Encyclopedia of INLAND WATERS

SECOND EDITION

VOLUME
ONE

Thomas Mehner, Klement Tockner

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ENCYCLOPEDIA OF INLAND WATERS, 2ND EDITION

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VOLUME 1

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ELSEVIER

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Library of Congress Cataloging-in-Publication Data
A catalog record for this book is available from the Library of Congress.

British Library Cataloguing-in-Publication Data
A catalogue record for this book is available from the British Library.

ISBN 978-0-12-819166-8

Publisher: Oliver Walter
Acquisition Editors: Priscilla Braglia
Content Project Manager: Paula Davies
Associate Content Project Manager: Greetal Carolyn
Designer: Christian Bilbow

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Klement Tockner is an internationally leading freshwater scientist, in particular in the research domains biodiversity, ecosystem science, and environmental management. He has published about 250 scientific papers including 180 ISI papers. He was editor-in-chief of the journal *Aquatic Sciences* (2005–2014) and is subject editor of the journal *Ecosystems*. He has published about 250 scientific papers including 180 ISI papers. In 2009, he edited a comprehensive book on European Rivers (Rivers of Europe, Elsevier; 2nd Edition in 2021). He is elected member of the Austrian Academy of Sciences and the German Academy of Sciences, Leopoldina.

Photo credit: David Ausserhofer

Thomas Mehner is vice director and senior researcher at the Leibniz Institute of Freshwater Ecology and Inland Fisheries in Berlin, Germany. He is limnologist and fisheries biologist by training, and has got his Diploma and Ph.D. at the University of Rostock (formerly East Germany) in 1992. In 1999, he had received his habilitation and venia legendi in limnology, which allowed him to start teaching as Privatdozent at universities. Since 1997, he has been working at IGB in several positions. He has published about 170 ISI papers, with primary focus on fish communities, lake food webs, and species interactions. However, his topical interests are broader, and he has authored and co-authored several publications on freshwater fisheries management, fish population genetics and evolutionary and behavioral ecology of aquatic organisms. He has been Handling Editor of the journals "*Aquatic Ecology*" and "*Freshwater Biology*" for several years, and he is currently member of the Editorial Boards of "Global Change Biology" and "Limnologica." Since spring 2018, he has been the president of the International Society of Limnology (SIL), the oldest and most international scientific society devoted to the study of inland waters. Thomas Mehner has taught M.Sc. courses at universities on limnology, fish ecology, fisheries management, and behavior and evolution. His one-week course on "Scientific Writing" for Ph.D. students has been run at 3 universities and in total 18 times, with >120 international students participating. He has trained many M.Sc. and Ph.D. students and supervised their theses, and he is actively mentoring undergraduates, graduates, and post-doc researchers.

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Damien Bouffard is leader of the aquatic physics lab at Eawag (Switzerland). He holds a Ph.D. from EPFL (with Ulrich Lemmin). After his Ph.D. he worked in Canada with Leon Boegman (Queen's U.), Ram Yerubandi (Environment Canada), and Joe Ackerman (Guelph U.) before returning to Switzerland as first assistant at EPFL with Alfred (Johny) Wüest. He has published over 70 peer-reviewed papers in aquatic physics and serves as associate editor for JGLR, AS, and HESS. His program research is focused on two axes: (i) linking the small-scale turbulence to the large-scale forcing with today a special interest in convective processes in lakes and (ii) aquatic physics as a tool to understand lake ecosystems. The later includes the use of 1D and 3D operational hydrodynamic models such as simstrat.eawag.ch or meteolakes.ch. Bouffard is also involved in promoting multidisciplinary and high-tech research on lakes, notably as member of the steering committee of the LéXPLORE floating research platform in Lake Geneva and in promoting open science in limnology with the web platform Datalakes-eawag.ch.

Debbie Chapman as a graduate of the University of London, Deborah Chapman started her research career as limnologist at the Freshwater Biological Association in the English Lake District. She subsequently became interested in monitoring the impacts of disposal of sewage sludge on aquatic organism and the potential for human health impacts from aquatic pollution. In 1986 she joined the United Nations Environment Programme's (UNEP) Monitoring and Assessment Research Centre (MARC) in London, participating in the international monitoring and assessment activities of UNEP and the World Health Organization (WHO), and assisting in global environment assessment programs. In 1988 she became the deputy director of MARC and took responsibility for the developing country workshops and training program, and global environment data review and compilation. After moving to Ireland in 1990, she worked as a freelance Environmental Consultant engaged mostly on international and developing country projects for WHO, UNEP, and other international organizations. She has assisted with the compilation of State of the Environment reports and has contributed to, edited, and produced more than 20 books on water resources and environmental management, including the internationally successful *Water Quality Assessments: A guide to the use of biota, sediments and water in environmental monitoring.*

In 1998 she joined UCC becoming the first lecturer in Environmental Science and then Head of Environmental Science in 2013. In recent decades her research interests have focused on water resources management, especially recreational and amenity lakes and reservoirs, developments and current practice in design and implementation of water quality monitoring programs, and human health risk assessment in relation to the use of freshwater resources and wastewater disposal. Drawing on 30 years of international experience, in 2015 she established the UNEP Global Environment Monitoring System for Water (GEMS/Water) Capacity Development Centre at UCC. This center delivers capacity development activities in water quality monitoring and

assessment worldwide for UNEP, including support for the Sustainable Development Goal indicator for good ambient water quality. She retired as director of the center in June 2021 and now acts in an advisory role and as an independent consultant.

Photo by Blythe White

Kendra Spence Cheruvelil is professor of limnology and co-director of the Data-intensive Landscape Limnology Laboratory at Michigan State University (MSU) in the Department of Fisheries and Wildlife (https://www.canr.msu.edu/fw/). She is also serving as Interim Dean of the Lyman Briggs College, which is MSU's residential college for studying the sciences and maths within their societal and global contexts (www.lbc.msu.edu). Kendra co-established the discipline of landscape limnology (https://bigdatalimno.org/research-themes/landscape-limnology/) and co-leads the LAGOS research program that is creating the research infrastructure to conduct big-data research on U.S. lakes (https://lagoslakes.org/). This large, collaborative, and interdisciplinary research program has been funded by the U.S. National Science Foundation and seeks to understand how global changes such as climate change and land use intensification affect lakes across regions and continents and through time. Dr. Cheruvelil also pushes the boundaries of how to conduct limnology research by using data-intensive science, science of team science, and open science approaches, tools, and perspectives to answer complex scientific questions. She also has an active research program to advance diversity and inclusion in the sciences (https://ee-stem.weebly.com/) and serves as an associate editor for the journals *Limnology & Oceanography Letters* and *Frontiers in Ecology & the Environment*. Prior to joining MSU, Dr. Cheruvelil was a faculty member in the Purdue University system. She has a dual Ph.D. from MSU in Fisheries & Wildlife and Ecology, Evolution, & Behavior (2004).

Photo by Shayenna Nolan

Catherine Febria is a Tier 2 Canada Research Chair in Freshwater Restoration Ecology and assistant professor at the Great Lakes Institute for Environmental Research (GLIER) & Dept. of Integrative Biology at the University of Windsor. Her research focuses on the ecology and restoration of small streams and wetlands in human-impacted landscapes, and the role of small waterways in supporting good ecosystem health in the Laurentian Great Lakes. She launched her lab—the Healthy Headwaters Lab—in 2019 and also wears multiple hats as co-director of the GLIER Organic Analysis & Nutrients Laboratory (a central research facility), associate director of FishCAST (an NSERC CREATE graduate student training program in Canada), co-chair of the International Science Advisory Panel for New Zealand's Biological Heritage National Science Challenge, coordinating editor with the journal *Restoration Ecology* and alumni fellow and contributing author with the Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services (IPBES). She previously held a postdoctoral role at the University of Maryland's Chesapeake Biological Laboratory (USA), the University of Canterbury (Aotearoa New Zealand). Her research has been published in the *Science*, *Nature Geoscience*, *Canadian Journal of Fisheries and Aquatic Sciences*, *Environmental Science & Technology*, and *Frontiers in Microbiology*, *Restoration Ecology*, *Proceedings of the Royal Society*, to name a few. She is co-founder of the Kindness in Science global initiative, and contributes actively to actions, scholarship and mentorship to advance justice, equity, diversity, and inclusion in academia.

Christian Griebler is full professor and head of the Limnology unit at the University of Vienna, Austria. He is a dedicated groundwater ecologist with core expertise in microbial ecology and biogeochemistry.

Kenneth Irvine has a broad range of multidisciplinary experience working on aquatic ecology, ecological assessment of surface waters, especially lakes and wetlands, and policy and related policies and management. After gaining a Ph. D. in 1987 at the University of East Anglia (U.K.) for a study on trophic ecology of shallow lakes, he worked for the U.K. Nature Conservancy Council, before moving to study ecosystem structure of Lake Malawi in Africa. He moved to Trinity College Dublin in 1994 Ireland. There, he continued work on the African Great Lakes, as well as building a research group working on ecological assessment in support of the EU Water Framework Directive. In 2011 he moved to IHE Delft Institute of Water Education, the Netherlands, as chair of Aquatic Ecosystems. Current work focusses on wetlands and capacity development in Sub-Sahara Africa. Recent work also includes a review of hydromorphology and links to policy. He currently sits on the Board of the Board of the *African Center for Aquatic Research and Education* (ACARE) and on the Scientific Advisory Board of the *Leibniz Institute of Freshwater Ecology and Inland Fisheries* (IGB), Berlin.

Wolfgang Junk was scientist of the Max-Planck-Institute for Limnology, Dep. Tropical Ecology, Plön during 1970–75.He was scientist of National Amazonian Research Institute, leader of the Dep. of Hydrobiology and Inland Fishery at Manaus, Brazil during 1976–79. and leader of the Working Group "Tropical Ecology" at the Max Planck Institute for Limnology in Ploen, Germany during 1980–2007.He is expertise in ecology and sustainable management of floodplains, land-water interactions, wetland classification. His main research areas arestudies on biomass, primary production, and decomposition of wetland plant communities; nutrient fluxes between land and water; adaptations of plant and animals to periodical drought and flooding; ecology of aquatic macrophytes and fish communities; biodiversity; conceptional considerations on river-floodplain systems, sustainable management of wetland resources and wetland protection with emphasis on the Amazon River floodplain and the Pantanal of Mato Grosso, Brazil. He supervised numerous M.Sc. and Ph.D. students and published more than 300 peer-reviewed publications, including several books and book chapters on Amazonian wetlands and the Pantanal of Mato Grosso. He received many honors, among them the Award of the Grande Cruz (the highest distinction of Brazil) for exceptional scientific performance, and the Cross of Merit First Class of the Federal Republic of Germany. He is corresponding member of the Academy of Sciences of Brazil.

Krantzberg is professor and lead for the engineering and public policy in the School of Engineering Practice and Technology at McMaster University offering Canada's first master's degree in engineering and public policy. Gail completed her M.Sc. and Ph.D. at the University of Toronto in environmental science and freshwaters. She worked for the Ontario Ministry of Environment from 1988 to 2001, as coordinator of Great Lakes Programs, and senior policy advisor on Great Lakes. Dr. Krantzberg was the director of the Great Lakes Regional Office of the International Joint Commission from 2001 to 2005. In 2007 she was appointed as an adjunct faculty member of the United Nations University Institute for Water and Environmental Health and participated in the twinning of the Laurentian and African Great Lakes (principally Lake Victoria). She has co-authored and edited 9 books and more than 200 scientific and policy articles on issues pertaining to ecosystem quality and sustainability and is a frequent speaker to media and the public. Her research interests include investigating Great Lakes governance capacity, analyzing interjurisdictional co-management arrangements internationally for application to the Great Lakes regime, and methods to better integrate science and engineering in policy formulation and decision-making.

Marie-Elodie Perga is associate professor of limnology at the University of Lausanne in Switzerland. Since receiving her Ph.D. from the University of Savoie-Mont Blanc (France), she has worked at the University of Victoria in Canada, and the French National Institute for Agronomy and Environment (France), before moving UNIL.

Because she is a Lindeman's groupie, her research lies at the interface of community ecology and biogeochemistry, through lake food webs and carbon processes. More recently, she added a pint of hydrodynamics with the intent to bridge physical and biogeochemical mechanisms, especially in alpine and high-altitude lakes. Her work covers centennial up to minute timescales through the combination of high-resolution paleo-records and high-frequency data from autonomous sensors.

She is also involved in promoting high-tech research on lakes, notably as a member of the steering committee of the LéXPLORE floating research platform in Lake Geneva, and in connecting science and management through a transdisciplinary network involving National Parks in France. She has published over 75 peer-reviewed papers and serves as associate editor for WIRES Water.

N. LeRoy Poff is professor of biology at Colorado State University and holds a partial appointment as distinguished professor at the University of Canberra, Australia. Since receiving his Ph.D. in 1989, his research has focused on understanding how natural and human-caused hydrologic variability regulates the interactions among species and the structure and function of riverine ecosystems. By developing techniques to quantify streamflow variability in ecologically meaningful terms and using species (functional) traits as generalized, mechanistic response variables, he has been a leader in advancing the field of hydroecology. Through his interdisciplinary and collaborative work, he has contributed fundamentally to the development of the field of "environmental flows," which aims to support sustainable management of streams and rivers at local to regional to global scales in the face of growing human water demands. His current interests are on developing better conceptual frameworks and decision support tools for science-based management of streams and rivers in our current period of rapid climate and ecological change.

Lars Rudstam is professor of fisheries and aquatic sciences in the Department of Natural Resources and the Environment, Cornell University (USA) and the director of the Cornell Biological Field Station. He has a master's degree from the Center for Limnology, University of Wisconsin-Madison and a Ph.D. from Stockholm University, Sweden. Rudstam has published over 250 papers ranging from lake physics to phytoplankton, zooplankton, mussels, mysids, fish, birds, and anglers, mostly about processes associated with food web interactions and ecosystem dynamics. He has worked in lakes in North America, Europe, and Asia as well as the Baltic Sea.

Stuart Warner works with the United Nations Environment Programme with a focus on helping countries to monitor and assess their freshwaters. He was born in England, he moved to Ireland in 2001 to work at University College Cork. Stuart has published in the areas of water quality monitoring and assessment and citizen science approaches to data collection. He has written reports on the capacity of countries to understand their freshwaters which highlight the challenges faced in different world regions. Recent efforts have focused on the development and implementation of a global water quality indicator, and the delivery of capacity development targeted at improving freshwater management. His professional interests include using both traditional and innovative approaches to understand and protect freshwater ecosystems.

Florian Wittmann is professor for physical geography and head of the Department of Wetland Ecology at the Karlsruhe Institute for Technology, Germany. He studied geography, geology, and botany at the Universities of Mannheim and Heidelberg, got his Ph.D. in physical geography at the University of Mannheim, and his lecturer qualification at the University of Bayreuth, Germany. He held post-doc positions at the Max Planck Institutes for Limnology and Chemistry, Germany, where he was working at the bilateral project between the Max Planck Society and the National Institute for Amazonian Research in Manaus, Brazil, for more than 15 years.

His research focuses on neotropical wetlands, with special interest in biogeography, plant species distribution, species diversity, forestry and sustainable management, remote sensing, biomass and primary productivity, and botany and vegetation ecology. Actually, he teaches at the Institute for Geography and Geoecology of the Karlsruhe Institute for Technology, Germany, and in the post-graduate program of Tropical Ecology—Botany at the National Institute for Amazon Research—INPA, Manaus, Brazil. He supervised numerous M.Sc. and Ph.D. students and published more than 150 peer-reviewed publications, including several books and book chapters on Amazonian wetlands.

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INTRODUCTION TO ENCYCLOPEDIA OF INLAND WATERS, 2ND EDITION

The surface of the earth is dominated by water. Water is fundamentally critical for the life forms we know. Not surprisingly, humans have always settled near the shores of oceans, rivers, and lakes. However, the amount of potentially drinkable, non-salty water on earth is much more limited, and hence inland waters are of particular focus to humans. Whereas lakes and rivers constitute the largely visible part of inland waters, wetlands and groundwater are less visible, and hence are often neglected in consideration of inland water systems. However, all inland water types constitute the centrally important resource for future life, and hence understanding the structure, functions, and interdependencies of inland waters is paramount for a sustainable development of the human population.

The science of inland waters is limnology, also called the queen of sciences because of its multidisciplinary nature, including aspects of biology, ecology, physics, chemistry, hydrology, and geology. Given the strong interactions between humans and inland waters, this set of disciplines has to be expanded toward medical sciences, toward technological disciplines such as engineering and construction, and toward social sciences, like sociology, psychology, and history. Ultimately, covering the full bandwidth of scientific disciplines related to inland waters requires a comprehensive approach.

It can be discussed whether a comprehensive topical coverage of the science of inland waters in the form of a printed Encyclopedia is still an approach worthwhile to be completed. In contrast to a classical lexicon, which addresses the meaning of key terms and definitions, an Encyclopedia bundles articles related to structures, processes, and concepts. If ideally structured, the reader of an Encyclopedia article will understand both details and the complexity of topics, and this knowledge may support informing others, whether in school and university teaching, or may be applicable to public discussion and information.

We are convinced that an edited volume such as this *Encyclopedia of Inland Waters* can still serve as a reference output for a discipline. The strong interactions between authors, section editors, and us, the editors-in-chief, were the foundation for generating a volume that reliably reflects scientific quality and correctness, in contrast to several web-based text compilations that are exposed to less rigorous quality controls. Nevertheless, the chosen structure of the Encyclopedia keeps the contributions by researchers or researcher groups, and hence perpetuates the flavor of individual perspectives on topics. By this approach, the *Encyclopedia of Inland Waters* does not rival, but complements several textbooks on limnology and aquatic ecology.

When discussing a second edition of the successful *Encyclopedia of Inland Waters* whose first edition was printed in 2009, the process has got its own dynamics. While the initial idea was primarily related to updating the chapters from the first edition, and adding a few fresh chapters on emerging topics, the intense consideration of what we think is relevant to understand inland waters has enforced a full re-structuring of the volume. The inclusion of sections on lakes and rivers was obvious, but the addition of sections on wetlands and groundwater became necessary to address the full set of forms in which inland waters are present on earth. When considering the strong interactions between humans and inland waters, a section on pressures on, and management of, freshwater systems became evidently necessary, and the addition of a section on social values of inland waters reflects the tight linkages between water and human beings. We complemented these six sections by a general section, in which structures and processes are outlined that are not specific to only one type of inland waters. And ultimately, we added a section on emerging topics; themes in research and methodology that are not yet fully fledged and hence often not properly covered in textbooks, but for which we think that they will become standard in future limnological research.

Inevitably, the outcome of such an endeavor is not perfect. Despite having enthusiastic section editors, finding and selecting authors or author groups for the more than 250 originally planned topics was more complicated than initially anticipated. Despite all efforts, we could not secure contributions to all topics, and hence we have to accept that there are thematic gaps also in the second edition of the Encyclopedia. Furthermore, we tried to apply a consistent chapter structure at least for all chapters that were freshly produced for the second edition. Yet, this structure could not be harmonized for the chapters we reproduced from the first edition. Finally, drafting, revising, editing, and producing a volume of this dimension under the conditions of the Covid-19 pandemic was an extra challenge. We appreciate the motivation, diligence, and patience of all contributors in these complicated times. The volume finally available is a wonderful piece of work that can emerge if professional expertise, creativity, and enthusiasm are combined via a shared vision.

Ultimately, we wish to thank Gene Likens for his original idea to create the *Encyclopedia of Inland Waters*. We followed his intentions and hope that the second edition of this book is a dignified continuation of his first collection of articles. In summer 2022, the International Society of Limnology (SIL) celebrates its centennial year of foundation. In 1922, August Thienemann and Einar Naumann founded an international society devoted to the study of inland waters, named Societas Internationalis Limnologiae Theoreticae et Applicatae. Now, 100 years later, we, the editors-in-chief of the second edition of the *Encyclopedia of Inland Waters*, offer this volume as a contribution to theoretical research and practical management of inland waters, in the sense of Thienemann and Naumann. We hope that it will be well received.

Thomas Mehner, Klement Tockner
Berlin and Frankfurt, March 2022

CONTENTS OF ALL VOLUMES

VOLUME 1

Fundamental concepts and theories

VOLUME 2

Structures and functions of Inland Waters - Lakes continued

VOLUME 3

Structures and functions of Inland Waters - Wetlands

VOLUME 4

Human pressures and management of Inland Waters

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FUNDAMENTAL CONCEPTS AND THEORIES

Section introduction: Fundamental Concepts and Theories of Inland Waters

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Introduction

Earth is a water planet, life originated in water, and all life on this planet (and everywhere else in the universe as far as we know) depend on water. Clearly, the study of inland waters—limnology—is critically important to humanity. Even though water is the most abundant liquid on Earth, most of the water is in oceans. Freshwater is a valuable resource that needs careful management both when it is in short supply and when there is too much of it causing floods. Inland waters contribute to our food supply, to our enjoyment through boating, swimming, wildlife watching, hunting and fishing, and to the beauty of the landscape. To me, limnology is also intellectually stimulating because its multidisciplinary nature. To understand how inland waters function, limnologists use concepts and theories from physics, chemistry, biology, ecology, geology, and their subdisciplines. In his introductory chapter, Gene Likens calls limnology the Queen of Sciences, as limnology includes aspects of so many natural science fields. It was therefore difficult to decide which fundamental concepts and theories to include in this section of the Encyclopedia of Inland Waters. Working with Thomas Mehner, I consulted the first edition of this encyclopedia (Likens, 2009), canvassed colleagues, and read limnology textbooks. The resulting 36 chapters by world-renowned experts range from an introduction to limnology by Gene Likens and how the science of limnology is organized by Jonathan Cole and Michael Pace, to the physical, chemical and biological concepts and theories that I consider fundamental to the field. Some chapters are updates of the chapters in the 1st edition, other chapters are completely new. Together these 36 chapters present the fundamental concepts and theories a reader interested in limnology and inland waters should know about. Note though, that fundamental concepts and theories are also discussed in other encyclopedia sections. I have organized the chapters below in subheadings of water budgets and flows, physical properties, chemical properties, ecological concepts, population interactions, and ecosystem processes. But sorting chapters with often multidisciplinary content are somewhat arbitrary. In particular, many chapters include effects on the whole system, an indication of the whole system thinking that permeates the science of limnology.

Water budgets and flows

Water is constantly evaporating from the surface of the oceans into the atmosphere, transported with winds, deposited on land as rain and snow and then flow back to the ocean. Without this hydrologic cycle, there would be no inland waters. Dale Robertson and Howard Perlman describe this cycle and the water budget, concepts requiring information on evaporation, precipitation, and water movement. Water travel back to the oceans in streams and rivers, and the nature of flowing water affect all organisms living in it. Turbulent and laminar flows as well as the theory of turbulent flows are described in the chapter by Alexander Sukhodolov, Oleksandra Shumilova and Bruce Roads. Water also accumulates in land depressions forming lakes and ponds, and how long time water remain in such waterbodies—the residence time—depends on the hydrology of the watershed and morphometry of the lake basin. Isabella Olesky and colleagues describe the relationship between hydrology and residence time, and how these attributes of lakes affect ecosystem processes, such as lake metabolism and biogeochemistry. Hydrology and residence time are clearly fundamental concepts for our understanding of inland waters.

Physical properties of water

Water is a different medium than air. It is 800 times more dense, 50 times more viscous, can dissolve chemicals, and has lower oxygen content, higher heat conductivity, higher light absorbance, and higher sound speed. Even though life originated in water, humans are terrestrial animals and do not have an intuitive understanding of living in water. Limnologists still need to understand the basic properties of this medium. Kenton Stewart and Joseph Atkinson describe the physical properties of water, including density, heat capacity, phase shifts (ice-water-vapor), sublimation, surface tension, viscosity, and colligative properties. Pressure received its own chapter by Atkinson, as it is central to currents, seiches, buoyancy, and solubility of gasses. Because of the differences between water and air, more energy is required to move through water than through air, especially when moving fast. On the other hand less energy needs to be invested in structural parts like skeletons and wood due to the buoyancy of water. Another difference is that it is harder to insulate body temperature from the surrounding water temperature due to the higher heat conductivity of water. The bioenergetics of aquatic organisms therefore includes functions for temperature and swimming speed in addition to the allometry of size, as described in the chapter on bioenergetics by Steve Chipps, David Deslauriers and Charles Madenjian. Temperature affects most ecological processes making inland water sensitive to climate change. Bart DeStasio and colleagues describes how temperature is a driving force in aquatic ecosystems affecting seasonality, growth rates, distribution and ecological interactions. The physical properties of water also affect light absorbance, light color at depth, and light scattering. Three chapters describe light in inland waters. Patrick Neale, Craig Williamson and Donald Morris describe these optical properties of water, with UV light receiving a more in-depth treatment by Williamson and Neale because of its potential harmful effects on organisms. How organisms are adapted to different light regimes and how they perceive light is described in the chapter on light as an ecological resource by Dina Leech and Sönke Johnsen.

Chemical properties of water

The chemical reactions occurring in water are fundamental to limnology. The chemical properties of water include concepts such as the structure of the water molecule itself, water's ability to dissolve various substances from ions and gasses to complex organic molecules, and the inclusion of H_2O in chemical reactions. Joseph Aldstadt III, Harvey Bootsma and Jessica Ammerman discussed these and other chemical properties of water in their chapter. Photochemical reactions break down organic matter as well as pollutants and are a major component of the carbon cycling and ability of inland waters to "self-depollution" as described by Anssi Vähätalo, Luca Carena and Davide Vione. Many other chemical reactions are mediated by organisms, including photosynthesis, chemosynthesis, methanogenesis, and nitrogen fixation. The chemistry of inland waters is the result of an integrated system of biological and chemical processes that build up and break down organic molecules and recycle nutrients. In his chapter on nitrogen—one of the most important nutrients in inland waters, Robert Howarth discusses the nitrogen cycle and the effect of excess nitrogen from human activities. The chapter by Roxanne Marino and Howarth goes into more detail on one part of the nitrogen cycle, nitrogen fixation, particularly by cyanobacteria. Chapters on the other important nutrients, like phosphorus, are in the sections specific to lakes and rivers. Chemosynthesis refer to the synthesis of complex organic compounds—the building blocks of life—from simple one-carbon molecules using energy from oxidation of a number of inorganic compounds. Alex Enrich-Prast and colleagues describe this process and the highly diverse group of bacteria and archaea involved. Methane received its own chapter by David Bastviken given its importance as a greenhouse gas and the complex processes leading to methane production. Carbon cycles, including the breakdown of organic compound and carbon dioxide production, are discussed in other sections of the encyclopedia. Photosynthesis uses energy from light to synthesize complex organic molecules. Organisms that have the ability to do photosynthesis include cyanobacteria and various phytoplankton and higher plants. The distribution of photosynthesis in inland waters is described by Martin Dokulil and Katrin Teubner. The details of the photosynthesis process are described by Dokulil as part of the lake section of this encyclopedia.

Ecological concepts and theories

Fundamental concepts describing how we organize the biology of inland waters include the individual, species, population, meta-population, food webs, and ecosystems. The chapter on biodiversity by Alan Covich stresses the importance of species in inland waters and describes the various groups present, their species richness, and some fascinating natural history. Populations are defined as collections of individuals of the same species that either interact evolutionarily through gene flow or can be considered to be affected by the same demographic processes like birth, death and harvest rates. The distinction between a genetic based and a demographic based definition of a population is described in the chapter by Matthew Hare and myself. When the dynamics of a population requires consideration of migrations from surrounding populations, we have meta-population dynamics. A meta-population is a collection of interacting populations, and the theory of meta-populations is described in the chapter by Kasey Pregler, Emily Chen and Stephanie Carlson. Populations exist within food webs, and the food web and its trophic structure are explained by Ursula Gaedke using Lake Constance as an example. Finally, the ecosystem concept is defined by William Lewis from a lake perspective as including both biotic and abiotic components and their interactions.

Interactions between populations

The processes that govern interactions between populations include competition, predation, commensalism and mutualism as well as the indirect interactions that emerge, such as apparent competition and buffering by alternate prey. For this encyclopedia, I selected concepts and theories with special relevance to inland waters. Each organism is using a subset of the environment, its niche. The niche is defined by William Lewis based on the multidimensional niche concept (Hutchinson, 1957), stressing the differences between the fundamental niche and the realized niche and the importance of niche overlap for competition between species. Predation is a major source of mortality and driving force in many aquatic ecosystems, and is the topic of the chapter by Jonathan Jeschke and colleagues. That chapter highlights the predation cycle and describes how predation is affected by prey defenses, swarming, prey offenses, and functional responses. When an animal feeds on another without killing it, such as parasites and disease organisms, the effects and dynamics are different. Spencer Hall shows how parasites and diseases affect populations and how these effects can (and should) be incorporated in food web models. Both predators and parasites have to meet their prey/host to interact making the distribution of animals in both space and time a critical part of these interactions. In many inland waters, vertical migrations are ubiquitous as animals react to changing light and food resources to optimize their growth and survival rates. This concept and the theories explaining diel vertical migration are described in the chapter by Luc De Meester, Thomas Mehner and Anne Scofield. More general predictions of the distribution of organisms requires understanding the decision rules that drive organisms to use certain habitat at certain times. Several approaches have been used to predict distributions, and these theories are explained in the chapter on spatial models by Milan Říha and Marie Prchalová. Interactions between organisms drive evolutionary changes, including arms races between predators and prey. It is now clear that such evolutionary changes can occur rapidly and affect ecological interactions, which in turn can drive further evolutionary changes. Such eco-evo dynamics is fundamental to the interactions between species and the topic of the chapter by Lynn Govaert and colleagues. Populations are also buffered by the presence of resting stages, both evolutionary and demographically. The "egg bank" allows genotypes to survive periods of adverse conditions. If conditions become more favorable in the future, delayed hatching of dormant eggs can "resurrect" past genotypes adapted to those conditions. The description and implications of dormancy are explained in the chapter by Nelson Hairston Jr. and Jennifer Fox.

Ecosystem processes

The last section on fundamental concepts and theories involves processes operating on the ecosystem scale, and how to study and understand them. Perhaps because the system boundaries of waterbodies consist of an air-water interface and is therefore easy to define, a whole systems approach was introduced early to the study of lakes by S.A. Forbes in 1887 in "A lake as a microcosm" and in the monographs on Lake Geneva introducing limnology as a science by Francois Alphonse Forel (the first volume published in 1892). Lakes were also the inspiration for Raymond Lindeman's (1942) classic study introducing trophic dynamics and quantitative ecosystem science. The field of ecosystem ecology in inland waters has advanced substantially since then and continues to generate new ecological concepts such as alternate stable states, regime shifts, resilience and tipping points (Scheffer and Carpenter, 2003). Tipping points and regime shifts describe how a system may relatively suddenly shift into a different state, perhaps an alternative stable state that is resilient to further change (a new regime). Small changes past a tipping point will cause large ecosystem changes due to non-linear dynamics and feedback loops. These are important concepts in inland waters as well as in science in general and are described in the chapter by Sarian Kosten, Annelies Veraart and Vasilis Dakos. Another way ecosystems can change dramatically implying a regime shift is by the arrival of new invasive species, a change that is typically irreversible. Biological invasions are reviewed by Reuben Keller and David Lodge. Further, ecosystems are affected by ecosystem engineers, a concept explained by Christine Mayer. Ecosystem engineers alter their physical habitat by their activities and by their physical presence, such as dam building beavers or reef building molluscs. Nutrient cycling is integral to ecosystem dynamics, and is affected not only by the chemistry of the water and the organisms present, but also by the ratio of nutrients within organisms—their ecological stoichiometry. This concept and its implications for organism growth and food web interactions are described in the chapter by Robert Sterner. The biomass size spectrum is a concept based on large organisms consuming smaller organisms and the allometric relationships inherent in body size. Biomass size spectra theory originated in biological oceanography and may be a particularly useful concept for aquatic systems. This theory is explained in the chapter by Gary Sprules. Note also that several chapters introduced earlier consider ecosystem processes, including the chapter by Olesky and colleagues on ecosystem consequences of residence time, by DeStasio and colleagues on the ecosystem effects of temperature, by Gaedke on food webs and by Lewis on ecosystems.

Many of these concepts and theories benefit from studies on long time scales and large spatial scales. Long term data are needed for assessing slowly changing systems, effects of long-lived organisms, and changes associated with human use, biological invasions and climate change. Long-term ecological data series of half a century or more do exist in some inland waters of the world (e.g., Magnuson et al., 2006; Jeppesen et al., 2012; Rudstam et al., 2016), but such data series are rare. There is an increasing number of large-scale, world-wide analyzes of limnological concepts and theories, partly shepherded through organizations like the Global Lakes Ecological Network (Hanson et al., 2016), the ability to collaborate world-wide through the internet, and the science of Big Data (e.g., Soranno et al., 2017). These large-scale syntheses are powerful, especially when available long-term data series can be combined and compared over large spatial scales (e.g., O'Reilly et al., 2015; Solomon et al., 2013). Paleolimnology can

provide longer data series. In the final chapter of this section, John Smol describes how paleolimnology has provided insights into the structure and function of pre-industrial ecosystem that helps us better understand the current state of our ecosystems and inland waters.

Acknowledgments

I like to thank the Editors-in-Chief, Thomas Mehner and Klement Tockner, for taking on this massive and important task and recruiting me to work on the fundamental concepts and theories section. I learned a lot and hope the readers will as well. A big thank you to all the contributing authors who stayed with the project during the time of a pandemic, and to our managing editor Paula Davies. The importance of understanding inland waters is increasing in this era of environmental change, and together we have contributed to an encyclopedia that will be useful to students and scientists of inland waters around the world.

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Inland Waters and Limnology☆

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This is an update of G.E. Likens, Inland Waters, in Encyclopedia of Inland Waters, Edited by Gene E Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00001-6.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Ecosystem An ecosystem is a spatially explicit unit of Earth that includes all of the organisms, along with all components of the abiotic environment, interacting together as a system, within its boundaries.
Inland waters Waters on or in the terrestrial portion of the Earth.
Limnology The scientific study of inland waters.
Saline Salty; approximating or exceeding the salt content of sea water.

Inland waters

All life on Earth is dependent in some way on water for providing a vital habitat, the milieu for biochemical reactions, electrochemical transformations, reproduction, food production, transportation, climate regulation, and for many other ecosystem services to biota. Some 75% of the Earth's surface is covered by water and ice, but most of this area (71%) contains water that is salty and is found primarily in oceans and seas. Inland waters are distributed among polar ice and glaciers, actively exchanged groundwater, freshwater lakes, and human-made impoundments (farm ponds and reservoirs), saline lakes, soil water, marshes/wetlands, and rivers and streams, in order of decreasing volume (Table 1). Although the areal extent and volume of freshwater lakes and rivers are relatively small, their interest and value to humans is huge as a source of drinking water, for transportation, food, recreation, and esthetics (Figs. 1–6). Recently, their importance as a significant source of carbon dioxide and methane flux to the atmosphere, as well as carbon storage in sediments, has become apparent from scientific study because of increased interest in the flux and balance of carbon for the Earth as related to the climate crisis.

Estimates of the worldwide dimensions of inland waters are changing as a result of the use of new technology, such as satellite observation of the Earth and increased computer power to deal with large and more complicated data sets. Scientists have estimated that freshwater lakes and impoundments (engineered dams and farm ponds) occupy a much larger proportion of the Earth's surface than previously thought (Table 2), overall comprising ~3% of the terrestrial surface of the Earth. Most inland waters in lakes, reservoirs, and rivers are shallow (less than a few tens of meters in depth), but a few are very deep. Lakes Baikal in Russia (Fig. 5) and Tanganyika in Africa are more than 1000 m deep. Lake Baikal with a maximum depth of 1620 m contains about 23,000 km^3 or 18% of the Earth's surface freshwater in its basin and is one of the oldest fresh water basins (formed >20 Mya). The five Laurentian Great Lakes (Superior, Michigan, Huron, Erie, and Ontario) in North America contain another 20% or so of the Earth's surface fresh water in their basins. A very large (possibly the largest) lake, Lake Vostok, exists below the ice in Antarctica, but relatively little is known about this lake. Antarctica contains some 70% of the Earth's freshwater, but most of it is locked up as ice. Because of glacial, tectonic, and volcanic activity, many areas have numerous basins now filled with water, thus forming "lake districts." Examples include the Patagonian region of South America, northern England, the upper midwestern and St. Lawrence regions of North America, and the Rift Valley of Africa. Many inland waters, such as the Dead Sea in Israel, are highly saline. The Black Sea and Caspian Sea in Eastern Europe, Great Salt Lake in United States, and Lake Corangamite in Australia are saline and very large. Some inland bodies of water, such as the Black Sea, Aral Sea and Caspian Sea, represent areas recently isolated geologically from the ocean. In many respects, including their name, they are much more like oceans than lakes. Recent human activities, for example water withdrawal, have greatly reduced the volume and areal extent of the Dead Sea, and particularly the Aral Sea.

☆*Change History:* November 2021. GE Likens made all of the updates. Photos and tables have been updated.

Table 1 Estimated volume of water on the Earth (thousands of km^3).[a,b]

	Volume (1000 of km^3)	*Percent of total water*	*Percent of total fresh water*
Oceans	1335040[a]	96.95	–
Glaciers, permanent groundwater	26350[a]	1.91	62.9
Groundwater	15300[a]	1.11	36.6
Ground ice, permafrost	22[a]	<0.01	0.1
Lakes and river impoundments	178[a]	0.01	0.4
Marshes, wetlands	11.5[b]	<0.01	<0.1
Saline lakes	85[b]	0.01	–
Incorporated in biota	1.12[b]	<0.01	<0.1
Total water on Earth	1377000[a]	100	–
Total fresh water on Earth	41,860	3.04	100

Percentages don't sum to 100 because of rounding.
[a]Based on Trenberth et al. (2007) and other sources.
[b]Based on Shiklomanov (1993) and other sources.

Fig. 1 Crater Lake, Oregon, United States. Photo by G.E. Likens.

Fig. 2 Tub Lake, Wisconsin, United States. Photo by G.E. Likens.

Unfortunately, there are no good estimates for the total area of small rivers and streams, yet the huge interface between these inland waters and their adjacent terrestrial drainage areas is one of the exciting and important subject areas in limnology. This interface is often occupied by lacustrine and riverine wetlands consisting of herbaceous-dominated marshes and forest- or shrub-dominated swamps. These wetlands often occupy much larger surface areas than do lakes and rivers. In addition to these transitional wetlands, wetlands also occur in depressions, seepages on hill slopes, and on poorly drained flat lands not adjacent to lakes and streams.

Fig. 3 Lake Tahoe, California/Nevada, United States. Photo by G.E. Likens.

Fig. 4 Chandalar Lake, Alaska. Photo by G.E. Likens.

Fig. 5 Lake Baikal, Russia. Photo by L.G. Rudstam.

The so-called lentic or standing, inland waters include lakes, ponds, pools, reservoirs, inland saline systems, and wetlands (swamps, marshes, bogs, fens). Lakes, ponds, and reservoirs are transient features of the landscape because as their basins fill with water, they immediately start to disappear as the basin fills with sediment. Of the 83,115 lakes with names in the conterminous US,

Fig. 6 Lake Taihu, China. Photo by L.G. Rudstam.

Table 2 Areas of water on the Earth (thousands of km^2).[a]

	Area (thousands of km^2)	*Percent of total*
World (total)	510,230	100
Land area	148,925	29
Oceans	361,305	71
Polar ice caps and glaciers	17,871	3.5
Fresh and saline lakes	4200	0.82
Inland seas	699	0.14
Rivers	360	0.071
Impoundments	335	0.066

[a]Compiled from Nace (1960), Wetzel (2001), Lehner and Döll (2004), Downing et al. (2006), and other sources.

897 are named "Mud" (Mud Lake, Mud Pond), the most common name (Soranno et al., 2020). Nevertheless, lakes esthetically represent some of the most beautiful "gems" of the landscape, e.g., Lake Tahoe, CA, United States; Lago Grey, Chile; Crater Lake, OR, United States; Lake Atitlan, Guatemala; Lake Pukaki, New Zealand; Lake Baikal, Russia. Lotic or running inland waters are referred to by different names (e.g., stream, brook, rivulet, river, headwaters, run, fork, creek [crick], kill, chalk stream, tributary) in English depending on the size and regional or cultural background. Obviously, water flows downslope by gravity, coalescing in networks from headwaters, into large rivers and eventually to the ocean. These networks of channels with flowing water may be simple or complicated, but flowing waters are challenging to study because the water is constantly moving, often in numerous channels (braided), and below ground.

A brief history of limnology

Limnology (from the Greek: limné = pool or pond; logos = discourse or study), the study of inland waters, is the scientific discipline focused on all inland waters of the Earth. These days, the term, limnology, may be replaced by or subsumed under other terms of scientific inquiry such as aquatic ecology, hydrobiology, or even hydrology. Initially, limnology lagged behind oceanography as a scientific discipline, as F. A. Forel in 1892, in his book (first volume) on Lac Léman (Lake Geneva, Switzerland/France), defined limnology as the oceanography of lakes.

Because successful limnological studies depend upon an understanding of the interactions of physics, chemistry, biology, meteorology, and hydrology for aquatic ecosystems, such as lakes, ponds, reservoirs, rivers, streams, and wetlands, limnological investigations often draw rather uniquely on a team of scientists with diverse interests and expertise. To do limnological research well, studies must incorporate biology, physics, chemistry, hydrology, geology, etc. into an holistic approach in order to make sense of the function, structure, and temporal change of a lake, pond, river, stream, or wetland. Such studies, focused on a systems approach, provide limnologists with a powerful and successful framework for addressing complicated environmental issues such as eutrophication and anthropogenic acidification. This integrative approach to the study of inland waters as complicated systems renders it the status as "queen" among the natural sciences.

The success and vitality of any endeavor is the product of its historical underpinnings. Limnology is no exception. The first work explicitly introducing limnology was Forel's three volumes on Lac Léman published in 1892, 1895 and 1904. In Eurasia, academic limnology has a long history with early, major centers of activity in Sweden (E. Naumann, S. Ekman, W. Rodhe), Germany (A. Thienemann, H. Elster, W. Einsele, W. Numann, W. Ohle, H. Sioli, D. Uhlmann), Denmark (K. Berg, C. Wesenberg-Lund, P. Jónasson), Norway (K. Strom), France (F.A. Forel, A. Delebeque, B. Dussart), Switzerland (L. Minder, E.A. Thomas), Spain

(R. Margalef), Austria (A. Ruttner-Kolisko, F. Ruttner, I. Findenegg), England (T.T. Macan, W.H. Pearsall, C.H. Mortimer, E.M. Wedderburn, J. Talling, J. Lund, W. Tutin), Japan (S. Yoshimura, S. Horie), Poland (A. Hillbrecht-Ilkowska), Russia (Yu. I. Sorokin; G.G. Winberg), and Italy (E. Baldi, V. Tonolli, L. Tonolli). This is a non-exhaustive listing of locations of major limnological centers and pioneers in the field. Austrian Professor F. Ruttner's early textbook (*Fundamentals of Limnology*, 1940) (Ruttner, 1940) had been a standard for years in Europe and in North America. He offered a course in hydrobiology (limnology) at Lunz, Austria in 1908, possibly the first such course in Europe.

In North America, Dr. J.G. Needham, who was appointed Assistant Professor of Limnology at Cornell University in Ithaca, New York in 1907, offered the first course on limnology in the United States in 1908 (Hairston and Likens, 2009). In 1911, he authored with J.T. Lloyd the first textbook on limnology—*Life of Inland Waters*. Although the book is broad in disciplinary coverage as expected for limnology, its focus was biological. Another major center for limnological studies was the University of Wisconsin-Madison, often referred to as the "birthplace of limnology in North America" because of the leadership and proficiency of E. A. Birge and C. Juday. Drs. Birge and Juday championed the systematic analysis of inland waters (Beckel, 1987). Courses in limnology and plankton were taught at the University of Wisconsin-Madison in 1909 by Chancey Juday. Other early pioneers in limnological studies in the United States and Canada included A.D. Hasler (Wisconsin), J. Reighard, F.E. Eggleton, P. Welch, H.B. Ward (Michigan), D.S. Jordan, D.G. Frey, S. Gerking, C.A. Kafoid, S.A. Forbes (Indiana), R. Patrick (Pennsylvania), L. Agassiz, G.C. Whipple, G.E. Hutchinson (New England), and F.R. Hayes, H.B.N. Hynes, F.E.J. Fry, D.S. Rawson, F. Rigler, J.R. Vallentyne (Canada). Again, this list is not exhaustive.

Some 39 professional limnological organizations exist in countries throughout the world. The International Association for Theoretical and Applied Limnology (Societas Internationalis Limnologiae) was founded in 1922 by E. Naumann and A. Thienemann and represents the international organization for limnology and limnologists (www.limnology.org). The name was changed in 2007 to the International Society of Limnology. Its mission "to... work worldwide, to understand inland aquatic ecosystems and to use knowledge, gained from research, to manage them," and its Congresses, now occurring every 2–3 years in different countries, attract limnologists from throughout the world. Other limnological professional societies, such as the Association for the Sciences of Limnology and Oceanography and the Asociación Española de Limnología, although originally more national/regional in origin and scope, are working to expand international memberships and activities. Dozens of limnological journals and periodicals are being published, including *Limnology and Oceanography*, *Journal of Paleolimnology*, *Journal of Crustacean Biology*, *Chinese Journal of Oceanography and Limnology*, and *Japanese Journal of Limnology*, on diverse topics and in many different languages.

The future of limnology

Historically, inland waters have been attractive to humans as a place to live, providing a convenient source of water, food, recreation, and transportation. Unfortunately, inland waters have also been a "convenient" receptacle for wastes. Flowing waters have been used especially for waste disposal by humans following the old adage, "out of sight, out of mind," and with little regard for other organisms, including humans, living downstream. Currently, freshwater ecosystems are much threatened and degraded because of pollution, human occupation and development of shorelines, and increased sediment loading and sedimentation. This degradation results from human activity such as agriculture, urbanization, and industrial activity, affecting the airshed or the catchment of these inland waters.

Water shortages for human use are common in many areas of Australia, the Middle East, Africa, Asia, and even in areas of eastern North America, long perceived to have abundant water. Serious water-quality problems are now occurring because of the pollution of surface waters by sediments, excess nutrients such as phosphate and nitrate, acids, mercury, pharmaceuticals, toxic algal/cyanobacterial blooms, human parasites, e.g., *Cryptosporidium* spp. and *Giardia* spp., and invasive alien species. Excess nutrient loading to inland waters has led to eutrophication (nutrient enrichment) of standing and flowing waters worldwide with resultant degradation (changes in species composition and diminishment of dissolved oxygen). Anthropogenic acidification from acid rain deposited on geologic areas with low buffering capacity has resulted in widespread degradation of lakes and rivers. Government action during the past few decades to lower emissions of sulfur dioxide and nitrogen oxides, the primary precursors to acid rain, have reduced this pollutant impact. Pollution of lakes and streams from atmospheric deposition of mercury, originating largely from combustion of fossil fuels and incineration of municipal waste, has resulted in health advisories for the consumption of fish throughout North America and Europe.

Inland waters are spatially explicit ecosystems that include all the organisms along with all components of the abiotic environment, interacting together as a system. The inland waters of the Earth result from the balance between precipitation, evapotranspiration, and runoff (Table 3; Clausen, 2017). The chemistry of inland waters is the result of how the chemistry of precipitation is transformed along hydrologic flow paths, by hydrologic factors (dilution or concentration such as by evaporation), biotic factors (such as plant uptake, storage and release, and microbial storage and transformation) and geologic factors (geochemical reactions). Clearly, all aspects of limnology as a science have to be considered. Using the ecosystem approach, the boundaries of a lake, pond, or river are ostensibly clear because the shorelines would appear to make quantitative, mass-balance calculations easier, but it has become apparent that there is a critical need to look "beyond the shoreline," that is, to the airshed and to the watershed or catchment, for evaluating human impacts on a body of inland water. Moreover, it is mostly impossible to judge the "health," condition, or value of an aquatic ecosystem from a causal observation from the shoreline. It is necessary to get inside the boundaries of the system to learn about these characteristics. Humanity needs water, and understanding the ecosystems of inland waters is vital to our future.

Table 3 Water balance for the Earth.

Fluxes	*Volume (km^3/year $\times$ 10^3)*	*Percent of total*
Evaporation from ocean	413	100
Precipitation to ocean	373	90.3
Water vapor transport from ocean to land	40	9.7
Precipitation to land	113	100
Evapotranspiration from vegetation	73	64.6
Runoff from land	40	35.4

Volume data from Trenberth et al., 2007.

Source: Modified from Clausen JC (2017) *Introduction to Water Resources*. Long Grove, IL: Waveland Press.

See Also: Emerging methods and topics: Macrosystems Limnology and Beyond: Re-Envisioning the Scale of Limnology; Fundamental concepts and theories: Hydrologic Setting Affects Ecosystem Processes; Paleolimnology: Long-Term Reconstructions of Environmental Change

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The Discipline of Limnology☆

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This is an update of J.J. Cole, Limnology as a Discipline, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00002-8.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Colloidal organic matter Very large molecules or aggregates that have properties intermediate between particles and truly dissolved substances.
Dispersion The spatial mixing of a solute in water or the spatial mixing of more than one water mass.
Eutrophication Nutrient enrichment that leads to increased autotrophic growth.
Food-web An assemblage of organisms that interact by consuming each other.
Piscivorous A predator that eats fish.
Secondary production The growth of consumer organisms.

Limnology—An integrative, multidisciplinary science

The objective of limnology is a comprehensive, integrated, scientific understanding of inland waters. As Gene Likens points out in this Encyclopedia, limnology can be viewed as the Queen of Science because of its inherent interdisciplinary nature. As the scientific study of inland waters, limnology incorporates knowledge of geological, physical, chemical, and biological processes at a range of spatial and temporal scales. Although some limnology textbooks greatly emphasize lakes, the inland waters within the purview of modern limnology include lakes, streams, rivers, ground water, and often wetlands. Like oceanography, limnology is a highly integrative and interdisciplinary science and frequently adopts an ecosystem perspective to approach research questions or applied problems. This need for integration to understand the dynamic processes of inland waters has been evident since the beginnings of limnology as a formal discipline in the late 19th century, and in this regard there is a striking parallel between the fields of limnology and oceanography. With one important caveat, it is instructive to think of limnology as "freshwater oceanography." Forel was a little too narrow for modern limnology when he referred to it in 1892 as the "oceanography of lakes." Nevertheless, both limnology and oceanography are focused on types of environment (as are atmospheric science or forestry) and both are integrative sciences constructed from the strengths of the traditional scientific disciplines. If we wear jackets or tee-shirts with the word "limnology" emblazoned on the back and someone asks what it is, this definition as "freshwater oceanography" seems to be the one that best conveys limnology to the general public or scientists from diverse fields. The important caveat is that many inland waters are saline. So, one has to be careful here with the analogy. In some ways it is unfortunate that Francois- Alphonse Forel (1841–1912), the first to use the term limnology, was both conversant with ancient Greek, and unwilling to compromise linguistic purism by combining perhaps a more widely recognized Latin word for inland water with the Greek "-logos" (the study of). The Greek, "limni" (λίμνη) can be translated as lake, pool, lagoon, or lough. Even if most people knew Ancient Greek, "limni" does not represent limnology well because limnologists study both flowing and standing waters, and a host of systems that are neither lakes, nor lagoons, nor loughs. More problematic is that, for the few non-Greek speakers among us, there is no familiar everyday cognate for "limni." Thus, we have a scientific endeavor that studies a resource that is critically important to human welfare but exists under a rubric that is not recognized by the general public. Many practicing limnologists, and some entire universities, have chosen to drop the term

☆*Change History:* October 2020. JJ Cole and ML Pace.

limnology and describe the discipline other ways, such as "water science," "aquatic science," "aquatic ecology," "freshwater ecology," or by a sub discipline (e.g., "freshwater microbiology"). None of these are perfect. Both aquatic and water could just refer to the ocean as well as to inland waters, and in most definitions, ecology is too biological to represent the full spectrum of science in limnology (but see Likens, 1992). Sometimes the term "hydrology" is used in place of limnology. While etymologically reasonable, hydrology, especially in North America, as a discipline is well entrenched as the study of the water cycle and the movement of water. Limnology and hydrology are related sciences, but are not synonyms. Certainly other disciplines with otherwise obscure Greek names have caught the imagination of the public. Is "astronomy" well recognized because of its cognates, or are we aware of "astro-" because the space program, and some of its more visible proponents, made sure of it?

Limnology—Integration and sub disciplines

Although the science of limnology is by definition integrative and comprehensive, limnology is built upon its interacting sub disciplines. We can recognize four or five major sub disciplines. Physical limnology is focused on water movement at all spatial scales (from large-scale water balances to turbulence); heat and gas transfers; the optical properties of water, and often, the effects of physical properties on chemical reactions or organism function, and vice versa. Geological limnology is concerned with the formation and morphology of lake basins and river networks, the record of past events recorded in sediments (paleolimnology) and the distribution of aquatic environments over the landscape (which could also be called geographical limnology). Chemical limnology attempts to understand (a) the distribution of chemical constituents in water bodies, (b) the transport and retention of these constituents, (c) the chemical and biological reactions that control the forms of these constituents. Because of the strong direct and indirect roles that organisms, and especially microbial organisms, have on many chemical constituents much of chemical limnology would be classified as biogeochemical limnology. Biological limnology is concerned with the numbers and kinds of organisms that inhabit inland waters; their evolutionary adaptations, genetic relationships, and autoecology; their trophic and behavioral interactions with other organisms; food webs; and the effects of organisms on ecosystem-level processes such as whole-system metabolism and the effects of organisms on major biogeochemical cycles. Because of its rapid growth and high visibility, paleolimnology should probably be treated as a subdiscipline separate from geology. Paleolimnologists use the geological, chemical, or organismal records preserved in sediments to reconstruct conditions in the aquatic system itself (usually lakes), in the watershed, or more broadly as a record of paleoclimatic conditions.

The teaching of limnology

Although limnology, as "freshwater oceanography," is a broad and interdisciplinary topic in theory and origin, the teaching of limnology has progressed mainly in university departments that are most closely associated with biology and ecology. Even the historic and famous Center for Limnology at the University of Wisconsin at Madison is part of the larger Department of Integrative Biology (formerly Zoology). Thus, the teaching of limnology at most institutions tends to emphasize biological aspects. Basic physics, chemistry, and geology are covered, but not in the depth to which biology is. Where there is a clear distinction in oceanography between Marine Biology (the study of marine organisms and their interaction with the marine environment) and Biological Oceanography (how organisms effect the biogeochemical cycles in the ocean and vice versa), these distinction are usually blurred in the modern teaching of limnology. Many courses in limnology are really courses in freshwater biology, with physics and chemistry playing a supporting role. Many students are able to take a course in limnology (under whatever name) without a strong background or prerequisite courses in either chemistry or physics. While limnologists sometime complain about either a decline in the field of limnology or lack of recognition (see Jumars, 1990), an internet search in Google during May 2020 (with no date restrictions) reveals there are 965,000 hits for the parameters "limnology and course." Adding the names "freshwater biology" and "aquatic science" brings the total to about 62 million hits. This value is comparable and a bit larger to the results of a search for "oceanography and course," which recovers 11.2 million hits and quite a bit less than the 159 million for "ecology and course." Thus the teaching of limnology continues to have adherents and visibility, but not nearly what it should have because of the importance and relevance of the topic. The basic principles of limnology are also covered in other course work. Frequently, high-school students will have had a section on limnology in a basic course in either Earth Science or Environmental Science, as will university students who follow a course of study in areas like Natural Resources, Ecology, or Conservation Biology.

Principal limnological text books

The material covered in principal texts used to teach limnology is generally broad but as suggested above tends to be more focused on biology as a discipline and lakes as an environment. These texts contrast with the broader integrative science aspirations of the field. G.E. Hutchinson's classic four-volume Treatise on Limnology devoted one volume to geography, physics, and chemistry with the other three covering biological topics: Volume 2—Introduction to Lake Biology and the Limnoplankton; Volume 3—Limnological Botany; and Volume 4—Zoobenthos (coauthored with Yvette Edmondson). Though wide ranging in the topics covered, the Treatise, nevertheless, is nearly entirely devoted to lakes. One of the founding textbooks is Ruttner's 1953 Fundamentals of

Limnology, which devoted about half its length to biology, and thus more to chemistry, physics, and geology, and does give a single chapter on flowing waters.

Table 1 lists some of the more popular English-language texts published since 2000. We do include several texts focused exclusively on streams and rivers such as Stream Ecology: Structure and Function of Running Waters by Allen and Castillo (2007) or Stream Ecosystems in a Changing Environment by Jones and Stanley (2016). Students may want to consults these texts for more detailed analysis of flowing water.

The most comprehensive of the modern textbooks are Wetzel's 2001 Limnology: Lake and River Ecosystems and Dodds and Whiles, 2019 Freshwater Ecology. Both texts explicitly include flowing waters, and both devote multiple chapters to physical and chemical topics. The Dodds and Whiles text gives a comprehensive definition of limnology as, "The study of continental waters." Interestingly, though the scope of Wetzel's text does cover the full field of limnology, Wetzel inexplicably defines limnology (p. 4) as ". . . the study of the structural and functional interrelationships of organisms of inland waters as they are affected by their dynamic physical, chemical and biotic environments." Kalff's 2002 Limnology, also covers both flowing and standing waters and defines limnology more simply as (p. 1) ". . . the study of lakes, rivers, and wetlands as systems . . ." Kalff goes on to suggest that limnology is the most successful of the ecological sciences. Dodson's (2005) Introduction to Limnology is structured differently than the other modern texts in several ways. It is the only text to provide a specific manual for teachers of limnology. The text is also hierarchical and ecological, moving from the diversity of organisms to populations, communities, and ecosystems, a design that is shared with some ecology texts. This text pays little attention to physics or chemistry but strongly includes the interaction of humans with aquatic environments. Similar to Dodson the text of Lampert and Sommer is ecological and one of the few limnology texts that covers evolution. Cole and Weihe (2016) provide a recent update to a text that has been through many editions (with Cole as the sole author of prior versions). This text is less biological than others with more emphasis on aquatic habitat types as well as physical and chemical topics. The first edition of The Encyclopedia of Inland Water. Oxford-Elsevier, edited by G.E. Likens and published in 2009, and the precedent of this volume, has become an important go-to text. The coverage is very comprehensive and the short chapters are useful as a way to start to investigate a particular topic. Two more textbooks, likely to come out in the near future are noteworthy. An update of a long-standing text by Moss will be published posthumously in 2020. Moss provides an ecologically oriented text with light coverage of physical and chemical topics based on review of the pre-publication table of contents. Finally, although R.G. Wetzel died in 2005, an update of his famous text book is in the works at present, with John Smol and Ian Jones as editors. Unlike Wetzel's original text, this new one is an edited book with different authors for the individual chapters.

Scientific journals—The publication of limnological research

Exciting limnological research competes for space in the top, broad scientific journals such as Science, Nature, Nature Geoscience, Bioscience, Proceedings of the National Academy of Science, and so on. Limnology competes reasonably well for this space but not under its own name. There are 33 papers in these journals that come up in a Web of Science search (1975 through 2020) using the keyword "limnology" and its linguistic expansions (e.g., limnological etc.). However, if we put in a search that includes limnology

Table 1 Some of the more widely used English language text books of limnology published since 2000. For texts with multiple editions the most recent version is listed and subtitles are included with main title.

Author	*Date*	*Title*	*Scope*	*Comment*
Wetzel	2001	Limnology: Lake and River Ecosystems	Comprehensive, geography, geology, physics, chemistry, biology	Strong summary of field at the time of publication
Kalff	2002	Limnology: Inland Water Ecosystems	Comprehensive with more strength in ecology and biogeochemistry than physics or chemistry	Extensive comparative analyses
Dodson	2005	Introduction to Limnology	Mostly biology	Structured like an ecology text
Lampert and Sommer	2007	Limnoecology: The Ecology of Lakes and Streams	Mainly biology, includes flowing waters	Includes evolution and adaptation, ecological research methods and approaches
Likens (editor)	2009	The Encyclopedia of Inland Water. Oxford-Elsevier Volume 1	Comprehensive, encyclopedia, includes flowing waters	Short chapters with multiple authors
Cole and Weihe	2016	Textbook of Limnology	Comprehensive, less biology than most texts, includes chapters on streams and wetlands	Organization moves from biology to physical and chemical topics
Brönmark and Hansson	2018	The Biology of Lakes and Ponds	Focuses on biology and standing waters	Integrates ecology, evolutionary biology with limnology
Dodds and Whiles	2019	Freshwater Ecology: Concepts and Environmental Applications of Limnology (Aquatic Ecology)	An ecologically oriented text but also includes considerable coverage of physics and chemistry	Coverage of flowing waters, management applications
Moss	2020	Ecology of Freshwaters: Earth's Bloodstream	Ecologically oriented text with some chemistry and physics as well as coverage of major aquatic environments	Publication planned for late 2020

(and its expansions) plus we add "aquatic ecology" or lake or river, there are many more papers. For these journals combined from 1975 to 2020 in Web of Science there are 3009 entries. A similar search using oceanography (and its expansions) or "marine ecology" or estuary or sea, we get almost threefold this, 9784 hits. This is about the same as a search for ecology (with expansions) in the same set of journals (5211). Using "ecology" and expansions to include "ecosystem" and "ecological" the search yields 8777 hits. So limnology holds it own in these very high impact journals but not quite as well as do ecology and oceanography.

Most limnological research is published in journals dedicated to limnology itself (some including oceanography) or to fisheries or more generally, ecology. Taking just the journals of the Ecological Society of America, for example Ecology, Ecological Applications, Ecological Monographs, Frontiers in Ecology and Environment, Ecosphere, there are 2732 papers that cover limnological topics. This number is about 13% of the total content of these journals. Twenty eight percent of the papers in the journal Ecosystems from 1998 to 2020 cover inland aquatic environments.

There are 10 journals included by Web of Science with the word "limnology" (or a linguistic variant) in the title; 37 more with the word "aquatic"; and many others that come under different names, such as Hydrobiologia or Freshwater Biology, for a rough total of about 70 (Table 2). This number is comparable to the 29 journals with the word "oceanography" (or a variant) and 87 with the word "marine." As in most scientific disciplines, the citation rates or impact factors among these journals are highly variable reaching as high of 5.2 for Limnology and Oceanography Letters. These factors are based on the most recent data available for all journals in the limnology grouping as listed by the Institute for Scientific Information (ISI). The higher-impact limnological journals are on a par with higher-impact field-oriented journals such as Ecology, Geology, and so on.

Limnology—Multiple scientific approaches

As with other aspects of ecosystem science, limnology employs multiple approaches. These can be classified, albeit imperfectly, as: observational; comparative; experimental; and theoretical (including modeling; see Carpenter et al., 1997).

Observational approach. The observational approach consists of measurements over time of key parameters of interest, often in a single system, and has dominated limnology in the past. The observational approach is descriptive. That is, measured variables, their changes over time or space, and their apparent interrelations can be depicted quite quantitatively, but the backbone here is the description of a state or change in state.

While the observational approach can suffer from being narrowly site-specific in some single-system studies, it forms the background of what we know about aquatic systems and how they vary over time. Further when such observations are sustained over time (long-term studies), or extended to include multiple systems, the observational approach becomes particularly powerful at detecting changes or long-term trends. Sometimes this approach can identify the factors that cause the observed changes, and this is often useful to management or policy about these resources.

Table 2 Leading limnological journals, ranked by Journal Impact Factor (JIF).

Rank	*Journal Title*	*Journal Impact Factor*
1	Limnology and Oceanography Letters	5.2
2	Water Resources Research	4.3
3	Limnology and Oceanography	3.8
4	Freshwater Biology	3.4
5	Canadian Journal Fish & Aq. Sci.	2.9
6	Limnology And Oceanography-Methods	2.5
7	Aquatic Sciences	2.4
8	Hydrobiologia	2.4
9	Freshwater Science	2.3
10	Journal of Great Lakes Research	2.2
11	Limnologica	1.8
12	Journal of Paleolimnology	1.6
13	Limnology	1.6
14	Inland Waters	1.5
15	Marine and Freshwater Research	1.5
16	Aquatic Ecology	1.4
17	Water and Environment Journal	1.4
18	Journal of Limnology	1.3
19	Journal of Freshwater Ecology	1.2
20	Water Environment Research	1.1

The JIF is the number of times an article was cited during a 2-year period, divided by the total number of articles published in that journal during that same period. Data are the most recent available from Journal Citation Reports Science Edition (Clarivate Analytics, 2020). Note than JIF varies over time and can change year to year.

Comparative approach. In the comparative approach researchers often choose to sample a wide variety and number of related aquatic systems and then formulate a relationship between aspects of these systems (e.g., lake size, river discharge rate, slope, pH, wind stress) and the objective of the study (phytoplankton biomass, bacterial secondary production, diversity of fishes, net gas flux rates). When these relationships are strong and based on reasonable connections between driver and observation, they can be used to predict conditions in a system that has not yet been sampled. When the relationships also have strong mechanistic underpinnings, they can be used in management as well. Examples include: the relationships between the loading or concentration of total phosphorus, and algal biomass (as chlorophyll-a) in lakes: the rate of phosphorus release from sediments over a gradient of sulfate concentrations (Caraco et al., 1989); how food chain length is related to lake size (Post et al., 2000): or how the fraction of dissolved and particulate organic matter derived from terrestrial organic matter relates to lake size, trophic richness and other variables (Wilkinson et al., 2013).

Experiments. Limnologists use experiments at many time and space scales ranging from short term manipulations of water in bottles or sediment cores, to more complex mesocosms, or artificial stream channels, to entire ecosystems. Experiments in bottles or mesocosms offer replicability but can be criticized for a lack of realism. Nevertheless, work on limiting nutrients for algal primary production; food preferences of zooplankton, the uptake and releases of chemicals from sediments, have been greatly advanced by work at these small and replicable scales. An interesting example is that of Howarth et al. (1993) who manipulated turbulence in large mesocosms to investigate its effects on cyanobacterial blooms. Because aquatic systems are discrete with observable boundaries, limnology has always been a leader in whole-ecosystem experiments, especially in smaller lakes and in streams. Whole-ecosystem experiments also suffer the limitation of being site specific, and from lack of strict controls, but can be used to look directly at a system's response to a perturbation and can be very useful from a management point of view. Manipulative experiments are designed to change the properties of a system (add nutrients; alter the food web; decrease available light; (Carpenter et al., 2005). Tracer experiments do not alter the system per se, but are designed to follow a process by adding a purposeful tracer (C or N isotope to follow the food web Wilkinson et al., 2014.); inert gas to measure gas exchange rates (Cole and Caraco, 1998); or an exotic or non-reactive solute to trace water movement or residence time (Peterson et al., 2001). Whole system experiments are difficult to replicate and require special care in their interpretations but can be very powerful. As demonstrations, especially to the general public, whole-system manipulations can be particularly convincing and evocative. For example, the addition of phosphorus and nitrogen to a lake without significant algal blooms almost always results in these blooms (Schindler 1977; Carpenter et al., 1997, 2001).

Modeling and theory. Modeling and theory are widely used, often in conjunction with data from comparative or long term studies, to test the theory of interest. Theoretical approaches are able to look at essentially any spatial or temporal scale and integrate knowledge across these scales. In fact, most data analysis contains some type of modeling. Some limnological models are designed to represent the physics of systems and the user can input local data (Imberger and Ivey, 1991), or to calculate primary production from continuous oxygen data in a stream or river (Holtgrieve et al., 2000). Others are designed for a specific use in a particular analysis (Carpenter and Brock, 2011).

The four basic approaches are used unevenly in the major subdisciplines of limnology (Fig. 1). In modern limnology some of the best studies combine aspects from the four basic approaches. A few examples are noteworthy. Combining long-term observations

	Geological	Physical	Chemical	Biological	Paleolimnology
Observational	XXX	XXX	XXX	XXX	XXX
Comparative	XXX	X	XX	XXX	XX
Experimental	?	X	X	X	?
Model/theory	X	XXX	XX	X	?

Fig. 1 Approaches used in the major subdisciplines of limnology. More X's means more commonly used. Thus, the observational approach (measurements over time in a single system) is widely used in all subdisciplines whereas whole-system experiments are rarely if ever attempted in paleolimnology or geology.

carried out in multiple lakes (observational plus comparative), Magnuson et al. (2000) used historical records of ice duration data on lakes to document a warming climate in the Northern Hemisphere over the past 150 years. Combining physical theory and experimental approaches, a number of researchers have added purposeful tracers to lakes, rivers and streams to estimate the physical basis of gas exchange and the factors that regulate it. In the work that led to the modern understanding of the causes of cultural eutrophication in lakes, we have all four legs of the table in play at various times. The comparative work of R.A. Vollenweider and colleagues showed the initial correlation between total phosphorus (TP) and chlorophyll-a levels among lakes. Further comparative work has revealed numerous factors such as lake depth, zooplankton community structure that modify the basic TP-chlorophyll relationships. Whole lake nitrogen and phosphorus additions revealed that phosphorus was necessary to stimulate large algal blooms. Again further experimental work that followed showed that the effect of a given level of TP loading could be modified by the presence or absence of piscivorous fishes. Models from the simple empirical type to more refined models that included the effects of hydraulic residence time were added and aided managers to predict the effects of a given increase or decrease in nutrient loads. A number of studies have followed the time course of eutrophication (Smith, 1997). An important example is the long-term work at Lake Washington, which was studied both before and after a large-scale sewage-nutrient diversion (Edmonson, 1991). The work on acid rain and its effects on aquatic ecosystems is a second excellent example of a topic that used all four legs of the table. The work included specific experiments on acid sensitivity of key organisms, following over long-term the changes in acidity, organisms and organism health in systems, comparative studies, direct, whole system experiments in lakes and streams, and rich modeling data that simulated acid from its deposition, through the watershed and into water bodies. Another research area that is richly developed in combining theory with both experimental and comparative approaches is the Lotic Intersite Nitrogen Experiment (LINX) which consists of a large network of stream sites all performing N-isotope addition experiments, linked to a common model to examine nitrogen retention and transformations (Peterson et al., 2001). The exciting work on regime shifts in shallow lakes is particularly strong in combining theory, experiments and long-term observation. This body of work endeavors to explain the factors that cause the observed sudden shifts from macrophyte to phytoplankton dominance in shallow systems. The advent of reliable instruments which can make high-quality continuous measurements of variables such as temperature, dissolved oxygen, pH, chlorophyll etc., has opened up a new approach. Persistent high-frequency measurements are being used to measure whole system primary production and respiration in lakes and in flowing waters and are beginning to be used to reveal the factors that regulate this metabolism. Some limnologists are exploring the value and challenges of a global network of persistent high frequency measurements. For example, the Global Lake Ecological Observatory Network is a grass-root, international collaboration organized around using these sensors in lake and reservoirs of the world (www.gleon.org).

Current and emerging themes in limnological research

Several consensus documents (Lewis et al., 1995; Wurtsbaugh et al., 2003) have attempted to summarize the key unifying and emerging themes in modern limnology. These are useful compilations because both are the results of workshops, sponsored by the scientific societies and funding agencies, and thus, have the consensus of more than a few individuals. Neither workshop attempted to be comprehensive; the list here, derived from both sources, is meant only to be illustrative of selected important themes with a few examples. The further reading lists a few studies under each topic where the reader can gain more information. More detailed information on some of these topics appears elsewhere in this Encyclopedia.

Principles governing aquatic food webs. This topic covers the role of consumers in determining the biomass, species composition and production of prey items and primary producers. How changes in piscivorous fish, by removal due to over fishing or addition by stocking, affect the rest of the food web and both algal and macrophytes communities. Fish manipulations have been used as a tool in managing freshwater ecosystems.

The origin, structure and roles of organic matter in natural waters. Organic matter affects the optical properties of water as well as pH and, through chelation, the degree of toxicity of certain metals. The amount of organic matter in a given system is governed by its production from within the system, the rate of input from the watershed and losses due to degradation by light and microbes. Researchers have also been interested in the role of terrestrial subsidies and how terrestrial organic matter does or does not enter the aquatic food web. In addition to the roles of organic matter, other researchers have been advancing our understanding of the chemical make up of dissolved and colloidal organic matter to achieve a molecular understanding of its macro-properties.

Hydrodynamics and fluid mechanics. There have been stunning achievements in recent years in understanding water movement and fluid dynamics in all aquatic ecosystems, largely as the result of improved instrumentation such as acoustic Doppler current profilers (ADCP). Interacting with the better measurements has improved theory for modeling thermal structure, advection, dispersion and turbulence. In streams, the ability to do tracer experiments has led to a much better understanding of temporary storage and mixing in eddies. The work on fluid dynamics extends to the effects on biological and chemical processes.

Biogeochemistry of aquatic ecosystems. The transport, retention and transformation of key elements such as carbon, nitrogen, phosphorus and more recently mercury, has been an important component in limnology for some time. Balancing input-output budgets often requires the identification of sources and sinks that were not known or realized to be important or biogeochemical reactions that were thought not to occur like the anaerobic oxidation of ammonia. As new toxic materials become of concern, their biogeochemistry becomes relevant and interesting, sometimes in surprising ways. For example, the creation of new, large hydro-electric reservoirs in Canada, Brazil and China has caused an enormous release of mercury, which is highly toxic.

Energetics of aquatic ecosystems. The study of energy as a basic currency in ecosystems is a pervasive theme in all types of ecosystems and particularly well developed in limnology and has a long history of study. An interesting modern extension has been the

expanded use of ecological stoichiometry which links the ratios of key elements in organisms (N, P, Si, C) to food webs and ultimately to energetic constraints (Sterner and Elser, 2002).

Land-water and atmosphere-water interactions. A key area in limnology is to explore the relationship of the conditions within an aquatic system (chemical constituents, biological productivity, etc.) to the system's links with its watershed or airshed. This endeavor includes the responses of an aquatic system to changes in land cover or land use. With climate change as a potential driver of new land use or land cover patterns, this area of research has become critically important as well as the system's geographical and hydrogeographical position in the landscape. Atmosphere-water interactions include the mechanisms, magnitudes, and of materials that enter and leave aquatic systems at the air water interface. The exchange processes include aeolian transport of particles, and the exchange of gases.

Ecosystem services. Aquatic environments provide many services to humans such as drinking water, fisheries, recreation, cooling water for power plants. These services are the result of natural processes such as the food webs that produce fish and the aggregated flows that provide power plant cooling waters. Disruption of these services can be costly and research is addressing the value of ecosystem services, the consequences of losing services, and resilience of services to various types of disturbance (e.g., storms, land use change).

Conservation of biodiversity. Inland waters support a rich diversity of flora and fauna and many species are imperiled due to pollution, loss of habitat, overharvesting, invasions of exotic species, and flow modifications. Sustaining and restoring endangered species requires understanding both population processes and the ecosystem dynamics that support species. Examples of successful conservation programs are often founded on sustaining or restoring habitats and particularly in flowing waters this requires attention to hydrology (e.g., minimizing low flow condition in a river). Despite examples of success, inland water biodiversity is declining as water resources are continually subjected to greater human pressures and development (e.g., dams).

Global limnology. Limnologists are increasingly interested in the global status of aquatic resources. Seemingly simple but nonetheless technically challenging problems are amenable to analysis using remote sensing and modeling. These include questions like how many lakes are there in the world, how are the number of volume of reservoirs changing globally, what is the total length and discharge of rivers globally and how are these properties changing. Answers to these questions open others such as what are the emissions of greenhouse gases from inland waters and how much carbon is stored in their sediments. Limnological research is achieving global scope with value for understanding the earth system and managing aquatic resources and regional and global scales.

The future of limnology as a discipline

There is no doubt that the comprehensive, integrative scientific understanding of inland waters (e.g., limnology) is critical to our understanding of the larger terrestrial matrix in which these aquatic systems are embedded. It is becoming increasingly clear the aquatic systems are often biogeochemical "hot spots" which regulate chemical cycles to a much greater extent than their small size would suggest. Certainly, inland waters are critically important habitats and resources for wildlife and humans alike. While the scientific study of these inland waters will continue, it is not clear to what extent that limnology will either maintain its independent identity, or be subsumed into ecology or earth science in the future.

See Also: Emerging methods and topics: Dust and Fog Effects on Inland Waters; Fundamental concepts and theories: Section introduction: Fundamental Concepts and Theories of Inland Waters; Lakes as Ecosystems; Nutrient Stoichiometry in Aquatic Ecosystems; Photochemical Reactions in Inland Waters; The Chemical Properties of Water; Structures and functions of Inland Waters - Lakes: Ecological Consequences of Climate Extremes for Lakes; Lake Ice Formation and Melt. Under-Ice Dynamics; Structures and functions of Inland Waters - Wetlands: Boreal and Temperate River Wetlands

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Hydrological Cycle and Water Budgets

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This is an update of T.N. Narasimhan, Hydrological Cycle and Water Budgets, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00010-7.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Component Specific pool of water in the hydrological cycle.
Evaporation Process where a substance in a liquid state changes to a gaseous state.
Evapotranspiration Process where water is transferred from the land to the atmosphere by evaporation from water and soil, and transpiration from plants.
Flux Flowing of water or a constituent per unit time.
Groundwater Water that exists in saturated zones beneath the land surface.
Hydrological cycle Also known as the water cycle, describes the continuous movement of water on, above, and below the surface of the earth.
Runoff Flow of water over the land surface to the stream network.
Soil-zone water Water retained in the unsaturated zone (zone between the land surface and the water table).
Storage Amount of water contained in a specific component of the water budget.
Surface water Any body of water above ground, including streams, wetlands, rivers, lakes, reservoirs.
Unsaturated zone Zone between the land surface and the water table.
Water budget An accounting of the rates of water movement and the change in water storage in all parts of the atmosphere, land surface, and subsurface.

*Deceased.

Introduction

The earth's geology, atmosphere, and life itself have been profoundly affected by water and the movement of water. The movement of water is the result of the hydrological cycle, which is a continuous exchange of water above, on, and in the earth. The hydrological cycle is characterized by the circulation of an almost insignificant fraction, about 0.01%, of the total water existing on the earth. Almost all biological creatures on land require freshwater for sustenance. Yet, remarkably, they have evolved and proliferated, depending on the repeated reuse of this small fraction of available water. The partitioning of water among the components of the hydrological cycle at a given location over a given time period constitutes a water budget. Water-budget evaluations are important to understand the geological and biological evolution of the earth and of practical value in environmental and natural-resource management on various scales. The purpose of this chapter is to describe the important components (often referred to as pools) of the hydrological cycle and water budgets relevant to inland waters and aquatic ecosystems.

Hydrological cycle

The hydrological cycle (National Oceanographic and Atmospheric Administration, 2020) is a continuous cycle with no beginning or end point, but the atmosphere is a good place to start (Fig. 1; Perlman and Evans, 2019). Atmospheric water vapor condenses and precipitates as rain or snow. Part of this precipitation is intercepted by vegetation canopies prior to reaching the ground. What precipitation does reach the ground either evaporates, percolates into the soil, or flows immediately (or after snow melting) over land as surface water and moves toward inland depressions, streams, rivers, and ultimately the oceans. Much of the surface water is intercepted along the way by wetlands, lakes, and reservoirs. The water that percolates into the soil either replenishes the soil-water zone, where it is available for uptake by plants, or continues downward to replenish aquifers and deeper groundwater reserves. Depending on soil characteristics, the water reaching aquifers (groundwater) flows relatively slowly from areas high in the landscape to areas lower in the landscape. Because of variability of the layers of soil and rock, the rate of downward movement of water can vary. Groundwater is transported horizontally and discharged in springs, streams, wetlands, ponds, lakes, or the ocean itself. At the land and water surface, surface water is subject to evaporation by solar radiation and to transpiration by plants as they consume water for photosynthesis. Collectively referred to as evapotranspiration, this transfer of water back to the atmosphere completes the hydrological cycle.

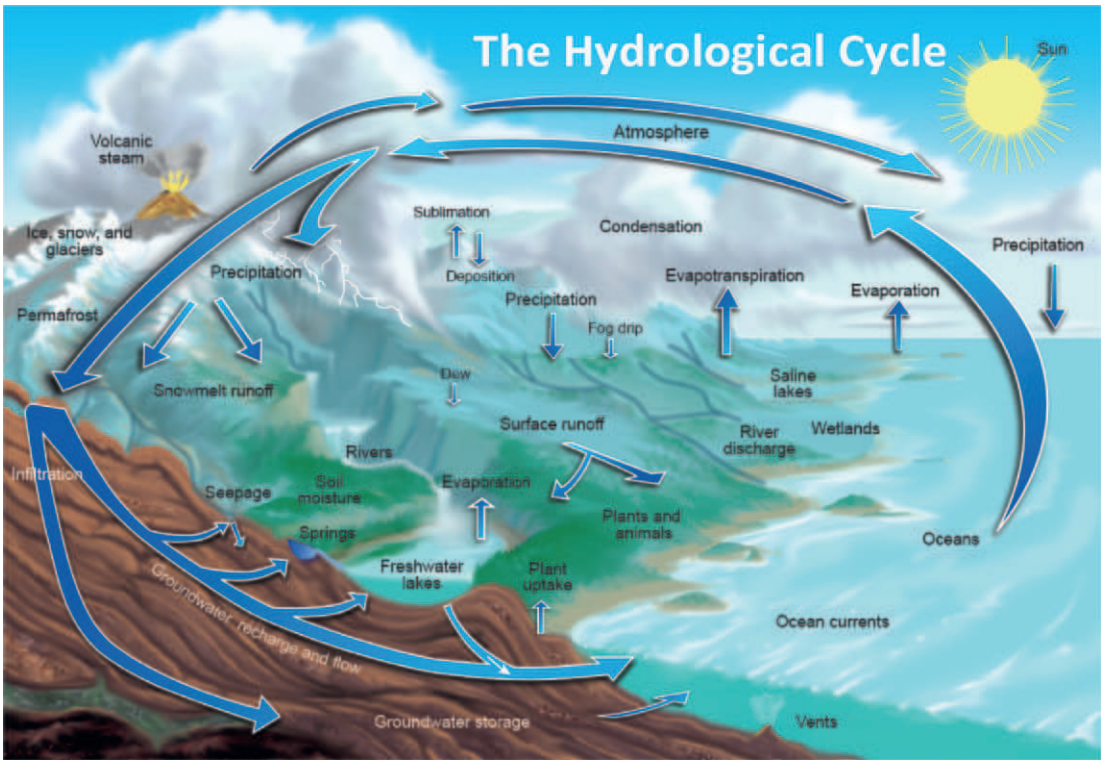

Fig. 1 Schematic of the hydrological cycle. Modified from Perlman H and Evans J (2019) *U.S. Geological Cycle*, *The Water Cycle*, https://www.usgs.gov/special-topic/water-science-school/science/water-cycle?

Table 1 Components or pools of water in the hydrological cycle, with their respective spatial and temporal scales.

Water source	*Water volume, in cubic kilometers*	*Percent of freshwater*	*Percent of total water*	*Spatial scale*	*Residence time*
Oceans, Seas, and Bays	1,340,000	–	96.480	Km to thousands of km	Thousands of years
Ice caps, Glaciers, and Permanent Snow	25,800	96.116	1.858	Km to thousands of km	Tens of thousands of years
Groundwater	22,600	–	1.627	Tens of meters to hundreds of km	Days to millions of years
Renewable (young)	*630*	2.347	*0.045*	Tens of meters to hundreds of km	Days to millions of years
Nonrenewable (old)	*22,000*	–	*1.584*	Tens of meters to hundreds of km	Days to millions of years
Soil-zone water	54.1	0.202	0.004	Meters to tens of meters	Weeks to years
Ground Ice and Permafrost	207	0.771	0.015	Km to hundreds of km	Days to millions of years
Lakes	190	–	0.014	Meters to hundreds of km	Weeks to years
Fresh	*108*	0.402	*0.008*	Meters to hundreds of km	Weeks to years
Saline	*95*	–	*0.007*	Meters to hundreds of km	Weeks to years
Artificial Reservoirs	10.8	0.040	0.001	Km to hundreds of Km	Weeks to years
Rivers	1.90	0.007	0.000	Meters to hundreds of km	Days
Atmosphere	12.9	0.048	0.001	Km to thousands of km	Days
Wetlands	14.1	0.053	0.001	Meters to km	Weeks to years
Seasonal snowpack	2.90	0.011	0.000	Meters to hundreds of km	Weeks to years
Biological Water	0.94	0.004	0.000	Less than meters	Minutes to years

Modified from Abbott BW, Bishop K, Zarnetske JP, Minaudo C, Chapin FS, Krause S, Hannah DM, Conner L, Ellison D, Godsey SE, Plont S, Marcais J, Kolbe T, Huebner A, Frei RJ, Hampton T, Gu S, Buhman M, Sayedi SS, Ursache O, Chapin M, Henderson KD, and Pinay G (2019) Human domination of the global water cycle absent from depictions and perceptions. *Nature Geoscience*, 12: 533–540, https://doi.org/10.1038/s41561-019-0374-y.0374.

The components or pools of water of the hydrological cycle, namely, the oceans (the biggest pool and one often not considered in surface water), atmosphere, surface water, soil-zone water, and groundwater are intimately interlinked over a variety of spatial scales (meters to thousands of kilometers) and temporal scales (days to millions of years). Estimates of the volume of water stored in each component or pool of the hydrological cycle for the entire earth, and the relevant spatial and temporal scales are summarized in Table 1, which is based on a synthesis of 80 recent modeling and empirical studies (Abbott et al., 2019).

Water is essentially an incompressible liquid, with high specific heat capacity and latent heats of melting and evaporation. Water exists in solid, liquid, and gaseous phases within the range of temperatures over which life, as we know it, is sustained. The relation between temperature and water density of fresh water is nonlinear. As temperatures decline, the density of water increases until water reaches 4 °C, with further cooling its density decreases until it reaches 0 °C. At 0 °C, water forms into ice and its density abruptly decreases by about 10%. After freezing, the density of ice slowly increases with further cooling. Ice being much less dense than water is the reason ice forms on the surface of lakes rather than lakes freezing solid. The nonlinear decrease in density as water warms from 0 to 30 °C is one of the main reasons that lakes and ponds thermally stratify into specific layers during summer. The bipolar nature of water enables it to trap nonelectrolyte molecules as well as charged ions. For these reasons, water is an active chemical agent, efficient transporter of energy and heat, and a carrier of dissolved and suspended substances. These attributes render water to be an extraordinary geological and biological agent.

The hydrological cycle is driven mostly by solar energy and gravity, and to a minor extent by geothermal heat and underground pressure. The earth's erosional and geochemical cycles exist because of water's ability to do mechanical work associated with erosion, chemically interact with rocks and minerals, and transport dissolved and suspended materials. Collectively, the hydrological and geochemical cycles constitute the vital cycles that sustain life. The interrelationships among these vital cycles can be conveniently understood by examining the components of the hydrological cycle.

Specific components (pools) of the hydrological cycle

Oceans, glaciers, ice caps, and snow fields

The oceans, seas, and bays are the biggest pool of water, followed by the glaciers, ice caps, and permanent snow field pool. Both of these pools are at the land surface, but they are not typically considered in the surface-water pool.

Surface water

Once precipitation reaches the earth's surface, the water that does not percolate into the ground becomes surface water. Surface water chemically breaks down rocks through actions of microbes, plants, and animals and solar radiation and physically breaks down rocks through weathering and erosion during its transport. The products of weathering are transported as sediments

(bedloads and suspended loads) and dissolved chemicals. In addition, water transports leaf litter and other decaying vegetation and animal matter. Sediments and organic matter together contribute to the cycling of life-sustaining nutrients. Habitats for flora and fauna along the course of a river depend, in very complex ways, on the texture of sediments as well as on their chemical makeup. Most runoff and streamflow is intercepted along its movement to the oceans by wetlands, ponds, and lakes, where its temperature and chemical makeup can be greatly altered. In addition, reservoirs built for many purposes intercept the flow.

Soil-zone water

Once water percolates into the soil, it is either retained in the soil zone (zone between the land surface and the water table also called the unsaturated zone) or it seeps down to the water table. Water in this unsaturated zone is referred to as soil-zone water. In the soil zone, water and air coexist. Soil-zone water, which is held in the pores by capillary forces, is not amenable for easy extraction by humans. However, plants can overcome the capillary forces and extract soil-zone water. With abundant availability of oxygen and carbon dioxide in this zone, the soil is an active chemical reactor, with microbially mediated aqueous reactions. In the soil zone, water movement is mainly vertical, with downward directed gravity flow and upward evaporative movement. Water moving down by gravity reaches the water table to recharge the groundwater pool.

Groundwater

Throughout the watershed, water enters the groundwater pool via infiltration, and driven by gravity or pressure from the soil and rocks above moves vertically down in areas of groundwater recharge. Depending on topographic relief and the distribution of permeable and impermeable layers, the vertical downward movement is resisted sooner or later, and the movement becomes more horizontal, and is discharged into streams or lakes. The journey of water from the time it enters the groundwater pool to the time it emerges back at the land surface is referred to as regional groundwater flow (Fig. 2; Carter, 1996). Regional groundwater flow constitutes a convenient framework for understanding the formation of sedimentary rocks and minerals, and the areal distribution of soils and aquatic ecosystems on land. Groundwater discharge typically occurs in perennial stream channels, wetlands, springs, low lying areas, and lakes. In these discharge areas, surface water and groundwater directly interact with each other, with important geological and biological consequences. For example, the spectacular tufa towers of Mono Lake in California represent precipitates of calcium carbonate resulting from a mixing of subaqueous thermal springs with the lake water. Areas where groundwater discharge occurs are referred to as hyporheic zones, which play an important role in stream ecology.

Regional groundwater flow provides a framework to interpret patterns of chemical processes in the subsurface. Water in recharge areas is generally rich in oxygen and carbon dioxide and can chemically break down minerals through corrosive oxidation reactions. However, available oxygen is consumed as water chemically interacts with the minerals along the flow path, and the oxidation potential of groundwater progressively decreases along the flow path. In swamps and wetlands of discharge areas, water typically has strong reducing (anaerobic) conditions. Between these two extremes, ambient conditions of acidity (pH) and redox state (Eh) govern the chemical makeup of water and the types of minerals and microbial populations that are compatible with ambient water

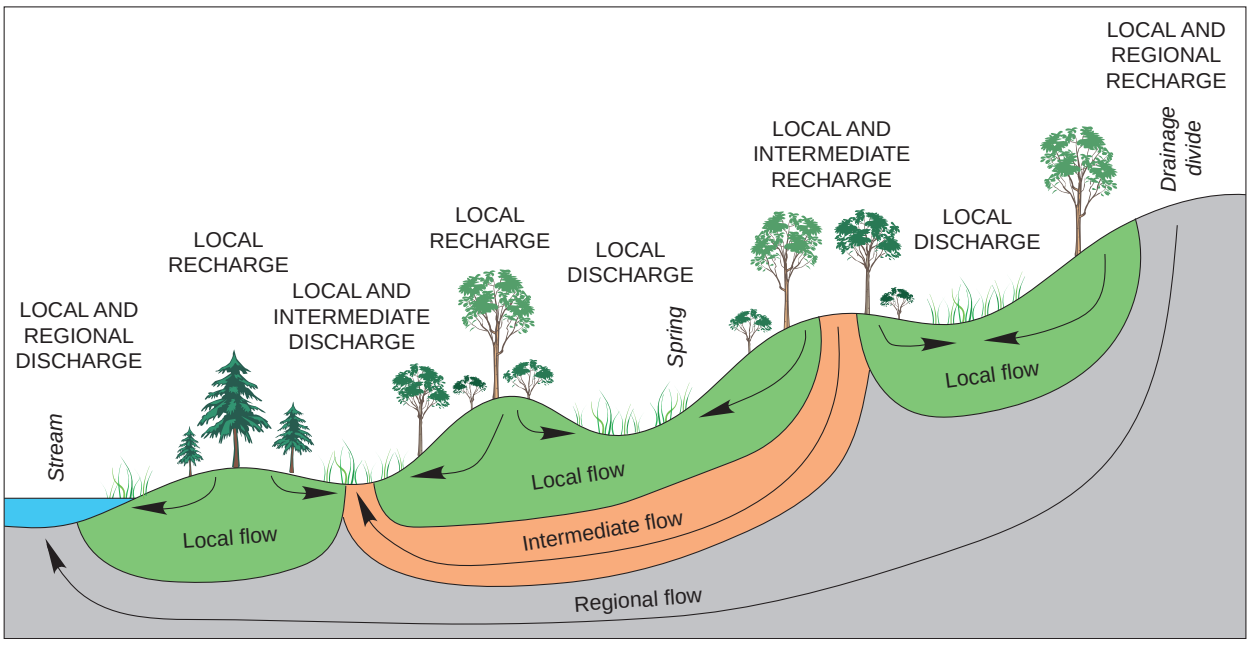

Fig. 2 Regional groundwater flow demonstrating local, intermediate, and regional flow patterns. Modified from Carter V (1996) Technical aspects of wetlands: Wetland hydrology, water quality and associated functions. In: *U.S. Geological Survey. National Water Summary on Wetland Resources. U.S. Geological Survey Water-Supply Paper 2425*. pp. 35–48.

chemistry. In general, the cation content of groundwater reflects the chemical makeup of the rocks encountered along the flow path, and the anion content is indicative of the progress of chemical reactions.

Nutrient cycling

The hydrological cycle is important to the transport and cycling of nutrients. A glimpse into connections to nutrient cycling can be gained by examining the role of water in the cycling of carbon, sulfur, and phosphorus. Almost all biological carbon originates from atmospheric carbon dioxide through photosynthesis by plants and phytoplankton. Water, essential for photosynthesis, is transferred by terrestrial plants from the soil via leaves to the atmosphere (transpiration). Water plays a dominant role in the decomposition and mineralization of organic carbon on diverse time scales, ultimately producing carbon dioxide or methane to be returned to the atmosphere.

Sulfur is a redox-controlled chemical element that plays an important role in metabolic reactions of plants. Under reducing conditions, sulfur is insoluble in water. Sulfate, in its most oxidized form, is water soluble, and is the form that sulfur usually enters plant roots. Sulfide minerals are oxidized in the presence of bacteria to sulfate and become available for uptake by plants. In plants, sulfur is fixed in a reduced form. Thus, sulfur from dead organic matter is mobilized by oxidizing waters to sulfate to sustain the sulfur cycle.

Phosphorus plays several important roles in the biological processes of plants and animals and often limits productivity in lakes. Phosphorus is water soluble only under narrow ranges of redox and pH. Because phosphorus does not readily form gaseous compounds, phosphorus is almost entirely transported with the movement of surface water and to a much lesser extent with the movement of groundwater. Because of the importance of phosphorus to the productivity in lakes and rivers, management actions are often taken to limit its transport, especially in runoff and wastewater effluent.

Energy balance

A discussion of the hydrological cycle with respect to inland waters is incomplete without mentioning its connections to the solar energy balance. The hydrological cycle is driven largely by solar energy. Just like water, solar energy is also subject to cyclic behavior. On the land surface, the energy received as incoming solar radiation (insolation used to heat streams and lakes) is balanced partly by outgoing longwave radiation, partly as sensible heat by convecting air columns, and partly as latent heat transferred by water from the land to the atmosphere during evaporation. Of the total solar radiation received from the sun, about 45% of the energy is returned to the atmosphere by water, a major fraction. Any significant perturbation to this natural cycle could influence global climate.

Summary

The concept of the hydrological cycle is quite simple. But, its importance to life on earth is profound. The hydrological cycle plays an overarching role in the cycling of solar energy, sediments, and chemical elements vital for life. Although it is clear that contemporary ecosystems reflect an evolutionary adaptation to the delicate linkages that exist among the various components of the hydrological cycle, it is also apparent that evolving life has affected the evolution of the hydrological cycle over geological time. Life, it appears, is simultaneously a product of the hydrological cycle and a factor causing changes in the cycle.

Water budgets

Humans, like plants and animals, have had to adapt to natural variability in weather and climate and now will have to continue to adapt to a changing climate. However, many individual components of the hydrological cycle (surface water, soil-zone water, and groundwater) lie within reach of human control and can be managed for human benefit. In this context, the concept of water budgets (Healy et al., 2007) becomes relevant.

Given a specific area with well-defined boundaries, constructing a water budget consists of quantifying the amount and relationships among inflow, outflow, and change in storage within a defined area (i.e., the transport or flux of water between each pool). This simple concept is as valid over the entire earth, over a river basin, or over a small rural community. In a world of stressed water resources, water budgets are becoming more important as a framework for wise and equitable water management.

Water is always in motion, and its budget is governed by the simple notion that the sum of inflows must equal sum of outflows plus a change in storage. Symbolically, this may be stated as:

$$PPT = R_{SW} + Q_{GW} + ET + \Delta SW + \Delta SoilW + \Delta GW + D_H \quad (1)$$

where PPT is precipitation, R_{SW} is runoff from surface water, Q_{GW} is groundwater flow, ET is evapotranspiration, SW is water in surface waters, SoilW is soil-zone water, GW is the water in groundwater storage, D_H is diversion out of the area being considered (diversions into the area would be negative), and Δ denotes change in storage. If the time interval of interest is smaller than a year, the terms involving change in storage cannot be neglected because the system is usually under transient conditions. If, however, the

time interval of interest is a year or several years, seasonal increases and decreases in storage typically cancel out, except for areas with large reservoirs, and the water budget equation reduces to a steady-state balancing of inflow and outflow:

$$PPT = R_{SW} + Q_{GW} + ET + D_H \quad (2)$$

Implicit here is the assumption that precipitation and diversions into the defined area constitute the only inflows, which is reasonable if one considers a watershed is enclosed by both surface-water and groundwater divides. However, the groundwater divide is not necessarily the same as the surface-water divide, especially for small areas. Also implicit is the assumption that there are no long-term changes in weather (i.e., climate changes) causing changes in the surface- and groundwater pools. If the area of interest is defined by open boundaries, additional terms representing water import and export must be added to the equations. The simplicity of the above equations belies the difficulties inherent in assessing the different components involved.

Specific flux components of water budgets

Precipitation

Perhaps the most widely measured quantity or flux in water budgets is precipitation. Precipitation represents a combination of rainfall and snowfall. In general, precipitation data obtained from aerially distributed rain-gaging stations are integrated over space to arrive at the total volume of water falling over an area during a period of interest.

Surface-water runoff

Surface-water runoff, estimated at a given location in a stream with flow meters or river-stage data supplemented by rating curves, represents outflow from the watershed upstream from that location. To help determine the water budget of a defined area, it is helpful to have a streamgage at the outlet of that basin.

Groundwater flow

The movement of groundwater in the subsurface is quantified with Darcy's Law, according to which the volume of water flowing through a given cross-sectional area per unit time is equal to the product of the hydraulic conductivity of the formation, the gradient of hydraulic head, and the cross-sectional area (Freeze and Cherry, 1979). In the field, hydraulic gradients can be obtained from water-table maps. These maps, in conjunction with the known hydraulic conductivity of the geological formations can be used to estimate groundwater flow. Groundwater flow is often defined using groundwater flow models or from surface-water streamgages using baseflow-separation techniques. Often groundwater movement is not constrained to surface-water basins making it difficult to quantify.

Evapotranspiration

Evapotranspiration includes evaporation from water surfaces and water transpired by plants. Evapotranspiration constitutes a significant percentage of the precipitation over the land surface. Yet, quantification of evapotranspiration is a difficult task. A gravimetric lysimeter provides a way of estimating evapotranspiration from a soil mass over the scale of a few cubic meters. For watersheds and river basins, it is customary to use a combination of empirical and theoretical methods. In one such approach, the concept of potential evaporation plays a central role. Potential evaporation is understood to be the amount (for example, millimeters) of water that would be evaporated from a pan at a given location, assuming unlimited supply of water, as from a deep lake. If precipitation at the location exceeds potential evaporation, the soil is assumed to hold a maximum amount of water in excess of gravity drainage. If precipitation is less than potential evaporation, then the actual evapotranspiration will be limited to what precipitation can supply. In this case, empirical curves are used to estimate soil-moisture storage based on precipitation deficit and the maximum water-holding capacity of the soil. With the availability of instruments of increased sophistication, energy budget methods are increasingly sought after to estimate evapotranspiration from watershed scale to continental scale. In these methods, the goal is to carry out an energy budget and isolate the amount of energy that is transferred by water from the land surface to the atmosphere as latent heat. This estimate is then converted to evapotranspiration. To support this model, data are generated from detailed micrometeorological measurements such as short-wave and long-wave radiation, temperature, humidity, cloud cover, and wind velocity. Another method for estimating evapotranspiration is to carry out an atmospheric water balance in a vertical column overlying the area of interest. In this method, evapotranspiration is set equal to the sum of precipitation and change in water vapor content of the column, less the net flux of water laterally entering the column. Often hydrodynamic energy mass-balance models are used to estimate evaporation from the surface of lakes and reservoirs.

Soil-water storage

In the field, water content of soils can be profiled as a function of depth with the help of neutron logs or by time-domain reflectometry, both which measure the dielectric capacity of moist soil in situ (International Atomic Energy Agency, 2000). In principle, the change in soil-water storage can be empirically estimated by carrying out repeat measurements with these instruments. However, these methods are of limited value when estimates are to be made over large areas.

The concept of field-water capacity, used widely by soil scientists and agronomists, denotes the quantity of water remaining in a unit volume of an initially wet soil from which water has been allowed to drain by gravity over a day or two, or if the rate of drainage has become negligible. The water that remains is held by the soil entirely by capillary forces. Field capacity depends on soil structure, texture, and organic content and is commonly measured to help in scheduling irrigation. Empirical curves presented by Thornthwaite and Mather (1957) provide correlations among field-water capacity, water retained in soil, and the deficit of precipitation with reference to potential evaporation. These curves can be used to estimate change in soil-water storage.

Groundwater storage

Changes in groundwater storage occur because of two distinct physical processes. At the base of the soil zone, as the water table fluctuates, change in storage occurs through processes of saturation or desaturation of the pores. In this case, change in groundwater storage per unit area is equal to the product of the magnitude of the water-level fluctuation and the specific yield of the formation, a parameter that is approximately equal to porosity. In the case of formations far below the water table, water is taken into storage through slight changes in the porosity, depending on the compressibility of the formations. In this case, change in groundwater storage can be estimated from the product of water-level fluctuation and the storage coefficient of the formations. Typically, changes in soil-water storage and groundwater storage are neglected in developing water budgets for specific areas.

Anthropogenic modifications to water budgets and water balances

Water budgets, at all spatial scales, are determined by the interaction and movement of water between its different components. Today's hydrological cycle is different than the natural-water cycle of thousands or millions of years ago because of the effects of human activity on specific components of the water budget and the movement of water between the components. The ways humans affect water budgets can be classified into three categories: water appropriation, land and environmental disturbance, and indirect consequences.

Water appropriation

People have appropriated water for their own uses throughout history. With the population of the earth now in the billions, withdrawals from surface water and groundwater affect the amount of water in each pool. Water is withdrawn from surface water for drinking-water needs, domestic and public-supply uses, industrial and commercial uses, and most significantly for agricultural uses. The results of these appropriations can be seen in some areas as a reduction of flows in rivers, lower water levels in lakes and reservoirs, and lowering water tables in aquifers. Taking water from one pool affects not only that pool, but also water movements in other parts of the hydrological cycle and water budget. If groundwater is withdrawn from aquifers faster than natural rainfall replenishes them, then groundwater levels fall, sometimes precipitously, as in the central United States (for example, see McGuire, 2017). Because groundwater contributes to flow in nearby rivers, falling groundwater levels can directly reduce streamflow, which can have further repercussions on water availability, water quality, and ecosystems.

Land and environmental disturbance

Another way people have affected water budgets and water balances is by landscape and hydrosphere disturbance. As people changed from their nomadic ways and began to cultivate crops and domesticate animals, agricultural practices began to modify the landscape. Although a single farmer modifying a field for crop planting will not upset the global water balance, billions of people manipulating the landscape over time have altered where water exists on earth and how it moves through the hydrological cycle. Even before industrial-sized machinery was used to modify landscapes, towns and roads were built, and streams and rivers were redirected to serve community needs. This trend continues today at an exponential rate and with large effects on the hydrosphere. The need for water has resulted in damming of rivers to produce reservoirs, which affects all aspects of a regional hydrosphere, from water quantity to water availability to water quality (Collier et al., 2000). The effects of these disturbances have consequences both on surface water and groundwater, which plays a major role in supplying water for the needs of people, especially the agricultural sector. Withdrawing groundwater faster than it can be replenished not only affect water budgets and water balances, but also affects the local area used by people. These effects can even alter the landscape, as is seen by the formation of sinkholes and land subsidence over large areas, such as in California (Poland, 1984).

Indirect consequences

On a global scale, the indirect consequences of human activities on the hydrosphere are perhaps the most significant, but also the most difficult to quantify and understand. These consequences have become increasingly apparent and people have begun to question what effects human activities will have on not only themselves but on all life on earth. These indirect consequences are often slow to develop, but they may take the most time and resources to alleviate. The most obvious causes of worldwide water-budget and water-balance changes are global warming and climate change and variability. People continue to engage in

activities that cause climate change and increased variability in weather, which may potentially lead to extreme changes to many aspects of the hydrosphere (Seneviratne et al., 2012). Climate change is contributing to rising sea levels (Thead, 2016), which affect the global water balance. The increased melting of icecaps and glaciers contribute additional freshwater to the oceans, possibly affecting ocean currents along with ocean ecosystems. Reduction of snow cover directly affects people that rely on consistent annual snowmelts for agriculture and daily water needs. Climate change is affecting weather and precipitation patterns worldwide, resulting in more variability in the occurrence and increased intensity of precipitation (Seneviratne et al., 2012), which in turn affect the hydrologic cycle. Lack of rainfall leading to droughts, and excessive and more intense rainfall leading to floods are having negative effects on the ability to supply food and water, the most basic of human needs. Perhaps the most precarious aspects of climate change are the likely changes in the hydrologic cycle that could affect food production. It is currently unknown how these changes will affect the earth's ecosystems and their ability to support human life.

Although we can quantify how human activities affect water budgets and water balances, it is difficult to interpret these changes and to predict how they will affect human, animal, and plant life in the future. Still, it is important to understand that significant effects have occurred and will continue to occur, possibly at an accelerated rate.

Two examples of water balances

Global water balance and fluxes

For the earth as a whole, precipitation and evapotranspiration (including evaporation from the oceans) are the two most dominant hydrologic fluxes, which on average balance one another. Based on a synthesis of studies by Abbott et al. (2019), precipitation and evapotranspiration for the earth are each about 490,000 km^3/yr; however, an imbalance exists between precipitation and evapotranspiration, if land and the oceans are considered separately. Over land, average annual precipitation is about 111,000 km^3/yr. Of this, evapotranspiration constitutes about 69,000 km^3/yr and runoff and groundwater flow to the oceans constitutes about 41,000 km^3/yr (36,000 km^3/yr from surface and subsurface flows and 5000 km^3/yr from groundwater), indicating a surplus of precipitation in comparison to evapotranspiration. Over the oceans, the average annual precipitation is about 381,000 km^3/yr, while evaporation is about 421,000 km^3/yr. The excess of evaporation over precipitation on the oceans is about equal to the runoff and groundwater flow from the land to the oceans.

Mercer Lake

Typically, water balances for inland waters are constructed over much smaller areas and used to assist in guiding specific management actions. An example of this is a water mass balance constructed for the drainage basin upstream from Mercer Lake, which is a small lake (72 ha) in northern Wisconsin. Because productivity in Mercer Lake is limited by phosphorus, decreasing phosphorus input is expected to reduce phosphorus concentrations in the lake and thus improve its water quality. Almost all phosphorus entering the lake is transported by water inputs; therefore, to quantify phosphorus inputs, it was necessary to first quantify the water inputs (Robertson et al., 2012). The gaged inlet to the lake was the largest source of water to the lake, supplying about 67% of its total input of water. Other sources were groundwater (16.9%, estimated with a groundwater model), precipitation (7.0%, measured at nearby meteorological stations), and the near-lake drainage (9.2%, estimated from nearshore gages). To determine the accuracy of the water inputs, monthly water balances were constructed by quantifying outflows from the lake (gaged stream), groundwater outputs (estimated with a groundwater model), and evaporation from the lake (estimated from nearby evaporation pans). These net inputs were compared with the change in the volume of the lake (change in storage, estimated from a lake morphometric map and measured water levels). Over a 2-year period, the average absolute monthly error was less than 5% of the total measured outflow from the lake. With the fluxes of water and their corresponding phosphorus concentrations for each source, water and phosphorus budgets were constructed for the lake and used to guide where management actions could be taken to reduce phosphorus input to the lake.

Concluding remarks

Modern science has shown that the observed behavior of the hydrological cycle can be understood and explained in terms of the laws of mechanics and thermodynamics. However, the ability of modern science to describe the hydrological cycle in precise detail and to predict the future behavior of its individual components with confidence is severely limited. The limitation arises from the many spatial and temporal scales in which the components interact, the complexity of processes, difficulties of access to observations, and sparsity of data, not to mention the role of living beings that defy quantification. Yet, our goal should be to draw upon our best science to use the world's limited supplies of freshwater wisely and equitably. This goal will be best achieved if we recognize the limitations of science, moderate our social and economic aspirations, and use science to help us adapt to the constraints imposed by the hydrological cycle.

See Also: **Fundamental concepts and theories**: Hydrologic Setting Affects Ecosystem Processes; **Human pressures and management of Inland Waters**: Hydromorphology: Case Studies; Hydromorphology: Overview and Assessment Methods; Hydromorphology—Interactions and Habitats; **Structures and functions of Inland Waters - Groundwater**: Groundwater and Surface Water Interaction; The Hydrology of Groundwater Systems - From Recharge to Discharge; **Structures and functions of Inland Waters - Lakes**: Lakes as Recorders of Earth Surface Dynamics From Yearly to Plurimillennial Time-Scales; **Structures and functions of Inland Waters - Rivers**: Dryland Rivers and Streams; Environmental Flows: Ecological Effects of Hydrologic Alterations, Assessment Methods for Rivers, Challenges and Global Uptake; Hydrology and Classification of Rivers for Management; Riparian Zones; **Structures and functions of Inland Waters - Wetlands**: Section introduction: Wetland Ecology; The Landscape Role of River Wetlands

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Comparative Primary Production☆

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This is an update of MT Dokulil, Comparative Primary Production, In *Encyclopedia of Inland Waters*, Edited by: GE Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00143-5.

This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editor Lars Rudstam.

Glossary

See also glossary in Dokulil (2021) Phytoplankton productivity. Bioc(*o*)enosis (ecological community, life assemblage) Interacting organisms living together in a biotope.
Biotope Area that supports its own distinctive community.
Community respiration (CR) Total respiration produced by organisms in a given community.
Ecosystem Complex of living organisms, their physical and chemical? environment, and all their interrelationships in a particular unit of space.
Gross accrual rate Gross biomass changes over time.
Gross primary productivity (GPP) Total amount of energy fixed by photosynthesis.
Habitat Type of natural environment in which a particular species lives. Habitat and biotope are related terms which interact (*biotope* and *habitat* are like *city* and *place of residence*).
Helophyte Any perennial marsh plant overwintering in the mud.
Net accrual rate Net biomass changes over time.
Net primary productivity (NPP) Amount of energy fixed less that respired.
Pleustohelophyte Plant free-floating on the water surface (e.g., *Eichhornia* or *Pistia*).
Standing crop Total above-ground biomass.

Introduction

Inland water bodies are an infinite variety of freshwater and saline lakes, ponds, man-made reservoirs, rivers, streams, swamps, and marshes (Downing, 2010; Downing et al., 2006, 2012). Total production of these lentic and lotic ecosystems comprises many photoautotrophic assemblages which inhabit a variety of habitats. Aquatic systems are conceptually divided into pelagic

☆*Change History:* August 2021. MT Dokulil and K Teubner prepared the update. All sections, figures and tables were updated.

(free-water), profundal (bottom), and littoral (shore) biotopes, as well as aquatic-terrestrial ecotones. Organisms range from microscopic forms, such as planktonic and benthic algae, via macroscopic visible life forms, such as filamentous algae and charophytes, to submersed and emergent macrophytes.

Primary production can be compared:

- between different components within the same freshwater ecosystem.
- between types of freshwater ecosystems.
- between climatic regions.
- in relation to other ecosystem types, such as semi-aquatic or terrestrial ecosystems.

Concepts

Comparison of primary productivity between ecosystems and compartments is based on different varieties of the *aquatic ecosystem concept* (Reynolds, 1997; Minshell et al., 1985) and the *biofilm concept* (Romaní et al., 2016). The river continuum and flood pulse concept are relevant for streams and rivers (Vannote et al., 1980; Junk et al., 1989; Tockner et al., 2000).

Estimation of productivity and production

In principle, the same or a similar terminology as outlined in Phytoplankton productivity (Dokulil, 2021) applies to the organisms considered here. Tracer techniques have been recently augmented by fluorescence methods. Corresponding to the variety of habitats and life forms, many different techniques and methods exist.

Modifications of conventional techniques are used to assess photosynthetic rates of microscopic and macroscopic algal assemblages. Productivity on substrates however is often estimated from algal accumulation as either area-specific (dN/dt, e.g., cells cm^{-2} d^{-1}) or biomass-specific rates (dB/dt, e.g., biomass cm^{-2} d^{-1}). The term *accrual rate* is also used for area-specific accumulation rates. Gross accrual and net accrual rates might be appropriate for biomass changes (biomass cm^{-2} d^{-1}) that do or do not respectively take gains and losses into account. Many procedures are used to estimate benthic algal biomass. Besides cell-counting methods, several inexpensive techniques are used to obtain estimates of biomass such as chlorophyll-a, algal group-specific pigments (marker pigments), dry mass, ash-free dry mass, C, N, or P content of the cells, all expressed usually per cm^2. These different measurements have their advantages and disadvantages. Inter-comparison of data is often difficult due to the multitude of units used.

Production of macroscopic algae and, especially, macrophytes is often deduced from *standing crop* census at times of maximum biomass development. Again, as outlined above, several different estimators of biomass are in use, making comparison of results difficult. Production of higher plants (macrophytes) is usually expressed as dry mass per unit area. It must be emphasized however, that standing crop estimates in macrophytes commonly refer to above ground biomass only, and do not take losses into account or assume them negligible.

Assessments of primary productivity in rivers often use an integrative approach. Total area-specific net production may be calculated for a river segment from diurnal changes in O_2 of the open water (Demars et al., 2015; Grace et al., 2015). Newly developed optodes for CO_2 concentration measurements (Atamanchuk et al., 2014) allow estimation of diel changes in CO_2.

Components of freshwater ecosystems

Benthic algae

Benthos refers to all organisms living on the bottom or associated with substrata. Terms largely synonymous with benthic algae are *Periphyton* and *Aufwuchs*, broad terms that apply to microbiota living on any substratum. *Biofilm* is another synonymous term frequently used in engineering applications. The nature of the habitat in which these organisms are found depends on the habitats present and on the size of the organisms. Macroalgae on substrata are in very different habitats than microalgae on the same substrate type, because they extend further into the surrounding water. However, one common criterion for habitats is the type of substrate:

- *Epipelic* algae live on inorganic or organic sediment. Characteristically, these are large motile diatoms, motile filamentous cyanobacteria, or large motile flagellates.
- *Epipsammic* algae live attached to grains in sandy sediments
- *Epilithic* algae live on hard, relatively inert substrata (gravel, pebble, cobble, stone surfaces).
- *Epiphytic* algae live on plants and larger algae
- *Epizooic* algae live on surfaces of animals.
- *Metaphyton* refers to algae of the photic zone not directly attached to substrata. Usually these are clouds of filamentous green algae.

Table 1 Summary of biomass and carbon fixation rates for algal components in wetlands.

Algal type	*Wetland*	*Chl-a [mg m^{-2}]*	*Dry weight [mg cm^{-2}]*	*C-fixation rate [g m^{-2} year^{-1}]*
Epipelon	Freshwater marsh	0.4–435		<0.1–29
	Salt marsh	20–231		28–341
	Tundra ponds			4–10
Epiphyton	Freshwater marsh	1–650		2–548
	Peat bog	2–238		
Metaphyton	Freshwater marsh		0.5–80	12–1120
	Shallow fish ponds		1–49	
	Peat bog		0–6	
	Cypress swamp		1–3	
Phytoplankton	Freshwater marsh	3–104		1–381
	Cypress swamp		0.34	
	Tundra ponds			0.6–0.9
	Salt marsh			100

Modified from Goldsborough LG and Robinson GC (1996) Pattern in wetlands. In Stevenson RJ, Bothwell ML and Lowe RL (eds.) *Algal Ecology. Freshwater Benthic Ecosystems*. pp. 77–117, San Diego: Academic Press. ISBN 9780080526942, Table II.

For a more detailed categorization of benthic algae refer to Poulíčkova et al. (2008). Attached algal assemblages in freshwaters are dominated by the three divisions (phyla) Cyanobacteria, green algae (Chlorophyta), and diatoms (Bacillariophyta). These attached groups can dominate whole-lake primary production in small oligotrophic lakes and dominate littoral zone primary production in clear lakes of all sizes (Vadeboncoeur and Power, 2017).

As primary producers, algae are fundamental for wetland ecosystems and their food web. Production estimations are summarized in Table 1 for a variety of algal and wetland types. Evidently, highest biomass and carbon fixation rates are attained by all components in freshwater marshlands but vary considerably. In tundra ponds, annual carbon uptake rates of the epipelon can be 10× higher than those of the phytoplankton.

Epipelic assemblages

Maximum photosynthetic rates of periphyton (epipelic microphytobenthic biofilm) ranged from 125 mg C m^{-2} d^{-1} to 425 mg C m^{-2} d^{-1} in the upper epilimnion of five United States lakes. Average littoral zone primary production did not depend on lake size or water column P concentration (Devlin et al., 2016). In an extremely turbid shallow lake, Neusiedler See, Austria, daily epipelic production ranged from 0.4–275 mg C m^{-2} d^{-1} with highest rates in winter under the ice (Khondker and Dokulil, 1988). Observations of epipelic microalgal production in an oxbow lake of the River Danube near Vienna varied from 7.6 to 223.5 mg C m^{-2} d^{-1} (average 107.35 mg C m^{-2} d^{-1}) with higher values in winter (Dokulil and Schiel, 2000).

Liboriussen and Jeppesen (2003) compared epipelic production in two contrasting shallow lakes, one turbid and P-rich, the other clear and low in phosphorus. Total annual production of phytoplankton plus epipelon was 190 g C m^{-2} year^{-1} in the turbid lake, 34% greater than the 141 g C m^{-2} year^{-1} in the clearwater lake. Phytoplankton accounted for 96% of the annual production in the turbid lake. Epipelic microalgal production dominated in the clear lake with 77%. Epiphytic production on reeds was low and did not vary significantly between the two lakes. In contrast to the clearwater lake where epipelon contribution varied little over the year, epipelic algal share to total production was 11–25% in winter but only 0.7–1.7% during summer due to changes in turbidity.

Epilithic and metaphytic assemblages

Epilithic primary production of *Cladophora*-dominated rocky substrata in western Lake Ontario was highest in spring (2.39 mg C g Dry Mass^{-1} h^{-1}), had negative specific photosynthetic rates by early summer (−0.76 mg C g DM^{-1} h^{-1}), and showed regrowth in late summer (1.98 mg C g DM^{-1} h^{-1}). Mean areal net epilithic production at the depth of peak biomass (2 m) was 405 mg C m^{-2} d^{-1}, averaged over the growing season from May to August. Net epilithic production exceeded planktonic primary production (Fig. 1) from the shoreline to the 12 m depth contour (Malkin et al., 2010).

An excellent example of the primary production by metaphytic species was provided for Lake Thingvallavatn, Iceland by Jónsson (1992). GPP, NPP and community respiration (CR) of epilithic *Ulothrix*, *Cladophora* and *Nostoc* communities is indicated in Fig. 2. Maximum production occurred in all cases in July when irradiance and temperatures were high. Annual net production per square meter was calculated as 127 g O_2 year^{-1} at 0.4 m depth, 177 g O_2 at 1 m depth, and 122 g and 82 g at 2 m and 6 m respectively.

Macrophyte (hydrophyte) communities

Investigations on macrophyte biomass and production are numerous. The most productive communities in the world are generally emergent macrophytes which are most common in lentic ecotones. In temperate zones they attain an annual production of 30–45 Mt. ha^{-1}, and in tropical regions 65–85 Mt. ha^{-1}. Submerged plants are less productive (Table 2). Maximum standing crop data for different species and climatic regions are summarized in Table 3 extracted from Kvet and Westlake (1998). Extended information on the structuring role of macrophytes is included in Jeppesen et al. (1998).

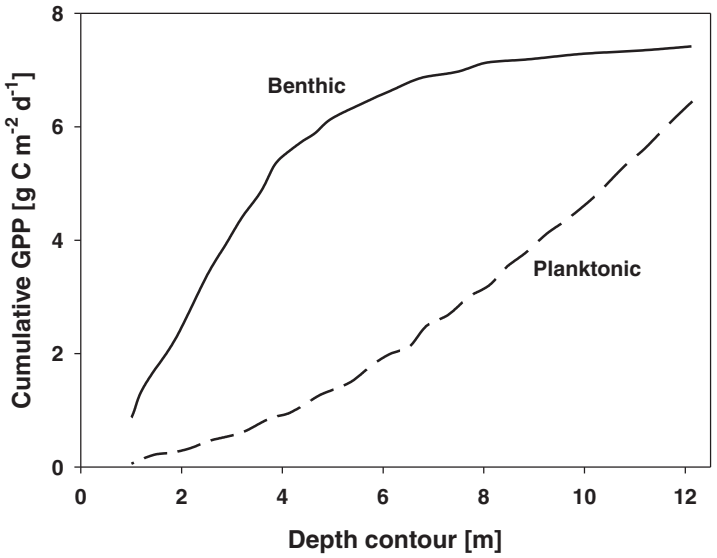

Fig. 1 Seasonal means of gross primary production per area cumulative through each depth starting at 1 m depth moving offshore in Lake Ontario. Modified from Malkin SY, Bocaniov SA, Smith RE, Guildford SJ and Hecky RE (2010) In situ measurements confirm the seasonal dominance of benthic algae over phytoplankton in nearshore primary production of a large lake. *Freshwater Biology* 55: 2468–2483. https://doi.org/10.1111/j.1365-2427.2010.02477.x.

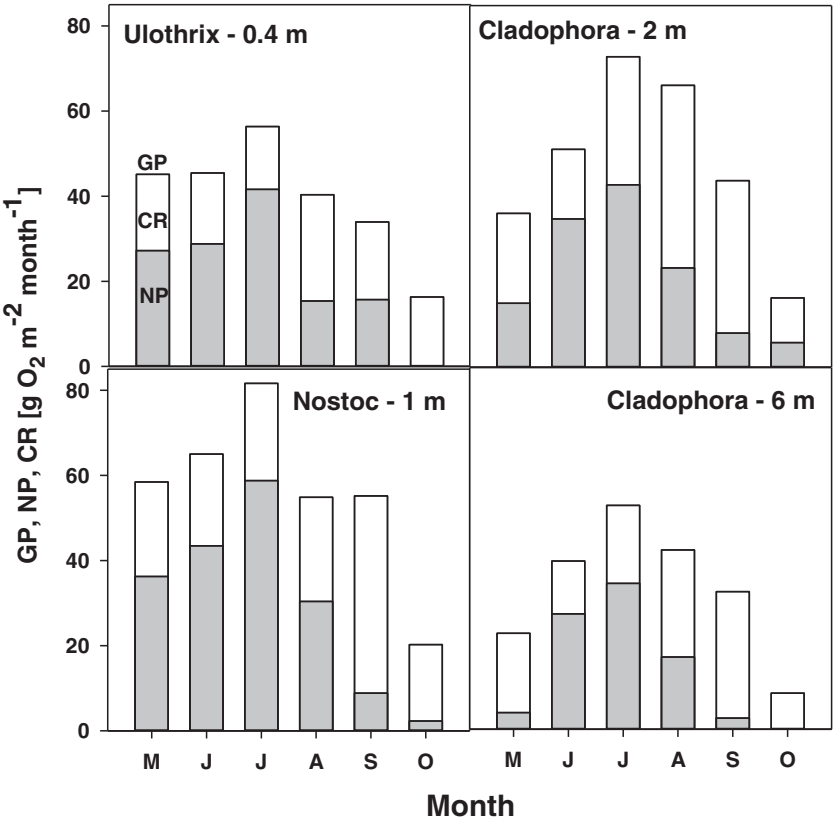

Fig. 2 Gross production (GP), net production (NP) and community respiration (CR) in the metaphytic (epilithic) communities of *Ulothrix* at 0.4 m depth, *Cladophora* at 2 and 6 m depth and *Nostoc* at 1 m depth in Lake Thingvallavatn, Iceland from May to October 1982. Data are monthly sums as g O_2 m^{-2} $month^{-1}$. Modified from Jónsson G.St. (1992) Photosynthesis and production of epilithic algal communities in Thingvallavatn. *Oikos* 64: 222–240. https://doi.org/10.2307/3545053.

Table 2 Annual net production of wetlands compared to other ecosystems.

Ecosystem	*Range of annual production [Mt dry wt ha^{-1} year^{-1}]*
Wetlands with helophytes	
Temperate	50–70
Tropical	60–90
Wetlands with pleustohelophytes	
Mostly tropical	40–60
Aquatic, freshwater	
Submerged macrophytes, temperate	5–10
Phytoplankton	15–30
Cultivated plants	25–85
Forests	20–60

Modified from Kvet J and Westlake DF (1998) Primary production in wetlands. In Westlake DF, Kvet J and Szczepanski A (eds.) *The Production Ecology of Wetlands*. Cambridge: University Press, https://doi.org/10.1017/CBO9780511549687.

Table 3 Seasonal maximum standing crop for species of above-ground vegetation of wetlands in different climatic regions as kg dry weight (wt) per meter square.

Climate	*Species*	*Standing crop [kg dry wt m^{-2}]*	*Country*
Tropical rain, no long dry season (rain forest)	*C. papyrus*	4.30	Uganda
	E. crassipes	2.40	Florida, United States
	P. repens	1.14	Brazil
	C. jamaicense	1.13	Florida, United States
	P. stratiotes	0.46	Florida, United States
	L. articulata	0.29	Malaysia
Tropical rain, long dry season (savanna)	*Arundo donax*	10.00	Thailand
	T. domingensis	2.54	Malawi
	S. molesta	0.60	Zambia
Arid (steppe and warm desert)	*C. papyrus*	3.60	Chad
	P. australis	3.60	Ukraine
	P. australis	3.20	Chad
	Typha sp.	2.00	Chad
	P. australis	0.60	Uzbekistan
Temperate rain (broad-leaved, evergreen or deciduous forest)	*T. angustata*	3.86	Kashmir
	P. australis	3.00	Austria
	C. papyrus	2.90	Kenya
	E. crassipes	2.13	Alabama, United States
	S. lacustris	2.00	Germany
	N. officinale	1.26	England
	C. lacustris	1.15	New York, United States
	G. maxima	1.00	England
	A. philoxeroides	0.84	Alabama, United States
	T. natans	0.52	Japan
Boreal (deciduous or needle-leaved, evergreen forest)	*S. lacustris*	4.20	Czech Rep.
	T. latifolia	3.60	Czech Rep.
	P. australis	3.30	Czech Rep.
	P. australis	3.00	Austria
	G. maxima	2.70	Czech Rep.
	S. erectum	1.90	Czech Rep.
	Typha glauca	1.50	Iowa, United States
	S. aloides	1.20	Belarus
	C. rostrata	1.10	Minnesota, United States
	S. sagittifolia	0.47	Belarus

Modified from Kvet J and Westlake DF (1998) Primary production in wetlands. In Westlake DF, Kvet J and Szczepanski A (eds.) *The Production Ecology of Wetlands*. Cambridge: University Press, https://doi.org/10.1017/CBO9780511549687.

Pelagic versus benthic production

The increases in water clarity associated with the declines in phytoplankton biomass during oligotrophication in the Laurentian Great Lakes had positive effects on benthic primary production. Phytoplankton production declined by 5–45% from the 1970s to 2000s but was compensated by benthic primary production, which increased by up to 190%. Autotrophic productive capacity of large aquatic ecosystems seems to be relatively resilient to shifts in trophic status, due to a redirection of production to the benthic zone. The autotrophic structure of large lakes can shift like the regime shifts in shallow lakes (Brothers et al., 2016).

The relation of benthic to planktonic primary production explored in 13 hemiboreal lakes indicates that one lake was clearly dominated by benthic production. Autotrophic structure of all other lakes was dominated by phytoplankton production possibly switching to benthic dominance from time to time. The benthic fraction varied from 0.01 to 0.94 in these lakes (Cremona et al., 2016).

The clear-water state in shallow lakes without macrophytes was largely maintained by benthic production, benthic-pelagic coupling and the capacity of periphyton to buffer impacts such as increased P-loading or fish removal as demonstrated by Genkai-Kato et al. (2012). Blanco et al. (2016) refined these findings for shallow lakes in Spain using biomass as an estimator. The response of epiphyton biomass to increasing phosphorus levels was unimodal, phytoplankton developed exponentially and submerged aquatic plant coverage decreased. Phytoplankton began to dominate when TP levels were greater than 30 μg P L^{-1}, a threshold for the turbid state.

Littoral primary production may dominate whole-lake autotrophic production in small lakes (Vesterinen et al., 2016). Periphyton production shifted a humic boreal lake towards net autotrophy with production exceeding destruction processes (Fig. 3). How important littoral production can be for higher trophic levels such as fish has been demonstrated by Vander Zanden et al. (2011) using data from 75 lakes (Fig. 4). Contribution of benthic primary production to total lake production varied between 0.1 and 1.0 with an average of 0.36 ± 0.24 in these 75 lakes (Fig. 4A). The contribution of benthic carbon to fish body carbon was higher than expected in most of the lakes (Fig. 4B).

Photophysiology of communities

There is considerable variation in the photosynthesis-irradiance relationship measured for benthic algae from wetlands (Table 4). Differences reflect the physiological state of organisms collected from diverse habitats but may also reflect differences in analytical methodology. Part of the variability in epiphytic assemblages with discrete three-dimensional physiognomy can be attributed to accumulated biomass because photosynthetic efficiency and biomass estimated as chlorophyll-a are inversely related (Fig. 5, Goldsborough and Robinson, 1996). Based on the few studies conducted, generalizations on the photosynthetic behavior of various algal assemblages are difficult to make since ranges of all three parameters are wide. Maximum chlorophyll-specific carbon

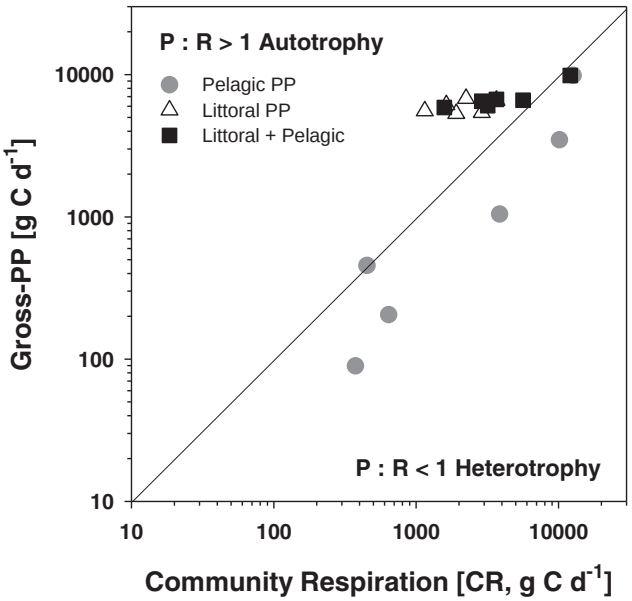

Fig. 3 Comparison of whole-lake gross primary production (GPP) and community respiration (CR) from pelagic and littoral habitats, both separately and in combination on a log-log scale. The line represents a GPP:CR ratio of 1. Data from a Finnish boreal lake modified from Vesterinen J, Devlin S, Syväranta J and Jones R (2016) Accounting for littoral primary production by periphyton shifts a highly humic boreal lake towards net autotrophy. *Freshwater Biology* 61(3): 265–276. doi: https://doi.org/10.1111/fwb.12700, Fig. 5.

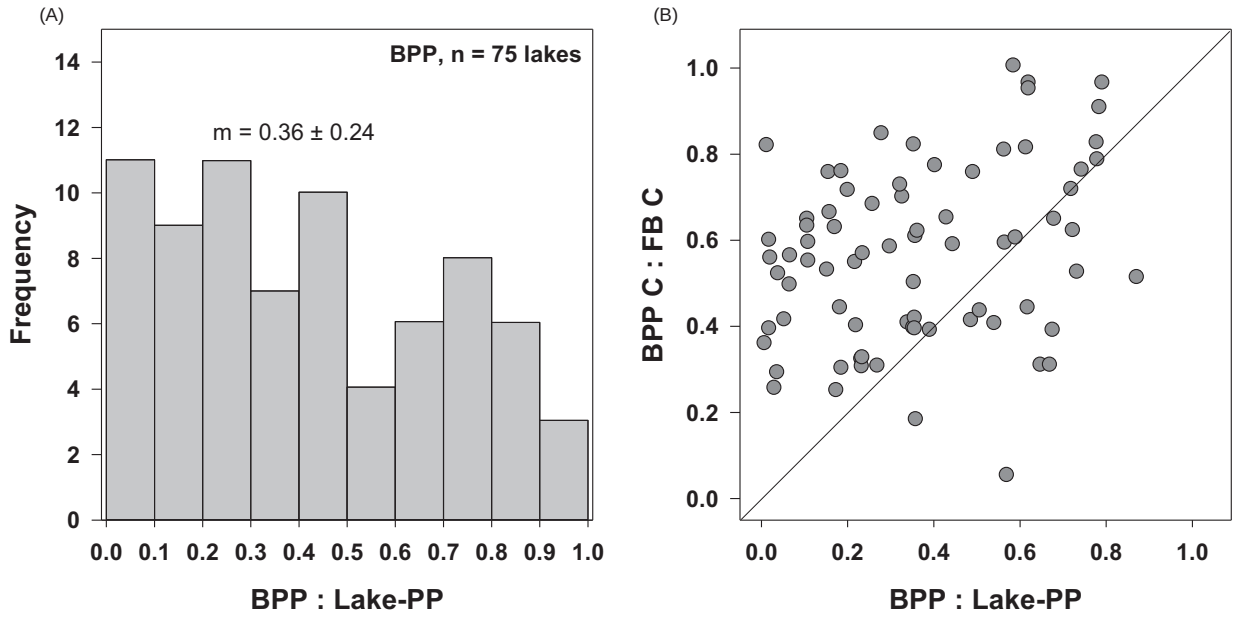

Fig. 4 Frequency of benthic algal contribution (BPP) to whole-lake primary production (Lake-PP) in (A). Benthic algal contribution (BPP) to whole-lake primary production (Lake-PP) related to mean benthic carbon contribution (BPP C) to fish body carbon (FB C) in (B). Data from 75 North American lakes. Modified from Vander Zanden MJ, Vadeboncoeur Y and Chandra S (2011) Fish reliance on littoral–benthic resources and the distribution of primary production in lakes. *Ecosystems* 14: 894–903. https://doi.org/10.1007/s10021-011-9454-6.

Table 4 Ranges of parameters derived from photosynthesis-irradiance curves (PE curves) for wetland algae.

Algal type	α [μg C μg Chl-a^{-1} h^{-1} (μE m^{-2} s^{-1})$^{-1}$]	E_K [μE m^{-2} s^{-1}]	P^*_{max} [μg C μg Chl-a^{-1} h^{-1}]
Epipelon	0.002–0.006	237–834	0.8–4
Epiphyton	0.008–0.016	198–659	0.5–21
Metaphyton	0.003–0.007	36–400	0.2–2
Phytoplankton	0.025–0.092	235–446	2–79

Examples of PE curves are in Fig. 6.

Modified from Goldsborough LG and Robinson GC (1996) Pattern in wetlands. In Stevenson RJ, Bothwell ML and Lowe RL (eds.) *Algal Ecology. Freshwater Benthic Ecosystems.* pp. 77–117, San Diego: Academic Press. ISBN 9780080526942.

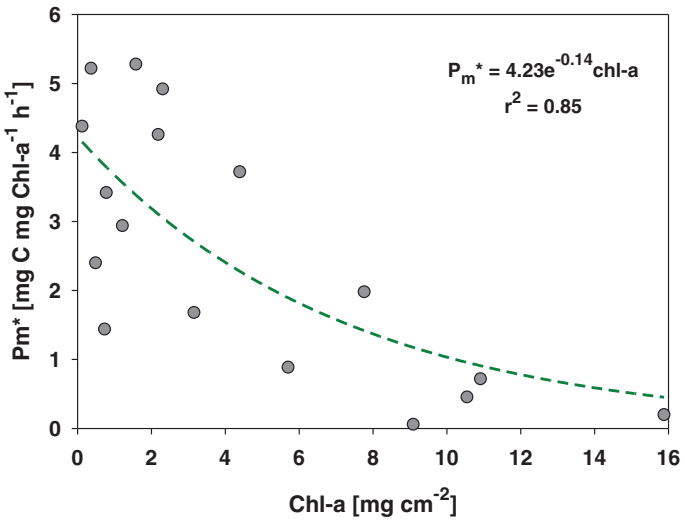

Fig. 5 Relationship between maximum chlorophyll-specific photosynthetic carbon uptake and biomass as chlorophyll-a of epiphytic algae. Modified from Goldsborough LG and Robinson GC (1996) Pattern in wetlands. In Stevenson RJ, Bothwell ML and Lowe RL (eds.) *Algal Ecology. Freshwater Benthic Ecosystems.* pp. 77–117, San Diego: Academic Press. ISBN 9780080526942, Fig. 1.

uptake of the metaphyton however, is comparatively small and light saturation (E_K) occurs at low light intensities. In turbid waters and under a macrophyte canopy irradiance can fall well below E_K (e.g., <5 μmol photons m^{-2} s^{-1} below a dense mat of *L. minor*). Evidence of photoinhibition in surface waters has been reported from only a few investigations.

Although many benthic habitats are characterized by extremely low light levels, shade acclimation is little documented in freshwater benthic algae. It is, however, a common response of phytoplankton and macrophytes in habitats characterized by low ambient irradiances. It is usually manifest in increased photosynthetic efficiency at low irradiances (increased α), lower photosynthetic rates at saturating irradiances (lower P_{max}), and decreased saturation parameters (E_K or E_{max}) as shown in Dokulil (2021, Fig. 1).. These functional changes typically reflect increased quantities of antenna pigments and decreased quantities of dark reaction enzymes. Shade acclimation theoretically buffers the photosynthesis-limiting effects of low irradiances. If respiratory losses are not too high, it will have a positive effect for production. One of the best documented shade acclimations by benthic algae originates from a study on a stream (Hill, 1996)—see below and Fig. 6. A comparison of P_{max} and α for epilithic algae and phytoplankton in Lake Huron indicate lower P_{max} values but higher α values for epilithic algae. These differences may be related to light adaptation and the lower in situ light levels found for epilithic algae (Fahnenstiel et al., 2003).

Freshwater ecosystems

The pelagic zone is reviewed in Dokulil (2021) Phytoplankton productivity.

Rivers

Organic carbon in rivers is either autochthonous or allochthonous. Autochthonous carbon derives from primary production within the river itself, while allochthonous carbon is based on decomposed products of terrestrial origin.

An inter-biome comparison of first to third order streams in North America (Mulholland et al., 2001) using open-water diurnal oxygen changes revealed three general patterns of whole ecosystem production:

(1) high gross primary production (GPP) with positive net ecosystem production (NEP)
(2) moderate GPP during daylight but negative NEP at all times.
(3) little or no GPP during daylight and negative NEP over the entire day.

In these streams, GPP ranged from <0.1–15 g O_2 m^{-2} d^{-1}. Variation of respiration was substantially lower, ranging from 2.4 to 11 g O_2 m^{-2} d^{-1}. The NEP was negative for all streams except one. Most of the streams were strongly heterotrophic with P:R ratios <0.25.

Photosynthetic active radiation (PAR) and soluble reactive phosphorus (SRP) explained 90% of the variation in GPP while NEP was correlated only with PAR ($r^2 = 0.53$). The rate of ecosystem respiration was poorly correlated with GPP, but SRP and the size of the transient storage zone explained 73% of the variation. In essence, stream metabolism is controlled by light, nutrient limitation and channel hydraulics across large geographic areas.

Rivers and streams often provide a mosaic of open sites exposed to full irradiance and sites shaded by patches of e.g., trees and bushes. Stream benthic algae have to cope and acclimate to such situations. An example of shade acclimation in stream benthic

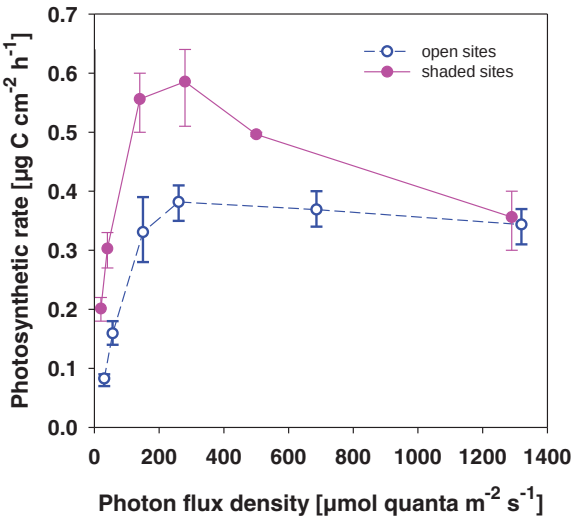

Fig. 6 Photosynthesis—irradiance (PE) response by stream periphyton at open sites and at sites shaded by vegetation. Data from North American streams. Modified from Hill W (1996) Effects of light. In Stevenson RJ, Bothwell ML and Lowe RL (eds.) *Algal Ecology. Freshwater Benthic Ecosystems.* pp. 121–148, San Diego: Academic Press. ISBN 9780080526942, Fig. 2.

algae is shown as photosynthesis–light energy (PE) curves in Fig. 6. At low light intensities, photosynthesis from the shaded sites (average light intensity 50 μmol m^{-2} s^{-1}) was twice that from the open sites (average intensity 1100 μmol m^{-2} s^{-1}). In these laboratory experiments, efficiency α is two times higher in the shaded assemblages. Shade acclimated communities saturate at lower intensities, have the highest P_{max}, and show clear evidence of photoinhibition not indicated in the results from the open site. Üveges and Padisák (2012) demonstrated that epilithic stream production strongly depends on canopy presence or absence. In an African watershed around Lake Tanganyika, stream productivity by benthic algae increase in regions of anthropogenic disturbance, mainly deforestation.

Temperature appears to be of secondary importance in determining seasonal changes in primary productivity of epilithon in streams. Little changes in net primary production are documented when temperature increases, suggesting that respiration increases at the same rate. Temperature however may interact with changes of other factors. The degree of photoinhibition can for instance be inversely correlated with water temperature. Temperature certainly sets an upper limit to areal primary productivity. As can be seen from Fig. 7 (DeNicola, 1996), maximum areal net primary productivity not corrected for biomass increases exponentially for temperatures <30 °C. The Q_{10} value (the relative increase associated with a temperature increase of 10 °C) for the regression in Fig. 7 is 2.9, like relations obtained for phytoplankton growth rates.

Algal biomass is used as an indicator of primary productivity in Table 5 to characterize different stream quality. Chalk streams and hypertrophic streams attain highest biomass and chlorophyll-a concentrations whereas acidic soft water streams are among the most unproductive (Hall et al., 2007; Janauer and Dokulil, 2006).

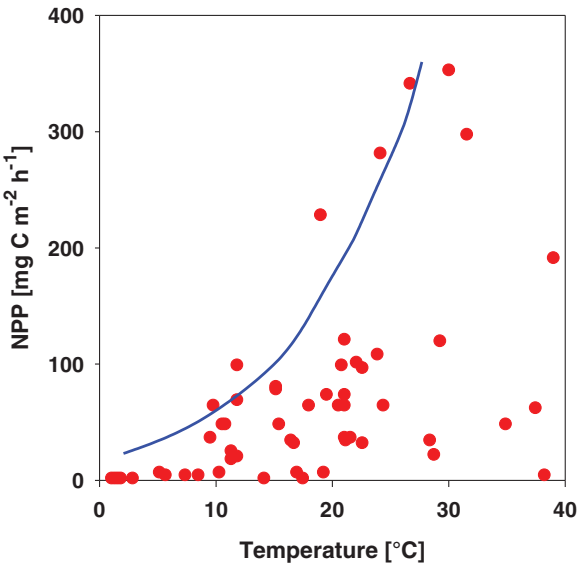

Fig. 7 Relation of areal net primary production in lotic epilithon assemblages with temperature. Curve determined by regression of maximum rates versus temperature, $r = 0.96$. Modified from DeNicola DM (1996) Periphyton responses to temperature. In Stevenson RJ, Bothwell ML and Lowe RL (eds.) *Algal Ecology. Freshwater Benthic Ecosystems*. pp. 149–181. San Diego: Academic Press. ISBN 9780080526942, Fig. 2.

Table 5 Algal biomass range as indicators of primary production in rivers of different qualities (expressed as ranges of nutrient N and P concentrations), and primary production estimates for streams modified and combined from Janauer G and Dokulil M (2006) Macrophytes and algae in running waters. In: Ziglio G, Siligardi M and Flaim G (eds.) *Biological Monitoring in Rivers. Applications and Perspectives*. pp. 89–109, Chichester: J. Wiley & Sons. ISBN: 978-0-470-86377-0, Table 1.6.2 and Hall, RO Jr, Thomas S and Gaiser EE (2007) Measuring freshwater primary production and respiration. In Fahey TJ and Knapp AK (eds.) *Principles and Standards for Measuring Primary Production*. pp. 175–203. Oxford: University Press, Table 10.1.

River type	*NO_3-N mg L^{-1}*	*PO_3-P mg L^{-1}*	*Biomass range minimum g m^{-2}*	*Chl-a maximum mg m^{-2}*
Soft water pH 4–5	0.06–0.35	<1	26	92
Soft water pH 6–7	0.5	1–2	40	178
Headwater chalk stream	4–5	10–30	50	200
Chalk stream	4–5	30–50	15–25	150–300
Hyper-eutrophic stream	5–15	1000–3000	25–50	150–250

River type	*PP mean g C m^{-2} d^{-1}*	*PP range g C m^{-2} d^{-1}*
Small stream—forested	0.2	0–0.7
Open-canopy streams	0.5	0.08–1.3
Spring/desert streams	4.1	1.5–7.4

In general, attached algal and cyanobacterial productivity and biomass development is moderate in mid-order streams (3–5) and in backwater areas but low in light-restricted, canopied or high-velocity portions of low-order streams and in more turbid large rivers. In the highly dynamic large rivers of the tropics, such as the Amazon and Paraná river ecosystems, productivity of different vegetation components becomes much more complicated.

Littoral of lakes

Although the productivity in the littoral of lakes is relatively high, their contribution to the overall lake production largely depends on the morphometry of the system. The pelagic/littoral ratio (P/L) permits an estimate of the importance of the littoral in relation to the pelagic zone. Since most of the lakes of the world are small, their P/L ratios are low. On a global basis, the littoral zone is clearly dominant over the pelagic among most standing-water and river ecosystems. Addition of wetland components results in low P/L ratios for nearly all inland water ecosystems.

Emergent plants are the most productive macrophytes in the littoral (Table 6). Floating leaved plants are intermediate and submersed macrophytes are the least productive macrophytes among the higher plants in the littoral. In oligotrophic lakes, the algal class of the Charophytes (stoneworts) often is more productive than the submersed vegetation. Littoral productivity increases 3–5 times when lakes become eutrophic. Since macrophyte biomass in the littoral is high and turnover slow (P/B <1) nutrients are less readily available in the littoral region. Macrophyte beds buffer the pelagic zone. In general, the littoral is more defined by biomass than turnover.

Effects of temperature on the productivity of lenthic periphyton indicate an increase with temperature mainly due to increased biomass since assimilation efficiency is usually lower at heated sites.

Reservoirs

Reservoirs range from small ponds to huge impoundments. Classification is mainly based on morphological and hydrological features. One important criterion is retention time reaching from through-flow (e.g., river-run dams) to very long residence times (e.g., storage reservoirs).

On a large scale, lakes and reservoirs are distinctly different in behavior and operation. At the small spatial and temporal scales at which algae operate they are generally similar in both habitats. Broadly, the same type of algae occurs. Responses to fluctuations in resource availability and the severity of processing constraints are similar in both types of waters (Naselli-Flores, 2013). The development of biomass and the rate of productivity is therefore like those commonly observed in lakes. Elongated or highly dendritic reservoirs, however, develop longitudinal gradients as a result of variable input from the tributaries, retention time and sedimentation of particles. Moreover, clay and other suspended solids can reduce under-water light availability to an extent that primary production is suppressed through light limitation even in reservoirs with high nutrient load. For example, the high average volume-based production of the south arm of the Barra Bonito Reservoir, Brazil is constrained to a shallow photic zone by the high clay load. The water column in the north arm with adequate nutrients and less clay-turbidity produces almost twice as much. Even the lacustrine region with less nutrients and low clay turbidity produces more than the nutrient rich but clay-loaded south arm (Oliveira, 1997).

Canyon shaped reservoirs develop distinct longitudinal gradients (Fig. 8). Chlorophyll-a concentration, low near the inflow, increases rapidly further down the reservoir. Plankton production is also low near the river mouth, reaching maximum values in the middle section of the reservoir declining thereafter towards the dam region (Rychtecký and Znachor, 2011).

The high and variable turbidity and the water-level fluctuations in many reservoirs preclude the development of moderately stable and diverse substrate habitats. Limited habitat, substrata, and light therefore often restrict development and productivity of attached algae. Turbidity, basin shape and retention time are the key variables controlling phytoplankton primary production in reservoirs.

Table 6 Annual net primary productivity in the littoral of lakes modified and combined from Wetzel RG (2001) Limnology. In: *Lake and River Ecosystems*. 3rd edn, San Diego: Academic Press. ISBN: 9780080574394, several Tables.

Type	*Climatic region or Trophic level*	*NPP g C m^{-2} $year^{-1}$*
P. australis	Temperate	80–800
	Tropical	>1000
Typha sp.	Temperate	1500–2500
	Tropical	3000–4000
Floating leave plants		50–1400
Submersed plants	Temperate	50–400
	Tropical	~2000
Littoral Periphyton	Oligotrophic	~40
	Eutrophic	160 – >400
Littoral Phytoplankton	Oligotrophic	~100
	Eutrophic	~1000

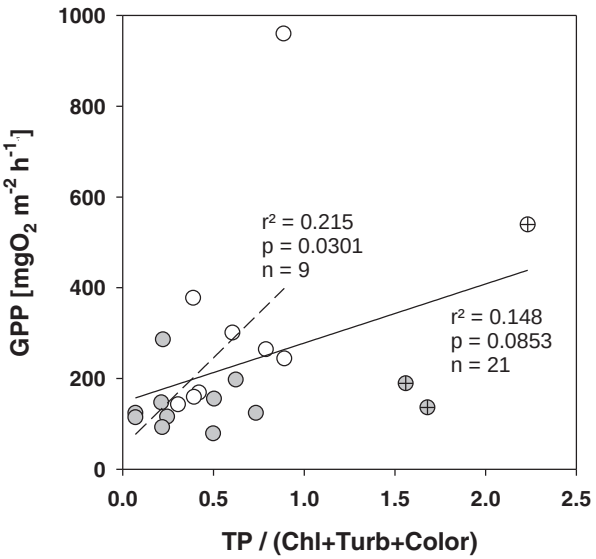

Fig. 8 The relationship of mean epilithic gross primary production (GPP) and a ratio of total-P (TP) to an index of water clarity (phytoplankton chlorophyll-a (Chl) + turbidity (TURB) + watercolor) in 21 lakes. Open circles represent lakes in limestone regions, closed circles are lakes in non-limestone basins. Regression lines are shown for all data and if hypereutrophic lakes are removed (⊕) from regression (———). Modified from DeNicola DM, de Eyto E, Wemaere A and Irvine K (2003) Production and respiration of epilithic algal communities in Irish lakes of different trophic status. *Archiv Hydrobiologie* 157: 67–87. https://doi.org/10.1127/0003-9136/2003/0157-0067, Fig. 5C.

Estimation of total lake production

Estimations of all components of lake primary production allowing calculation of production for the whole lake are not common. Two examples are given from Löffler (1979) and Nõges et al. (2010) in Table 7. Average total carbon uptake amounts to 3310 mg C per square meter and day in the shallow Neusiedler See, Austria bordering Hungary. With 83%, reed (*P. australis*) is the largest contributor, followed by *Utricularia* and phytoplankton (7% each). All other components are of minor importance. In Lakes Peipsi

Table 7 Estimation of total lake production from measurements of individual components Three examples from Austria and Estonia.

Neusiedlersee, Austria Component	*Annual Average [mg C m^{-2} d^{-1}]*	*%*
Phytoplankton (pelagial, open lake)	235	7.10
Phytoplankton (littoral, within reed belt)	20	0.60
Epiphytic algae (on *Phragmites*)	11.6	0.35
Epipelic algae (on the sediment surface)	50	1.52
Submersed macrophytes	12	0.36
Pleustophytes (*Utricularia* spp.)	242	7.32
Helophytes (*P. australis*)	2740	82.75
Total	3310.6	
Peipsi, Estonia		
Phytoplankton	1.9	15.64
Epiphytes	0.02	0.16
Macrophytes	10.5	84.20
Total	12.42	
Võtsjärv, Estonia		
Phytoplankton	5.04	41.9
Epiphytes	0.01	0.10
Macrophytes	6.97	58.00
Total	12.02	

Comment to Neusiedlersee: 1.3 m mean depth, area ~320 km^2 (about 60% covered by a *Phragmites* reed belt).
Extracted from several authors in Löffler H (ed.) (1979) *Neusiedlersee: The Limnology of a Shallow Lake in Central Europe*. The Hague: Dr. W. Junk Publisher. 10.1007/978-94-009-9168-2; Nõges T, Luup H and Feldmann T (2010) Primary production of aquatic macrophytes and their epiphytes in two shallow lakes (Peipsi and Võrtsjärv) in Estonia. *Aquatic Ecology* 44(1): 83–92. https://doi.org/10.1007/s10452-009-9249-4.

and Võrtsärv, Estonia, macrophytes dominate littoral primary production in both lakes (*P. perfoliatus* in Lake Peipsi and *P. perfoliatus* and *Myriophyllum spicatum* in Lake Võrtsärv) (Table 7). Vadeboncoeur and Steinman (2002), (Table 4) proved that periphyton can contribute between 1% and 92% of whole-lake primary productivity in a range of lakes world-wide, depending on surface area, mean depth, trophic state and phosphorus gradient (Vadeboncoeur et al., 2003, 2008).

In the littoral zone of Lake Mikolajskie, Poland, attached algae contributed 41% to annual primary production per m^2, submersed macrophytes 28%, metaphyton 21%, and phytoplankton 10%. In a littoral zone overgrown with emergent vegetation, the contribution was almost twice as high from macrophytes (57%) and phytoplankton (20%), the share from attached algae decreased to 23% and metaphyton dropped to a negligible amount of only 0.1% (Pieczyńska, 1970).

Production of attached algae is usually higher in eutrophic shallow lakes when compared to oligotrophic deep lakes. Average annual production of epiphytic algae in Priddy Pool, a shallow lake in England, was estimated to 63.9 mg C m^{-2} h^{-1} which is 95% of the total amount (67.2 mg C m^{-2} h^{-1}). The remaining 3.3 mg C m^{-2} h^{-1} are almost equally shared by epipelic algae and phytoplankton. In contrast, attached algae contributed 28%, epipelic algae 29% and phytoplankton 42% to the average total production of 12.6 mg C m^{-2} h^{-1} in the deep oligotrophic Lake Pääjärvi in Finland. Total production in eutrophic lakes is much higher (in this case five times) and shifted towards attached algae (Wetzel, 2001, Table 19–11).

Benthic algal production in a gradient of lake size proved to be a function of light saturated photosynthesis (BP_{max}) and light availability (Vadeboncoeur et al., 2008). The maximum possible contribution of benthic algae to total lake production was largely determined by the depth ratio (DR $\hat{z}/z_{max}$) and light attenuation while light quality has no significant effect. In addition, periphyton productivity is a function of total phosphorus concentration ($BP_{max} = 28.1 * TP + 0.24$). Similarly, epipsammic algal production contributed 75–95% to total production at 0.5 m depth but decreased to less than 15% below 3 m in a shallow lake (Üveges et al., 2011). Estimates of net production for shallow epilithic algal communities in 21 lakes of different depth and trophic status in Ireland range from 51 to 958 mg O_2 m^{-2} h^{-1} (circa 16–319 mg C m^{-2} h^{-1}). Although overall GPP did not significantly depend on chl-a, lakes in limestone areas differed from those in non-limestone areas (Fig. 9). Alkalinity and turbidity significantly explained GPP and NPP while colour and turbidity were related to respiration (DeNicola et al., 2003).

Besides all these environmental constraints, water-level changes can severely affect total lake production through effects on the littoral vegetation as exemplified in Table 8 using data from a wetland on the shores of Lake Manitoba. Epiphytic and particularly metaphytic algae totally dominated the littoral algal productivity. Production rates declined markedly as mean water level raised by half a meter.

It is difficult to generalize the quantitative contribution of the types of algal assemblages to gross primary production in wetlands. Few studies have been sufficiently inclusive to measure all potential producers. In constructed wetlands in Illinois, United States, epiphytes contributed 1–65% to total primary production. Annual primary production by epipelon was estimated to be 4–10 g C m^{-2} $year^{-1}$, as compared to 1 g C m^{-2} $year^{-1}$ for phytoplankton and >15 g C m^{-2} $year^{-1}$ for the emergent macrophyte *C. aquatilis* in an Alaskan tundra pond (Miller, 2013). In a dystrophic wetland of South Carolina, contribution by littoral algae, including all possible types, was estimated to over one-third of net primary production, whereas macrophytes made up the remainder (Schalles and Shure, 1989). In a shallow clear-water lake, micro-phytobenthos contributed more than 70% (5.4 g C m^{-2} $year^{-1}$) to total production on an aerial basis while phytoplankton contributed less than 30% (2.2 g C m^{-2} $year^{-1}$) as stated in Goldsborough and Robinson (1996).

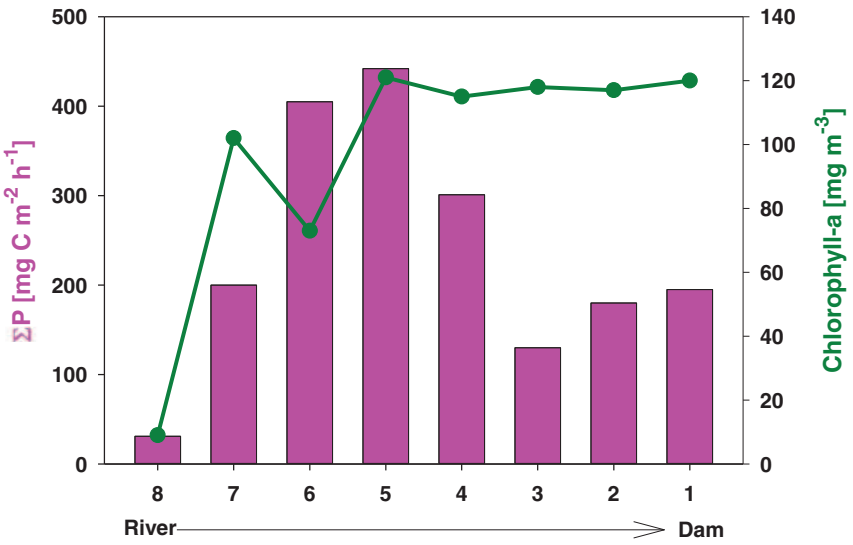

Fig. 9 Longitudinal profile of integrated water column productivity rate (areal production) and chlorophyll-a from the river to the dam in a Canyon-type reservoir in the Czech Republic. Compiled from Rychtecký P and Znachor P (2011) Spatial heterogeneity and seasonal succession of phytoplankton along the longitudinal gradient in a eutrophic reservoir. *Hydrobiologia* 663: 175–186. https://doi.org/10.1007/s10750-010-0571-6.

Table 8 Effect of different water level regimes on primary productivity of attached and planktonic components in a wetland of Manitoba, Canada.

	Mean algal biomass [mg Chl-a m^{-2}]	*Mean daily productivity mg C m^{-2} d^{-1}*		
		Water level		
		Low	*Medium*	*High*
Phytoplankton	7	169	209	225
Epipelon	4	32	47	15
Epiphytes	67	1003	813	353
Metaphyton	530	2863	2372	1338
Total		4067	3441	1931

Modified from Wetzel RG (2001) Limnology. In: *Lake and River Ecosystems*. 3rd edn, San Diego: Academic Press. ISBN: 9780080574394.

Climatic regions

There is no obvious correlation between standing crop data for species of wetland vegetation and climate (Table 3). High standing crop of around 4 kg m^{-2} are found from tropical to boreal regions. Values below 0.2 kg m^{-2} are equally widespread. Obviously, biomass development of emergent vegetation in wetlands is generally affected by local factors such as species composition, micro-climate, soil and grazing more than by climate.

Summarized across larger climatic regions however, large differences in the production of organic matter appear (Table 9). Production of submersed macrophytes triples on average in the tropics while production from emergent vegetation doubles compared to temperate regions.

In an early analysis based on data collected during the world-wide International Biological Program (IBP), latitude and altitude alone explained 49% of the variance of phytoplankton production; chlorophyll, as a substitute for biomass, and latitude explained 79%. Thus it appears that the geographical position on the globe and biomass are largely responsible for the productivity of freshwater ecosystems. Moreover, biomass and productivity reflect the nutrient levels of freshwater systems. Both are therefore dependent on the trophic level.

Comparison to other ecosystems

The best current estimate of global net primary production (NPP) is 104.9×10^{15} g of C $year^{-1}$ (104.9 Pg C y^{-1}) which is about 200×10^{9} tons dry weight per year, assuming 50% carbon in dry weight. The oceans contribute 46%, while production on land, including freshwaters, contributes 54%. A more detailed break-down of NPP for various ecosystem types is presented based on Lieth (1975) and Roehm (2005) in Table 10. All freshwater systems, lakes, streams, swamps and marshes contribute 3.9% to total continental NPP, and about 2.5% to total global NPP. Almost half of NPP on land is produced by tropical forests, while tundra, alpine and desert ecosystems together contribute only 2.4%. Cultivated land produces about 8% of NPP on land. However, per unit area, the range of wetland production is equal or higher than the production of cultivated plants or forests (see Table 2).

A clear latitudinal gradient of increasing productivity from boreal through temperate to tropical conditions has been established for lakes by Field et al. (1998). Similar trends are observed in grassland, tundra, and cultivated crops. Global NPP peaks on either side of the equator with a wide shoulder of higher productivity between 30 degrees and 60 degrees north, and a smaller peak between 30 degrees and 45 degrees south (Fig. 10).

Table 9 Annual primary production of aquatic communities.

Type of ecosystem	*Average net organic dry production [Mt ha^{-1} yr^{-1}]*	*Range of production [Mt ha^{-1} yr^{-1}]*
Lake phytoplankton	2	1–9
Submersed macrophytes		
Temperate	6	1–7
Tropical	17	12–20
Emergent macrophytes		
Temperate	38	30–45
Tropical	75	65–85

From Wetzel RG (2001) Limnology. In: *Lake and River Ecosystems*. 3rd edn, San Diego: Academic Press. ISBN: 9780080574394.

Table 10 Net annual primary productivity estimates for plant associations of the world.

Ecosystem type	*Net primary productivity (NPP) per unit area dry weight [g m^{-2} or t km^{-2}]*		*World NPP [10^9 t]*
	Range	*Mean*	
Lakes and streams	100–1500	400	0.8
Swamps and marshes	800–6000	3000	6.5
Cultivated land	100–4000	650	9.1
Tropical forests	1000–3500	2200	37.4
Temperate forests	600–2500	1250	14.9
Boreal forests	400–2000	800	9.6
Wood and shrubland	200–1200	700	6.0
Savanna	200–2000	900	13.5
Temperate grassland	200–1500	600	5.4
Tundra and alpine	10–400	140	1.1
Desert	10–250	90	1.6
Extreme desert	0–10	3	0.07
Total continental		*782*	*117.5*
Open Ocean	2–400	125	41.5
Upwelling zones	400–1000	500	0.2
Continental shelf	200–600	360	9.6
Algal beds and reefs	500–4000	2500	1.6
Estuaries	200–3500	1500	2.1
Total marine		*155*	*55.0*
Average globe		*336*	*172.5*

Modified and combined from Lieth H (1975) Primary production of the major vegetation units of the World. In Lieth H and Whittaker RH (eds.) *Primary Productivity of the Biosphere. Ecological Studies (Analysis and Synthesis)* vol. 14. Berlin: Springer. https://doi.org/10.1007/978-3-642-80913-2_10, Table 10-1; Likens GE (1975) Primary production of inland aquatic systems. In Lieth H and Whittaker RH (eds.) *Primary productivity of the Biosphere*. New York: Springer. https://doi.org/10.1007/978-3-642-80913-2_10, Table 15-1; Roehm CL (2005) Respiration in wetland ecosystems. In del Giorgio PA and Williams PJ (eds.) *Respiration in Aquatic Ecosystems*. pp. 83–102. Oxford: University Press. https://doi.org/10.1093/acprof:oso/9780198527084.001.0001. Table 6.1.

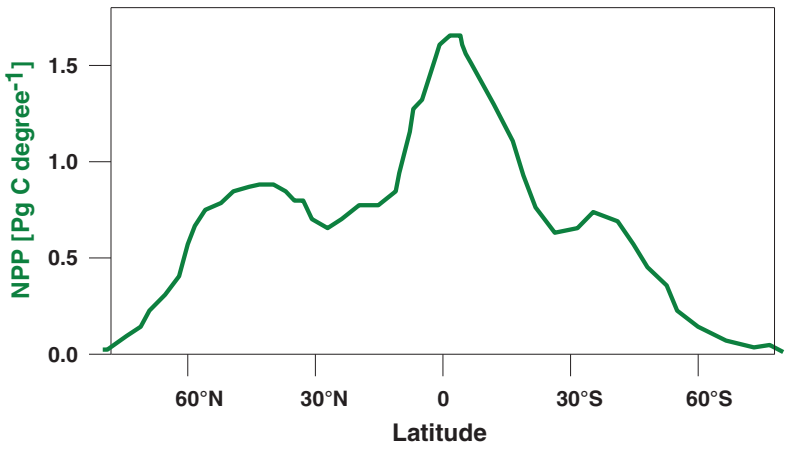

Fig. 10 Latitudinal distribution of the global net primary production. Modified from Field CB, Behrenfeld MJ, Randerson JT and Falkowski P (1998) Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science* 281: 237–240. https://doi.org/10.1126/science.281.5374.237.

Average values of productivity are broadly related to biomass for the ecosystem types in Table 10. For a given NPP value however, biomass varies widely. Thus production-biomass (P/B) ratios (e.g., kg produced per year per kg biomass) are 17 for aquatic communities, 1–2 for helophytes, 0.29 for terrestrial systems, and 0.042 for forests. Differences are mainly due to size of the producers, as smaller organisms such as algae have much higher turnover rates and produce more per unit biomass. In contrast, forests are slow growing and accumulate large portions of biomass in supporting tissue or dead material.

More productivity data from various ecosystems as well as global production can be found in Dokulil (2019) and Dokulil and Qian (2021).

Conclusions

Comparative primary productivity of autotrophic freshwater organisms was attempted for different habitats, biotopes and ecosystems. Results indicate that contribution of distinct communities (biocenoses) to overall production vary greatly depending on the type and size of the ecosystem, the trophic status and the relative importance of the littoral or benthic zone. Although knowledge of various assemblages has generally advanced, several questions remain including the coupling between benthic and pelagic production, the relative importance of different primary producers along morphometric and productivity gradients, the importance of littoral vegetation to overall primary production, and how primary producers will be affected by climate change.

Knowledge gaps

- The function of various freshwater assemblages across a spectrum of ecosystems varying in morphometry and trophic conditions.
- Evaluation of further details of benthic-pelagic interactions.
- Contribution and importance of organisms and communities to food web structure.
- Importance of littoral vegetation, both micro- and macrophytes, for the overall production of freshwater ecosystem types.
- Significance of components in freshwater ecosystem during progressive climatic change.

See Also: Emerging methods and topics: Dust and Fog Effects on Inland Waters; Remote Sensing of Inland Water Quality; Structures and functions of Inland Waters - Lakes: Benthic Algae in Lake Littoral Habitats; Lacustrine Phosphorus Cycling; Phytoplankton Productivity; Structures and functions of Inland Waters - Rivers: High Latitude Rivers: Ecosystems Shaped by Environmental Extremes; Structures and functions of Inland Waters - Wetlands: Section introduction: Wetland Ecology

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Physical Properties of Water☆

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This is an update of K.M. Stewart, Physical Properties of Water, in Encyclopedia of Inland Waters, edited by Gene Likens Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00007-7
This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Buoyancy Net gravitational force acting on a submerged object.
Colligative properties Properties that change when a solute is added to water.
Compressibility Tendency for a substance to change volume due to an applied pressure.
Density Amount of mass of a substance contained in a unit volume.
Heat capacity Energy required to raise 1 g of a material 1 °C.
Heat of fusion (melting) Heat released (added) for a phase change between solid and liquid.
Heat of vaporization (evaporation) Heat released (added) for a phase change between liquid and gas.
Surface tension Tensile or "pulling" force per unit length of a line on the interface between two materials that do not intermix (i.e., at an air/water interface or at a boundary between a liquid and a solid).
Viscosity A measure of the internal friction or resistance exerted on one substance (gas, liquid, or solid) as that substance tries to flow or move through the same or another liquid; defined in terms of the relationship between shear stress and rate of strain.

Introduction

Water is an indispensable and remarkable substance that makes all forms of life possible. Speculation about possible past or present life on other planets within our solar system, or on any extraterrestrial body somewhere within the universe, is conditioned on the evidence for or against the existence of past or present water or ice. Humans can and did survive and evolve without petroleum products (gas and oil), but cannot survive without water. Water is the most important natural resource on Earth.

Liquid water can be formed through hydrogen bonding and electrostatic attraction of two slightly positively charged atoms of the gaseous hydrogen (H) and one slightly negatively charged atom of the gaseous oxygen (O) to form one molecule of water (H_2O). Fig. 1 provides two views of that polar molecule. Figs. 1A and B show the somewhat lopsided or asymmetrical arrangement of two smaller hydrogen atoms, separated by an angle of approximately 105°, and a larger oxygen atom. Fig. 1A is a simple 'ball and spoke' representation and Fig. 1B shows the shared electron orbits, positive (+) and negative (−) poles, and the number (eight each) of protons and neutrons in the nucleus of the oxygen atom.

The relative elemental simplicity of water is somewhat deceptive because of the great influence that some of the unusual properties of water have on the physics, chemistry, and biology of the world generally, and on the distribution of life specifically. The following discussion describes briefly some of these unusual properties and provides examples of how these properties may help us understand the world of inland waters. For more information on the chemical properties of water, see Aldstadt et al. (2021) in Further Reading.

☆*Change History*: October 2021. JF Atkinson updated the text and added several components, primarily in the density, viscosity, pressure, and isotope sections. Minor changes were made throughout text.

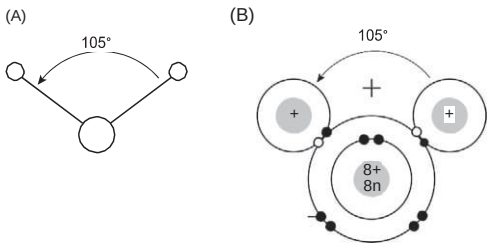

Fig. 1 Two schematic representations (A) and (B) of a water molecule. Modified from various sources.

Density and specific weight

Density may be defined simply as the amount of weight or mass contained in a specific volume. Typically, density is more often reported in units of mass per unit volume, while weight is the force of gravity acting on that mass. The nominal density of water at 4 °C is 1000 kg m^{-3} or 1 g cm^{-3}. Table 1 lists a few comparative densities (rounded to two decimal places) of two liquids (water and mercury) and several selected solids. The specific weight is found as the product of density and gravitational acceleration, i.e., $\gamma = \rho g$, where γ is the specific weight, ρ is density, and g is gravitational acceleration. The nominal specific weight of water is 9810 N m^{-3} (Newtons per cubic meter). Note that a mass of 1 g is equivalent to a weight of 9.8 N on Earth.

Density differences in inland waters may be caused by variations in the concentrations of dissolved salts, by changes in the water temperature, and by changes in pressure. However, the impact of pressure is small and generally ignored. Compressibility is a measure of the relative change in volume in response to an applied change in pressure. It is usually expressed in terms of a coefficient of compressibility, K, defined as

$$K = -\frac{1}{V}\frac{dV}{dp} = \frac{1}{\rho}\frac{d\rho}{dp} \tag{1}$$

where V is volume and dV is a change in volume resulting from a change in pressure dp. The negative sign accounts for the fact that V decreases under higher pressure, so that K is reported as a positive quantity. The second part of Eq. (1) is an alternative representation for K in terms of density. Since density changes inversely to volume, this expression does not have a negative sign. For water at 0 °C, K has a value of about 5×10^{-10} Pa^{-1}. Even at a depth of 2000 m (deeper than any inland water body), the relative change in density (or volume) is just under 1%. All liquids can be safely considered to be incompressible, that is, their volume or density does not change with applied pressure, but water is especially so. For a truly incompressible fluid, $K = 0$.

Fixed or uniform additions of salts tend to cause linear increases in the density of water. In contrast, fixed or uniform changes in the temperature (both below and above 4 °C) cause nonlinear changes in the density of water (see Table 2). The density of pure water is maximum at a temperature of 4 °C (3.98 °C to be precise). It is at this temperature that the interatomic and intermolecular motions and intermolecular distances of water molecules are least. One consequence of this reduction is that more molecules of H_2O can fit into a fixed space at 4 °C than at any other temperature. This compaction allows the most mass per unit volume and thus the greatest density. If salt is added, the temperature of maximum density drops slightly. It is especially noteworthy that the temperature at which water has the maximum density is above its freezing point. In fact, it is this property that allows life as we know it to exist in lakes. Imagine what would happen if water reached its maximum density just at the point where ice forms. In regions where ice forms in winter, it would sink and form a perpetual layer at the bottom, unless enough thermal energy was able

Table 1 Some comparative densities of water and other substances or elements.

Substance	*Density (g cm^{-3})*
Wood	
Seasoned balsa	0.11–0.14
Seasoned maple	0.62–0.75
Seasoned ebony	1.11–1.33
Water	1.00
Calcium	1.55
Aluminum	2.70
Iron	7.87
Lead	11.34
Mercury	13.55
Uranium	18.95
Platinum	21.5

Information from multiple sources.

Table 2 Comparative densities of average ocean water (salinity nominally 3.5% by weight, or 35 parts per thousand), freshwater ice, and pure distilled water at different temperatures.

Temperature (° C)	*Density (g cm^{-3})*
20	1.02760, ocean water (salinity 3.5%)
0.0	0.9168, freshwater (ice)
0.0	0.99987, pure water (from here on)
2.0	0.99997
3.98–4.00	1.00000
6.0	0.99997
8.0	0.99988
10.0	0.99973
12.0	0.99952
14.0	0.99927
16.0	0.99897
18.0	0.99862
20.0	0.99823
22.0	0.99780
24.0	0.99733
26.0	0.99681
28.0	0.99626
30.0	0.99568
32.0	0.99505

Values from Hutchinson (1957), Pinet (1992), and Weast and Astle (1979).

to reach the bottom to cause melting. Entire lakes and ponds could be completely frozen, thus eliminating habitat for aqueous biota. Our own ability to use water from lakes in cold regions would be severely compromised.

The primary reason we are interested in density is because mixing processes that control the fate and distribution of chemical and biological species are largely dependent on density stratification (the tendency for water layers of decreasing density to stack up on top of layers with higher density) and its resistance to wind induced mixing. For the vast majority of inland lakes, only vertical differences in salt concentrations and temperatures are of significant influence for mixing processes. Because the differences in densities, within a few degrees above and below 4 °C, are very slight, it takes relatively little wind energy to induce substantial vertical mixing when water temperatures are within those ranges. An example period, for those lakes that become covered with ice in the winter, would be shortly before an ice cover develops and shortly after the ice cover departs. Because energy is required to work against gravity forces, it takes much more energy to cause extensive mixing when density differences are high, such as is common between the usually warm upper waters and colder lower waters of temperate zone lakes during summer. The greater the top-to-bottom differences in temperature, the greater the top-to-bottom differences in density and, consequently, the greater is the energy required for wind-induced mixing.

There is an old, but still valid, cliché in the northern hemisphere that '... it is cold up north and warm down south.' Water temperatures in more northerly temperate zone lakes tend to average cooler than those of more southerly tropical lakes. Interestingly, although the upper-water summer temperatures in tropical lakes are somewhat higher than those of temperate lakes, the lower-water temperatures in tropical lakes are substantially higher than those ordinarily found in the lower waters of temperate zone lakes. It might therefore seem that there would be a relatively easy top-to-bottom mixing of the water in tropical lakes. Indeed, some shallow tropical lakes, with only slight top-to-bottom temperature differences, may experience this situation. However, because of the nonlinear increases in water density with temperature, tropical lakes can be surprisingly stable and resistant to much vertical mixing. Table 2 provides a listing of some comparative densities. Let us consider two hypothetical lakes with just a 2 °C spread between their lower and upper waters. For example, if a temperate zone lake in the spring, not long after the ice departed, had lower and upper waters of 4.0 °C and 6.0 °C, respectively, the density difference would be 1.00000–0.99997 = 0.00003 g cm^{-3}. In contrast, a warmer tropical lake whose lower and upper water temperatures may be 26.0 °C and 28.0 °C, respectively (i.e., with the same temperature difference), would have density differences that are much greater (0.99681–0.99626 = 0.00055 g cm^{-3}). Thus, the top-to-bottom ratio or density difference in these two lakes with a temperature difference of just 2 °C would be 55/3 or ~18 times greater in the tropical lake than in the temperate lake. This example is only hypothetical, but it shows the nonlinear influence of density changes with temperature, a property of water that influences the stratification and mixing of lakes around the world.

Pressure

Pressure p can be divided into hydrostatic pressure and dynamic pressure. Dynamic pressure is due to water movement and its full description is beyond the scope of this article (see Atkinson 2021 in Further Reading for further information on pressure). In addition, due to usually small velocities in lakes, consideration of hydrostatic pressure is often sufficient for most applications.

The (hydrostatic) pressure at any depth h is equal to the weight of water that sits above the point at which the pressure is calculated, per unit of horizontal surface area. Assuming density is constant, it is easily shown that pressure can be calculated simply as

$$p = \gamma\, h. \tag{2}$$

where $\gamma = \rho g$ is known as the specific weight and is calculated as the product of density ρ and gravity (g). Note that this calculation assumes $p = 0$ at the water surface. Using this datum, the pressure value is known as relative, or gauge pressure. Absolute pressure is equal to relative pressure plus the air pressure at the water surface. It is much more common to use gauge pressure readings.

Heat capacity/specific heat

Heat is a form of energy and, as such, we can measure changes in the temperature of a given volume of a substance and determine its heat capacity. Water is the common standard used and its heat capacity is defined as the amount of heat needed to increase the temperature of 1 g of water by 1 °C; this amount of heat defines a calorie. The number of calories needed to raise 1 g of a substance by 1 °C is termed its specific heat. For water, the value is 1 cal g^{-1} or 4.18 J g^{-1} (1 cal is equivalent to 4.18 J; Joule is the SI unit for heat). That quantity may not seem like much, but compared to other materials, the heat capacity, or specific heat of water (1.00 cal g^{-1}) is much greater than that of most other substances (Table 3).

Along with their ever changing and mesmerizing aesthetic qualities, inland waters are of immense importance in the storage and release of heat. In terms of freshwater lakes, the influence of their heat capacity can be seen most easily around very large lakes located in inland areas of temperate zone latitudes. It is in these areas that even larger swings in seasonal air temperature would ordinarily occur in the absence of those lakes. Parts of the immediate surrounding areas of Lake Baikal in Russia (this is actually the world's deepest freshwater lake as well as the one with the greatest volume of water, Kozhov, 1963) and the five Laurentian Great Lakes of North America are prime examples of the 'thermal buffering' these large lakes provide to their surroundings because of their large heat capacity.

For humans, this may result in some 'beneficial economic consequences' as portions of a lake's heat capacity are slowly released or 'shed' to down-wind regions as the fall and winter seasons progress. The immense thermal capacity of Lake Baikal, for example, is such that the lake and its immediate environments are roughly 10 °C warmer in December and January, and about 7 °C cooler in June and July, than in the cities of Irkutsk (about 50 km to the west of the southern half of Lake Baikal) and Ulan-Ude (about 70 km to the east of the lake). Several coastal and near-coastal regions of the Laurentian Great Lakes also provide impressive beneficial evidence of the influence of the Great Lakes' heat capacity. There may be reduced costs associated with home and business heating in some nearshore regions. An extended or milder autumnal period permits greater production in near-shore plantations of fruit trees and vineyards. Economic benefits also may accrue in some nearshore regions of higher terrain during winter, when enhanced snows permit additional winter skiing, snowmobiling, and other winter sports.

However, some influences of a lake's heat capacity have detrimental economic consequences. There are costs involved with snow removal, increased vehicular accidents (because of slippery roads), the corrosion of cars (attributable to higher use of road salts), and the potential long-term ecological changes associated with lake and stream salinization. There also are greater heating costs in spring as cooler water bodies extend their cooling influence inland. In addition, in late fall and winter (northern temperate zones), before an ice-cover develops, heavy snows may result when water vapor, being formed by evaporation off a relatively warm lake, is buoyed into much colder arctic air crossing the lake. Intense, 'lake-effect' snow storms tend to have their greatest impact at the downwind end of a lake after very cold arctic air has moved across the long axis of a lake and deposited its snows. These events may be part of broader synoptic patterns, but sometimes they are in very narrow bands of heavy snowfall that may bring auto traffic, schools, and businesses to a stop. In the Great Lakes region of North America, three of the better known areas for this phenomenon are (1) portions of the Upper Peninsula of Michigan on the southeastern shore of Lake Superior, (2) the southeasterly and easterly

Table 3 The specific heat of selected substances compared to that of ice, pure water, and ammonia.

Substance	*Specific heat (cal g^{-1})*
Aluminum	0.215
Copper	0.092
Gold	0.030
Lead	0.030
Silver	0.056
Zinc	0.092
Ethyl alcohol	0.60
Ice (at 0 °C)	0.51
Water	1.000
Ammonia	1.23

Information from multiple sources.

shores of Lake Ontario, especially the Tug Hill Plateau area of New York State, and (3) the easterly end of Lake Erie, around Buffalo, NY (Eichenlaub, 1979). Indeed, the Laurentian Great Lakes have been considered 'weather factories' capable of causing twists of climate found in few other parts of the world.

Heat of fusion/melting

This property is just the amount of heat exchanged during a phase shift from either liquid water to solid ice, or from solid ice to liquid water. One gram of water at 0.0 °C can be converted to ice at 0.0 °C if 80 cal (79.72 cal g^{-1}, to be precise) are released in the process. The same quantity, i.e., 80 cal, is required to melt that 1 g of ice back to 1 g of water. No further caloric additions or subtractions are needed to effect the phase shift. Because of the heat needed to melt ice, researchers might intuitively expect to see a brief but substantial drop in the mean or weighted lake-water temperature when the ice cover of a lake melts in the spring season. For example, consider a hypothetical northerly latitude and a 20-m deep lake in late winter (March), and that the lake is covered with 50 cm of ice at 0.0 °C. Furthermore, assume that the weighted mean temperature of the 1950 cm (essentially 1950 g) water column below the ice is 3.0 °C. The heat content of that water column would be 5850 cal (1950 g × 3 cal g^{-1} = 5850 cal). Assuming that there are no further gains or losses of heat to the lake, the amount of heat required to melt the ice would be 3680 cal (80 cal g^{-1} × 50 cm of ice x 0.92 g cm^{-1}, allowing for density of pure ice rounded to two decimals, it is about 3680 cal). If some of the caloric content of the water column could be used to melt all the ice, the total caloric content would drop to 2170 cal (5850 cal – 3680 cal = 2170 cal). If those 2170 cal were now equally distributed within a 1-cm^2 square and 20-m (2000 cm, essentially 2000 g) deep water column, the mean water temperature would need to drop from 3 to 1.08 °C (2170 cal/2000 cal = 1.08 °C). A drop of about 2 °C during the melting of ice would be large!

However, the temperature decline during ice-off is less as the ice generally melts over an extended period of time, from several days to several weeks, not suddenly. Half or more of the total ice thickness may be lost from the top of the ice by melting from warming air temperatures, not necessarily from waters that are just above freezing below the ice. Because of its *albedo* (percent of incoming solar radiation that is reflected back into space), dark or open water generally reflects only a small fraction of the incoming solar radiation, whereas white snow cover on a frozen lake can reflect a large fraction of incident radiation. Indeed, snow cover extending into the spring period can delay the date the ice disappears. However, with increasing amounts of solar radiation, rising air temperatures, melting snows, and darkening ice, the water below the ice may be gaining some heat from solar inputs at the same time it is losing heat in melting an overlying ice cover. Therefore, do not expect a big drop in mean water temperature as an ice cover melts on a lake.

Heat of vaporization/condensation

As was the case for 'Heat of Fusion/Melting,' the heat of vaporization/condensation also represents the amount of heat exchanged during a phase shift. For vaporization, it is the quantity of heat (540 cal g^{-1}) needed to convert 1 g of water to 1 g of water vapor. The same amount of heat is exchanged or released in the phase shift during the condensation of 1 g of water vapor to 1 g of water.

Aquatic scientists may be naturally impressed with the large amount of heat exchanged (80 cal g^{-1}) in the phase shift from water to ice, or from ice to water, but the amount of heat exchanged (540 cal g^{-1}) in the phase shift from water to water vapor, or water vapor to water is 6.75 times larger (540/80 = 6.75). Although the importance of this large amount of heat exchange via vaporization or condensation may be underappreciated by humans, it is huge. On a small but critical scale for life, water evaporating off perspiring warm-blooded animals, including humans, helps maintain body temperatures within narrow survivable limits. On a global scale, the seemingly endless phase shifts between liquid water and water vapor in the atmosphere are key determinants in the redistribution of water and heat within the hydrological cycle around the world.

Isotopes

An *isotope* is one of two or more forms of the same chemical element. Different isotopes of an element have the same number of protons in the nucleus, so they have the same atomic number, but a different number of neutrons giving each elemental isotope a different atomic weight. Isotopes of the same element have different physical properties (melting points, boiling points, etc.) and the nuclei of some isotopes are unstable and radioactive. For water (H_2O), the elements hydrogen (atomic number 1) and oxygen (atomic number 16) each have three isotopes: ^{1}H, ^{2}H, and ^{3}H for hydrogen; ^{16}O, ^{17}O, and ^{18}O for oxygen. In nature, the ^{1}H and ^{16}O isotopes are by far the most common (greater than 99.7% of oxygen is in the ^{16}O form). In water, the water molecule may be given as $^{1}H_2O$ or hydrogen oxide, $^{2}H_2O$ or deuterium oxide, and $^{3}H_2O$ or tritium oxide, which is the radioactive species. Both of the latter two are sometimes called heavy water because of their increased mass. However, the phrase 'heavy water' gained notoriety primarily because of the association of $^{2}H_2O$, or deuterium oxide, also called the deuterated form of water, in the development of nuclear weapons. Many elements have isotopes, but the isotopes of hydrogen and oxygen are of particular interest because fractionation occurs in vapor–liquid–solid phase changes. Heavier molecular species tend to be enriched in the condensation phase and lighter molecular species in the vapor phase.

This phase difference has been used in studies of paleoclimate changes by looking at the ratio of $^{18}O/^{16}O$ in ice or ocean sediment cores. Because of the greater tendency for ^{16}O to evaporate, seawater is slightly enriched in ^{18}O, relative to fresh water or polar ice, which is made up of the evaporated water. Thus, a higher $^{18}O/^{16}O$ ratio in an ice core indicates a warmer climate (less ice production). Similarly, analysis of sea shells in ocean sediment cores can help identify general climate variations, since shells are made of calcium carbonate, $CaCO_3$, which includes oxygen, and a higher $^{18}O/^{16}O$ value indicates a colder climate, since more ^{16}O would be frozen in ice and the sea water would be more enriched in ^{18}O.

Some isotopes also can be used to great advantage as tracers in understanding water movements and exchanges within atmospheric, oceanic, lake, stream, and ground water systems. For example, in a recent study Yeung et al. (2015) showed that photosynthetically produced O_2 is depleted in the heavier oxygen isotopes, and suggested that "Similar signatures may be widespread in nature, offering new tracers of biological and geochemical cycling." Other studies have shown that ^{18}O concentrations can be used as a tracer that is related to particular source conditions, including photosynthetic processes and the production of phosphate.

Sublimation

Water is said to be sublimated, sublimed, or undergo sublimation when it passes directly from a solid (ice) stage to a gas (vapor stage) without becoming a liquid in between. The latent heat of sublimation, i.e., the heat required to make the form of water change from ice to a water vapor, is 679 cal g^{-1}. This quantity is larger than the heat required to melt ice (80 cal g^{-1}) and vaporize water (540 cal g^{-1}), which combined is (80 + 540 = 620 cal g^{-1}). Because there may be multiple heat sources and sinks (e.g., the air above the ice and the water below the ice) associated with changing ice thickness on frozen Temperate Zone lakes, it is a challenge to assess the quantitative role that sublimation may play in those changes.

Some practical effects of sublimation may be visualized by observing a reduction in the volume of some dry ice (solid CO_2) or camphor. In another example, after several weeks of continuing subfreezing temperatures and deep frost, and assuming that no deicing salts were used, sublimation is most likely responsible for the slow disappearance of an ice sheet over the surface of a frozen sidewalk. Sublimation also is the main process by which wet clothes, which were hung out to dry in subfreezing temperatures, may actually dry. In the latter case, the water on the clothing quickly freezes to ice, but then slowly vaporizes through sublimation, and the clothes dry. In more recent years, freeze-dried vegetables, fruits, and other products (including instant coffee) provide other examples where the practical application of sublimation is utilized to both market and preserve food.

Surface tension and cohesiveness

Surface tension may be regarded as the resistance offered by liquid water to forces attempting to deform or break through the surface film of water. The interface between two immiscible fluids behaves like a stretched membrane, and surface tension comes from intermolecular attraction, or cohesion. At an interface between two fluids or between a fluid and a solid container, the fluid molecules try to pull the interface inward. The surface tension is then defined as the tensile force per unit length of the line at the interface. It is an interesting property and, for water, the surface tension, measured in force per unit length, e.g., Newtons per meter (N m^{-1}), is high and shows a slight increase as the temperature falls from 100 °C (0.0589 N m^{-1}) to 0 °C (0.0765 N m^{-1}).

An interesting application of surface tension is in calculating the size of raindrops. It can be shown that a simple mass balance for a spherical droplet may be written as

$$\sigma(2\pi R) = (p_1 - p_2)\ \pi R^2 \tag{3}$$

where σ is surface tension, R is the radius of the droplet, and p_1 and p_2 are the pressures inside and outside the droplet, respectively. If the pressures are known (depending on local meteorological conditions), then the radius of the droplet can be determined.

The properties of surface tension and cohesiveness also work together in shaping the small rounded water droplets seen on a table top or a car windshield. The primary force for restoring larger wind-generated surface and internal waves of lakes is gravity, but the primary force for restoring the much smaller capillary waves or ripples on a lake's surface is the surface tension of the water itself.

The surface tension of water is sometimes used to advantage in parlor games in which someone claims that he/she can float a more dense (than water) steel needle on less dense water. When the needle is lowered slowly and carefully with its long axis paralleling the surface of the water, it may be possible to 'float the needle' because the high surface tension of the water may prevent the needle from sinking. Do not try this by lowering one of the sharp ends of the needle first, because a point application of the needle will not provide enough length for the surface tension to work on, it will exceed the surface tension of the water film, and the needle will sink rapidly.

There is a specialized community of organisms, sometimes called neuston, associated with the surface film. For many observers of nature, it is always fascinating to see small insects such as pond skaters or water-striders (*Gerris* sp., within the insect order Hemiptera), and whirligig beetles (*Gyrinus* sp. and *Dineutes* sp., within the insect order Coleoptera), running around on the surface of ponds, sheltered lakes, and some streams. Because of padded ends on the long middle and hind feet of water striders, and the much shortened but paddle-like feet of the whirligig beetles, the high surface tension of the water is such that the insects may dimple, but not break through, the surface film.

Viscosity

This property may be thought of as the internal friction or resistance exerted on one substance (gas, liquid, or solid) as that substance tries to flow along or move through the same or another liquid. One way of visualizing the influence that liquids or semiliquids of progressively greater viscosities might exert is to take three glass marbles (same diameter and density) and drop one in each of three similarly sized glasses, one glass containing water, one light oil, and one honey, all at the same temperature. The marble would descend quite rapidly in water, more slowly in the light oil, and very much more slowly in the glass of honey. In this example, honey, with the highest viscosity, exerts the most friction or resistance to movement through it. Viscosity is usually measured in poises (P, defined as N s m^{-2}) or centipoises (cP =0.01 P). Water at 20 °C has a viscosity of 0.01002 P or 1.002 cP.

It should be noted that the rate of passive descent through a liquid reflects the density of the liquid itself as well as the surface area and density of the substance moving through it. Viscosity changes with water temperature in that viscosities decrease as water temperatures rise and increase as water temperatures fall. Most fish are sufficiently powerful, slippery from mucous on their skin, and shaped so they can 'slip through' water relatively easily. In contrast, tiny zooplankton, with multiple projections on their body, are ordinarily challenged as they attempt to move in any direction and particularly so when moving in cool waters.

An important application of viscosity is in calculating shear stress (an important property in the equations of motion for water). Water is known as a Newtonian fluid, in which the shear stress due to molecular cohesive forces is proportional to the rate of strain, also calculated as the velocity gradient, and the proportionality coefficient is the molecular viscosity, i.e.,

$$\tau = \mu \frac{du}{dy} \tag{4}$$

where τ is the shear stress (force acting on a plane of fluid parallel to the flow direction, per unit area), μ is viscosity, and du/dy is the velocity gradient normal to the plane on which τ is calculated. Note that this form of dependence between shear stress and strain differentiates fluids from solids, for which it is much more common to assume a linear dependence of shear stress on strain (not rate of strain). In many situations flow is often turbulent, in which case the shear stress is more dependent on flow properties and not the fluid properties.

Colligative properties

There are four special properties of water that are significantly altered or modified when solutes are added to and dissolve in water. The alterations or modifications of a colligative property (regarded as a binding property) may be predictable in dilute solutions when the number of solute particles is known. It is the number of solute particles, not their chemical nature, that determines the extent to which a property is modified.

The four colligative properties of water are *vapor pressure* (when water is in equilibrium with its own vapor), *osmotic pressure* (the pressure controlling the diffusion of a solvent across a semipermeable membrane), *boiling point* (the temperature at which water undergoes a phase shift to a gas), and *freezing point* (the temperature at which water undergoes a phase shift to a solid). Even at standardized pressures and temperatures, the extent to which a property is modified depends on the number of solute particles added. Generally, if we add a fixed number of solute particles of a sugar or salt to a liter of pure water, there would be some consequences. The vapor pressure would be lowered but the osmotic pressure would rise. The boiling point would be elevated a bit above the usual boiling point of 100.0 °C (also termed boiling-point elevation). In the latter case, a watery mixture with solutes (e.g., a well-mixed soup being heated for a meal) would have to get hotter than the boiling point of pure water before it would boil. The freezing point would be lower than 0.0 °C. A practical application of this (also termed freezing-point depression) is easily seen in parts of the northerly Temperate Zone in winter, following the application of deicing salts to melt the ice and snow on roads and sidewalks. Although not a colligative property as such, a simple increase in physical pressure also lowers the melting point of ice (~0.007 °C/atm) and helps form snowballs (when the snow is not too cold) and forms a lubricating layer of water under the blade of an ice skate.

See Also: Fundamental concepts and theories: Flowing Water, Turbulent and Laminar Flows; Optical Properties of Water; Temperature as a Driving Factor in Aquatic Ecosystems; Structures and functions of Inland Waters - Lakes: Biophysical Interactions in Phytoplankton; Bottom Boundary Layers; Currents in Stratified Water Bodies: Internal Waves; Heat Budget of Lakes; Small-Scale Turbulence and Mixing: Energy Fluxes in Stratified Lakes; Surface Mixed Layers in Lakes

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Pressure

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This is an update of J.F. Atkinson, Pressure, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, https://doi.org/10.1016/B978-012370626-3.00009-0.
This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editor Lars Rudstam.

Nomenclature

$\vec{a}$	Acceleration
A	Area
f	Coriolis parameter
$\vec{F}$	Force
g	Gravitational acceleration
g'	Reduced gravity (relative buoyancy)
k_a	A constant
p	Pressure
p_d	Dynamic pressure
p_h	Hydrostatic pressure
r	Radial position
u, v, w	Velocity components in x, y, and z directions, respectively
W	Weight
x, y, z	Coordinate directions (z is vertical)
Δx	Length of curved segment projected in z direction, defined in Fig. 7
γ	Specific weight
ν	Kinematic viscosity
$\vec{\Omega}$	Earth's rotation
ω	Angular Velocity
ρ	Density

Introduction

Pressure is an example of a surface stress (defined as force per unit area), and is important in many problems of fluid mechanics, as well as in a variety of chemical and biological responses in natural water bodies. In this article, we deal primarily with the analysis of the physical impacts of pressure, and provide several examples of biological responses to variations in pressure, including algae, fish, and humans.

The study of fluid mechanics is ultimately the study of the response of a fluid to applied forces, subject to certain constraints such as continuity, or mass conservation, momentum and energy conservation, and constitutive functions including the relationship between shear stress and rate of strain. Stress is defined as force per unit area on which the force acts. Fluid forces can generally be divided into body forces and surface forces. Body forces act on all the fluid within a defined control volume, or fluid element, while surface forces act on the surface that encloses that volume. Furthermore, surface forces can be separated into those that act either normal to or in the plane of (called shear forces) the surface of interest (Fig. 1). Problems that are addressed on the basis of force balances include calculation of forces acting on a pipe bend or forces acting on a sluice gate or canal lock. Solutions to these types of problems would be needed in the design of a pipe distribution system or for structures in an open channel flow, respectively.

For differential analysis of fluid flow, such as would be used in describing details of the velocity distribution, stresses are generally of more direct interest than forces. Normal stress is called pressure, and pressure at a point has the same magnitude in all

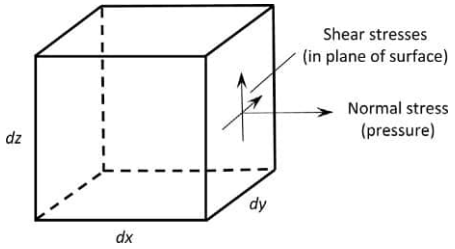

Fig. 1 Stresses acting on one surface of a small fluid element.

directions. Although by mathematical convention, the normal stress in Fig. 1 is considered positive as shown, pointing outwards from the fluid element, pressure is considered positive as a compressive stress (pointing inwards), since fluids cannot withstand tension forces. Thus, pressure acting on a fluid element as a result of the surrounding fluid is the negative of the normal stress and points inward on all faces of the element.

In general, pressure can be divided into two parts, the hydrostatic and dynamic components. Hydrostatic pressure is generated by the force of gravity acting on fluid that lies above a particular point of interest at which the value of pressure is desired, and dynamic pressure is due to the movement of the fluid. As shown below, hydrostatic pressure can be assumed in many analyses of fluid flow, especially in environmental applications where water velocities are low. For so-called Newtonian fluids, which encompass most fluids of practical interest including water, it is assumed that the shear stress is proportional to the rate of strain, which in turn can be approximated by the velocity gradient in the direction normal to the surface on which the shear stress acts. This characteristic is a fundamental difference between the mechanical description of fluids and solids, where for solids the shear stress is often assumed to be directly proportional to strain. Thus, in a static fluid, or in a fluid that is moving but in which there are no velocity gradients, the only forces to consider are the body and normal forces.

In the present article, although many of the concepts apply to fluids in general, it will be assumed that the main fluid of interest is water, either fresh or saline. The main property of interest that pertains to water and is useful for the analysis of pressure distributions is that of incompressibility, meaning that the density of the fluid is not a function of pressure. In addition, a normal right-handed Cartesian coordinate system is assumed.

Hydrostatic pressure

As the name implies, hydrostatic pressure (here denoted by p_h) is the pressure that is exerted under conditions of no or little fluid motion. To understand how p_h varies, first consider a small element of fluid within a larger volume of that same fluid (Fig. 2). The top of this element is at a depth h below the water surface. Similar to Fig. 1, the element has sides dx, dy, and dz, aligned with each of the respective coordinate directions. The forces acting on the element include its own weight and the forces of the surrounding fluid acting on the surface of the element. Since there is no fluid motion, or more precisely, no relative motion of the fluid element with respect to its surroundings, the only surface force to consider is pressure. If the element is to be in equilibrium, and therefore to remain motionless (as a result of Newton's First Law), the forces acting on it in each direction must be in balance.

In Fig. 2, the sides of the fluid element are numbered for convenience, with sides 1 and 2 referring to faces with perpendiculars (to the faces) along the x direction, sides 3 and 4 referring to sides with perpendiculars along the y direction, and sides 5 and 6 with perpendiculars along the z direction. Note that the z direction is oriented parallel to the direction of gravity, but points positive upwards. If p_h is the pressure at the center of the element, then pressures along each of the faces can be expressed in terms of p_h using a truncated Taylor Series expansion, and force (product of stress and area on which it acts) balances in each of the three coordinate directions may be written as

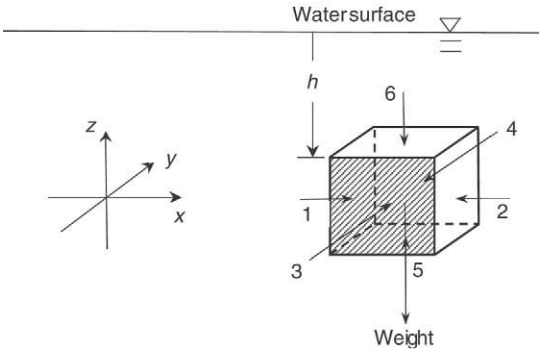

Fig. 2 Forces acting on a small fluid element under static conditions; forces include the weight of the fluid enclosed by the rectangular surface and the pressure acting on each of the faces (six total) of the element. Face 3 is the front (shaded) and face 4 is the back.

$$(x)\ p_{h1}(dydz) = p_{h2}(dydz) \Rightarrow \left(p_h - \frac{\partial p}{\partial x}\frac{dx}{2}\right) = \left(p_h + \frac{\partial p}{\partial x}\frac{dx}{2}\right) \tag{1}$$

$$(y)\ p_{h3}(dxdz) = p_{h4}(dxdz) \Rightarrow \left(p_h - \frac{\partial p}{\partial y}\frac{dy}{2}\right) = \left(p_h + \frac{\partial p}{\partial y}\frac{dy}{2}\right) \tag{2}$$

$$(z)\ p_{h5}(dxdy) - p_{h6}(dxdy) - g(\rho dxdydz) = 0 \Rightarrow \left(p_h - \frac{\partial p}{\partial z}\frac{dz}{2}\right) = \left(p_h + \frac{\partial p}{\partial z}\frac{dz}{2}\right) + \rho g dz \tag{3}$$

where p_{hi} is the hydrostatic pressure acting on face i, g is gravitational acceleration, the products $(dxdy)$, $(dxdz)$, and $(dydz)$ are the areas of each of the faces of the element, and ρ is the fluid density, which is assumed to be constant over the small volume $(dxdydz)$. Note also that dx, dy, and dz are assumed to be small enough that any variations in p_{hi} over the area of the side may be neglected. Eq. (3) differs from Eqs. (1) and (2) only in that the fluid weight is included in the force balance. Eq. (1) and Eq. (2) show

$$\frac{\partial p_h}{\partial x} = \frac{\partial p_h}{\partial y} = 0 \tag{4}$$

In other words, p is constant on a horizontal plane. Eq. (3) can be simplified as

$$-\frac{\partial p_h}{\partial x} = \gamma \tag{5}$$

where $\gamma = \rho g$ is known as the specific weight of the fluid. If density is constant this result can be integrated between two points z and $(z + \Delta z)$ to obtain

$$p_h(z + \triangle \mathbf{z}) = p_h(z) - \gamma \triangle \mathbf{z} \tag{6}$$

This is the basic equation of hydrostatic pressure variation in a constant density fluid, where pressure decreases linearly with increased elevation in a fluid (or, increases linearly with increasing depth). For environmental applications it is more common to express pressure in terms of depth h. If $p_h = p_0$ at the surface (where $h = 0$), then

$$p_h(h) = p_0 + \gamma h \tag{7}$$

(note that $\Delta h = -\Delta z$ since h and z are oriented in opposite directions). This relationship is illustrated in Fig. 3.

If $p_0 = 0$ is assumed, then the pressure acting on the top surface of the fluid element in Fig. 2 is simply the weight of water sitting above the element ($= \gamma\ hdxdy$), divided by the area ($dxdy$). Using similar reasoning, the pressure at the water surface is actually the weight of air above the surface, per unit area (note that pressure can be defined in terms of weight, whether or not the density is constant, but if density is not constant the weight must be determined by integration of the density distribution). In fact, Newton long ago deduced that air has mass by determining that water could be pumped up a tube by extracting air at the top only to a maximum height of about 10 m (33 ft). The reason for this result is because the weight of a column of water 10 m high weighs approximately the same as a similar column of air stretching through the entire atmosphere. Atmospheric pressure changes slightly with weather and with location (elevation), but is usually assumed to be 14.7 psi, 1 atm, or about 101 kPa.

For convenience, the pressure at the water surface is in fact often taken as zero, which facilitates the interpretation of pressure in terms of weight of water above a given point of interest, as shown above. Pressures written with respect to real air pressure as a reference, or boundary condition, are said to be 'absolute' pressures, whereas pressures written in terms of zero pressure at the water surface are said to be 'gauge' pressures. In absolute terms, pressure at a depth of 10 m is approximately double what it is at the water surface, and pressure increases by approximately 1 atm (101 kPa) for every 10 m increase in depth. The lowest possible pressure in absolute terms is zero, which is the pressure in deep space. Gauge pressures, however, may take negative values (indicating a vacuum). In the remainder of this article all pressures are assumed to be in 'gauge' terms.

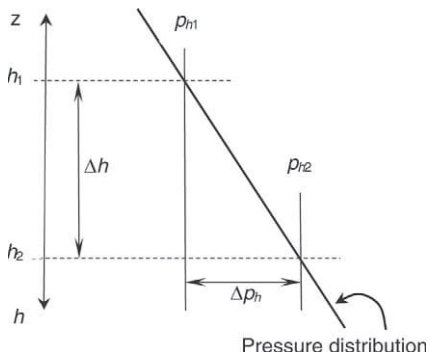

Fig. 3 Pressure variations in a static fluid with constant density.

A further outcome of the constant density assumption is that the pressure difference between two points at different vertical locations in the fluid may be found from Eq. (7) as:

$$p_h(h_2) = p_h(h_1) + \gamma(h_2 - h_1) \tag{8}$$

This relationship holds for either gauge or absolute pressures.

As noted in Eq. (5) and shown in Fig. 3, hydrostatic pressure generally increases with depth, at a rate γ. However, pressure may be forced to increase upwards, if a fluid were to be subjected to a downward acceleration with a magnitude greater than g. For example, consider a fluid in a container (so there is no relative movement of fluid particles with respect to each other) subjected to a downward acceleration of magnitude α, while still assuming gravity is effective, in which case an extra force would have to be included in the above analysis, and Eq. (5) would become:

$$-\frac{\partial p_h}{\partial z} = \rho(g - \alpha) \tag{9}$$

Note that α is negative for downward acceleration. Then if the magnitude of α were greater than g, the pressure would increase upwards in the fluid since the pressure gradient would be positive. Similarly, if the acceleration was upward, (a +g) would be additive, and the magnitude of the pressure gradient would be (a + γ). For a fluid mass in free-fall, $\alpha = -g$ and there is no effective weight, since there is no resistance to gravity, Eq. (9) would result in a zero vertical gradient, and pressure would be constant everywhere within the falling mass (equal to zero, in gauge pressure terms).

For fluids being accelerated in the x or y directions, the appropriate force, or stress would have to be included in either Eq. (1) or (2), depending on the direction of the force, and in general the corresponding pressure gradient would no longer be zero. If a force were applied to accelerate a fluid in a container in a horizontal direction, say in the x direction with magnitude α_x, then Eq. (1) would have to include this force and the resulting gradient would be:

$$-\frac{\partial p_h}{\partial x} = \rho a_x \tag{10}$$

If the container had a surface open to the atmosphere, the gradient in Eq. (10) would be exhibited by a gradient in surface elevation (Fig. 4), where pressure along a horizontal line would be directly proportional to water depth. This result occurs since there is still no relative motion of fluid in any part of the container, relative to fluid in any other part of the container, so hydrostatic pressure would still be seen in the vertical direction. An example of this type of problem would be a tanker truck carrying water with a free surface and accelerating (or decelerating) along a highway. Using the above results, it is possible to calculate the maximum acceleration possible before water would spill over the sides of the tank.

The situation is similar for a fluid in solid-body rotation. Considering a fluid rotating around a vertical axis, applying a similar force balance in the radial direction as was previously done in vertical and horizontal directions (Eq. (1) or (2)) results in:

$$\frac{\partial p_h}{\partial r} = \rho\omega^2 r \tag{11}$$

where r is the radial coordinate and ω is the angular velocity. Note that centrifugal acceleration is equal to $\omega^2 r$. Upon integrating Eq. (11), assuming constant density, pressure is found to vary parabolically with radial distance, and then considering a surface open to the atmosphere, the fluid surface will take a parabolic shape as well, since in this case rotation (about a vertical axis) does not affect forces or pressure distribution in the vertical direction. Although of interest in many applications of fluid mechanics, situations in which a fluid is artificially accelerated, either linearly or in rotation, are rare for environmental applications, except for large systems in which the rotation of the earth must be taken into consideration. This case is addressed below, but otherwise, situations with rotation are not considered further here.

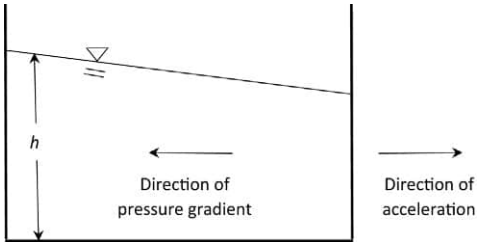

Fig. 4 Response of water surface in a container of fluid of constant density and with a surface open to the atmosphere being accelerated to the right; along the bottom, $Ph = \gamma h$, where h is the depth at any location.

Density variations

When density is not constant, its variation with depth must be known in order to integrate Eq. (5) to obtain the pressure distribution. For example, if density increases linearly with depth, $d\rho/dz = -k$, where k is a positive constant, then the pressure variation would vary with z^2. As previously noted, when working with water, the incompressibility assumption may be applied, so the density is not affected by pressure (density of water becomes a function of pressure only in the deepest parts of oceans), and for inland waters it may be assumed that density depends on temperature and salinity only. This relationship is expressed through an equation of state,

$$\rho = \rho(T, S) \tag{12}$$

where T is temperature and S is salinity. For most inland waters, salinity is small enough (or zero) that only temperature variations are important. For fresh water, the temperature of maximum density is 4 °C, and the variation of density with temperature may be approximated by a parabolic function such as:

$$\rho = \rho_0\left[1 - 0.00663(T-4)^2\right] \tag{13}$$

where $\rho_0 = 999.97$ kg m^{-3} is the density at 4 °C and T is temperature in °C.

Independent of any density stratification, Eq. (5) must still hold. For example, it can easily be shown that lines of constant density must be horizontal in a static fluid, since equilibrium would not otherwise be possible. To see this result, consider a force balance applied to the fluid element as shown in Fig. 5. With lines of constant density oriented as shown, ρ increases downward and also while moving along a horizontal line towards the right. According to Eq. (5), the pressure would then also increase while moving along a horizontal line to the right (assuming a horizontal water surface), resulting in a non-zero pressure gradient in the x direction, which violates Eq. (4). This situation is impossible in a static fluid, although it may be possible in a fluid moving in a body of water large enough that the earth's rotation (i.e., Coriolis acceleration) could generate a pressure gradient (tilt in water surface) to counter-balance the pressure gradient associated with the horizontal density gradient. See section below on Equations of Motion.

Hydrostatic forces on submerged surfaces

In addition to development of the fluid equations of motion (see below), understanding of pressure has practical applications in calculating forces acting on submerged objects. In general, both hydrostatic and dynamic pressures must be considered, but initially we look at hydrostatic forces only.

To start, consider a submerged rectangular planar surface oriented at an angle θ with respect to horizontal, in a fluid as shown in Fig. 6 (note that the submerged surface is shown in an oblique view). To simplify the discussion, it is assumed that the fluid has constant density, although the general approach here is easily extended to conditions of varying density. As discussed above, the pressure at any depth h is $p_h = \gamma h$, which acts perpendicularly on the surface, indicated on the projection of the surface to the right in Fig. 6. The differential force acting on a small area element of the surface dA is $dF = p\,dA = \gamma h B\,dh(\sin\theta)^{-1}$, where B is the width of the surface. Note that dh is assumed to be small enough that pressure may be assumed to be approximately constant over the area dA, which is oriented horizontally. The total pressure force is then obtained by integrating dF between the limits h_1 and h_2,

$$F = \gamma B(sin\theta)^{-1}\int_{h_1}^{h_2} h\,dh = \frac{\gamma B}{2sin\theta}\left(h_2^2 - h_1^2\right) \tag{14}$$

This force may be decomposed into horizontal and vertical components,

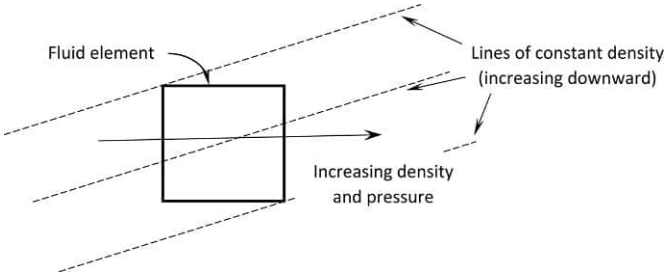

Fig. 5 Fluid element in fluid where lines of constant density are tilted.

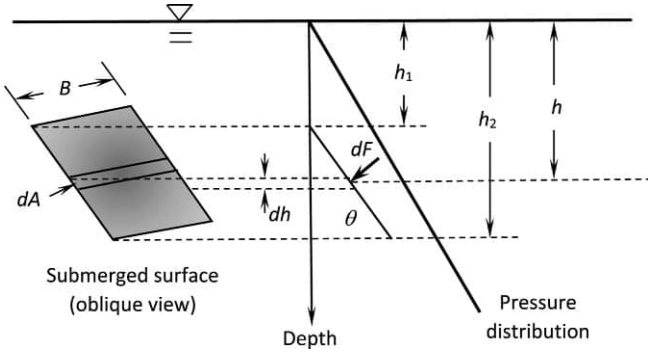

Fig. 6 Hydrostatic forces acting on a submerged planar surface, oriented at angle θ with respect to horizontal.

$$F_{hor} = -\left[\frac{\gamma B}{2sin\theta}\left(h_2^2 - h_1^2\right)\right]sin\theta = \frac{\gamma B}{2}\left(h_2^2 - h_1^2\right); F_{vert} = -\left[\frac{\gamma B}{2}\left(h_2^2 - h_1^2\right)\right]cos\theta \tag{15}$$

where the negative signs indicate forces in the negative coordinate directions. It is useful to note that the pressure at the area centroid of the surface p_{hc} is:

$$p_{hc} = \gamma\frac{(h_1 + h_2)}{2} \tag{16}$$

If this pressure acted on the entire area of the surface, given by $B(h_2 - h_1)(\sin\theta)^{-1}$, the result is identical to Eq. (14). In fact, it can be shown that this is a general result, i.e., that the total pressure force on a submerged planar surface may be calculated as the product of the surface area and the pressure evaluated at the area centroid. It also can be shown (see 'Further Reading') that the location of the resultant pressure force acts through the centroid of the pressure prism defined by the pressure distribution. Similarly, using moment balances it can be shown that the resultant vertical force acting on a horizontal surface passes through the centroid of that area.

For submerged curved surfaces, consider forces acting on the control volume designated by the cross-hatched area shown in Fig. 7. Applying a force balance in the horizontal direction gives:

$$F_{sx} = \frac{\gamma B}{2}\left(h_2^2 - h_1^2\right) \tag{17}$$

where F_{sx} is the force of the curved surface acting on the control volume in the x direction (pointing to the right), B is the width of the surface into the page, and the right-hand-side of Eq. (17) is pressure force acting on the right side of the control volume, given by Eq. (14). In the vertical direction, the force balance gives:

$$F_{sz} = (\gamma h_1)B\Delta x + \gamma V_f \tag{18}$$

where F_{sz} is the force of the curved surface acting on the control volume in the z direction (assumed to point upwards), Δx is the length of the curved segment projected in the vertical direction, and Vf is the cross-hatched volume. The first term on the right-hand-side of Eq. (18) is the pressure force acting on the top surface of the control volume, and the second term is the weight of fluid in the control volume. Eqs. (17) and (18) show that the forces acting on a curved surface may be calculated by considering the projected areas of the surface in the horizontal and vertical directions. In other words, the shape of the surface does not matter, except in so far as it determines the control volume (cross-hatched area in Fig. 7).

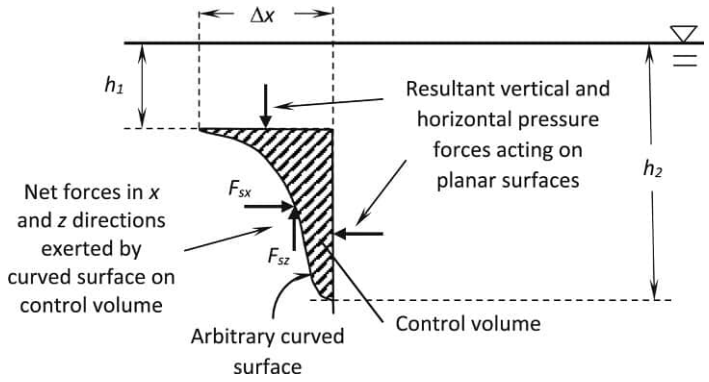

Fig. 7 Pressure forces acting on a curved surface.

Buoyancy

Buoyancy is directly related to hydrostatic pressure, and may be considered as the net upward vertical force due to pressure acting on the surface of a submerged object. This result can be seen by considering an arbitrarily shaped object of weight W and volume V submerged in a fluid of constant density ρ (Fig. 8). A surface is drawn below the object to illustrate a space defined by vertical sides drawn everywhere tangential to the object, intersecting a horizontal plane (this surface is the area of the object projected vertically). A volume of fluid V_f is contained above the object and bounded horizontally by the vertical tangents. The forces acting on the object are the forces of fluid acting on its upper and lower surfaces, F_1 and F_2, respectively, and the object's weight W. There are no net forces in the horizontal direction because there are no horizontal variations in pressure. The force F_1 is simply the weight of fluid sitting above the object, occupying volume V_f. The force F_2 acting on the lower surface is the same as the weight of fluid that would have occupied the volume $(V + V_f)$—this can be seen by thinking of a column of fluid with a surface drawn around the lower half of the object and applying the same sort of force balance as above and noting that pressure is the same upwards as downwards. The force balance for the object in the vertical direction is then:

$$\rho V_f + W = \rho\left(V + V_f\right) \text{ or } F_1 + W = F_2 \tag{19}$$

This result shows that the weight of the object is balanced by the weight of fluid that has been displaced by the object. The displaced weight of fluid is called the buoyancy force, i.e.:

$$F_B = \gamma V \tag{20}$$

where F_B is the buoyancy force. It should be emphasized that the depth at which the object rests is arbitrary, unless the density of the ambient fluid varies, as is its shape. The most important consideration is the displaced volume. If the average density of the object (total mass divided by V) is equal to the density of the fluid, the object will be in equilibrium at any location in the water column. If the density of the object is greater than that of the fluid, it will sink until it hits the bottom. If the density is less than that of the fluid, the object will be partially submerged, with the degree of submersion depending on the relative difference in densities and the displaced volume. Sometimes reference is made to the 'submerged weight' of an object, which is simply the actual weight minus the weight of displaced fluid in which the object is placed. Buoyancy is what allows ships, which are typically made of materials much denser than water, to float. The ship simply has to be designed so that the weight of displaced water is greater than the weight of the ship and all its contents.

Applying a force balance to fluid elements in a fluid with density stratification gives rise to the concept of 'relative buoyancy,' where the density of the fluid element is not the same as the density of its surroundings. There is a net reduced effect of gravity since the weight of the fluid element is partially offset by buoyancy. For analysis of these situations, the net effective gravity is referred to as reduced gravity, or relative buoyancy, defined by:

$$g' = g\frac{\rho_r - \rho}{\rho_r} \tag{21}$$

where ρ_r is a reference density value, usually taken as that of the surrounding fluid. Reduced gravity appears in problems associated with density-stratified flows, and may take positive or negative values, depending on the relative values of ρ and ρ_r.

Dynamic pressure

As previously noted, dynamic pressure is associated with fluid motion. The simplest illustration of dynamic pressure is obtained by considering the Bernoulli equation, which for cases of steady flow, constant density, and negligible friction (or viscosity) may be written as:

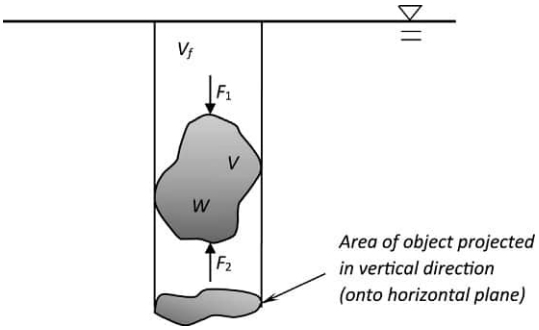

Fig. 8 Object submerged in a fluid of constant density.

$$\frac{v^2}{2g} + \frac{p}{\gamma} + z = H \tag{22}$$

where v is the fluid velocity and H is a constant known as the Bernoulli constant, or total head, and is given by conditions of the problem. This equation is usually applied to compare conditions at two locations along a streamline in the flow, but such application must be done with care to be sure all the conditions mentioned above are satisfied, particularly the negligible head loss assumption (i.e., no frictional losses). Each of the four terms in Eq. (22) has units of length. The first term is known as the velocity head, the second is the pressure head, and the third is the elevation head, or simply elevation. Definitions of these terms, as well as concepts of hydraulic grade line (HGL) and energy line (EL) for open channel flow applications are shown in Fig. 9. The Bernoulli equation represents a statement of conservation of energy, where H represents the total energy of the flow, expressed in units of (vertical) length, or head. To consider this equation in terms of real energy units, Eq. (22) would be multiplied by mass and by g.

The EL is a graphical representation of the magnitude of H. The HGL is a graphical representation of the sum of the pressure head and elevation. This sum is known as the piezometric head. In a system where energy is conserved, the EL, or magnitude of H, is at a constant level when moving from one location to another in the flow. In other words, considering two sections in the flow as in Fig. 9, the total head should be the same at both sections, $H_1 = H_2$ (note that velocity is assumed to be uniform at each cross section in this example—more detailed discussion is needed when velocity gradients are considered). The Bernoulli equation is developed for comparison of conditions at different points along a common streamline, or in the case of irrotational flow as is usually assumed for open channel flow, for any two points in the flow field. By considering a case where velocities are zero everywhere, Eq. (22) reduces to a statement of hydrostatic pressure, where $(p\gamma^{-1} + z)$ is a constant. This result is consistent with the earlier result Eq. (7).

In a moving fluid there is a sort of inverse relationship between velocity and pressure, as indicated in Eq. (22). That is, regions of higher velocity generally have lower pressures, and vice-versa. This is the main effect, for example, that produces lift in airfoils and allows aircraft to fly. Airfoils are designed so that there is a faster flow of air over the top of the airfoil than over the bottom, resulting in lower pressure on the top than on the bottom, and a net upward force. For applications in water flow, a typical problem might involve calculating the pressure force acting on an object submerged in a flow. A simple situation of this type is illustrated in Fig. 10, where a flat plate is placed perpendicular to a moving stream of water. At point 1 the velocity is v_1, the pressure is p_1, and the elevation is z_1. At point 2, which is at the surface of the plate, the velocity is (ideally) zero, while the elevation $z_2 = z_1$. Applying the Bernoulli equation then gives:

$$\frac{v_1^2}{2g} + \frac{p_1}{\gamma} + z_1 = 0 + \frac{p_2}{\gamma} + z_2 \Rightarrow p_2 = p_1 + \rho\frac{v_1^2}{2} \tag{23}$$

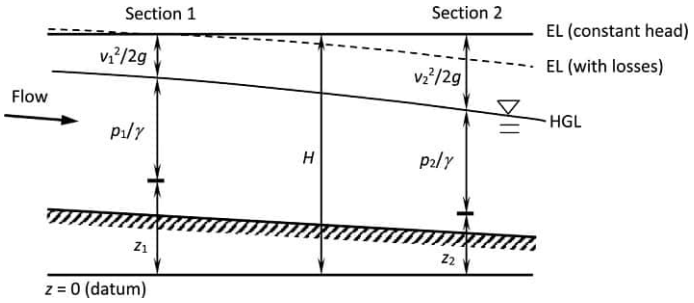

Fig. 9 Definition of head terms for Bernoulli equation Eq. (22). For hydrostatic pressure variations the sum of the elevation and pressure heads is equal to the elevation at the water surface, the position of which is also known as the hydraulic grade line (HGL). The energy line (EL) represents the elevation of total head; in an energy-conserving system the EL is horizontal, but in cases where there is energy loss, as may be induced by friction, the EL slopes downward in the direction of flow (shown as a dashed line).

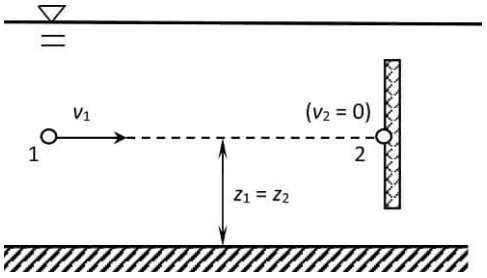

Fig. 10 Dynamic pressure force acting on planar surface in moving stream of water; point 2 is a stagnation point.

Point 2 is known as a stagnation point, which is defined anywhere the velocity is zero, and the second term on the right-hand-side of Eq. (23) is the dynamic pressure component. In this case, in which v_2 is zero, the dynamic pressure acting at point 2 attains the highest value possible, and it is known as the stagnation pressure. When comparing pressures at two points in a fluid, any difference due to different velocities comes from a dynamic pressure effect, which depends on the difference in velocity heads.

In general, to calculate the total pressure force acting on a submerged object with flow around it would require an integration of the pressure distribution on the surface of the object, which as described previously would require detailed knowledge of the velocity distribution. Fortunately, in many cases a simpler approach may be applied, based on general force balance and continuity considerations.

For example, consider calculations of force acting on a sluice gate as shown in Fig. 11. Again assuming constant velocities at each cross section (see "Introduction" and "Hydrostatic pressure"), an integral momentum equation may be applied, along with the continuity and Bernoulli equations, to solve for the net hydraulic (pressure) force acting on the gate. For simplicity it is assumed that the flow section pictured here has a width of one unit of length into the page. This allows the problem to be viewed as two-dimensional flow, since the one unit of width will appear in all force and flow expressions and will thus cancel. Considering a control volume consisting of the water between sections, and assuming steady flow, continuity states that the flow rate of water entering the control section must be the same as the flow leaving, so:

$$v_1 h_1 = v_2 h_2 \tag{24}$$

With the channel bed as datum and neglecting friction head loss, the Bernoulli equation gives:

$$\frac{v_1^2}{2g} + h_1 = \frac{v_2^2}{2g} + h_2 \tag{25}$$

where h is the piezometric head defined above, which in open channel flow is essentially the same as the water depth. If h_1 and h_2 are known, Eqs. (24) and (25) can be used to find the velocities at each section, and therefore the flow in the channel.

One further equation needed here is the integral momentum equation, which allows an interpretation of forces acting on a control volume in terms of momentum flux passing across the surfaces bounding that volume. Applied to the conditions shown in Fig. 11, the result is:

$$-(\rho q_1)v_1 + (\rho q_2)v_2 = p_{c1}h_1 - p_{c2}h_2 - F_g - F_f \tag{26}$$

where $q = vh$ is the two-dimensional flow rate, or flow per unit width, p_c is the (hydrostatic) pressure evaluated at the centroid of each cross section (recall previous discussion of forces on submerged surfaces), F_g is the total force exerted by the gate on the fluid in the control volume, assumed to act in the negative x direction, and F_f is the total friction forces acting on the fluid in the control volume. Note that it is not important which direction is assumed for F_g; if the result of the calculations is negative, it means the wrong direction had been assumed, but the numerical result is correct.

Eq. (26) is a statement of force balance that also accounts for the apparent forces exerted by momentum transport as fluid enters and leaves the control volume. The force imparted by momentum transfer is what must be balanced to prevent a garden hose from flying around when water is flowing out of the nozzle, for example. The force F_g is the net integrated effect of the pressure distribution on the gate, resulting from both hydrostatic and dynamic components, and is found using Eq. (26) without needing to actually calculate the pressures directly. Thus, with a simple measurement of depths upstream and downstream of the gate, the net force on the gate is found, where the force on the gate is in the opposite direction as the force found from Eq. (26).

Pressure in the equations of motion

In several of the above examples it has been implicitly assumed that the pressure variation was approximately hydrostatic, even in the case where velocity was not zero. This assumption is evaluated in this section, which explores the impact of pressure differences on the equations of motion, as would be used in developing mathematical models of flows and circulation for environmental analyses in lakes and streams. The primary equations governing fluid flow consist of statements of conservation of mass

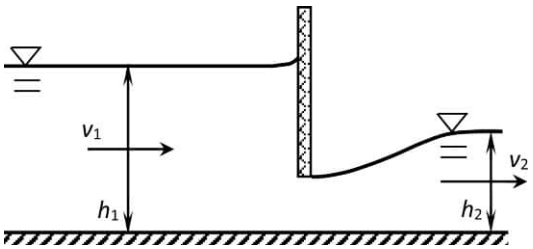

Fig. 11 Forces acting on a sluice gate in (two-dimensional) open channel flow.

(continuity), momentum, and energy. Of particular interest here are the momentum equations, or Navier–Stokes equations, which in component form are written as:

$$\frac{\partial u}{\partial t} + u\frac{\partial u}{\partial x} + v\frac{\partial u}{\partial y} + w\frac{\partial u}{\partial z} - fv = -\frac{1}{\rho}\frac{\partial p}{\partial x} + \upsilon\nabla^2 u \tag{27}$$

$$\frac{\partial v}{\partial t} + u\frac{\partial v}{\partial x} + v\frac{\partial v}{\partial y} + w\frac{\partial v}{\partial z} + fu = -\frac{1}{\rho}\frac{\partial p}{\partial y} + \upsilon\nabla^2 v \tag{28}$$

$$\frac{\partial w}{\partial t} + u\frac{\partial w}{\partial x} + v\frac{\partial w}{\partial y} + w\frac{\partial w}{\partial z} = -\frac{1}{\rho}\frac{\partial p}{\partial z} - g + \upsilon\nabla^2 w \tag{29}$$

where u, v, and w are the velocity components in the x, y, and z directions, respectively, f is the Coriolis parameter, defined as twice the daily rotation rate of the earth times the sine of the latitude, $\vec{\nabla}$ is the gradient vector ($\nabla^2 = \vec{\nabla} \cdot \vec{\nabla}$), and υ is kinematic viscosity. For inland waters, except for very large lakes such as the Laurentian Great Lakes of North America, the Coriolis terms may be neglected. Also, it is easily seen that in the case of no motion, $u = v = w = 0$, Eqs. (27)–(29) reduce to Eqs. (4) and (5). In most cases of natural flows, the motions are predominantly horizontal, so w is small, as are vertical accelerations, so that all terms in Eq. (29) are negligible except for the first two terms on the right-hand-side, consistent with hydrostatic pressure variation in the vertical direction. There are certain situations where this is not the case, such as during fall or spring overturns in lakes, or when looking at wave motions, but these situations are generally of limited temporal duration. It should be noted that assuming a hydrostatic pressure variation in the vertical direction does not necessarily imply any assumption for horizontal pressure gradients.

For applications in model development for inland waters, it is useful to explore the impact of the pressure term in the Navier-Stokes equations. Here, consider the vector form of Eqs. (27)–(29):

$$\frac{\partial \vec{v}}{\partial t} + \vec{v} \cdot \vec{\nabla}\vec{v} + 2\vec{\Omega} \times \vec{v} = \vec{g} - \frac{1}{\rho}\vec{\nabla} p + \upsilon\nabla^2 \vec{v} \tag{30}$$

where $\vec{\Omega}$ is the earth's rotation vector. The pressure term, as discussed previously, may be considered as the sum of hydrostatic and dynamic components, where the hydrostatic part may be written as:

$$\rho_h = \rho_r - \int_{z_r}^{z} \rho g dz \tag{31}$$

where p_r is a reference value at $z = z_r$. Note that Eq. (31) is simply the integrated form of Eq. (5). Letting $p = p_h + p_d$, where p_d is the dynamic pressure, and substituting Eq. (31), the pressure gradient term in Eq. (30) may be written as:

$$\frac{1}{\rho}\vec{\nabla} p = \frac{1}{\rho}\vec{\nabla} p_r - \frac{g}{\rho}\vec{\nabla}\int_{z_r}^{z} \rho dz + \frac{1}{\rho}\vec{\nabla} p_d$$

$$= \frac{1}{\rho}\vec{\nabla} p_r - \frac{g}{\rho}\int_{z_r}^{z} \vec{\nabla}\rho dz - g\vec{\nabla} z + g\frac{\rho_r}{\rho}\vec{\nabla} z_r + \frac{1}{\rho}\vec{\nabla} p_d \tag{32}$$

Then, substituting Eq. (32) into Eq. (30) and applying the Boussinesq approximation (neglect density variations except in the buoyancy term), the result is:

$$\frac{\partial \vec{v}}{\partial t} + \vec{v} \cdot \vec{\nabla}\vec{v} + 2\vec{\Omega} \times \vec{v}$$

$$= -\frac{1}{\rho_0}\vec{\nabla}(p_r + p_d) + \frac{g}{\rho_0}\int_{z_r}^{z} \vec{\nabla}\rho dz - g\vec{\nabla} z_r + \upsilon\nabla^2 \vec{v} \tag{33}$$

where ρ_0 is a (constant) reference density value, usually taken as the density at 4C in freshwater systems (i.e., maximum density). On the right-hand-side of Eq. (33), the gradient of reference pressure, $\vec{\nabla} p_r$, may usually be neglected. The second term is the effect of density variations, which are important for stratified fluids, and the third term is the effect of reference surface gradients (such as waves). Also, as previously mentioned, the Coriolis term on the left-hand-side will often be negligible. Along with continuity and energy equations, Eq. (33) or a simplified version may serve as a general starting point for developing models of fluid motion in natural waters.

Biological responses

The above discussion focuses on the physical description of pressure, how it varies in a fluid, and how forces are manifested on submerged objects. Other considerations apply to various species that live or at least spend some of their time in water, and examples of issues related to algae, fish, and humans are presented briefly here.

For submerged objects buoyancy is the primary force of interest. As shown previously, buoyancy is the net result of pressure forces in the vertical direction. Pressures in horizontal directions, or at least in the direction of movement, are of interest in determining drag that must be overcome to maintain such movement. (Actually, the resistance to movement, in general, is called drag, which is a combination of both pressure and friction forces. For larger bodies, however, pressure is the more significant contribution to drag.) The simplest biological response and movement in the water column is achieved through the process of buoyancy regulation, which is used by certain species of algae to position themselves optimally in regions of preferable temperature, light, and nutrient availability. These algae are mostly of the blue-green type (or cyanobacteria), which also can cause nuisance and even harmful (toxic) blooms. Buoyancy regulation is achieved by increasing or decreasing gas volume in vesicles in the cells. By increasing or decreasing volume, the displaced water and hence the buoyancy force acting on the cell is altered. Increasing volume increases the buoyancy force and causes the cell to rise, and up to fivefold variations in rising or falling rates have been observed. The actual rate of rise depends on the density structure of the water column in which the organism floats, since buoyancy is the weight of the displaced water, which changes as a function of density.

For fish the physical interactions with the water environment are more complicated, due to locomotion. Some fish make use of a gas-filled cavity, called a swim bladder, or gas bladder, to maintain buoyancy and stability. Additional uplift forces can be obtained by swimming, using the same Bernoulli effect noted above that allows airplanes to fly. However, this dynamic lift is achieved only when there is forward motion. With respect to the swim bladder, in order to maintain a constant buoyancy, the volume of the bladder must remain approximately constant as the fish swims in different depths where pressure changes, and this requires some interesting physiological responses. Near the surface, the pressure in the water is close to atmospheric pressure, but as previously described, pressure increases by about 1 atm for every 10 m of depth. Unlike water, air is compressible and volume decreases as pressure increases, so there is a tendency for reduced buoyancy at greater depths. In order to maintain neutral buoyancy within a water column, an effort must be made by the fish with swim bladders to keep the volume of their swim bladder constant. Methods of maintaining some 'hydrostatic equilibrium' varies among different groups and species of fish. This maintenance is usually done by slight secretions or resorptions of gas within the swim bladder itself, or by release of gas through a duct. 'Physoclists' are fish (e.g., the perch, *Perca fluviatilis*) that have special gas secreting and resorbing sites on the swim bladder wall that let the fish descend or ascend, respectively. 'Physostomes' are fish (e.g., the eel, *Anguilla anguilla*) that have a pneumatic duct that extends from the swim bladder to the esophagus. Such a duct allows these fish to release, or 'burp' some expanding gas as the fish ascends. Still other fish (e.g., castor oil fish, *Ruvettus pretiosus*) are able to maintain neutral buoyancy through alterations in their quantities of lipid storage. Interestingly, fish like tuna (e.g., the little Pacific mackerel tuna, *Euthynnus affinis*) and sharks have no swim bladders. This latter group, as well as species like dolphins, gain hydrodynamic lift by their shape, but they must swim continuously to keep from sinking.

Perhaps of more direct interest for humans is the attention one must pay to pressure when diving. As a diver moves into deeper or shallower water, the pressure changes and affects the balance between concentrations of gases in the dissolved (liquid) and gaseous phases, following Henry's Law. This law expresses the equilibrium between the dissolved phase concentration of a gas and its pressure in the surroundings. In essence, as outside pressure increases, gases are 'pushed' into the dissolved phase. The problem for divers occurs when they ascend too quickly following a deep dive. As pressure is reduced, gases move into the gaseous phase, and if pressure is reduced too rapidly, the gas cannot leave the blood stream quickly enough and gas bubbles, mostly nitrogen, form in the blood. In other words, the re-dissolution process does not have enough time to accommodate the gasses moving out of solution due to the pressure change. This situation leads to 'the bends,' also known as decompression or caisson sickness. This latter name comes from the situation where workers would work in pressurized caissons, or boxes lowered in streams for construction of structures such as bridge towers—the interior of the caisson was pressurized to equal that of the surrounding water to prevent water from entering the work area, and workers leaving the pressurized area too quickly would suffer the same symptoms as divers who ascended too quickly from a dive. This was a significant problem in the building of the Brooklyn Bridge, for example. Symptoms of 'the bends' include pain in the joints, muscle cramps, sensory system failure, and, in extreme cases, even death.

It is important to recognize that different species have different responses to pressure variations. The above examples represent only a small sampling of these reactions, and how pressure and its net vertical force, buoyancy, is important in regulating our physical environment.

See Also: Fundamental concepts and theories: Physical Properties of Water

Further reading

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Relevant websites

http://padi.com—Diving information and diving tables
http://www.americandivecenter.com/deep/preview/pd04.htm—Diving information and diving tables
http://hyperphysics.phy-astr.gsu.edu/Hbose/pman.html—General discussion of water pressure
http://www.atozdiving.co.nz/waterpressure.htm—Calculator for pressure in salt water

Flowing Water, Turbulent and Laminar Flows

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Boundary layer The layer of fluid within a solid surface such as a riverbed.
Flowing water A general term for brooks, creeks, and rivers.
Laminar flow A flow in which fluid particles move on smooth paths in layers moving smoothly past the other layers in the fluid.
Mixing layer Turbulent flow evolving between parallel flows of different velocity.
Shallow flow The flow which horizontal scales are much larger than its vertical scales.
Shear stress The tangential component of internal force applied to a unit area within fluid.
Turbulence model A relation between shear stress and velocity gradients in the fluid.
Turbulent flow A flow in which fluid particles move on chaotic paths in small unit volumes of fluid which also move chaotically around each other.
Turbulent jet Turbulent flow evolving around fluid moving with higher speed inside the ambient fluid with low velocity.
Turbulent wake Turbulent flow developing around and past an obstruction in the flow.

Introduction

Flowing inland water is an umbrella term for brooks, creeks, and rivers whose waters are moved by the action of gravity and friction forces. Their motion takes place within irregular boundaries imposed by alluvial or bedrock channels. Both these channel types are subject to the intermittent and inhomogeneous processes of erosion, transport, and deposition that result in irregular shapes of the channel surface (Leopold, 2006; Rhoads, 2020). These irregularities force waters to move in the directions orthogonal to the main flow thereby distorting patterns of streamlines from regular and parallel (laminar flow) to irregular and chaotic (turbulent flow). Turbulent flows are the most common and thereby most important kind of flowing waters (Yalin, 1992; Rhoads, 2020). For instance, turbulent instabilities in the flow structure may locally enhance erosion and deposition processes at the opposing banks which eventually increase the local curvature of the channel (Sukhodolov et al., 2017). The curvature of flow streamlines induces centrifugal forces which are counter-balanced by pressure-gradients and generate a secondary flow that further enhances channel alterations. Thereby feedbacks among turbulent flows and sediment transport processes result in the self-regulating adjustments that sustain the form of natural fluvial systems (Grinvald and Nikora, 1988; Yalin, 1992).

Besides their significance for geomorphological processes, flowing waters represent a valuable abiotic component of fluvial ecosystems. Flow rates and patterns of turbulent flows determine transport and mixing of oxygen, nutrients, and pollutants. Distinctive flow patterns form specific habitats for many species of aquatic life. Aquatic biota may also impose strong feedback to the flow by shaping the structure of their habitat. A good example is the interaction between aquatic and riparian vegetation and the river flow.

Although understanding of flowing waters has been attracting the attention of scientists for centuries, their accurate quantitative prediction has been proven elusive due in part to the lack of a general theory of turbulent flows. Therefore, available quantitative

methods describing turbulent flows are based either on semi-empirical techniques or case-specific computational models (Pope, 2000). This article provides an abbreviated overview of the essential physical processes associated with flowing waters and turbulent flows. The simple case of turbulent open-channel flow in wide and straight riverbed is considered first as it introduces the boundary layer theoretical framework. Then spatial non-uniformities of the flow fields that result in the development of horizontal shear layers are considered along with the effects of the riverbed friction on the dynamics of these layers. Further complications in the pattern of turbulent flows are considered using the example of a turbulent jet moving through a discordant river confluence. An illustration of a wake flow past an exposed gravel-bed bar concludes this overview of the basic types of turbulent flows in flowing waters. Conceptual and theoretical approaches are illustrated with the examples of the original field studies completed by the authors.

Turbulent and laminar flows

In contrast to solids, water flows under the action of external forces because its ability to resist a deformation is quite modest. A quantity, which shows how much the water resists the rate of deformation, is the dynamic viscosity μ (8.9×10^{-4} Pa s at 25 °C). The ratio of inertial forces to viscous forces $Re = \rho\, U\, L/\mu$ is the Reynolds number, where L is the characteristic linear scale, U is the flow speed and ρ is water density. The Reynolds number allows distinguishing between *laminar* and *turbulent* flow regimes. Laminar flow is smooth and it occurs at low Re values ($Re < 2300$ in water pipes), while turbulent flow exhibits irregular patterns of motion (Fig. 1) and occurs at high Re values ($Re > 2900$ in water pipes). Historically mathematical theories focused on the laminar flows first, but turbulent flows represent a general case and particular solutions of quantitative theories of turbulent flow can readily provide analytical treatment of laminar flows. Therefore, the rest of the article is focusing on the turbulent regime of flowing water.

Flow classifications

River flows originate at defined sources like channel head or the junction of two streams, and evolve under continued action of gravitational (G) and frictional (F) forces (Leopold, 2006). At the most basic level, flow in rivers can be classified according to whether or not the rate of flow remains constant over time (*steady flow*) or changes (*unsteady flow*), and whether or not the rate of flow remains constant over space (*uniform flow*) or changes over space (*varied flow*). In the case of steady, uniform flow gravity and friction forces are equal ($G = F$). However, in unsteady flow the forces are unbalanced ($G \neq F$) over time, whereas in varied flow they are unbalanced over space. When $G > F$ the flow accelerates, whereas if $G < F$ the flow decelerates.

Motion of water in fluvial systems is a continuous process of energy transformation. Potential energy of water $\rho\, g\, H$ transforms into kinetic energy $\rho\, U^2$, where g is the gravity acceleration, and H is the flow depth. A ratio between those two forces $\mathrm{Fr} = U/\sqrt{gH}$, the Froude number, allows distinguishing between *subcritical* ($Fr < 1$), *critical* ($Fr = 1$), or *supercritical* ($Fr > 1$) flow states. Subcritical flows are typical for lowland rivers and are characterized by smooth, undisturbed water surfaces (Fig. 2). When flow is in the critical

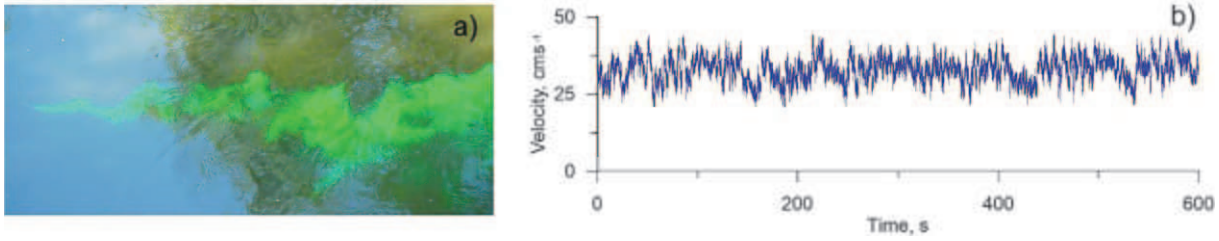

Fig. 1 Patterns of turbulent flow measured in the lowland river Spree: (A) visualization of flow by continuous point-source injection, and (B) a pattern of flow velocity at a point.

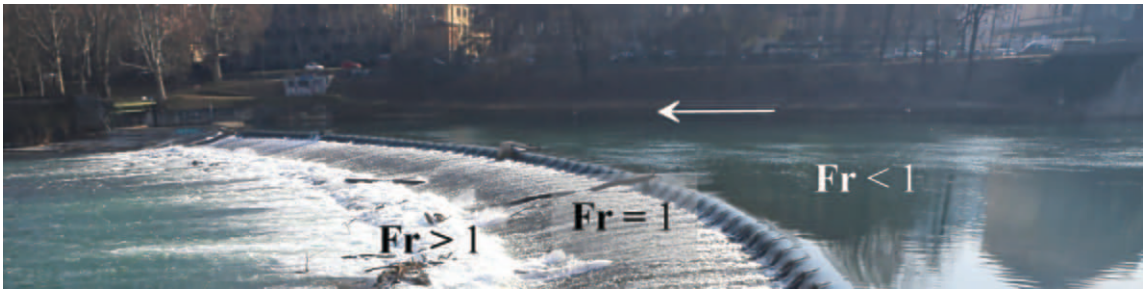

Fig. 2 Patterns of subcritical, critical and supercritical flow at the weir on the Po River, near Turin, Italy.

regime standing waves develops on its surface, which becomes distorted into breaking waves in the supercritical flow (Fig. 2). Both critical and supercritical regimes are the local features in mountain torrents, though they may also be observed in lowland rivers during floods. Transitions between subcritical and supercritical regimes may produce hydraulic drops, or abrupt decreases in flow depth, whereas transitions between supercritical and subcritical regimes result in hydraulic jumps, or abrupt increases in flow depth.

Hydraulic resistance

Flowing waters originate in uplands and flow downhill into larger rivers, lakes, seas, or oceans. They flow within channels with a certain longitudinal gradient $S = \Delta z/\Delta x$, where Δz is the difference in elevation occurring along a streamwise distance Δx. The shear stress associated with the gravitational force per unit area oriented along the inclined plane of the channel bed is ρgHS. Assuming that the gravitational force is balanced by friction force over the streambed, one readily obtains a coefficient of hydraulic resistance $c_f = 2gHS/U^2$. This equation can be rewritten as the Chezy formula $U = C\sqrt{HS}$, where C is the Chezy coefficient. Another common equation is the Manning-Strickler formula $U = H^{2/3}S^{1/2}/n$, where n is the Manning coefficient. Historically both Chezy Manning-Strickler formulae were developed on a purely empirical basis that postulated a certain relationship between depth and velocity. Thereby most empirical hydraulic resistance coefficients are related to c_f and their values have been empirically quantified. Standard manuals report for rivers that the values of the Chezy coefficient vary from 30 to 70, and the Manning coefficient ranges from 0.020 (lowland rivers) to 0.2 (flow over floodplains with terrestrial vegetation).

Although the theory of uniform open-channel flow is capable of describing bulk characteristics of turbulent flows in rivers, the spatial variability of flowing waters always limits the accuracy of this theory. The spatial variability is a distinctive feature which provides diversity of habitat for aquatic life and is therefore a key factor determining patchiness in the community structure of aquatic organisms. This is why it is important to understand and predict complex patterns of turbulent flows correctly. The following sections illustrate spatial patterns of turbulent flows in rivers and illustrate the approaches that quantify the processes producing those patterns.

Fundamentals of turbulent flow theory

The theory of turbulent flows is based on the fundamental physical laws of mass and momentum conservations - incompressible Navier-Stokes equations, which relate instantaneous velocities to the external and internal forces acting on the fluid (Pope, 2000). A fundamental technique allowing analytical and statistical treatments in practical applications of the Navier-Stokes equations is the Reynolds decomposition. With this technique the flow velocity at a point u_i at a time moment t can be represented as $u_i(t) = \overline{u}_i + u'_i(t)$, where overbar indicates time averaging, and subscript refer to a velocity component in the 3-D space. Applying the Reynolds time-averaging operator to the Navier-Stokes equations, the latter translates to a set of the Reynolds-averaged Navier-Stokes (RANS) equations, which relate $\overline{u}_i$ to external and internal forces but contain additional terms $-\rho\overline{u'_i u'_j}$ called Reynolds stresses. Modeling of turbulent flows for practical applications is based on solving RANS together with certain relations between mean velocities and the Reynolds stresses (Pope, 2000; Nezu and Nakagawa, 1993). Turbulence models are usually developed by carrying out experiments in hydraulic labs and verified with the data measured in natural flowing waters. The principles of modeling and the use of the theoretical framework are illustrated on the practical examples in the following sections.

Models of turbulent flows

Turbulence models which are used in RANS relay on a Boussinesq hypothesis according to which the Reynolds stresses is related to the gradients of mean velocity as $-\rho\overline{u'_i u'_j} = \nu_T d\overline{u}_i/dx_j$, where ν_T is turbulent viscosity. The necessity to quantify turbulent viscosity involves schematizations of turbulent flows and provision of typical values or functions for this quantity. On the very basic level turbulent flows are classified as *confined* or *free* turbulent flows (Fig. 3A). Flow confinement may be imposed by a solid boundary such as riverbed, or by the boundary at the interface with a gas or fluid in a solid state (ice). Free turbulent flows are formed when velocity gradients are imposed by an intrusion of flow with flow velocity exceeding that of the ambient flow (jet), by a presence of an obstruction which creates a local velocity deficit (wake), or because of junction of flows differing in their velocities (mixing layer). Because the width of alluvial channels W is usually many times larger than flow depth $W/H > 20$, the jets, wakes and mixing layers, whose lateral scales are not confined sideward by solid boundaries, becomes confined between the river bed and free surface. Such turbulent flows are classified as *shallow* mixing layers, jets and wakes (Jirka and Uijttewaal, 2004).

Turbulent boundary layer

Rivers flow within their alluvial or bedrock channels, whose permeability is generally weak. Therefore velocities in a river cross-section reduce to zero at the bottom and bank and they are maximal at the surface in the center of the channel. In a steady uniform flow not close to the river banks, the gravitational shear-stress component ρgHS is balanced by friction over the boundary that produces a shear stress within the water column $\tau(z) = -\rho\overline{u'w'}$, where τ is Reynolds shear stress, and u', w' are turbulent fluctuations (standard deviations) of velocity in the streamwise and vertical directions, h is the local flow depth, and z is distance

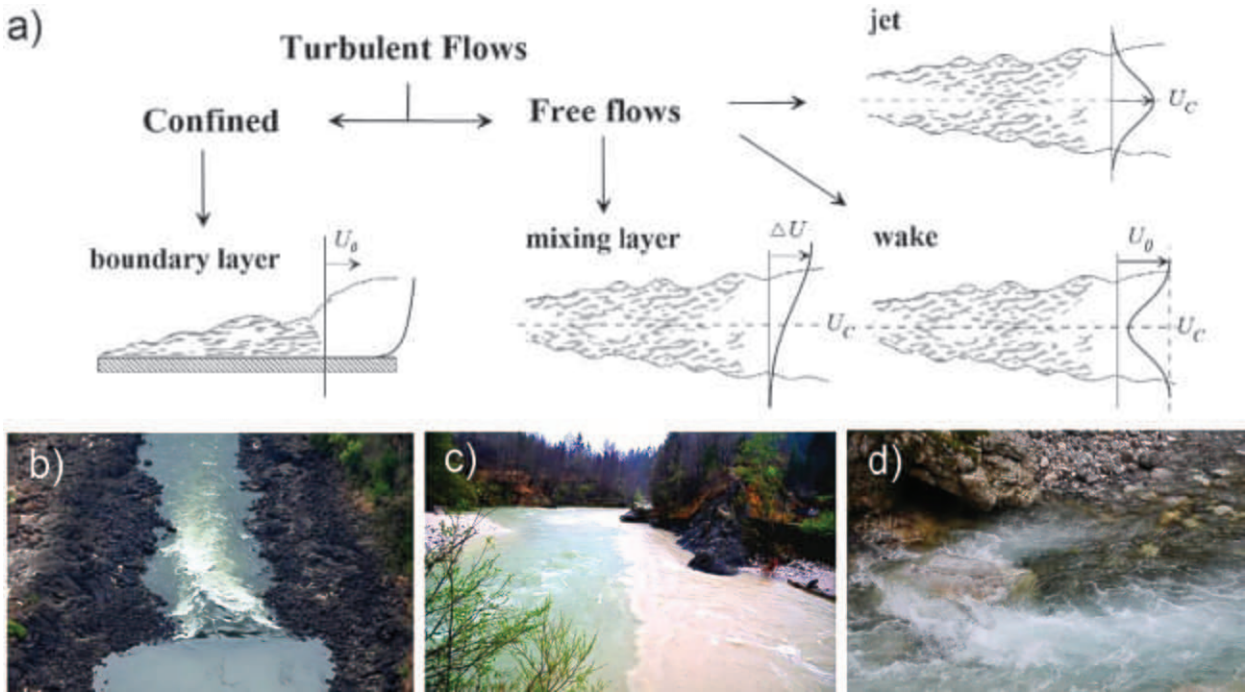

Fig. 3 (A) Classification scheme of turbulent flows, (B) and example of a jet structure at the rapid N17 of the Zambezi River, (C) a mixing layer at the confluence of the Soča and Koritnica Rivers, and (D) a wake downstream of a boulder in the Tolminka River.

from the riverbed. Analytical solution of simplified RANS for this case of quasi-two dimensional uniform open-channel flow predicts that shear stress is linearly distributed over the flow depth

$$\tau = \tau_0(1 - z/H) \tag{1}$$

with a maximum, bed shear stress $\tau_0 = \rho gHS$, at the riverbed. Then an important velocity scale - the *shear velocity* is defined as $u_* = \sqrt{\tau_0}/\rho = \sqrt{gHS}$. Prandtl's mixing length theory for boundary layers suggests that the velocity gradient near the boundary is $d\bar{u}/dz = \kappa u_*/z$, where $\kappa = 0.4$ is the von Karman constant. Eq. (1) together with the mixing length theory and Boussinesq hypothesis yields the parabolic profile for the turbulent viscosity over the flow depth $\nu_T = \kappa u_* z(1 - z/h)$. Integration of $\tau = \nu_T d\bar{u}/dz$ with (1) and assuming a parabolic profile of turbulent viscosity, yields a logarithmic profile for mean streamwise velocity

$$\frac{\bar{u}}{u_*} = \frac{1}{\kappa} \ln \frac{z}{k_s} + B \tag{2}$$

where k_s is a characteristic height of roughness elements, and $B = 8.5$ is a constant of integration. Integrating (2) over river depth provides a logarithmic law of resistance illustrating the effect of riverbed friction on the depth-averaged mean velocity

$$\frac{C}{\sqrt{g}} = \frac{1}{\kappa}\left(\ln \frac{z}{z_0} - 1\right), z_0 = exp\ (\ln k_s + \kappa B) \tag{3}$$

Experimental and field studies provide evidence that boundary layer theory predicts the behavior of flow in natural rivers quite well. Fig. 4 illustrates the performance of the theory by comparing Eqs. (1)–(3) with the data collected in Germany and Italy (Sukhodolov et al., 1998; Sukhodolov and Sukhodolova, 2019). Mean velocities are normalized as $\zeta = exp\,[\bar{u}\kappa/u_* - ln\,(H/z_0)]$. Measured vertical profiles of Reynolds shear stress show the effect of riverbed roughness (Fig. 4A). With an increase of mean diameter of riverbed material, the distance from the riverbed at which measured values separate from the linear profile (1) is increasing. This layer from the riverbed up to the point of separation (indicated by arrows at Fig. 4A) is called the roughness sublayer. Recent extensions of the boundary layer theory based on double averaging methodology provide also a quantitative assessment of the flow turbulence in the roughness sublayer.

The boundary layer theory is intensively used in hydraulic, geomorphologic and ecological studies in flowing waters. It guides the surveys of the velocities by suggesting that depth averaged velocity is measured at $z/H = 0.4$ and Eq. (2) is used to evaluate the shear velocity u_* from the measured velocity profiles.

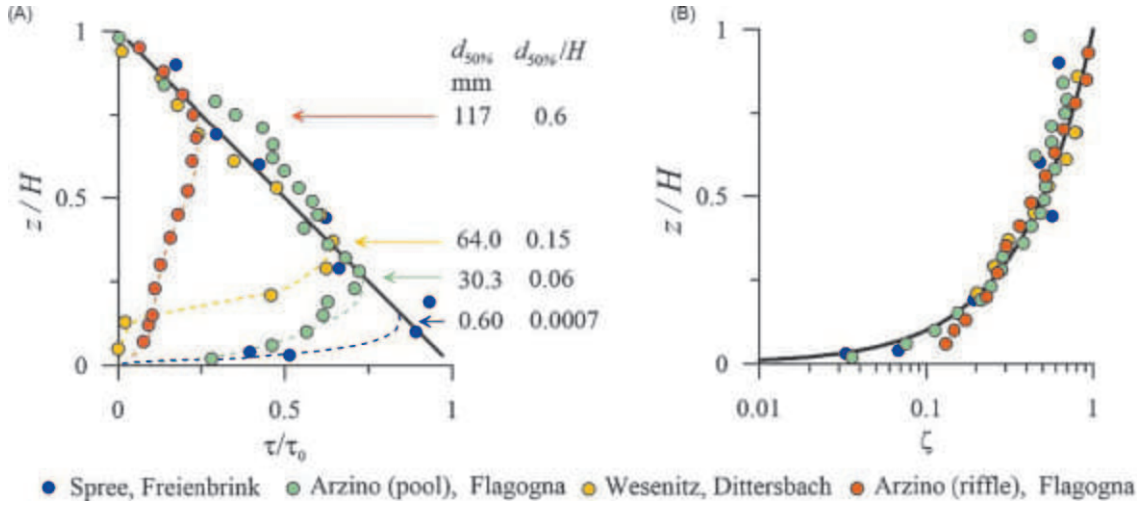

Fig. 4 Boundary layer theory of the turbulent open-channel flow and its comparison with the measurements in natural rivers: (A) the vertical profile of normalized Reynolds shear stresses (solid line is Eq. (1), arrows indicate the height of roughness sublayer, and $d_{50\%}$ is mean diameter of riverbed material), and (B) the vertical profile of normalized streamwise velocities (solid line is Eq. (2)).

Mixing layer

Brooks, creeks and rivers comprise fluvial networks of streams whose channels are interconnected to each other through the nodal locations called confluences (Rhoads, 2020). Because of differences in geology, hydrological regime, and land use on the watersheds of joining streams their waters often differ in volume, sediment content and temperature (Fig. 3C). Lateral velocity gradients occurring at a confluence between merging flows produce flow patterns similar to those of turbulent mixing layers (Fig. 3A). Velocity difference ΔU within confluences generates turbulent structures which exchange momentum between merging flows by which they reduce ΔU in the downstream of the confluence. Because of shallowness of fluvial systems ($H << W$), the larger-scale lateral turbulent structures become affected by the smaller-scale turbulence generated in the boundary layer over the riverbed. This smaller-scale turbulence enhances dissipation of larger-scale turbulence and affects its generation thereby reducing the streamwise growth of the mixing layer width δ as (Sukhodolov et al., 2010)

$$\delta(\mathrm{x}) = \alpha\frac{\Delta \mathrm{U}_0}{\mathrm{U}_0}\mathrm{x}\left(1 - \frac{\beta}{2\Delta \mathrm{U}_0}\mathrm{x}\right), \beta = \frac{\mathrm{g}}{\mathrm{U}_0}\left(\Delta \mathrm{S_f} + \Delta \mathrm{S_{xy}} - \Delta \mathrm{S_x}\right), \tag{4}$$

where $\alpha = 0.11$ is a spreading rate, ΔS_f, ΔS_{xy}, ΔS_x are the differences in friction slopes, lateral and streamwise energy gradients, respectively, the subscript 0 is referring to the origin of mixing layer ($x = 0$). The lateral profile of depth-averaged velocities $\tilde{u}$ in the mixing layer is described as

$$\tilde{\mathrm{u}}(\mathrm{y})/\Delta \mathrm{U} = 0.5\tanh\ (2\mathrm{y}/\delta), \tag{5}$$

where y is the lateral distance with the origin in the middle of the mixing layer y_c. Differentiating Eq. (5) and assuming constant turbulent viscosity, the Boussinesq hypothesis yields the reciprocal hyperbolic cosine profile for the lateral Reynolds stress

$$-\frac{\overline{\mathrm{u'v'}}}{\Delta \mathrm{U}^2} = \frac{\nu_\mathrm{T}}{\delta \Delta \mathrm{U}}\cosh^2(2\mathrm{y}/\delta), \nu_\mathrm{T}/\delta\Delta \mathrm{U} = 0.01. \tag{6}$$

Eqs. (1)–(6) provide the theoretical framework for predicting turbulent flow in shallow mixing layers. Fig. 5 illustrates the performance of the theory by comparing Eqs. (1)–(6) with the results of field-based experiments completed in Italy and Germany (Sukhodolov and Sukhodolova, 2019). In these experiments the width of the mixing layer at short distance from the origin ($x/H < 20$) growths similar to a free mixing layer (Fig. 5A). As the distance increases the lateral larger-scale turbulence becomes strongly affected by the bed friction and further downstream the dynamics of the mixing layer width is accurately predicted by shallow mixing layer theory (Fig. 5A). The depth-averaged profiles of streamwise velocity inside the shallow mixing layer agree with the predictions of Eq. (5) (Fig. 5B). Measured lateral profiles of lateral Reynolds shear stress also confirm that assuming the constant turbulent viscosity provides a reasonably accurate model for the shallow mixing layers (Fig. 5C).

The theory of mixing layers has valuable implications for studies of pollutant spread in fluvial networks, transport of suspended sediments and effects of aquatic and riparian vegetation on flow dynamics (Jirka and Uijttewaal, 2004; Rhoads, 2020).

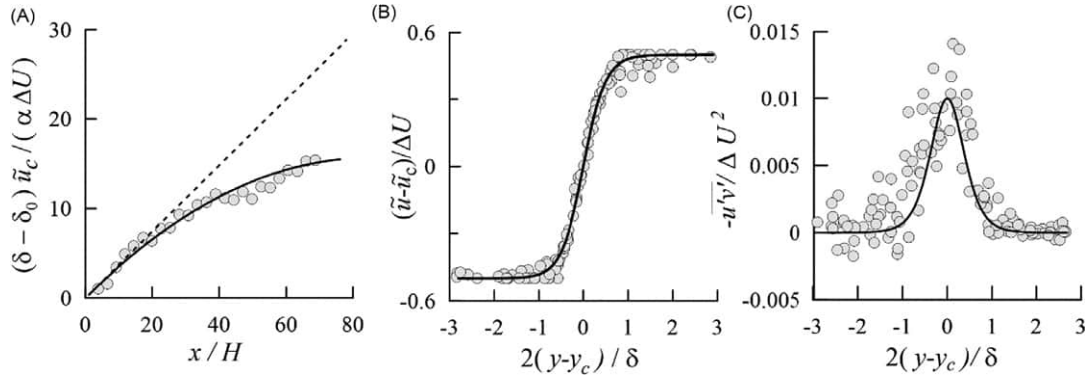

Fig. 5 Shallow mixing layer theory of the turbulent flow and its comparison with the field-based experiments in rivers: (A) dynamics of a shallow mixing layer width (solid line is Eq. (4), dashed line is dynamics of a free mixing layer), (B) normalized depth-averaged velocity across the mixing layer (solid line is Eq. (5)), and (C) lateral profile of normalized Reynolds shear stress measured in the mid-depth (solid line is Eq. (6)).

Turbulent jets

In the upper parts of fluvial networks, the tributaries may have substantially larger gradients of riverbeds and even overhanging channels in the bed rocks. Such tributary streams will also have velocities faster than those in the main rivers. By entering the waters of the main river, the flow from the tributary keeps moving for some distance with gradual loss of momentum, which drives the flow through the ambient water (Fig. 6A). At the interface with the ambient waters evolve two turbulent mixing layers, one on each side of the potential core of a jet. Theoretical and experimental research shows that velocity excess in a free plane jet is decaying with the distance from the origin (x) as $\overline{u}_{max}(x) = 1/\sqrt{x}$. A lateral profile of mean streamwise velocity in the jet is represented by an exponential function

$$\overline{u}/\overline{u}_{max} = \exp\left(-A\eta^2\right), \eta = 2y/b, \tag{7}$$

$$-\frac{\overline{u'v'}}{\overline{u}^2_{max}} = \gamma \frac{\exp\left(-A\eta^2\right)}{\sqrt{A}\eta}\left[1 - \exp\left(-A\eta^2\right)\right], \tag{8}$$

where $\gamma = 0.066$ is the spreading rate for plane jets, $A = 0.693$ is a constant, and b is the width of a jet. Following the method of turbulence modeling based on the Boussinesq hypothesis, one obtains a lateral profile of the Reynolds shear stress. Although results

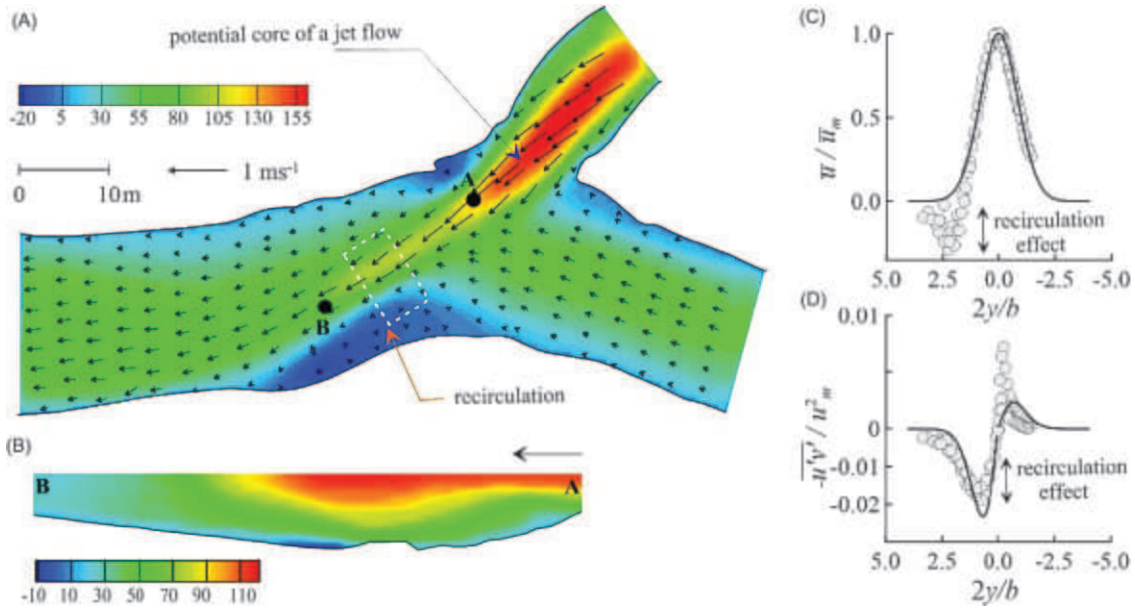

Fig. 6 Turbulent jet at a discordant river confluence of the Ledra with the Torrente Sorgive die Bars, Italy: (A) velocity vectors near the free surface of the flow (color scale shows velocity magnitude in cms^{-1}), (B) longitudinal section of streamwise velocity field (points A-B indicate beginning and end of the section), (C) lateral profile of normalized streamwise velocity near the free surface (location of profiles is shown by the dashed rectangle, solid line is Eq. (7)), and (D) lateral profile of normalized Reynold shear stress near the free surface (solid line is Eq. (8)).

of field studies show that in natural rivers the simple turbulence theories agree with measurements in the central part the jet, complex flow structure of the ambient stream may produce significant deviations from the theory (Fig. 6) (Sukhodolov et al., 2017). The effects of flow recirculation can be especially strong, which enhance lateral gradients and increase turbulence structures both in size and magnitude (Fig. 6C and D).

Besides the importance of jet models for confluences, these turbulent flows are also of a fundamental importance for understanding flow structures in the riffle-pool and step-pool sequences, and within engineering structures (e.g., dams, fish passages, and groyne fields).

Turbulent wakes

Diversity in fluvial ecosystems is perceived in a context of a tight link between spatial heterogeneity in environmental factors and biota. Central to this topic is the flow heterogeneity produced by natural in-stream obstructions such as boulder clusters, log jams, and patches of riparian and aquatic vegetation. Turbulent flows evolving around these obstructions are referred to as turbulent wakes. Downstream these obstructions the width of a free wake δ_w increases as a root square of distance $\delta_w = \sqrt{x/D}$, where D is the diameter of an obstruction. However, in shallow fluvial environments the shallowness may restrict the growth of the wake. This effect is quantified by the stability parameter $S_w = c_f D/H$. For $S_w \leq 0.2$ the wake's dynamics is similar to a free wake and at $S_w > 0.5$ the wake width is not laterally expanding. Lateral velocity profiles in a turbulent wake can be scaled with a velocity differential as characteristic velocity scale as

$$\frac{|\tilde{u}_c - \tilde{u}|}{\Delta U} = \exp\left[-A\left(\frac{2y}{\delta_w}\right)^2\right]. \tag{9}$$

Differentiating Eq. (9) with a constant turbulent viscosity, the Boussinesq hypothesis yields the lateral profile for the Reynolds stress

$$-\frac{\overline{u'v'}}{\Delta U^2} = -4A\varepsilon\frac{2y}{\delta_w}\left[-A\left(\frac{2y}{\delta_w}\right)^2\right], \varepsilon = \nu_T/\Delta U\delta_w, \tag{10}$$

where $\varepsilon = 0.01$is a constant. Performance of wake theory is illustrated by comparing Eqs. (9)–(10) to the results of field-based experiments in a gravel bed river (Fig. 7) (Sukhodolov and Sukhodolova, 2014; Shumilova et al., 2021). In turbulent flows past solid objects a recirculation zone forms immediately downstream of the obstruction (Fig. 7A). The width of the wake assumes the dynamics of a free wake for some distance that is then stabilized by bed friction further downstream (Fig. 7A). The lateral profile of depth-averaged streamwise velocity across the shallow wake agrees with the predictions of Eq. (9) (Fig. 7B). A good agreement can be also concluded for the lateral profiles of lateral Reynolds shear stress predicted with Eq. (10) (Fig. 7C).

Conclusions and knowledge gaps

This chapter briefly reviews the main features distinguishing laminar and turbulent flows in flowing waters and it focuses on the turbulent flows and on the concepts of their modeling. These are illustrated with four basic types of turbulent concepts: boundary layer, mixing layer, jet and wake. For each of these flows turbulence modeling is illustrated by applying the Boussinesq hypothesis with appropriate assumptions on the turbulent viscosity. Predictions of turbulence modeling are compared to the results of field-based experiments completed on rivers in Germany and Italy.

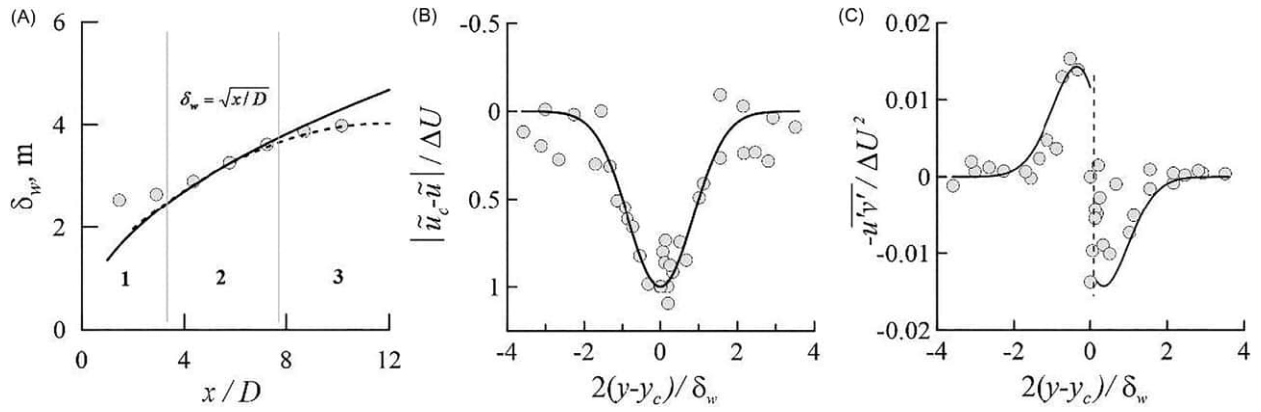

Fig. 7 Turbulent wake past a deposition bar in a gravel bed river: (A) dynamics of the wake width in the downstream (solid line corresponds to a free wake and dashed line is shallow wake), (B) normalized mean streamwise velocity profile in the wake (solid line is Eq. (9)), and (C) the lateral profile of normalized lateral Reynolds stress (solid line is Eq. (10), the dashed line shows the centerline).

Although turbulent flows and their modeling are considered complex and difficult to predict, advances in the past decades have led to substantial progress in our understanding of these flows. Especially important is the development of theoretical, field, experimental and numerical studies of shallow turbulent flows, which allows separation of different sources and the contributions of physical forces. Because of their mathematical simplicity and clearly defined parameters, analytical models of turbulent shallow flows are easy to incorporate into complex mechanistic models of river ecosystem such as individual-based models of aquatic organisms.

Mutual interaction between flow, channel, and biota at different spatial and temporal scales ranging from a sediment grain to the scale of a river reach, and from milliseconds to hundreds of years complicate unambiguous studies of turbulent flows in natural environments. Therefore, available data on model parameters of river flows include significant scatter that leads to uncertainties in prediction of magnitudes and patterns of flows. Some of this uncertainty reflects the fact that most theoretical, laboratory, and field studies investigate or assume uniform steady flow, while in nature these flows are always an idealization. To overcome these limitations, further research needs to address the following knowledge gaps:

- effects and feedbacks of free surface dynamics;
- hydrodynamics and turbulent flow structure in large rivers;
- details of turbulent flow structure in riffle-pool sequences;
- hydrodynamics of river flows during floods.

See Also: Structures and functions of Inland Waters - Lakes: Currents in Stratified Water Bodies: Internal Waves

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Relevant websites

https://youtu.be/5wXjvzqxONI—Down by Karman Street: Hydrodynamics of fluvial wakes past large in-stream natural objects and their implications for riverbed morphology.
https://youtu.be/gM-Zr-rhflY—Where rivers meet: Transport and mixing at river confluence.
https://youtu.be/fbZclyal_yQ—Turbulence and sand waves: Field studies of flow structure over moveable sandbed.

Optical Properties of Water☆

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This is an update of D.P. Morris, Optical Properties of Water, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00069-7.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

1% Attenuation depth, $z_{1\%}$ (m) The depth to which 1% of subsurface irradiance of a given wavelength penetrates in the water column. Using subsurface measurements gives a surface reference that excludes albedo and thus more accurately reflects water transparency.
Absorptance (A, unitless) Fraction of flux that is absorbed across the medium relative to the incident flux.
Absorption coefficient (a, m^{-1}) Rate of flux decrease due to absorption with thickness of the medium.
Beam attenuation coefficient (c, m^{-1}) Flux lost from a beam of light as a result of both absorption and scattering, per unit thickness of the medium.
Diffuse attenuation coefficient (K_d, m^{-1}) Rate of decrease of subsurface irradiance with depth.
Irradiance (E, W m^{-2} or Q, μmole quanta m^{-2} s^{-1}) Measure of the radiant power (E) or quantum flux (Q) within a wavelength range, incident per unit area on a surface.
Photosynthetically active radiation (PAR) Irradiance in the 400–700 nm wavelength range, as either radiant power (W m^{-2}) or quantum flux (μmole quanta m^{-2} s^{-1}).
Scatterance (B, unitless) Fraction of flux that diverges from the parallel beam as it passes through a medium relative to the incident flux.
Scattering coefficient (b, m^{-1}) Rate of flux decrease due to scattering with thickness of the medium.
Spectral slope (S, nm^{-1}) The slope of the plot of the natural log of the absorbance versus wavelength for a specified wavelength range such as all UV (280–400 nm).
Volume scattering function (β, steradian^{-1}) Angular distribution of scattered flux.
Zenith The point in the sky directly overhead from the location of interest.

The nature of light

Sunlight is essential for photosynthesis which provides the energy essential to all but a few of the simplest microbial communities in aquatic ecosystems. Sunlight is also critical in structuring aquatic ecosystems. Seasonal variations in the heat energy provided by sunlight are responsible for thermal stratification and mixing regimes in aquatic systems.

The term "light" is commonly referred to as that portion of the electromagnetic spectrum that is visible to the human eye. This visible light accounts for a very narrow portion of the electromagnetic spectrum that ranges from cosmic rays to radio waves. Although some electromagnetic radiation originates from outside our solar system (indeed some as remnants of the "Big Bang"), an overwhelming majority of the electromagnetic radiation reaching the Earth originates from the Sun.

☆*Change History*: January 2021. PJ Neale and CE Williamson updated abstract, text and further readings. Figs. 4, 5 and 7 were revised with updated information. One annotation in Fig. 8 was corrected.

All electromagnetic radiation should be viewed as having two fundamental properties, which include both a physical entity (photons/quanta) and wave properties. Thus, electromagnetic radiation is a transverse wave of energy that behaves as a particle with a defined momentum. The photon carries energy in the form of a wave; each discrete photon has a distinct wavelength and frequency associated with it. The wavelength (λ, m) and frequency (ν, Hz) of electromagnetic radiation are inversely related by

$$\lambda = c/\nu \tag{1}$$

where c is the speed of light (3.0×10^8 m s^{-1} in a vacuum). When dealing with light, it is more typical (and convenient) to express wavelength in units of nanometers (10^{-9} m).

The energy content of discrete photons (in Joules) of electromagnetic radiation is inversely related to wavelength via the Planck equation

$$\varepsilon = h\nu = hc/\lambda \tag{2}$$

where h is Planck's constant (6.63×10^{-34} J s).

The bulk of solar radiation spans wavelengths from approximately 100–3000 nm (Fig. 1). A relatively small proportion of this spectrum corresponds to 'visible' light (400–700 nm). Wavelength bands within the visible spectrum are perceived as colors by the human eye. The perceived colors of blue (450–500 nm), green (500–550 nm), yellow (550–600 nm), orange (600–650 nm) and red (650–700 nm) are all associated with distinct wavelength bands within the visible spectrum. Wavelengths of ultraviolet radiation are shorter than the visible spectrum (200–400 nm) while those of infrared radiation are longer (700–3000 nm).

Planck's Eq. (2) can be used to calculate the energy content of photons associated with any of these wavelengths. Relative to photons with a wavelength of 665 nm (a major absorption peak for chlorophyll *a*), infrared photons at 1000 nm contain only 66% of the energy. In contrast, photons associated with UV-B radiation at 300 nm contain 221% of the energy compared to those at 665 nm. This explains why UV-B radiation can cause erythema (sunburn) while infrared radiation produces only a gentle warming sensation.

Even more ecologically significant than the phenomenon of vision, light provides the energy necessary for photosynthesis. The energy utilized in photosynthesis is restricted to a relatively narrow spectrum referred to as "photosynthetically active radiation" (PAR). Interestingly, and probably not coincidentally from an evolutionary perspective, PAR and visible light are essentially identical (400–700 nm). The long wavelength limit of PAR is defined because photons at a wavelength greater than 700 nm have too little energy to overcome the biochemical threshold for production of electrons by photosystems I and II used in photosynthesis. In contrast, the intensity of the solar spectrum drops off sharply below 400 nm (Fig. 1) so there is little energetic benefit to be derived from harvesting the shorter (UV) wavelengths. Although vision and photosynthesis utilize only a narrow band of the solar spectrum, the region from 400 to 700 nm contains almost 45% of the energy output of the sun (at Earth's surface). Evolution of vision and photosynthesis to use this narrow band resulted from a balance between available solar radiation and the optimum energy content per photon for biological systems.

As a result of the nature of electromagnetic radiation, the radiant flux density, or irradiance, of light may be quantified in one of two ways: by counting quanta or measuring energy. Each method has utility with respect to the study of aquatic systems.

Full summer sunlight at the surface of the Earth delivers a quantum flux density (Q) of approximately 1.2×10^{21} quanta m^{-2} s^{-1} of visible light. Frequently, Q is expressed in terms of moles of photons (1 mol of photons = 6.02×10^{23} photons, also known as 1 Einstein). Thus, a "full sun" value of Q for a typical summer day at noon is approximately 2000 μmole of visible (or PAR) quanta per square meter per second. Alternatively, PAR may also be measured as radiant power, the flux of energy (joules) per square meter per

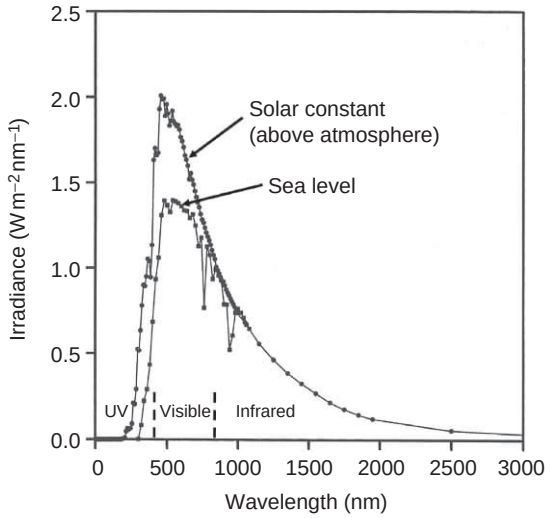

Fig. 1 Spectral distribution of sunlight above the atmosphere and at sea level.

second (E). A "full sun" value for PAR irradiance reported in energy units is approximately 430 J m^{-2} s^{-1} or 430 W m^{-2} (1 J s^{-1} = 1 W).

If the distribution of quanta or energy is known across the solar spectrum, it is possible to convert between the two sets of units using Planck's Eq. (2). Often instrumentation to precisely measure the spectral distribution of quanta or energy in sunlight is not available. In these cases, a conversion factor may be applied based on a typical spectral distribution of sunlight at the Earth's surface. Morel and Smith (1974) found that for solar radiation in the visible (and PAR) spectral range, a conversion factor of 2.77×10^{18} quanta J^{-1} was accurate to a within few percent over a variety of sky conditions for measurements made in the air. This factor (Q/E) is equivalent to 4.6 μmole quanta J^{-1}.

Role of the atmosphere

Solar flux just outside Earth's atmosphere is referred to as the "solar constant" and has a value of approximately 1373 W m^{-2}. Reflectance, scattering, and absorption of light in the atmosphere can reduce this amount by 15–80% before reaching Earth's surface. Scattering and absorption do not influence all wavelengths equally, thus significant changes in the spectral distribution of sunlight will occur as light penetrates the atmosphere.

Scattering of light by gas molecules in the atmosphere is proportional to $1/\lambda^4$ (as described by Rayleigh's law). Some of this light is back scattered into space while some is scattered forward and reaches the Earth's surface as skylight. Since scattering is inversely related to λ^4, the shortest wavelengths are preferentially scattered in the atmosphere, causing a cloudless sky to appear blue. Although not visible, large fluxes of short wavelength UV radiation can reach the surface of the Earth as scattered skylight (in contrast to direct sunlight). In addition to gas molecules, aerosols and water vapor (as clouds) in the atmosphere can also contribute to light scattering.

The absorption of light by the atmosphere is largely a result of naturally occurring oxygen, ozone, carbon dioxide, and water vapor. Anthropogenic air pollution may also have significant effects in some regions.

Ozone strongly absorbs high-energy UV-B radiation and essentially prevents light of wavelengths shorter than 290 nm from reaching the surface of the Earth. Water vapor and carbon dioxide strongly absorb some specific bands of infrared radiation and are significant as 'greenhouse' gases. Fig. 1 compares the spectral distribution of light above the atmosphere and at sea level.

Cloud cover can be effective in both reflecting and absorbing light in the atmosphere. The transmissivity of thick cumulus clouds may be as little as 10% while that of high stratus clouds may be as high as 70%. The transmissivity of total solar radiation can be as high as 86% under dry, cloudless, and "clean" atmospheric conditions. According to Gates (1962), the average annual transmissivity of the atmosphere over a region in the Northern Hemisphere was 47%. Reflectance and back scattering of light into space accounted for a loss of 34% while 19% was lost via atmospheric absorption.

The role of latitude

Latitude plays a critical role in determining solar flux at Earth's surface (E_0), by its influence on sun angle and day length (Fig. 2). Insolation generally declines with increasing latitude through its influence on sun angle. The flux density (irradiance) on a flat surface declines in proportion to the cosine of the incident angle of the sun (angle from the vertical, often referred to as the zenith angle). For example, just considering the effect of sun angle, direct solar irradiance at a zenith angle of 60 degrees (sun 30 degrees above the horizon) is half of what it is when the sun is directly overhead (zenith angle 0 degrees). However, during summer, this phenomenon is countered by increasing day length. The net result is that during mid-summer, high latitude regions may actually receive greater daily insolation than the equatorial regions. Thus, the maximum daily insolation received at the surface of Earth does not vary significantly with latitude (disregarding any variations in atmospheric conditions). The most profound influence of

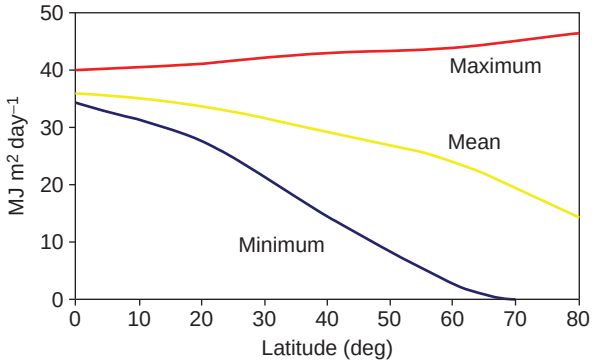

Fig. 2 Maximum, minimum, and mean daily irradiance at different latitudes at the surface of the Earth. Data do not account for regional differences in cloud cover.

latitude on insolation is in determining the minimum daily insolation. During winter, increasing sun angle is accompanied by decreasing day length at high latitudes. In fact, daily insolation falls to zero in polar regions during the winter.

Reflectance, scattering, and absorption of light by the atmosphere also increase with sun angle. Loss of light by scattering and absorption are both a function of the amount of atmosphere traversed. The atmospheric path length is inversely proportional to the cosine of the solar zenith angle. Thus, the atmospheric path length is roughly doubled when the sun is 30 degrees above the horizon than when being directly overhead. For this reason, the transmissivity of the atmosphere will vary greatly according to both latitude and time of day.

Reflectance at the air-water interface

Light at the surface of a water body may be reflected. Unless rereflected or scattered back to the aquatic system from the atmosphere or the surrounding landscape, this light is lost from the system. The amount of light reflected from the water's surface is related to the incident angle of the sun (zenith angle), as described in the Fresnel equation

$$r = \frac{1}{2}\left\{\left[\frac{\sin(\theta_a - \theta_w)}{\sin(\theta_a + \theta_w)}\right]^2 + \left[\frac{\tan(\theta_a - \theta_w)}{\tan(\theta_a + \theta_w)}\right]^2\right\} \tag{3}$$

where r is the reflection of unpolarized light as a fraction of the incident light, Θ_a is the zenith angle of the sun, and Θ_w is the angle of the light transmitted into the water (i.e., the angle of the incident light beam refracted by the air-water interface). The angle of transmitted light is related to the angle of incident light by Snell's law, $n_a \sin\theta_a = n_w \sin\theta_w$ where $n_a = 1$ and $n_w = 1.33$ are the indices of refraction of air and water, respectively. Reflectance for a flat body of water with the sun directly overhead (i.e., $\Theta_a = 0$ degrees) is approximately 2% and remains relatively low for zenith angles of up to about 60 degrees ($r < 6\%$). As the zenith angle approaches 90 degrees, reflectance increases rapidly (e.g., r is approximately 60% at 80 degrees). At small zenith angles, surface disturbances (i.e., small waves) have very little influence on reflectance but at more extreme zenith angles (>60 degrees) reflectance can be increased by as much as 20%. Large waves in combination with high zenith angles may reduce reflectance by decreasing the effective zenith angle between the water's surface and the sun. Reflectance of light from frozen water bodies has been estimated to be as much as 75–95%; however, this value depends on the quality of the ice and particularly the amount of snow.

This discussion of reflectance deals solely with direct solar radiation. Reflection of diffuse solar radiation striking the surface of the water as a result of scattered skylight is difficult to determine precisely because the angular distribution of light is unknown.

Inherent optical properties

Once photons penetrate the air–water interface of aquatic systems they may only be scattered or absorbed. The extent to which either of these phenomena may occur is governed by three parameters: absorption coefficient, scattering coefficient, and the volume scattering function. These three parameters are often referred to as "inherent optical properties" because they only depend on the constituents of the aquatic medium and not on the geometry of the light field.

To define these parameters, it is necessary to consider an infinitesimally thin layer of medium being illuminated at right angles by a parallel beam of light (Fig. 3). The fraction of flux that is absorbed across the medium relative to the incident flux is defined as the absorptance (A) and the fraction of flux that diverges from the parallel beam of incident flux is referred to as the scatterance (B)

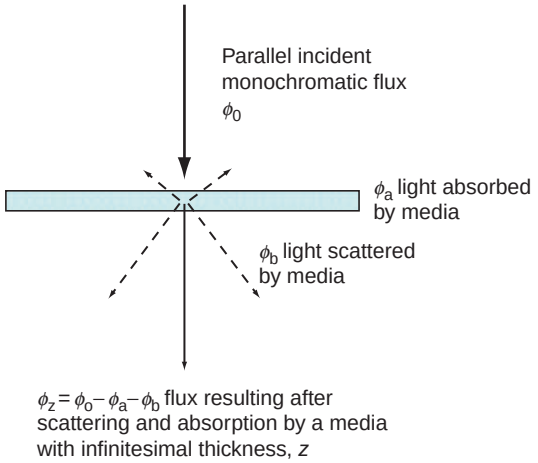

Fig. 3 Schematic diagram illustrating absorption and scattering of light by an infinitesimally thin layer of water.

$$A = \Phi_a/\Phi_0 \tag{4}$$

$$B = \Phi_b/\Phi_0 \tag{5}$$

where Φ_0 is the incident flux of the parallel beam of light, Φ_a is the flux absorbed and Φ_b is the flux scattered by the thin medium. If we represent the change in absorptance (ΔA) and scatterance (ΔB) with infinitesimal changes in the thickness of the medium (Δz), we can estimate the absorption coefficient (a) and the scattering coefficient (b)

$$a = \Delta A/\Delta z \tag{6}$$

$$b = \Delta B/\Delta z \tag{7}$$

The beam attenuation coefficient (c), an additional inherent optical property, is simply an expression of the amount of flux lost from the beam of light as a result of both absorption and scattering, per unit thickness of the medium

$$c = a + b \tag{8}$$

The absorption coefficient, scattering coefficient, and beam attenuation coefficient each have units of 1/length and are typically expressed as per meter.

Another inherent optical property of the aquatic medium is the volume scattering function (β). As light is scattered within a medium, the photons may be dispersed in a variety of different directions. The volume scattering function defines the angular distribution of the resulting scattered flux. This function differs according to the medium but generally describes a radially symmetrical cone of distribution around the direction of the incident beam.

Scattering

Scattering of light in aquatic ecosystems can be thought of as the deflection (reflection) of photons at a large number of angles due to water and its dissolved and particulate constituents. Although scattered photons are largely distributed in a radially symmetrical cone around the direction of the incident beam, there is a finite statistical probability that photons may be deflected in any direction. Scattered photons that are deflected back may leave the aquatic ecosystem along with their energy content. Scattering varies with wavelength according to the differential absorption and scattering characteristics of the aqueous medium. In very clear aquatic ecosystems, the greatest amount of scattering occurs in UV wavelengths. These systems appear blue because blue is the shortest visible wavelength backscattered that is detected by the eye. Systems with large concentrations of dissolved organic carbon appear yellow/brown because blue photons are strongly absorbed and thus not available to be backscattered to the eye of the observer.

Scattering may be greatly influenced by the nature of particulate material in an aquatic ecosystem. For instance, fine glacial "flour" may be highly reflective and can enhance scattering at the mouth of rivers draining glaciers and lakes receiving glacial meltwater. White calcium carbonate (marl) at the bottom of lakes may also enhance scattering (reflectance) in shallow systems or in the water column of deeper systems if sediments are resuspended by wind driven mixing. In contrast, organic particulate material (colloids of humic substances, detritus, etc.) may strongly absorb rather than scatter photons. The net result of scattering is that it can greatly increase the path length (Δz) taken by a photon as it passes through an aqueous medium. For instance, it is not uncommon for the "average" photon to travel a path of 1.2 m (as a result of multiple scattering events) before reaching a depth of 1 m in an aquatic ecosystem. Scattering also has important implications for aquatic photosynthetic organisms because scattered photons are available from all directions (including the bottom) and not just that oriented toward the downward welling light.

Absorption

Photons of light may interact with the electron shell of molecules and be absorbed. During this process, the photon is destroyed but its energy is transferred to the molecule that absorbed it. This energy is used to transition electrons from the ground state to higher energy levels. Molecules can have very distinct absorption spectra because the energy content of some photons (Eq. (2)) match exactly the energy required for the electron transition. The energy of absorbed photons may be used to break chemical bonds or generate electrons (in the case of photosynthesis). However, because energy has to be conserved, the energy of all absorbed photons is eventually released in aquatic ecosystems as heat.

Light absorption can be measured with a spectrophotometer, which is an instrument specifically designed to measure the absorbance of light by a medium of known thickness. Values obtained by spectrophotometers are known equivalently as absorbance (A) or optical density (OD). Here, we use the latter term (OD) to avoid confusion with the related but different property of absorptance (Eq. (4)). Using a spectrophotometer, optical density (OD) can be calculated as

$$OD = \log_{10} \frac{I_0}{I_z} \tag{9}$$

where I_0 is the intensity of incident light and I_Z is the intensity of light transmitted through the medium. If we arrange the system so that any light scattered in the medium is also included in our measurement of I, we can use Eq. (9) to determine the absorption coefficient (a) of the medium

$$a = \frac{2.303\ OD}{Z} \tag{10}$$

where 2.303 is the constant to convert base 10 to natural logarithms and Z is the path length of the medium. The absorption coefficient is given in units of 1/path length (typically m^{-1}). Under ideal measurement conditions, the result of Eq. (10) is identical to the theoretical absorption coefficient as defined in Eq. (6).

In aquatic ecosystems, photons may be absorbed by the water itself, dissolved substances, and particulate material. Pure water is not a colorless liquid. As is obvious by observing very deep, clear systems, water is a blue liquid. This color implies that there is significant spectral variation in absorption over the visible region. As seen in Fig. 4, the absorption of light by pure water decreases from the UV to a minimum in the blue range of the visible spectrum then increases substantially from 430 to 760 nm. Following a small decline centered around 810 nm, absorption increases markedly through the infrared region, peaking at about 975 nm. In the infrared, the absorption coefficient is more than 100 times greater than in the UV and visible region (compare left- and right-hand axes in Fig. 4). The strong absorbance peak in the IR region highlights the great importance of infrared radiation in influencing the heat budgets of aquatic ecosystems.

Dissolved organic matter (DOM) plays the most critical role in influencing the absorption spectrum of natural waters in the visible and UV wavelengths. The colored fraction (typically yellow/brown) of DOM is referred to as chromophoric dissolved organic matter (CDOM). This material consists mainly of humic and fulvic compounds originating from the decomposition of terrestrial plant material under anaerobic conditions. DOM released from microalgae and other aquatic plants is another source. DOM is typically characterized by its carbon content, dissolved organic carbon (DOC). The global mean concentration for DOC in freshwater systems is approximately 5 mg C L^{-1} but can vary widely ($\ll$1 mg C L^{-1} in very clear systems to >100 mg C L^{-1} in bogs). CDOM is generally an important component of DOM in high DOC lakes. As seen in Fig. 5, the presence of CDOM causes an exponential increase in absorption from the short visible wavelengths through the UV-B region of the spectrum. The slope of this exponential curve (S, $\ln(a)$ vs. $\lambda_{280-400nm}$) has been measured for a variety of freshwater systems and averages –0.0181 nm^{-1}. S typically ranges between –0.020 and –0.010 nm^{-1} and seems to be related to qualitative differences in CDOM (likely due to CDOM source or photobleaching). CDOM has the greatest influence on short wavelength UV radiation but also strongly affects the absorption of visible light (especially blue). The optical property often referred to as "color" is typically measured as the absorption coefficient at 440 nm and is a reflection of CDOM concentration for a particular aquatic ecosystem. In systems with high CDOM concentrations, absorption of PAR can significantly reduce light available for photosynthesis. Because of the shape of the absorption spectrum, much smaller concentrations of CDOM can effectively absorb damaging solar UV-B radiation, producing refugia from damaging UV at depth in aquatic systems. Above approximately 600 nm, CDOM has little influence on the absorption spectrum. Other dissolved constituents of aquatic systems (e.g., nitrate) may also absorb light but their specific absorption coefficients are very low compared to that of CDOM. Thus, these compounds will only be optically significant in systems with very low concentrations of CDOM.

Suspended particulate matter may also absorb light in aquatic systems (Fig. 6). Phytoplankton evolution has produced photosynthetic pigments that are highly efficient at absorbing light in the PAR and UV spectrum. These cells often contain a variety

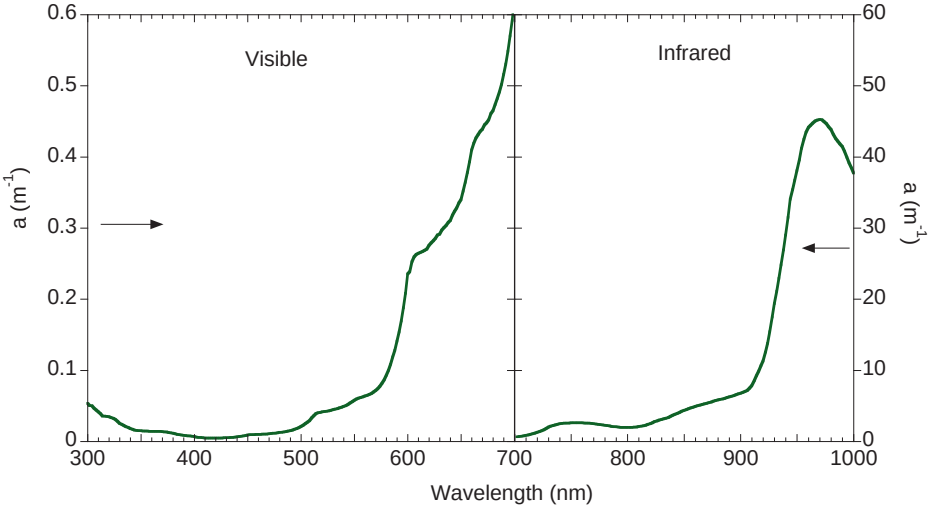

Fig. 4 Spectral distribution of the absorption coefficient for pure water. Measurements were made with a spectrophotometer, with air as reference. Note that the absorption coefficient in infrared is plotted using the right hand y-axis, which has a 100 times larger scale than the left hand y-axis for the UV and visible.

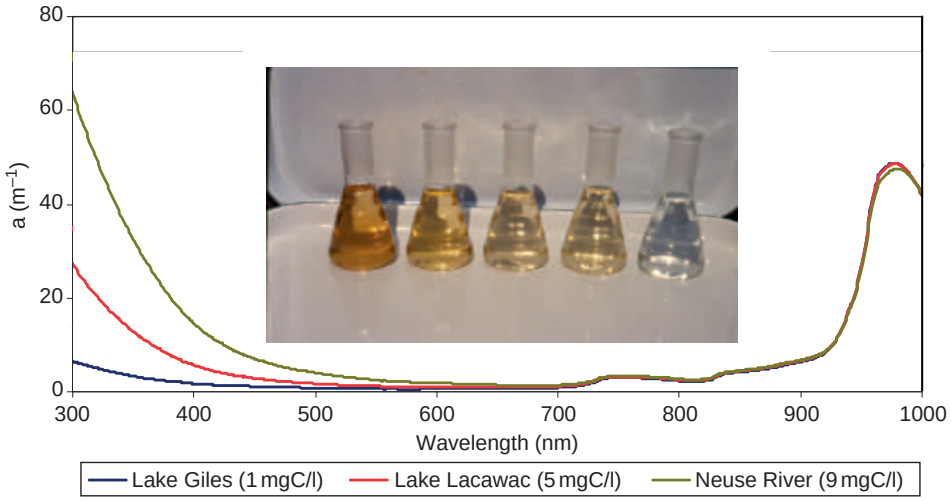

Fig. 5 Spectral distribution of absorption for filtered water from lakes with different concentrations of CDOM. The inset shows the visual color of four lake water samples ranging from approximately 1 to 15 mg C L^{-1} of dissolved organic carbon. Measurements were made with a spectrophotometer referenced to air.

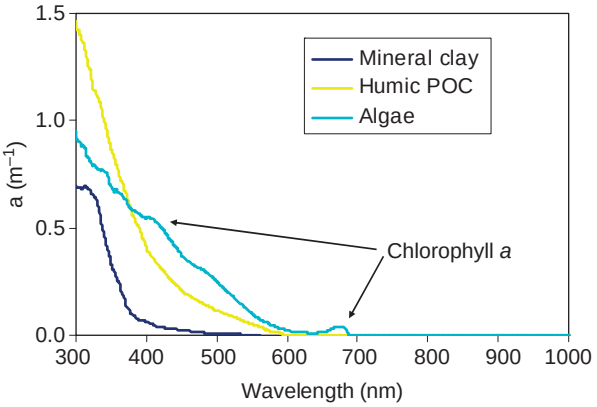

Fig. 6 Spectral distribution of absorption for three categories of particulate material commonly found in aquatic ecosystems. These are only examples, the shape and absolute size of the peaks will depend upon the composition and concentration of these materials in the water column. The "fingerprint" of the chlorophyll *a* absorption peaks (665 and 425 nm) can be seen in the sample of algae. Data were obtained using spectrophotometry and the quantitative filter pad technique.

of accessory pigments (e.g., carotenoids, chlorophyll *b*, and chlorophyll *c*, etc.) as well as chlorophyll *a*. As seen in Fig. 6, the absorbance peaks of chlorophyll *a* (425 and 665 nm) are often apparent in the spectral analysis of suspended particulate matter over and above that of accessory pigments. Systems with high concentrations of CDOM may also have significant amounts of suspended organic colloids composed of humic matter. The chemical composition and absorption spectrum of this particulate matter is often similar to that of CDOM (compare Figs. 5 and 6). Fig. 6 also shows an absorption scan for mineral clay particles. In contrast to either phytoplankton or colloidal CDOM, kaolin (a type of clay) exhibits very little absorption above 400 nm. However, mineral particles make an important contribution to scattering that extends across the spectrum (see "Scattering" section).

Optical properties of aquatic ecosystems

The transparency of aquatic systems is represented by a value referred to as the extinction coefficient or diffuse attenuation coefficient (K_d). This value may be determined empirically for an aquatic system using the following equation:

$$E_{dz} = E_{d0}\, e^{-K_d z} \tag{11}$$

where E_{dz} is the downward welling irradiance at depth z, E_{d0} is the downward welling irradiance just below the water's surface, and K_d is the diffuse attenuation coefficient. K_d has units of reciprocal depth (typically m^{-1}). As demonstrated in the previous section, the attenuation coefficient in aquatic systems will be influenced by absorption and scattering by pure water (K_{water}), by materials dissolved in the water ($K_{dissolved}$), and by particulate material ($K_{particulate}$). Thus, the total measured diffuse attenuation coefficient for a given system will be the sum of each of the partial diffuse attenuation coefficients.

As illustrated by data presented in Figs. 4–6, each of these partial diffuse attenuation coefficients have a strong spectral component. Thus, the relative contribution of each of these partial diffuse attenuation coefficients to the total diffuse attenuation coefficient will vary substantially across the solar spectrum and between systems. For instance, due to the spectral distribution of CDOM absorption, $K_{dissolved}$ in lakes comprised an average 68% of K_{total} at 305 nm compared to only 33% for PAR. In contrast, K_{water} contributes a much larger fraction (>95%) of K_{total} in the infrared portion of the spectrum than do the other partial diffuse attenuation coefficients. For lakes in general, the concentration of CDOM is the single most important determinant of K_d in the UV region of the spectrum while a combination of both CDOM concentration and phytoplankton biomass are significant determinants of K_d for PAR.

Plots showing examples of the extinction of light in an aquatic ecosystem are shown for Lake Superior, MI (Fig. 7). The top panel shows the comparative depth penetration of different wavelengths of solar irradiance, with lighter gray tones indicating higher

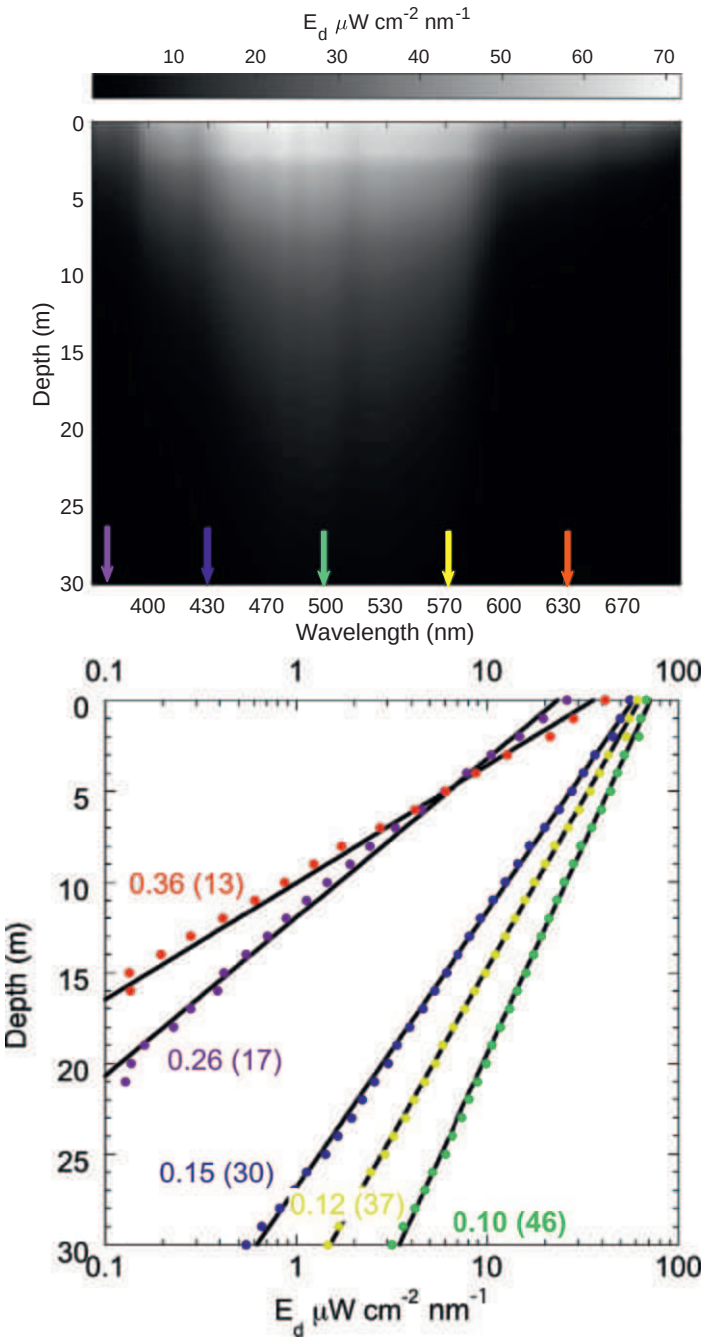

Fig. 7 Attenuation of downward welling irradiance (E_d) in Lake Superior. In the top panel, the extent of vertical penetration of irradiance from 370 to 700 nm (horizontal axis) with depth (vertical axis) is shown. Flux intensity is scaled by gray scale at top. In the bottom panel the line of best fit is plotted through the data points of ln(E_d) vs. depth for selected wavelengths indicated by arrows in upper panel. The negative slope of this line is the value of K_d for each wavelength. The values of K_d ($z_{1\%}$) are provided. Data from Mouw CB, Ciochetto AB, Grunert B and Yu A (2017) Expanding understanding of optical variability in Lake Superior with a 4-year dataset. *Earth System Science Data* 9: 497–509.

irradiance. The intensity of incident irradiance (i.e., at a depth of 0 m) follows from the data presented in Fig. 1, where the highest value of radiant flux (E_d in this case) is in the wavelength range of 470–530 nm (blue to green) with a progressive decrease in surface flux toward both the shorter (UV) and longer (red) wavelengths. As would be expected from the exponential form of Eq. (11), irradiance decreases quickly with depth such that 90% of PAR irradiance is attenuated in the first 18 m. Blue and green wavelengths, in addition to having the highest flux, also penetrate the deepest. Below 18 m in this near-shore area of Lake Superior, a diver in the water would see almost monochromatic bluegreen light as little remains of the rest of the spectrum. The color (wavelength) of this deepest penetrating light varies between lakes depending primarily on the absorption spectrum (Figs. 5 and 6), varying from a deep blue in lakes with low CDOM and particulates to yellow in lakes with a high concentration of these constituents.

Light of each of the wavelengths diminishes through the water column with a characteristic slope. Using Eq. (11), the value of K_d for each wavelength can be derived from the negative slope of the plot of $\ln(E_{dz})$ vs. depth. To illustrate, irradiance on a log scale is plotted (Fig. 7, bottom panel) for five selected wavelengths shown by the color-coded arrows along the lower axis of the upper panel. For near-shore Lake Superior, the highest K_d is in the red and the lowest K_d is in the green.

Since K_d is an exponential rate constant, it is often difficult for the general public to embrace it as an estimate of water column transparency. A more generally understandable parameter is the 1% attenuation depth for light. This parameter is the depth in the water column at which 99% of the surface irradiance has been attenuated. This parameter is useful in that for PAR it approximates the compensation depth, a depth at which daily photosynthesis = respiration, above which there is net oxygen production, and below which there is net oxygen consumption. The 1% attenuation depth for any given wavelength or wavelength range can be calculated as

$$z_{1\%} = \frac{4.61}{K_d} \tag{12}$$

where $z_{1\%}$ is the 1% attenuation depth (m) and K_d is the diffuse attenuation coefficient (m^{-1}). The value 4.61 is the $-\ln(1\%)$. Lower values of K_d correspond to higher water column transparency. In Lake Superior (as well as many other aquatic systems) the low transparency in the UV is due to the presence of CDOM which in this case accounts for more than 70% of the lake water absorbance at 370 nm (Mouw et al., 2017). The relationship between K_d and λ generally follows the relationship between the absorption coefficient (a) and λ observed in different concentrations of CDOM (Fig. 5).

The transparency of PAR in aquatic ecosystems can vary tremendously. Fig. 8 shows the vertical penetration of PAR in five lakes that span a range of transparency typically found in aquatic systems. In extremely clear Lake Correntoso, $z_{1\%}$ is in excess of 45 m while 99% of PAR is attenuated in the first meter of Little Echo Lake, which has moderate concentrations of chlorophyll a (~6 mg L^{-1}) and a high concentration of CDOM (~23 mg C L^{-1}).

One method of estimating the transparency of visible light (PAR) in aquatic systems is the Secchi disk. First used in the 1860s, the black and white Secchi disk (20 cm diameter) is lowered through the water column on a calibrated line. The depth at which the disk disappears is termed the Secchi depth (z_{sd}).

Although the Secchi depth can vary between users, light conditions, and surface conditions, generally the $z_{1\%}$ for PAR corresponds to approximately 2–3 times z_{sd}. The value of Secchi measurements lies not in its accuracy, but in its ease of use and the extremely long records of transparency based on this simple and inexpensive device.

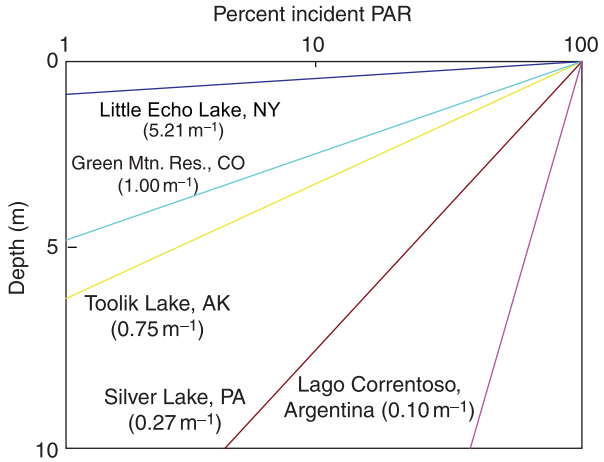

Fig. 8 Penetration of PAR for lakes with widely differing transparency. Diffuse attenuation coefficients are provided for each lake (K_d).

Conclusion

In conclusion, light is critical in structuring aquatic ecosystems. Seasonal variations in the heat energy provided by sunlight are responsible for thermal stratification and mixing regimes so fundamental to aquatic systems. The energy of sunlight used in photosynthesis forms the foundation of all but the simplest microbial communities on Earth. Thus, an understanding of the nature of light, and how it interacts with the atmosphere and the water column, is fundamental to our understanding of how aquatic ecosystems function.

Acknowledgment

CEW acknowledges support from NSF OPUS DEB 1950170.

See Also: Fundamental concepts and theories: Diel Vertical Migration; Ecosystem Engineers in Freshwater Ecosystems; Light as an Ecological Resource; Structures and functions of Inland Waters - Groundwater: Biogeochemical Cycling of Carbon and Nitrogen in Groundwater—Key Processes and Microbial Drivers; Structures and functions of Inland Waters - Lakes: Benthic Algae in Lake Littoral Habitats; Biophysical Interactions in Phytoplankton; Lakes as Recorders of Earth Surface Dynamics From Yearly to Plurimillennial Time-Scales; Measurement and Variability of Lake Metabolism; Structures and functions of Inland Waters - Rivers: Algae and Primary Production of Streams and Rivers Ecosystems

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Further Reading

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Ultraviolet Radiation☆

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This is an update of C.E. Williamson, P.J. Neale, Ultraviolet Light, in Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00076-4.

Glossary

1% Attenuation Depth (m) The depth to which 1% of subsurface irradiance of a given wavelength penetrates in the water column. Using subsurface measurements gives a surface reference that excludes albedo and thus more accurately reflects water transparency. When estimated from epilimnetic diffuse attenuation coefficients the attenuation depths may be somewhat greater than the actual attenuation depths due to higher absorptivity of the deeper hypolimnetic waters.

Biolabile The degree to which a compound such as dissolved organic matter is available for biological uptake, usually by microbes.

Chromophore A molecular structure that absorbs photons, usually in a wavelength selective fashion.

Diffuse attenuation coefficient ($K_{\lambda d}$, m^{-1}) Exponential rate of decrease of subsurface irradiance with depth which varies by wavelength.

Dobson Unit (DU) A measure of total column content of a gas, frequently used for ozone. The thickness of the layer (in 10's of μm's) of the total mass of the gas in the column at standard temperature and pressure (STP, 0 °C, 1 atm). For example, 300 DU = 3 mm of ozone at STP.

Dose ($J\ m^{-3}$ or $J\ g^{-1}$) Total radiant energy in a given wavelength range absorbed by a specific chromophore (per volume or per mass). Compare exposure.

Dose Rate ($W\ m^{-3}$ or $W\ g^{-1}$) Measure of the radiant energy absorbed per unit time ($J\ s^{-1}$) by a specific chromophore (per volume or per mass). Compare irradiance.

Erythemal UV index (UVI) A derived unit that expresses the potential for sunburn in Caucasian humans estimated by multiplying the solar irradiance spectrum by the CIE action spectrum for sunburn (McKinlay and Diffey, 1987) and multiplying by 40 (for irradiance in $W\ m^{-2}\ nm^{-1}$).

Irradiance (E or E_λ, $W\ m^{-2}$, or $W\ m^{-2}\ nm^{-1}$) Measure of the radiant power within a wavelength range or at a given wavelength, λ, incident per unit area on a surface; exposure rate. Compare dose rate. Fluence rate is the analogous term for radiant power (energy received per unit time, $J\ s^{-1}$) from all directions to a point.

Photobleaching The removal of a chromophore in a chemical compound induced by the absorption of photons.

Photodegradation Photochemical transformation of a molecule into lower molecular weight fragments, usually by oxidation (photooxidation).

☆*Change History*: March 2021. CE Williamson and PJ Neale updated the abstract, text and further readings. Figure 4 was revised with updated information.

Photolabile The degree to which a chemical compound is susceptible to being broken down by photolysis.
Photolysis The cleavage of chemical bond induced by the absorption of photons.
Photooxidation Oxidation reactions induced by absorption of photons.
Radiant Exposure (H or H_λ, J m^{-2}, or J m^{-2} nm^{-1}) The total amount of radiant energy within a wavelength range or at a given wavelength, λ, incident on a surface. Compare dose. Fluence is the analogous term for radiant energy received from all directions to a point.
Reactive oxygen species (ROS) Potentially damaging highly reactive forms of oxygen such as hydrogen peroxide, superoxide or hydroxyl radicals, or singlet oxygen.
Spectral slope (S, nm^{-1}) The slope of the plot of the natural log of the absorbance versus wavelength for a specified wavelength range such as all UV (280–400 nm), UV-A (320–400 nm), or UV-B (280–320 nm).
Total column ozone The amount of ozone in the entire atmospheric column over a given area, expressed in Dobson Units.
Zenith The point in the sky directly overhead from the location of interest.

Introduction

The important role of UV in inland aquatic ecosystems went largely unrecognized for many years because it was believed that incident solar UV was rapidly absorbed within the surface waters. Although a few early studies demonstrated that UV penetrated many meters into the water column of highly transparent lakes, these studies were unappreciated. Instrumentation for measuring underwater UV was not widely available for many years and few measurements were made of UV attenuation in inland waters. This all changed following the discovery of severe ozone depletion in Antarctica (the "ozone hole") in the mid-1980s and subsequent evidence for ozone depletion and elevated UV exposure in the Arctic and even temperate latitudes. Submersible UV radiometers became more widely available to study this disturbing global UV trend and recognition of the importance of UV in inland waters has increased in recent decades.

While ozone is the major UV-absorbing substance in the atmosphere, colored, or chromophoric dissolved organic matter (CDOM) is the primary UV-absorbing substance in most inland waters. Variations in CDOM concentrations in inland waters contribute far more to the regulation of underwater UVR than variations in atmospheric ozone. The strong CDOM-driven gradients in UV transparency in inland waters lead underwater UV exposure to vary by orders of magnitude across water bodies. High elevation alpine waters often exhibit the highest levels of underwater UV exposure due largely to low CDOM concentrations, while lowland waters with extensive wetlands in their watersheds that contribute to high CDOM production have lower UV transparency. The sensitivity of UV transparency of inland waters to CDOM changes related to natural and anthropogenic disturbances makes UV transparency a good sentinel of environmental change. Climate warming and other disturbances including UV can in turn alter concentrations and quality of CDOM in inland waters and contribute to strong temporal and spatial gradients in underwater UV exposure. It is these strong and dynamic gradients in underwater UV exposure and the sensitivity of UV transparency to environmental change that drive the need to understand the causes and consequences of UV exposure in inland waters.

Main topics/concepts

Wavelengths and units of measurement

Ultraviolet radiation can be separated according to wavelengths into UV-C (200–280 nm), UV-B (280–320 nm) and UV-A (320–400 nm). The Commission Internationale de l'Eclairage, CIE (International Commission on Illumination) uses 280 nm to separate UV-C and UV-B, 315 nm to separate UV-B and UV-A, and 400 nm to separate UV-A and photosynthetically active radiation (PAR). Some investigators use 290 nm and 320 nm as breakpoints. Here we adopt the 280 and 320 nm wavelengths to separate out the types of UV as these are most commonly used in aquatic studies (Hargreaves, 2003; Hargreaves et al., 2007; Kirk, 2011). While PAR is most commonly measured in quantum units (moles of photons), UV is more commonly measured in energetic units. Radiant flux of UV is measured in Watts (J s^{-1}), radiant exposure (dose or fluence) in J m^{-2}, and irradiance (dose rate, fluence rate, or radiant flux density) in W m^{-2}.

Atmospheric controls on incident UV in inland waters

The amount of solar UV radiation incident on inland waters is influenced by sun angle, elevation, cloud cover, and atmospheric aerosol and ozone concentrations. Sun angle (usually measured from the zenith, directly overhead), is the most important determinant of UV exposure due to two primary mechanisms. The length of the slant path through the atmosphere is a function of zenith angle. Longer paths through the atmospheric increase absorption and scattering. In addition, at higher angles the incident beam is projected over a larger area. Changes in sun angle drive the diurnal and seasonal variation in UV (Fig. 1), and most of the UV variation with latitude. Aerosols and clouds are the most important factors affecting the day-to-day variation in incident UV (Fig. 1), primarily by scattering radiation back to space. Aerosols scatter the shorter UV wavelengths more efficiently than visible light, so UV can be substantially lowered by "hazy" conditions even under apparently "sunny" conditions. Under most conditions, aerosol and

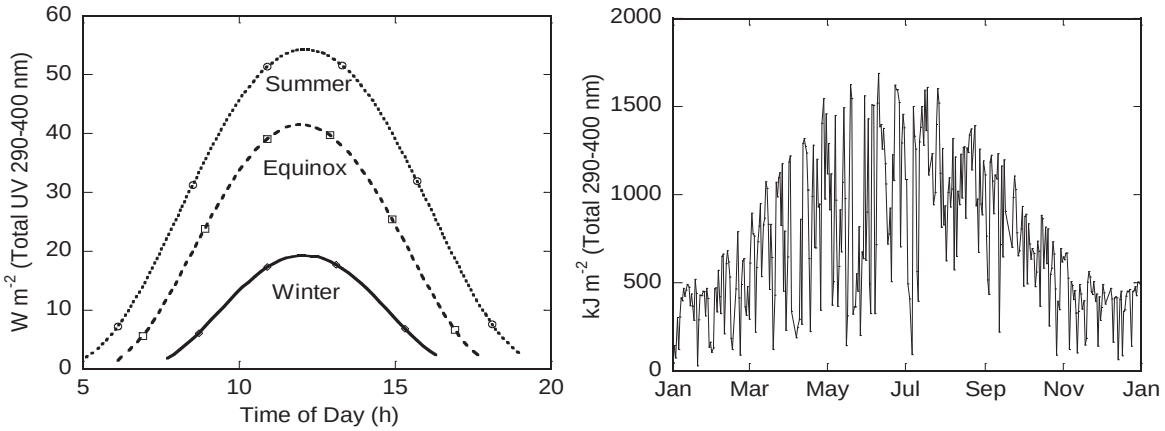

Fig. 1 Example plots for diurnal and annual variation in total UV radiation (290–400 nm) for summer and winter solstices and equinoxes (left panel, fall shown, spring is similar) at a temperate location (Edgewater, MD, United States, ~39°N latitude). The diurnal curves show maximum (clear sky) irradiance (W m^{-2}) calculated using a radiative transfer model. The annual curve is for total daily UV (J m^{-2}) as measured at the Smithsonian Environmental Research Center (Edgewater, MD, United States) for 2003 (right panel). The annual range for total daily UV at this latitude is a factor of three, a similar range of variation occurs day-to-day due to variations in cloud cover, aerosols and ozone.

molecular (Rayleigh) scattering divert so many UV photons from a straight path (direct beam) that UV exposure is primarily from sky (diffuse) light. The ratio of diffuse to direct light increases with shorter wavelengths. This phenomenon leads to much more variability ("noise") in underwater vertical profiles of visible and long-wavelength UV than shorter-wavelength UV during wavy rather than calm conditions.

Clouds are less wavelength-selective than are aerosols, but can still have different effects on UV than visible light. This is another consequence of the higher diffuse/direct ratio in UV: clouds blocking the solar disc, but not the sky, have only a small effect on UV. Incident irradiance can actually exceed "clear sky" levels when high clouds not actually covering the sun act as reflectors. Uniform cloudiness, on the other hand, has about the same effect on UV as visible light, usually >50% overall reduction.

Ozone absorbance is the most wavelength selective of all atmospheric controls on UV, absorbing essentially all UV shorter than about 290 nm and having little effect for wavelengths longer than 330 nm. Because of existing concentrations of atmospheric ozone, only UV-A and UV-B components impinge on inland waters. Total column ozone in the atmosphere varies across Earth's surface and with season independent of any of the ozone depletion events reported in recent decades. Column ozone generally varies from about 240 Dobson units (DU) at the equator to over 440 DU near the North Pole. The seasonal variation in ozone is minimal at the equator with a range between 240 DU and 260 DU. At the North Pole ozone ranges more widely from 280 DU in September to over 440 DU in March. At the South Pole the seasonal variation in the absence of the ozone hole ranges from less than 300 DU in the austral fall to over 340 DU in the austral spring.

The combination of a sun angle closer to the zenith and the reduced ozone at the equator leads inland waters in tropical regions to be exposed to much higher UV levels than temperate, boreal, or polar systems. A major exception to this is in regions with severe ozone depletion. For example, the World Health Organization uses an erythemal UV index that ranges from 1 to 18 to reflect potential biological damage (sun burn in this case). This UV index generally ranges from 4 to 10 in temperate zones and from 10 to 16 in the tropics. During ozone hole events total column ozone in Antarctica can be depleted to levels less than 100 DU. Although UV indices around Antarctica are typically low at all times due to the southerly location, it increases from 1–3 to 4–6 in coastal locations under ozone-depleted air masses and values as high as 12 have been observed.

The potential for increased exposure to damaging UV as a consequence of ozone depletion inspired the Vienna Convention for the Protection of the Ozone Layer in 1985 and the Montreal Protocol on Substances that Deplete the Ozone Layer in 1987. These international agreements were successful in reducing the levels of anthropogenic ozone-depleting substances in the atmosphere and subsequently the rate of stratospheric ozone depletion. The beginning of a significant long-term trend of recovery of ozone over Antarctica has now been documented. However, current concentrations of chlorine and bromine in the stratosphere are still adequate to catalyze depletion of nearly all of the ozone in the critical 14–21 km altitude layer of the polar vortex. Ozone depletion now varies greatly from year to year depending on the temperature of the stratosphere (which is being affected by climate change). The 2019 "ozone hole" was one of the smallest on record while 2020 had the 12th largest ozone hole observed over the past 40 years. Full recovery to the levels observed in the 1970s is not expected until the middle of the 21st century.

Environmental regulation of underwater UV exposure and impacts

Measuring UV transparency

Submersible radiometers are used to measure depth profiles of UV at various wavelengths. These profiles follow an exponential trend and thus appear as straight lines when plotted on a logarithmic scale in a semi-log plot (Fig. 2). The slope of this line, the rate of exponential decrease, is the diffuse attenuation coefficient ($k_{\lambda d}$, m^{-1}) which is specific to a given wavelength λ. Derived from the

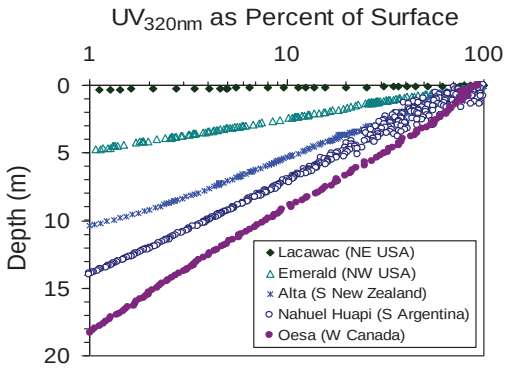

Fig. 2 Depth profiles for five selected lakes showing the wide variation in UV attenuation in inland waters. The intersection with the vertical axis shows the depth to which 1% of the subsurface 320 nm UV penetrates, referred to as the 1% attenuation depth ($Z_{320nm1\%}$). Wavelengths in the 320 nm range are among the most highly damaging solar radiation when you combine the solar spectrum with a biological weighting function to get the biologically effective exposure (see Fig. 9).

$k_{\lambda d}$ (often just k_d is used, but attenuation is strongly wavelength dependent) is the depth at which UV declines to 1% of the surface value, the 1% attenuation depth ($z_{\lambda 1\%}$, m), which is an overall measure of UV transparency for a given wavelength. For more general information about the derivations of $k_{\lambda d}$ and $z_{\lambda 1\%}$ see Kirk (2011).

Effects of CDOM on UV transparency

UV transparency can vary greatly among inland water bodies with the 320 nm 1% attenuation depths ranging from a few centimeters to well over 10 m (Fig. 2). This variation is largely a function of dissolved organic carbon (DOC), the optically active component of which is colored dissolved organic matter (CDOM) (Fig. 3). Environmental change, and "browning" of water due to observed increases in CDOM can similarly reduce UV transparency within a single water body leading to strong long-term changes in UV transparency (Fig. 4).

A wide variety of dissolved and particulate compounds contribute to the UV transparency and hence underwater UV exposure levels in inland waters. The most important of these is CDOM. Similar to ozone, CDOM selectively absorbs shorter wavelengths of solar radiation, leading to more rapid attenuation of shorter wavelengths in the water column (Fig. 5). CDOM also plays a major role in determining the depth of the surface mixed layer in small lakes and ponds which will in turn influence UV exposure of non-motile planktonic organisms in this stratum. During winter ice formation CDOM is excluded such that clear ice with few air bubbles is more UV transparent than unfrozen water. Air bubbles and snow cover dramatically decrease transmission of UV by ice. In lakes with anoxic hypolimnia the oxidation of ferrous iron to ferric iron may cause substantial increases in UV absorbance. DOM can complex with the iron and increase its retention in the surface waters, thus decreasing UV transparency.

CDOM in inland waters may come from autochthonous sources such as algae or macrophytes, but the primary source is generally allochthonous sources derived from the leaching and decomposition of terrestrial vegetation within the surrounding watershed. Peat-based wetlands can be particularly strong sources of allochthonous CDOM to associated water bodies. Allochthonous CDOM is generally composed of more refractory, higher molecular weight compounds that are more highly UV-absorbing and

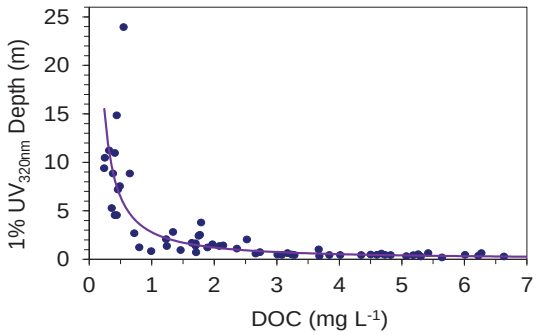

Fig. 3 Variation in UV attenuation among lakes as a function of DOC concentration. The depth to which 1% of 320 nm UV penetrates as estimated from diffuse attenuation coefficients is shown for a series of glacial lakes from the northern and southern hemisphere. Each data point represents one lake. Note the strong inflection point below about 1–2 mg L^{-1} DOC, indicating the high sensitivity of these low DOC lakes to small changes in DOC inputs. Modified from Fig. 1, page 1026 in Williamson CE, Stemberger RS, Morris DP, Frost TM and Paulsen SG (1996) Ultraviolet radiation in North American Lakes: Attenuation estimates from DOC measurements and implications for plankton communities. *Limnology and Oceanography* **41**: 1024–1034, Copyright (1996) by the American Society of Limnology and Oceanography.

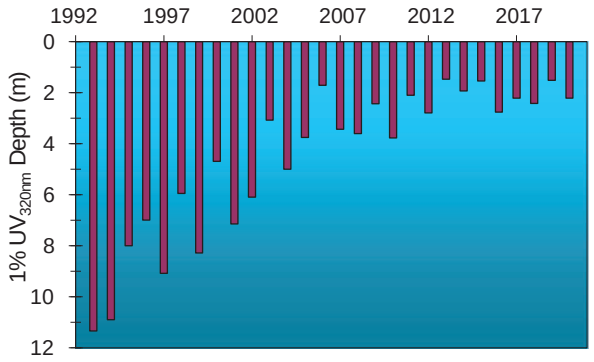

Fig. 4 Trends of changing UV transparency in an eastern Pennsylvania, United States lake in recent decades. The changes in the actual measured 1% 320 nm UV attenuation depth in Lake Giles are plotted for the past 27 years. These decreases in UV transparency over time are due largely to "browning," a phenomenon documented in lakes across large regions of northern Europe and northeastern North America where both the concentration and color of CDOM have been increasing over time.

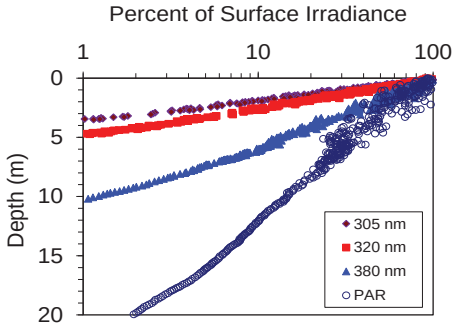

Fig. 5 Attenuation of 305, 320, and 380 nm UV and PAR in Lake Giles, NE Pennsylvania, United States showing the wavelength-dependent attenuation with depth in the water column that is characteristic of most lakes. In lakes with extremely low concentrations of CDOM such as Lake Tahoe, the 380 nm UV may actually attenuate less rapidly than longer wavelength PAR due to the peak transparency of pure water in the short wavelength blue which is close in wavelength to UV-A.

thus more photolabile. Autochthonous CDOM on the other hand is composed of smaller molecular weight compounds that are less UV-absorbing and correspondingly less photolabile but more biolabile. When exposed to solar UV radiation CDOM undergoes important photochemical changes that involve photolysis and photobleaching, rendering it less UV-absorbing and more aliphatic. Photobleaching of CDOM in combination with other seasonal changes in hydrologic inputs and biota can substantially increase the UV transparency of inland waters during the summer months (Fig. 6). In endorheic hypersaline lakes the long residence time of CDOM leads it to be strongly photobleached and much less UV absorbing.

Effects of elevation, plankton, and particulates on UV transparency

Living organisms in alpine waters are exposed to particularly high levels of UV radiation. Shorter wavelength UV-B (300 nm) may increase by as much as 24% per 1000 m in elevation due to the shorter pathlength through the atmosphere. The low densities of terrestrial vegetation in alpine ecosystems also reduce the inputs of UV-absorbing CDOM into alpine waters (Fig. 7). The timing of ice-out in alpine environments is often close to summer solstice, thus exposing aquatic organisms to maximum UV levels at very low temperatures that slow down DNA repair enzymes.

In extremely low DOC alpine systems and in higher DOC hypereutrophic, algal-rich systems phytoplankton may play an important role in regulating UV transparency. While zooplankton are known to increase visible transparency in lakes during seasonal "clear-water phases" through their grazing on phytoplankton, the contribution of zooplankton to seasonal increases in UV transparency is small relative to photobleaching of CDOM. In highly turbid systems like glacial lakes and shallow, wind-mixed reservoirs, suspended particulates may play a primary role in reducing UV transparency (Rose et al., 2014; Olson et al., 2018).

Mechanisms of UV damage in aquatic organisms

UV can cause substantial damage to a wide variety of aquatic organisms ranging from viruses, bacteria, and phytoplankton to zooplankton, fish, and amphibians (Peng et al., 2016; Alves and Agusti, 2020). Direct and indirect mechanisms of UV damage influence critical cellular processes in aquatic organisms ranging from DNA replication and transcription to cell survival, growth, motility, photosynthesis, orientation, and nutrient uptake. The relative importance of overall exposure versus irradiance (often

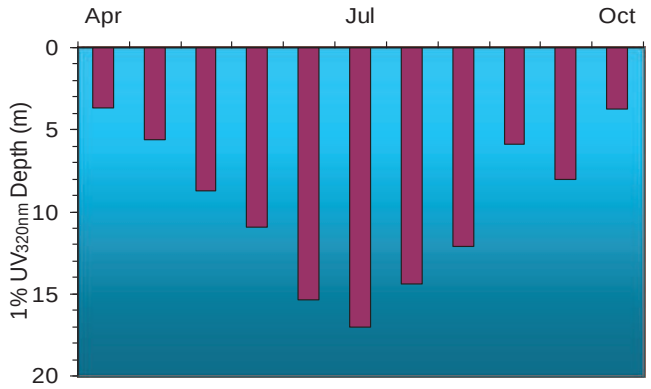

Fig. 6 Seasonal variation in UV transparency in Lake Giles, a low DOC lake in northeastern Pennsylvania, United States. These seasonal changes are largely driven by photobleaching, with minimal change in DOC concentrations. Values are expressed as the 1% attenuation depth for 320 nm UV from epilimnetic diffuse attenuation coefficients. Note the change in the 1% attenuation depth from 3 m in April to over 15 m in mid-July. This is an extreme example of the more subtle seasonal changes that are observed in most lakes. Actual depths to which UV penetrates may be somewhat less when UV penetrates into the hypolimnion where UV transparency may be lower. Modified with permission from Fig. 4 in Williamson CE, Hargreaves BR, Orr PS and Lovera PA (1999) Does UV play a role in changes in predation and zooplankton community structure in acidified lakes? *Limnology and Oceanography* **44**: 774–783. Copyright (1999) by the American Society of Limnology and Oceanography.

Fig. 7 Watersheds of alpine Lake Alta in New Zealand with very little vegetation (left) and temperate lowland Lake Lacawac in the northeastern United States with abundant vegetation (right). The amount of vegetation in the surrounding watershed is a key source of CDOM inputs and thus variations in UV transparency among inland waters.

referred to imprecisely as "dose" and "dose rate" respectively, see glossary) in causing UV damage is a major concern. The reciprocity principal argues that damage is a function of total dose and independent of dose rate. However, the presence of active repair processes generally invalidates the reciprocity principle because repair of UV damage permits high survival rates over long periods of low exposure. Short-term periods of exposure to high dose rates of UV often have a much more severe effect on organism survival ("one bad day" hypothesis).

Primary mechanisms and targets of UV damage

There are two primary mechanisms of UV damage to living organisms at the subcellular level: damage by direct absorption of UV by a molecule or complex, and damage through the production of reactive oxygen species (ROS). Biomolecules that absorb the shorter wavelength, higher energy UV are most susceptible to direct damage. DNA and RNA are the two most highly UV-absorbing biomolecules, and due to its lower turnover rate in the cell, DNA is considered the primary target of UV damage. The primacy of DNA damage has given rise to the use of DNA dosimeters to assess DNA damage in the environment. These are small quartz tubes with DNA solutions that provide an assessment of potential DNA damage to aquatic organisms by examining the UV-induced photoproducts in the absence of repair processes that do occur in living cells. The primary photoproduct in UV-irradiated DNA is the cyclobutane pyrimidine dimer (CPD), followed by the pyrimidine (6–4)pyrimidone dimer [(6–4)PD]. While CPDs are the most abundant photoproduct (up to 80–90% of total photoproducts), the (6–4)PD photoproducts may be as much as 300 times more cytotoxic than the CPDs due to their effectiveness at blocking DNA polymerase.

The second major type of UV damage results from the production of ROS that cause cell damage, like hydrogen peroxide, singlet oxygen, and hydroxyl and superoxide radicals. The lower energy, longer wavelengths of UV are largely responsible for ROS production both in organisms and the surrounding water. Damage from ROS may be at sites within the organism that are remote from the site of UV exposure. The short half-life of most UV-induced ROS prevents them from accumulating in inland waters. The exception is hydrogen peroxide with a half-life on the order of a few hours to a day.

UV damage to proteins and lipids

UV can influence protein metabolism through inhibition of nitrogen uptake and thus the rate of protein synthesis. The absorption of UV by aromatic amino acids makes many proteins susceptible to UV damage including nitrogenase, the enzyme responsible for nitrogen fixation. Structural proteins can be damaged by UV due to the disruption of covalent sulfur bonds that are important in tertiary protein structure. UV damage of proteins in the lens of the eye can lead to cataracts in aquatic organisms as in humans. Damage to proteins is also thought to be the major reason for inhibition of photosynthesis by UV through largely UV-A damage to photosystem II and the RUBISCO pathway. The double bonds in many lipids also absorb UV and combined with lipid peroxidation can damage lipid-rich membranes.

Importance of spectral composition

The division of UV into the three bands gives a rough indication of biological threat—increasing from A to C. The biological effect varies almost continuously with wavelength for several reasons. The energy of a photon is inversely proportional to its wavelength (Planck's Law). Thus UV-C is the highest energy and has the greatest effect per photon while UV-A has the least. The effectiveness of short wavelength UV, however, increases more rapidly with decreasing wavelength than the increase in photon energy because biomolecules have higher absorbance at shorter wavelengths. Thus effectiveness typically rises exponentially with decreasing wavelength, with the slope and shape varying for different effects (Fig. 8). Processes driven by DNA damage have a characteristically different shape than when damage is also induced by production of ROS. Effectiveness curves are termed biological weighting functions (BWFs), and must be considered when comparing responses to exposures that differ in spectral composition such as experiments with artificial lamps versus natural solar exposures (Fig. 9).

Mechanisms to reduce UV damage

There are three possible levels of response of aquatic organisms to reduce UV damage in nature: behavioral avoidance, photoprotection by sunscreens or antioxidants, and molecular repair following the damage.

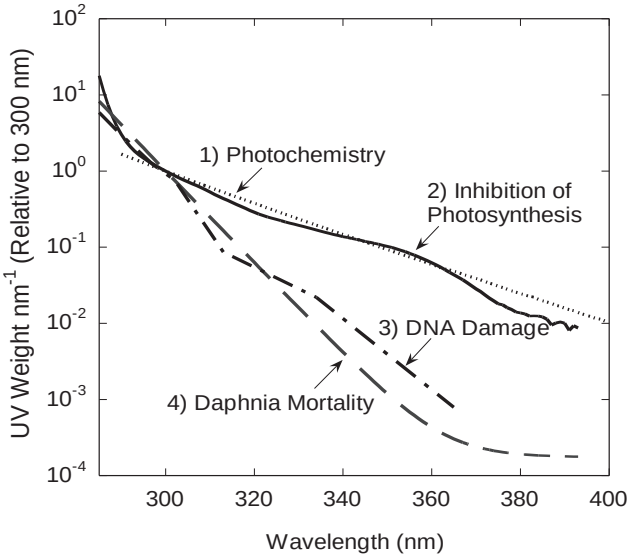

Fig. 8 Photochemical weighting function for production of hydrogen peroxide (ROS that contribute to CDOM photobleaching) (1), and biological weighting functions (BWFs) for the effect of UV on inhibition of photosynthesis, average for natural populations of phytoplankton (2), DNA damage in alfalfa seedlings (3), and mortality of *Daphnia* (4). Note the shape is different when ROS are important (1 and 2) versus when DNA damage is important (3 and 4). The weights have been normalized to 1 at 300 nm. Data sources are (1) and (2) Neale PJ and Kieber PJ (2000) Assessing biological and chemical effects of UV in the marine environment: Spectral weighting functions, In RE Hester and RM Harrison [eds.], *Causes and Environmental Implications of Increased UV-B. Radiation. Issues in Environmental Science and Technology*. pp. 61–83, Royal Society of Chemistry. (3) Quaite FE, Sutherland BM and Sutherland JC (1992) Action spectrum for DNA damage in alfalfa lowers predicted impact of ozone depletion. *Nature* **358**: 576–578. (4) Williamson CE, Neale PJ, Grad G, De Lange HJ and Hargreaves BR (2001) Beneficial and detrimental effects of UV radiation on aquatic organisms: Implications of variation in spectral composition. *Ecological Applications* **11**: 1843–1857.

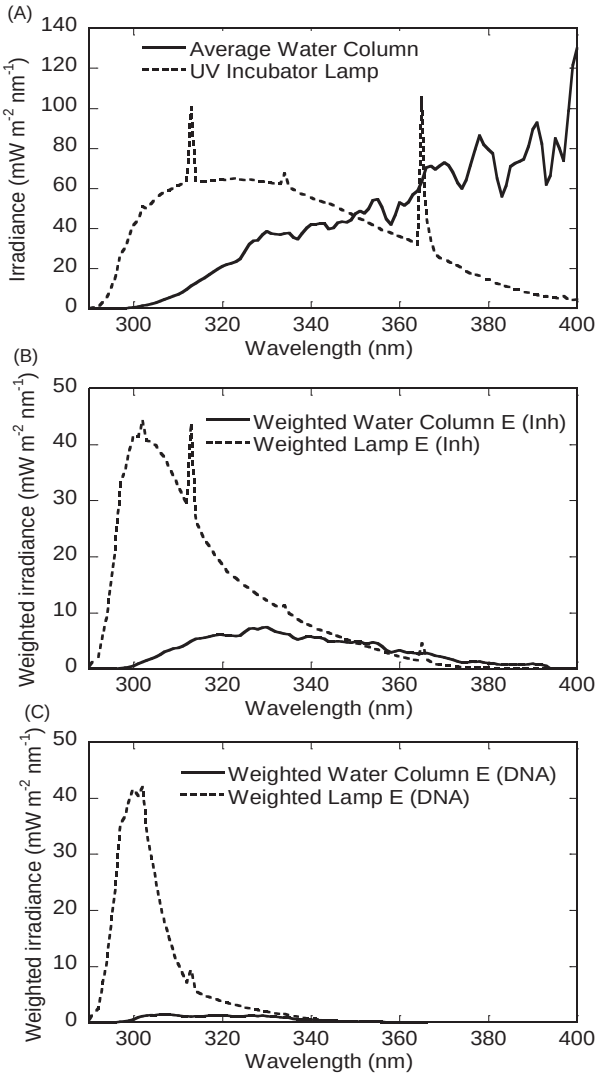

Fig. 9 Spectral distribution of UV (280–400 nm) in a UV incubator (Phototron) using fluorescent lamps (combination of Spectronics XX15-B and UVA-340, Q-Panel) and the average spectral irradiance in a shallow water column (1.5 m deep) (Rhode River, MD, United States, near summer solstice, noon, 40°N latitude). (A) unweighted radiation; (B) radiation weighted by the BWF for inhibition of photosynthesis in natural phytoplankton populations; (C) radiation weighted by the BWF for DNA damage in alfalfa. The BWFs are shown in Fig. 8. Total (280–400 nm) UV is the same for the unweighted spectra, but the lamps emit a greater proportion of more damaging UV-B, so that the weighted irradiance in the incubator is >3 times higher for inhibition of photosynthesis and >11 times higher for DNA damage compared to water column irradiance. Source for spectra: Rhode River—Litchman E and Neale PJ (2005) UV Effects on photosynthesis, growth and acclimation of an estuarine diatom and cryptomonad. *Marine Ecology Progress Series* **300**: 53–62.; Williamson CE, Neale PJ, Grad G, De Lange HJ and Hargreaves BR (2001) Beneficial and detrimental effects of UV radiation on aquatic organisms: Implications of variation in spectral composition. *Ecological Applications* **11**: 1843–1857.

Behavioral avoidance of UV damage

Behavioral avoidance of UV requires the ability to detect UV (photoreceptors sensitive to UV) as well as the ability to avoid UV (motility). A wide range of aquatic organisms do have UV photoreceptors including some bacteria, phytoplankton, protozoa, annelids, mollusks, crustaceans, and fish. Negative phototaxis to longer wavelength PAR may also be effective in UV avoidance. However, the selective absorption of the short-wavelength damaging UV-B irradiation by ozone and DOM create wide variations in UV:PAR ratios. The disproportionate increase in damaging UV-B with decreasing wavelength may lead to UV damage under scenarios of ozone depletion or reduced DOM if organisms cannot detect and avoid UV ("solar ambush" hypothesis). Exposure to UV-B can also damage both motility and orientation behavior, rendering any potential phototactic avoidance less effective.

Several species of zooplankton and fish can detect and avoid UV. *Daphnia* have UV photoreceptors with peak absorption at 348 nm and can avoid damaging UV in situ by downward migration. The larval and juvenile stages of some species of fish have photoreceptors with absorption peaks in the UV-A range. Laboratory studies have demonstrated that these UV-A photoreceptors

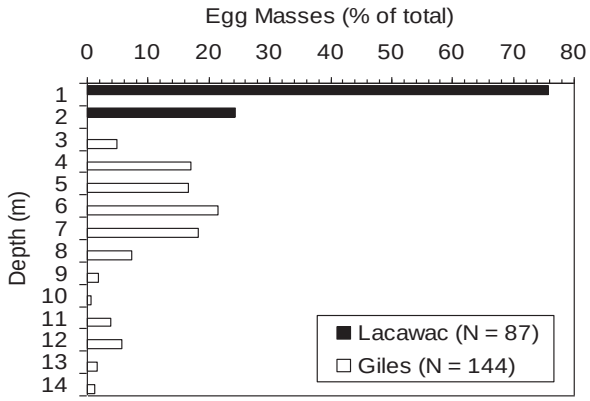

Fig. 10 Spawning depth of yellow perch (*Perca flavescens*) in two lakes in the same geographic area, one of high (Giles) and one of low (Lacawac) UV transparency. Note that all eggs in Lake Giles were spawned deeper than 2 m, while in Lake Lacawac all eggs were spawned at depths shallower than 2 m. It is not known whether the deeper spawning in the high UV lake is a result of UV avoidance behavior or differential survival coupled with strong fidelity to spawn at natal sites. Deposition of eggs in the deeper, colder waters may slow development and hatching and consequently reduce the time available for perch to reach the critical size needed to survive the following winter. Modified with permission from Fig. 3 in Huff DD, Grad GG and Williamson CE (2004) Environmental constraints on spawning depth of yellow perch: The roles of low temperature and high solar ultraviolet radiation. *Transactions of the American Fisheries Society* **133**: 718–726.

may enhance feeding in larval fish, and field experiments have demonstrated the ability of juvenile Coho salmon (*Oncorhynchus kisutch*) to avoid solar UV in shallow streams. Yellow perch (*Perca flavescens*) spawn deeper in more UV transparent lakes, but it is not clear that this is a behavioral response (Fig. 10).

Protection against UV damage: Sunscreens and defense compounds

There are two major types of UV photoprotective compounds: sunscreens that absorb UV radiation directly and antioxidants that reduce damage from ROS. Some compounds serve both functions. Sunscreens are less effective in very small organisms such as bacteria where the pathlength of a UV photon is too short to be effectively absorbed before causing damage. Photoprotective compounds present in aquatic organisms include carotenoids, mycosporine-like amino acids (MAAs), and melanin. Carotenoids have absorption peaks in the short-wavelength blue range but this absorption extends into the UV, thus allowing absorption and dissipation of UV energy as heat. Carotenoids are also important quenching agents that react with ROS to reduce levels of cellular damage. Environmental concentrations of carotenoids are not consistently correlated with UV exposure, and plant-derived carotenoids in zooplankton may actually reach their highest concentrations in colder waters under non-peak UV conditions, suggesting that their function is not only one of photoprotection.

Mycosporine-like amino acids (MAAs) are photoprotective compounds with absorption peaks generally in the 310–360 nm range; with some functioning also as antioxidants. The MAAs derive their name from fungi where they were initially discovered to be abundant during sporulation. Fungi, bacteria, and algae are the only groups that can synthesize MAAs because they have the shikimate pathway, a biochemical pathway related to the pathway used to produce photoprotective flavonoid compounds in higher plants. Animals must acquire MAAs through their diet. The production of MAAs is photoinducible and MAA concentrations in both phytoplankton and zooplankton are known to be correlated with environmental UV exposure.

Among the crustacean zooplankton, cladocerans generally have low concentrations of carotenoids and MAAs but a few species do utilize melanin. Copepods have little melanin but depend heavily on carotenoids and MAAs. In marine copepods, and thus by inference in freshwater copepods, ingestion of MAAs may increase fitness. Though some fish use melanin for photoprotection, especially in juvenile stages, it is often lacking in their epidermal layers. Melanin is common in the epidermis of many amphibians, particularly in early developmental stages such as eggs and larvae. Some fish secrete UV-absorbing compounds in their mucus while others have UV-reflective guanine-based compounds in their scales.

Several common antioxidant enzymes and vitamins in algae are capable of reducing oxidative damage from ROS produced during UV exposure, but little is known about how widespread this process is in other aquatic organisms. These compounds include superoxide dismutase (SOD), glutathione peroxidase, ascorbate peroxidase, catalase, vitamin E (α-tocopherol) and vitamin C (ascorbic acid).

Molecular repair of UV damage

UV-induced DNA lesions can be repaired by a variety of molecular processes including photoenzymatic repair (PER, also referred to as photorepair or photoreactivation), nucleotide excision repair (NER), and base excision repair (BER). PER is mediated by a single enzyme, photolyase, which requires UV-A or visible light for activation. Thus, PER is often referred to as "light repair". PER is specific to damage induced by UV and is present in a wide range of organisms but not all species. NER and BER on the other hand are not

specific to UV damage and are universal among all organisms. NER is often referred to as "dark repair" because it does not require UV-A or visible light but rather depends on the metabolic energy of ATP. In bacteria the recA gene codes for a protein that promotes DNA recombinational repair. Exposure to UV transforms the recA derived protein into a proteinase that destroys a repressor and subsequently enables the expression of a suite of DNA repair genes. Because these DNA repair processes are enzyme-dependent, they are often less effective at lower environmental temperatures.

Interactive and indirect effects of UV in aquatic ecosystems

Perhaps the most compelling role of UV in inland waters is not the potential for direct damage, but how it interacts with other important limnological and ecological stressors across gradients of UV transparency. Organisms that respond to UV by behavioral avoidance may be forced into habitats where temperature, food, or potential predators are suboptimal. For example, migration by zooplankton or egg deposition by amphibians and fish into deeper, cooler waters may reduce rates of growth and reproduction, or expose them to higher levels of tactile invertebrate predators.

Aquatic organisms ranging from bacteria and phytoplankton to zooplankton and fish have UV photoreceptors and can use UV as an environmental cue. Coral reef fish use UV in mate selection, but this has yet to be investigated in freshwater fish. Similarly, in the African Rift lakes there is evidence that a narrowing of the spectral transmission of water due to pollution has influenced mate selection and contributed to the decline of the species richness of African Cichlids. The transparency loss is primarily in the UV range but its importance has not been investigated.

Variation in UV tolerance among organisms at different trophic levels may alter aquatic food webs. For example, UV exposure can inhibit uptake of critical nutrients such as N and P as well as alter the concentrations and quality of pigments, proteins, lipids, and fatty acids in phytoplankton with important consequences for their productivity and nutritional quality to zooplankton grazers. Zooplankton that respond to UV by increasing their concentrations of dietary photoprotective compounds may increase their susceptibility to visual predators. In shallow lakes and ponds UV-sensitive tactile predators such as *Chaoborus* may benefit from the refuge from underwater exposure to UV caused by increases in CDOM, thus permitting them to decimate certain of their prey species. While bacteria in surface waters can suffer direct damage from UV, the generation of biolabile DOM by UV photolysis may enhance bacterial productivity, which can also be enhanced by increased release of DOM by phytoplankton subjected to UV stress.

UV exposure of a variety of anthropogenic pollutants such as polycyclic aromatic hydrocarbons (PAH) can enhance their toxicity. The primary mechanism of this phototoxicity is the production of ROS by the photosensitizer (PAH or other), with subsequent biological damage such as lipid peroxidation by the ROS. The phototoxicity of PAHs such as pyrene, fluoranthene, and anthracene is driven much more by UV-A, even though some absorb both UV-B and UV-A, due to the greater number of UV-A versus UV-B photons present in incident solar radiation, and the more rapid attenuation of UV-B versus UV-A in the water column. Due to the role of ROS, oxygen concentrations may alter phototoxicity. Diel variation in metal speciation and photodegradation of compounds such as methyl mercury suggest that UV may also play a role in the phototoxicity of heavy metals. Phototoxicity may also be ameliorated by complexation of contaminants with DOM, or enhanced by UV photolysis of CDOM and subsequent release of toxic compounds.

Climate change can alter the importance of UV in inland waters by modifying cloud cover, aerosols, stratospheric ozone, and CDOM inputs from the surrounding watershed (Williamson et al., 2019). Increases in dissolved CO_2 can also alter the sensitivity of algal photosynthesis to UV inhibition. Decreases in precipitation combined with increased temperatures reduce the saturation and inundation of soils with water, resulting in better oxygenation of soils and more complete decomposition of dead organic matter to inorganic C rather than CDOM. Consequent reductions in CDOM can dramatically increase the UV transparency of lakes (Williamson et al., 2016). UV spectral composition can be used as an assay to sort out whether these responses to climate change are due to alteration of autochthonous or allochthonous processes. The spectral slope (280–400 nm) is generally steeper for CDOM from autochthonous sources than for CDOM from allochthonous sources. Photobleaching of allochthonous CDOM produces a characteristic bending of the absorbance spectrum with a steeper slope at short wavelengths and shallower slope at longer wavelengths.

Conclusion/synthesis

Ultraviolet (UV) is short wavelength, high energy solar radiation that plays multiple different roles in inland waters. At high exposure levels, UV has sublethal and lethal effects on organisms ranging from bacteria, phytoplankton, and protozoa to zooplankton, benthic invertebrates, fish, and amphibians. While UV is mutagenic, carcinogenic, and can cause a variety of other damage in living organisms, small amounts of UV may actually be quite beneficial (Williamson et al., 2001). For example, a small amount of UV at potentially damaging wavelengths less than 315 nm is necessary for the synthesis of vitamin D, while longer wavelength UV activates DNA repair enzymes and serves as an environmental cue in mate selection and foraging behavior in fish as well as in the vertical migration of zooplankton. Solar UV exposure can kill parasites, pathogens, and vectors of disease such as mosquito larvae in surface waters, thus aiding in the disinfection of water supplies. UV also plays important roles in biogeochemical processes including carbon cycling and the ecotoxicology of heavy metals and pesticides. UV stimulates photodegradation as well as photobleaching of CDOM, contributing to seasonal variations in water transparency. While ozone is the primary regulator of UV in the atmosphere, variations in the quantity and quality of CDOM in inland waters are much more important regulators of

underwater UV exposure than atmospheric ozone. The strong CDOM-driven gradients in UV transparency in inland waters lead underwater UV exposure to vary by orders of magnitude across inland waters. High elevation alpine waters often exhibit the highest levels of underwater UV exposure, while lowland waters with inundated watersheds with high CDOM production have low UV transparency. The sensitivity of UV transparency of inland waters to CDOM changes related to natural and anthropogenic disturbances makes UV transparency a good sentinel of environmental change.

Knowledge gaps

- Data on the UV transparency of inland waters remain sparse, but are essential to elucidate the role of this high energy radiation in aquatic ecosystems.
- While we know a great deal about the negative effects of UV on aquatic organisms, most studies of UV effects on aquatic organisms have been in the laboratory. More field data under natural solar UV radiation are needed due to the critical importance of differences in the spectral composition of UV from artificial versus solar sources. Biological weighting functions are needed for more organisms as well due to the fact that wavelength matters to the biological response.
- While we know that UV can alter the balance of trophic interactions due to the differential effects of UV on different trophic levels, we still have only very limited appreciation for the net effects of UV at the community and ecosystem levels.
- The balance of the beneficial *vs.* detrimental effects of UV, and whether or not this balance varies across trophic levels is necessary to understand community and ecosystem level effects.
- The interactive effects of UV and other environmental factors such as temperature and pH have been demonstrated in many cases, but their net effects remain poorly understood.
- While UV has in several cases been demonstrated to have positive effects on certain zooplankton and other aquatic species, we still do not understand the underlying mechanisms of these positive effects. Do they relate to resolving vitamin D deficiencies, reducing parasites, pathogens, competitors or predators, or other mechanisms?
- While solar UV radiation has been repeatedly demonstrated to have the ability to kill parasites and pathogens, the relative sensitivity of hosts versus pathogens still needs to be elucidated in order to understand the net effects of UV exposure on host-parasite interactions and infectious diseases.

Acknowledgment

CEW acknowledges support from NSF OPUS DEB 1950170 and NSF LTREB 1754276.

See Also: Fundamental concepts and theories: Diel Vertical Migration; Ecosystem Engineers in Freshwater Ecosystems; Light as an Ecological Resource; Optical Properties of Water; Structures and functions of Inland Waters - Groundwater: Biogeochemical Cycling of Carbon and Nitrogen in Groundwater—Key Processes and Microbial Drivers; Structures and functions of Inland Waters - Lakes: Benthic Algae in Lake Littoral Habitats; Biophysical Interactions in Phytoplankton; Lakes as Recorders of Earth Surface Dynamics From Yearly to Plurimillennial Time-Scales; Measurement and Variability of Lake Metabolism; Structures and functions of Inland Waters - Rivers: Algae and Primary Production of Streams and Rivers Ecosystems

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http://www.epa.gov/sunwise/uvindex.html—United States Environmental Protection Agency (US EPA) UV Index Page—Provides UV Forecasts.

http://www.cpc.ncep.noaa.gov/products/stratosphere/uv_index/uv_current_map.shtml—United States National Oceanic and Atmospheric Administration UV Index Page—Provides UV Forecasts.

http://www.nasa.gov/vision/earth/environment/ozone_resource_page.html—United States National Aeronautics and Space Administration (NASA) Ozone Resources, Including Documenting Size of Ozone Holes.

The Chemical Properties of Water☆

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This is an update of J.H. Aldstadt, H.A. Bootsma, J.L. Ammerman, Chemical Properties of Water, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, https://doi.org/10.1016/B978-012370626-3.00008-9.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Dipole moment A measure of the polarity of a chemical bond between two atoms in a molecule, due to separation of positive and negative charges in a molecule. The dipole moment of water is 1.85 D (debye), or 6.17×10^{-30} C · m (coulomb-meter).
Heat of fusion The amount of energy required to transform a quantity of a substance from a solid state to a liquid state at a constant pressure.
Heat of vaporization The amount of energy required to transform a quantity of a substance from a liquid state to a gaseous state. It is a function of pressure and, to a smaller degree, temperature.
Hydrogen bond Non-covalent bond between water molecules, due to the electrostatic attraction between a hydrogen proton in one molecule and the electronegative oxygen in another molecule.
Major ion Cations (positively charged) and anions (negatively charged) that contribute the majority of salinity in water. In most aquatic systems, major ions are conservative, meaning their concentration is minimally affected by biological processes.
Nutrient From a limnological perspective, nutrients are elements such as nitrogen, phosphorus and iron required for the growth of algae and photosynthetic cyanobacteria. Note that this differs somewhat from the description of the term when applied to animal nutrition, in which case it can include organic compounds that serve as an energy source.
Solvation The process by which solvent molecules (such as water) surround and interact with solute ions or molecules. Solvation of a solute by water is referred to as hydration.
Surface tension Attractive force exerted on the surface molecules of a liquid by underlying molecules, making the liquid assume a shape that results in minimal surface area. Measured as the energy required to increase the surface area of a liquid by a unit of area.

> Water is H_2O, hydrogen two parts, oxygen one, but there is also a third thing, that makes it water and nobody knows what that is. D.H. Lawrence (1929).

Introduction

Water is the most abundant molecule on Earth. In spite of being so common, water is quite unusual—from its high melting and boiling points to its tremendous solvating power, high surface tension, and the largest dielectric constant of any liquid. In this chapter, we present an overview of the chemical properties of water and their implications for aquatic ecosystems. The phrase "chemical property" is context-dependent, which we define in general as a description of the way that a substance changes its

☆*Change History:* November 2020. H. Bootsma updated and revised the text in the "Dissolved Gases", "Major Ions", and 'Nutrients" sections. Minor edits made in the "Structure of Water" section for clarification. Revised and updated Figs. 8 and 9. Updated the "Further Reading" section with two references: Nilsson and Pettersson (2015), and Tainter et al. (2011). Added a glossary.

identity in the formation of other substances. A universally accepted set of chemical properties does not exist in the same way that there is, more or less, a standard set of physical properties for a given substance. Whereas a given substance has intrinsic physical properties (such as melting point), by our definition chemical properties are clearly tied to change. In addition to reactivity, a substance's "chemical properties" also typically include its electronegativity, ionization potential, preferred oxidation state(s), coordination behavior, and the types of bonding (e.g., ionic, covalent) in which it participates. Because these properties are extensively studied in general chemistry courses, we will not further discuss them here. Rather we move beyond the basic general chemistry concepts and focus upon water in a limnologic context—particularly, its bulk fluid structure and aspects of its chemical reactivity in the hydrosphere.

In the following pages, we begin by briefly reviewing the molecular structure of water, and then discuss models for its structure in "bulk" solution. We then turn our attention to the hydration of ions and an overview of important reactions that involve water, including acid-base, complexation, precipitation, and electron transfer. We conclude with a discussion of trends and patterns in the chemical composition of freshwater that are fundamental to the field of limnology.

The structure of water

Knowledge of the structure of water is the basis for understanding its unique chemical and physical properties. Like the other non-metallic hydrides of the elements of Group 16 in the periodic table, water is a triatomic molecule that forms a non-linear structure. In terms of group theory (which is used to explain the physical properties of a molecule based on its properties of symmetry), water has two planes of symmetry and a twofold rotation axis, and is therefore assigned point-group C_{2v}. The H—O—H angle is 104.5 degrees, formed as a result of the distortion of the O—H bond axes by the two pairs of non-bonding electrons on the oxygen atom. Although water is often described as having four sp^3-hybridized molecular orbitals in a slightly distorted tetrahedral geometry, models based solely upon that configuration fail to accurately predict the properties of liquid water, particularly the extent and influence of hydrogen bonding on the structure of the bulk fluid state. However, a tetrahedral geometry is in fact present in the solid state, giving rise to the sixfold axis of symmetry that is characteristic of ice, and in large part is the basis of the networks that form in the bulk liquid, though in a rapidly fluctuating dynamic state.

Models for the bulk fluid structure of water are a function of the non-covalent van der Waal's forces that exist between water molecules. There are five major types of van der Waal's forces that occur between neutral molecules and ions in solution: (a) London (or dispersion) forces, in which transient dipoles form by variations in electron density between neutral molecules; (b) Debye forces, in which the dipole of a molecule induces the formation of a dipole in an adjacent neutral molecule; (c) Keesom forces, which form between neighboring dipoles; (d) Coulombic forces, the electrostatic attraction (and repulsion) of ions; and (e) hydrogen bonds, which involve the electrophilic attraction of a proton to electronegative atoms such as oxygen and nitrogen. All of these forces are present in aqueous solution to varying degrees—hydrogen bonding being the most dominant. The high negative charge density of the oxygen atom relative to the high positive charge density of the hydrogen atom creates a large (1.84 D) electric dipole moment for the water molecule (Fig. 1). Because of the large dipole moment, the partial positive charge on the H atom is attracted to electron density, while the partial negative charge on the O atom causes the attraction of electrophilic H atoms. In this way, hydrogen bonds are formed, representing the strongest of the van der Waal's forces that exist between neutral molecules. While each hydrogen bond is approximately 20 times weaker than a typical covalent bond, each water molecule can participate in multiple hydrogen bonds—one to each H atom and one (or more) to each non-bonded pair of electrons on the O atom.

The key to understanding the structure of bulk water—and its abnormal properties—is understanding the way that non-covalent hydrogen bonds affect its intermolecular interactions. Although one might expect that the random translational motion of molecules in a liquid results in an amorphous structure, the extensive network of hydrogen-bonded molecules in the liquid state

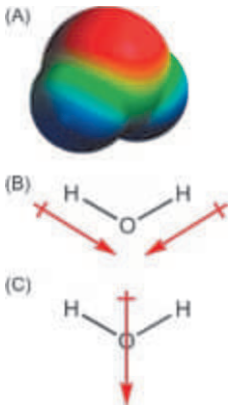

Fig. 1 (A) The distribution of electron density in molecular water (red = high, blue = low). Representation of the electric dipolar nature of molecular water, as contributing dipoles along each O—H axis (B) and as a net dipole (C).

of water gives rise to a surprisingly high degree of order. Water has considerable short range order out to at least ~10–15 Å from the 2.75 Å diameter water molecule (1 Å is 10^{-10} m). Hydrogen bonds are certainly not peculiar to water, but in water they form such elaborate, extensive, and strong networks that they create a "bulk" structure with significant order, order that is in fact maintained up to its boiling point.

A great deal of research has been devoted to improving our understanding of water's structure in condensed phases (ice and liquid)—broadly divided into studies of short-range and long-range order, the latter defined as beyond approximately 15 Å. These research endeavors have been both theoretical and empirical, with theoreticians employing advanced computational tools for molecular modeling, and experimentalists armed with a wide variety of spectroscopic techniques. Models for the structure of water in the solid-phase (various forms of ice) generate little controversy because theoretical models can be directly verified by crystallographic and neutron-scattering techniques. Because of the much more limited atomic motion in the solid state, crystallographic methods have provided an accurate picture of the various ices that form as a function of temperature and pressure. The most common type of ice under ambient conditions is hexameric ice, in which six water molecules are hydrogen-bonded to form a hexagonal ring, as shown in Fig. 2. The most stable state for this structure is a so-called "chair" conformation (analogous to cyclohexane), in which H—O · · · · · H bonds alternate around the ring (where — is a covalent and · · · · · is a hydrogen bond). Also shown in Fig. 2 is the "boat" conformation, an energetically less stable conformation than the "chair" structure. Each O atom has a nearly tetrahedral arrangement of H atoms surrounding it, in which two H atoms are covalently bonded and two non-covalently as hydrogen bonds. The sixfold axis of symmetry found in ice (Fig. 3) is the result of the building blocks of cyclic hexamers.

Unlike models for ice, much controversy continues to surround models for the structure of liquid water. This may be somewhat surprising given that water is a simple molecule, yet general agreement on a realistic model remains elusive despite the application of powerful computational and experimental approaches. Predicting the precise arrangements of hydrogen-bonded neighboring water molecules is challenging because the structures are in a state of rapid flux (at sub-picosecond timescales). Some insight into the structure of bulk water can be gleaned by examining the structural changes that occur upon the melting of ice. When ice melts, the increase in temperature causes a slight disruption of the hydrogen-bonded network, thereby initially causing the ice crystalline lattice to collapse. Whereas the structure of ice is >80% ordered, only an approximately 10% decrease in order occurs upon transition to the liquid phase, resulting in a heat of fusion (334 joules per gram) that is small relative to the heat of vaporization (see below). In this way, much if not most of the short-range order is maintained, and this short-range order persists to the boiling point at 100 °C, where the order is essentially lost completely. The partial collapse of the ordered environment during melting results in slightly more compact hexameric chairs. Consequently, water has the very unusual property of maximal density at a temperature that is higher than its melting point. Above 4 °C, further disruption of the intricate networks of cyclic hexamers by more intensive thermal agitation causes the structures to become more open with a consequent decrease in water's density.

Water forms clusters in the liquid state. The presence of "ice-like" structures in water, based on not only hexameric but also pentameric and octameric building blocks, along with "free" swimming water molecules in more amorphous regions, is the generally accepted model (Fig. 4). However, there have been intriguing studies that suggest that there are regions that are far more complex than the structures analogous to ice. Curiously, one of the earliest is found in Plato's dialogue *Timaeus*, where the ancient Greek's classification of matter—Earth, fire, air, and water—is described in mathematical (geometric) terms. In Plato's view, water is the most complex structure, taking the form of an icosahedron. A regular icosahedron has 20 faces, with five equilateral triangles meeting at each of the 12 vertices. Thus, along with the dodecahedron, these regular convex polyhedral comprise the famous "Platonic Solids." This ancient conception of water may seem quaint, yet it is strikingly similar in concept to several recent

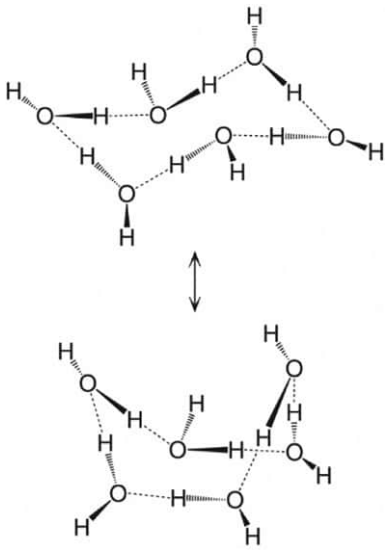

Fig. 2 The arrangement of hexagonal water into a "chair" conformation (top) and less stable 'boat' conformation (bottom).

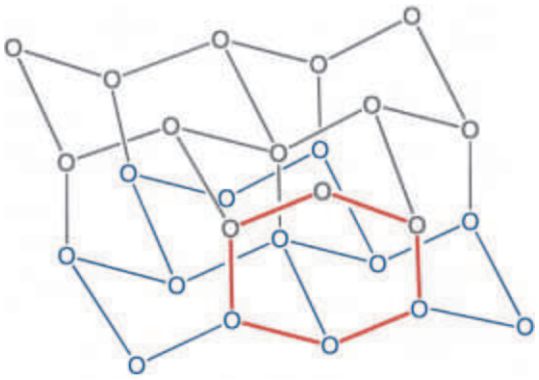

Fig. 3 The structure of the most common form of ice (hexagonal ice), an arrangement based upon the HOH "chair" hexamer. Each oxygen atom is at the approximate center of a tetrahedron formed by four other oxygen atoms. The sixfold axis of symmetry is shown in red for a layer of water "chairs" (black) overlaying another layer (blue). (Hydrogen atoms are not shown for clarity.)

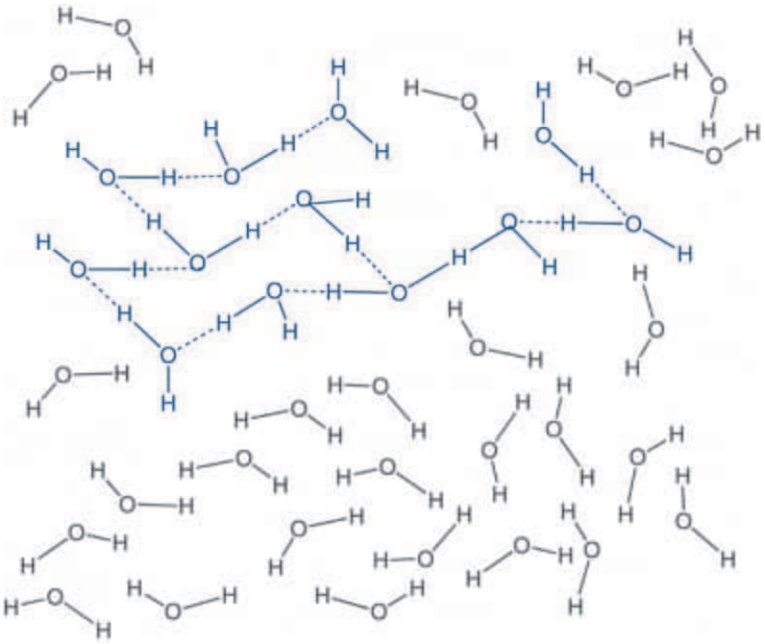

Fig. 4 Proposed models for the structure of bulk water. (Top) The "flickering cluster" model, with ice-like ordered regions highlighted in blue surrounded by amorphous regions where little short-range order is present. (Bottom) Molecular modeling and some experimental evidence suggests that quite complex structures, such as dodecahedra (left) and icosahedra (right), may also exist.

theoretical models of the structure of water in the bulk liquid phase. Clusters based on dodecahedra and icosahedra have been proposed by molecular modeling and supported by experiment to exist in water—though the evidence remains somewhat controversial. Early work by Searcy and Fenn on protonated water clusters by molecular beam mass spectrometry found that a large peak in the spectrum was present, i.e., for a cluster of unusual stability, that corresponded to 21 water molecules—a so-called "magic number." Speculation arose that the structure of this "magic" cluster was a dodecahedral complex of 20 water molecules, each vertex occupied by an oxygen atom and a hydronium ion trapped within (e.g., as in clathrates). Recent work by Dougherty and Howard has indeed found evidence for dodecahedral clusters, and Chaplin has proposed a theoretical model for the formation of icosahedral clusters, a model that has been supported by recent neutron scattering experiments.

The polarity of the water molecule and the hydrogen bonding that results from this polarity have important biological implications. Molecular cohesion produces surface tension that is strong enough to support small animals like water striders and the basilisk lizard, allows for the formation of drops and bubbles, and along with adhesion (attraction to charged surfaces) allows for the transport of water through plants by capillary action. The hydrogen bond also results in a high heat of vaporization (2444 joules per gram at 25 °C and 1 atm), so that evaporation is an important temperature regulation mechanism for both lakes and endothermic animals.

Solvation by water

Ions in aqueous solution interact with one another and with other non-electrolytes, and their presence in water's dipolar electronic field creates relatively strong non-covalent bonds such that the hydrated ion is the form that undergoes further interactions and chemical reactions, with consequent implications for the rates of these processes. Only in the gas phase do "bare" (unsolvated) ions exist; in the liquid phase, all ions are hydrated to some degree.

To appreciate the solvating power of water, the solubility parameter (δ) provides a useful measure, defined as the ratio of the energy required to completely break all intermolecular forces that maintain the liquid state to the molar volume. We represent δ quantitatively as:

$$\delta = \sqrt{\left(\frac{\Delta E_v}{V}\right)}$$

where ΔE is the total energy required to vaporize a solute and V is molar volume. One can think of δ as the "cohesive energy density" of a substance. Of course, δ correlates strongly with polarity, with water not surprisingly having the highest value of δ when compared to other common solvents (Fig. 5).

Before studying an example of the structure of a hydrated metal ion, we recognize that each water molecule is already "solvated" to a very high degree of structural complexity. And because of the auto-ionization reaction of water, which can be represented as a net reaction:

$$H_2O \rightleftharpoons H^+ + OH^- \quad (1)$$

Protons and hydroxide ions are formed that also become hydrated. Realistic structures of the reaction (1) products continue to be the subject of debate, but much evidence suggests that a more realistic way to describe the auto-ionization of water is:

$$6H_2O \rightleftharpoons (H_2O)_2H^+ + (H_2O)_3OH^- \quad (2)$$

Proposed structures for these ions are shown in Fig. 6. For convenience, the simplistic products of reaction (1) are commonly used in the literature. However, more complex structures, such as those depicted in Fig. 6, are themselves not yet fully accepted as realistic.

For ions in aqueous solution, the structures formed by hydration reactions are driven by geometric and electronic factors. The number of water molecules that coordinate as ligands to an ion typically varies from four to nine, and is a function of factors that include ion size, the number of vacant orbitals present, and the degree of ligand-ligand repulsion. Given the great interest in pollution by toxic metals, our understanding of cation hydration is more extensive than for anions, yet hydration of the latter should not be surprising given the dipolar nature of water as a ligand.

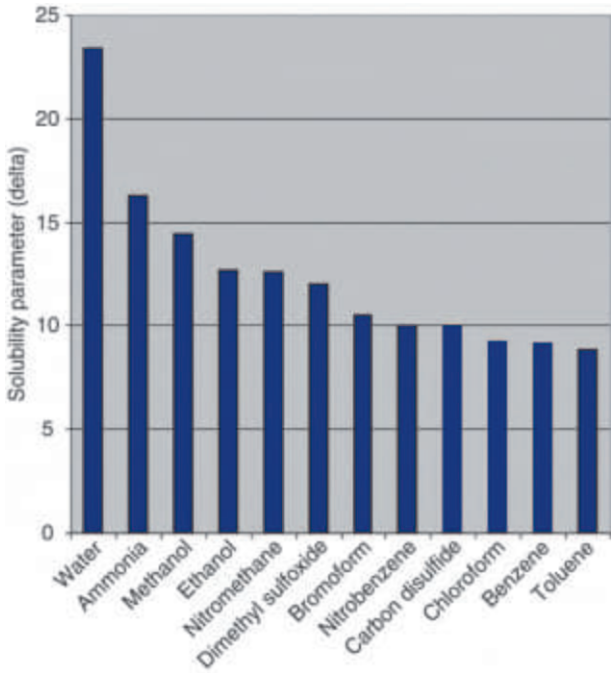

Fig. 5 A comparison of Hildebrand's solubility parameter (δ) for various liquids (25 °C).

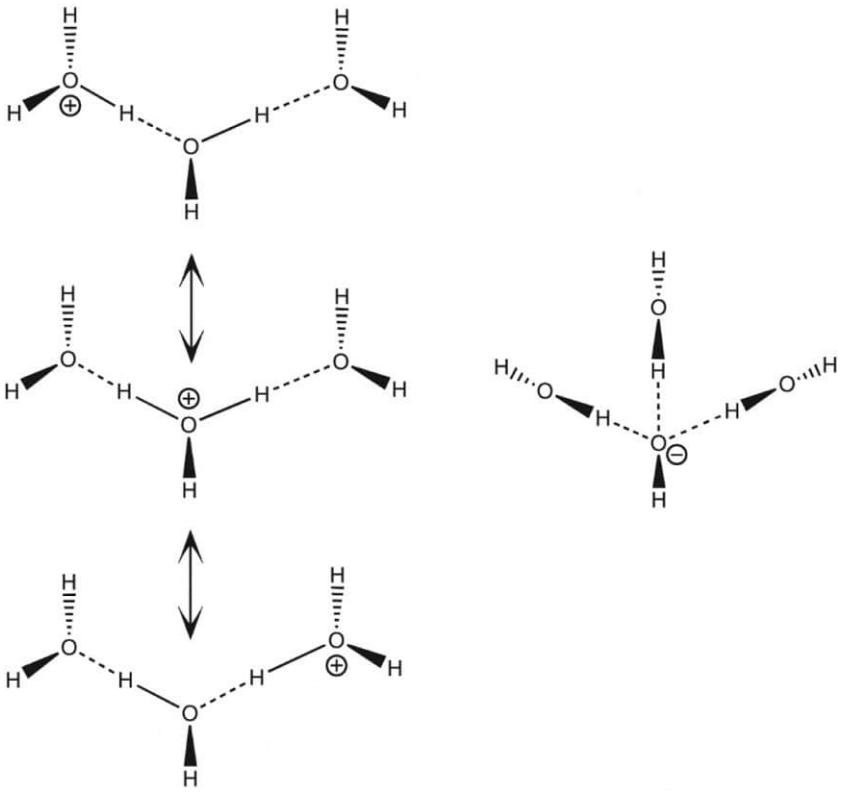

Fig. 6 'Proton hopping' among three water molecules which together constitute a more accurate representation of a hydrated proton ($H_5O_2^+$). The center structure is the most energetically stable of the three shown. A more realistic structure for solvated hydroxide ion ($H_7O_4^-$) is also shown (right). Hydrogen bonds are denoted by dashes (–).

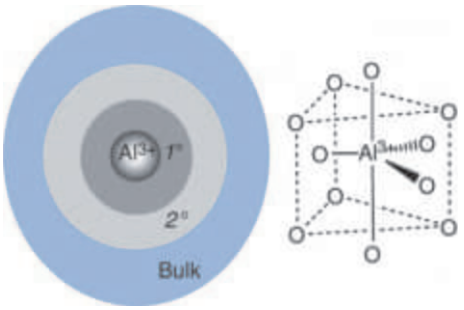

Fig. 7 The "concentric shell" model (left) for the hydration spheres surrounding a cation, showing the primary, secondary, and bulk solution shells. The primary hydration shell of aluminum ion (right), a tricapped trigonal prismatic geometry in which only the O atom positions for the 11 coordinating water molecules are shown.

In Fig. 7, the "concentric shell" model for the hydration of an ion is illustrated for aluminum ion, which exists under ambient conditions in the +3 oxidation state. Three regions form the shells – an inner layer, known as the primary (1°) shell, an intermediate layer known as the secondary (2°) shell, and a third region comprised of the bulk fluid. The structure of the 1° shell is highly ordered, as shown in Fig. 7 for the tri-capped trigonal prismatic arrangement of 11 water molecules closely surrounding the trivalent cation. In the 2° shell, the influence of the Al(III) ion's high charge density would create a more loosely held though structurally defined layer. The bulk fluid extends beyond the 2° shell where the range of the ion's force field has no apparent effect on the fluid structure. It is important to note that the concentric shell model is simplistic, focusing on the strongest inner layers that are present. That is, the model ignores long-range ordering effects, which because of their weakness are inherently difficult to study. For example, studies have shown that for Pb(II) in aqueous solution, the surrounding water is affected by the electronic field of the heavy metal ion to a distance corresponding to ~90 layers of intervening water molecules. Only beyond ~90 layers does the bulk water reflect the "undisrupted" structural state of a pure solution of water.

The reactivity of water

While we may tend to think of water as relatively inert, it is actually a very reactive molecule, with the oxygen atom behaving as a strong electrophile and the protons involved in auto-ionization reactions. However, water's reactivity is attenuated by its extensive hydrogen-bonding. The eightfold mass ratio between water's single relatively heavy (O) atom and two light (H) atoms, and the charge inequity that exists between them, gives rise to a rapid exchange of protons between adjacent water molecules ("proton hopping"). In a pure solution of water, proton hopping among water molecules is constantly occurring at a high rate (Fig. 5). Even at pH 7 where it is slowest, it occurs on the order of 1000 times per second. In studies of hydrogen-bonding and the solvation of ions by water, the exchange of protons is even faster than the millisecond time scale observed for a bulk solution of pure water. Nevertheless, water is treated as a stable molecule because the net structure (H—O—H) is maintained despite its intrinsic dynamic state.

Fundamentally, chemical reactions occur as means for a species (atom, molecule, or ion) to increase its thermodynamic stability. We can generally classify chemical reactions into two broad categories: (i) those that involve changes in oxidation state, and (ii) those that involve changes in coordination environment. While the former redox processes stand alone, the latter type of reaction can be divided into acid-base, complexation, and precipitation reactions. We can illustrate these three sub-categories of coordination reactions by the example of a series of hydrolytic reactions involving the Al(III) ion:

$$\begin{aligned}
&Al^{3+}_{(aq)} + H_2O \rightleftharpoons Al(OH)^{2+}_{(aq)} + H^+_{(aq)} && pK_1 = 8.2\\
&Al(OH)^{2+}_{(aq)} + H_2O \rightleftharpoons Al(OH)_2{}^{+}_{(aq)} + H^+_{(aq)} && pK_2 = 19.0\\
&Al(OH)_2{}^{+}_{(aq)} + H_2O \rightleftharpoons Al(OH)_{3\,(s)} + H^+_{(aq)} && pK_3 = 27.0\\
&Al(OH)_{3\,(s)} + H_2O \rightleftharpoons Al(OH)_4{}^{-}_{(aq)} + H^+_{(aq)} && pK_4 = 31.4
\end{aligned} \qquad (3)$$

The subscript "aq" denotes "in aqueous solution," a reminder that all of these species are hydrated, the structures of which are not shown. While none of the reactions above cause changes in oxidation states, all are acid-base reactions because of the generation of a (hydrated) proton. All can be classified as complexation reactions as well because of hydroxide ion acting as a ligand in its coordination to the metal cation, with the formation of complex cations and anions (with the exception of the third reaction). For the third reaction, because of the formation of a solid product, we classify it as a precipitation reaction. Chemical reactions in the environment that involve water as a reactant or product—that is, each type of reaction illustrated above as well as redox reactions—represent an enormous volume of scholarly work; the interested reader is therefore referred to the "Further Reading" listed at the end of this chapter and elsewhere in this *Encyclopedia*.

Aquatic biogeochemistry

The chemistry that is mediated by water in natural aquatic systems varies in space and time. Often this variability is expressed in the form of trends and patterns, and by understanding their causes it is possible to gain insight into the mechanisms that control water chemistry. Ultimately, variation in the chemistry of lakes and rivers can be attributed to three controlling factors: (1) physical processes and properties, including lake morphometry, weather, and climate; (2) geologic setting; and (3) biological factors, including the abundance and composition of biota within the water body and its watershed. Each of these factors may in turn be influenced by human activities. A discussion of how these factors influence water chemistry is best facilitated by examining some observed patterns for three important classes: dissolved gases, major ions, and nutrients.

Dissolved gases

The dissolved gases of primary interest in most aquatic ecosystems are oxygen and carbon dioxide. Both of these molecules are non-polar, so as they partition at the air-water interface their hydration by water is minimal and consequently their solubility is very low. The only van der Waal's forces that act upon them are very weak Debye forces, in which water's strong dipolar field induces a transient dipole in the non-polar molecule's electronic field. These gases are of primary importance because they both influence and reflect biological processes. Because they are regulated primarily by photosynthesis and respiration, they serve as tracers of electron flow (i.e., energy flow) in an ecosystem. Reactions that convert energy into an organic form will reduce CO_2. In the case of photosynthesis, energy is derived from light and water is the electron donor, with the resultant production of O_2. CO_2 can also be reduced by chemoautotrophic bacteria using other alternate electron donors such as ammonium (NH_4^+), methane (CH_4), and hydrogen sulfide (H_2S). In each case, anabolic processes result in the reduction of CO_2 to form organic compounds. Conversely, the microbial decomposition of organic material results in the production of CO_2, which is accompanied by the reduction of electron acceptors that are used by various microbial taxonomic groups in an order that corresponds to the free energy yield: $O_2 > Mn^{3+/4+} > Fe^{3+} > NO_3^- > SO_4^{2-}$. Following depletion of all these electron acceptors, CO_2 itself can serve as an electron acceptor during

microbial methanogenesis. As a result of decomposition, a vertical redox gradient is created in the water column and/or the underlying sediment, in which the concentrations of the various electron acceptors vary with depth.

The effect of photosynthesis and decomposition on concentrations of dissolved O_2 and CO_2 is modulated by hydrodynamics and lake-atmosphere gas exchange. In systems that are vertically stratified due to a chemically- or thermally-driven density gradient, prolonged separation of deep water from the atmosphere results in deep waters being CO_2 supersaturated and hypoxic or anoxic. In lakes that are well mixed, anoxia may occur in the underlying sediment.

For lakes of a given size and within a geographic/climatic region, dissolved gas concentrations can vary according to the loading of nutrients and organic carbon. Lakes with high nutrient loads will exhibit large diurnal fluctuations in surface dissolved O_2 and CO_2 concentrations, because of high photosynthetic rates during the day and high respiration rates at night. Lakes with high organic carbon loads may be persistently supersaturated with CO_2 and undersaturated with O_2.

Temperature is a key property that determines the solubility of gases in water (Fig. 8). This has ramifications both for the distribution of dissolved gases within lakes, and for the relationship between climate and dissolved gases, especially O_2. Within large, deep temperate lakes in which plankton metabolism is generally slow, there is usually sufficient dissolved O_2 at all depths to support aerobic organisms. Smaller lakes that stratify may develop an anoxic hypolimnion, with the probability of anoxia increasing with the duration of stratification and lake productivity. In tropical lakes and rivers, warm temperatures result in lower O_2 solubility and higher decomposition rates, making these systems more prone to anoxia than their temperate counterparts.

While oxygen retains its molecular structure when dissolved in water, carbon dioxide reacts with water to form carbonic acid, which dissociates to form bicarbonate and carbonate ions, as well as H^+:

$$H_2O + CO_2 \rightleftharpoons H_2CO_3 \rightleftharpoons H^+ + HCO_3^- \rightleftharpoons 2H^+ + CO_3^{2-} \quad (4)$$

Therefore, processes that influence the concentration of dissolved CO_2 in water also affect pH. At pH > 6.5 the formation of bicarbonate and carbonate ions results in a concentration of total dissolved inorganic carbon ($CO_2 + HCO_3^- + CO_3^{2-}$) that is much greater than that of CO_2 alone. As a result, oceans and lakes have absorbed much more of the anthropogenically CO_2 produced since the industrial revolution than they would have if CO_2 did not react with water.

Major ions

Major ions are those that contribute significantly to the salinity of water. Major cations generally include Ca^{2+}, Mg^{2+}, Na^+, and K^+, while major anions include HCO_3^-, CO_3^{2-}, Cl^-, SO_4^{2-}, and sometimes NO_3^-. All these species are of course solvated by water, and the concentric shells that are formed may extend relatively far into the "bulk" water. The absolute and relative abundance of the hydrated major ions in rivers and lakes are controlled by three factors: basin geology, rainfall, and evaporation—crystallization processes. Hence geographic variations in major ion composition can be related to one or more of these factors. For example, the relatively low Ca^{2+} concentrations in lakes and rivers of Precambrian Shield regions of North America and northern Europe reflect the dominance of igneous granite in their watersheds, while the high sodium and chloride concentrations of lakes in many dry regions are due to evaporative concentration of these salts. Because the above three factors differentially influence various major ions, the salinity and relative abundance and distribution of ions can be used to infer which of these processes is most significant for a given water body (Fig. 9).

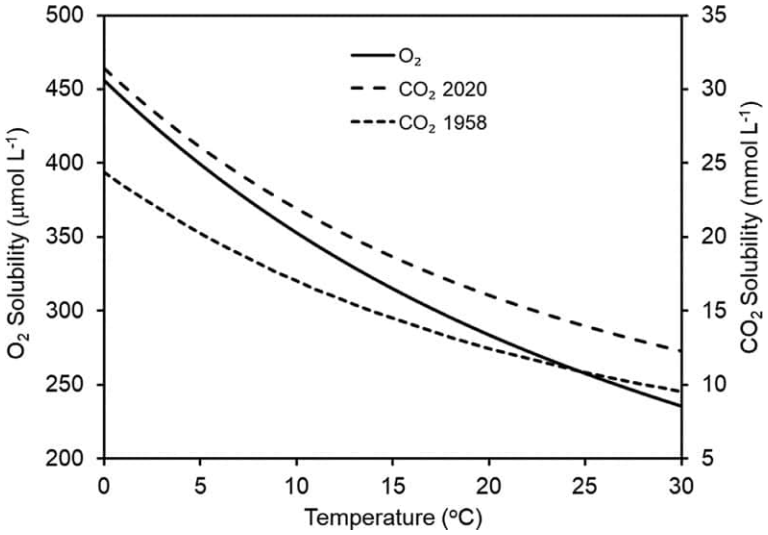

Fig. 8 The solubility of oxygen and carbon dioxide in freshwater at a pressure of 1 atm. CO_2 solubility is shown for both 1958 (when the global average atmospheric CO_2 concentrations was 316 ppm) and 2020 (when the global average was 407 ppm).

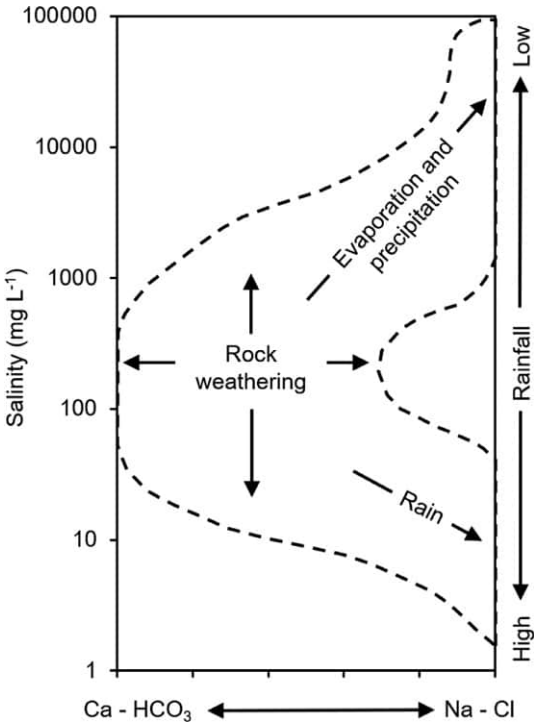

Fig. 9 Influence of geology and climate on salinity and major ion composition of inland waters. Some exceptions to this pattern occur, especially in Africa, where a combination of intense weathering, low Ca^{2+} concentrations in rock, and evaporative concentration can result in moderately high salinities that are dominated by Na^{+} and HCO_3^{-}.

Nutrients

Most algae require a minimum of 17 essential nutrients to grow. The nutrient that limits algal growth in a water body depends on the availability of these nutrients relative to algal demand. In most water bodies, phosphorus or nitrogen is the limiting nutrient, but trace elements such as iron and molybdenum may also be limiting in some systems.

The effects of accelerated nutrient loading to lakes and rivers resulting from human activities, referred to as eutrophication, are well documented in the scientific literature, and are not addressed here. Phosphorus input to lakes and rivers is controlled primarily by rock composition and weathering intensity, but its availability to algae is influenced by the availability of other elements, and by biologically mediated processes. In iron-rich waters, inorganic phosphorus is bound as insoluble ferric phosphate or adsorbed onto ferric oxides and oxyhydroxides, and such systems tend to be unproductive and phosphorus-limited. In calcareous regions, including the Laurentian Great Lakes, calcium minerals may serve as a source of phosphorus through weathering, but this phosphorus is often biologically unavailable because of adsorption to minerals such as calcium carbonate and precipitation with calcium to form apatite. The equilibrium between dissolved and particulate phosphorus is influenced by redox potential, with phosphorus dissolution often being accelerated under anoxic conditions. Such conditions also promote denitrification, through which biologically available nitrate is ultimately reduced to nitrogen gas, which cannot be assimilated by most algae. Over an annual cycle, water column anoxia is more prevalent in tropical lakes than in temperate lakes, which may increase the recycling of phosphorus while enhancing denitrification. As a result, nitrogen limitation of algal growth tends to be more common in the tropics. These patterns can be modified by lake depth. In deep lakes, phosphorus may be sequestered more efficiently into sediment. Consequently, such lakes tend to have lower concentrations of phosphorus in the water column relative to shallow lakes with similar external phosphorus loads.

Conclusion

Primarily because of an extensive network of hydrogen bonding, water is structurally complex and has very unusual properties, with important consequences for biological and biogeochemical processes. Ions and molecules are solvated by water, and the resulting structures affect their reactivity and hence their toxicity, transport, and fate. To understand how nutrients and pollutants are transformed by their interaction with water is essential to understanding the dynamics of the Earth's hydrosphere. Furthermore, these chemical transformations affect how these compounds are transported to other environmental compartments (e.g., the lithosphere and biosphere).

Water is said to be the most studied molecule. Yet while theory and experiment have greatly improved our knowledge of water's structure, important questions remain only partially answered. In particular, questions concerning the structure of water in the liquid state, specifically how hydrogen bonding determines long-range ordering effects, continue to intrigue researchers. Given the astonishing properties of such a simple molecule, one might conclude that hydrogen bonding is indeed that "third thing" to which D.H. Lawrence was alluding to in the 1929 quote at the beginning of this article.

See Also: Fundamental concepts and theories: Pressure; Structures and functions of Inland Waters - Lakes: Surface Mixed Layers in Lakes

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Relevant Websites

http://www.lsbu.ac.uk/water/—"Water Structure and Science" by Professor Martin Chaplin, London South Bank University, London, England, UK.
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Photochemical Reactions in Inland Waters☆

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This is an update of A.V. Vähätalo, Light, Photolytic Reactivity and Chemical Products, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00110-1.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Apparent quantum yield Efficiency of photochemical reaction, expressed per mol of photons absorbed by an unknown mixture of compounds such as CDOM.
BAPs Biologically available photoproducts, which are generated when biologically non-labile dissolved organic matter is photochemically transformed into biologically labile forms.
CDOM Chromophoric dissolved organic matter, the major absorber of solar radiation in surface waters. Defined as an absorption coefficient "m^{-1}" in sensu stricto, but also as a mixture of dissolved organic compounds able to absorb solar radiation in sensu lato used in this article.
CDOM(S_1) The first short-living (<1 μs) excited singlet state of a CDOM-molecule after the absorption of a photon.
CDOM(T_1) or ^{3}CDOM* The short-living (>1 μs) excited triplet state of a CDOM-molecule formed from CDOM(S_1) and capable of mediating indirect photochemical reactions.
Direct photochemical reactions Reactions where the primary absorber will be transformed.
Indirect photochemical reactions Reactions mediated by sensitizers and PPRIs.
Photobleaching Photochemical transformation, which decreases absorbing or fluorescing properties of dissolved organic matter.
PPRIs Photochemically produced reactive intermediates such as $^1O_2$, CDOM(T_1) and reactive oxygen species (e.g., $^{\bullet}OH$).
Quantum yield Efficiency of a photochemical reaction expressed in unit such as mol of photochemical product per mol of photons absorbed by a known compound.
Scavenger A compound which reacts with PPRIs.

☆*Change History*: July 2021. Anssi V. Vähätalo, Luca Carena, and Davide Vione updated the title of article as "Photochemical reactions in inland waters." Two authors, Luca Carena and Davide Vione, have been added. The text in the entire article has been edited for clarity. Earlier section "Contribution of Photochemistry to the Biogeochemistry of Organic Matter" has been removed. Two new sections "Photodegradation of pollutants" and "Photochemical reactions and climate change" have been added.

Sensitizer The primary absorber of sunlight for indirect photochemical reactions.
Singlet oxygen, $^1O_2$ The first activated form of molecular oxygen produced in the reaction between CDOM(T_1) and O_2.

Introduction

Photochemical reactions take place in surface waters and on irradiated surfaces of organic or inorganic substrates. The prerequisite for photochemical reactions is the absorption of radiation. Section "Mechanisms of photochemical reactions" explains the mechanistic principles of photochemical reactions. They start from the primary photophysical events, but the following thermal secondary reactions are responsible for chemical transformations.

Photochemical transformations modify the molecular composition of dissolved organic matter. Section "Photochemical transformations" illustrates how photochemistry changes the composition of the natural and xenobiotic organic matter as well as metals associated to them. The transformation of nitrogen-, phosphorus- and iron-containing compounds are treated separately as they produce nutrients, which contribute to the productivity of aquatic ecosystems. Although most photochemical transformations are mediated by chromophoric dissolved organic matter, CDOM, and concern dissolved compounds, this section introduces also heterogeneous photochemical transformations on solid surfaces and material adsorbed on them.

The importance of photochemical transformations depends on their rates. Section "Photochemical reaction rates" examines the rates of photochemical transformations in surface waters. Often it is easiest to estimate the photochemical rates in the environment based on (apparent) quantum yields measured in the laboratory. Section "Photochemical reaction rates" introduces models, which use spectral (apparent) quantum yields for the estimation of rates in surface waters. These models also reveal the spectral solar radiation responsible for the photochemical reactions and can describe the attenuation of photochemical reaction rates with depth into a water column.

Finally, Section "Photochemistry, food webs and climate change" points out that photochemical transformations are coupled to the biological communities and their metabolism. This section also outlines likely changes in the photochemistry of inland water under predicted scenarios of climate change.

Mechanisms of photochemical reactions

Primary photophysics and subsequent secondary chemical reactions

During the absorption of radiation, a photon ($h\nu$) delivers its energy (250–400 kJ mol^{-1} at the wavelengths 280–500 nm) to the absorber molecule and excites the molecule from its ground state (S_0) to the first excited electronic singlet state (S_1; Vione et al., 2014). In surface waters, chromophoric dissolved organic matter (CDOM) dominates the absorption of photolytic solar radiation. In a strict sense, CDOM is an optical property of water bodies, an absorption coefficient with a unit of m^{-1}. This article takes a broader definition, where CDOM refers also to dissolved organic compounds, which can absorb solar radiation. The absorption event can be described as: CDOM(S_0) + $h\nu$ → CDOM(S_1). Excited CDOM releases its excitation energy mostly as heat (with 0.95–0.98 probability) but also as fluorescence (probability of ~0.01; CDOM(S_1) → CDOM(S_0) + $h\nu$) at the nanosecond time scale. The excited singlet state of CDOM may be converted into an excited triplet state (T_1, probability of 0.001–0.04; CDOM(S_1) → CDOM(T_1)). The excited triplet state of CDOM has > microsecond-lifetime and may undergo secondary (thermal) chemical reactions, but it can also transfer its excitation energy to another compound or release it as heat or a photon (phosphorescence).

Numerous reaction pathways are available for excited states e.g., homolysis or heterolysis of bonds, ionization, intermolecular oligomerization, intramolecular rearrangements, and photoisomerization. Because the energy of a photon can be larger than the dissociation energy of a chemical bond, the excited molecules may dissociate (probability of $\leq 10^{-5}$) or ionize (e.g., CDOM + $h\nu$ → CDOM$^+$ + $e^-_{(aq)}$; probability of 10^{-3}–10^{-4}). The fragmentation may take place via homo- or heterolysis of σ- and π-bonds e.g., next to the carbonyl functional groups of CDOM (e.g., type I and II Norrish reactions). The fragmentation of excited molecules results in radical species (such as organoperoxy radicals), which can further lead to the expulsion of carbon monoxide, carbon dioxide, or other small molecules.

The excited CDOM (triplet states in particular) can transfer their excitation energy to other molecules (McNeill and Canonica, 2016). Dissolved dioxygen is a common acceptor of this energy. Transfer of energy or an electron to O_2 generates singlet oxygen, $^1O_2$, or superoxide, $O_2^{\bullet -}$, respectively. The latter can be further reduced to hydrogen peroxide, H_2O_2, and hydroxyl radicals, $^\bullet$OH. The generation of these reactive oxygen species causes photochemical consumption of O_2. The hydroxyl radical is the most reactive oxygen species and can react effectively with organic and inorganic matter as well as cause oxidative damage to organisms. In surface waters, the lifetime of H_2O_2 can be longer than several hours, while those of $^1O_2$, $O_2^{\bullet -}$, and $^\bullet$OH are often much lower than a second. The photochemical formation of reactive oxygen species can proceed also via photolysis of nitrate and nitrite as well as via photo-Fenton reactions involving iron. The reactive oxygen species along with excited CDOM-molecules are examples of photochemically produced reactive intermediates (PPRIs).

The photochemical reactions concerning the primary absorber are called direct photochemical reactions. A direct photoreaction takes place, e.g., when a CDOM-molecule absorbs solar radiation and becomes photochemically transformed. An example is the photobleaching of CDOM, where the light absorbed by CDOM decreases the absorption coefficient of CDOM itself. If photochemical reactions concern molecules other than the primary absorber, they are called indirect photochemical reactions and the primary absorber is called a sensitizer. In these cases, photochemically produced reactive intermediates mediate chemical reactions and may even target molecules, which cannot absorb solar radiation themselves.

Photochemical transformations

Photochemistry of organic carbon

In many fresh waters, the major part of organic carbon (50–90%) consists of a diverse group of dissolved compounds, which can form high molecular weight (>1000 g mol^{-1}) colored aggregates (CDOM), traditionally called humic substances (Nebbioso and Piccolo, 2013). These aggregates are too large for a direct microbial uptake and are rich in chromophoric non-hydrolyzable aromatic moieties, which make them biologically non-labile but sensitive to photochemical degradation.

The most abundant single photochemical product of CDOM is carbon dioxide (CO_2). It typically originates as a scission of carboxylic groups, which are abundant functional groups in (C)DOM (Fig. 1, Doane, 2017). Photochemical reactions produce low

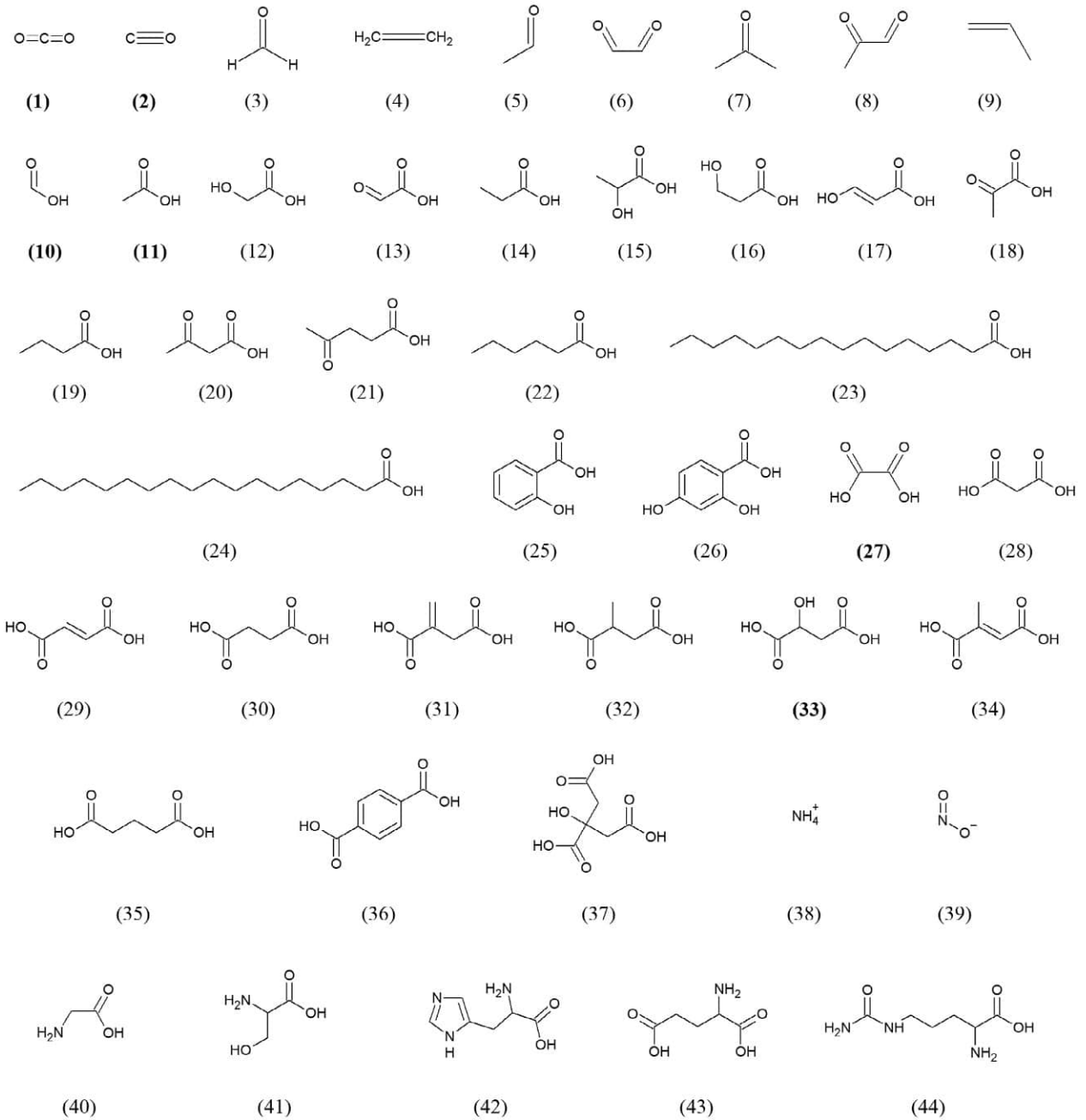

Fig. 1 Identified photoproducts of natural dissolved organic matter. The most abundant products are marked with bold. **(1)** carbon dioxide; **(2)** carbon monoxide; (3) formaldehyde; (4) ethene; (5) acetaldehyde; (6) glyoxal; (7) acetone; (8) methylglyoxal; (9) propene. *Monocarboxylic acids*: **(10)** formic acid; **(11)** acetic acid; (12) glycolic acid; (13) glyoxylic acid; (14) propionic acid; (15) lactic acid; (16) 3-hydroxypropanoic acid; (17) 3-hydroxy-2-propenoic acid; (18) pyruvic acid; (19) butanoic acid; (20) 3-oxobutanoic acid; (21) levulinic acid; (22) hexanoic acid; (23) hexadecanoic acid; (24) octadecanoic acid; (25) salicylic acid; (26) 2,4-dihydroxybenzoic acid. *Di-tricarboxylic acids*: **(27)** oxalic acid; (28) malonic acid; (29) fumaric acid; (30) succinic acid; (31) methylene succinic acid; (32) 2-methylsuccinic acid; **(33)** malic acid; (34) 2-methylfumaric acid; (35) pentanedioic acid; (36) terephthalic acid; (37) citric acid. *N containing products*: (38) ammonium; (39) nitrite; (40) glycine; (41) serine; (42) histidine; (43) glutamic acid; (44) citrulline. Sources: (Kieber, Zhou and Mopper, 1990; Mopper et al., 1991; Backlund, 1992; Allard et al., 1994; Wetzel, Hatcher and Bianchi, 1995; Corin, Backlund and Kulovaara, 1996; Kulovaara et al., 1996; Bertilsson and Tranvik, 1998; Kieber, Li and Seaton, 1999; Riemer et al., 2000; Tarr et al., 2001; Shiller et al., 2006).

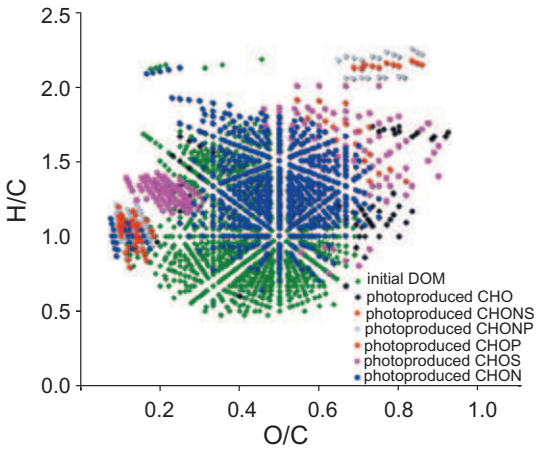

Fig. 2 Van Krevelen diagram for the photochemical transformation of DOM. Each dot refers to an assigned molecular formula containing carbon (C), hydrogen (H), oxygen (O), nitrogen (N), sulfur (S) and phosphorus (P) atoms arranged according to H/C and O/C-ratios in the formulas. Initial DOM refers to the composition of DOM prior to an exposure to solar radiation. Photoproduced CHO, CHONS, CHONP, CHOP, CHOS and CHON refer to the photochemically produced new formulas containing C, H, O, N, S and P atoms (Rossel et al., 2013).

molecular mass organic compounds from CDOM (Fig. 1). Identified abundant products include carboxylic acids, few carbonyl compounds, volatile alkenes and carbon monoxide (Fig. 1). Fourier-transform ion cyclotron resonance mass spectrometry has shown that photochemistry transforms a major portion of compounds, which collectively make up DOM (Fig. 2). A large portion of DOM-molecules and their photochemical transformation products consists of carbon, hydrogen and oxygen atoms (Figs. 1 and 2). Photochemical reactions lead to disappearance of some compounds, create new compounds, but decrease eventually the molecular diversity upon prolonged irradiation (Fig. 2). Photochemically produced compounds can also contain nitrogen, phosphorus and sulfur atoms (Fig. 2).

Photochemical reactions typically decompose aromatic moieties, decrease the molecular mass of CDOM and increase the oxidation number of compounds e.g., through an introduction of functional groups containing oxygen (Riedel et al., 2016). These photochemical transformations increase the water solubility of humic acids, decrease the light absorption of CDOM, decrease the adsorption of CDOM on surfaces as well as the sorption of hydrophobic organic chemicals on CDOM, and change the composition of functional groups (ligands) responsible for the chelation of metals. In some instances, photochemical reactions can cross-link molecules into di- or oligomers and cause the precipitation of CDOM.

As CDOM typically consists of biologically non-labile organic matter, its photochemical transformation into small molecular mass organic photoproducts generates biologically labile substrates for bacterioplankton (Fig. 1). These biologically available photoproducts (BAPs) are quickly consumed by bacterioplankton. Thus, in addition to the direct photochemical mineralization of CDOM to CO_2, a combined action of photochemistry and microbial respiration based on BAPs facilitates the mineralization of organic carbon. When photochemical reactions cross-link biologically labile compounds together into less labile forms, they slow down biological consumption of labile compounds.

Solar radiation decomposes the fluorophores and the light absorbing moieties of CDOM in a process called photobleaching. An extensive photobleaching requires the presence of O_2. The photochemical loss of carbonyl chromophores, their transformation into low molecular weight organic compounds, and the destruction of aromatic and quinone-structures of CDOM are likely responsible for photobleaching. Under extensive exposure to solar radiation, photochemical reactions can destroy the chromo- and fluorophores of organic matter completely. The photobleaching of CDOM takes place faster than the mineralization of DOC. After complete photochemical loss of chromophores, DOM consists of non-chromophoric compounds that cannot be transformed by direct photolysis. Because CDOM is largely responsible for the absorption of UV- and short wavelength visible radiation, photobleaching increases the penetration of solar radiation into the water column, and thus interferes with the exposure of organisms to UV radiation, the light availability of photosynthetic organisms, and the thermal stratification of the water column.

Photochemistry of nitrogen

Photochemical reactions can release ammonium (NH_4^+) from dissolved organic nitrogen when the concentration of dissolved organic nitrogen (DON) is high and that of NH_4^+ is low (<6 μM, Tarr et al., 2001). The proposed mechanism for the photochemical release of NH_4^+ includes a photoreaction of organic amines with ketones and aldehydes to produce imines, which hydrolyze to NH_4^+. The photoproduction of nitrite (NO_2^-), primary amines, and amino acids along with NH_4^+ provides a source of biologically labile nitrogen (Fig. 1). The photochemical reactions mineralize more carbon than nitrogen, and therefore decrease the C/N-ratio of DOM.

In the presence of high concentration of NH_4^+ (>8 μM) or NH_3, photochemical reactions can also incorporate these inorganic N-species into DON. In addition, photochemical reactions can convert aromatic amino acid (tryptophan) and protein (in the presence of CDOM) into less bioavailable forms.

Photochemistry of phosphorus

Ferric iron, Fe(III), binds phosphate ion (PO_4^{3-}, hereinafter P_i) tightly and can associate with organic matter, CDOM, to form Fe(III)-P_i-CDOM (Gerke, 2010). The phosphorus of these associations is not readily available for organisms. Photochemical reactions can release phosphate from Fe(III)-P_i-CDOM. When these associations absorb solar radiation, ferric iron, Fe(III), can be photoreduced into ferrous iron, Fe(II), and the phosphate ion is released. Unlike many photochemical reactions of CDOM, the photoreduction of ferric iron and subsequent release of phosphate can proceed with high quantum yields. The photochemical release of P_i from Fe(III)-P_i-CDOM may be an important pathway in some environments for converting non-bioavailable P into bioavailable form.

The coupling of photo-oxidation of organic matter to the photoreduction of metals

Metals can associate with organic matter and can become photochemically reduced via a ligand-to-metal charge-transfer pathway when exposed to natural solar radiation (Fig. 3). For example, when organic matter is associated with ferric iron, its light absorption and the probability for photochemical transformation increases. Photochemical reactions can reduce ferric iron to more soluble ferrous iron and at the same time oxidize organic matter e.g., via decarboxylation-reaction, which can lead to production of CO_2 and hydrogen peroxide (H_2O_2). Ferrous iron, Fe(II), is often quickly oxidized to ferric iron, Fe(III), in a dark process, which consumes dissolved oxygen or reactive oxygen species. If H_2O_2 is the oxidizer of Fe(II), the process produces hydroxyl radicals via the Fenton reaction: Fe(II) + H_2O_2 → $^{\bullet}$OH + Fe(III). When solar radiation produces both Fe(II) and H_2O_2, this reaction is known as photo-Fenton reaction (Vione et al., 2014).

Photodegradation of pollutants

Photochemical reactions transform contaminants and contribute to the self-purification of water bodies. Many pollutants absorb sunlight, and absorption triggers their direct photochemical transformation. The direct photolysis of contaminants is most efficient in waters with low CDOM-content, because CDOM decreases the availability of light to contaminants and, therefore, their rates of direct photolysis.

Indirect photochemical reactions can also transform pollutants, which cannot absorb solar radiation themselves (Remucal, 2014). The major sensitizers for the indirect photochemical transformation of contaminants are CDOM, nitrate and nitrite (Fig. 4). Indirect photochemical transformations involve the PPRIs, of which the main ones are $^{\bullet}$OH, $^1O_2$, CDOM(T_1) and the carbonate radical, $CO_3^{\bullet-}$ (Fig. 4). The PPRIs are photochemically generated by the sensitizers and quickly consumed by scavengers or otherwise quenched (Fig. 4). For example, DOM is a major scavenger of $^{\bullet}$OH and $CO_3^{\bullet-}$ (Fig. 4). Effective scavenging keeps the steady-state concentrations of PPRIs at low level, such as 10^{-15}–10^{-18} mol L^{-1} for $^{\bullet}$OH.

Although scavenging and quenching consume PPRIs effectively, the comparatively minor reactions of PPRIs with contaminants are of prime importance in the ecology of rivers and lakes (Remucal, 2014; Vione et al., 2014). PPRIs react with man-made pollutants (e.g., pesticides, pharmaceuticals and personal care products, industrial chemicals) to induce their transformation, which often leads to partial or even complete detoxification. Unfortunately, in some cases the transformation intermediates can be more toxic/harmful/mutagenic than their parent compound. This means that the actual impact of photochemical processes on the environmental status of water bodies has to be assessed on a case-by-case basis: (i) in the same water body, some pollutants may

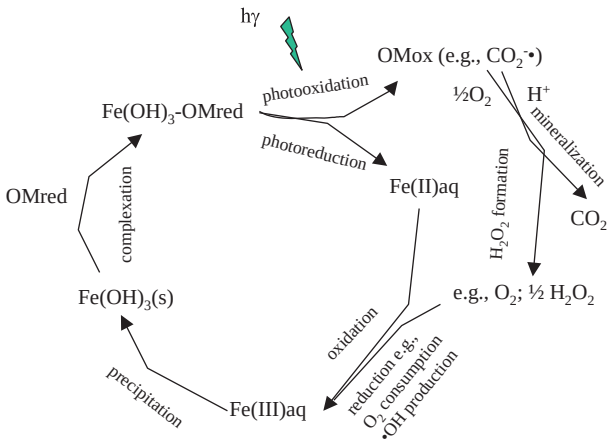

Fig. 3 Schematic representation of the aquatic photo-redox cycling of iron and its coupling to the oxidation of organic matter (OM) in illuminated surface waters. Fe(II)aq = dissolved ferrous iron; Fe(III)aq = dissolved ferric iron; Fe(OH)$_3$(s) = ferric hydroxide; OMred = reduced organic matter, which is a ligand for Fe(III); Fe(OH)$_3$-OMred = a complex between reduced OM and Fe(III); OMox = oxidized organic matter; $CO_2^{\bullet-}$ = carboxylic radical. The oxidation of Fe(II) with hydrogen peroxide is called the Fenton reaction (H_2O_2 + Fe(II) → Fe(III) + $^{\bullet}$OH + OH^-) and generates hydroxyl radicals (Sulzberger, 1992).

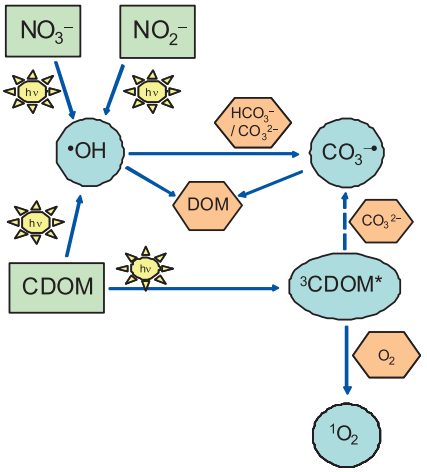

Fig. 4 Schematic of the main processes leading to the generation of photochemically produced reactive intermediates, PPRIs, in surface fresh waters. These PPRIs play a major role in pollutant attenuation. The rectangles represent the photosensitizers, ellipses the PPRIs, and hexagones the main scavengers. Note that $^3CDOM^* = CDOM(T_1)$ (Vione et al., 2014).

undergo detoxification but others may produce hazardous intermediates; (ii) the same pollutant may be detoxified in some water bodies but be transformed into harmful compounds in others, depending on different environmental conditions.

The occurrence of PPRIs depends on water quality. In particular, the concentration of DOC regulates the pathways of photoreactions (Fig. 5). Low-DOC waters favor the reactions involving $CO_3^{\bullet -}$, especially if pH and alkalinity are also high, because HCO_3^- and (predominantly, at pH > 8) CO_3^{2-} are the sources of $CO_3^{\bullet -}$. Intermediate-DOC waters are favorable environments for $^\bullet OH$ and for the direct photolysis (see below), while high-DOC waters favor the reactions induced by $CDOM(T_1)$ and $^1O_2$ (Fig. 5).

Heterogeneous photochemistry

Photochemistry can modify particulate organic matter or organic matter adsorbed on the surfaces. The photochemical reactions associated with surfaces are called heterogeneous in contrast to the homogenous photochemistry of dissolved molecules.

Heterogeneous photochemical reactions take place on any surfaces exposed to photolytic solar radiation, e.g., on the surfaces of sediment or particles in suspension. For example, irradiation can reduce ferric iron of particulate iron oxides and release it into solution as ferrous iron (Doane, 2017). Concomitantly with the photoreduction of iron(III), organic carbon adsorbed on particles is oxidized and O_2 consumed. Solar radiation can mineralize, and decrease the molecular mass of, organic matter adsorbed on the

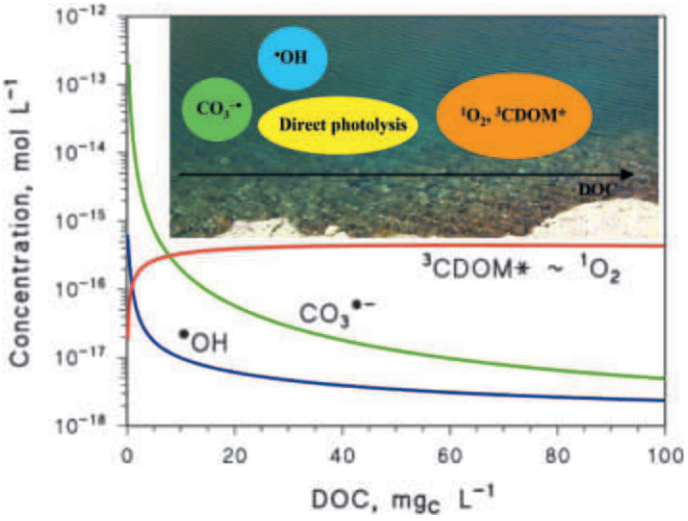

Fig. 5 DOC trend of the steady-state concentrations of the main PPRIs occurring in surface waters, under fair-weather summer sunlight at mid-latitude, for a water column depth of 3 m. Note the logarithmic scale on the Y-axis, which was needed to accommodate the very different concentration values. The insert provides qualitative insight into the relative role played by direct photolysis and indirect photochemistry in different environmental (DOC) conditions. Note that $^3CDOM^* = CDOM(T_1)$.

surfaces of mineral (e.g., clay) particles. This process decreases the adsorption of CDOM on surfaces and leads into the dissolution of DOC. Such DOC is biologically labile compared to organic matter adsorbed on the surfaces of mineral particles.

Photochemical reactions also interfere with the decomposition of particulate dead organic matter (detritus) such as senescent phytoplankton or macrophytes (King et al., 2012). The (photosynthetic) pigments are primary absorbers of solar radiation, and they are susceptible for photolysis in detrital plants with non-functional photoprotective apparatus. The photolysis of pigments in surface waters is an important pathway for their decomposition, because pigments decompose ineffectively in dark anaerobic sediments.

The lignin of vascular plant detritus is highly susceptible for photolysis (King et al., 2012). The photochemical decomposition of lignin can break down the structural integrity of detrital plant material, enhance the leaching of particulate organic matter into DOM, and induce the loss of particulate organic matter. Photochemical reactions can also directly mineralize detrital plant material into CO_2. The exposure of detrital leaves to solar radiation can increase or decrease microbial activity on leaves, possibly depending on the diagenetic state and the bioavailability of detrital leaves.

Photochemistry can transform organic matter differently in frozen (ice/snow surfaces on glaciers and lakes) than in liquid water. Freezing can create highly concentrated microenvironments on the surface of snow/ice and in channels between ice crystals. Photochemical condensation is more common in highly concentrated solutions associated with snow/ice than in dilute solutions e.g., in lake water.

Photochemical reaction rates

Photochemical reactivity of organic matter

Photochemical reactivity of organic matter describes the susceptibility of organic matter to photochemical transformation and is quantitatively described by a quantum yield (often abbreviated by ϕ). The ϕ for a photochemical reaction describes the magnitude of a certain reaction (for example with a unit "mol of photochemical product") in relation to the number of photons absorbed (mol of absorbed photons).

The variability of ϕ-values is large among different photochemical reactions (Fig. 6). An example of high reactivity is the ϕ-value around one for the photochemical transformation of ferrioxalate (Fig. 6). In this case, every photon absorbed by ferrioxalate reduces Fe(III) to Fe(II). An example of a lower quantum yield is the photochemical production of hydroxyl radicals from nitrate: $NO_3^- + h\nu (+H^+) \rightarrow NO_2 + {}^{\bullet}OH$. The quantum yield for this reaction is ~0.01 (Vaughan and Blough, 1998; Fig. 6). The quantum yield is

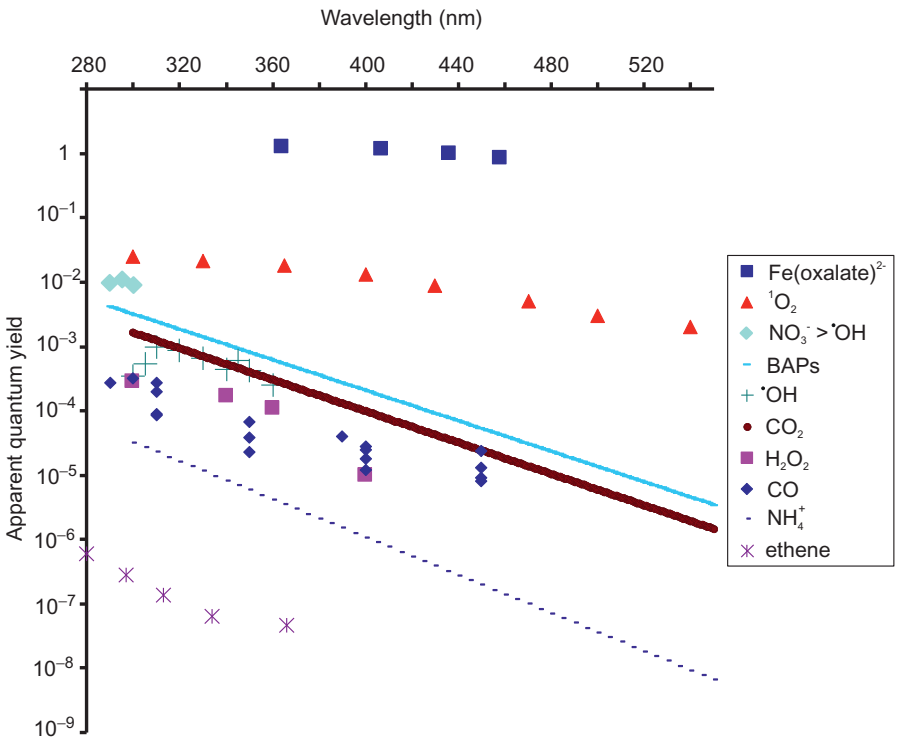

Fig. 6 Apparent quantum yield for the photochemical reactions of CDOM and those of nitrate and ferrioxalate. Photoreduction of ferrioxalate ($Fe(oxalate)^{2-}$) (Demas et al., 1981; Faust and Zepp, 1993). $^{\bullet}OH$ production from photolysis of nitrate (Vaughan and Blough, 1998). Photoproduction of singlet oxygen ($^1O_2$) from Suwannee River natural organic matter (Partanen et al., 2020). Biologically available photoproducts (BAPs) in Altamaha River, United States (Miller et al., 2002). CO_2 photoproduction in L. Valkea-Kotinen (Vähätalo et al., 2000). $^{\bullet}OH$ photoproduction from Suwannee River fulvic acid (Vaughan and Blough, 1998). H_2O_2 photoproduction in Sharpes Bay (Scully et al., 1996). Photoproduction of carbon monoxide (CO) in Satilla and Suwannee River, L. Kinoshe, Houghton wetland and Okefenokee Swamp (Valentine and Zepp, 1993; Gao and Zepp, 1998). NH_4^+ photoproduction in the Baltic Sea (Vähätalo and Zepp, 2005). Ethene photoproduction in Shark River (Riemer et al., 2000).

typically assumed to be spectrally independent for a defined photochemical reaction, when initiated by light absorption by a known compound (Kasha's rule, which is usually valid with a few exceptions). Examples that follow Kasha's rule are the photoproduction of $^{\bullet}OH$ from nitrate in the environmentally significant UV-B and UV-A wavelength ranges, and the direct photolysis of most organic contaminants.

For the photochemical reactions associated with CDOM, the light absorption cannot be assigned to any specific compound, because the chromophores of CDOM contribute to light absorption collectively. In these cases, the quantum yields receive a prefix "apparent," the ϕ-values are low (typically <0.02) and have a strong spectral dependence (Fig. 6). The apparent ϕ-values often decrease exponentially with increasing wavelength, likely reflecting the heterogeneity of chromophores and the photochemical reactivity of thousands of compounds in CDOM. Examples of these types of reactions are the photoproduction of $^1O_2$, BAPs, CO_2, $^{\bullet}OH$, H_2O_2, CO and ethene by irradiated CDOM (Fig. 6). The exponential spectral dependence of ϕ-values can be approximated as (Vähätalo et al., 2000): $\phi_\lambda = c \exp(-d\,\lambda)$, where ϕ_λ is the apparent quantum yield at the wavelength λ, c is an apparent quantum yield at a reference wavelength λ (e.g., mol product mol photons^{-1}), and d is a spectral slope coefficient for ϕ_λ (nm^{-1}). This approximation is shown as lines in Fig. 6, where the ϕ-values for the photoproduction of BAPs, CO_2 and NH_4^+ are reported in the logarithmic scale.

Regulators of the photochemical reactivity of organic matter

The characteristics of DOM and environmental conditions affect the photochemical reactivity of DOM. For example, the ϕ-values for the mineralization of DOC can vary 10-fold in different water bodies depending on pH, the concentration of iron and O_2, as well as the quality of CDOM. CDOM exported from organic soils without previous exposure to solar radiation is most sensitive for the photochemical transformations (Cory et al., 2018). The first exposure to solar radiation decomposes the most photoreactive parts of DOM (e.g., the aromatic structures) and can decrease the photoreactivity of DOM quickly. Later the decrease in ϕ-values is more gradual when DOM has been already exposed to solar radiation e.g., in large lakes with long water retention times.

The rates of photochemical reactions depend on temperature but to a lesser degree than typical chemical reactions. Typical activation energies for photochemical reactions are 10–30 kJ mol^{-1}. The activation energies 10 and 30 kJ mol^{-1} correspond to 1.5- and 3-times faster rates at 25 °C than at 0 °C, respectively. By comparison, the rates of chemical reactions can be 4–5 times faster at 25 °C than at 0 °C.

Estimating the rates of photoreactions in the environment

The rates of photochemical reactions related to CDOM depend on (i) the amount of spectral solar irradiance, (ii) its absorption by CDOM and (iii) the spectral apparent quantum yield for the reaction (Cory et al., 2018). The volumetric photochemical transformation rate of DOM at the depth z (pr_z, e.g., mol m^{-3} day^{-1}) can be expressed as:

$$pr_z = \int_{\lambda\ \min}^{\lambda\ \max} Q_{s,z,\lambda}\, a_{CDOM,\lambda}\, \phi_\lambda\, d\lambda \tag{1}$$

where $Q_{s,z,\lambda}$ is the scalar photon flux density at λ and depth z (e.g., mol photons m^{-2} d^{-1} nm^{-1}; Fig. 7A), $a_{CDOM,\lambda}$ is the absorption coefficient of CDOM at λ (m^{-1}; Fig. 7B), and ϕ_λ is the apparent quantum yield for the photochemical reaction at the wavelength λ (mol product mol absorbed photons^{-1}; Fig. 7C). The integration range refers to the solar radiation contributing to the photochemical reaction from the shortest λ_{min} to the longest λ_{max} wavelengths (nm). The term $Q_{s,z,\lambda}$ describes photon flux density to a point from all directions. Fig. 7A–D illustrate the use of Eq. 1 for the estimation of the volumetric photochemical mineralization rate of DOC at three depths in a humic lake.

The areal rate for photochemical transformation of CDOM over the entire water column (pr, e.g., mol m^{-2} day^{-1}) can be expressed as:

$$pr = \int_{\lambda\ \min}^{\lambda\ \max} Q_{a,\lambda}\, a_{CDOM,\lambda}/a_{tot,\lambda}\, \phi_\lambda\, d\lambda \tag{2}$$

where $Q_{a,\lambda}$ represents mol of photons absorbed by the water column (mol photons m^{-2} day^{-1} nm^{-1}; Fig. 7E), and the ratio $a_{CDOM,\lambda}/a_{tot,\lambda}$ describes the contribution of CDOM to the total absorption coefficient, $a_{tot,\lambda}$ (Fig. 7F). Fig. 7E–H illustrate the use of Eq. (2) for the estimation of the areal photochemical mineralization rate of DOC.

Similar equations as Eqs. (1) and (2) hold for the photochemical generation of PPRIs by irradiation of CDOM, NO_3^- and NO_2^-, and for the direct photolysis of pollutants (Vione, 2020). The relevant set of equations can be included into software that predict the direct and indirect phototransformation kinetics of contaminants, due to the action of sunlight. One such examples is APEX (Aqueous Photochemistry of Environmentally-occurring Xenobiotics), a software that predicts the photochemical lifetime of contaminants based on (i) pollutant properties: absorption spectrum, direct photolysis quantum yield and second-order reaction rate constants with PPRIs, and (ii) environmental features: sunlight spectrum and irradiance, depth and chemical composition of natural water (Vione, 2020).

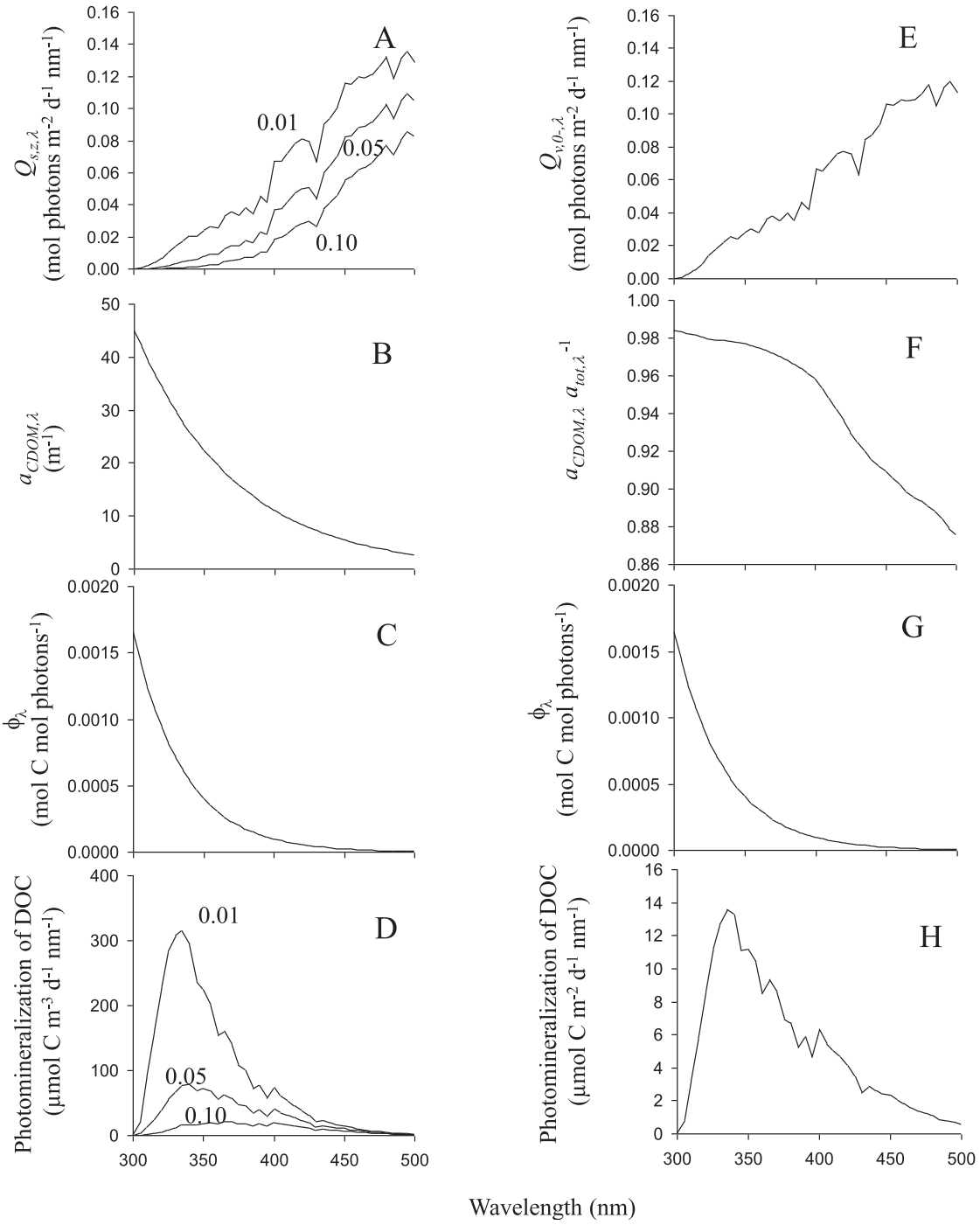

Fig. 7 Modeling the photochemical production of CO_2 from DOC in Lake Valkea-Kotinen at three depths (panels A–D, Eq. 1) and over the entire water column (panels E–H, Eq. 2). Volumetric CO_2 photoproduction rates at three depths: (A) Solar scalar photon flux density at the depths of 0.01, 0.05 and 0.10 m, (B) the absorption coefficient of CDOM, (C) the apparent quantum yield spectrum for CO_2 photoproduction, and (D) the action spectra for CO_2 photoproduction rates at the depths of 0.01, 0.05 and 0.10 m. Areal CO_2 photoproduction rate over the entire water column. (E) Vector photon flux density just below the surface, (F) the proportion of radiation absorbed by CDOM, (G) the apparent quantum yield spectrum for CO_2 photoproduction, and (H) the action spectrum for CO_2 photoproduction over the entire water column (Vähätalo et al., 2000).

Solar radiation spectrum responsible for photochemical reactions and the attenuation of photochemical rates with depth

The UV- and short wavelength visible part of solar radiation are mostly responsible for photochemical reactions in surface waters, as illustrated by the action spectra for CO_2 photoproduction in Fig. 7D and H. Although the UV-B radiation (290–315 nm) has high energy per photon, it contributes only 0.1% to the global radiation (290–3000 nm). Therefore, the less energetic but more abundant UV-A (315–400 nm, ca. 6% of global radiation) is often mostly responsible for photochemical reactions. The solar radiation peaks at the visible range of spectrum (400–700 nm, ca. 50% of global radiation), but at that range of spectrum the energy of photons is lower and much of the radiation is absorbed by suspended particles and by H_2O.

The short wavelength solar UV radiation contributes a lot to photoreactions in a narrow stratum close to surface (Fig. 7D). Such UV-radiation attenuates quickly in the water column and, therefore, radiation at longer wavelengths (UV-A and visible radiation) becomes more important for photochemical reactions at deeper depths (Fig. 7A and D).

The optical characteristics of water bodies regulate the attenuation of both the solar UV radiation into water columns and the photochemical reaction rates. Because solar UV-A radiation is often mostly responsible for the photochemical transformation of DOM, the attenuation of solar UV-A radiation into the water column approximates the attenuation of many photochemical reactions. Photochemical reactions can reach a depth of ~30 m in the most transparent water bodies, but they are limited into depths of less than 0.1–0.2 m in waters rich in suspended particles or CDOM as exemplified by Lake Valkea-Kotinen in Fig. 7. On solid surfaces, such as plant detritus or sediments, the solar UV radiation and photochemical transformations are limited to a very narrow (<1 mm) surface stratum.

The rates of photochemical reactions in the environment

In water bodies with high light extinction coefficients, CDOM absorbs solar UV radiation effectively and the rates of resulting photochemical reactions (such as photochemical production of CO_2) can exceed the corresponding rates of biological processes (such as respiration) in a narrow surface stratum (Cory et al., 2014). In these cases, photochemical rates also attenuate steeply with depth and their overall importance depends on the depth of the water column.

It is often more informative to examine the rates per area, as those rates give more information about the role of photoreactions on the biogeochemistry of whole ecosystems. Table 1 presents examples of areal rates of photochemical reactions measured directly, calculated according to Eq. (2) or from mass balances. The summertime rates for the photochemical mineralization of DOC range from 1000 to 24,700 μmol C m^{-2} day^{-1} in the 20 freshwaters exemplified in Table 1. In the perspective of the epilimnion or the

Table 1 Areal summertime rates for the photochemical production of CO_2, biologically available photoproducts (BAPs) and NH_4^+ over the entire water column.

Rate μmol m^{-2} day^{-1} (% of BR or BCD)	*Site (depth of integration)*	*References*
DOC → CO_2		
3700–4800[a] (>7–11% of BR)	Four lakes, Sweden (1.5–7.5 m epilimnia)	Granéli et al. (1996)
4200* (3% of BR)	Rio Negro, Brazil (50-m water column)	Amon and Benner (1996)
2690* (11% of BR)	Neusiedler See, Germany (1-m epilimnion)	Reitner et al. (1997)
1000* (30% of BR)	Lake Valkea-Kotinen (1-m epilimnion)	Vähätalo et al. (2000)
1700–2250[a]	Lake Skervatjern, Norway	Salonen and Vähätalo (1994)
1000[c]	Lake Tuscaloosa, United States	Vähätalo and Wetzel (2004)
3000–5000[c]	Seven lakes, Canada	Molot and Dillon (1997)
1100[c]	Parker River estuary	Pullin et al. (2004)
4200[c] (20% of BR)	Lake Öreträsket, Sweden (whole lake)	Pers et al. (2001)
1280[a,c] (31% of BR)	Lake Plěsné, Czech Republic (whole lake)	Kopáček et al. (2004)
24700[c] (1051% of BR)	Imnavait Creek, Alaska	Cory et al. (2014)
DOC → BAPs		
3800[c] (10% of BCD)	Lake Skärhultsjön (3.5 m epilimnion)	Bertilsson and Tranvik (1998)
780[c] (11% of BCD)	Lake Valkea-Kotinen (1-m epilimnion)	Vähätalo et al. (2003)
1600[c]	Parker River estuary	Pullin et al. (2004)
900–3000[c]	Coastal seawater 0–65°N	Miller et al. (2002)
570[a,c] (<20% of BCD)	Coastal	Moran and Zepp (1997)
3040[c] (129% of BCD)	Imnavait Creek, Alaska	Cory et al. (2014)
DON → NH_4^+		
29–44[c]	A coastal lagoon	Buffam and McGlathery (2003)
71[c]	Lake Valkea-Kotinen	Vähätalo et al. (2003)
16–102[c]	Offshore Baltic Sea	Vähätalo and Zepp (2005)
23–26[c]	Coastal Baltic Sea	Vähätalo and Järvinen (2007)

The rate of photochemical CO_2 production is given as a percentage of bacterial respiration (BR). The contribution of BAPs is given in percentages of bacterial carbon demand (BCD).

* = measured, [c] = calculated, [a] = mean annual rate.

BR = bacterial respiration = biological mineralization of DOC; BCD = bacterial carbon demand in the epilimnion.

entire water column, the photochemical mineralization of DOC typically corresponds to 3–31% of the biological mineralization of DOC, but in some cases exceeds bacterial respiration (Table 1).

Altogether, solar radiation mineralizes 13–35 Tg C $year^{-1}$ DOC directly to CO_2 in freshwaters and contributes 10% to the CO_2 evasion from inland waters (Koehler et al., 2014). Rivers transport photoreactive CDOM from the inland waters to the coastal waters. In the coastal waters, solar radiation mineralizes 31–58 Tg C $year^{-1}$ of the DOC transported by rivers (Aarnos et al., 2018). The mineralization of freshwater DOC is larger in the coastal than in the inland waters, because the mixing of CDOM from river water to low-CDOM seawater and the advection of river plumes over extensive areas facilitate the photochemical transformation of CDOM.

The photochemical production rate of BAPs ranges from 570 to 3800 μmol C m^{-2} day^{-1} and has often similar magnitude as direct photochemical mineralization to CO_2 in the examples reported in Table 1. The total impact of solar radiation on the mineralization of DOC consists of direct photochemical mineralization (DOC → CO_2) and microbial mineralization of BAPs (BAPs → CO_2). BAPs can satisfy 10–20% of bacterial carbon demand in the epilimnion or the mixed layer of coastal ocean (Table 1). The rates of photochemical production of ammonium from dissolved organic nitrogen are one to two orders of magnitude lower that the rates concerning DOC (Table 1).

Photochemistry, food webs and climate change

Responses of food webs to the photochemical transformation of organic matter

Bacteria are the primary consumers of dissolved organic matter and the first component of the food web to respond to the photochemical transformation of DOM (Cory et al., 2018). When photochemical reactions break down aromatic compounds into bioavailable substrates, bacterial communities may suppress the gene expression of enzymes for degradation of aromatic compounds (Nalven et al., 2020). Photochemically produced low molecular mass compounds are typically enriched in carbon relative to the essential N- or P-nutrients, and more oxidized than is CDOM before exposure to solar radiation (Fig. 1). Therefore, BAPs often support more respiration than the production of new bacterial biomass and result in a reduced bacterial growth efficiency. The BAPs favor bacterial strains, such as *Polynucleobacter necessarius* subspecies *asymbioticus*, which can efficiently consume them (Hahn et al., 2012). Bacterioplankton species consuming BAPs are most abundant during summertime when the concentration of BAPs is highest. When BAPs increase bacterial production, the increased production transfers first to the grazers of bacterioplankton (e.g., flagellates and ciliates) but can extend up to metazooplankton (*Daphnia*). The nutrients released from CDOM through photochemical reactions, such as nitrogen, phosphorus and iron, also support phytoplankton (Vähätalo et al., 2011).

Photochemical reactions can also decrease the bioavailability of organic matter, when they act on biologically labile organic matter such as proteins or other fresh organic matter produced by phytoplankton or macrophytes. For example, solar radiation can cross-link simple unsaturated fatty acids and NH_3 and consequently decrease the bioavailability of both carbon (fatty acids) and nitrogen (NH_3) substrates.

The same solar UV-radiation that transforms CDOM into biologically labile forms also causes harmful effects on organisms, for example via formation of thymidine dimers in DNA (pairing of two consecutive bases on one single strand), which can cause misreading during transcription or replication and even the stop of the replication. The sensitivity of organisms to UV-radiation varies and the net impact of UV-radiation on food webs depends on the balance between the beneficial and harmful effects.

Photochemical reactions and climate change

By deeply affecting the chemistry and hydrology of surface waters, climate change may modify the photochemical processes in aquatic environments (Vione and Scozzaro, 2019). For example, increased runoff exports CDOM from soils to the water bodies and causes browning of inland waters in the Boreal region. An increase in the DOC concentration usually slows down the phototransformation of pollutants. As suggested by Fig. 5, an enrichment in CDOM favors the CDOM(T_1)/$^1O_2$-induced processes at the expense of the $^{\bullet}OH/CO_3^{\bullet-}$ reactions and direct photolysis. For example, browning inhibits the $^{\bullet}OH$-induced transformation of phenylurea herbicides into toxic N-formyl compounds. In contrast, browning is expected to enhance the CDOM(T_1)-induced transformation of the drug (lipid regulator) metabolite clofibric acid into toxic 4-chlorophenol.

Additional predicted impacts of climate change are (i) increased summer stratification period in lakes; (ii) longer ice-free period, and (iii) alternation of water scarcity with flood events, because a similar amount of average precipitation will be distributed over fewer rainy days. (i) Water stratification enhances the photobleaching of CDOM, the penetration of sunlight, and the direct photochemical transformations in the epilimnion. At the same time, a larger amount of matter may be protected from photochemical transformation in the dark hypolimnion, and the photochemical turnover time in the perspective of the entire lake may increase. (ii) Compared to the albedo of water, the albedo of ice and snow is high and limits the sunlight available to photochemical reactions in aquatic systems. Therefore, a longer ice-free period will increase photochemical processes in the water column of lakes. This increase is highest during earlier melting of ice in spring, because sunlight is more intense than with delayed freezing in early winter. (iii) Water scarcity usually increases the importance of photochemical reactions. Decreasing water levels enhance photochemistry because sunlight reaches a higher fraction of the water column. In the case of rivers there would be the additional effect of a decreased water flow velocity during drought events. Therefore, the same river stretch could accommodate water for longer in water-scarcity conditions, which provides a longer time scale for photoreactions to operate. In some cases, enhanced photochemistry in rivers during droughts might offset the higher levels of contaminants that would result from lesser dilution of the wastewater inputs.

Conclusion

Photochemical reactions in sunlit surface waters modify the chemical properties of natural and anthropogenic organic matter and shift the speciation of metals. The rates of photochemical reactions can exceed those of other transformations carried out by biological or thermal abiotic processes in a narrow surface stratum or shallow waters. Photochemical transformations provide an ecosystem service by re-mineralizing organic matter and self-depolluting surface waters. Photochemical processes couple to biological processes and this interplay speeds up remineralization of organic matter. Photochemical transformations of organic matter partially support the aquatic food webs and modify their composition.

Knowledge gaps

Although many works have been published about photochemical reactions taking place in inland waters, several aspects of these processes still have to be completely understood. For instance, there is still debate about the chromophores and pathways that account for light absorption by CDOM, which is the main source of photochemical processes in surface waters. Moreover, the photoproduction mechanisms of some PPRIs by irradiated CDOM are still unclear, such as $^{\bullet}OH$ radicals. As far as the photodegradation of pollutants is concerned, there is need of additional data about phototransformation products and about their toxicity towards aquatic organisms. This kind of information would be helpful to assess the ecological impacts of photochemical reactions in inland waters. Finally, the evaluation of several real-case studies such as drought events, e.g., by means of modeling tools will allow for a better understanding of the effects of climate change on the photochemistry of surface waters.

See Also: **Human pressures and management of Inland Waters**: Emerging and Less Commonly Recognized Chemical Contaminants: Organic Micropollutants; The Role of Wetlands in Mitigating Impacts From Diffuse Agricultural Loads; **Structures and functions of Inland Waters - Groundwater**: Ecology of the Hyporheic and Parafluvial Zone; **Structures and functions of Inland Waters - Lakes**: Lacustrine Phosphorus Cycling; Measurement and Variability of Lake Metabolism; The Carbon Cycle in Lakes: A Biogeochemical Perspective; **Structures and functions of Inland Waters - Rivers**: Effects of Dams on Rivers; **Structures and functions of Inland Waters - Wetlands**: Wetland Soils: Physical and Chemical Properties and Biogeochemical Processes

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Chemosynthesis☆

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This is an update of A. Enrich-Prast, D. Bastviken, P. Crill, Chemosynthesis, in Encyclopedia of Inland Waters, edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00126-5.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Acetogenesis Synthesis of acetate as cell carbon from CO_2 via the acetyl-CoA pathway.
Anabolism Anabolic metabolism can be understood as a coordinated metabolic activity for construction processes in which macromolecules are synthesized, which results in the formation of more complex molecules from simpler ones, both for cell growth and for its maintenance.
Anaplerotic metabolism Inorganic carbon assimilation in central physiological pathways of cell metabolism. These include the presence of carboxylases, e.g., pyruvate carboxylase and phosphoenolpyruvate carboxylase which recycle and incorporate inorganic carbon into TCA cycle intermediates.
Anoxic Denotes the absence of molecular oxygen (O_2).
Autotroph Organism that derives the carbon needed for biosynthesis from inorganic molecules (carbon dioxide) independent of their energy source. *Photoautotrophs* and *chemoautotrophs* obtain their energy from sunlight and the oxidation of inorganic molecules respectively.
Bacterial growth efficiency The fraction of the total carbon in the metabolized substrates that is used for biomass production (the remainder is used for energy generation). Bacterial growth efficiency is usually calculated as the bacterial production divided by the sum of bacterial production and bacterial respiration.
Bacterial production Production of bacterial biomass C per time unit.
Carbon fixation The formation of organic biomolecules from inorganic carbon (e.g., CO_2).

☆*Change History*: November 2021. F Machado-Silva and C Signori were invited to new contributions. A Enrich-Prast, F Machado-Silva, D Bastviken, P Crill, and C Signori worked on the whole text. All sections have been updated, Table 3 has been updated, and Figure 6 has been included.

Catabolism Catabolic or oxidative metabolism is the metabolic activity used to degrade molecules to produce simpler constituents and energy. All biochemical reactions that aim to break down or unfold molecules to release of energy necessary to carry out various metabolic activities. It is in catabolism that carbohydrates, lipids and proteins, for example, are broken down into smaller, simpler products.
Chemolithotrophic heterotrophs Organisms that use energy from the oxidation of reduced inorganic compounds to support growth on organic substrates as carbon source.
Chemosynthesis Can be defined as the biological production of organic compounds from inorganic C-1 molecules (e.g., carbon dioxide and methane) and nutrients using the energy generated by the oxidation of inorganic (e.g., hydrogen gas, hydrogen sulfide, ammonium) or organic C-1 (e.g., methane, methanol).
Chemosynthetic mixotrophs Organisms that utilize at the same time CO_2 and organic carbon compounds as carbon source and/or organic and inorganic substrates as energy source.
Chemotrophs Organisms that use chemical reactions as energy source. *Chemoorganotrophs* or *chemolithotrophs* obtain their energy for biosynthesis or energy conservation via aerobic or anaerobic respiration from the oxidation for organic or inorganic molecules respectively.
Chironomids A family of non-biting midges. Larval stages can be found in surface sediments in most freshwater habitats. The larvae of some species are tolerant to low O_2 conditions.
Dark carbon fixation Term widely used in aquatic sciences and applies primarily to chemosynthetic reactions where organic matter production occurs without sunlight.
Electron acceptor A chemical entity that accepts electrons transferred to it from another compound. It is an oxidizing agent that, by accepting electrons, is itself reduced in the process.
Electron donor A chemical entity that donates electrons to another compound. It is a reducing agent that, by donating electrons, is itself oxidized in the process.
Endosymbiosis Term for a symbiotic relationship when one organisms live inside another organism and when both organisms benefit from this relationship.
Epilimnion The uppermost surface wind mixed water layer of a thermally stratified lake.
Fermentation The incomplete anoxic degradation of organic matter resulting in e.g., small organic acids, alcohols, H_2 or CO_2.
Heterotrophs Organisms relying on organic matter as their source of carbon.
Hypolimnion The bottom water layer in thermally stratified lakes positioned below the strong temperature gradient.
Metabolism Metabolism describe the various chemical reactions existing in organisms that ensure structural and energy needs, such as the synthesis and breakdown of biomolecules. The biochemical reactions can be classified into two major metabolic processes: anabolism and catabolism.
Mineralization The complete degradation of organic matter to CO_2 under oxic conditions, or CO_2 and CH_4 under anoxic conditions.
One-carbon (C-1) compounds Carbon dioxide (CO_2) and carbon monoxide (CO) are examples of inorganic molecules and methane (CH_4), methanol (CH_3OH), methylamine (CH_3NH_2) and methane thiol (CH_3SH) are examples or organic molecules.
Oxidation Describes the loss of electrons by a molecule, atom or ion.
Oxycline The steep O_2 concentration gradient that represent the border between oxic and anoxic environments.
Phototrophs Organisms that use sunlight as energy source.
Phylogeny The study of evolutionary relatedness among various groups of organisms.
Primary production The production of organic matter from carbon dioxide (CO_2).
Redox (Shorthand for reduction/oxidation reaction) describes all chemical reactions in which atoms have their oxidation number (oxidation state) changed.
Reduction Describes the gain of electrons by a molecule, atom or ion.
Syntrophic consortia Term for the aggregates of different microbial groups depending on each other for optimizing their metabolic energy yield. En example is H_2 producing fermenting bacteria living together with H_2 utilizing methanogenic or sulfate reducing bacteria. The organization into a consortium result in an efficient and rapid H_2 transfer to the H_2 utilizing bacteria and the rapid removal of H_2 increase the thermodynamic energy yield of the fermentation process.
Thermodynamic energy yield ($\Delta G_0'$) The amount of Gibbs free energy yielded in a chemical reaction.

Introduction

All known life forms depend on the biosynthesis of complex organic compounds. Hence, the capability to produce such biomolecules from abiotic carbon sources, e.g., one-carbon (C-1) compounds such as carbon dioxide (CO_2) and methane (CH_4) was, and still is crucial for the development of life. The formation of biomolecules from C-1 compounds, often referred to as carbon fixation or autotrophy, requires energy. *Chemosynthesis* can be defined as the biological production of organic compounds from C-1 compounds and nutrients using the energy generated by the oxidation of inorganic molecules, e.g., hydrogen gas, hydrogen sulfide, ammonium, or C-1 organic molecules, e.g., methane, methanol. This process contrasts with *photosynthesis*, a process in which organic compounds are synthesized from CO_2 using energy generated from sunlight radiation.

Table 1 Classification of microbial metabolism on the basis of energy source, the type of electron donor and the type of carbon source.

Energy source				
Chemical	*Chemo-*			
Light	*Photo-*			
Electron donor				
Inorganic		*-litho-*		
Organic		*-organo-*		
Carbon source				
CO_2			*-auto-*	
Organic			*-hetero-*	
Both			*-mixo-*	
				-troph

Reproduced from Overman J (2006) Principles of enrichment, isolation, cultivation and preservation of prokaryotes. In: Dworkin M, Falkow S, Rosenberg E, Schleifer K-H and Stackebrandt E (eds.) *The Prokaryotes*. (3rd edn.), vol. 1, pp. 80–136. New York: Springer.

Organisms that use sunlight as energy sources are called *phototrophs* and those that use chemicals are called *chemotrophs* (Table 1). Chemotrophs can be classified as *chemoorganotrophs* or *chemolithotrophs* depending on their use of organic or inorganic energy sources, respectively (Table 1). The term chemolithotroph literally means "chemical rock eaters" and is used to designate organisms that derive energy by the oxidation of inorganic molecules and the transfer of electrons either aerobically or anaerobically to other chemical acceptors for biosynthesis or energy conservation (Overman, 2006).

Many chemosynthetic organisms are usually referred to as *chemoautotrophs*. The term *autotroph* (self-feeding) denotes organisms that derive their metabolic carbon from CO_2 independent of their energy source. *Photoautotrophs* and *chemoautotrophs* obtain their energy from sunlight and the oxidation of inorganic molecules, respectively (Table 1). All chemoautotrophs are chemosynthetic organisms, but not all autotrophs are chemosynthetic.

Some chemosynthetic organisms can assimilate organic molecules, i.e., they are anabolically heterotrophic. There are also facultative chemolithoautotrophs that can grow autotrophically or heterotrophically depending on conditions such as substrate availability. Chemolithotrophic heterotrophs use energy from the oxidation of reduced inorganic compounds to support growth on organic substrates as carbon sources. Chemosynthetic mixotrophs are organisms that at the same time utilize CO_2 and organic carbon compounds as carbon sources and/or organic and inorganic substrates as energy sources. These classifications based on the energy and carbon sources and on electron acceptor utilization are reviewed in Table 1.

Redox processes associated with chemosynthesis are important drivers of many biogeochemical cycles and have profound roles in the production and cycling of climate forcing trace gasses such as CH_4 and N_2O. In addition, chemosynthetic processes have to be considered in studies regarding biochemical or microbial diversity, ecosystems and the origin of life on Earth. It is likely that the earliest self-sustaining metabolism was based on chemosynthesis. This hypothesis is supported by the fact that many of the deepest branching lineages of the phylogenetic tree contain chemoautotrophic organisms.

This chapter primarily focuses on autotrophic chemosynthesis, i.e., inorganic carbon fixation, and aims to present chemosynthesis from an inland water perspective. In aquatic sciences, the term "dark carbon fixation" is widely used and applies primarily to chemosynthetic reactions where organic matter production occurs without sunlight. Considerations of all existing processes associated with chemosynthesis, their biochemistry and the organisms involved is outside the scope of this chapter and can be found in the more specialized literature listed in Further Readings.

Carbon fixation pathways

The most studied CO_2 fixation pathways for chemosynthesis are the Calvin-Benson-Bassham cycle and the reductive acetyl-CoA pathway (also known as Wood-Ljungdahl pathway), of a total of six CO_2 fixation pathways. The other four pathways are the reductive tricarboxylic acid (rTCA) cycle, the 3-hydroxypropionate (3-HP) bicycle, the 3-hydroxypropionate/4-hydroxybutyrate (3-HP/4-HB) cycle and the dicarboxylate/4-hydroxybutyrate (DC/4-HB) cycle. The Calvin cycle is the only one observed in eukaryotes. Here the first step of CO_2 fixation is the Rubisco reaction combining CO_2 with the 5 carbon compound Ribulose-1,5-bisphosphate and forming a 6 carbon compound that is later cleaved into two molecules of glycerate 3-phosphate that are used in cellular anabolism. The reductive acetyl-CoA pathway leads to the fixation of CO_2 into acetate. This is the main pathway of acetogenic microorganisms. Methylotrophs can metabolize C-1 compounds as energy and carbon sources by three major assimilation pathways: (1) the Calvin cycle, (2) the Ribulose monophosphate (RuMB) pathway, and (3) the serine pathway (Fig. 1). For all aerobic methylotrophs, formaldehyde is a central intermediate, which is partly oxidized to CO_2 and is partly assimilated into cell carbon via the serine or RuMB pathways (Lindstrom, 2006). Other methylotrophs are able to oxidize C-1 compounds to CO_2 with subsequent assimilation via the Calvin cycle. For chemosynthetic sulfate-reducers the synthesis of acetyl-CoA from CO_2 has been demonstrated to occur via the citric-acid cycle or the CO-dehydrogenase pathway.

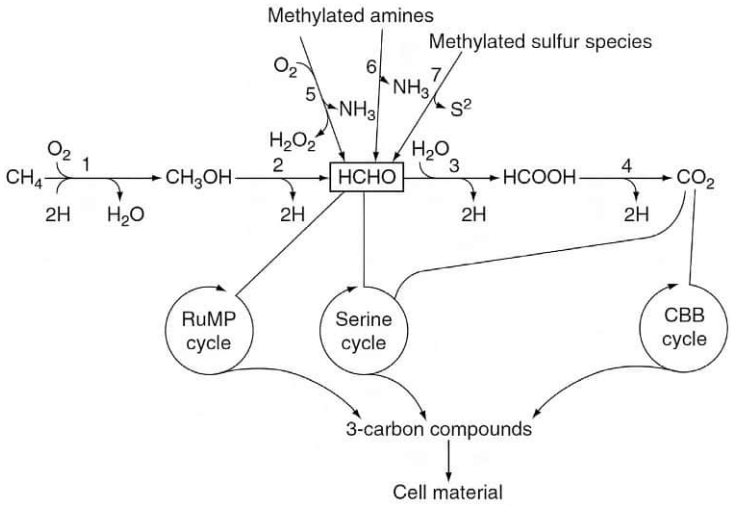

Fig. 1 Metabolism of one-carbon compounds in aerobic methylotrophic microorganisms. (1) Methane monooxygenase; (2) methanol dehydrogenase; (3) formaldehyde oxidation system; (4) formate dehydrogenase; (5) halomethane oxidation system; (6) methylated amine oxidases; (7) methylated amine dehydrogenase and (8) methylated sulfur dehydrogenase or oxidase. RuMB is ribulose monophosphate, CBB is the Calvin-Benson-Bassham cycle. For more information about RuMP, Serine, CBB and other carbon fixation pathways we refer to Dworkin et al. (2006). Some of the cycles such as CBB are also described in most general microbiology textbooks. Reproduced from Lindstrom ME (2006) Aerobic methylotrophic prokaryotes. In: Dworkin M, Falkow S, Rosenberg E, Schleifer K-H and Stackebrandt E (eds.) *The Prokaryotes* (3rd edn.) vol. 2, pp. 618–634. New York: Springer.

Energetics of chemosynthesis

Redox reactions involving the transfer of electrons from reduced compounds (*electron donors*) to more oxidized molecules (*electron acceptors*) are important in the energy metabolism of all organisms. Electron transfer in redox reactions is used both for ATP production and for acquiring reducing power for biosynthesis, e.g., production of NADPH. In this text, both mechanisms are included when considering the energy yield of the reaction. A limited number of inorganic redox reactions are used for chemosynthesis. Examples of such reactions, along with their thermodynamic energy yield ($\Delta G^{\circ\prime}$), are presented in Table 2. In general, chemosynthetic microorganisms grow very slowly, and growth rates may be limited by the energy yield of the associated redox reactions. However, energy limitation is not always the case. For example, the doubling time of anaerobic ammonium oxidizers (ANAMMOX) in the laboratory varies from 11 days to 3 weeks, a much higher value than for aerobic ammonium oxidizers, although the biomass yield and Gibbs free-energy change of both anaerobic and aerobic groups is approximately the same. This means that the low growth rate of ANAMMOX bacteria is not caused by inefficient energy conservation but by other constraints such as a low substrate conversion rate (Thauer et al., 1977).

Chemosynthetic organisms and associated redox processes

Chemosynthetic organisms are highly diverse in terms of phylogeny, substrate requirements, morphology, habitats, and metabolism. They can be strictly aerobic, strictly anaerobic, or facultative anaerobes. Similarly, some are strictly autotrophic, while others can metabolize either heterotrophically or mixotrophically depending on the environmental conditions and substrate availability. Major identified groups of chemoautotrophs and associated key processes are presented briefly below. It should be remembered that much of our information is based on studies of specific strains grown in the laboratory and many aspects of the organisms and their metabolism in situ are still unknown.

Ammonium and nitrite oxidizers

Since the first discovery of nitrification, this process has always been attributed to the action of a two-step aerobic chemosynthetic process in which ammonium is oxidized to nitrite, and nitrite is then oxidized to nitrate by ammonia oxidizers and nitrite oxidizers (Table 2). However, single nitrifiers that can oxidize ammonia to nitrate, complete ammonia oxidizers (COMAMMOX), have been identified and isolated (van Kessel et al., 2015). These microorganisms are members of the genus *Nitrospira* and have a higher affinity for ammonia than all studied ammonia-oxidizing bacteria and archaea but a low affinity for nitrite. The COMAMMOX metabolism is highly efficient, producing a high biomass yield per mol of ammonia oxidized. These microorganisms are widespread in terrestrial and freshwater habitats, but their relative activity in inland waters in relation to other groups of nitrifiers is still unknown.

Table 2 Examples of the principal redox reactions associated with chemosynthesis and their Gibbs free energy yields ($\Delta G_0'$).

Processes	*Substrates*[a]		*Products*	*$\Delta G_0'$ (kJ mol substrate^{-1})*[b]
Aerobic				
Methane oxidation[c]	$CH_4 + 2O_2$	→	$CO_2 + 2H_2O$	−818
Hydrogen oxidation	$2H_2 + O_2$	→	$2H_2O$	−237
Ammonium oxidation	$2NH_4^+ + 3O_2$	→	$2NO_2^- + 4H^+ + 2H_2O$	−275
Nitrite oxidation	$2NO_2^- + O_2$	→	$2NO_3^-$	−76
Sulfur oxidation	$H_2S + 2O_2$	→	$SO_4^{2-} + 2H^+$	−796
Sulfur oxidation	$2HS^- + 2H^+ + O_2$	→	$2S^0 + 2H_2O$	−209
Sulfur oxidation	$S^0 + 2H_2O + O_2$	→	$SO_4^{2-} + 4H^+$	−587
Thiosulfate oxidation	$S_2O_3^{2-} + H_2O + 2O_2$	→	$2SO_4^{2-} + 2H^+$	−823
Iron oxidation[d]	$4Fe^{2+} + 4H^+ + O_2$	→	$4Fe^{3+} + 2H_2O$	−31
Iron oxidation[d]	$4FeS_2 + 14H_2O + 15O_2$	→	$4Fe(OH)_3 + 16H^+ + 8SO_4^{2-}$	−164
Anaerobic				
Sulfate reduction	$4H_2 + SO_4^{2-} + H^+$	→	$HS^- + 4H_2O$	−152
Sulfite reduction	$3H_2 + SO_3^{2-} + 2H^+$	→	$H_2S + 3H_2O$	−173
Sulfite reduction	$H_2 + S^0$	→	H_2S	−34
Thiosulfate reduction	$2H^+ + S_2O_3^-$	→	$SO_3^{2-} + HS^- + H^+$	−22
Hydrogenotrophic methanogenesis	$4H_2 + CO_2$	→	$CH_4 + 2H_2O$	−131
Methanogenesis	$H_2 + CH_3OH$	→	$CH_4 + H_2O$	−113
Methanogenesis	$4CO + 2H_2O$	→	$CH_4 + 3CO_2$	−210
Methane oxidation[c]	$CH_4 + SO_4^{2-} + H^-$	→	$CO_2 + HS^- + 2H_2O$	−21
Methane oxidation[c]	$CH_4 + 2NO_3^- + 4H^+$	→	$CO_2 + N_2 + 4H_2O$	−766
Methane oxidation[c]	$CH_4 + 4NO_2^- + 8H^+$	→	$CO_2 + 2N_2 + 6H_2O$	−928
Acetogenesis	$4H_2 + 2CO_2$	→	$CH_3COOH + 2H_2O$	−95
Acetogenesis	$4CH_3OH + 2CO_2$	→	$3CH_3COOH + 2H_2O$	−93
Acetogenesis	$4H_2 + 2HCO_3^- + H^+$	→	$CH_3COO^- + 4H_2O$	−105
Ammonium oxidation (ANAMMOX)	$NH_4^+ + NO_2^-$	→	$N_2 + 2H_2O$	−238
Iron reduction	$H_2 + FeOOH + H^+$	→	$Fe^{2+} + 2H_2O$	−110
Manganese reduction	$2S^0 + 2H_2O + MnO_2$	→	$H_2S + SO_4^{2-} + 2H^+ + Mn^{2+}$	−297

The more negative $\Delta G_0'$, the greater the energy yield.

[a]The first substance is the electron donor and the last the electron acceptor.

[b]Standard Gibbs free energy ($\Delta G_0'$) in kJ mol substrate^{-1}, at pH 7 and 25 °C.

[c]The main carbon sources for all processes is CO_2. The main carbon sources for methane oxidizers are CH_4 or C-1 compounds.

[d]Calculations for Fe^{2+} at pH 2.

Modified from Thauer RK, Jungermann J, and Decker H (1977) Energy conservation in anaerobic chemotrophic bacteria. *Bacteriological Reviews* 41:100–180.

Nitrifiers fix CO_2 via the Calvin cycle but, to a minor extent, also via the phosphoenolpyruvate carboxylase pathway. Some nitrifiers use the reverse tricarboxylic acid cycle (TCA cycle), where CO_2 is eventually fixed into acetyl-CoA and pyruvate. By convention, the ammonium oxidizers are characterized by the prefix Nitroso- and the nitrite oxidizers by the prefix Nitro-, i.e., yielding strain names like *Nitrosomonas* and *Nitrobacter*, respectively. The two groups of gram-negative bacteria are not phylogenetically related. Some heterotrophic bacteria, fungi, and algae can also oxidize ammonium to nitrate in a process known as heterotrophic nitrification. This process depends on the oxidation of organic compounds and, distinct from chemosynthetic nitrification, is not related to energy generation. The relative importance of heterotrophic nitrification in inland waters has not yet been clarified (Ward, 2011).

Ammonium and nitrite oxidizers are slow-growing bacteria with doubling times that can vary from 7 to 10 h in the laboratory and up to weeks in natural environments depending on conditions (Andersson et al., 2006). Aerobic ammonium oxidation is regulated by oxygen and substrate availability, temperature, and pH. Under low oxygen tension, aerobic ammonium oxidizing bacteria can act mixotrophically using CO_2 and organic compounds as carbon sources and can also reduce nitrite (NO_2^-) to nitric oxide (NO) and nitrous oxide (N_2O). Ammonium oxidizers grow very well at low ammonium concentrations, and can survive ammonium starvation for up to a year. Under anoxic conditions, some ammonium and nitrite oxidizers can also denitrify.

Anaerobic ammonium oxidation (ANAMMOX) is utilized by members of the order Planctomycetales to oxidize ammonium using nitrite as the electron acceptor (Table 2). The bacteria that perform this process are very slow-growing organisms using different metabolic pathways compared to aerobic ammonium oxidizers, such as the use of nitrite as an electron acceptor for ammonium oxidation and as an electron donor for the reduction of carbon dioxide (Kuenen, 2008).

Sulfur reducers

Chemosynthetic sulfur-reducers transfer electrons to oxidized sulfur compounds, e.g., sulfate, in association with a respiratory type of energy conservation (Table 2). Sulfate reduction usually occurs via heterotrophic anaerobic respiration, i.e., oxidation of organic matter. However, sulfate-reducing bacteria are metabolically very versatile, and many can utilize H_2 as an electron donor to synthesize cell material from both acetate and CO_2 (mixotrophs) or only from CO_2 (chemolithoautotrophs). Some sulfate-reducing bacteria can use nitrate and nitrite as electron acceptors, even in the presence of sulfate. The end product of this reaction is ammonium and not N_2 as it is for denitrifiers. In the absence of sulfate or other inorganic electron acceptors, some sulfate reducers can grow by fermentation of several organic substrates (Li et al., 2018).

Sulfur oxidizers

Reduced sulfur compounds such as sulfide (H_2S), thiosulfate ($S_2O_3^{-2}$), tetrathionate ($S_4O_6^{-2}$), and elemental sulfur (S^0) are used as the electron donors by sulfur oxidizers (Table 2). Such organisms are capable of performing extensive chemosynthesis in inland waters having high concentrations of e.g., hydrogen sulfide, sulfide, and sulfur (Table 3). Reduced sulfur compounds are usually formed as a product of anaerobic heterotrophic respiration with sulfate, but some waters receive large inputs of sulfide via groundwater. Oxygen is the most common electron acceptor, but other potential electron acceptors such as nitrate have been proposed. Sulfur reducers and oxidizers can be active under extreme pH, temperature, and saline conditions. Phototrophic H_2S oxidizers use carbon dioxide as the electron acceptor, and evidence of light-dependent sulfide consumption across stratified environments suggests that this process should be pervasive rather than relying on the presence of other chemical oxidants (Hanson et al., 2013).

Iron and manganese oxidizers

In aquatic environments, iron and manganese are found both in oxidized (Fe^{3+} and Mn^{4+}) and reduced (Fe^{2+} and Mn^{2+}) forms depending on pH and O_2 concentrations (Table 2). Dissimilatory Fe^{3+} and Mn^{4+} reduction are processes by which microorganisms transfer electrons from the oxidized to the reduced form of the metal. Most Fe^{3+} reducers seem able to reduce Mn^{4+} as well. Fe^{2+} and Mn^{2+} are more soluble than Fe^{3+}. The oxidized forms (Mn^{4+} and Fe^{3+}) are highly insoluble at neutral pH but highly soluble at low pH. Recent studies indicate that sediment microorganisms may be able to access particle-associated Fe^{3+} in spite of its low solubility and that some freshwater environments have the potential for anaerobic oxidation of methane coupled to the reduction of iron and manganese mediated by particular groups of archaea and bacteria that play an important role in the regulation of methane fluxes (Bar-Or et al., 2017).

Methanogens

Methane-producing microorganisms belong to the Archaea domain and are called methanogens. Methanogens are strict anaerobes that can be found in a variety of environments across extreme pH, temperature, and salinity conditions. Methanogens are limited in their capacity to use different substrates, with acetate and CO_2/H_2 being the most common. The use of acetate is a heterotrophic process whereas hydrogenotrophic methanogens rely on H_2 as the electron donor and CO_2 as the carbon source and hence carry out a chemosynthetic process (Table 2). About half of the described species of methanogens are hydrogenotrophic. Methanogens are abundant in habitats with very low availability of oxygen, sulfate, nitrate, Fe^{3+}, and Mn^{4+}, i.e., competitive substrates. In the presence of these electron acceptors, methanogens are thermodynamically out-competed (Table 2) for reduced substrates, e.g., H_2 and acetate. Hydrogenotrophic methanogenesis contribution to total methane production varies from 0% to 100% in lake sediments, and temperature is one of its main regulating factors, as higher temperatures usually favor hydrogenotrophic methanogenesis (Conrad et al., 2007).

Methylotrophs

Methylotrophs are chemosynthetic microorganisms that can utilize C-1 organic molecules as their sole source of carbon and energy (Anthony, 1978). Methylotrophs are phylogenetically diverse, and they obligately require an available methylated compound (methylated amines, halogenated methanes, and methylated sulfur species). Many methylotrophs are capable of N_2 fixation and can use N_2 as a nitrogen source. Those methylotrophs capable of growth on methane are distinguished as methanotrophs. Methane is the main electron donor for methanotrophs, but other C-1 compounds like methanol, methylamine, or carbon monoxide, and formate can also be used. Limited amounts of CH_4 have been shown to be produced by bacteria by methylphosphonate degradation and demethylation of osmotica such as dimethylsulfoxide, methylamines, and methanol.

Methanotrophs

Methane oxidizers have been divided into two groups (Type I, II), depending on their internal cell structure and carbon assimilation pathway (Murrell, 2010). Type I assimilate C-1 carbon via the ribulose monophosphate cycle and are α-Proteobacteria, while Type II

Table 3 Examples of in situ chemosynthesis rates in various aquatic systems.

System	Primary Electron Donor[a]	Habitat[b]	Max S_2^-/NH_4^+/CH_4 (μM)[c]	Volumetric rate (mmol $m^{-3}day^{-1}$)	Areal rate (mmol m^{-2} day^{-1})	% of total C fixation	Area integration[a,d]	Notes[e]	Source
Scheldt estuary, Netherlands/ Belgium Tidal estuary	NH_4^+	w	nd/150/nd	0.01–3.6				Higher rates in freshwater part	1
Ilersjön, Sweden Eutrophic lake	CH_4	w	nd/nd/138	0–1.0	0.6–1.4	1–6	WL	MBP corresponded to 4–120% of HBP	2
Mårn, Sweden Eutrophic, humic lake	CH_4	w	nd/nd/56	0–1.0	0.1–0.6	2–7	WL	MBP corresponded to 2–39% of HBP	2
Lillsjön, Sweden Humic lake	CH_4	w	nd/nd/68	0–0.3	0.01	0.3–5	WL	MBP corresponded to 0.5–14% of HBP	2
Scheldt estuary, Netherlands Tidal estuary	S^{2-}, NH_4^+	sed	8000/2500/nd		3–36			Chemos corresponded to 18–32% of SOC	3
Deep Alpine Lake Maggiori, Italy	ns	w	nd/nd/nd	0.09($\pm$0.01)	5.5($\pm$0.4)	87		Deep Hypolimnon $\sim$350 m	4
Lake Cadagno, Switzerland Meromictic lake	ns	w	0.3/60/nd	20–188	260	ca 50	WL		5
Lakes Banyoles, Vilar, Cisó, Estanya, Spain Stratified with oxygen-sulfide interfaces	S^{2-}	w	2625/nd/nd	$<$188		ca 40			6
Ebro River salt wedge, Spain Estuary	ns	w	20/74/nd	0.5–10	2.4–5	37–61	ox/an		7
Lakes Vilar, Cisó, Estanya, Spain Sulfide-rich stratified lakes	S^{2-}	w	799/nd/nd		6.2–148.2	31–61			8
Lakes La Cruz, Lagunillo del Tejo, El Tobar, Arcas, Vilar, Spain Stratified karstic lakes	S^{2-}	w	950/198/nd	$<$82		3.8–31.4			9
Big Soda Lake, United States Saline lake	ns	w	12,059/2500/ nd		2.5–57	1–72	1 m^2	Chemos 30% of C fixation annually	10
Photic Zone at Lake Candagno	S^{2-}	w	430/nd/nd	6.3($\pm$2.5)		10($\pm$2)	ox/an	Chemosynthesis corresponds to 10% of CO2 fixation of phototrophic sulfur bacteria	11
Flathead Lake, EUA	NH_4^+	w	nd/nd/nd	0.08				Oligotrophic lake	12
Rhône river estuary, France Non-tidal estuary	NH_4^+	w	nd/10/nd	0.02–0.15				Higher rates in freshwater part	13
Lake Cisó, Spain Monomictic lake, gypsum rich drainage area	ns	w	5000/nd/nd		5.8–141	11–75	1 m^2		14
L Kinneret, Israel Monomictic lake	S^{2-}	w	382/79/nd	0.8–80	26–44	8–92	ns	Chemos 20–25% of C fixation annually	15
Solar Lake, Sinai Saline lake, seepage from sea into lake	S^{2-}	w	1000/nd/nd	0–35		Up to 33	WL		16
Saanich inlet, Canada Stratified fjord	ns	w	15/nd/nd	0–2					17

L Mekkojärvi, Finland Humic, acidic lake	ns	w	nd/29/nd	0–7.5		>50 during stratification	ns		18
Coromina lagoon in karstic lacustrine system of Lake Banyoles, Spain	S^{2-}/CH_4	w	450/nd/nd	7.2–17.2	26–41.2	39–61		Maximum rates at chemocline	19
Lake Baikal, Russia Large, deep, permanently stratified	ns	sed	nd/20/nd		0.03–0.1	<2	1 m^2		20
Antarctic Subglacial Lake Whillans	ns	w	nd/nd/nd	0.003				sulfide oxidation	21
Antarctic Subglacial Lake Whillans	ns	sed	nd/nd/nd	0.008				sulfide oxidation	21
Meromictic karstic Lake Banyoles in Catalonia (Spain)	S^{2-}	w	nd/nd/nd	0.1–0.2		3–9		Epilimnion, higher rates and relative contribution in winter than summer	22
Meromictic karstic Lake Banyoles in Catalonia (Spain)	S^{2-}	w	nd/nd/nd	0.3–12		52–83		Chemocline, higher rates and relative contribution in winter than summer	22
Meromictic karstic Lake Banyoles in Catalonia (Spain)	S^{2-}	w	nd/nd/nd	0.3–2		70–73		Hypolimnon, higher rates and relative contribution in winter than summer	22
Boreal lakes (4), Sweden Thermally stratified seasonally	ns	sed	nd/nd/nd		0.2–4.2			Chemos corresponded to 8–37% of HBP and 3–16% of SOC	23
Tropical lakes (7), Brazil Shallow non-stratified water column	ns	sed	nd/nd/nd		0.01–1.7			Chemos corresponded to 0.4–80% of HBP and 0.1–9% of SOC	23
Tropical lakes (9), Brazil Shallow non-stratified water column	ns	sed	nd/nd/nd		0.1–1.2			Chemos corresponded to 0.3–3% of HBP and 0.01–0.8% of SOC	24
Polar Meromictic Lake Bol'shie Khruslomeny at the White Sea Coast	S^{2-}/CH_4	w	17,000/nd/1000	0.4–2.83		ca 25		Higher rates below ice than in upper mixed layer in summer	25
Polar Meromictic Lake Bol'shie Khruslomeny at the White Sea Coast	S^{2-}/CH_4	w	17,000/nd/1000	8.0–8.9		100		Chemosynthesis peak in chemocline in both winter and summer. Higher rates in winter	25
Polar Meromictic Lake Bol'shie Khruslomeny at the White Sea Coast	S^{2-}/CH_4	w	17,000/nd/1000	2.9–7.7		100		Hypolimnion displayed higher rates in winter during ice cover	25
Guanabara Bay, Brazil Eutrophic estuary	ns	w	nd/nd/nd	0–0.0005				Chemos corresponded to <5–89% of HBP	26
Rodrigo de Freitas Lagoon, Brazil Eutrophic and impacted lagoon	ns	w	nd/nd/nd			30–43		Chemos corresponded up to 10% of HBP	27
Rybinsk reservoir, Russia Hydroelectric reservoir on the Volga River	ns	w		0.03–1.8				Chemos up to 50% of microbial production in bottom layers and 1–2% in non-stratified water column	28
Kuybyshev reservoir, Russia Hydroelectric reservoir on the Volga River	ns	w	132/nd/nd	0–2.3		5	1 m^2	Chemos limited by O_2 and CH_4 or H_2 concentrations	28
L Belovo, Russia Meromictic lake	S^{2-}	w	4471/nd/nd	0–2.3					29

(*Continued*)

Table 3 (Continued)

System	Primary Electron Donor	Habitat	Max S_2^-/ NH_4^+/CH_4 (μM)	Volumetric rate (mmol $m^{-3}day^{-1}$)	Areal rate (mmol m^{-2} day^{-1})	% of total C fixation	Area integration	Notes	Source
L Gek-Gel, Russia Meromictic lake	S^{2-}	w	79/111/nd	0–1.6	18	99	ns		29
L Maral-Gel, Russia Meromictic lake	S^{2-}	w	7/nd/nd	0–4.2					29

Sources: (1) Andersson et al. (2006), (2) Bastviken et al. (2003), (3) Boschker et al. (2014), (4) Callieri et al. (2014), (5) Camacho et al. (2001), (6) Casamayor (2010), (7) Casamayor et al. (2001), (8) Casamayor et al. (2008), (9) Casamayor et al. (2012), (10) Cloern et al. (1983), (11) Di Nezio et al. (2021), (12) Dodds and Priscu (1991), (13) Feliatra and Bianchi (1993), (14) Garcia-Cantizano et al. (2005), (15) Hadas et al. (2001), (15) Jorgensen et al. (1979), (16) Juniper and Brinkhurst (1986), (17) Kuuppo-Leinikki, and Salonen (1992), (18) Llirós et al. (2011), (19) Maerki et al. (2006), (20) Mikucki et al. (2016), (21) Noguerola et al. (2015), (22) Santoro et al. (2013), (23) Santoro, et al. (2021), (24) Savvichev et al. (2020), (25) Signori et al. (2018), (26) Signori et al. (2020), (27) Sorokin (1964), (28) Sorokin (1970).

[a]ns denote not specified.

[b]w indicates water column and sed denotes sediment.

[c]nd denote no data.

[d]WL denotes that area integration was made on a whole lake basis taking the volumes of different water layer into account. 1 m^2 denotes that a 1 m^2 water column was used, and ox/an indicates that depth integration was made over the oxic/anoxic interface only.

[e]Chemos, MBP, HBP, SOC denote chemosynthesis, methanotrophic bacterial production, heterotrophic bacterial production, and sediment oxygen consumption, respectively.

Modified from Enrich-Prast A, Bastviken D and Crill PM (2009) Chemosynthesis. *Encyclopedia of Inland Waters*, pp. 211–225. Oxford Elsevier.

assimilate C-1 compounds via the serine pathway and are γ-Proteobacteria. Both types utilize the enzyme methane-monooxygenase (MMO) to oxidize methane to methanol. Methanotrophs are found in most environments with both methane and O_2. Methanotrophs generally are able to oxidize ammonium to nitrite, while some ammonium oxidizers can oxidize methane and incorporate some methane as cell material, but methanotrophs and ammonium oxidizers are taxonomically different (Strous and Jetten, 2004).

Anaerobic methane oxidation has been reported in sediments and the water column in inland waters (Deutzmann et al., 2014). This process appears to be mediated by microbial consortia as some isotopic studies suggested that methane is not directly utilized by sulfate- or nitrate-reducing bacteria. Methanogens may incorporate light CO_2 from methane oxidation into their cell material or may use some of the light CO_2 produced by the anaerobic oxidation to make the very highly depleted CH_4 (>−100‰) (Bastviken et al., 2003; Sanseverino et al., 2012), which is seen in some marine and freshwater sediments. The presence of multiple active pathways of anaerobic methane oxidizers is associated with the availability of different electron acceptors in reduced river beds, including nitrite, nitrate, sulfate, and ferric iron (Table 2). Nitrite and nitrate-dependent anaerobic oxidation of methane could be the most important in regulating methane emissions from sandy riverbeds (Shen et al., 2019). The diversity of pathways is greatest where methane concentration is highest, suggesting a link between the diversity of anaerobic methane oxidation pathways and methane availability.

Hydrogen oxidizers

Molecular hydrogen (H_2) is a powerful electron donor in cellular metabolism in both prokaryotes and eukaryotes. The capability of using H_2 is spread across many taxonomic groups of different and independent phylogenetic origins. Hydrogen oxidation occurs in restricted habitats and is catalyzed by hydrogenase enzymes. Aerobic hydrogen oxidizers, sulfate reducers, methanogens, acetogens, and cyanobacteria are some groups that metabolize H_2. The main biogenic source of H_2 is anaerobic metabolism and the fermentation of organic matter in sediments. However, the H_2 turnover time in sediments is estimated to be on the order of 2 min, and therefore, almost all H_2 that is produced in the sediment is rapidly consumed. H_2 concentrations in lake sediments vary from 1 to 150 nM. The main sedimentary H_2 consumers that have been studied are methanogens and sulfate-reducing bacteria, and both groups compete for H_2. Sulfate reducers out-compete the methanogens in the presence of sulfate because they have a higher affinity for H_2 and there is a higher thermodynamic yield for the reaction and thus a higher growth yield (Table 2). The occurrence of one or the other process seemingly depends on sulfate availability which is often low in most inland waters but not in coastal environments. The importance of and competition for H_2 in anoxic microbial metabolism is illustrated by the development of consortia of fermenters and H_2 oxidizers. Such consortia facilitate "interspecies hydrogen transfer," a process whereby H_2 that is produced by the fermenter is rapidly transported to the H_2 consumer. This favors the H_2 consumer and keeps H_2 concentrations low, which increases the energy yield of the fermentation.

As demonstrated in the field and laboratory-based investigations, soil bacteria consume molecular hydrogen (H_2) from the Earth's atmosphere and serve as the main sink in the global biogeochemical H_2 cycle. Hydrogenases catalyze the conversion of H_2 to protons and electrons. Recent genomic and metagenomic studies have identified other bacteria within the phyla Acidobacteria, Proteobacteria, Planctomycetes, Chloroflexi, and Verrucomicrobia. Recent evidence shows acidobacteria are active and abundant members of diverse atmospheric H_2-oxidizing communities detected in temperate soils (Giguere et al., 2021).

Acetogens

Acetogens are organisms that utilize the acetyl-CoA pathway for the synthesis of acetate as cell carbon from CO_2. Homoacetogen is a more specific term and is often used to describe organisms that only produce acetate. However, most acetogens that use the acetyl-CoA pathway often form products other than acetate, such as butyrate, succinate and ethanol. Acetogens are anaerobes, but they can tolerate small amounts of O_2. Acetogens can grow chemoautotrophically on H_2, but also heterotrophically depending on environmental conditions (Table 2). Because CO_2 is the most common terminal electron acceptor for acetogens, CO_2 availability may regulate their growth and determine what substrate will be metabolized. However, other electron acceptors can also be used, allowing these microbes to adapt to a wide range of redox conditions and optimize their growth efficiency. Their competitive ability for H_2 increases when alternate electron acceptors, e.g., nitrate, are used.

Spatial and temporal distribution of chemosynthesis in aquatic environments

Chemosynthesis depends on the presence of both reduced and oxidized compounds to be used as electron donors and acceptors, respectively. At oxic-anoxic interfaces, the simultaneous access to reduced and oxidized substrates, e.g., S^{2-}, NH_4^+, or CH_4, and O_2, creates thermodynamic gradients that can support chemosynthesis (Schlegel and Jannasch, 2006; Stahl et al., 2006). However, electron acceptors other than O_2, such as NO_3^-, SO_4^{2-}, Fe^{3+}, can also be used, and thereby, other interfaces, e.g., the sulfide-nitrate interface, may also be important (Figs. 2 and 3). In general terms, chemosynthesis is expected to be most extensive at sites with steep redox gradients like sediments (Stahl et al., 2006; Santoro et al., 2021) and stratified water columns (Schlegel and Jannasch, 2006; Stahl et al., 2006; Casamayor et al., 2008) and can also exist over small scales within microbial mats, biofilms, and crumbs of organic matter in more oxic environments (Fig. 2). In stratified lakes, a more significant contribution of carbon production through chemosynthesis would come from chemoclines. They have steep redox gradients where the energy yield of redox reactions must

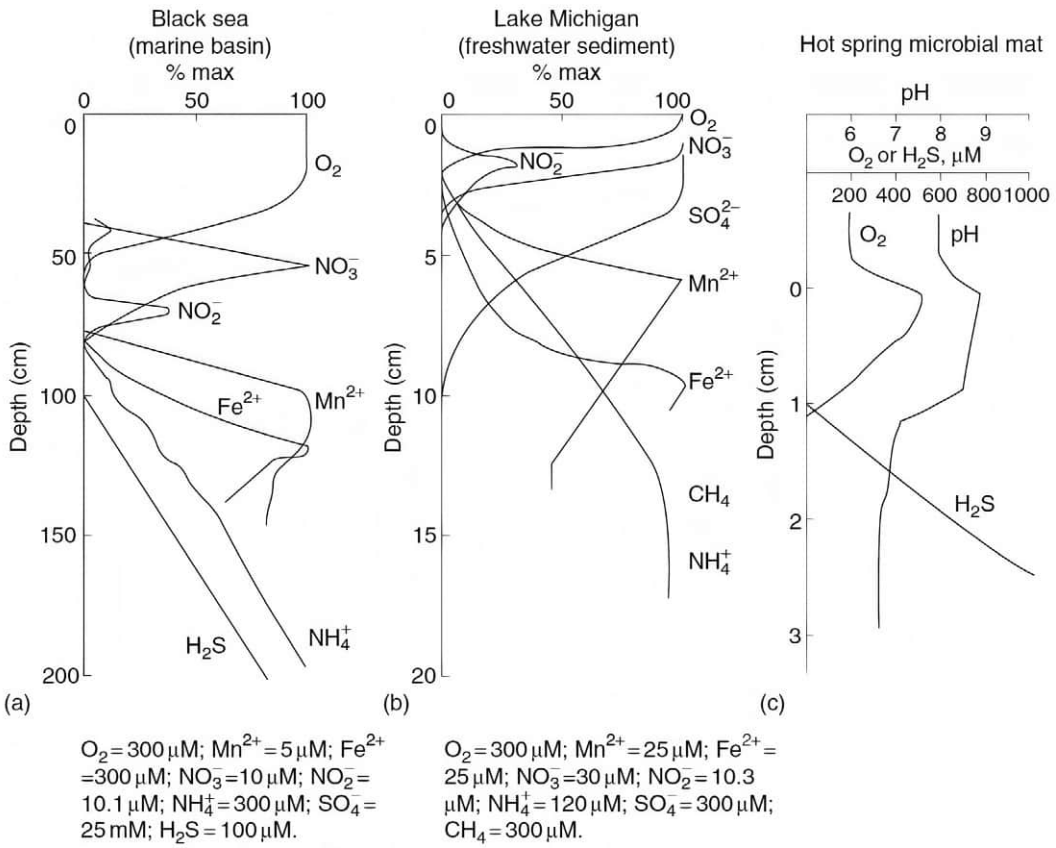

Fig. 2 Distribution of oxidized and reduced compounds related with chemosynthesis at: (A) the water column from the Black Sea; (B) the sediment from Lake Michigan and (C) a hot spring microbial mat. The scales vary from hundreds of meters in the water column, to centimeters and millimeters at the sediment and microbial mat respectively. Note the different scales at the y-axis. Reproduced from Stahl DA, Hullar M and Davidson S (2006) Prokaryotes and their habitats. In: Dworkin M, Falkow S, Rosenberg E, Schleifer K-H and Stackebrandt E (eds.) *The Prokaryotes*. (3rd edn.), vol. 1, pp. 299–327. New York: Springer.

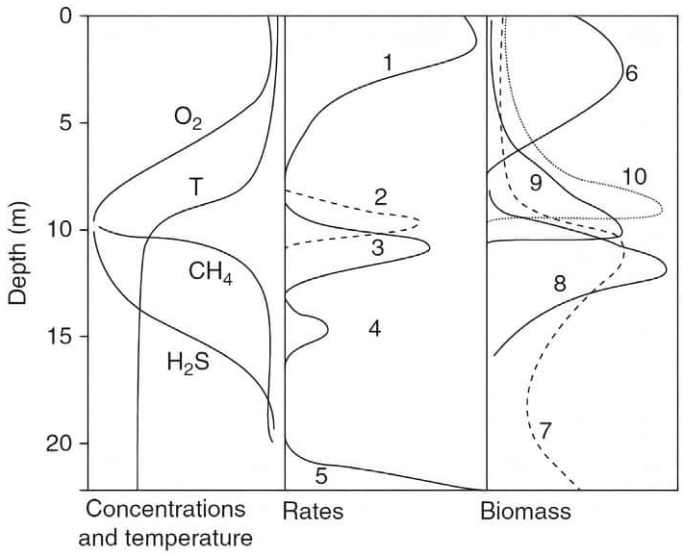

Fig. 3 Idealized vertical profiles in a temperate lake during summer stratification according. Note that this illustration is conceptual only and that absolute concentrations, rates, or biomasses are not given. Profiles: (1) CO_2 fixation in the light (oxygenic photosynthesis); (2) dark CO_2 fixation; (3) CO_2 fixation in the light (anoxygenic photosynthesis); (4 and 5) sulfate reduction; (6) biomass of algae and cyanobacteria; (7) total bacterial biomass; (8) biomass of phototrophic bacteria; (9) biomass of protozoa and (10) biomass of Copepoda and Cladocera. Chemosynthesis is directly related with profiles 2, 4, 5, 6 and 7 and indirectly with profiles 9 and 10 as microbial biomass formed via chemosynthesis is consumed by predators. From Schlegel HG and Jannasch HW (2006) Prokaryotes and their habitats. In: Dworkin M, Falkow S, Rosenberg E, Schleifer K-H and Stackebrandt E (eds.) *The Prokaryotes*. (3rd edn.), vol. 1, pp. 137–184. New York: Springer.

support effective CO_2 uptake rates. Inland waters with seepage of reduced compounds of geochemical origin can also be important for chemosynthesis. Examples include hot springs and lakes fed by sulfide-rich groundwater (Yang et al., 2011).

Chemosynthesis seems to be a quantitatively important carbon fixation pathway in shaded ecosystems. Caves are a very appropriate environment for chemosynthesis. For instance, the Movile Cave in Romania is flooded by thermomineral groundwater that is completely anoxic with high amounts of CH_4 and H_2S. Microbial mats can be seen on the water surface, and the cave ecosystem is supported exclusively by chemoautotrophic production of methane- and sulfur-oxidizing bacteria. Some studies reported that the Frasassi caves in Italy and both the Lower Kane Cave and Cesspool Cave in the USA are also important sulfidic ecosystems sustained via chemosynthesis (Kumaresan et al., 2014).

Direct studies of in situ chemosynthesis in inland waters (usually measured as dark fixation of $H^{14}CO_3$) have mostly addressed oxic-anoxic interfaces in sulfide-rich water columns (Table 3). These studies confirm a highly stratified distribution of the chemosynthesis with the highest rates of radiocarbon incorporation at the oxic-anoxic interface. Some cases also suggest considerable chemosynthetic activity in the anoxic water below the interface (Figs. 3 and 4). The most likely explanation for anoxic chemosynthesis is that electron acceptors other than O_2 are being used deeper in the anaerobic water column or are being supplied by high temperature water-rock interactions. The stratified location of the associated redox processes implies that chemosynthesis is generally most extensive in narrow zones at redox interfaces under field conditions (Fig. 4).

Due to the limited number of systems in which chemosynthetic carbon fixation has been measured, the spatial distribution of chemosynthesis among different types of inland waters is poorly known at present. Very high rates of chemosynthesis have been measured in saline sulfide-rich water columns (Table 3), but comparable methods to estimate chemosynthesis have so far rarely been reported from sulfide-poor water columns, where chemosynthesis associated with other redox reactions could dominate. Increasing ammonium oxidation associated chemosynthesis with decreasing salinity along the Scheldt estuary (see Table 3) indicates that sulfide and ammonium may be important electron donors for chemosynthesis in different environments. It has also been proposed that sulfide oxidizers could thermodynamically out-compete ammonium oxidizers in sulfide-rich environments. Substantial chemosynthesis associated with electron donors other than sulfide is possible.

In some aquatic systems, chemosynthetic processes appear to account for a major share of the total carbon fixation and may exceed 90% of the total carbon fixation under certain conditions (Table 3), contributing significantly to primary productivity and as a relevant energy source for aquatic food webs. The highest rates have been reported for saline sulfide-rich environments, such as mono- or meromictic lakes with haloclines from temperate and boreal regions. Lakes fed by sulfide-rich groundwater also have high rates of chemosynthesis. In contrast, other aquatic ecosystems such as estuaries, lagoons and rivers that often lack chemoclines usually have relatively lower rates of chemosynthesis, although the relative contribution of chemosynthesis in these systems may

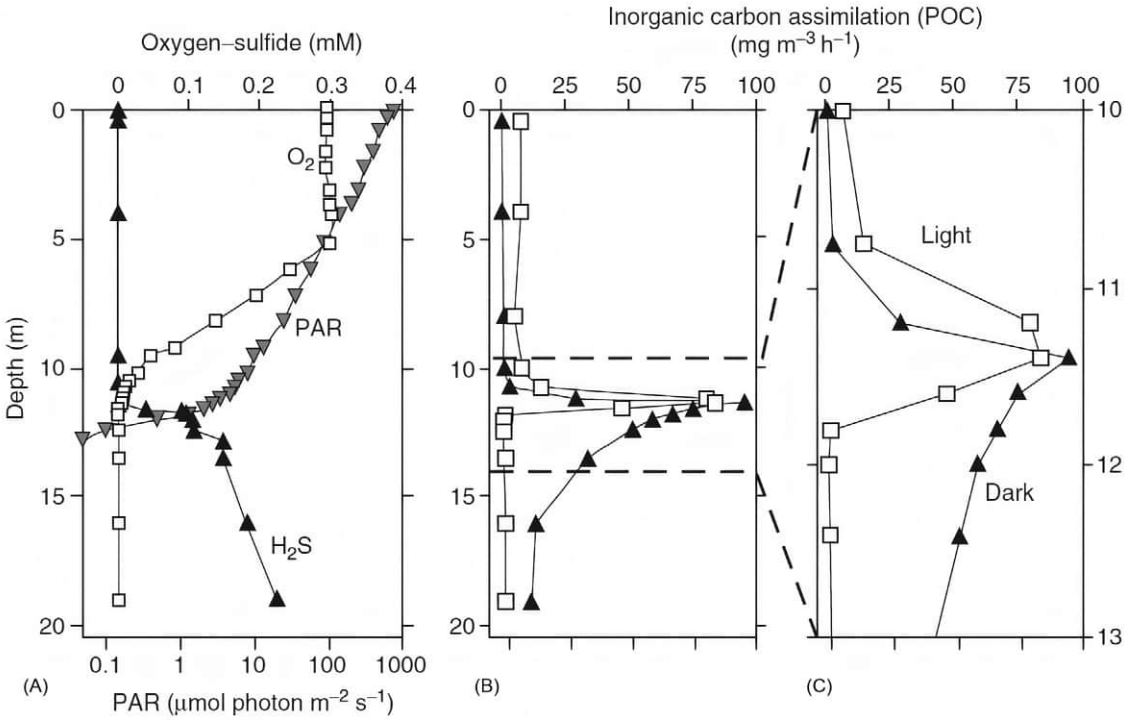

Fig. 4 Concentrations of H_2S and O_2, and PAR (A), and light versus dark CO_2 fixation (B) in Lake Cadagno, Switzerland, September 13, 1999, at noon. (B_1) represent detailed rates from B between 10 and 13 m. Reproduced from Camacho A, Erez J, Chicote A, Florín M, Squires MM, Lehmann C and Backofen R (2001) Microbial microstratification, inorganic carbon photoassimilation and dark carbon fixation at the chemocline of the meromictic Lake Cadagno (Switzerland) and its relevance to the food web. *Aquatic Sciences* 63: 91–106.

vary spatially and can be important when compared to other microbial processes like heterotrophic bacterial production and oxygen consumption (Table 3). However, the identification of carbon fixation in the dark in extremely heterogeneous environments and in close relation to the hydrological cycle remains a challenge due to the small spatial and time scale intensification of biogeochemical processes, also referred to as hotspots and hot moments. More efforts are needed to improve our understanding of the extent to which chemosynthesis contributes to total CO_2 fixation in inland waters and sediments.

Sediment-water interfaces of aquatic environments offer sites of rapid organic matter deposition and degradation. In many cases, organic matter inputs are faster than the oxygen diffusion into the sediment, and microbial activity may deplete oxygen in the superior millimeters, creating a steep thermodynamic chemical gradient with high chemoautotrophic potential. In Subglacial Lake Whillans in Antarctica, dark carbon fixation is at least three times higher in the sediment than in the water column due to a diverse microbial community consisting of bacteria and archaea that are close relatives of species known to use reduced compounds of N, S, or Fe, and CH_4 as energy sources (Mikucki et al., 2016). Some chemosynthetic processes can reach rates up to three orders of magnitude higher in the sediment (dominated by diffusional processes) than in the water column (dominated by advective processes), favored by a combination of different factors that influence the formation of microhabitats and consequently the reduction or oxidation of chemical elements. An extensive microbial metabolism in the anaerobic sediment below the top centimeter indicate that the anaerobic chemoautotrophic processes below the oxic surface layer may be relevant for the overall sediment processes of tropical lacustrine systems (Santoro et al., 2021). Dark carbon fixation may be greater in the sediment than in the water column at volumetric rates; however, rates per area should be used for standardized comparison between habitats.

Although symbiosis is well known and much more investigated in marine ecosystems, chemosynthesis can occur inside macrofauna in inland waters. Peat mosses (*Sphagnum* sp.) can have methane oxidizers in their tissue which seems to be associated to water table level (Putkinen et al., 2012). Mussels of the genus *Congeria* from Late Miocene of Lake Pannon, an ancient lake in eastern and central Europe had large, heavy shells that likely formed with chemosymbiosis and suggest a long-life span that contrasts with the extant genus *Mytilopsis*, which tends to form temporary boom-and-bust populations during cyclic shifts in the epilimnion/hypolimnion when carbon uptake is favored by chemosynthesis production (Harzhauser and Mandic, 2004). Anchialine caves in the Yucatan peninsula characterized by steep chemocline showed evidence of *Typhlatya* shrimp harboring endosymbiotic mutualistic bacteria and taking advantage of chemosynthesis to survive under extreme conditions (Pakes et al., 2014).

The temporal distribution of chemosynthesis is related to the development of redox gradients. Water column studies indicate chemosynthesis is most extensive during stratification, which usually depends on seasonality. The turbulence of advective processes is reduced, and slower diffusional processes allow the development of the necessary thermodynamic/redox gradients. In sediments overlain with oxic water, redox gradients are likely to be permanently present, although the oxygen penetration and consequently the depth of the redox interfaces may vary over time due to hydrodynamics combined with other environmental conditions, e.g., turbulent mixing, insolation, and wind. Dark carbon fixation may be greater during winter stratification than in summer, when ice cover promotes more stable conditions that favor steeper redox gradients and low light decrease competition with photosynthetic microorganisms for dissolved components (Table 3).

Implications of chemosynthesis in aquatic ecosystems

Chemosynthesis and carbon cycling

The highly stratified distribution of free-living chemosynthetic microorganisms implies that intensive rates of chemosynthesis can be spatially restricted. In some systems, chemosynthetic processes appear to account for a major share of the total carbon fixation and may exceed 90% of the total carbon fixation under certain conditions (Table 3). The highest rates have been reported for saline, sulfide-rich environments, such as mono- or meromictic lakes with haloclines. Lakes fed by sulfide-rich groundwater also have high rates of chemosynthesis. Saline inland waters with haloclines may dominate globally in terms of water volume, especially if the Caspian Sea, Lake Baikal, the African rift lakes, and large estuaries such as the Baltic Sea are included in the accounting. However, inland waters without haloclines and with moderate to low concentrations of sulfide are more abundant by numbers. The limited data from such non-saline inland waters makes it unclear to what extent chemosynthesis contributes to the total CO_2 fixation.

The contribution of chemosynthesis to overall carbon fixation in aquatic ecosystems is limited by the availability of electron donor substrates, e.g., sulfide, ammonium, etc. In most inland waters, the electron donors that are the energy source for chemosynthesis typically originate from the degradation of organic matter. Organic matter is typically produced by photosynthesis, either in the aquatic system itself or in the terrestrial surroundings transported to the aquatic environment. Hence, from an energetic point of view, most chemosynthesis in inland waters is indirectly driven by sunlight energy, given the dependence of chemosynthesis on photosynthesis supplying organic material (Fig. 5). An exception would be systems with an extensive supply of electron donors from hydrothermal or geochemical external sources (Yang et al., 2011). Therefore, chemosynthesis should only be able to dominate carbon fixation relative to aquatic photosynthesis in (1) systems receiving substantial input of organic matter from the surroundings, or (2) systems with large inputs of reduced substrate compounds directly suitable as electron donors, e.g., waters receiving reduced compounds of geochemical origin such as hot springs or some saline sulfide-rich lakes.

In addition to chemosynthesis, heterotrophic inorganic carbon uptake has been reported for a wide range of organisms from prokaryotes and fungi to vertebrates, compensating for dependence on organic matter (Braun et al., 2021). More than 20 carboxylases are known to form an integral part of the central and peripheral metabolic pathways of heterotrophic metabolism, e.g., in gluconeogenesis, the synthesis of fatty acids, amino acids, vitamins, nucleotides, the assimilation of leucine, and anaplerosis.

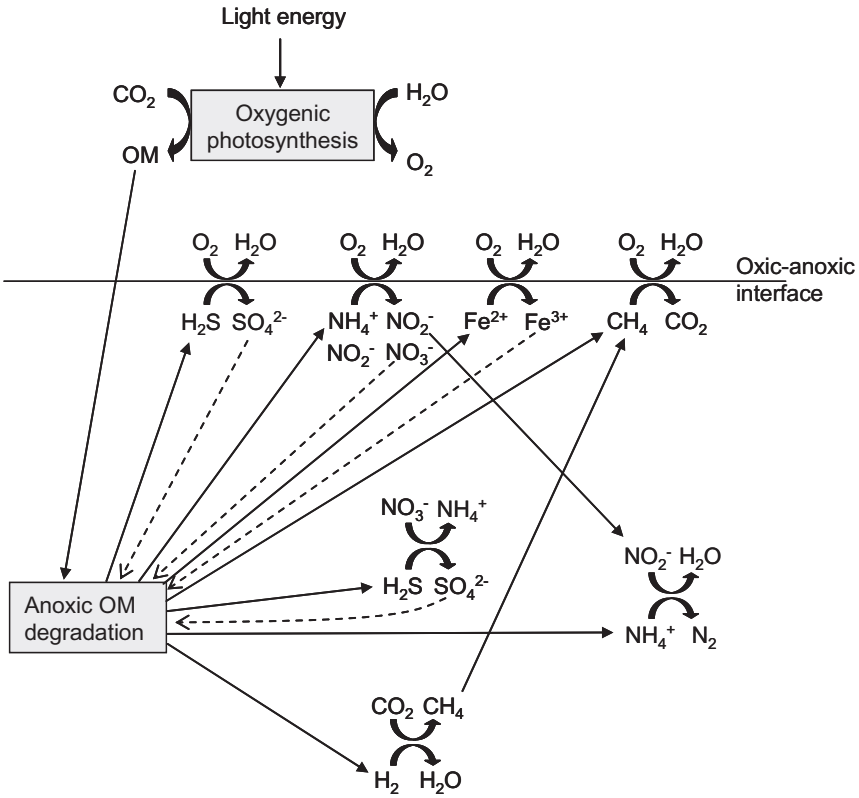

Fig. 5 Illustration of the connections between some redox processes associated with chemosynthesis and anoxic organic matter (OM) degradation. Solid arrows indicate contribution of reduced compounds produced by anoxic OM degradation processes. These reduced compounds function as electron donors in the redox processes associated with chemosynthesis. The contribution of OM (functioning as electron donor in anoxic OM degradation) from oxygenic photosynthesis is also indicated. Note that OM can be both produced in the aquatic system (aquatic photosynthesis) and transported from the terrestrial surroundings (i.e., depend on terrestrial photosynthesis). Dashed arrows indicate re-supply of oxidized compounds that can function as electron acceptors in anoxic OM degradation. From Enrich-Prast A, Bastviken D and Crill PM (2009) Chemosynthesis. *Encyclopedia of Inland Waters*, pp. 211–225. Oxford Elsevier.

The most important CO_2 fixation pathway in all organisms is anaplerosis, which replaces endogenous components of the tricarboxylic acid (TCA) cycle with either inter- or extra-cellular exogenous products. Although dark carbon incorporation appears to function at low levels in heterotrophic bacteria, it has been suggested that the carboxylase activity increases in situations of organic matter deficiency and slow growth (Moran and Miller, 2007). Then, these processes may significantly contribute to the total dark carbon fixation.

Chemosynthesis and climate

Globally, it is now clear that climate changes can be caused by changes in atmospheric content of radiatively important gasses including CO_2, CH_4, and N_2O in the atmosphere. Chemosynthetic processes are directly related to the natural production and consumption of these gasses. Inland waters can be simultaneously both carbon sinks for organic matter accumulating in sediments and major sources of climate forcing gasses such as CO_2 and CH_4. Chemosynthetic processes are involved in both production and consumption of CH_4 and nitrous oxide. Wetlands and lakes together contribute more than 75% of the natural CH_4 emissions to the atmosphere (Tranvik et al., 2009; Saunois et al., 2020). However, these CH_4 emissions would be much higher without CH_4 oxidation since freshwater aquatic CH_4 oxidation may consume >50% of the produced CH_4 (probably much higher in marine systems) and thereby substantially limit emissions (Sawakuchi et al., 2021). While the N_2O emission from inland waters to the atmosphere is relatively low, N_2O emission rates per surface area are substantially higher in reservoirs than in rivers. Short events of massive N_2O emissions have been reported in tropical floodplains suggesting that N_2O emissions from inland waters may be spatially and temporally localized and could be overlooked.

Chemosynthesis and food webs

Chemosynthesis can contribute carbon to food webs both through endosymbiosis (see above) and by direct or indirect predation on chemosynthetic microorganisms. Stable isotope studies confirm that carbon fixed by chemosynthesis enters food webs, although the magnitude and importance of this contribution are still unknown (Fig. 6). Chemosynthetic biomass is generally depleted in ^{13}C

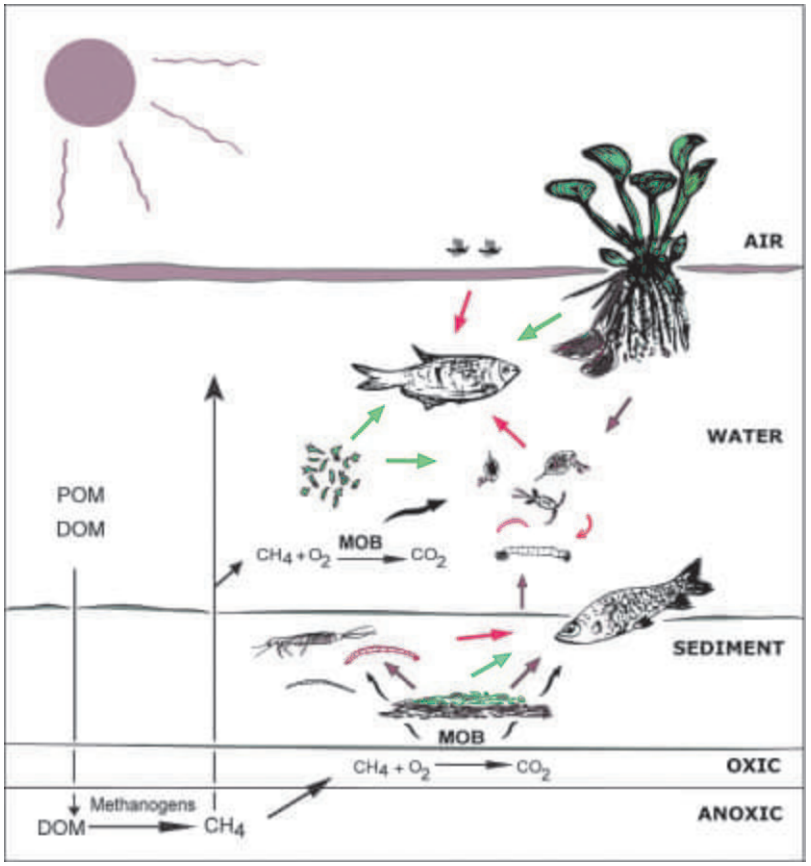

Fig. 6 Schematic illustration of the incorporation of carbon of aerobic methane oxidizing bacteria (MOB) into the food web of a tropical shallow lake. Particulate and dissolved organic matter (POM and DOM, respectively) of autochthonous and allochthonous origin support anaerobic methane (CH4) formation. CH_4 is oxidized by MOB and CH_4-derived carbon is transferred to higher trophic levels subsidizing pelagic and benthic organisms, reaching the fish level. Arrows with different colors indicate potential food sources: black- MOB; green-herbivory on phytoplankton and/or plant material; blue- herbivory on bottom filamentous algae; red-carnivory on aquatic and/or terrestrial organisms; brown detritivory. Reproduced from Sanseverino AM, Bastviken D, Sundh I, Pickova J and Enrich-Prast A (2012) Methane carbon supports aquatic food webs to the fish level. *PLoS One* e42723. doi: 10.1371/journal.pone.0042723.

relative to terrestrial organic carbon in inland waters, while ^{34}S signatures can be used to trace the contribution of sulfide-dependent chemosynthesis. Several studies in freshwater ecosystems have reported ^{13}C depleted values from tissues of organisms and have also suggested that oxidizing bacteria would be an important food source for different trophic levels.

The use of carbon isotopes to identify different organic matter sources and to elucidate carbon flow in food webs has shown that non-symbiotic metazoans also assimilate CH_4 carbon. The transfer of carbon and energy from CH_4 to higher food web levels was confirmed by the presence of fatty acids diagnostic for methane-oxidizing bacteria (MOB) in animal tissues. The first evidence came from ^{13}C content of zooplankton that is frequently found to be ^{13}C-depleted compared to seston particles in size range of their prey (Bastviken et al., 2003). In general, $\delta^{13}C$ signatures in methane in surface and bottom water of lakes are relatively ^{13}C-depleted compared to organic matter sources indicating a significant contribution of methanogens to the flow of energy and carbon to zooplankton, insects, and fish. In addition, the presence of MOB-fatty acids was first detected in tissues of larval chironomids, aquatic insects abundant in many freshwater environments, and then found in fish tissues (Sanseverino et al., 2012). These findings demonstrated that CH_4 could be a significant carbon source not only for the microbial food web and primary consumers but also for higher trophic levels (Fig. 6). Another example of the importance of chemoautotrophic production is associated with sulfidic waters in caves and karst aquifers. Examples included the Lower Kane Cave and Cesspool Cave (United States), Movile Cave (Romania) and Frasassi cave system (Italy) which all supports diverse terrestrial and aquatic invertebrate communities and can be considered subterranean biodiversity hotspots (Kumaresan et al., 2014).

Chemosynthesis and element cycling

Redox-driven biogeochemical element cycling plays a key role in organic matter cycling in aquatic ecosystems. As already mentioned in this chapter, redox processes associated with chemosynthesis are crucial for the biogeochemical cycling of many

common elements. For example, nitrogen cycling depends upon nitrification (ammonium oxidation to nitrite, primarily a chemoautotrophic process) and chemosynthesis is therefore vital for remineralization of nitrogen, and indirectly for denitrification. Another example is anaerobic CH_4 and ammonium oxidation which have been estimated to account for more than 75% and 30–50% of all marine CH_4 oxidation and ammonium oxidation (Strous and Jetten, 2004). The overall importance of these processes in inland water ecosystems is still unknown, but the number of lakes and rivers where these processes have been measured is increasing. There are many other examples where chemosynthetic processes are critical in biogeochemistry, including the cycling of sulfur, iron, and manganese (Table 2). From a general element cycling point of view, chemoautotrophic microorganisms function as catalysts for a large number of redox reactions, greatly increasing reaction rates.

Knowledge needs

Even after more than a decade from the publication of the first version of this chapter, it is remarkable how few new studies related to chemosynthesis in inland waters have been published. New methodologies in Molecular Biology have emerged that have been revelatory of the detail and metabolic complexity of the microbial communities that fix and cycle the biological processes important to planetary climate processes. It is exciting that more holistic studies combining microbial community structure with in situ-simulated rates obtained from the traditional dark ^{14}C fixation and other isotopic and biogeochemical methods are beginning to appear. The determination of specific chemosynthetic pathways through genetics, genomics, and multiple isotopic observations and experiments will enhance our knowledge of biogeochemical processes related to chemosynthesis in aquatic ecosystems. Scientists need to combine all information related to in situ rates of the chemosynthetic process(es) involved and the main actors in chemosynthetic primary production to have a complete understanding of ecosystems.

From the ecological perspective, more studies on chemosynthesis in inland waters are still needed, both in the water column and in sediments comprising spatial (geographically and vertically) and temporal dynamics. More detailed measurements with new technologies in non-saline waters, in sediments, and in common microenvironments such as biofilms will be very valuable. A focus on non-sulfide-dependent chemosynthesis would also supplement current data greatly, e.g., redox processes associated with iron or manganese could potentially be important in many soft water ecosystems and even for the management of water quality. It would also be interesting to further investigate the anaerobic (non-O_2 dependent) chemosynthesis shown to be extensive in some anoxic hypolimnia where it is unclear which electron acceptors are used (Fig. 3). Important processes are likely ignored because of the limited number of systematic studies in many common types of inland waters. The importance of chemosynthesis as a source of organic matter to macrofauna, with or without endosymbiosis, is another important area of study to understand food webs. Chemical redox interfaces induce high microbial activity, and high biomass, representing hot spots of microbial food web interactions. In addition, chemosynthesis could be very important for specific species having certain feeding strategies or depending on endosymbiotic microorganisms. An apparent extension of the studies examining the carbon transfer from chemosynthetic organisms to higher trophic levels would help to quantify the magnitude of this contribution.

Finally, it should be noted that chemosynthetic microorganisms provide important ecosystem services, such as providing and cycling carbon to shaded systems, mitigating climate forcing trace gas emissions to the atmosphere, and removing environmental pollutants. The fact that their function is ultimately linked to biogeochemical elemental cycles suggests that they can influence, and be strongly influenced by, climate and land-use changes. Floods and droughts exacerbate hydrological fluctuations in water balance and alter the linkages between surface and groundwater. Intensification of the hydrological cycle is likely to alter redox gradients in space and time. We also need to understand the importance of dark carbon fixation in the hydrological cycle and pursue new links between microscale processes to more fully understand the large-scale cycling of biogeochemical elements in aquatic systems.

See Also: Structures and functions of Inland Waters - Lakes: Bottom Boundary Layers; Structures and functions of Inland Waters - Wetlands: Restoring Riparian Peatlands for Inland Waters: A European Perspective; Wetland Soils: Physical and Chemical Properties and Biogeochemical Processes

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Methane[☆]

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This is an update of D. Bastviken, Methane, in Encyclopedia of Inland Waters, edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00117-4.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Emission Flux in a specified direction given by the context—often from an environment or source to the atmosphere.
Flux Transport of a compound without specification of the transport direction.
Greenhouse gas Gasses that absorb infrared light in the atmosphere, thereby delaying the heat transport through the atmosphere towards space, resulting in warming of the atmosphere.
Methane (CH_4) The most reduced organic compound. Formed in e.g., anaerobic microbial metabolism upon degradation of organic matter. An effective energy carrier for food webs and society and represents a powerful greenhouse gas.
Methane oxidation Processes resulting in transformation of methane into carbon dioxide and water.
Methanogenesis The microbial processes resulting in methane formation.

Introduction

Methane (CH_4) is a major product of organic matter decomposition in freshwater environments. CH_4 is both produced and consumed in aquatic environments. This results in local within-system carbon cycling providing a link between anoxic and oxic processes or habitats. CH_4 produced in anoxic sediments can represent an overlooked carbon source for aquatic food webs in oxic habitats. Recently, it has been shown that oxic methane production in surface waters can occur with amounts and implications being discussed. The local consumption of CH_4 is not complete and CH_4 emissions from inland waters represent a substantial greenhouse gas contribution to the atmosphere. The aim of this chapter is to review various aspects of CH_4 cycling in inland waters, including:

1. the fundamentals of CH_4 formation and oxidation in aquatic environments,
2. the contribution of CH_4 dynamics to overall carbon cycling in aquatic systems,
3. the potential contribution of CH_4 carbon to aquatic food webs,
4. the role of CH_4 emissions in linking aquatic carbon cycling and global atmospheric chemistry and climate regulation.

[☆]*Change History*: November 2021. D Bastviken updated all sections.

CH_4 is an odorless organic trace gas melting at −182.5 °C and boiling at −161.5 °C (Haynes, 2016). It is combustible at concentrations of 5–15% in air and it represents the major component of natural gas, biogas and marsh gas (Liao et al., 2005). CH_4 has a Henry's law constant of 1.29×10^{-3} M atm^{-1} (1.27×10^{-5} mol m^{-3} Pa^{-1}) at 25 °C, expressing a low water solubility (Wiesenburg and Guinasso, 1979). CH_4 absorbs infrared radiation with strong adsorption bands between 1 and 13 μm. The greenhouse warming potential, a function of atmospheric residence time and radiative properties, is approximately 28–32 times greater than for carbon dioxide (CO_2) on a molecular basis over a 100 year timescale (Myhre et al., 2013). The atmospheric mixing ratio of methane has more than doubled over the past 250 years and has increased from 1.5 to near 1.9 ppmv between 1977 and 2018 (Saunois et al., 2020). It has been estimated that CH_4 accounts for approximately 20% of the increase in the greenhouse gas effect observed since the mid-1700s.

CH_4 is constantly being degraded in the atmosphere by photo-oxidative and hydroxyl radical associated processes (Saunois et al., 2020). The estimated lifetime of CH_4 in the atmosphere is 8–12 years. Hence, steady-state or increasing atmospheric concentrations require large continuous emissions from various sources.

CH_4 formation

Biochemical and microbiological aspects of methanogenesis

The CH_4 in the atmosphere is primarily of biogenic origin as determined by its ^{14}C age (Saunois et al., 2020). Most biological production of CH_4, methanogenesis, is anaerobic and performed by methanogenic archaea. They share some characteristics including high intracellular concentrations of co-enzyme F_{420} (resulting in autofluorescence after stimulation under a fluorescence microscope), the presence of the enzyme methyl co-enzyme M methylreductase and the presence of unique phospholipid membrane components (Garcia et al., 2000).

The anaerobic methanogenesis (AMG) relies on a limited number of low molecular weight substrates (Garcia et al., 2000; Segers, 1998). The two principal pathways are acetotrophic (acetate dependent) and hydrogenotrophic (H_2 dependent) methanogenesis, respectively. In the former case, acetate (CH_3CO_2H), is cleaved into CH_4 and carbon dioxide (CO_2). During hydrogenotrophic methanogenesis, H_2 reacts with CO_2 forming CH_4 and H_2O. Other low molecular weight organic molecules, such as formate, methanol, dimethyl sulfide (DMS), tri-, di- and monomethylamines and ethylamine can also be used for methanogenesis, but acetate or H_2 and CO_2 are believed to be the quantitatively most important substrates. Thereby AMG represents a terminal step of anoxic organic matter degradation (Table 1). Before the terminal anoxic degradation can occur, complex organic substrates have to undergo several degradation steps (Fig. 1). Complex organic matter is fermented to intermediate fermentation products including acetate, H_2 and CO_2, which can then be utilized in methanogenesis. Typically this requires the activity of several different bacterial groups, which organize in syntrophic consortia facilitating the transfer of the reaction products between cells. In the presence of oxidized compounds that can function as electron acceptors, e.g., nitrate (NO_3^-), manganese (IV) (Mn^{4+}), iron (III) (Fe^{3+}) and sulfate (SO_4^{2-}), terminal degradation steps like denitrification, iron reduction, manganese reduction and sulfate reduction may yield more energy than methanogenesis (Table 1). Hence, because microorganisms capable of utilizing alternative terminal electron acceptors often have a superior energy gain, and sometimes also more efficient substrate uptake systems (greater substrate affinity), they are likely to outcompete methanogenic archaea. Thereby, the presence of alternate electron acceptors inhibits AMG (Table 2).

Recently, oxic methane production (OMP) in lake water has been highlighted (e.g., Hartmann et al., 2020). Mechanisms are not yet clear but OMP have been associated with cyanobacteria and photosynthesis and methylphosphonates and trimethylamine have been discussed as precursors. AMG in anaerobic micro-niches in oxic waters have also been suggested. There is an ongoing discussion on the extent, regulation, and implications of OMP in various inland waters (e.g., DelSontro et al., 2018; Günthel et al., 2019; Peeters et al., 2019).

Table 1 Examples of redox reactions used in the microbial degradation of organic matter.[a]

Process	*Substrates*		*Final products*		$-\Delta G^\circ$ *kJ/mol* e^- *(pH = 7)*
	e^- *donor*	e^- *acceptor*			
Aerobic respiration	OM	O_2	CO_2	H_2O	125
Denitrification	OM	NO_3^-	CO_2	N_2	112
Manganese reduction	OM	Mn(IV)	CO_2	Mn(III), Mn(II)	95
Iron reduction	OM	Fe(III)	CO_2	Fe(II)	24
Fermentation	OM	OM	CO_2	LMWOM, H_2	5–60
Sulfate reduction	LMWOM	SO_4^{2-}	CO_2	S^{2-}	18
Methanogenesis	LMWOM, H_2	LMWOM, CO_2	CO_2	CH_4	14–28

[a]The general principle of these metabolic processes is that organisms gain energy by transferring electrons from an electron (e^-) donor to an e^- acceptor. The e^- donor has to be more reduced than the e^- acceptor to allow energy gain. The difference in degree of reduction or oxidation between the e^- donor and acceptor is roughly proportional to the energy gain. $-\Delta G^\circ$ indicates the energy yielded from the listed processes. Values of $-\Delta G^\circ$ are related to specific reactions in Zehnder and Stumm (1988) and should only be used for comparison between the different processes in the table. OM and LMWOM denote organic matter and low molecular weight organic matter (i.e., fermentation products), respectively.

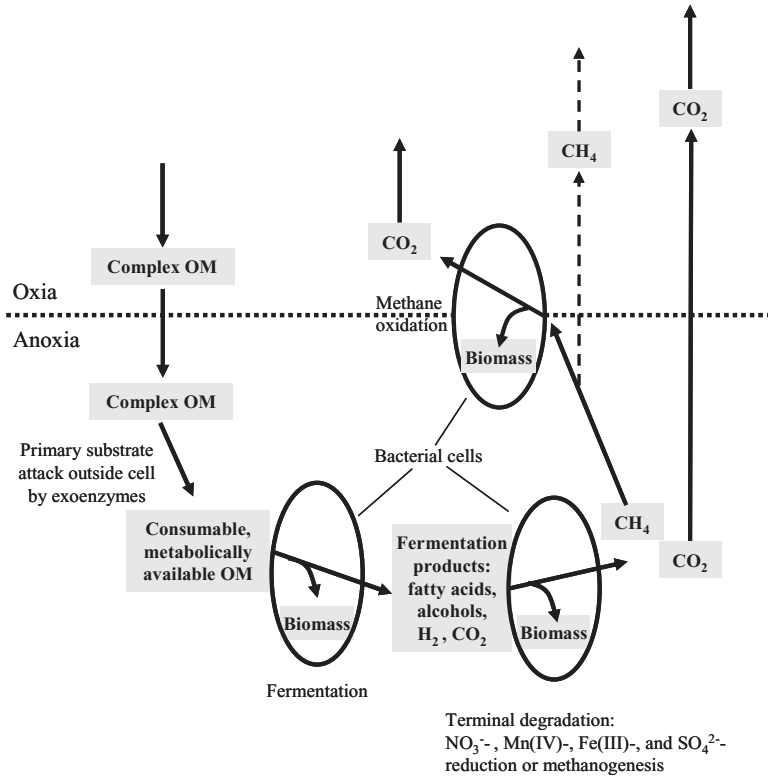

Fig. 1 Simplified illustration of anoxic degradation of organic matter and of CH_4 oxidation in an aquatic sediment. Complex polymeric organic matter (OM) reaching the sediment is subjected to hydrolysis and fermentation to low molecular weight intermediary products. Production of CH_4 is one of several alternative terminal anoxic degradation processes. CH_4 oxidation, primarily occurring at the oxic-anoxic interface, results in the formation of CO_2 and biomass from CH_4. Some CH_4 may escape oxidation and leave the system leading to emissions. See text for details.

Table 2 Effects of some environmental factors on CH_4 production rates in aquatic systems.[a]

Environmental factor	*Effect on CH_4 production (±)*	*Notes*	*Sources*[b]
O_2	–		1, 6
Alternative electron acceptors (NO_3^-, Fe^{3+}, Mn^{4+}, SO_4^{2-})	–		2, 6, 7
Temperature	+	Q_{10} 4.1 ± 0.4; Arrhenius activation energy 0.62–1.27 eV (data from wetland and lake systems)	1, 2, 4, 5, 6, 8, 10
pH	Variable	Community dependent pH optimum	6, 8
Roots	+ by OM leakage and root decay – by O_2 leakage	+ probably dominate	6
Availability of recently produced OM	+	Yields indirect relation between system primary productivity and CH_4 production	6, 8, 9
Physical disturbance	+ at low intensity – at high to moderate intensity	Effects may differ among environments and communities	3, 6
Sulfide	– above threshold conc.	Thresholds of 0.1–1 mM found	6

Sources: (1) Boon and Mitchell (1995), (2) Conrad (2002), (3) Dannenberg et al. (1997), (4) Duc et al. (2010), (5) Marotta et al. (2014), (6) Segers (1998), (7) van Bodegom et al. (2004), (8) Whalen (2005), (9) Yavitt et al. (2000), (10) Yvon-Durocher et al. (2014).

[a]Positive and negative effects are denoted by + or –, respectively. OM denotes organic matter.

[b]Only examples of sources given. Sources 2, 5, and 7 are reviews representing many studies on the regulation of methanogenesis.

Environmental factors affecting anaerobic methanogenesis

The effects of various environmental factors on AMG are summarized in Table 2 (factors affecting OMP remain to be established). It is now established that many methanogenic archaea can tolerate substantial O_2 exposure even though O_2 inhibits AMG. Likewise, the inhibition by sulfate is not strict, but primarily results from substrate competition. The temperature optimum of AMG is usually well above in situ temperatures, and the potential CH_4 production rates increase about fourfold if the temperature increases by 10 °C (Table 2). Therefore, AMG has a substantially higher temperature sensitivity than photosynthesis or overall organic matter respiration. pH within the natural variation found in aquatic habitats does not seem to limit methanogenesis directly but can affect what substrates are available and used. Under low pH, acetotrophic methanogenesis seems to be favored, while higher pH favors H_2 dependent methanogenesis. Often both acetotrophic and hydrogenotrophic methanogenesis occur simultaneously in sediments with either process contributing between 20% and 80% of the overall AMG.

Spatial distribution of methanogenesis in freshwater environments

AMG is restricted to environments with low concentrations of alternate electron acceptors (e.g., O_2, NO_3^-, Mn^{4+}, Fe^{3+}, and SO_4^{2-}), at the same time having a high enough concentration of the AMG substrates needed. Such conditions are common in freshwater sediments. If the sediments are overlain with oxic water, or in the proximity of roots of aquatic plants from which O_2 diffuses into the sediment, there is often a redox gradient over a few mm to cm's in the sediment. In this gradient, the organic remineralization processes using alternate electron acceptors often occur in the energy yield sequence according to the order in Table 1. In these cases AMG dominates terminal organic matter degradation in subsurface sediments or at longer distance from the roots, where the other electron acceptors are depleted. If the sediment is overlain with anoxic water and lacks roots contributing O_2, AMG may dominate terminal organic matter degradation in the whole sediment column. In wetlands, the depth distribution of AMG often depends on the position of the ground water table which regulates the availability of O_2 and other electron acceptors.

So far there is little evidence of significant rates of AMG in anoxic water columns, possibly due to low concentration of substrates relative to that found in the sediment. It is also possible that the establishment of stable syntrophic microbial consortia is more difficult in the water column due to higher turbulence than in the sediments, and this may also restrict methanogenesis. Anoxic microenvironments such as digestive tracts of animals or the interior of suspended detrital particles are sites of AMG that may be of importance for the depth distribution of CH_4 in the oceans, but in freshwaters the sediments appear to be the dominant source. The recent discussion about OMP has highlighted the potential for CH_4 production also in surface oxic lake water (e.g., Hartmann et al., 2020).

CH_4 oxidation

Aerobic methane oxidation

The fact that CH_4 is the most highly reduced organic compound means that energy can be gained by the oxidation of CH_4 in the presence of O_2 or other potent oxidants. Aerobic methane oxidizing bacteria (MOB) take advantage of this by using CH_4 as energy and carbon source and O_2 as electron acceptor. MOB oxidize CH_4 sequentially to methanol, formaldehyde, formate, and finally to CO_2. The intermediate product, formaldehyde (CHO) is a primary carbon source for growth.

MOB have been identified in several phyla including Proteobacteria (Gammaproteobacteria and Alphaproteobacteria classes), Verrumicrobia, and Methylomirabilota (Smith and Wrighton, 2019). Studies of isolated strains from these groups have revealed differences in morphology, membrane structures, resting stages and metabolic pathways. Some phospholipid fatty acids represent biomarkers unique for MOB and can be used for identification and biomass estimation. The key enzymes responsible for the CH_4 oxidation are the methane monooxygenases (MMOs). There are both particulate and soluble types of MMOs. Particulate MMO appears to be common to most MOB while soluble MMO is not. Some MOB are obligately methanotrophic, while other are methylotrophic and can use methyl groups on various small organic molecules. A chemically diverse catalytic capacity has been found for soluble MMO, including the oxidation of many aromatic and alicyclic organic compounds, and oxidative dehalogenation of halomethanes, haloalkanes and haloalkenes. Ammonia monooxygenase, used by ammonia oxidizing bacteria is similar to MMO and many MOB may be able to perform ammonia oxidation. Another link to nitrogen cycling, although not specifically associated with MMO, is that many MOB can fix molecular nitrogen (N_2) at low O_2 concentrations (Kallistova et al., 2017; Smith and Wrighton, 2019).

Environmental factors affecting CH_4 oxidation

Aerobic CH_4 oxidation depends on the presence of both CH_4 and O_2 (Table 3). CH_4 oxidation rates appear less sensitive to temperature than methanogenesis (Tables 2 and 3). There is no clear pattern regarding how pH affects CH_4 oxidation rates, possibly due to local adaptations to various pH ranges by the microbial communities. Likewise, the effects of ammonium and nitrate are contradictory and seem to differ between environments (Table 3). High salinity inhibits CH_4 oxidation as does high light intensity. Light can also indirectly favor CH_4 oxidation by enhancing photosynthesis and thereby oxygenation of sediments or water columns.

Table 3 Effects of some environmental factors on aerobic CH_4 oxidation rates (MOX) in aquatic systems (anaerobic oxidation of methane. AOM, is discussed separately in the text).[a]

Environmental factor	*Effect on CH_4 oxidation (±)*	*Notes*	*Sources*[b]
CH_4	+	Given that O_2 is available	9, 10, 11
O_2	+	Given enough CH_4 present; + or – at high O_2 levels debated	4, 5, 9, 10, 11, 12
Temperature	+	Q_{10} 1.4–2.4 (data from wetland and lake systems)	8, 11, 13
pH	Variable effect	pH optimum may vary among communities	4, 8, 13
Salinity	–	Reduction from 40 mM, total inhibition from 9%	8
Light	– (direct effects) + (indirect effects)	Indirect effects related to photosynthesis and O_2 dynamics	2, 3, 6
Nitrogen (NH_4^+ or NO_3^-)	Debated	Both + and – effects found	1, 4, 5, 7
Roots	+	Through O_2 release	8
Season		Highest MOX during summer in sediments	8

Sources: (1) Bodelier and Laanbroek (2004), (2) Dumestre et al. (1999), (3) King (1990), (4) King (1992), (5) Liikanen and Martikainen (2003), (6) Murase and Sugimoto (2005), (7) Rudd et al. (1976), (8) Segers (1998), (9) Sundh et al. (2005), (10) Sundh et al. (1995), (11) Thottathil et al. (2019), (12) van Grinsven et al. (2020), (13) Whalen (2005).

[a]Positive and negative effects are denoted by + or –, respectively.

[b]Only examples of sources are given. Source 4, 8, and 13 are review papers representing many studies.

Anaerobic oxidation of CH_4

It can be thermodynamically favorable to oxidize CH_4 using any electron acceptor that gives a higher energy yield than methanogenesis (see Table 1). The anaerobic oxidation of CH_4 (AOM) by syntrophic interactions between bacteria performing sulfate reduction and reverse methanogenesis, respectively, was first discovered in marine environments. In inland waters, AOM coupled to reduction of sulfate, nitrate, (denitrification), iron or manganese have been shown (Kallistova et al., 2017). Anaerobic CH_4 oxidation can be considerable, particularly in saline environments, but in freshwaters anaerobic CH_4 oxidation often appears to be of less importance compared to aerobic CH_4 oxidation.

Spatial distribution of aquatic CH_4 oxidation

Aerobic CH_4 oxidation is most extensive at the oxic-anoxic interface where both O_2 and CH_4 are available. The oxic-anoxic interface can be situated in the surface sediment, in deeper sediments close to roots releasing O_2, or in the water column (Fig. 2). The zone with extensive CH_4 oxidation is usually confined to a layer only a few millimeters thick in the sediment, but can be extended over decimeter or meter scales in the water column. The location of this zone varies with time depending on how the oxygenation of the water varies temporally. For example, in a lake which develops an anoxic hypolimnion during summer stratification, the most extensive CH_4 oxidation is expected at the oxic-anoxic interfaces in the water column and in the shallow sediment at depths above the oxycline. During the rest of the year most of the CH_4 oxidation would be expected to occur in the sediment surface if the water column is oxygenated. In wetlands, the oxic-anoxic interface, and thereby the zone of CH_4 oxidation follows the movements of the ground water table (Le Mer and Roger, 2001).

Similarly, anaerobic CH_4 oxidation is favored where both the substrate (CH_4) and a suitable electron acceptor are present at adequate levels. If anaerobic CH_4 oxidation depends on syntrophic relationships, the process may be sensitive to physical disruption such as turbulence breaking microbial associations, and this may limit the distribution in the water column.

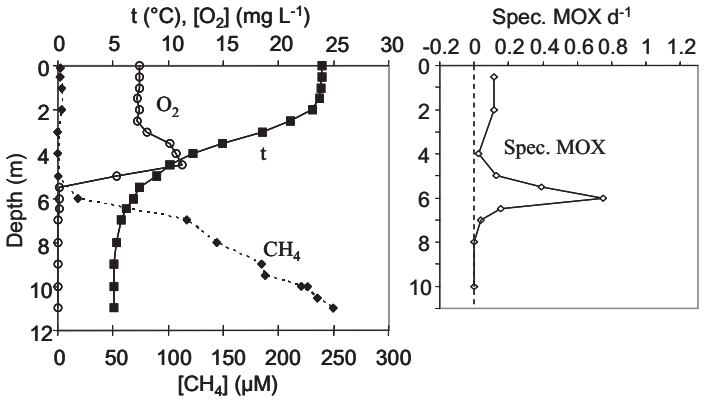

Fig. 2 Example of water column profiles of temperature (t), O_2 concentration ($[O_2]$), CH_4 concentration ($[CH_4]$), and specific CH_4 oxidation rates (Spec. MOX; the fraction of the present CH_4 being oxidized each day), in a temperate lake during summer stratification. Data from Paul Lake, Northern Michigan, USA, July 2001.

At marine hydrocarbon seeps CH_4 oxidation can occur in association with animals (e.g., endosymbiotic MOB in mussels; Nix et al., 1995). In freshwaters, methane oxidation may be enhanced by the extended zones with redox gradients forming in the burrows created by benthic fauna (e.g., chironomids; Kiyashko et al., 2004).

Aquatic CH_4 dynamics

CH_4 concentrations in aquatic environments

The CH_4 concentrations in sediments or water columns are the consequence of formation rates, import rates, CH_4 oxidation rates and rates of export to the water column or the atmosphere. High porewater concentrations, at which CH_4 is saturated at the prevailing pressure, are typical for subsurface sediment layers, and excess CH_4 that is produced will then form bubbles. If surface sediments are oxygenated, CH_4 oxidation can keep CH_4 concentrations low (<10 μM) at the sediment surface. If the sediment is overlain with anoxic water and CH_4 oxidation in the sediment is low, concentrations will be high in the whole sediment resulting in greater export to the water. CH_4 concentrations in anoxic parts of stratified water columns can exceed 1000 μM. Consequently, steep concentration gradients influenced by physical transport patterns and CH_4 oxidation are frequently found in stratified waters (Fig. 2). In strongly stratified systems, lack of advective transport may efficiently trap CH_4 below the thermocline. In such cases most of the surface water CH_4 may be derived from shallow sediments above the thermocline and OMP in surface water (e.g., Bastviken et al., 2008). CH_4 concentrations in well mixed oxygenated parts of water columns are typically ranging from 0.01 to 10 μM. The equilibrium concentrations relative to the atmosphere range from 0.002 to 0.005 μM at an atmospheric CH_4 partial pressure of 2 μatm and temperatures of 0–40 °C, meaning that inland waters are generally supersaturated.

Rates of CH_4 formation and oxidation

Most available assessments of CH_4 production and oxidation rates in sediments are based on incubations of sediment slurries. Slurries are made to ensure well mixed conditions and to avoid the development of gradients that may affect CH_4 production. It is well recognized that such measurements, although providing good potential production rates under experimental conditions, may not reflect actual in situ rates. In situ rates are more difficult to measure and different approaches have been tried including studies of intact sediment cores and whole system CH_4 budgets. Table 4 provides an overview of some CH_4 production, CH_4 oxidation, and CH_4 release rates in lake sediments acquired by different methods. CH_4 production rates range from almost zero to 68 mmol m^{-2} day^{-1}. In oxic surface sediment, 50–95% of the produced CH_4 was oxidized. CH_4 release, representing the net transport of CH_4 to the water, may to a large extent depend on CH_4 oxidation rates and regulation by the O_2 penetration depth has been suggested. The release of CH_4 to the water column in previously studied lakes was 0.04–46 mmol m^{-2} day^{-1} (Table 4). Production or release values greater than 2.9 mmol m^{-2} day^{-1} only occurred in the more nutrient rich systems (mesotrophic or eutrophic), indicating some influence of nutrient levels, probably indirectly by affecting supply rates and quality of the sediment organic matter as well as the frequency of anoxia in bottom waters.

The oxidation of CH_4 in the water column is highly dependent on the mixing regime and the depth of lakes. Hence, reported water column oxidation rates are highly variable ranging from zero in deep anoxic water layers to very high rates in the oxycline where O_2 and CH_4 concentrations gradients meet (Fig. 2) or during lake overturn periods when concentrations of both CH_4 and O_2 are elevated throughout the entire water column. Rates can vary from zero to 27 mmol m^{-3} day^{-1} at individual depths and areal CH_4 oxidation rates, taking the average depth into account, range from 0 to 31 mmol m^{-2} day^{-1} (Table 5). Apparently, a large proportion of the CH_4 entering the water column will get oxidized (45–100%; Table 5). Hence, considering both surface sediments and water columns, CH_4 oxidation substantially reduces the amount of dissolved CH_4 that can be emitted from aquatic environments by diffusion across the water-atmosphere boundary layer.

CH_4 and aquatic food webs

To explain observations that zooplankton and chironomids are frequently depleted in ^{13}C relative to assumed food sources such as algae and bulk particulate organic matter, they have to partly rely on more ^{13}C-depleted carbon sources (Grey, 2016). Biogenic CH_4, and consequently also the biomass of MOB are very depleted in ^{13}C. Accordingly, studies using ^{13}C or MOB phospholipidic fatty acids (PLFA) as tracers of food web connections indicate that CH_4 carbon transformed to MOB biomass can support higher food web levels (Fig. 3); a result that has also been supported by carbon mass balances. CH_4 oxidation in aquatic environments is extensive and the high MOB growth efficiency ranging from 0.15 to 0.8 means that a high proportion of the consumed CH_4 is transferred to biomass. The production of MOB biomass can be of the same order of magnitude as the total heterotrophic bacterial production and even comparable to the primary production in some lakes (Table 6). Therefore, MOB biomass could represent a substantial food resource in many aquatic environments. Until now, there are examples that CH_4 carbon indeed can substantially support zooplankton and chironomid populations, at least in some lakes, during some seasons (e.g., when CH_4 oxidation can be extensive compared to algal production), or for zooplankton or benthic animals preferentially feeding at oxic-anoxic interfaces (Table 7). There is also support that CH_4 carbon can reach fish biomass. However, there are also studies showing negligible food web contributions of CH_4 carbon and the overall extent of a methanotrophic microbial loop is still poorly understood. While it is likely that CH_4 carbon can substantially support aquatic food webs in some cases, future studies are needed on under what conditions this is important.

Table 4 Examples of CH_4 production and oxidation rates in sediment, or net diffusive flux from sediment to water in lakes.[a]

Lake	*Trophic state*	*Method*	*Sediment origin*	*O_2 regime in water above sediment in situ*	*Sediment CH_4 production* *mmol m^{-2} day^{-1}*	*CH_4 oxidation in surface sediment* *% of production*	*Net CH_4 flux from sediment to water* *mmol m^{-2} day^{-1}*	*Source*
Fuchskuhle	Acid	Slurry incubation	Profundal		0.4–1.2			4
Dagow	Eu	Slurry incubation	Profundal		0.7–13			4
Kevätön	Eu	Slurry incubation	Profundal		27–68			12
Ontario	Meso	Slurry incubation	Prof + Litt		0–42.5			16
Stechlin	Oligo	Slurry incubation	Profundal		0.3–1.2			4
Two Siberian lakes	Dys	Radioisotopes	Prof + Litt		0.006	67%		7
Washington	Meso	Benthic chamber	Profundal	oxic	0.6	50%	0.2–0.3	11
Tuusulanjärvi	Eu	Conc gradient calc	Profundal	oxic	4.5			8
Postilampi	Eu	Conc gradient calc	Profundal	anoxic	6.6			8
Soiviojärvi	Eu	Conc gradient calc	Profundal	oxic	0.5			8
Takajärvi	Eu	Conc gradient calc	Profundal	oxic	0.3			8
Ranuanjärvi	Eu	Conc gradient calc	Profundal	oxic	4.8			8
Lokka	Eu	Conc gradient calc	Profundal	oxic	0.03			8
Luiminkajärvi	Meso	Conc gradient calc	Profundal	oxic	1.7			8
Porttipahta	Meso	Conc gradient calc	Profundal	oxic	1.6			8
Big Soda Lake	Saline	Conc gradient calc	Profundal	anoxic			2.9	9
Mono Lake	Saline	Conc gradient calc	Profundal	anoxic			1.3	5
Kevätön	Eu	Intact cores	Profundal	oxic	1.9–9.4	66–95%	0.1–3.2	12
Illersjön	Eu	Intact cores	Profundal	anoxic	1.1–2.4			1
Mårn	Eu and Dys	Intact cores	Profundal	anoxic	1.1			1
Constance	Meso	Intact cores	Profundal	oxic	0.5	93%	0.04	6
Biwa	Meso	Intact cores	Profundal	oxic	0.002–1.2	90%		14
Biwa	Meso	Intact cores	Littoral	oxic	1–8.8	90%		14
Lillsjön	Dys	Intact cores	Profundal	anoxic	0.6			1
Frain's Lake	Eu	Hypolimnion budget	Profundal	anoxic			3.8–9.8	10
Wintergreen	Eu	Hypolimnion budget	Profundal	anoxic			10–46	18
St George	Meso	Hypolimnion budget	Profundal	anoxic			5–14.8	3
Third Sister	Meso	Hypolimnion budget	Profundal	anoxic			3.2–4.5	10
Onodaga	Meso	Hypolimnion budget	Profundal	anoxic			5.6–11.9	13
Mendota	Eu	Whole lake budget	Profundal	anoxic			35.8	5
Lake 227	Eu	Whole lake budget	Profundal	anoxic			10.8	17
Lake 227	Eu	Whole lake budget	Littoral	oxic			0.8	17
Paul	Oligo	Whole lake budget	Littoral	oxic			3.2	2
Paul	Oligo	Whole lake budget	Thermocline	oxic			0.1	2
Paul	Oligo	Whole lake budget	Profundal	anoxic			11.7–13.8	2
Peter	Oligo	Whole lake budget	Littoral	oxic			3.0	2
Peter	Oligo	Whole lake budget	Thermocline	oxic			0.4	2
Peter	Oligo	Whole lake budget	Profundal	anoxic			12.1–14.3	2
Hummingbird	Eu	Whole lake budget	Littoral	oxic			2.4	2
Hummingbird	Eu	Whole lake budget	Profundal	anoxic			4.9	2

Sources: (1) Bastviken et al. (2002), (2) Bastviken et al. (2008), (3) Bédard and Knowles (1991), (4) Casper (1992), (5) Fallon et al. (1980), (6) Frenzel et al. (1990), (7) Gal'chenko et al. (2001), (8) Huttunen et al. (2006), (9) Iversen et al. (1987), (10) Kelly and Chynoweth (1980), (11) Kuivila et al. (1988), (12) Liikanen et al. (2002), (13) Matthews et al. (2005), (14) Murase et al. (2005), (15) Oremland et al. (1987), (16) Roy et al. (1994), (17) Rudd and Hamilton (1978), (18) Strayer and Tiedje (1978).

[a]Lake trophic states based on definition total phosphorous concentrations (TP; $\mu g\ P\ L^{-1}$) denoted are eutrophic (Eu; TP 24–96), mesotrophic (Meso; TP 12–24), oligotrophic (Oligo; TP 0–12). Acidotrophic (Acid) and dystrophic (Dys) denote low pH and high levels of colored organic matter, respectively, as defined by the source. Profundal (Prof) or littoral (Litt) sediment, and in one case sediment in contact with the thermocline water layer (metalimnion) is represented. The studies have been grouped based on the approach (see original source for method details). Mean values or ranges are given. CH_4 leaving the sediment by ebullition is not accounted for by sediment CH_4 production values, meaning that total sediment CH_4 production may be greater.

Table 5 Examples of methane oxidation rates in lake water columns.[a]

Lake	*Lake information*	*CH_4 oxidation*			*% CH_4 oxidized*[b]	*Sources*
		mmol m^{-3} day^{-1}	*day^{-1}*	*mmol m^{-2} day^{-1}*		
Lake Kevätön, Finland	Hyper eutrophic	0–27		15–31		9
Lake 227, Canada	Eutrophic, summer stratification	0–9.6		1.2	100	11, 12
Lake 227, Canada	Eutrophic, fall overturn	1–17.3		2.9	60	12
Lake Mendota, Unitec States	Eutrophic, summer stratification			10.6	45	3
Ilersjön, Sweden	Eutrophic, summer and winter stratification	0.004–3.3	0.01–0.21	0.6–4.3	57–90	1
Mårn, Sweden	Eutrofic, humic, summer and winter stratification	0.001–2.3	0.01–0.8	0.7–1.2	64–100	1
Lake Kasumigaura, Japan	Eutrophic, shallow, 5 whole years studied	0.02–1.1	0.01–6.5		74	14
Lake Nojiri, Japan	Mesotrophic, fall overturn	0–19.8	0.04–1	1	94	15
Williams Lake, United States	Whole year study			6.6		13
Shingobee Lake, United States	Whole year study			20		13
Lillsjön, Sweden	Dystrofic, summer and winter stratification	0.001–0.3	0–0.1	0.4–0.7	69–100	1
Lake Mekkojärvi, Finland	Dystrophic, fall overturn			3.3–4.2		8
Valkea-Kotinen, Finland	Dystrophic, whole year study			1.2	80	7
Lake Tanganyika, East Africa	Meromictic			0–9.6		10
Lake Kivu, Central Africa	Meromictic	0.04–0.9				5
Big Soda Lake, United States	Saline, Anaerobic CH_4 oxidation	2×10^{-3}–85×10^{-3}	5.6×10^{-4}–8.1×10^{-4}	1.4		4
Mono Lake, United States	Alkaline, saline, primarily anaerobic CH_4 oxidation	4×10^{-5}–$4.8 \cdot 10^{-2}$	1.3×10^{-4}–7×10^{-3}	0.07–0.7		6
Paul	Oligotrophic, clear, Whole-lake CH_4 budget, Jun-Aug	0.3–5.6		2.3–2.6	64	2
Peter	Oligotrophic, clear, Whole-lake CH_4 budget, Jun-Aug	0.2–6.3		2.9–3.6	63	2
Hummingbird	Eutrophic, humic, Whole-lake CH_4 budget, Jun-Aug	0.2–2.4		2.4	55	2

Sources: (1) Bastviken et al. (2002), (2) Bastviken et al. (2008), (3) Fallon et al. (1980), (4) Iversen et al. (1987), (5) Jannasch (1975), (6) Joye et al. (1999), (7) Kankaala et al. (2006a), (8) Kankaala et al. (2006b), (9) Liikanen et al. (2002), (10) Rudd (1980), (11) Rudd and Hamilton (1975), (12) Rudd and Hamilton (1978), (13) Striegl and Michmerhuisen (1998), (14) Utsumi et al. (1998a), (15) Utsumi et al. (1998b).

[a] Various methods were used including monitoring CH_4 concentration decline over time in closed vessels, changes in $\delta^{13}CH_4$ values, or ^{14}C based approaches. Studies attempting to quantify actual in situ rates were selected (i.e., potential rate measurements in incubations with substantial additions of CH_4 were not included). Averages or ranges are reported.

[b] Of the CH_4 reaching the water column.

CH_4 and whole system carbon cycling

Methanogenesis is the dominating terminal organic matter degradation process in anoxic freshwater environment. The significance of CH_4 cycling compared to overall carbon cycling in aquatic environments is large where comparisons have been made. Methanogenesis has been reported to account for 20–56% of the total carbon mineralization in lakes (Table 6). CH_4 oxidation can be comparable to primary production and has the potential to rapidly consume large amounts of O_2. In isolated water bodies, CH_4 oxidation has caused hypoxia or anoxia, resulting in fish kill events. CH_4 emissions may correspond to up to 37% of the primary productivity (Table 6). Altogether, the existing comparisons indicate that CH_4 dynamics can represent a substantial proportion of the total carbon cycling in some aquatic systems. This means that lakes and wetlands represent environments where CO_2, fixed by terrestrial and aquatic primary production, is converted to CH_4 with a relatively high efficiency.

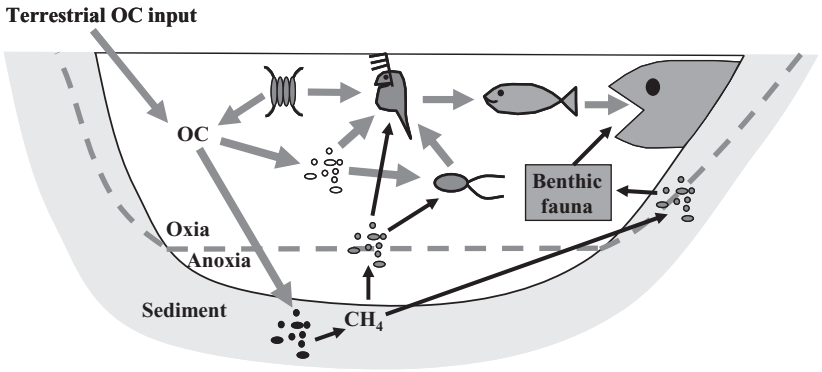

Fig. 3 Schematic illustration of how CH_4 carbon can be incorporated into aquatic food webs. Organic carbon (OC) from terrestrial sources or aquatic primary production (symbolized by Scenedesmus algae) reach anoxic sediment where methanogenic archaea (black dots) produce CH_4. At the oxic-anoxic interface in the water column or in sediment, CH_4 oxidizing bacteria (gray dots) transform CH_4 carbon to bacterial biomass that can be grazed upon by pelagic or benthic bacterivores. Narrow black arrows illustrate the potential routes for CH_4 carbon to various food web levels. The large gray arrows symbolize the classical food web carbon transfer including the microbial loop. (The arrows were made different to make the figure easier to read, and size does not represent quantities or rates).

Table 6 Comparisons between parts of the CH_4 cycling and other parts of the carbon cycling in some freshwater environments.

Lake	*System/Study information*	*Comparison*	*Sources*
Methanogenesis (AMG)			
7 North American lakes		AMG accounted for 19–87% of the anaerobic or 20–25% of the total C mineralization	4, 13, 14
Ryans I Billabong, Australia	Small shallow oxbow lake	AMG accounted for 30–60% of the sediment carbon flux or at least one third of total wetland respiratory carbon losses	3, 7
Pantanal, Brazil	Various waters on floodplain	AMG represented 20% of total heterotrophic metabolism in water and sediment	9
Lake St George, Ontario, Canada	Mesotrophic	AMG accounted for 56% of organic carbon mineralization during lake stratification	2
Lake 227, Canada	Eutrophic, dimictic	AMG equal to 55% of C input from runoff and atmosphere, and 13% of primary production	17
Methane oxidation (MOX)			
Lake Tanganyika, East Africa	Meromictic	MOX $\geq$ primary productivity on annual basis	16
Mekkojärvi, Finland	Dystrophic	Water column MOX rates during fall overturn similar to rates of primary production during July	12
Lake Sebasticook, Maine, United States	Hypereutrophic	MOX accounted for 62–70% of hypolimnetic O_2 demand	15
Lake 227, Canada	Eutrophic, dimictic	MOX consumed all available O_2 under ice during winter resulting in water column anoxia and widespread suffocation of fauna	17
Lake Constance	Mesotrophic	MOX corresponded to 9% of the sediment O_2 demand	8
Methane oxidizing bacteria (MOB)			
Lake Plußsee, Germany	Eutrophic, hypolimnion	MOB biomass 1.4–3% of total bacterial biomass	6
Three Swedish lakes	Two eutrophic lakes and one dystrophic lake	MOB growth rates 0.5–119% of heterotrophic bacterial production, or 0.3–7% of primary production. MOB biomass 5.4–41% of total bacterial biomass at different depths in the water column	1, 19
Lake Nojiri, Japan	Mesotrophic	Production of MOB biomass during fall overturn similar to primary production	20
Lake Kjelåsputten, Norway	Dystrophic	Production of MOB biomass similar to all C fixation by heterotrophic bacteria	10
Valkea-Kotinen, Finland	Dystrophic	Production of MOB biomass equivalent to 23–81% of heterotrophic bacterial production and 5–10% of primary production	11
CH_4 emission			
Wintergreen Lake, Michigan, United States	Small, shallow, hypereutrophic	Summer CH_4 emissions corresponded to 24–37% of summer productivity	18
Everglades, Florida, United States	Plant mediated wetland flux	CH_4 emissions corresponded to 3–14% of net ecosystem production	5

AMG, MOX, and MOB denote anaerobic methanogenesis, oxic methane oxidation, and methane oxidizing bacteria, respectively.

Sources: (1) Bastviken et al. (2003), (2) Bédard and Knowles (1991), (3) Boon and Mitchell (1995), (4) Capone and Kiene (1988), (5) Chanton et al. (1993), (6) Eller et al. (2005a), (7) Ford et al. (2002), (8) Frenzel et al. (1990), (9) Hamilton et al. (1995), (10) Hessen and Nygaard (1992), (11) Kankaala et al. (2006a), (12) Kankaala et al. (2006b), (13) Kuivila et al. (1988), (14) Mattson and Likens (1993), (15) Mayer et al. (1982), (16) Rudd (1980), (17) Rudd and Taylor (1980), (18) Strayer and Tiedje (1978), (19) Sundh et al. (2005), (20) Utsumi et al. (1998b).

Table 7 Examples of studies suggesting utilization of CH_4 carbon by different parts of the food web at least in some of the studied lakes or taxa, or during some of the studied seasons.

Food web compartment	*System studied*	*Methods (Indicator of CH_4-carbon, and type of study)*	*Sources*
Zooplankton	Billabongs, Australia	^{13}C, field observations	2
Zooplankton	Humic lakes	^{13}C, field observations	8
Zooplankton	Eutrophic and humic lakes, Sweden	^{13}C, carbon mass balance, field observation	1
Zooplankton	Polyhumic lake, Finland	^{13}C, carbon mass balance, laboratory and field experiments	9
Zooplankton	Polyhumic lake, Finland	^{13}C, fatty acids, carbon mass balance, laboratory and field experiments	14
Chironomids	Large mesotrophic Lake Biwa, Japan	^{13}C, field observations	11
Chironomids	Eutrophic lakes, Germany	^{13}C, field observations	5
Chironomids	Forest lakes, Finland	^{13}C, field observations	7
Chironomids	Large mesotrophic Lake Biwa, Japan	^{13}C, fatty acid composition, field observations	10
Chironomids, several other invertebrates, fish (*Curimatidae*)	Pantanal, Brazil	^{13}C, field observations	3
Chironomids	Eutrophic lake, Germany	^{13}C, microbial community analyzes, field observations	4
Off shore chironomids and oligochetes	Small oligotrophic arctic lakes, Canada	^{13}C, field observations	6
Several macroinvertebrates	Small stream, Japan	^{13}C, ^{15}N	12
Fish, macroinvertebrates, zooplankton	Tropical floodplain lake	^{13}C, fatty acids	13

Sources: (1) Bastviken et al. (2003), (2) Bunn and Boon (1993), (3) Calheiros (2003), (4) Eller et al. (2005b), (5) Grey et al. (2004), (6) Hershey et al. (2006), (7) Jones and Grey (2004), (8) Jones et al. (1999), (9) Kankaala et al. (2006b), (10) Kiyashko et al. (2004), (11) Kiyashko et al. (2001), (12) Kohzu et al. (2004), (13) Sanseverino et al. (2012), (14) Taipale et al. (2009).

CH_4 emissions from inland waters

Flux pathways

Emission of CH_4 from freshwater ecosystems to the atmosphere can occur in several different ways (Fig. 4):

1. *Ebullition* via bubbles released from the sediment that rapidly pass through the water column. Most of this CH_4 thereby escapes CH_4 oxidation. The ebullition rate is related to CH_4 formation rates in the sediment and also to the hydrostatic pressure and sediment coherence that has to be overcome to allow release of the bubbles. Ebullition is often depth dependent and most extensive from shallow sediments where the hydrostatic pressure is low (Fig. 5), although highest ebullition rates are sometimes found at high depths in steep-sided basins where sediment focusing leads to highest sediment and organic matter accumulation at deeper water. The relation to hydrostatic pressure allows weather to influence the timing of bubble release, and a higher occurrence of ebullition has been observed coincident with drops in the air pressure (Table 8) due to storms or frontal passages. Where ebullition depends on biogenic AMG there can be a bubble recharge-time between ebullition events, while in systems fueled by either geogenic CH_4 or where biogenic CH_4 produced over extensive sediment volumes are channeled to specific spots, more continuous ebullition has been observed (e.g., in some thermokarst systems).
2. *Continuous background flux of dissolved CH_4 from the water surface* (usually called diffusive emission as explained below). The transport of dissolved CH_4 from the sediment through the water column occurs primarily along concentration gradients through advective processes or eddy diffusion (turbulence enhanced diffusion). Very low diffusion rates similar to molecular diffusion may occur across stably stratified water layers at the sediment-water interface, across water column density gradients, or across the diffusive boundary layer at the water-atmosphere interface. As these lower diffusion rates are considered rate limiting (compared to the turbulence enhanced diffusion), this flux is often named "diffusive flux." Because the transport of dissolved CH_4 is much slower than transport by ebullition, a large portion of dissolved CH_4 is oxidized in oxic sediments or water layers (Tables 4 and 5), resulting in low CH_4 concentrations in surface waters. However, due to the poor solubility of CH_4, surface freshwater is still nearly always oversaturated (3–3000 times oversaturation given a concentration interval of 0.01–10 μM) with respect to atmospheric CH_4 (1.8 ppmv). The diffusive flux is regulated by the concentration difference between the water and the air, and by factors affecting the physical transport rate across the water-air interface. Accordingly, the diffusive flux is enhanced by high surface water concentrations or by high turbulence in the surface water making more water coming in contact with, and exchanging gas with the air per time unit (Table 8).
3. *Episodically enhanced flux of dissolved CH_4*. This can occur (a) when deep anoxic and CH_4 rich water in stratified water bodies is mixed up to the surface and comes in contact with the atmosphere during lake circulation (in some papers referred to as "storage flux"). Much of the CH_4 stored in the anoxic water can in this way be vented to the atmosphere over a timescale of days. It is still discussed to what extent enhanced water column CH_4 oxidation during lake overturn can reduce the storage flux, and estimates of how much of the stored CH_4 was oxidized instead of emitted range between >50% and 5%. If substantial parts of this stored

CH_4 are emitted, the storage flux represents a significant flux pathway in many freshwaters (Table 9; Fig. 6). Partial upwelling of CH_4-rich deep water can lead to several such events apart from the full lake circulation events. Episodically enhanced diffusive flux can also occur after (b) ice-out if the surface water suddenly being exposed to the atmosphere after being under the ice is rich in CH_4. Another and more immediate enhanced ice-melt flux occur if (c) there are considerable amounts of CH_4 in bubbles trapped under or in the ice, being released when the ice melts (Denfeld et al., 2018). Overall, more research is needed to constrain all types of episodically enhanced fluxes.

4. *Flux through rooted emergent plants*. Many aquatic plants transport air to the roots to supply them with O_2. Such gas transport systems also transfer gasses such as CH_4 from the roots to the leaves and the atmosphere. These transport systems can be pressurized (e.g., *Typha* spp., *Phragmites* spp., *Nuphar* spp.) or passive (e.g., *Carex* spp., *Peltandra* spp., *Eriophorum* spp.) depending on the plant species. These plants function as conduits for CH_4 that enters the roots allowing rapid transport to the atmosphere bypassing the zones of CH_4 oxidation. At the same time fewer bubbles have been noted where emergent plants are growing. For some species, diel patterns in the transport as an effect of light and solar heating on the plant physiology has been proposed (Table 8).
5. *Transport* via *microbubbles* have been suggested to explain continuous fluxes that were higher than expected from the continuous diffusive flux, in the absence of detectable bubbles as for ebullition (Prairie and del Giorgio, 2013; McGinnis et al., 2015). The formation of pure CH_4 micro bubbles in surface water are typically not physically possible given that the surface inland waters are rarely supersaturated towards 100% CH_4 (although the water is generally supersaturated towards an atmosphere with 2 ppm CH_4). If microbubbles are generated by other processes (e.g., turbulence, or O_2 supersaturation) dissolved CH_4 may however diffuse into such bubbles. Overall, the extent and importance of this microbubble transport pathway is not yet clear.
6. *Specific emission pathways for hydropower reservoirs* include emissions in turbines and in downstream rivers (Johnson et al., 2021; Harrison et al., 2021). Such emissions can be very large if deep anoxic and CH_4-rich water is drawn into the turbine, and therefore hydropower reservoir design is highly important for the associated CH_4 emissions.

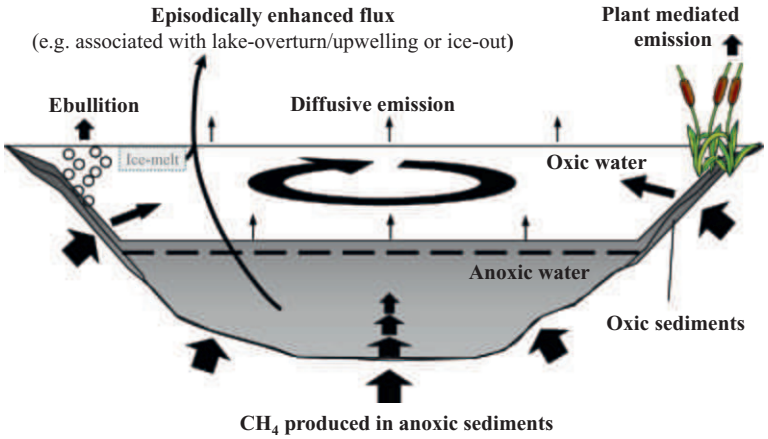

Fig. 4 Illustration of CH_4 emission pathways and transport patterns in a stratified lake with anoxic bottom water. The gray area represents the zone where CH_4 oxidation may be extensive given availability of suitable electron acceptors. When possible anoxic electron acceptors have been depleted CH_4 will start to accumulate in the bottom water, while most of the CH_4 oxidation occur at the oxic-anoxic interface in the water column or in the surface of the shallow sediment. See text for details. Adapted from Bastviken D, Cole J, Pace M and Tranvik L (2004). Methane emissions from lakes: Dependence of lake characteristics, two regional assessments, and a global estimate. *Global Biogeochemical Cycles* 18: GB4009 (12 pages), with permission from American Geophysical Union.

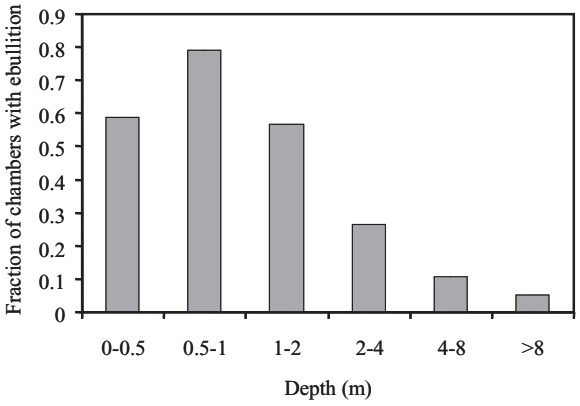

Fig. 5 Fraction of floating chambers receiving ebullition over a 24 h period at different depths. Data are based on 242 measurements in 11 lakes. Adapted from Bastviken D, Cole J, Pace M and Tranvik L (2004). Methane emissions from lakes: Dependence of lake characteristics, two regional assessments, and a global estimate. *Global Biogeochemical Cycles* 18: GB4009 (12 pages), with permission from American Geophysical Union.

Table 8 Examples of environmental variables being related with different types of CH_4 emission from open water of lakes and reservoirs (upper part of table) and vegetated lake shores and wetlands (lower part of table).[a]

Frameworks of study				*Sources*
Biome	*Ebullition*	*Diffusive flux*	*Episodic flux*	
Multi-biome	Lake area, latitude, T_w, T_{air}, HD, time of the day, TP, DIP, CH_{4surf}, Chl-a, PP, DOC, water level fluctuations, river inlets, z, DTS, P_{air}, sediment trapping/focusing, seasonal energy input	Lake area, latitude, T_w, T_{air}, HD, time of the day, TP, DIP, nutrient levels, CH_{4surf}, Chl-a, PP, DOC, water level fluctuations, river inlets, z, DTS, Areal storage	Lake area, TP, DOC, AVF, CH_{4surf}, DO, Sed OM	2, 3, 9, 10, 37, 43
Subarctic				19, 31, 36, 41, 42
Boreal				20, 26, 42
Temperate				27, 28, 29
Tropic				4, 5, 11, 34

Area with emergent aquatic vegetation (wetlands and lake littoral zones)	*Ebullition*	*Diffusive flux*	*Sources*
Peat	P_{air}		38
Danish wetland		Light-DO-MOX[b]	24
	Plant flux or total emission		
Boreal littoral winter emissions	Total flux related to late summer water level, early winter precipitation, and summer biomass production		25
Lake Vesijärvi, Finland. Littoral transect	T_{sed}, plant biomass		23
Boreal littoral zones with Equisetum fluviatile, *Schoenoplectus lacustris* and *Phragmites australis*	Species composition, plant biomass, plant growth dynamics, sediment temperature and type of sediment		21, 22
Typha and Cladium stands in the Everglades	Diel variability if active gas transport. No diurnal pattern if (passive) gas transport. Spatial variability due to biomass and production		6
Hemiboreal wetland	Flux irregular over 24 h but no consistent diel pattern regardless of plant species or active/passive gas transport		30
Sallie's Fen, New Hampshire	Total flux correlated with climate and weather-related variables such as peat temperature, precipitation, net radiation, soil moisture profiles		16
Boreal Mire	Total flux related to depth of water table and presence of vascular plants		17
Freshwater marshes in Sanjiang plain, China	Species composition, water depth; diel variability related to redox potential		12–14
Wetlands in Greenland, Iceland, Scandinavia, and Siberia	Total flux related with temperature and microbial substrate availability. Freeze-in emissions can be important		7, 34
Sub-arctic wetlands, Sweden	Total flux related with temperature, hydrology, plant community, and alterations in permafrost distribution		8
Overall wetland emissions	Total flux related with NEE or NPP, WTD, T_{LST}, T_{air}, vegetation composition, electron acceptors, soil pH, permafrost regime, MOX		1, 14, 18, 32, 33, 35, 39, 40, 43

Sources: (1) Abdalla et al. (2016), (2) Aben et al. (2017), (3) Bastviken et al. (2004), (4) Bastviken et al. (2010), (5) Barbosa et al. (2020), (6) Chanton et al. (1993), (7) Christensen et al. (2003), (8) Christensen et al. (2004), (9) Deemer et al. (2016), (10) Deemer and Holgerson (2021), (11) DelSontro et al. (2011), (12) Ding et al. (2004b), (13) Ding et al. (2005), (14) Ding et al. (2002), (15) Evans et al. (2021), (16) Frolking and Crill (1994), (17) Granberg et al. (2001), (18) Harriss et al. (1993), (19) Jansen et al. (2019), (20) Juutinen et al. (2009), (21) Kankaala et al. (2005), (22) Kankaala et al. (2003), (23) Kankaala et al. (2004), (24) King (1990), (25) Larmola et al. (2004), (26) MacIntyre et al. (2021), (27) Maeck et al. (2013), (28) Mattson and Likens (1990), (29) Michmerhuizen et al. (1996), (30) Milberg et al. (2017), (31) Natchimuthu et al. (2016), (32) Oh et al. (2020), (33) Peltola et al. (2019), (34) Peixoto et al. (2015), (35) Pirk et al. (2015), (36) Rasilo et al. (2015), (37) Sieczko et al. (2020), (38) Tokida et al. (2005), (39) Treat et al. (2018), (40) Whiting and Chanton (1993), (41) Wik et al. (2014), (42) Wik et al. (2016), (43) Yvon-Durocher et al. (2014).

[a]Abbreviations as follows: T_w, T_{air}, water and air temperature, respectively; HD, hydrodynamics (includes turbulence driven by wind or density patterns); TP and DIP, total and dissolved inorganic phosphorous; CH_{4surf}, surface water methane concentrations; Chl-a, chlorophyll a; PP, primary productivity; DOC, dissolved inorganic carbon; z, water depth; DTS, distance to shore; P_{air}, barometric pressure; AVF, anoxic volume fractions; DO, dissolved concentrations of molecular oxygen; Sed OM, sediment organic matter content; MOX, aerobic methane oxidation; NEE, net ecosystem exchange; NPP, net primary production; WTD, water table depth; T_{LST}, land surface temperature. Areal storage means the CH_4 storage in the water column per m^2.

[b]Indirect effect by light on diffusive emissions since light affect O_2 concentrations which in turn affect CH_4 oxidation rates and thereby water CH_4 concentrations.

Table 9 Examples of CH_4 emissions from littoral zones or wetlands. Biome subsections in the table are denoted by headings with bold text. Averages or ranges are given.[a]

Location	*CH_4 emission (mmol m^{-2} day^{-1})*	*Dominating plants/Notes*	*Sources*
Subarctic wetlands	7.8		4
Manitoba wetlands (northern study area of BOREAS)	0.6–22		2
Tundra wetlands, northeast Siberia	0–17.6		10
Boreal wetlands	13.8		4
Swedish mires	0.5–14.8		11
Lake Ekojärvi littoral, Finland	27.8	*P. australis*	9
Lake Ekojärvi littoral, Finland	2.2	*S. lacustris*	9
Lake Ekojärvi littoral, Finland	1.7	*Equisetum fluviatile*	9
Lake Ekojärvi littoral, Finland	1.0	*N. lutea*	9
Lake Ekojärvi littoral, Finland	1.0	*S. gramineum*	9
Lake Ekojärvi littoral, Finland	0.5	*P. natans*	9
Lake Kevätön littoral, Finland	4.4	Hypereutrophic, mixed plant community	8
Lake Mekrijärvi littoral, Finland	3.0	Mesotrophic, polyhumic, mixed plant community	8
Temperate wetlands	5.8		4
Colorado wetlands:			12
Dillon	0.01	Mixed plant communities	12
Long	0.9	Mixed plant communities	12
Pass	0.1	Mixed plant communities	12
Red Rock	5.5	Mixed plant communities	12
Red Rock	12.6	*Nuphar lutea* stand	12
Rainbow	2.4	Mixed plant communities	12
Temperate Sphagnum bog, Japan	28.1	Marsh trefoil (*Menyanthes trifoliata*)	14
	18.1	*P. australis*	14
	4.4	*Sphagnum* sp.	
Natural wetlands in China	3.2		6
Wuliangsu Lake, western China	3.2	*P. pectinatus*	7
	22.3	*P. australis.* Marked seasonal and diurnal variation	7
Everglades, Florida	8.9	Typha stands; 90% through plants	3
	2.8	Cladium stands	3
Tropical wetlands	11.7		4
Orinoco River floodplain, Venezuela:			
Flooded forest	6.8	63% emitted as ebullition.	13
Floating macrophytes	1.6	52% emitted as ebullition.	13
Amazon floodplain:			
Wetlands	24.4		5
Macrophytes	36.9		5
Flooded forests	6.9		5
Grass mats	24.4	64% emitted as ebullition	1
Flooded forests	13.7	54% emitted as ebullition	1

Sources: (1) Bartlett et al. (1988), (2) Bubier et al. (2005), (3) Chanton et al. (1993), (4) Crill (1996), (5) Devol et al. (1988), (6) Ding et al. (2004a,b), (7) Duan et al. (2005), (8) Juutinen et al. (2003), (9) Kankaala et al. (2003), (10) Nakano et al. (2000), (11) Nilsson et al. (2001), (12) Smith and Lewis (1992), (13) Smith et al. (2000), (14) Sugimoto and Fujita (1997).
[a]Only examples from the numerous published wetland studies are given. For more information see e.g., Bartlett and Harriss (1993), Harriss et al. (1993), Peltola et al. (2019), Ringeval et al. (2011), Treat et al. (2018), Wetzel (2001), Whalen (2005), and Yavitt et al. (1997).

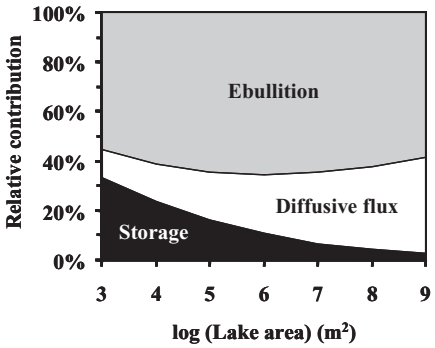

Fig. 6 Relative contribution of different open water methane flux pathways versus lake area. Based on data from 73 boreal and temperate lakes. Reproduced from Bastviken D, Cole J, Pace M and Tranvik L (2004). Methane emissions from lakes: Dependence of lake characteristics, two regional assessments, and a global estimate. *Global Biogeochemical Cycles* 18: GB4009 (12 pages), with permission from American Geophysical Union.

The contribution of different flux types and their regulation

Plant mediated emission and ebullition dominates CH_4 emissions from most lakes and wetlands. Ebullition often (but not always) accounts for about 50% or more of the open water emission (Fig. 6). However, it should be emphasized that ebullition, being episodic and having a heterogeneous spatial distribution, is challenging to quantify by the temporally and spatially limited measurement efforts typically being feasible, and a general underestimation of ebullition has been hypothesized.

At a small-scale level (<1 m^2), emission rates are regulated by a combination of CH_4 production and oxidation rates, and transport. In turn, this small-scale regulation depends on larger scale environmental factors as summarized in Table 8. In general, open water emissions from lakes seem related to lake area (Fig. 7), lake morphometry, and the amount and degradability of the organic matter reaching the sediments. Wetland emissions, dominated by plant-mediated flux, depend on sediment or peat temperature, the depth of the water table, plant community composition and biomass, and net primary production. In northern areas, alterations in the permafrost distribution are important by affecting the surface hydrology, inundation and plant community structure.

Open water mean emissions from lakes typically range between 0.01 and 20 mmol m^{-2} day^{-1}, while the range for wetland and plant mediated emissions is 0.01–40 mmol m^{-2} day^{-1}, with higher rates under conditions characterized by higher temperature and higher primary productivity. Smaller lakes have higher emissions per m^2 than larger lakes (Holgerson and Raymond, 2016). Rivers also emit CH_4 with total mean rates >8.5 mmol m^{-2} day^{-1} reported (Stanley et al., 2016). Fluxes have been linked to a large number of environmental variables (Table 8). Temperature and primary productivity regulating net supply of organic matter substrates for methanogenesis and microbial metabolic rates, and also being linked with physical forcing in various ways, seems to be key variables. Other variables, linked to transport may determine the residence time of CH_4 in the systems, thereby regulating the time for methane oxidation and the share of the produced CH_4 being emitted. There is growing concern that inland water CH_4 emissions are highly climate sensitive for multiple reasons including the strong direct temperature sensitivity, the enhancement of fluxes in lakes forming in tundra areas with melting permafrost (thermokarst lakes), and the enhancement of primary productivity from the combination of eutrophication and elevated temperature (e.g., Marotta et al., 2014; Wik et al., 2016; Yvon-Durocher et al., 2014).

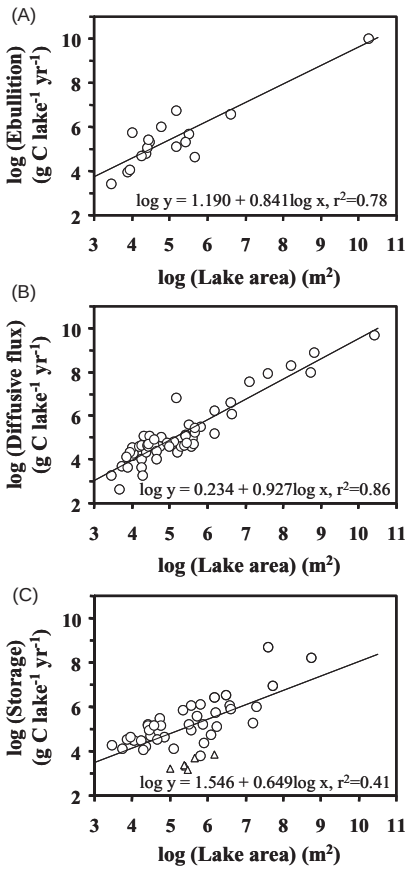

Fig. 7 Ebullition (A), diffusive flux (B), and water column methane storage during stratification periods (C) for lakes of different size. The triangles in panel C represent lakes without anoxic parts of the water column. Linear regression lines are given in the graphs. Adapted from Bastviken D, Cole J, Pace M and Tranvik L (2004). Methane emissions from lakes: Dependence of lake characteristics, two regional assessments, and a global estimate. *Global Biogeochemical Cycles* 18: GB4009 (12 pages), with permission from American Geophysical Union.

Reservoirs also emit CH_4 (Johnson et al., 2021; Harrison et al., 2021; IPCC, 2019). Old reservoirs have been suggested to emit CH_4 at rates similar to or somewhat higher than lakes. However, recently established reservoirs can emit much higher amounts of CH_4 due to the flooding of soils and rapid transformation of soil organic matter to CH_4. Consequently, reservoir fluxes are highly variable, with emissions being very low in some reservoirs, while very high emissions have been observed from shallow reservoirs in warm climate regions. Such emissions may offset the climate benefits with hydropower in some cases, making reservoir CH_4 emissions important to consider when prioritizing between different sustainable energy sources for the future. Recent work provides best estimates of reservoir emissions of 10–22 Tg CH_4 $year^{-1}$ (Johnson et al., 2021; Harrison et al., 2021).

Plant mediated emissions are highly variable based on local conditions (Table 9). Global CH_4 emissions from natural wetlands range between 100 and 222 Tg CH_4 $year^{-1}$ Other inland waters, including lakes, reservoirs, and running water, have been estimated to contribute 48–212 Tg CH_4 $year^{-1}$. Given total natural and anthropogenic global emissions estimates of 524–896 Tg CH_4 $year^{-1}$, natural wetlands and other inland waters account for in the order of 19–25% and 11–24%, respectively (Saunois et al., 2020). It has been estimated that lakes, various types of reservoirs or artificial impoundments, and running water contribute approximately 70%, 13%, and 17% to the global mean inland water fluxes, respectively (Saunois et al., 2020). Notably, inland water emissions is seen the most uncertain part of the global CH_4 budget and numbers provided here are recent estimates awaiting further refinements. Considerable uncertainty can be linked to the uncertainties in total inland water and wetland areas, to the distinction between various types of inland waters and wetlands which strongly impact fluxes and are important for flux modeling, and to spatiotemporal patterns in the various fluxes.

Knowledge needs

The knowledge about CH_4 in inland waters still suffers from scarcity of long-term systematic and coordinated data collection at multiple sites. Such efforts are key to determine e.g., climate impacts on CH_4 dynamics and emissions. Given the increasing evidence of strong temperature sensitivity and seasonality, future data collection face the challenge to cover all seasons adequately in spite of practical and financial constraints. It is also clear that variability at multiple scales e.g., across diel, seasonal and among-year time frames, should be considered. It should be noted that low latitude regions have received much less attention than high latitudes, yet low latitudes may contribute the greatest fluxes and the greatest flux changes in the future (Bastviken et al., 2011; Borges et al., 2015; Marotta et al., 2014). It would be highly beneficial to further constrain process regulation, flux rates, and area distributions in ways that are compatible with large-scale modeling (Matthews et al., 2020). Previously neglected fluxes, such as large emissions via trees in flooded forested wetlands (Pangala et al., 2017), also need attention and will challenge the traditional distinctions between environment types (such as "lakes" versus "wetlands"), as these definitions are not necessarily compatible with the key environmental features regulating CH_4 dynamics and emissions. For example, both lakes and wetlands can include partially open water areas and areas with emergent aquatic plants and the extent and characteristics of theses specific land cover types (open water versus water with emergent plants) are more important for CH_4 dynamics and flux regulation than if we define the environment as a lake or a wetland. In addition, method development towards easier and less expensive CH_4-measurements would be highly beneficial to resolve all types of CH_4-related knowledge gaps more effectively.

An important challenge is to estimate how CH_4 emissions from inland waters will be affected by climate change as emissions are considered highly sensitive to climate and there is a risk of increased CH_4 emissions in a warmer future. At the same time, some studies point towards the potential of MOX to prevent increased emissions (Oh et al., 2020). In any case, such emission feedback responses represent important links between aquatic methane cycling and the future climate.

Acknowledgments

I wish to thank Patrick Crill and Nguyen Than Duc for very valuable comments on the 1st edition manuscript.

See Also: Fundamental concepts and theories: Chemosynthesis; Structures and functions of Inland Waters - Lakes: Bottom Boundary Layers; Structures and functions of Inland Waters - Wetlands: Restoring Riparian Peatlands for Inland Waters: A European Perspective; Wetland Soils: Physical and Chemical Properties and Biogeochemical Processes

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Nitrogen☆

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This is an update of R. Howarth, Nitrogen, In Encyclopedia of Inland Waters, Edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00098-3.
This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Anoxic Oxygen-free, lacking oxygen.
Denitrification The process of converting nitrate to molecular N_2; also called dissimilatory nitrate reduction.
Eutrophic Characterized by high levels of primary production and high algal biomass.
Hypoxic Having oxygen present at only low concentrations (generally less than 2–3 mg/l).
Nitrification The oxidation of ammonium to nitrite and nitrate by bacteria.
Nitrogen fixation The conversion of molecular N_2 into reactive nitrogen compounds such as ammonium.
Nutrient limitation The condition of rate of growth of production by photo-autotrophs being less than maximum due to a constraint by one or more nutrients, usually phosphorus or nitrogen.
Oligotrophic Characterized by low levels of primary production and low algal biomass.
Oxic Having oxygen present.
Primary production The rate of accumulation of new biomass by plants, algae, and photosynthetic bacteria through photosynthesis.
Rhizosphere The roots, rhizomes, and associated micro-organism of a vascular plant.

Introduction

Nitrogen is an essential element for life and is the fourth most abundant element in the living biomass (by moles) after hydrogen, carbon, and oxygen. Nitrogen is in all amino acids and nucleotides, and therefore in all proteins and nucleic acids. Nitrogen is also a major component of the chitin that makes up the cell walls of fungi and the exoskeletons of aquatic insects and crustaceans. Together with phosphorus, nitrogen limits rates of primary production in most of the ecosystems on Earth, including inland waters. However, unlike phosphorus, nitrogen has a very active oxidation–reduction cycle, and nitrogen in nature exists in valence states from −3 to +5. Curiously, and unlike the biogeochemical cycle of any other major element, most of the nitrogen on Earth is present with an intermediate valence state of 0 (as molecular, gaseous N_2). More than any other major element cycle, human activity has accelerated the nitrogen cycle leading to many critical changes in the aquatic ecosystems.

Forms and transformations of nitrogen

Nitrogen occurs as both organic and inorganic nitrogen in aquatic ecosystems. Frequently, the organic forms dominate, including both particulate organic nitrogen (PON) and dissolved organic nitrogen (DON). The PON not only includes the nitrogen in living organisms, but also large amounts of nitrogen in detritus or dead organic matter. The DON consists of a wide range of organic substances, including simple substances such as free amino acids. Much of the DON, however, consists of higher molecular weight compounds. Most of the DON in natural waters has never been chemically characterized at the level of individual compounds because of the analytical challenge of measuring thousands of unknown substances, each often present at relatively low concentrations.

The inorganic nitrogen in aquatic ecosystems includes dissolved N_2 gas, oxidized ions such as nitrate (NO_3^-) and nitrite (NO_2^-), the reduced ammonium ion (NH_4^+), and the reduced ammonia gas (NH_3). Nitrate is the most oxidized form of nitrogen (valence

☆*Change History*: October 2021. RW Howarth updated all sections. Figs. 1, 3, and 4 are new.

state of +5), while ammonia and ammonium are most reduced (valence state of −3). Ammonium is a weak acid that in solution is in equilibrium with ammonia gas, which is a base. The equilibrium constant for this relationship is $10^{-9.3}$. Thus, ammonium is more dominant whenever the pH is less than 9.3, as is almost always the case in aquatic ecosystems. At pH = 8.3, the ammonium concentration is 10-fold greater than the ammonia concentration. At pH = 7.3, the ammonium concentration is 100-fold greater than the ammonia concentration. Since ammonia is a gas, it can be volatilized to the atmosphere. The rate of loss is a function of the ammonia concentration, and so this process is much greater at higher pHs, where higher concentrations of ammonia are favored.

The vast majority of the nitrogen on the Earth is present as N_2 gas. This becomes biologically available only through bacterial nitrogen fixation, fixation by lightning or volcanic activity, or fixation by human activity. Before the industrial revolution, bacterial nitrogen fixation was by far the major mechanism for the creation of reactive, biologically available forms of nitrogen on the planet. Increasingly, human activity is fixing nitrogen, and this now exceeds the natural biological nitrogen fixation globally and dominates the nitrogen cycle in many regions, as discussed below.

The primary forms of reactive nitrogen assimilated by algae, rooted plants, fungi, and bacteria are nitrate, nitrite, ammonium, and ammonia. Once taken up, nitrate and nitrite are reduced to ammonium in processes called assimilatory nitrate or nitrite reduction. Ammonium – whether taken up directly or formed by assimilatory reduction in the organism – is used by plants, algae, and microorganisms to produce organic nitrogen compounds. The organic nitrogen of plants, algae, and microorganisms can flow through a food web to animals, and detrital PON and DON is decomposed by bacteria and fungi. The organic nitrogen eaten by animals or decomposed by microorganisms is excreted as ammonium or sometimes as urea, a low-molecular weight compound that is quickly hydrolyzed to ammonium in water. These processes of releasing nitrogen back to the environment are called nitrogen mineralization (Fig. 1).

The forms of inorganic, reactive nitrogen are converted from one to another in aquatic ecosystems through a variety of bacterially mediated processes. Ammonium is oxidized to nitrate in a process called nitrification, an energy-yielding process. The nitrifying bacteria that catalyze the reaction gain energy and use this energy to fix carbon dioxide into new bacterial biomass, a process called chemosynthesis. The energy yield of the reaction is low compared with many chemosynthetic processes based on oxidizing sulfur or iron compounds, and so the growth of nitrifying bacteria is slow. Nitrification rates are in part a function of the population size of nitrifying bacteria; where mortality on the bacteria is high due to grazing, the slow growth result keeps population sizes low, and rates of nitrification can be very low, allowing ammonium to accumulate.

Nitrate is reduced to nitrite and nitrite is reduced to N_2 in a process called denitrification, also called dissimilatory nitrate reduction. The bacteria that catalyze these reactions are heterotrophic bacteria that gain their energy from the degradation or organic matter; they use the nitrate or nitrite as an electron acceptor, very much as plants and animals and many other microorganisms use oxygen as an electron acceptor for respiration. Since the energy yield of respiring organic matter using nitrate as the electron acceptor is somewhat less than when using oxygen as the electron acceptor, denitrification tends to occur only when oxygen is absent or present at very low levels. This is frequently the case in aquatic sediments, and often in the bottom waters of stratified lakes and estuaries. Denitrification is the major sink for reactive nitrogen in natural ecosystems. At the global scale, denitrification serves to balance nitrogen fixation and maintains N_2 gas as the major form of nitrogen on the planet.

Many of these nitrogen-cycle processes have been understood in broad brush since the early years of the 20th century, but other nitrogen processes have been discovered only in the past 30–40 years. One of these is denitrification based on chemosynthetic oxidation of sulfide or reduced iron rather than respiration of organic matter. Another is the anaerobic oxidation of ammonium to N_2 (ANAMOX), which is also a chemosynthetic process. And a third is the dissimilatory reduction of nitrate to ammonium (DNRA). The DNRA process is a form of respiration, with organic matter being consumed using nitrate as the electron acceptor; however, the

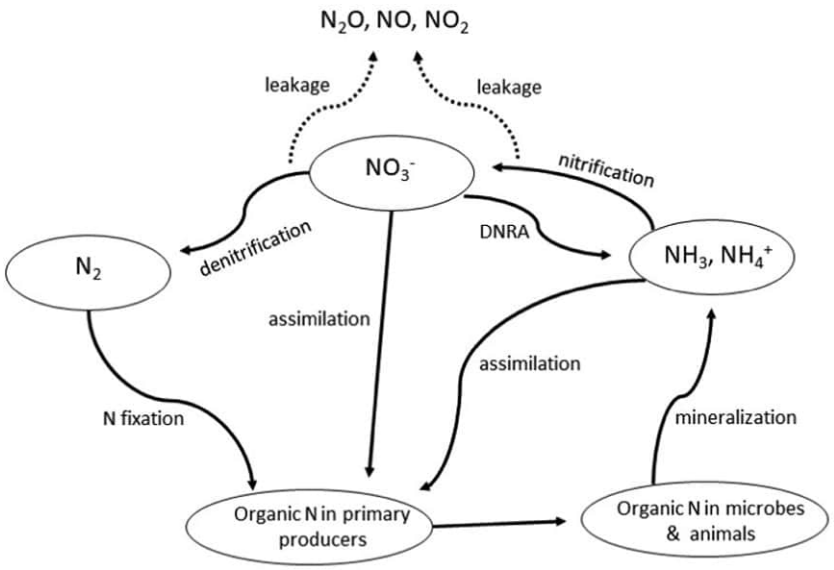

Fig. 1 Simplified diagram of the nitrogen cycle in aquatic ecosystems.

nitrogen is reduced to ammonium rather than to N_2. Unlike denitrification, DNRA conserves the nitrogen in the ecosystem in a reactive, biologically available form. The controls that may make denitrification or DNRA more important in any particular situation remain imperfectly known, but evidence suggests that DNRA may dominate in sediments that are more reducing and have higher concentrations of dissolved sulfides (Burgen and Hamilton, 2007).

Nitrogen cycling at the ecosystem scale

The nitrogen budget of most lakes, streams, and rivers is dominated by nitrogen inputs from their watersheds and often include flows through groundwaters as well as in surface waters. As discussed elsewhere within this encyclopedia, bacterial nitrogen fixation can be an important source, but in most aquatic ecosystems this is far less than the inputs from upstream sources. Direct deposition from the atmosphere can also be an important input of nitrogen, that is nitrogen inputs in rain and snowfall as well as uptake of nitrogen gases by the water body from the atmosphere and deposition of nitrogen particles onto the water surface. However, only in aquatic ecosystems with very small watersheds does the direct deposition of nitrogen from the atmosphere rival the input of nitrogen in stream and river flow and in groundwaters. Estuaries can receive nitrogen inputs from adjacent coastal ocean sources, as well as from their watersheds.

In most aquatic ecosystems, the rate of nitrogen uptake by plants, algae, and microorganisms is far greater than the rate of inputs from external sources, and the nitrogen needs of primary production and uptake by bacteria and fungi is supported by rapid recycling of nitrogen within the ecosystem. In oligotrophic lakes, the rate of uptake of nitrate and ammonium by phytoplankton is generally 50- to 100-fold more than the rate of input of nitrogen from external sources. In highly productive eutrophic lakes, the rate of nitrogen uptake by phytoplankton is often 10- to 30-fold greater than the rate of external inputs. In some very productive coastal salt marshes with huge inputs of nitrogen delivered by twice-daily tides, nitrogen uptake by the primary producing organisms is roughly equal to the external nitrogen inputs, but this is an extreme case of very high inputs.

In streams and rivers, the uptake of nitrogen and other nutrients can be considered in the context of spiraling distances, or the average distance over which an atom flows before being assimilated by plants, algae, bacteria, or fungi. In streams that are not heavily impacted by humans, this distance may be just meters to perhaps a hundred meters. After assimilation, the nitrogen atom is eventually remineralized and moves downstream again; again, on average, it moves the same spiraling distance. In larger rivers, the distances can be much greater, up to tens or hundreds of kilometers or even greater. And in landscapes with heavy human influences, the distances can be much greater; for instance, the spiraling distance for nitrogen in a ditch draining agricultural lands may be kilometers or more.

Denitrification can be a major sink of nitrogen in aquatic ecosystems, including wetlands, lakes, reservoirs, estuaries, streams, and rivers. Denitrification can occur in anoxic waters, such as often occur in stratified lakes and estuaries. However, in these stratified systems, the rate of supply of nitrate into the anoxic waters is often low, keeping rates of denitrification relatively low. Denitrification readily occurs in the sediments of virtually all inland water ecosystems due to low oxygen levels, and rates can be high when nitrate concentrations in the overlying waters are high. Commonly in many sediments and in wetland soils, nitrification and denitrification co-occur in close proximity in microzones where oxygen is present (for nitrification) and absent (for denitrification). This coupled nitrification–denitrification can account for a majority of the denitrification in aquatic ecosystems. The coupling of these processes is favored by the bio-irrigating activities of animals and by the rhizosphere of vascular plants.

In aquatic ecosystems with an oxygenated water column, the percentage of the nitrogen inputs that are denitrified is well predicted as a function of the water residence time and the depth of the water. This reflects the interaction time of the nitrogen with the sediments, the site of denitrification. The percentage loss of nitrogen is greater in ecosystems that are shallower and that have longer water residence times. At the landscape scale, the water residence time is frequently more important. Thus, the loss of nitrogen through denitrification tends to be greater in lakes and reservoirs than in streams and rivers (Howarth et al., 1996, Fig. 2).

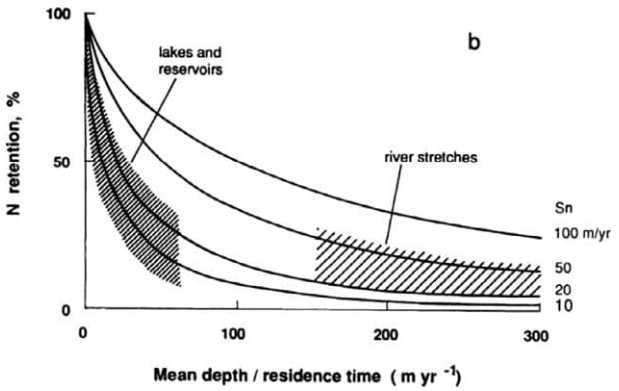

Fig. 2 The percentage of nitrogen inputs to aquatic ecosystems that is lost through denitrification as a function of depth and residence time of the system. Modified from Howarth RW, Billen G, Swaney D, Townsend A, Jarworski A, Lajtha A, Downing J. A., Elmgren R., Caraco N, Jordan T, Berendse F, Freney J, Kueyarov V, Murdoch P, and Zhao-Liang L (1996) Riverine inputs of nitrogen to the North Atlantic Ocean: Fluxes and human influences. *Biogeochemistry* 35: 75–139.

Nutrient limitation of net primary production

In most natural ecosystems, rates of net primary production tend to be limited by the availability of just one or two elements, usually nitrogen, phosphorus, or both. While the primary producers require many other elements, these generally are in abundant supply compared to nitrogen and phosphorus. Despite many decades of research, some disagreement continues to exist regarding nutrient limitation in freshwater lakes. Classic work by David Schindler and his colleagues using whole-lake nutrient additions clearly showed phosphorus to be the limiting nutrient (Schindler et al., 2008; Higgins et al., 2018), as did cross-system studies by Richard Vollenweider and others, showing phosphorus levels to be well correlated with phytoplankton biomass across a wide range of lakes. Phosphorus limitation may well be the norm for mesotrophic to eutrophic lakes, that is lakes of moderate to high productivity, at least in the temperate zone. However, oligotrophic, very low productivity lakes are often limited by nitrogen or co-limited by nitrogen and phosphorus. And some limnologists argue that nitrogen limitation may be more common in mesotrophic and eutrophic lakes than often appreciated, based on the ratio of total nitrogen to total phosphorus in the lakes, as is discussed further below. For temperate-zone estuaries, there is a clear tendency for nitrogen to be the nutrient most limiting net primary productivity. As is discussed in the section below, human activity has greatly accelerated the nitrogen cycle, leading to massive increases in nitrogen inputs to estuaries in many parts of the world. Nitrogen is now the largest source of pollution in estuaries, and in the United States, two-thirds of estuaries are moderately to severely degraded from nitrogen pollution and the eutrophication it causes (Vitousek et al., 1997; Carpenter et al., 1998).

Whether nitrogen or phosphorus is more limiting is a function of the relative availabilities of these two elements in the ecosystem (Howarth and Marino, 2006; Elser et al., 2009). Although there is some plasticity in the elemental composition of phytoplankton, the variation is relatively small and the ratio of nitrogen to phosphorus in phytoplankton biomass is usually in the range of 16:1 by moles (the "Redfield ratio," named after Alfred Redfield who described the relationship between water chemistry and phytoplankton composition in the world's oceans in the 1930s). In ecosystems where the ratio of available nitrogen to phosphorus in the water is well above 16:1, phosphorus is in relatively short supply and will be more limiting to net primary production. In ecosystems where the nitrogen:phosphorus ratio of available nutrients is well below 16:1, nitrogen is in relatively short supply (compared with the needs of the phytoplankton) and will be more limiting. The ratio of dissolved inorganic nitrogen (the sum of nitrate, nitrite, ammonium, and ammonia) to dissolved inorganic phosphorus is a reasonable indicator of the ratio of dissolved nitrogen and phosphorus in many cases and can be used to infer whether nitrogen or phosphorus is more limiting, if the ratio is sufficiently above or below 16:1. However, dissolved inorganic nutrients often recycle quite quickly in the water column of aquatic ecosystems, and so concentrations are not always a reliable indicator of supply. Further, most analytical methods for measuring dissolved inorganic phosphorus overestimate this quantity by some unknown amount due to inclusion of some organic phosphorus and positive interference from arsenic.

The ratio of available nitrogen to phosphorus within an ecosystem is a function of both the ratio in the external inputs of these elements and the processing of nitrogen and phosphorus within the ecosystem. Often, the nitrogen to phosphorus ratio in nutrient inputs from watersheds are well above 16:1, which tends to drive the aquatic ecosystems towards phosphorus limitation. In contrast to lakes, estuaries receive nutrients both from upstream watersheds and from ocean waters. The ocean waters are frequently phosphorus rich and somewhat depleted in nitrogen (relative to the Redfield ratio). This is one of the reasons that estuaries may be more prone to nitrogen limitation.

A variety of processes within an ecosystem can change the availabilities of nitrogen and phosphorus. Of particular importance for phosphorus is the adsorption to sediment particles. This lowers concentrations of dissolved inorganic phosphorus, and therefore makes phosphorus limitation more likely. The presence of competing ions in seawater makes adsorption less in estuaries than in freshwaters, and inorganic phosphorus that is adsorbed to suspended sediment particles in rivers is largely desorbed and becomes soluble in estuaries as the salinity increases. This tends to make phosphorus limitation less likely (and nitrogen limitation more likely) in estuaries than in freshwater ecosystems (within the constraints set by the inputs of nitrogen and phosphorus, and the influences of other biogeochemical processes).

Both nitrogen fixation and denitrification can have large influences on the availability of nitrogen in aquatic ecosystems. Briefly, nitrogen fixation by planktonic cyanobacteria is an important process in many lakes that helps to alleviate nitrogen shortages and can contribute to phosphorus limitation in freshwaters, providing the deficit of nitrogen availability to phosphorus is not too large. In stark contrast, nitrogen fixation by planktonic cyanobacteria seldom, if ever, occurs in even strongly nitrogen-limited estuaries at salinities greater than 10 parts per thousand. This is probably a result of the high sulfate concentrations in seawater interfering with the uptake of molybdenum by planktonic cyanobacteria in estuaries; molybdenum is required for nitrogen fixation. It is interesting to note that sulfate levels are sometimes high and sometimes not in inland saline lakes. As a result, nitrogen fixation is a major process in some saline lakes but not in others. In saline lakes where nitrogen fixation occurs, the process helps to alleviate nitrogen shortages and maintain phosphorus limitation, while high sulfate lakes without significant nitrogen fixation are often nitrogen limited.

Scientists who study nutrient limitation in lakes have used a variety of approaches, and this has contributed to the ongoing debate about the prevalence of phosphorus and nitrogen limitation (Howarth and Marino, 2006; Paerl et al., 2016; Higgins et al., 2018). Often, researchers will use short-term bioassays. In this approach, nitrogen, phosphorus, or some other element is added to water samples in bottles and any change in phytoplankton biomass or productivity over a few days to a week is noted. While this can provide very useful information, the approach has many difficulties. One of the greatest of these is that the time frame may not allow for some important biogeochemical processes, such as nitrogen fixation, to occur. In experiments with nutrient additions to

whole lakes over growing seasons and years, researchers have demonstrated that temporary shortages of nitrogen that result from fertilizing with phosphorus and nitrogen at ratios below 16:1 can be alleviated by planktonic nitrogen fixation, and that the lakes remain phosphorus limited over these longer time frames. But such a response would not be observed in a short-term bioassay, which might instead suggest nitrogen limitation. The nitrogen limitation would in fact be only a short, transient feature.

A less ambiguous way to study nutrient limitation has come from longer-term, whole-lake experiments and experiments with large tanks or bags designed to mimic important components of the ecosystem over time periods of a growing season or longer (mesocosm experiments). Such experiments have clearly shown a prevalence for phosphorus limitation in moderately productive lakes and for nitrogen limitation in estuaries in the temperate zone.

The ratio of nitrogen to phosphorus can also be used to infer nutrient limitation in aquatic ecosystems. However, seldom if ever do scientists have direct information on the ratio of available nitrogen to phosphorus, so inferences are made from data on inorganic, dissolved nutrients or data on total nitrogen and phosphorus. For the reasons discussed above, the ratio of dissolved inorganic nitrogen to phosphorus cannot unambiguously indicate nutrient limitation by a particular nutrient, when close to the Redfield ratio of 16:1. But ratios of more than 1000:1 are common in many lakes, clearly indicating phosphorus limitation in these lakes. And the inorganic nitrogen to phosphorus ratio in estuaries is often less than 1:1, which indicates strong nitrogen limitation. For most lakes, the ratio of total nitrogen to total phosphorus is considerably less than the ratio of inorganic dissolved nitrogen and phosphorus, although typically greater than the Redfield ratio of 16:1. Based on statistical analyses across lakes, limnologists have suggested that when the total nitrogen to total phosphorus ratio is less than 29:1, nitrogen may be more important than phosphorus in regulating phytoplankton biomass (Dolman et al., 2016). However, this has not been independently verified with long-term experimental data.

Human acceleration of the nitrogen cycle

Human activity has altered the nitrogen cycle more than that of any other major element on Earth (Vitousek et al., 1997; Galloway et al., 2004). Prior to the industrial and agricultural revolutions, the vast majority of reactive nitrogen on the planet was created by bacterial nitrogen fixation, and this rate of creation was balanced over geological time by denitrification. Now the creation of nitrogen by humans to produce synthetic nitrogen fertilizer through the Haber–Bosch process exceeds the rate of natural fixation on the continents. This process was not invented until 1909 and did not see widespread production until after World War II, but in the years since 1960, synthetic nitrogen fertilizer has come to dominate agriculture and has helped power the green revolution that has allowed the human population to expand to over 7.9 billion people. The inadvertent creation of reactive nitrogen during fossil fuel combustion also adds to the global nitrogen cycle.

The influences of human activity on the nitrogen cycle vary across the regions of the globe. Because of the high chemical reactivity and high biological demand for nitrogen, most forms of reactive nitrogen (i.e., nitrogen other than N_2 gas) do not cycle globally, but rather at the scale of large regions. The natural rates of nitrogen fixation in terrestrial ecosystems are much higher in the tropics, whereas more of the fertilizer use and fossil fuel combustion to date has occurred in temperate regions. This has started to change somewhat in recent decades as fertilizer use and fossil fuel combustion increase in South Asia and tropical South America. Nonetheless, to date the largest changes in nitrogen cycling have occurred in the temperate zone in Europe, the United States, and China. The flow of nitrogen in large rivers in these areas has increased 15-fold or more due to human activity, with much of this increase occurring since 1980 in Europe and the United States and since 2000 in China.

Globally, the use of synthetic nitrogen fertilizer has driven most of the increase in nitrogen cycling. This is also clearly the case in many regions, including the Mississippi River basin (Fig. 3; Howarth et al., 2021). However, in some regions such as New England in the northeastern United States, the combustion of fossil fuel has been a larger contributor. This fossil fuel combustion leads to pollution of the atmosphere with oxidized nitrogen compounds. Their deposition onto the landscape contributes to the flux of nitrogen to aquatic ecosystems. Much of the nitrogen is deposited onto forests, which retain a great deal of it, and some falls on urban and suburban lands, where retention is much less. The movement of nitrogen in animal feeds and in food for humans can also be significant in many regions. Note the large export of nitrogen in food and feed from the Mississippi River basin, a flux that exceeds the flow of nitrogen in the waters of the River itself, and the large import of nitrogen to New England in food and feeds (Fig. 3, Howarth et al., 2021).

One of the largest consequence on aquatic ecosystems of the human acceleration of the nitrogen cycle has been the eutrophi cation of estuaries and other coastal waters. Eutrophication is the excess production of organic matter by phytoplankton and benthic plants and algae, and it has led to oxygen-deprived waters (anoxic and hypoxic zones, sometimes called “dead zones”) in many areas, as well as habitat degradation, loss of biotic diversity, and increased incidences and extent of harmful algal blooms. One of the world’s largest dead zones occurs every summer in the northern Gulf of Mexico, caused by the large flux of nitrogen down the Mississippi River.

Nitrogen has contributed to eutrophication in some freshwater lakes as well, quite likely including Lake Victoria in Africa and Lake Taihu in China (Paerl et al., 2016). However, in general nitrogen is less likely to cause eutrophication in freshwater lakes than in estuaries simply because nitrogen limitation of net primary productivity is less common in lakes. Nonetheless, some recent evidence suggests that toxic phytoplankton blooms may be aggravated in lakes by high levels of nitrogen, even when net primary production is severely phosphorus limited. The oligotrophic and mesotrophic Finger Lakes of New York State are clearly phospho-rus limited, as indicated both by experiments and ratios of inorganic nitrogen to phosphorus that are commonly greater than

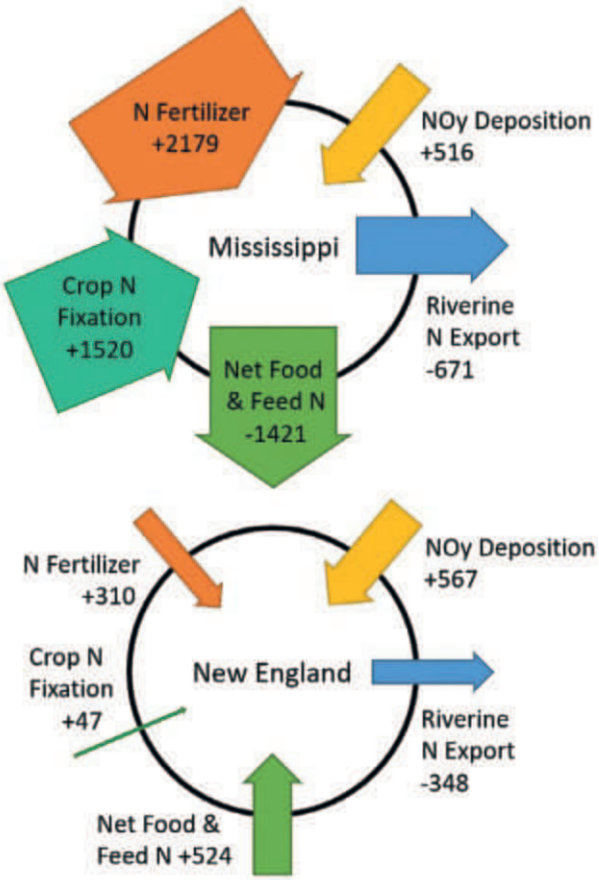

Fig. 3 Comparison of inputs of nitrogen to the landscape from human activity and exports of nitrogen in rivers, in kg nitrogen per square meter per year. Top shows the Mississippi River basin. Bottom shows all watersheds and rivers in New England. Note that the movement of nitrogen in food for humans and animal feeds is a net import in New England but a net export for the Mississippi River basin. Reprinted from Howarth RW, Chan F, Swaney DP, Marino RM, and Hayn M (2021). Role of external inputs of nutrients to aquatic ecosystems in determining prevalence of nitrogen vs. phosphorus limitation of net primary productivity. *Biogeochemistry* 154: 293–306.

1000:1. In recent years all of these Finger Lakes have experienced blooms of toxic cyanobacteria, often referred to as harmful algal blooms even though the cyanobacteria are not actually algae. One hypothesis for the occurrence of these blooms is that high nitrogen levels can promote higher concentrations of toxins such as microcystin in the cyanobacteria. The toxins can reduce grazing by zooplankton on the cyanobacteria, and thereby lead to a bloom with high cyanobacteria biomass even if the growth rate of the cyanobacteria is low due to low phosphorus. Some experimental evidence supports higher amounts of toxins when nitrogen levels are greater (Baker et al., 2018), although the connection to lower grazing and mortality has not yet been proven. In light of this hypothesis, cyanobacteria can be viewed to become a dominant part of the phytoplankton community in lakes under two conditions: when nitrogen levels are high and phosphorus levels are low to moderate, leading to highly toxic cyanobacteria that are not fixing nitrogen, and when nitrogen levels are low and phosphorus levels are high, which encourages nitrogen-fixing cyanobacteria (Fig. 4).

Another impact of accelerated nitrogen cycling on freshwater ecosystems comes from acid rain. Both sulfuric and nitric acids contribute to acid rain. Much of the focus historically has been on sulfuric acid, and that has led to some measurable progress in reducing sulfur emissions to the atmosphere. Reductions in NOx, the precursor for nitric acid, have been far less, and nitric acid is therefore growing as an overall source of acid rain. This nitric acid – which comes from fossil fuel combustion and is the same nitrogen deposition that contributes to nitrogen flows to estuaries – is the major source of acid rain now in some regions.

The deposition of ammonia gas and ammonium particles can also contribute to the acidification of inland waters. Most of the ammonia in the atmosphere comes from volatilization from agricultural sources, and particularly from large animal feedlot operations. Ammonia is a base, and so acts to raise the pH of precipitation. In this technical sense, ammonia counteracts acid rain. However, the ammonia and ammonium deposited onto terrestrial ecosystems or directly onto aquatic ecosystems can be nitrified to nitrate, as discussed above. This chemical transformation produces large quantities of acid – 1 mol of proton acidity generated for every mole of nitrate created from the oxidation of ammonia and 2 mol for every mole of nitrate created from the oxidation of ammonium ion. Consequently, the deposition of ammonia and ammonium also can contribute substantially to the acidification of inland waters.

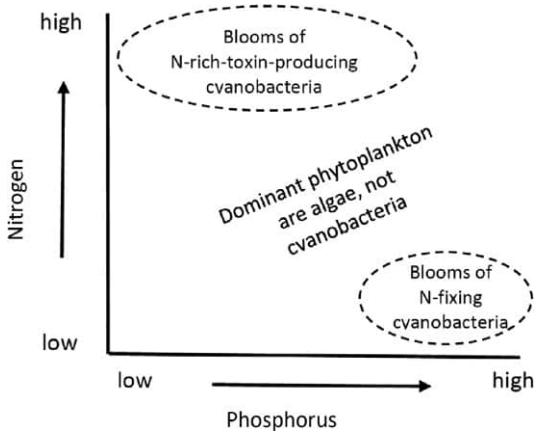

Fig. 4 In freshwater lakes, nitrogen-fixing cyanobacteria are favored under conditions when nitrogen availability is low and phosphorus availability is high, particularly when the N:P ratio is less than the Redfield ratio of 16:1 (lower right corner). Cyanobacteria may also be favored under conditions of low to moderate phosphorus but high nitrogen, although cyanobacteria will not fix nitrogen under these conditions. The high nitrogen may allow the cyanobacteria to produce nitrogen-rich toxins, thereby lowering their mortality rate from grazing by zooplankton (upper left corner).

Nitrate in drinking water for humans is also of concern, and a standard of 10 mg nitrate-N per liter is set in most of the world's nations, based on advice from the World Health Organization. Such a standard has existed since the early 1960s in the United States, and was originally set over concern about "blue-baby syndrome," a disease in infants where nitrate binds to hemoglobin in the blood, interfering with oxygen transport, and turning the blood blue. Studies over the past few decades have suggested that nitrate in drinking water poses many other health risks, including risk of a variety of cancers and a variety of developmental issues, and perhaps at levels below the drinking water standard. This topic has been much debated over the past 20 years, with some arguing that nitrate is a natural occurrence in saliva that the human body may actually manipulate to reduce bacterial infection. However, evidence shows a strong carcinogenic risk from nitrate in drinking water, probably due to the formation of nitrosomines, which are highly carcinogenic compounds. The best current evidence suggests a strong interaction between nitrate exposure and other dietary considerations: nitrate in vegetables such as spinach seems to pose little risk, while nitrate in drinking water combined with a high red-meat and low vegetable and fruit diet poses a major risk. Nitrate in drinking water at levels well below the current drinking water standard can pose a risk, in association with poor diet. Unfortunately, many of the drinking water sources in the world – including the developed world – exceed the current drinking water standard, and concentrations of nitrate in drinking water are rising (Townsend et al., 2003).

Nitrogen poses health risks beyond those of direct toxicity or carcinogenicity from nitrate, to both humans and natural animal populations. The toxicity of ammonia to aquatic animals is well known and is a major problem in waters heavily polluted from sewage or animal wastes. A more subtle aspect is the indirect effect of nitrogen on animal vectors that carry disease. For example, parasitic diseases of amphibians can increase markedly as eutrophication proceeds: nutrient pollution (probably phosphorus) in freshwaters in temperate-zone areas can lead to increased parasite releases from snails, which are an intermediary host, and cause massive disease in frogs and salamanders. The disease-causing organism is closely related to schistosomiasis, a major disease for humans in many tropical areas. An increase in snail populations as a result of nitrogen-based eutrophication in tropical reservoirs and lakes could lead to a similarly large increase in schistosomiasis. The temperate-zone studies on amphibian disease show an increased risk of disease resulting not only from an increase in snail populations as eutrophication progresses, but also a huge increase in the release of parasites from each snail. In another study, malaria has increased in some coastal areas of Brazil due to nitrogen-induced increases in eutrophication in mangrove swamps leading to increased abundances of mosquitoes that carry the malaria parasite.

One aspect of the human acceleration of the nitrogen cycle demands particular attention: the gas nitrous oxide (N_2O) presents severe challenges to the global environment. Laughing gas, as it is sometimes called, is an effective pain-killing drug sometimes used by dentists. It is also a long-lived gas in the Earth's atmosphere, with a residence time estimated at 120 years. Concentrations are rising rapidly. The gas catalyzes the destruction of ozone in the stratosphere, and increasingly nitrous oxide is responsible for ozone holes that allow excessive UV–B radiation to penetrate to the Earth's surface. Nitrous oxide is also a major absorber of infra-red energy, and therefore is a potent greenhouse gas that contributes to global warming. The Intergovernmental Panel on Climate Change considers nitrous oxide to be nearly 300-fold more powerful than carbon dioxide in terms of its long-term effect on global warming. Nitrous oxide is produced as a leakage-produce of both nitrification and denitrification. The rapid increase in the concentration of this gas in the atmosphere is clearly a side effect of the global acceleration of the nitrogen cycle by human activity.

See Also: Fundamental concepts and theories: Nitrogen Fixation; Nutrient Stoichiometry in Aquatic Ecosystems; Structures and functions of Inland Waters - Groundwater: Biogeochemical Cycling of Carbon and Nitrogen in Groundwater—Key Processes and Microbial Drivers; Structures and functions of Inland Waters - Lakes: Phytoplankton Growth and Nutrients; Structures and functions of Inland Waters - Rivers: Ecological stoichiometry in streams; Structures and functions of Inland Waters - Wetlands: Wetland Soils: Physical and Chemical Properties and Biogeochemical Processes

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Nitrogen Fixation☆

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This is an update of R. Marino, R.W. Howarth, Nitrogen Fixation, In Encyclopedia of Inland Waters, Edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00099-5.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Anoxic Oxygen-free, lacking oxygen.
Autotroph An organism that fixes carbon dioxide (CO_2) and converts it into organic matter; photoautotrophs use light as the energy source to fix the carbon dioxide; photo-autotrophs include plants, algae, cyanobacteria, and other photosynthetic bacteria that use reduced substances such as hydrogen sulfide rather than water as an electron donor; chemo-autotrophs do not use light but rather use the energy released from oxidizing reduced chemical substances to fix carbon dioxide.
Benthic In or on bottom sediments.
Cyanobacteria Photosynthetic bacteria, often called "blue green algae"; these organisms can use fixed nitrogen in the environment and many, but not all, species are also capable of fixing atmospheric N_2.
Denitrification A bacterial respiration process that takes place in the absence of oxygen; nitrate is converted to N_2 gas through a series of steps involving nitrogen oxides.
Diazotroph Microorganisms (bacteria and archaea) that can fix atmospheric N_2 into a biologically available form of nitrogen such as ammonia.
Eutrophication The process of increased growth and production of algae and other plant life in an aquatic ecosystem in response to excessive nutrient inputs.
Heterocyst A specialized, thick-walled non-photosynthetic cell that is the site of nitrogen fixation in many species of cyanobacteria.
Heterotroph An organism that gains its energy for life's processes by consuming organic carbon compounds produced by autotrophic organisms. All animals, all fungi, and many bacteria are heterotrophs; animals and many fungi and bacteria consume the organic matter by respiring it to carbon dioxide, using oxygen as the electron acceptor; some bacteria use other electron acceptors instead, such as nitrate or sulfate; and some bacteria and fungi gain energy through fermenting organic matter, where no inorganic electron acceptor is used and instead electrons are transferred from one type of organic molecules to another.
Nitrogen fixation The process of converting molecular N_2 to reactive, biologically available forms.
Nitrogenase The enzyme that catalyzes the fixation (reduction) of N_2 to NH_3.
Nutrient limitation The condition where the rate of growth and production of biomass by photoautotrophs is less than maximum owing to a lack of one or more nutrients, usually phosphorus or nitrogen.
Oxic Having oxygen present.
Planktonic Living in the water column of an aquatic ecosystem and largely dependent upon motion of the water for movement.
Primary production The creation of organic biomass by living organisms, using simple inorganic molecules (water, carbon dioxide, nutrients) and light or chemical energy.
Prokaryotic Describing an organism that lacks a cell nucleus or other organelles bound by membranes; bacteria and archaea are prokaryotes.
Salinity The content of dissolved salt and other minerals in water, usually used in the context of ocean waters or salt lakes; salinity is generally reported in units of parts per thousand, or grams of dissolved salts per kilogram (or liter) of water.
Stereochemistry The aspect of chemistry relating to the spatial arrangement of atoms within molecules. Stereochemistry is important in the reactivity of molecules.

☆*Change History*: October 2021. R Marino and RW Howarth updated the text and added in-text references to this entire article, updated the legend for Fig. 1, and updated the further readings.

Introduction to biological nitrogen fixation in aquatic systems

Nitrogen fixation is the bacterial process whereby molecular N_2 gas is converted to reactive, biologically available forms of nitrogen. The vast majority of nitrogen on Earth is present as molecular N_2, and is not available to living organisms other than those that can fix nitrogen for growth. Before the advent of the agricultural and industrial revolutions, biological nitrogen fixation was the only significant process creating new nitrogen to support fixation of carbon dioxide into energy-rich organic matter (primary production) in Earth's ecosystems. It is an ancient process, having evolved more than 3 billion years ago. Since nitrogen is an essential element for life as well as one of the two macro-elements frequently limiting primary productivity in ecosystems (along with phosphorus) at the global scale, the process of nitrogen fixation is essential for life (Vitousek and Howarth 1991).

In nature, the ability to fix atmospheric N_2 into a form of reactive nitrogen that can be used by organisms is limited to a specialized group of prokaryotes (diazotrophs) that use an enzyme (nitrogenase) to catalyze the reaction. There is a wide variety of these organisms, including bacteria that use organic carbon (heterotrophs), and bacteria that fix inorganic carbon dioxide (CO_2) into biomass (autotrophs). The autotrophs include photosynthetic cyanobacteria, so named because of the blue-colored photosynthetic pigment they contain to capture light energy, other photoautotrophs (such as the purple sulfur bacteria that use hydrogen sulfide rather than water as the reducing agent in photosynthesis), and chemo-autotrophic bacteria that use inorganic chemical energy rather than light energy. The latter two types of nitrogen-fixing bacteria only live in environments hostile to most organisms whereas cyanobacteria can thrive in a wide range of aquatic habitats and have mechanisms which help them grow and persist during periods of adverse environmental conditions (Carr and Whitton, 1982). Nitrogen-fixers can either live freely in the environment, or symbiotically in association with other organisms. The cyanobacteria that are capable of fixing atmospheric N_2 have a unique ecological role in aquatic ecosystems, as they are the only group of organisms on Earth that can fix both inorganic carbon and nitrogen in an oxic (oxygen-containing) environment.

In inland waters heterotrophic bacteria, and cyanobacteria (primarily from the order Nostocales) are responsible for most of the nitrogen fixation that occurs. The rates of nitrogen fixation and the resulting nitrogen input to an ecosystem from this process vary greatly among lakes and other inland water bodies. In general, when biological nitrogen fixation is an important contributor to the nitrogen economy of an aquatic ecosystem, high rates of nitrogen fixation by cyanobacteria living in the plankton of the water column are the primary reason. Cyanobacteria and other autotrophic bacteria living in the benthos (sediments) or in assemblages attached to surface substrate of shallow water bodies, marshes, and streams can also fix nitrogen at high rates and provide a locally important source of nitrogen to the communities they support. Benthic nitrogen fixation by photoautotrophs in very low-nutrient lakes where light can penetrate to much of the bottom area can constitute a significant source of nitrogen to these systems. Because cyanobacteria can thrive in a wide range of aquatic habitats and have the unique ability to fix N_2 while carrying out oxygenic photosynthesis, most of this chapter is devoted to a discussion of cyanobacterial nitrogen fixation in inland water environments. Nonetheless, nitrogen fixation by heterotrophic bacteria is fairly ubiquitous in sediments and can be significant in the nitrogen cycle of some aquatic ecosystems.

Before considering the rates of biological nitrogen fixation in inland waters and general factors which influence this process, it is useful to understand a bit about how nitrogen fixation is estimated in natural systems. The most commonly used method remains the acetylene reduction assay, introduced in the late 1960s by Ralph W.F. Hardy and colleagues (Capone, 2019). This relatively simple and highly sensitive technique indirectly assays nitrogen fixation by measuring the conversion of acetylene gas, a structural analog for N_2, to ethylene gas. The reactions that reduce N_2 gas to ammonium (fixed reactive N) and reduce acetylene to ethylene are both catalyzed by the nitrogenase enzyme present in all organisms capable of biological nitrogen fixation. It is necessary to assume a fixed relationship between acetylene reduced and N_2 fixed by the enzyme. Variation in this ratio due to physiological and environmental factors is the primary source of uncertainty in estimating field N_2 fixation rates using the acetylene reduction method, although sampling and incubation techniques can also affect measured rates. Nitrogen fixation can be also assayed directly by measuring the incorporation of a stable isotopic form of N_2 (^{15}N) into biomass (Wannicke et al., 2018), or by measuring the change in dissolved N_2 in a sample over time relative to a biologically inactive tracer (Kana et al., 1994). The latter measurement allows a direct estimate of N fixation when the microbial process of denitrification is insignificant, such as in a fully oxic water column, and an indirect estimate when both processes are present such as in sediments (An et al., 2001).

Rates of biological nitrogen fixation vary tremendously across the wide range of aquatic ecosystems where measurements have been made. In addition to the variation and uncertainties inherent in the methodologies used, a number of environmental factors acting at levels from the cellular up to the ecosystem and the region act to influence the rates and relative importance of nitrogen fixation in different inland water environments. Nonetheless, some patterns and generalities have emerged. This article is intended as a summary of these concepts, and not as an exhaustive review of the literature on nitrogen fixation in inland aquatic environments.

Nitrogen fixation by heterotrophic bacteria in sediments

Heterotrophic bacteria fix nitrogen in virtually all sediments. The rates reported for the sediments in lakes and estuaries tend to be low to moderate, from 0.002 to 0.3 g N m^{-2} $year^{-1}$ (Howarth et al., 1988a). Such rates are low compared with those mediated by cyanobacteria in many lakes or rates by heterotrophic bacteria found in many terrestrial ecosystems. Nitrogen fixation rates are

generally higher when the organic matter content of the sediment is greater. In marine and freshwater ecosystems where vascular plants are present (including marshes, swamps, bogs, and submerged macrophyte and seagrass beds) nitrogen fixation rates in the sediments are more variable, and can be much higher than in unvegetated sediments in similar environments. For Temperate Zone systems measured rates generally range from 0.5 to 4 g N m^{-2} $year^{-1}$ (Howarth et al., 1988a; Scott et al., 2008), values which are more typical of many terrestrial systems. Nitrogen fixation rates in the sediments of seagrass beds in subtropical and tropical coastal water bodies are often higher than in temperate systems, and range from approximately 1 to 20 g N m^{-2} $year^{-1}$ (Howarth et al., 1988a). The higher rates of fixation in wetlands and seagrass beds as compared with unvegetated lake or coastal marine sediments are probably a result of the greater availability of labile organic matter associated with the plants as a substrate to fuel the process. Although rates of nitrogen fixation are fairly similar in saltmarshes and freshwater wetlands, the resulting nitrogen is a much more significant input to freshwater systems because the latter are often much more closed systems. For example, nitrogen fixation was estimated to contribute 1–2% of the total nitrogen input to a salt marsh in New England (United States), as compared with 60% of the nitrogen input to a freshwater bog in the same region (Howarth et al., 1988a).

In sediments, the microbial process that counters nitrogen fixation as a nitrogen input is denitrification, where fixed inorganic nitrogen is converted back to a gas and lost from the system. Rates of denitrification also tend to increase with greater organic matter in sediments, and so the processes of nitrogen fixation and denitrification tend to vary in parallel. Denitrification rates are generally found to be similar to or greater than heterotrophic nitrogen fixation rates in aquatic ecosystems (Seitzinger, 1988). As a result, sediments of inland aquatic ecosystems tend to either show no net nitrogen flux out to the overlying water or serve as a net nitrogen sink annually despite heterotrophic nitrogen fixation, although recent work in estuarine sediments suggests the net balance of the two processes fluctuates temporally in response to changing conditions (Newell et al., 2016). In some wetlands as well as lakes and estuaries where light penetrates to the bottom there can be additional nitrogen fixation associated with sediments owing to the activity of autotrophic nitrogen-fixing bacteria on the surface sediments (see "Nitrogen Fixation by Benthic and Epiphytic Cyanobacteria" later in this chapter).

The nitrogenase enzyme that is essential for nitrogen fixation is readily poisoned by oxygen. Oxygen seldom penetrates into sediments below the first millimeter or two, and so does not inhibit nitrogen fixation by heterotrophic bacteria in most sediments. On the other hand, when oxygen is present in an environment, it may severely constrain nitrogen fixation by these bacteria. For example, essentially no nitrogen fixation by heterotrophic bacteria occurs in the oxygenated water columns of lakes, probably because of the deleterious effect of oxygen on nitrogenase activity. Some nitrogen fixation is associated with heterotrophic bacteria on leaf litter and other organic matter aggregates in streams where decomposition lowers oxygen in microzones, but rates are typically quite low, again perhaps due to the high level of oxygen in flowing water.

Nitrogen fixation is considered energy-intensive relative to many other biological processes, as it requires breaking a N—N triple bond using a specific metalloenzyme complex. As such, the process of synthesizing nitrogenase and reducing N_2 to create a source of fixed nitrogen for growth is often viewed as energetically "expensive" to the organism when compared with the uptake of fixed inorganic nitrogen present in the environment, or the synthesis of other cellular compounds. However, this appears not to be the case for N_2 fixation by heterotrophic bacteria in anoxic (no oxygen present) sediments. Moderate to high rates occur in the presence of elevated concentrations of ammonium (NH_4^+) typically present in porewaters as a result of decomposition and remineralization. Since bacteria can readily assimilate the ammonium and thereby have a plentiful supply of nitrogen, the fact that they also fix N_2 indicates that it "costs" them little to do so. However, ammonium at high levels has been shown to inhibit the rate of nitrogen fixation in some sediments, perhaps keeping these rates lower than otherwise might occur (Howarth et al., 1988b). As discussed later, nitrogen fixation by cyanobacteria and particularly those most commonly found in the plankton of inland waters, may be a much more energy-expensive process to the organisms, in part because of the need to build and maintain structures that protect the nitrogenase enzyme from deactivation by oxygen produced during photosynthesis.

Nitrogen fixation by planktonic cyanobacteria in freshwater lakes

Nitrogen fixation by planktonic cyanobacteria varies greatly among lakes, and rates are related to the overall nutrient (trophic) status. Rates of N_2 fixation typically range from 0 to 0.003 g N m^{-2} $year^{-1}$ in oligotrophic (very low-nutrient) lakes, from 0.01 to 0.1 g N m^{-2} $year^{-1}$ in mesotrophic lakes, and from 0.2 to16 g N m^{-2} $year^{-1}$ in eutrophic (highly enriched) lakes (Howarth et al., 1988a; Higgins et al., 2018). Planktonic nitrogen fixation is generally not an important term in the nitrogen budgets of oligotrophic and mesotrophic lakes, and contributes less than 1% of the nitrogen inputs to most of these ecosystems. On the other hand, nitrogen fixation can be very important in the nitrogen economy of eutrophic lakes, with studies showing from 5% to 86% of the total nitrogen load to the ecosystem from this source.

The most important species of planktonic cyanobacteria that fix nitrogen in lakes belong to the genera *Anabaena*, *Aphanizomenon*, and *Nostoc*, which can rapidly reproduce and form large blooms (high biomass) under optimal conditions (Carr and Whitton, 1982). These species form long chains or filaments of cells, which can differentiate to allow photosynthesis to occur in most cells (vegetative) and nitrogen fixation to occur at the same time, in specialized, non-photosynthetic cells called heterocysts (Fig. 1). Heterocysts form in response to low intracellular concentrations of nitrogen, as a result of low availability of nitrogen in the environment. The heterocysts have a thick wall that protects nitrogenase from oxygen; this adaptation allows nitrogen fixation to occur in fully oxic environments. The energy necessary for nitrogen fixation comes from carbon fixed in the photosynthetic cells, which is transferred to the heterocysts. To support the energy required for nitrogen fixation, many photosynthetic cells are needed per one heterocyst cell.

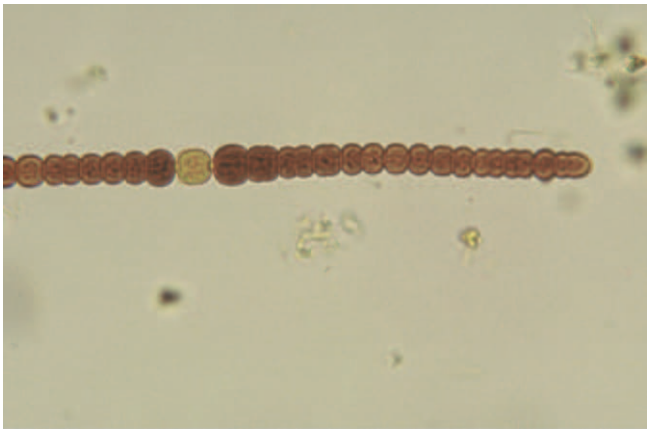

Fig. 1 Photograph of an *Anabaena* filament with heterocyst, stained for contrast. Heterocyst appears yellow, vegetative cells are orange-brown. Courtesy of Colleen Kearns, Cornell University.

Heterocysts develop in regularly spaced intervals of vegetative cells. Rates of both cyanobacterial growth and nitrogen fixation are generally higher when there are at least 15–20 vegetative cells per heterocyst cell (Stal, 2015). Filamentous cyanobacteria can be very sensitive to grazing: zooplankton can quickly shorten chains (and thereby reduce the number of photosynthetic cells available to support nitrogen fixation in a heterocyst) both by breaking chains into pieces and by eating along the end of a chain (Chan et al., 2006). As a result, grazing by zooplankton can constrain the development of a cyanobacterial bloom in nitrogen-depleted waters, by limiting nitrogen fixation and so nitrogen availability for further growth (Howarth and Marino, 2006). Significant reduction in cyanobacterial abundance by some types of zooplankton and filter-feeding bivalves has been observed in some inland waters, although many nitrogen-fixing cyanobacteria species often contain toxic chemical compounds as a protection against grazing. These defensive compounds may be less of a factor for grazers in the early stages of a cyanobacteria bloom, when filaments are developing and available nutrients and energy are needed for producing more vegetative cells rather than such accessory protective compounds. Also, some of the pigments in cyanobacteria cells at this stage of growth contain nitrogen-rich amino acids, making the cells a potentially high-quality food source. In addition to the ecological factors such as grazing that influence the extent of planktonic cyanobacterial growth and nitrogen fixation, there are other chemical and physical factors recognized to be important (Howarth et al., 1988b). These factors include light and the related parameters of turbulence and mixing depth, and the availability of essential macro-nutrients nitrogen (N) and phosphorus (P) and essential trace metals (iron, Fe and molybdenum, Mo). Other characteristics of the system, such as pH or dissolved organic carbon concentration, can interact with one or more of the primary factors to influence cyanobacterial population dynamics. The relative importance of any one factor in controlling nitrogen fixation in a water body varies depending on physical, biogeochemical, and ecological factors, as depicted in Fig. 2.

In contrast to nitrogen fixation by heterotrophic bacteria in anoxic sediments, nitrogen fixation by planktonic cyanobacteria appears to be an energetically more expensive process for the cells. Most of the energy cost of fixation is not in the catalysis of the reaction per se but rather in synthesizing and then protecting nitrogenase from oxygen, and perhaps the cost of assimilating trace metals that are required for nitrogenase in its predominant form: iron and molybdenum. The biological availabilities of both these metals are likely to be much greater in anoxic sediments than in an oxic water column (Howarth et al., 1988b). For iron, the greater availability under anoxic conditions in large part simply reflects the higher solubility of reduced iron compared to oxidized iron. For molybdenum, the chemically stable form found under oxic conditions in the pH range of most natural waters is molybdate. This anion can be difficult for bacteria to assimilate because of its close similarity in effective size and stereochemistry to the sulfate anion. The latter is far more abundant in inland waters, particularly in estuaries and some saline lakes. As such, the cellular uptake system needs to be more selective for molybdate, which likely requires more energy for synthesis than a lower affinity transport system (Marino and Howarth, 2016). In anoxic environments, molybdenum is present in different chemical forms, which may be more biologically available.

It is most advantageous to planktonic cyanobacteria to invest energy in heterocyst and nitrogenase synthesis to obtain nitrogen via the nitrogen fixation process when other sources of available nitrogen for growth are low. Further, even when concentrations of inorganic nitrogen are low, nitrogen fixation by planktonic cyanobacteria is not likely to occur if the N:P ratio of inorganic nitrogen and phosphorus in the environment is well above that needed for synthesis of phytoplankton biomass (the so-called Redfield ratio of 16:1, moles N to mole P, after Alfred Redfield, the scientist who first described this relatively constant relationship in oligotrophic ocean waters). Under these conditions, the growth of the cyanobacteria is more limited by phosphorus than by nitrogen. Nitrogen-fixing cyanobacteria generally have a high overall requirement for phosphorus (Carr and Whitton, 1982), and the biomass of planktonic cyanobacteria in freshwater lakes is often positively correlated with high concentrations of phosphorus in the water. The highest rates of nitrogen fixation are typically found when available nitrogen concentrations are low, available phosphorus concentrations are high, and the molar N:P ratio is below 16:1.

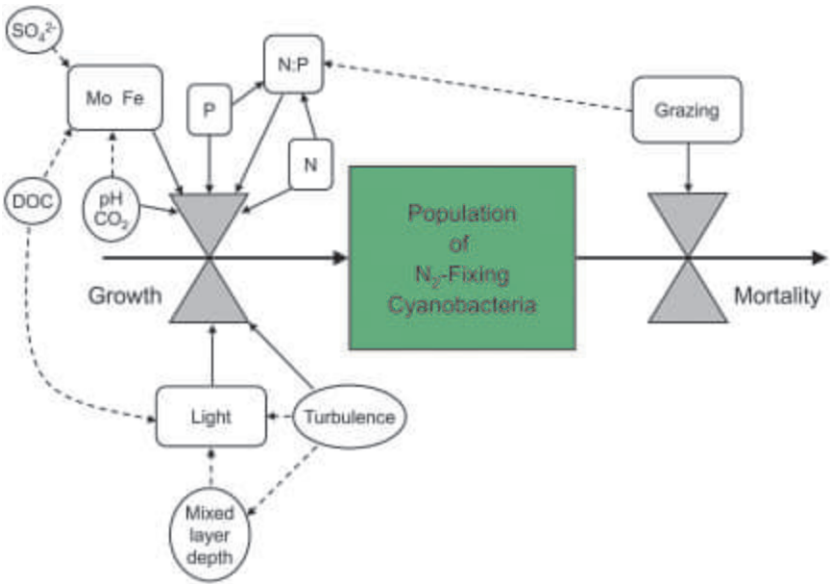

Fig. 2 Schematic representation of the factors that control growth and N_2 fixation by cyanobacteria in the plankton of lakes and estuaries. Dashed lines indicate indirect effects by acting to alter the availability of the direct factor; DOC is dissolved organic carbon; SO_4^{2-} is the sulfate anion.

In a series of classic experiments that began in the 1970s at the Experimental Lakes Area in Canada, David Schindler and colleagues demonstrated that planktonic nitrogen fixation can help maintain phosphorus limitation of net primary productivity in eutrophic lakes (Schindler, 1977; Higgins et al., 2018). For several years, they fertilized a lake with nitrogen and phosphorus, with an N:P ratio of total inputs of 32:1 (by moles). Under these conditions, phytoplankton growth is phosphorus-limited and sufficient dissolved inorganic nitrogen is present to meet the needs of the phytoplankton. No cyanobacteria were observed in the plankton. Then the experimental protocol was changed, reducing the nitrogen inputs while leaving the phosphorus input unchanged, with the N:P ratio of total inputs was 14:1. This was expected to induce a slight limitation of nitrogen to phytoplankton growth, but this did not occur. Rather, large populations of planktonic cyanobacteria grew in the lake and fixed a sufficient quantity of nitrogen such that net primary production in the lake remained limited by phosphorus. However, in some highly P-enriched lakes when the N:P ratio is very low, planktonic N fixation cannot fully alleviate the nitrogen deficit (Paerl et al., 2015; Hayes et al., 2019).

Nitrogen fixation by planktonic cyanobacteria in saline waters

Many of the world's lakes are composed of saline waters. These lakes typically occur in arid or semi-arid regions and have no drainage outlet. As a result, salt accumulates over time due to evaporation, and the salt content and composition of these types of lakes is quite variable. Nitrogen-fixing planktonic cyanobacteria are common in many of these lakes, and sometimes fix nitrogen at very high rates. Surprisingly, high rates have been observed even in oligotrophic (i.e., very low nutrient) salt lakes. For example, nitrogen fixation by cyanobacteria in Pyramid Lake, Nevada, United States, was measured as $2\ g\ N\ m^{-2}\ year^{-1}$, a rate more characteristic of eutrophic than oligotrophic freshwater lakes. In some years, nitrogen fixation is estimated to contribute roughly 80% of the total nitrogen input to Pyramid Lake (Howarth et al., 1988a). However, nitrogen-fixing cyanobacteria are not present in the plankton of many saline lakes even when conditions seem optimal—primary production is limited by nitrogen, concentrations of nitrate and ammonium are low, concentrations of dissolved inorganic phosphorus are high, and the N:P ratio is well below the Redfield ratio of 16:1 (Marino et al., 1990).

The controls on nitrogen fixation in saline lakes have received relatively little study, but the chemistry of the lakes is one major factor explaining variation in rates of nitrogen fixation. The specific dissolved substances that dominate the salinity in salt lakes vary greatly. In some saline lakes, sulfate is the dominant anion, while in others, chloride, carbonate, or other anions dominate. Growth and nitrogen fixation by planktonic cyanobacteria can be adversely affected by the high concentrations of sulfate found in some lakes because of an inhibition of molybdenum uptake, as discussed earlier. Thus, nitrogen-fixing cyanobacteria are most likely to be abundant in the plankton of salt lakes where the sulfate concentration is low. Salinity itself does not appear to be a constraint on growth and nitrogen fixation until salt concentrations reach very high levels (50–70 g per liter or more, about 1.5–2 times seawater levels) (Marcarelli et al., 2006).

Nitrogen-fixing cyanobacteria are present in the plankton of some estuarine ecosystems as well, although they are surprisingly rare, and generally are found to be significant only when the salinity is less than 10 parts per thousand (the salinity of open ocean

seawater is approximately 35 parts per thousand). Much of the Baltic Sea and its estuaries have a salinity below 10 parts per thousand, and nitrogen-fixing cyanobacteria are often present in high abundances (Moisander et al., 2003). A few other estuaries have reported cyanobacteria that persist at higher salinities, but these are ecosystems that tend to experience wide changes in salinity over the season; the cyanobacteria blooms typically originate during times when there is high freshwater inflow and the salinity is at or near zero parts per thousand, and then persist for some time as the salinity increases (Marino et al., 2006). Note that nitrogen-fixing cyanobacteria such as *Trichodesmium* that are commonly found in oligotrophic, warm, oceanic waters can be advected onto continental shelf regions and contribute new nitrogen (Mulholland et al., 2012) but are not significant nitrogen fixers in estuaries. For the vast majority of estuaries that have been studied, including all those in North America and in Europe outside of the Baltic Sea, nitrogen-fixing cyanobacteria have not been reported at salinities much above 8–10 parts per thousand (i.e., mesohaline and saline systems). This is a marked contrast with freshwater lakes, as many higher salinity estuaries typically have nutrient inputs and conditions that strongly promote nitrogen limitation of phytoplankton (Howarth et al., 2021).

What processes act to exclude nitrogen-fixing cyanobacteria from the plankton of most estuaries? Part of the answer again lies with sulfate, the second most abundant anion in seawater. Sulfate is a conservative constituent of seawater and estuarine waters, and so the sulfate concentration varies in direct proportion to the overall salinity. The concentrations of sulfate found in mesohaline and saline estuaries can significantly inhibit molybdate assimilation by heterocystous cyanobacteria. This is not an absolute constraint on nitrogen fixation, but does make molybdate uptake energetically costly by requiring more specificity (higher affinity) in the transport system, and therefore can negatively affect the growth rate of the cyanobacteria (Marino et al., 2003). Experimentally measured maximum growth rates for heterocystous planktonic cyanobacteria isolated from estuarine systems tend to be an average of four times lower than those for the same genera from freshwater systems (Marino et al., 2002).

As discussed earlier, heterocystous cyanobacteria growth can also be susceptible to grazing by zooplankton, because of the need to have enough photosynthetic cells per heterocyst in a filament to support differentiation and nitrogen fixation. A slower growth rate increases this vulnerability to grazing and is a negative feedback to the overall rates of production of cyanobacterial biomass and nitrogen fixation. Experiments have demonstrated that when grazing by zooplankton is suppressed in saline estuarine waters, heterocystous cyanobacteria can grow in the plankton and fix nitrogen, even when they are not observed under natural (and nitrogen-limited) conditions (Chan et al., 2006). The interaction of sulfate-induced slow growth rate and grazing by zooplankton is an important factor acting to exclude blooms of nitrogen-fixing cyanobacteria from the plankton of saline, nitrogen-depleted estuaries.

Nitrogen fixation by benthic and epiphytic cyanobacteria

When sufficient light reaches the bottom of an aquatic ecosystem to support photosynthesis, benthic nitrogen-fixing cyanobacteria frequently occur. This is true in both freshwater and saline inland waters, and in streams, particularly where current velocities are low and so hydrodynamic disturbance to the mats is minimal. There is relatively little information on nitrogen fixation by cyanobacteria in streams, however, the conditions most conducive to high rates appear to be similar to those in other freshwaters: low inorganic nitrogen availability and high phosphorus, high light, and warmer water temperatures (Marcarelli et al., 2008). In addition to free-living heterocystous cyanobacteria typically found in the benthic and periphyton communities of streams under favorable conditions, there are a few species of diatoms that have cyanobacteria capable of fixing nitrogen living within their cells (endosymbionts). Nitrogen fixation in stream ecosystems is generally patchy and influenced by microhabitat characteristics like substratum type in addition to the nutrient and seasonal environmental factors mentioned above. As such, nitrogen fixation is usually only important locally in river ecosystems.

In freshwater lakes, rates of nitrogen fixation by benthic cyanobacteria tend to be fairly low and range from 0 to 0.3 g N m^{-2} $year^{-1}$ (Howarth et al., 1988a). Rates are frequently higher in oligotrophic lakes than in mesotrophic and eutrophic lakes, since the light intensities at the sediment surface tend to be higher owing to lower phytoplankton productivity and lower concentrations of dissolved organic substances that attenuate light. Benthic nitrogen fixation by cyanobacteria generally constitutes a small proportion of the nitrogen budget of mesotrophic and eutrophic lake ecosystems, but fixation may be important in oligotrophic lakes. For example, benthic nitrogen fixation by cyanobacteria contributes an estimated 6% of the total nitrogen inputs to Mirror Lake (New Hampshire, United States) and 32% of the total nitrogen inputs to Lake Tahoe (California and Nevada, United States) (Howarth et al., 1988a). Some studies have found that grazing on benthic cyanobacteria can reduce nitrogen fixation, although often the effect is small. Other studies have shown a stimulative effect from grazing, sometimes because the light availability to the cyanobacteria increased as overlying sediment and competing phototrophic organisms are removed, or because the supply of phosphorus increased.

Rates of nitrogen fixation associated with marine and saline lake cyanobacterial mats can be very high, ranging from 1 to 75 g N m^{-2} $year^{-1}$ (Howarth et al., 1988a) The nitrogen fixation rates measured at the high end of this range occur in tropical marine environments and are some of the highest reported for any type of ecosystem globally. High rates of nitrogen fixation (10–30 g N m^{-2} $year^{-1}$) have also been reported associated with cyanobacterial mats in constructed wetlands and in salt marshes in both England and the Northeastern United States (Scott et al., 2008; Howarth et al., 1988a). However, these well-developed cyanobacterial mats are usually fairly limited in area, and so nitrogen fixation is generally not an important term in the overall nitrogen budgets of the larger ecosystems in which the mats exist. The factors that lead to the sometimes extremely high rates of nitrogen fixation in coastal marine cyanobacterial mats remain poorly known, but reducing conditions within the mats may result in chemical species of iron and molybdenum that are more readily available to the cyanobacteria, as well as limit oxygen

inactivation of nitrogenase. Thus, as with heterotrophic fixation in anoxic sediments, the energetic cost of the fixation to these cyanobacteria may be low. Such physiologically favorable conditions, combined with high light in the mat environments, likely support high rates of nitrogen fixation.

Nitrogen fixation by cyanobacteria also occurs in seagrass beds, an important coastal marine habitat. These cyanobacteria grow as epiphytes on seagrass leaves and on surface sediments in between the grasses. The seagrass leaves provide a high surface area substrate in the photic zone for the autotrophic N fixers, and overall fixation rates can sometimes be quite high. The conglomeration of organic material that accumulates on seagrass leaves in nutrient-rich estuarine systems can also support some heterotrophic nitrogen fixation in anoxic microzones, though when both light and dark fixation are assayed, higher rates are generally found in the light. In the sediments of these systems, it is not clear whether nitrogen fixation by autotrophic nitrogen fixers is more significant per unit area than that of heterotrophic bacteria. The relative contribution of each to the overall nitrogen economy of the beds likely depends on a number of factors including seagrass growth patterns and overall biomass, water column depth and clarity, nitrogen and other nutrient availability, and other bacterial processes in the sediments which influence nitrogen fixation, such as sulfate reduction.

Conclusions

The process of biological nitrogen fixation is carried out exclusively by a relatively few species of prokaryotes, capable of living in a very wide diversity of aquatic conditions. In most inland waters where biological nitrogen fixation is an important component of the nitrogen economy of the ecosystem, the fixation occurs in either the sediments or the water column, and is fueled either directly (cyanobacteria) or indirectly (heterotrophic species) by light energy. Heterotrophic bacteria fix nitrogen in virtually all lake and estuarine sediments, at low to moderate rates relative to cyanobacteria. Sediment nitrogen fixation is generally higher when the organic matter content of the sediment is greater, and is often balanced or exceeded by nitrogen losses through the microbial process of denitrification. Nitrogen fixation by benthic (sediment and mat) and epiphytic autotrophs can be high under optimal conditions of light and nutrient availability and thereby is important to the local environment of the organisms. However, the area of this type of habitat is limited in most inland waters and so such fixation usually constitutes only a small portion of the total nitrogen input to the ecosystem. An exception is oligotrophic lakes, where nitrogen fixation by benthic cyanobacteria can be a significant overall nitrogen input.

Nitrogen fixation by planktonic cyanobacteria varies greatly among lakes and is generally not of great importance in the nitrogen budgets of oligotrophic and mesotrophic lakes, but can be very important in the nitrogen economy of eutrophic lakes where phosphorus is often present in excess of nitrogen. Heterocystous species of cyanobacteria are the major nitrogen-fixers in both freshwater and saline lakes and estuarine environments. There is a marked contrast in the significance of these N-fixing organisms in the plankton of freshwater versus estuarine systems; when similarly nitrogen-limited, large blooms are often observed to occur and act to alleviate nitrogen deficits in freshwater, but rarely if ever in estuaries. This is in part owing to a greater inhibitory effect of sulfate, present in much higher concentration in estuaries and some saline lakes than in freshwaters, on molybdate uptake. Molybdenum is necessary for synthesis of the most abundant and efficient form of the enzyme nitrogenase which is essential for biological nitrogen fixation, and thus for growth on N_2. Slower growth leaves filamentous cyanobacteria more susceptible to control by grazing and limits development of blooms that can contribute significant nitrogen to an aquatic system via fixation. Several additional chemical, physical, and ecological factors and interactions also influence the extent of cyanobacterial growth and fixation of "new" nitrogen in inland waters. As population and land use pressures around inland waters increase and nutrient enrichment of these systems accelerates, along with changing and intensifying climate patterns, the relative constraints on this important biological process may shift. Current management strategies for controlling eutrophication and problematic algal blooms may need to be re-examined and altered as a result (Conley et al., 2009).

See Also: Fundamental concepts and theories: Nitrogen; Nutrient Stoichiometry in Aquatic Ecosystems; Structures and functions of Inland Waters - Groundwater: Biogeochemical Cycling of Carbon and Nitrogen in Groundwater—Key Processes and Microbial Drivers; Structures and functions of Inland Waters - Lakes: Phytoplankton Growth and Nutrients; Structures and functions of Inland Waters - Rivers: Ecological stoichiometry in streams; Structures and functions of Inland Waters - Wetlands: Wetland Soils: Physical and Chemical Properties and Biogeochemical Processes

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Biodiversity of Inland Waters

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This is a update of AP Covich, Biodiversity of Aquatic Ecosystems, in *Encyclopedia of Inland Waters*, edited by GE Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00200-3.

This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editor Lars Rudstam.

Glossary

Biodiversity A measure of the number of species and their relative abundances in an assemblage or region, together with the genetic composition and the phylogenetic relationships represented by the community.
Dominance A measure of the degree to which species in a community deviate from equal abundance, i.e., degree of inequality in abundance.
Endemic species Species that live in a specific location, which may either be small (e.g., a specific lake or spring) or large (a specific continent).
Facilitation The concept that some species can enhance the effectiveness of other species in terms of their complementary ecosystem functions.
Functional group Species that have the same or very similar role in ecosystem processing of organic matter (e.g., primary producers, herbivores, predators, or decomposers).
Hydraulic connectivity The degree of linkage among surface and subsurface waters for a particular geographic zone or drainage basin.
Redundancy The concept that species that may partially substitute for one another within a functional group to sustain an ecosystem process.
Species richness The number of species in an ecological community; species richness is one aspect of biodiversity.

Introduction

The astounding diversity of species found among inland waters has attracted a great deal of interest since Hutchinson (1959) asked, "Why are there so many species?" How does it happen that inland waters comprise only 0.01% of the Earth's total amount of water and cover only 0.8% of the Earth's surface, yet these ecosystems support approximately 6% of all described species?

No single factor determines the biodiversity of inland waters. However, one explanation for this remarkable diversity is the high potential for isolation of inland waters across a wide range of temperatures and salinities. These isolated populations can evolve various adaptations to avoid their competitors and predators and increase their chances for coexistence with others species. Because isolated ecosystems are not easily colonized, endemic species can evolve and adapt to specific habitats over many generations resulting in large number of species in the geologically oldest inland waters (Brooks, 1950; Schön and Martens, 2004; Hampton et al., 2018). Many of the endemic species in inland waters occur in lakes that originated more than 100,000 years ago and some of these species-rich ancient lakes have persisted over millions of years (Albrecht et al., 2020a).

The degree of isolation can change over time. In coastal rivers and lakes, some marine-derived species adapted to freshwater as they continued to migrate back to coastal waters to complete their life cycles. But fragmentation of coastal rivers can isolate populations during periods of sea-level change which can result in speciation but also extinctions (e.g., Dias et al., 2014; Miura et al., 2020). Similarly, lakes and ponds are affected by major floods and severe droughts that alter regional hydrologic linkages and change connectivity among these systems. In general, major differences in the age and origins of inland water ecosystems as well as adaptations for dispersal and tolerance of variability in key environmental factors, along with human impacts all can interact to determine species distributions and, therefore, biodiversity of inland waters.

Measuring biodiversity and its use as indices of the environment

Numerous methods are used to measure freshwater species diversity and to document the number of species lost. The earliest measures were based on lists of species that occurred in different locations ("species richness"). Additional measures such as "evenness" or relative abundance of species are also useful and both species richness and evenness are combined in the commonly used Shannon-Wiener index of diversity. Species richness, evenness and the observed log-normal distributions of species abundance were recognized early as having important biological attributes that could be analyzed mathematically (Fisher et al., 1943; Simpson, 1949). These early studies generated new interest in the ecological conditions that caused some species to be rare while others were relatively abundant in samples from different locations (Magurran, 2004).

Measures of biodiversity are also used as indices of environmental quality including those based on freshwater algal, fish, or benthic macroinvertebrate species (Bandeira et al., 2013). Indices based on diatom species richness and evenness were among the first to rely on extensive datasets on species and dominance distributions relative to changes in salinity, acidity, and nutrients as well as flow conditions for monitoring water quality (Patrick and Palavage, 1994). Among macrophytes, early studies showed that species of charophytes were especially intolerant of high nutrient concentrations, especially dissolved phosphorus (Hutchinson, 1975; Lambert and Davy, 2011). Changes in distributions of submerged macroalgae (such as charophytes) and aquatic mosses, are now widely used to monitor rates of eutrophication in deep lakes where increased densities of phytoplankton, especially cyanobacteria, can decrease light penetration and lead to the elimination of macrophytes (Ecke, 2018). Because many taxonomic groups of aquatic insects have extremely high numbers of widespread genera with different levels of tolerance for organic pollution, they also are widely used to measure water quality. Increases in relative abundance of some of these taxa indicate high concentrations of dissolved oxygen and good water quality. For example, the EPT density index is based on the observed relative abundances of the insect orders Ephemeroptera (E), Plecoptera (P) and Trichoptera (T) compared to the total number of individuals of all aquatic insect orders in the samples. High relative abundance of EPT taxa in a sample indicates good water quality based on high levels of dissolved oxygen and low concentrations of toxins (Valente-Neto et al., 2018; Goncharov et al., 2020). The ratio of the number of native to non-native species is also used to measure water quality and habitat condition ("ecological integrity") of freshwaters (Ruaro et al., 2020). Multi-metric indices include environmental as well as biotic factors for regional and nation-wide studies of habitat suitability and water quality (Bolding et al., 2020). These metrics integrate changes in key chemical and physical factors that can affect biotic distributions over a range of time scales. However, many threats to native species losses are not effectively included in these metrics because populations and individuals of species can differ in their responses to toxins (Collen et al., 2014; Cadmus et al., 2019; Taddei et al., 2021).

Biodiversity of major groups of plants and animals

Here, a brief overview of some of the most diverse groups of aquatic organisms illustrates general patterns of biodiversity in inland waters. These examples show that evolutionary history is critical for understanding how diverse communities have developed and how species interact in complex food webs. This summary also provides some insights into the natural and anthropogenic processes that influence species richness and species distributions across inland waters.

Primary producers and decomposers

The number of species in major groups of plants and animals in inland waters differs greatly on a regional basis. For example, there are 12 major groups of algae with more than 770 genera (many with numerous species) known to occur in North America. These diverse groups of algae differ in their nutrient and light requirements as well as their fundamental cell biology. Distinctions among these groups reflect differences in their modes of photosynthesizing and tolerances for different ranges of salinity and water temperatures (Wehr et al., 2015). Most algae are well adapted for wide dispersal by birds and other animals. Along with other freshwater species, there are concentrations of endemic algal species in the photic zone of some very old, deep lakes (e.g., Boedeker et al., 2018). Worldwide, the most diverse group is the green algae (chlorophytes) with over 400 genera and thousands of species in inland waters. Many of these species live in open waters as planktonic (floating) species while benthic species grow attached to surfaces (rocks, sediments, larger plants, and animals). Most species of green algae are free-living but some are parasitic or endosymbiotic (living inside animal species such as freshwater sponges and hydra). The green flagellated algae occur in a wide range of habitats including ponds, lakes, rivers, as well as ice and snow. This group of flagellates includes about 100 genera (44 in North America) and over 1000 species. A single genus, *Chlamydomonas*, has more than 400 species worldwide. Other green algae lack flagella and are typically planktonic. There are approximately 200 genera and thousands of species, the most commonly known genus of chlorophytes is *Chlorella*. Some groups of green algae have large cells and are macroscopic (e.g., charophytes such as *Chara* and *Nitella*). Many species form filamentous colonies of small single cells. The microscopic diatoms constitute another highly diverse and widely distributed group of algae characterized by cell walls composed of silica and can be unicellular or form multicellular colonies. Some species live on hard and soft surfaces; others remain suspended, floating in open waters.

Some other major groups of primary producers, such as "blue-green algae" (cyanobacteria) and euglenoids are sometimes classified differently because of their unique cell biology. Both cyanobacteria and euglenoids photosynthesize and are considered algae by many biologists. Currently, 'blue-green algae' are considered as bacteria, in part because they lack a nucleus. Cyanobacteria are among the earliest life forms on Earth and formed extensive layered rocks of calcium carbonate (stromatolites) as early as

3.5 billion years ago. Cyanobacteria can adapt to wide range of salinities and temperatures (e.g., Iniesto et al., 2021) and include about 120 genera in North America. Many of these species are important because they fix atmospheric nitrogen. Blooms of these organisms cause taste and order problems in water treatment processes and some species produce toxins. Euglenoids have flagella and can move in water. There are 800 named photosynthetic euglenoids in 13 genera worldwide. Another algal group, the dinoflagellates, has distinct flagellar morphology and pigmentation with about 35 genera in North America. Some species produce distinct cysts that are adapted for dispersal and persistence in sediments. A few species are toxic and known to cause serious water-quality problems. Freshwater red algae comprise about 180 species and some species of *Batrachospermum* can dominate low-nutrient, spring-fed streams (Necchi Jr., 2016). Brown algae are the least diverse, with only six freshwater genera and seven species worldwide (many more species are marine). They grow primarily on rocky surfaces in streams and lakes.

The aquatic fungi and bacteria are very widespread and play essential roles in breaking down organic matter (dead leaves, wood, and dead organisms). On a global scale, these microbes are essential for processing dead organic matter and recycling carbon in freshwaters (Tiegs et al., 2019). Different microbes provide food for many types of consumers (detritivores), especially aquatic insects and juveniles of many other groups. There are approximately 600 species of freshwater fungi with about 340 ascomycetes and 300 deuteromycetes. The environments, only 10 species occur in inland waters. Chytridiomycetes have about 1250 species but most are terrestrial or marine (Shearer et al., 2007). Freshwater chytrids degrade chitin, cellulose, and lignin. One species, *Batrachochytrium dendrobatidis*, is known to parasitize and kill certain types of amphibians. This species, along with other factors, contributes to large-scale declines in some frog populations where tadpoles are infected with chytrid fungi (Barnum et al., 2021).

A high diversity of aquatic vascular plants (macrophytes such as littoral submerged, floating, and emergent vegetation) provides important food, cover, and structure in many inland waters across a wide range of latitudes and altitudes (Alahuhta et al., 2020). Some species of aquatic mosses grow in bright light in shallow waters on rocky substrata of rivers and other species grow in low-light levels in deep, clear lakes (e.g., 20 species of *Fontinalis*). Other species (e.g., *Sphagnum*) live in bogs with relatively acidic waters low in nutrients. Ferns and liverworts occur primarily in vernal pools along with a high diversity of other plants capable of growing in habitats with fluctuating water levels. Aquatic vascular plants include 88 families and over 2600 species of angiosperms with a few groups of gymnosperms in wetlands and several types of aquatic ferns (Chambers et al., 2008). The 'horsetail' or 'scouring rush' (*Equisetum fluviatile*) is widely found in wetlands and riparian zones; it is related to the earliest land plants that predate the flowering plants (angiosperms and gymnosperms). Other familiar shoreline plants are flowering plants such as cattails (e.g., *Typha latifolia*), sedges (e.g., *Carex stricta*), rushes (e.g., *Juncus canadensis*), and papyrus (*Cyperus papyrus*). Submerged plant species are especially diverse in persistent habitats with optimal conditions for growth and reproduction such as clear water and stable water levels. Floating species are well adapted to variable water levels and can shade out submerged macrophytes and algae. Floating plants typically have roots that can take up dissolved nutrients in the water but are not anchored to the sediments, unlike many of the submerged and emergent species that are rooted in the sediments. Floating ferns (e.g., *Azolla*, *Salvinia*) and flowering species (e.g., *Trapa*, *Eichhornia*) can cover the surface of lakes and reservoirs, resulting in decreased fisheries and increases in mosquito and snail vectors of human diseases. For example, the water hyacinth (*Eichhornia crassipes*) is a native of South America and was initially distributed as an ornamental plant. Now it is widely distributed in warm waters and can contribute to limiting boat traffic and to major declines in fisheries as it did in Lake Victoria, West Africa, following deoxygenation of the waters. Duckweed (*Lemna*) is another example of problematic floating species and is the smallest flowering aquatic plant. Duckweed grows quickly in nutrient-rich waters and is widely used as a plant bioassay for laboratory toxicological studies. Dense populations of *Lemna* have created numerous problems for water intakes and cooling systems. Major 'blooms' of duckweed have created spirals of massive plant production repeatedly in Lake Maracaibo, Venezuela, a very large coastal lake, where petroleum production is concentrated. Submerged invasive species, such as the widespread *Hydrilla verticillata*, can dominate some warm-water lakes and create problems for fisheries and boating especially when they are not consumed by native herbivores (Langeland, 1996; Shivers et al., 2018).

Aquatic animals

The estimated number of known freshwater animal species exceeds 100,000, and more are being discovered each year, especially in tropical ecosystems. The greatest species diversity in inland waters occurs among the invertebrates. Collectively, they provide a wide array of food for many aquatic and terrestrial consumers, including humans. Their ecological roles and habitat preferences are generally well understood but vary in response to environmental conditions (Thorp et al., 2015). Aquatic insects are the most species-rich group; their estimated abundance varies greatly among families. Dipterans (true flies) are extremely diverse and widespread (Courtney and Cranston, 2015). This order includes 30 families and some 7000 species just in North America with more than 45,000 species globally. One species-rich family Chironomidae (midges) has more than 300 genera and more than 4000 species. Chironomids occur on all continents, including the Antarctica, and on most large oceanic islands. These species live in streams, lakes, and wetlands, and some species occupy wet dead wood. Beetles (Coleoptera) are also extraordinary diverse; however, only 5% of the coleopteran species are aquatic. Even so, this order has about 12,000 aquatic species, similar to the diversity of the caddisflies Trichoptera but lower than the Diptera (Yee and Kehl, 2015). Some species of beetles are highly effective predators. For example, *Dytiscus* spp. inject their prey with digestive enzymes that liquefy and digest a wide range of prey sizes and types. Dysticid "diving beetles" include 4200 species in 175 genera and are worldwide in distribution. Other predatory species occur among the 900 species in 11 of the 36 families of gyrinid beetles. Aquatic beetles can control mosquito larvae in temporary habitats and generally can affect colonization by other aquatic insects (Pintar and Resetarits Jr., 2020). A unique mode of feeding occurs among elmid beetles that bore into submerged dead wood that increases microbial breakdown and nutrient recycling

(e.g., Valente-Neto and Fonseca-Gessner, 2011). Unlike in marine waters, there are relatively few invertebrate groups that have evolved means to feed on dead wood. However, some tropical species of catfishes have microbiomes that allow them to digest wood and other foods (McDonald et al., 2019).

Other aquatic insects that are widely distributed in a many different types of inland waters include the odonates (dragonflies and damselflies) with more than 5680 species. Most of the species occur at low latitudes, especially in the neotropical and oriental tropics. The larvae have developed specialized modes of feeding while in the aquatic phase of their life cycle. Their extendible jaws and complex visual system are especially effective at capturing their prey that range from small invertebrates to tadpoles and small fishes (Kalkman et al., 2008). Another adaptation among the larvae of *Aeshna palmata* is their use of abdominal movements to lure their prey within striking distance (Edgehouse and Brown, 2014). These odonates have not evolved morphological "fish lures" as described for some freshwater mussels (Sietman et al., 2018) or turtles (Drummond and Gordon, 1979), but their behavior is effective in attracting some of their invertebrate prey.

Other less diverse groups are used to compare water quality besides the many species of aquatic insects. Globally there are about 1100 freshwater species of Oligochaeta (Timm and Martin, 2015). Some oligochaetes live in sediments and on submerged plants, insects and bryozoans, snails and sponges (Brinkhurst and Gelder, 2001; Corbi et al., 2005). There is high diversity in Lake Baikal with about 190 species of oligochaetes and more than 70% are endemic and have distinct niches in this extremely deep, well-oxygenated lake (Martin et al., 2019). The largest family (Tubificidae) has about 1000 species. These "blood worms" have oxygen-retaining blood (hemoglobin). *Tubifex tubifex* is found in organic-rich, fine sediment that accumulate in highly eutrophic waters characterized by low dissolved oxygen. They are used as indicators of excessive nutrient inputs that increase organic production leading to excessive decomposition and low dissolved oxygen. Some are freeze-dried and sold as aquarium food for tropical fishes. *Tubifex* can also serve as critical links in the parasite life cycle of *Myxobolus cerebralis* that causes whirling disease in some species of salmonid fishes (Nehring et al., 2016), causing regional economic losses from decreased recreational fishing.

Macroinvertebrates that provide other ecosystem services such as biofiltration include the freshwater sponges (and the bivalves described below). Sponges often attach to hard surfaces and form colonies, while filtering suspended particles in clear lakes and streams. Some species of sponges have evolved to live in extreme environments such as salt lakes and caves. Unlike marine habitats, inland waters have relatively few species of sponges (Van Soest et al., 2012). There are 45 genera with 219 acknowledged freshwater species with the highest diversity in Neotropics with 65 species in 23 genera (Manconi and Pronzato, 2007). Some of the largest and more diverse sponges occur in Lake Baikal (Kenny et al., 2019). Other endemic species live in several other ancient lakes such as Tanganyika, Malawi, Ohrid, Tiberius, Poso, Titicaca and Tana. In contrast, *Spongilla lacustris* is widely distributed and its green colonies contain symbiotic algae (zoochlorella and yellow-green algae) also found in hydra. Closely associated insect species are the spongilla flies (*Climacia* and *Sisyra*), caddisfly larvae (*Ceraclea*), and chironomid midge larvae (*Xenochironomus xenolablis*), which use sponges as protective cover and food.

The Mollusca account for more than 6000 freshwater species (Böhm et al., 2020). There are more than 1200 species of freshwater bivalves in 19 families. The largest family of mussels is the Unionidae, which has 674 species (Graf and Cummings, 2007, 2015). Many of these species are important for biofiltration and biomonitoring but are at risk of extinction (Vaughn, 2010, 2018). Part of the vulnerability of some species is based on their complex life cycles that require dispersal by fishes. Some mussels have species-specific connections with certain fish species that disperse the larvae. The female bivalve releases small larvae (dart-like glochidia) that attach as parasites on fish gills during a period of larval development and dispersal. A few mussel species have evolved a 'mantle flap' of tissue that resembles a prey item that lures the host fishes closer and into range of release of the glochidia by the female mussel as the fish attacks the lure. For example, *Lampsilis reevesiana* is a mussel that uses a lure resembling a small fish (Fig. 1) and attracts smallmouth bass and rock bass as dispersal agents. If these fish are rare or absent, the life cycle of the mussels are disrupted. Overharvesting, water pollution, water diversions and dam construction continue to threaten populations of native mussels. Bivalves also create major ecological problems. Invasive species (e.g., Asian clam *Corbicula fluminea*, zebra mussel *Dreissena polymorpha*, quagga mussel *Dreissena rostriformis bugensis*) have spread widely through lakes and rivers in North America with a

Fig. 1 A female 'broken ray' mussel (*Lampsilis reevesiana*) with a modified mantle flap of tissue that resemble a small fish. The mussel moves the flap to attract fish hosts to disperse larval mussels. From: www.pearl-guide.com/forum/pearl-books-resources/1137-unio-gallery.html.

cascade of effects resulting from their filtering. Declines have occurred among open-water zooplankton and some bottom-dwelling molluscan and crustacean species. Other bottom-dwelling species have increased as a result of changes in the sediments produced by these bivalves (Vaughn, 2010).

Gastropods are also very diverse with 4800 species worldwide and more than 600 species of freshwater snails in 15 families in North America. Some species of freshwater snails have evolved from intertidal marine species and others from terrestrial progenitors (Strong et al., 2008). Thin-shelled snails are widespread and well adapted for dispersal, while the thicker-shelled species are more restricted in their dispersal in ability (Pyron and Brown, 2015). Most species live in shallow waters and are often associated with littoral macrophytes where they graze on attached algae. Spatial gradients of snail distributions are well studied in the exceptionally clear waters of Lake Baikal where 148 gastropod species are known to occur and 78% of them are endemic. There are 80 endemic species between 20 and 30 m that are abundant. The number declines with depth and 39 endemic species are found deeper than 100 m, below the photic zone; only a few species occur at depths greater than 500 m (Sitnikova, 2006). Other variables also determine snail distributions. For example, endemic limpets that are found in deep hydrothermal vents and oil seeds in Baikal (Sitnikova and Shirokaya, 2013; Stelbrink et al., 2015). Unique endemic limpets occur in insular lakes in Sulawesi (Indonesia) where at least three species of planorbid limpets (*Protancylus*) live exclusively as epizoans on endemic pachychilid gastropods (*Tylomelania*). These limpets brood their young beneath their outer mantle, a type of parental care that is distinct among lacustratine pulmonate snails (Albrecht et al., 2020b).

In general, snail morphology and life histories vary greatly in ancient lakes and rivers where endemic species evolved distinct adaptations. Most species in recently formed freshwater habitats have relatively small, smooth, thin shells. Although thin-shelled snails are well adapted for rapid growth and wide dispersal, they are less adapted to avoid shell-breaking predators (Covich, 2010). For example, several endemic freshwater snails such as *Tiphobia horei* (Fig. 2) have evolved in Lake Tanganyika in the African Rift Valley, the second oldest and deepest lake in the world (Livingstone, 2003). Their shells are characterized by sharp spines that are

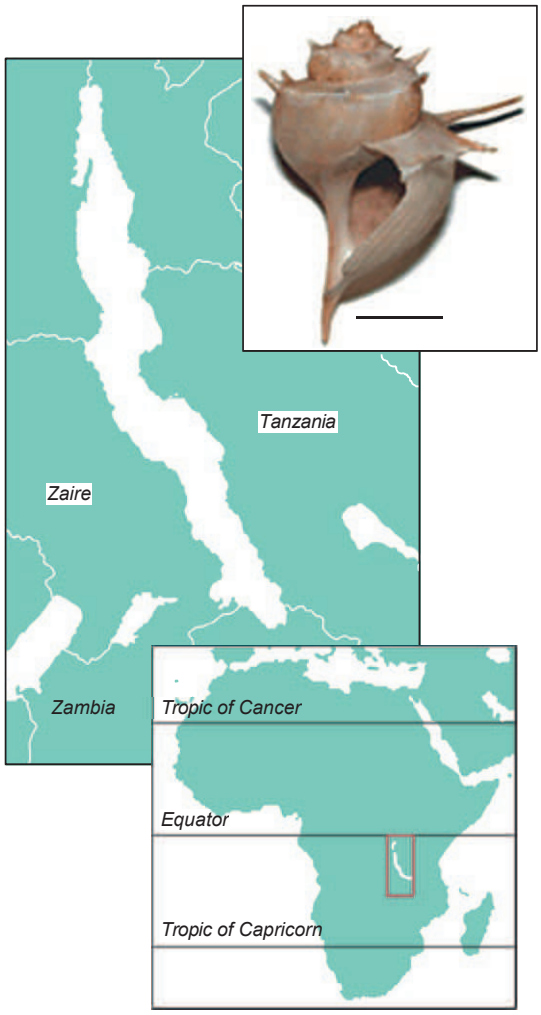

Fig. 2 A deep-water snail, *Tiphobia horei*, from Lake Tanganyika with spinose shell adapted to avoid predation by shell-breaking fishes. From: Livingstone DA (2003) Global climate change strikes a tropical lake. *Science* **301**: 468–469. The 1 cm scale indicates that these thin spinose shells are relatively large for freshwater gastropods.

anti-predator adaptations as often occurs among species of marine snails (Vermeij, 2019). These spinose shells have developed apparently in response to specialized shell-breaking cichlid fishes and crabs in this ancient lake (Marijnissen et al., 2008). Several near-shore snail species of *Lavigeria* in Lake Tanganyika grow into a size refuge once they are larger than 15 mm in shell length and spend more time on various surface substrata during the day. Predatory crabs are unable to break these large shells. Consequently, the snails are able to graze efficiently in the brightly illuminated microhabitats. In these well-lit waters, the snails accumulate a thick cover of algae that grows on their shells, creating a symbiotic snail-epibiotic algal relationship (Lukens et al., 2017). Another example of complex inter-relationships in this ancient lake occurs among one of the many cichlid fish species, *Telmatochromis temporalis*. This fish has two size morphs. The smaller individuals protect their eggs by laying them in empty snail shells of *Neothauma tanganyiicense* that occur in light brown sandy sediments. Individual fish among this dwarf morph change their color when moving across the sand from a pale to a dark color after they enter the shells seeking cover and protecting the eggs (Takahashi, 2019).

The Crustacea constitute another large group with about 10,000 species. Many are abundant and have key roles in freshwater ecosystems (Covich, 2015; Thorp et al., 2015). Crustaceans include a wide range of sizes of organisms from large river shrimp, such as *Macrobrachium carcinus*, which as adults are the size of marine lobsters, to smaller organisms such as cladocerans, copepods and ostracods. The cladocerans ('water fleas' such as *Daphnia magna*) include about 80 genera with some 4000 species. These crustaceans are also well adapted for wide dispersal by forming resistant stages, which are transported by birds and other animals. Most species are grazers on planktonic algae, while others are benthic and feed on sediments and algae growing on larger aquatic plants. Copepods are other important planktonic and benthic grazers. Harpacticoid copepods include about 300 species, calanoid copepods about 575 species, and cyclopoid copepods about 490 species in freshwaters. Some of the cyclopoids are parasitic on fishes. These zooplankton are often very abundant seasonally and many species have adapted to avoid fish predators by migrating into deep waters during daylight hours. The ostracods are small, mostly bottom-dwelling consumers with a worldwide distribution in inland waters with more than 2000 species in about 200 genera (Smith et al., 2015). Only a few ostracod species swim into open waters. Most species consume algae and dead organic matter (detritus). Some species are commensal and attach to the carapace of crayfishes. Ostracods live in a wide range of lakes, ponds, vernal pools, and caves, with some specialized species being restricted to saline waters while others are only found in calcium-rich waters or in small pools ('tanks') of bromeliads growing on tropical trees. Like other small crustaceans, these species are passively dispersed long distances by animals. However, most ostracod species are distributed in a single zoogeographic region and many species are endemic (Martens et al., 2008). For example, ostracods have evolved high concentrations of endemic species in ancient lakes such as Baikal (Schön et al., 2017) and Tanganyika (Schön et al., 2014).

The amphipods occupy a wide range of habitats from exceptionally deep lakes to ponds, vernal pools, and caves. There are some 1870 species and subspecies of amphipods; high concentrations of species are found in Lake Baikal (Siberia), Lake Titicaca (Peru), Tasmania, and the southeastern United States. For example, the amphipod *Acanthogammarus godlewskii* is one of the many unique species in Lake Baikal. It has sharp lateral spines that serve as effective adaptations to avoid cottid fish predation (Fig. 3). This crustacean species is one of more than 260 species of amphipods in 50 genera in Lake Baikal. Spinose armature also evolved among amphipod species in Lake Titicaca, apparently in response to predation by some of the endemic cyprinodontid killifish (*Orestias* spp.).

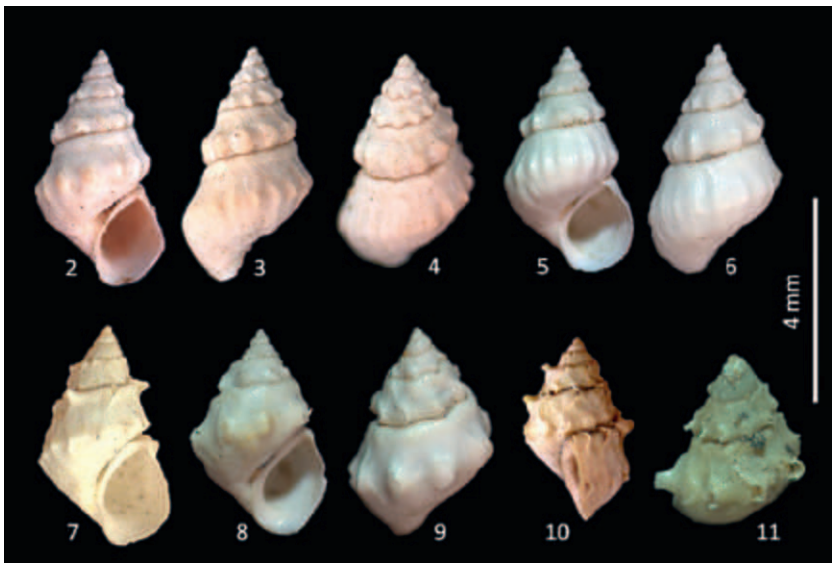

Fig. 3 Diversity in the variability of gastropod defensive morphology, 11 shells of a new species, Mexipyrgus viescaenis from Viesca, Choahuil, Mexico. From: Czaja A, Estrada-Rodríguez JL and Romero-Mendez U (2015) A new species of the genus Mexipyrgus Taylor, 1966 (Caenogastropoda: Truncatelloidea: Cochliopidae) from late Holocene spring deposits in Viesca, Coahuila, Mexico. *Nautilus* **129**: 163–168.

There are only about 70 freshwater species of the largely marine group of mysid or opossum shrimps. They are highly mobile and remain out of sight during daylight hours to avoid visual predators such as large fishes. Species in the *Mysis relicta* group are large zooplankton that undergo vertical migrations to limit their exposure to fish predators, others are littoral species that hide under rocks or among plants during the day. Mysids are omnivores and can be important predators on smaller zooplankton. Non-native mysid species were intentionally introduced in some lakes to enhance salmonid fisheries production but the unexpected cascade of changes was often detrimental to sustaining stable food webs (Ellis et al., 2011; Ricciardi et al., 2012). Because of their ability to migrate daily into a deep-water refuge, mysids are well adapted to exert major impacts on zooplankton prey populations and can compete with fish that feed on zooplankton (Gal et al., 2006).

Decapods are among the most diverse groups of crustaceans. For example, the total worldwide number of described crayfish species is over 640, and they are concentrated in two centers of diversity (Crandall and Buhay, 2008). The first is the southern Appalachian Mountains and the southeastern United States, where crayfish occur in subsurface waters as well as in small streams, rivers, lakes, wetlands, and springs. In all of North America there are over 340 crayfish species. The second center of diversity is located in southeast Australia where the largest freshwater crayfishes (*Astacopsis gouldi*) occur in Tasmanian rivers and are reported to weigh over 6 kg and live for 40 years. The Murray River crayfish (*Euastacus armatus*) is another very large Australian species that has evolved a spinose carapace (hard exoskeleton or shell) and large chelae (claws).

Crabs also occur in inland waters and have strong claws that can crush a wide range of animal prey, fruits, and nuts; their diversity is especially high in Neotropical, African, and Asian waters. Over 1300 species of freshwater crabs complete their life cycle independently of marine environments (Yeo et al., 2008; Cumberlidge et al., 2014). For example, some marine-derived species of freshwater crabs are known to have expanded their dispersal into coastal rivers during cycles of sea-level expansion and contraction throughout the Pleistocene. The diversity among species of *Parathelphusa* was not driven only by these regional fluctuations but was complexly connected with earlier dispersal events to rivers and ancient lakes in parts of southeast Asia (Klaus et al., 2013; Poettinger and Schubart, 2014). Some freshwater crabs are semi-terrestrial (amphibious) and link aquatic and terrestrial ecosystems. Freshwater crab species have evolved numerous endemics on large, isolated islands such as Madagascar, with six genera. The co-evolution of crabs and snails is widely documented in mainland and insular freshwaters (von Rintelen et al., 2004; Schubart and Ng, 2008; Marijnissen et al., 2009; Covich, 2010).

Freshwater shrimp also evolved from marine ancestors as they adapted physiologically and behaviorally to moving upstream into large coastal rivers, headwater streams, and lakes (De Grave et al., 2008; Bauer, 2013). Insular habitats have relatively high diversity of endemic species as in Madagascar. New species continue to be found among Indonesian insular lakes in Sulawesi (von Rintelen et al., 2020; Klotz et al., 2021). One endemic species of atyid shrimp (*Caridina spongicola*) found shelter and food in freshwater sponges and another species (*Limnocaridina iridinae*) associates with a bivalve species (*Iridina* sp.) in Lake Tanganyika (Zitzler and Cai, 2006; von Rintelen et al., 2007). Many inland waters of China are occupied by unique species of shrimps. Lake Tanganyika and the Amazon River basin also have unique endemic genera of shrimps.

Some benthic macroinvertebrates are associated with complex feeding behavior and numerous species interactions such as the many types of leeches. They are active predators and ectoparasites found in association with a wide range of larger invertebrate and vertebrate species. They are prey for many species such as fishes, snakes, salamanders and some invertebrate predators (Govedich and Moser, 2015). Leeches (Hirudinida) occur globally, except in Antarctica, with over 400 species in 91 genera in wetland, stream and lake habitats. Two ancient lakes, Siberian Lake Baikal and Balkan Lake Ohrid, each have 10 endemic species (Sket and Trontelj, 2008). The leech fauna of Lake Baikal consists of a total of 28 species. These species parasitize endemic amphipods and other species; for example, *Baicalobdella* infects sculpin fishes (Kaygorodova and Sorokovikova, 2014). Leeches affect the health of host species by causing ulceration, hemorrhage, and inflammation. Leech attachment sites can open the host to bacterial and virus infections as well as transmit trematodes, cestodes, nematodes and parasitic flagellates.

Several groups of invertebrates are among the smaller and often unnoticed species. Rotifers are microscopic, multicellular animals sometimes called 'wheel animalcules,' based their rings of cilia that appear to rotate like spinning wheels in the microscope. Rotifers are very abundant, functionally important consumers, and comprise about 2000 species. A single tropical lake can contain more than 200 species, while fewer species are often encountered in temperate-zone lakes, springs, vernal pools and ponds (Segers, 2008; Brown et al., 2020). They are primarily filter-feeding herbivores and detritivores, although a few species are predators and some are parasitic. Size and shape of some species is modified by the presence of predators (induce spine formation) and by their diet (vitamin E induces larger individuals). Most rotifers live as solitary, planktonic individuals but some species are attached (sessile) to plants, rocks, and other hard surfaces and about 25 species are colonial. Rotifers are prey for larger zooplanktonic species of insects and crustaceans.

Other small invertebrates include the approximately 1300 species of free-living freshwater flatworms (Planaria or Turbellaria). Most species live in crevices of well-oxygenated sandy, stony or muddy sediments in rivers and lakes or on macrophytes leaves and roots while some are found in streams that flow through caves. Flatworms can switch from living in the littoral zone to living in the open water depending on the relative risk to predation and to food quality (Dumont et al., 2014). Some planarians (triclades) are cannibalistic while others are predatory on zooplankton or on oligochaetes, chironomids, amphipods and other benthic invertebrates. A few species are ectosymbionts that live on crustaceans, snails, insect larvae and turtles where they ingest algae and small prey suspended by the host-generated turbulence (Noreña et al., 2015). Triclads are widely known for their ability of regenerate and are used in laboratory studies where identical individuals are useful to test responses to various manipulations independent of genotype. Some species of *Girardia* have well-studied life cycles, distributions, and ecology because they are enteric

parasites and create health concerns for humans relative to drinking untreated stream water. *Girardia tigrina* was introduced to Europe and *Girardia dorotocephala* was introduced to Hawaii from North America (Sluys et al., 2005).

The free-living nematodes are additional micro-metazoans that live in sediments of many inland waters (Poinar Jr., 2015). They range over a wide range of sizes and can occur at high densities (>1 million individuals per m^2). Along with other meiofauna they provide essential roles in nutrient cycling and in benthic food webs (Traunspurger, 2013; Majdi and Traunspurger, 2015). Some feed on bacteria and algae while others are predators and all are subject to predation by other groups of meiofauna, benthic macroinvertebrates, and some vertebrates (Abebe et al., 2008; Hodda et al., 2009). Nematodes are another group that evolved relatively high numbers of species in Baikal with about 65% of the more than 100 species considered as endemics (Naumova and Gagarin, 2019).

Another widely distributed group are the small "water bears" or tardigrades. Their common name derives from their movement behavior and use of multiple claws on their legs to hold on to surfaces, especially aquatic mosses and other macrophytes. Videos of their walking demonstrate interesting jumps and quick moves along with their slow forward motion. Those living in freshwaters are well adapted to a broad range of temperatures that allows them to survive in freezing conditions, intense UV radiation, complete desiccation in very dry environments, and even exposure to vacuum pressure in outer space. Although some species commonly reproduce parthenogenetically, many other species produce resistant eggs during periods of stress that also allow for local and regional dispersal (Nelson et al., 2015; Schill, 2019).

Because of their size, and often their important economic value, vertebrate distributions are generally more completely documented than invertebrate distributions. There are more than 20,000 known vertebrate species in inland waters, including nearly 18,000 species of freshwater fishes (Lévêque et al., 2008; Su et al., 2021). More than 1600 fishes are known just from the Amazon River basin (Albert et al., 2020). Other major concentrations of fish diversity occur in the Congo River (Stiassny et al., 2011) and in the Mekong River (Chea et al., 2017). In the African Rift Valley Lakes, remarkable species 'flocks' have apparently evolved in isolation from other lakes during prolonged dry periods. Approximately 250 cichlid species evolved in Lake Tanganyika, more than 800 in Lake Malawi and some 500 in Lake Victoria. Very rapid evolution of endemic cichlids is known from Central American crater lakes in Nicaragua. Hybridization can greatly increase the genetic and phenotypic diversity of cichlid flocks and result in important differences in morphology, feeding behavior and coloration. The extraordinary diversity of cichlids indicates the importance of understanding appropriate spatial and temporal scales in analyzing rates of speciation (Genner et al., 2007; Meier et al., 2017; Rometsch et al., 2020).

Turtles are another widespread, diverse group of vertebrates that play important roles in food webs of inland waters (Stanford et al., 2020). Their potential for long life and variations in life-cycle traits and local spatial distributions (e.g., seasonal movements and home ranges) are well known from studies that have recaptured marked individuals (e.g., Sexton, 1959, 1995) or used radio tracking to define travel patterns (Rowe, 2003). There are interesting differences among their life histories in that some species have indeterminate growth while others do not. Females among many species are known to reproduce late in life. For example, female Blanding's turtles (*Emydoidea blandingii*) can increase their reproductive output after 65 years of age by slowing their growth rates and allocating more energy to reproduction (Congdon et al., 2003). Turtles feed on many types and sizes of plants and animals as they mature. These ontogenetic shifts in diet increase the potential for coexistence among age classes. Among the unique fauna are the alligator snapping turtles (*Macroclemys temminckii*) in southern US that evolved a lingual lure that is moves to attract fish prey (Drummond and Gordon, 1979). This use of "fish lures" is very different from the way mussels attract fish to serve as dispersal agents (Fig. 1), but demonstrates the complexity of species interactions in diverse food webs. Many turtles are at risk from habitat fragmentation, pollution and overharvesting in many areas, especially in tropical waters where human population growth is threatening their future (Rhodin et al., 2018).

Global patterns of biodiversity in inland waters

One limitation in understanding patterns in global biodiversity is that hypotheses regarding the formation of species assemblages in various kinds and ages of inland aquatic habitats often are based on information from a limited subset of well-studied species. Another limitation is the incomplete geological, environmental, and historical information in many regions, especially from tropical inland waters. Even so, the examples in the previous sections regarding the highly uneven distribution of the number of species in different major groups of freshwater organisms demonstrate some biogeographic distributions that provide insights about speciation and the potential loss of species from centers of diversity. The dispersal ability of different groups is also important. Species of plants and invertebrates that are adapted for inland waters have generally evolved some means of dispersal. Many have resistant stages (seeds, hardened egg capsules, etc.) that allow for transport and colonization as well as persistence in "seed banks" that can regenerate populations (species "resurrection" from lake sediments) when favorable conditions occur (Hairston and Fox, 2009). The "ubiquity hypothesis" proposed for the smallest organisms (algae, bacteria, fungi, and some small invertebrates) suggest that those species are widely and uniformly dispersed (Fenchel and Finlay, 2004; Fontaneto and Hortal, 2013). The presence of such species in a given waterbody reflects current environmental conditions rather than isolation and dispersal. It is clear that some species have stages in their life histories that allow them to become inactive during stressful conditions (e.g., Vyverman et al., 2010). Other species such as fishes, turtles, and mammals (e.g., beavers, otters, raccoons) are excellent swimmers while some are strong flyers (e.g., wading birds, some insects). Thus, many species can disperse over long distances during some periods of their life cycle or in response to environmental change.

Unlike most marine and terrestrial ecosystems, the biodiversity of inland waters is generally independent of latitude. Fish distributions are an exception with a clear latitudinal gradient of more species in the tropics (Lévêque et al., 2008; Leroy et al., 2019; Miller, 2021; Su et al., 2021). In general though, the biodiversity of the major groups of invertebrates does not follow latitudinal trends or has a single explanation for predicting species assemblages (e.g., Dumont, 1994; Gillooly and Dodson, 2000; Les Eyzies and de Ciencias Biologicas, 2013). This lack of a latitudinal pattern is a result of the highly isolated nature of many inland waters and their varied types of geological origin (such as glaciation, tectonic activity, and dissolution of limestone).

Freshwater biodiversity generally reflects the major differences in the geological origins and ages of inland waters. However, because of the great variation in persistence of inland aquatic habitats, there is no single physical variable that adequately predicts how many species of any taxonomic group will share a given habitat. Some inland water habitats dry out completely every year, while others remain permanently wet. The large flowing rivers, deep lakes, and extensive wetlands frequently are colonized by dispersing species. These ecosystems can have many endemic species that coexist and coevolve in spatially distinct habitats over millennia. Dispersal, colonization, and local extinction explain a community's natural species composition over time.

It is clear that system age is important. Most inland waters can be considered temporary in a geologic sense in that they can eventually fill with sediments, dry out, or change physically and chemically in other ways over geological and historical time scale. For example, the North American Great Lakes took their present form during the last glacial retreat, only some 12,000 years ago. However, there are some very old lakes with remarkable species. Lake Baikal is the deepest (>1600 m maximum depth) and oldest lake in the world with an exceptionally long geologic history (more than 25 million years old) and extremely low nutrient concentrations. Lake Baikal contains 20% of the Earth's freshwater and has maintained one of the highest biodiversity found in any inland water with a large number of endemic species in several different groups. Shifts in Baikal's many complex environmental gradients over its long geological and evolutionary history affected the evolution of this unique biota; biota that is threatened by ongoing effects of climate change and landuse (Timoshkin et al., 2016; Hampton et al., 2018). Other lakes that are millions of years old are Tanganyika, Malawi, Victoria, Ohrid, Biwa, and Titicaca and the early dispersal of some groups to these isolated sites led to evolution of unique species and species "flocks." These ancient inland waters have attracted intensive research on the mechanisms of speciation (Schön and Martens, 2004; Hampton et al., 2018). In general, fluctuations in lake levels from climate-changes and paleohydrology over millions of years have created numerous endemic species in ancient lakes. For example, the evolution of species "flocks" and many endemic species of diatoms, gastropods, amphipods and fishes in Lake Titicaca resulted from regional changes in evaporation-precipitation ratios that altered water levels and sizes of several lakes with internal drainage (endorheric) throughout the central Andean high plateau (Jurado-Rivera et al., 2020; Zapelloni et al., 2021). Other ancient lakes, like Lakes Tanganyika and Malawi are especially well known for the large concentrations of endemic cichlid fishes. This is also true for Lake Victoria, but this lake is not as old and may have been affected by drought during the Pleistocene, which lowered the level of this lake, possibly accelerating the rate of evolution among the highly diverse cichlid fishes in perhaps just 15,000 years. However, short-term changes from recently introduced species have altered the diversity of native species in Lake Victoria. Population reductions of endemic cichlids followed the introduction of the Nile perch (*Lates niloticus*) in the 1950s; an introduction intended to increase sport fisheries and commercial harvests. Unfortunately, concentrations of endemics that have evolved from a single ancestral line can be vulnerable to rapid novel environmental changes such as introductions of non-native species as in Lake Victoria or the warming of surface waters and earlier melting of ice cover as is occurring in Lake Baikal (Njiru et al., 2010; Hampton et al., 2018).

Most of the 10 largest rivers are also ancient, highly diverse ecosystems. The Amazon River is the largest and has by far the highest mean annual discharge and drainage area. This basin also contains the largest number of freshwater fish species and has a high species richness of crustaceans and many other taxa. Other large tropical rivers such as the Congo (Stiassny et al., 2011) and Mekong (Chea et al., 2017) also have unique fish species diversity as a result of their complex channel networks, high-velocity barriers, and seasonal connections to large wetlands that provide numerous types of habitats. The evolution of different species in large rivers can result from isolation of habitats by very deep channels with complex rapids and by exceptionally high current velocities that separate populations on one side of the river from populations on the other side (e.g., Markert et al., 2010). Isolation also occurs from differences in flows and substrata associated with rapids (Hrbek et al., 2018) as well as by adaptations for traversing steep waterfalls (e.g., Hongjamrassilp et al., 2021; Ebner et al., 2021).

Additional insights about species diversity and biogeography are based on species that live in extreme environments of temperature and salinity as well as in dark caves, deep groundwaters, springs, and intermittent habitats (Gibert et al., 2009; Pipan et al., 2020). These species demonstrate a wide range of unique evolutionary adaptations that illustrate the physiological limits to distributions in very different habitats (Benvenuto et al., 2015; Baxter and Zalar, 2019). For example, brine shrimp (*Artemia*) dominate in hypersaline waters that few other species can tolerate, and are highly productive in those lakes. Their life cycle includes production of "resting eggs" that can withstand low-saline conditions until the environment is again appropriate for the eggs to hatch (e.g., Barnes and Wurtsbaugh, 2015). Many other well-studied examples are known from a wide range of salinities of inland waters in arid central Australia and South America (e.g., Bayly, 1993). Isolated springs in arid regions have large numbers of endemic species that are threatened by increased frequencies of drought and diversion of groundwater (e.g., Shepard, 1993; Box et al., 2008).

Biodiversity in freshwater habitats on islands provides opportunities to evaluate the importance of age as well as area and isolation of freshwater habitats relative to source areas (Arnott, 2009; Covich, 2009; Burress et al., 2018). Well-adapted species colonize these insular habitats either by dispersal from other freshwaters or by adapting to freshwaters from near-shore marine habitats. For example, in the south Pacific, Lake Wisdom is a deep crater lake on a recently formed volcanic island that is known to be younger than nearby Lake Dakataua, another caldera in West New Britain, Papua New Guinea. More species of aquatic plants and

aquatic invertebrates are found in the older lake but there are some similar species in both lakes. These shared species were most likely transported by birds and includes similar species on other nearby islands (Ball and Glucksman, 1980). Crater lakes can also be linked to springs and small streams flowing from the lakes. These small streams can function as corridors for movements among molluscan, decapod, insect, turtle, salamander and fish species, allowing for relatively rapid colonization of the lakes from marine-derived species that have adapted to low salinities in coastal rivers.

Hydrologically isolated lakes, springs and wetlands are similar to oceanic islands in that only species with special adaptations can colonize them. The duration of isolation may allow evolution of distinct endemic species, especially in arid regions where long distances separate potential sources of dispersal. Speciation may result in species flocks in permanent springs, ancient rivers, and deep lakes. Radiation (extensive development of new species) of some taxa can occur rapidly. For example, gastropod speciation is well documented in both large, ancient ecosystems and in small streams, springs, and groundwater habitat. Rapid radiations of some amphipod and gastropod species are apparently the result of micro-geographic isolation resulting from changing water levels during periods of rapid shifts in precipitation and the isolated nature of many spatially distinct small habitats. Genetic analyses are increasingly demonstrating the importance of these modes of speciation. High diversity of endemics and accumulation of species from both this process of speciation and slow rates of colonization from other regions can create distinct 'hot spots' of regional biodiversity. One of the most extensively studied clusters of spring-fed lakes and rivers occurs in the Chihuahuan Desert in northwest Mexico. The ecoregion contains a high concentration of endemic species that resulted from a long series of fluctuations in rainfall and groundwater levels (Czaja et al., 2015, 2020). Endemic species of fishes, turtles, shrimps, snails and an exceptionally high diversity of cyanobacteria have evolved in a complex food web. Some of the Mexican species of snails have sculptured shells that lower their risk to fish predation (Fig. 3).

Overall, there is a general relationship between size, age, geomorphology, and hydrology that influences species diversity of inland waters. However, unlike marine and terrestrial ecosystems, latitudinal diversity gradients are lacking for many groups of freshwater plants and animals, in part due to the high diversity of Baikal and other very old, deep lakes outside the tropics.

Loss of biodiversity

The highest rates of extinction in recent decades have occurred among freshwater species. These rates of loss are several times greater than those of terrestrial species or marine species. Inland water species are increasingly threatened from pollution, overharvesting, as well as dams and reservoirs that block dispersal corridors and that change natural flow regimes (Winemiller et al., 2016). Pollution and siltation have increased rates of extinction and loss of diversity through habitat degradation or complete elimination of some freshwater habitats. Recent increases in global transport of nonnative species are also changing distributions of some intentionally and accidentally introduced species from aquaculture, sport fisheries, and aquarium trades (Ricciardi, 2007; Havel et al., 2015). The impacts of these losses are further compounded by the negative effects of many invasive species and increased appropriations of freshwater for human needs at the expense of native species (Dudgeon, 2020; Rico-Sánchez et al., 2020). Loss of native freshwater species is a major concern because of the ethical values associated with preserving native species in protected areas and the value of native species for human use as well as for scientific study of evolutionary and ecological processes.

Although many species are well studied in inland waters, a large number remain taxonomically, ecologically, and behaviorally incompletely or entirely unknown, especially in tropical regions (Dudgeon, 2020). These major gaps limit our current understanding of the long-term impacts of species losses in aquatic ecosystems and the ability to predict sustainable production of ecosystem services. Most ecologists expect that rapid shifts in community composition will likely result in loss of important ecosystem processes and related ecosystem services (Covich et al., 2004). Once one species is locally or globally extinct, other species may not be adequate substitutes for the lost species in sustaining ecosystem processes. Partial species replacement or 'compensation' can occur in some cases for short periods of time (e.g., Frost et al., 1995), but complete, long-term functional replacement is unlikely because most native species have adapted to a lengthy history of different, and sometimes extreme, environmental changes. Consequently, assumed substitutability of "substitute species" in a particular functional group is unjustified without long-term studies (e.g., Lake et al., 2000). Loss of key species can not only affect short-term nutrient cycling but also diminish fisheries production (McIntyre et al., 2007) and sever connections among freshwater and terrestrial ecosystems (Naeem et al., 2012). Many decades of research have demonstrated that biodiversity in inland waters has economic value and a variety of ecological and social values (Heal et al., 2005; Heino et al., 2021). Despite this recognition, the remarkable biodiversity of species in inland waters is increasingly in need of protection and effective management to sustain essential ecosystem services (Dudgeon et al., 2006; Reid et al., 2019; Stanford et al., 2020). Much more information is needed on global distributions of species and their function in the ecosystem (Collen et al., 2014).

See Also: Fundamental concepts and theories: Paleolimnology: Long-Term Reconstructions of Environmental Change; The Ecological Niche in Aquatic Ecosystems; Human pressures and management of Inland Waters: Biological Invasions: Impact and Management; Structures and functions of Inland Waters - Groundwater: Biodiversity of Invertebrates in Springs; Structures and functions of Inland Waters - Lakes: A Diversity of Primary Producers in Lakes; Zooplankton Diversity and Variation Among Lakes; Structures and functions of Inland Waters - Rivers: Biodiversity Conservation of Aquatic Ecosystems; eDNA and Bioassessment of Rivers; Energetics and Food Webs in Large Rivers; Structures and functions of Inland Waters - Wetlands: Patterns in Freshwater Fish Diversity; Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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Populations in Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Carrying capacity, K The maximum population size of a given species that can be sustained by a specific environment. It is an attribute of the environment where the population exists.

Demographically correlated populations Two or more groups of individuals with correlated vital rates (survival, fecundity) or population growth rates over time.

Dispersal/migration These two words are used as synonyms as is the convention in population genetics. Both terms refer to the movement of individuals away from their birth place. Demographic consequences of that movement depend on intraspecific and ecological interactions after dispersal whereas evolutionary consequences depend on interbreeding after dispersal.

Effective population size, N_e In small populations genetic drift causes greater random changes in allele frequencies between generations than it does in large populations. However, the census number of adults is relatively uninformative about the strength of drift because demographic factors such as skewed sex ratio, high variance in reproductive success, and fluctuations in census population size over time can all increase genetic drift for a given census population size. If we consider an imaginary, demographically "ideal" population that has none of these factors enhancing genetic drift, then N_e = the size of the ideal population that would experience drift as strongly as the observed focal population. For the theoretical ideal population N_e = census N, but in most real populations N_e is 5–10 times lower than census N.

Evolutionarily correlated populations Two or more groups of individuals with correlated patterns of gene frequency variation over time.

Gene flow (effective migration, mN_e) Genes travel as a function of dispersal, but only get passed on to the next generation and generate "gene flow" if an immigrant interbreeds. Thus, gene flow is an evolutionary process. The per generation rate of gene flow is the product of the migration rate, m, and genetically effective population size of the receiving population, N_e.

Genetic drift Random changes in allele frequencies between generations due to finite population size. The alleles in a cohort of offspring are a sample from the previous (parental) generation. Chance differences in survival and reproduction contribute to sampling error. Smaller populations experience stronger genetic drift.

Intrinsic rate of increase, r (instantaneous rate of increase) The difference between instantaneous birth and death rates. A parameter in the logistic growth equation that indicates the per capita growth rate per unit time.

Logistic population growth A sigmoid population growth model that describes the exponential increase at low population size and decreasing rate of population growth as the population approaches its carrying capacity.

Metapopulation A set of spatially discrete populations that exchange migrants and in which some extinction and recolonization of habitat patches occurs. The term is often used more loosely as any spatial array of subpopulations that exchange migrants to some limited degree. If there is enough connectivity to make the subpopulations demographically correlated then the whole system is a population, not a metapopulation.

Phylogeography The use of molecular markers (e.g. DNA variation) to trace the extended genealogy within and among populations of a species to understand demographic history and evolution of the populations.

Introduction

"Population" refers to a group of individuals of the same species that interact more with each other than with other individuals of that species. Such a general definition serves well in many contexts, but any deeper investigation tends to be from a particular perspective shaped by specific questions. To understand population dynamics and persistence probabilities an ecologist might focus

on competitive or facilitative interactions in the context of predation and disease, whereas a demographer is focused on immigration and emigration and their effects on the life table and population growth. Similarly, an evolutionary lens puts focus on reproductive interactions of residents and immigrants and the impact of gene flow on random population genetic changes (genetic drift), the deleterious consequences of inbreeding, and how these processes interact to affect adaptive potential. Because different kinds of interactions are more important for various questions about a population, the definition of population boundaries might differ across studies, especially when physical boundaries that limits distributions are fuzzy.

In freshwater aquatic systems there is often a discrete landform that imposes population boundaries - a lake shore or watershed perimeter. Neither of these boundaries are necessarily absolute, that is able to contain a closed population (no immigrants; entirely self-recruiting). Lakes and ponds typically have inlet and outlet connections and watersheds can connect at their downstream junction. Nonetheless, for many species these landforms enforce a discrete population structure with relatively few migrants. At the other end of the spectrum are macrogeographic watersheds containing semi-continuously distributed species. Is the entire watershed a population? In these cases interactions are quantitatively greater and qualitatively different within local habitats than across distances much greater than the average dispersal distance. It is in these less discrete contexts that useful population definitions often depend on the question being asked, and as a consequence there are many definitions that have been applied.

The working definition of a population is also important for conservation and management. Leaving aside the reality that political jurisdictions often impose population definitions for the purposes of conservation, restoration or management of harvest, it is critical that management plans properly account for the ecological, demographic and evolutionary forces that affect population dynamics.

For an operational definition it is useful to focus on process rather than pattern because habitats are dynamic, and population boundaries vary as a function of habitat. Population abundance and spatial distribution are patterns that might suggest where one population ends and another begins. Demography entails the processes wherein individual traits like fecundity and survival (vital rates), along with immigration, emigration, and habitat quality, determine the local trajectory of population size change. If populations on two adjacent habitat patches change in synchrony, then the pattern suggests one population occupies both habitat patches. If we find that the species has a growing population in one habitat patch and is declining in the other, the two habitats have different populations and the demographic process lens helps identify the scale at which distinct management actions may be needed. Similarly, if two populations have different gene frequencies, that is a pattern that implies evolutionary differentiation and the need to manage the populations separately.

In this chapter we follow others in arguing for distinct definitions of demographic and evolutionary populations (Waples and Gaggiotti, 2006; Cooper and Hurd, 2019). We will address demographic and evolutionary population definitions conceptually first, and then address operational metrics for delineating populations.

The ecological population paradigm

Demographic and ecological processes often are considered together under an "ecological population paradigm." Thus, many definitions have focused on proximity and interactions; "A group of individuals of the same species that co-occur in space and time and have an opportunity to interact with each other" (Waples and Gaggiotti, 2006). Boundaries have been conceptualized as defining the spatially most inclusive set of individuals for which the rate of intraspecific interactions is much higher within the grouping than across groupings (Millstein, 2010). Others have emphasized the degree of immigration and emigration over some time period (Cooper and Hurd, 2019) in defining the population. The key feature of a population under the ecological paradigm is that population dynamics, i.e. births and deaths, are determined locally within an ecologically cohesive group. Unfortunately, very little theory has been developed to guide expectations for how low the immigration rate, m, needs to be to maintain independence of the group's population dynamics from that of surrounding populations. Hastings (1993) used coupled 2-population deterministic models to demonstrate a complex relationship between dispersal rate and the independence of local population dynamics. The analysis suggested a strong dependency of results on the intrinsic rate of population growth for intermediate migration rates, but in general $m < 0.1$ (10% immigration per generation) led to independent population dynamics (Hastings, 1993). However, White et al. (2011) found a substantial amount of coupling at $m = 0.1$ between the demography of two populations when one was experiencing strong harvest pressure. More work is needed; it may be premature to use $m < 0.1$ as a threshold for identifying discrete management units (Palsbøll et al., 2007).

The evolutionary population paradigm

Whereas competition and perhaps cooperation within a shared niche are the currency of cohesion under the ecological paradigm, the degree of evolutionary independence for a population is determined by a different kind of interaction - reproduction - and the source and magnitude of gene flow. Genetic drift is the random genetic change that occurs within and between generations. It shifts allele frequencies with unpredictable directionality at a rate that is the inverse of population size. Genetic drift reduces genetic variation within populations and causes differentiation among populations that may lead to populations evolving into new reproductively isolated species.

Recent and contemporary processes have effects on populations that are overlayed and intertwined with phylogeographic history. In particular, natural selection often generates spatial variation in organismal traits so dramatic that it shapes our perception of deep population divisions, as often reflected in subspecific taxonomy. In fact, however, adaptive traits can evolve relatively quickly compared to the deep history generating phylogeographic structure. Also, strong natural selection can maintain adaptive differences between populations even when a considerable amount of gene flow connects them (Lenormand, 2002; Richardson et al., 2014). Genomic studies are showing how portions of a genome that contribute to local adaptive trait variation can have lower realized gene flow than other regions of the genome (Martin and Jiggins, 2017). Thus, the degree of evolutionary correlation among subpopulations, and the implications for population definitions, often vary across the genome for a given history of migratory exchange and diversifying selection. Although genomics is being harnessed in ever more efficient ways to probe this complexity and interpret it in terms of evolutionary processes relevant to population management, this chapter primarily focuses on the more inevitable and predictable process of gene frequency differentiation caused by genetic drift.

Aspects of demography can alter the rate of genetic drift for a given population size (e.g., sex ratio, variance in reproductive success), so drift theory is based on an index of population size that accounts for these variables - the genetically effective population size or N_e. Leaving aside the N_e details (see glossary), a small reproductively cohesive group will experience more random genetic change per generation than a large group. The rate of gene flow can be thought of in terms of the proportion of immigrants per generation, m, but unlike the demographic rate m, only immigrants that reproduce contribute to gene flow so the evolutionary parameter refers to *effective* migration. Evolutionary process, and more specifically the degree of evolutionary independence of a population, are determined by the product of effective population size (N_e) and the immigration rate (m).

The number of effective migrants per generation (mN_e) is related to the degree of evolutionary independence, leading to disparities in the degree of evolutionary and demographic consequences for low levels of exchange. It can be surprising how few effective migrants are sufficient to maintain genetic homogeneity among spatially discrete populations compared to maintaining demographic homogeneity. With some simplifying assumptions, the theoretical turning point between evolutionary independence (leading to local fixation or loss of alleles at migration-drift equilibrium) vs. reproductive cohesion (maintaining genetic homogeneity among subpopulations and minimizing local allelic diversity losses) occurs at $mN_e = 1$. This led to the "one migrant per generation" rule in conservation biology describing the level of exchange desired to prevent evolutionary isolation. Mills and Allendorf (1996) examined some genetic and nongenetic factors that complicate applications of this rule and suggested that $1 < mN_e < 10$ provides a more generally useful quantitative threshold for exchange rates above and below which evolutionary correlations are more predictable.

Comparing the ecological and evolutionary paradigm

The ecological and evolutionary paradigms provide different definitions of a population because, for a given spatial pattern of average dispersal for individuals inhabiting fragmented habitat, demographic correlations trend toward zero at smaller concentric scales than evolutionary genetic drift correlations (Fig. 1). This process-based difference is sometimes used to posit ecological exchangeability when the demography of a species is correlated between two habitat patches, or evolutionary exchangeability if gene flow levels have prevented genetic drift from fixing different alleles in the two patches (Templeton, 1989). In practice, this distinction is sometimes aligned with management or policy goals with demographically correlated patches of individuals representing the minimum possible spatial "management unit" whereas criteria for "evolutionary significant units" focus on measures of evolutionary independence (Crandall et al., 2000).

Discrepancies in the demographic and evolutionary impacts of migration can cut both ways. As a result of mate choice or aspects of local adaptation it is possible to have immigration that influences demography (e.g. through competition) but has little to no gene flow effect. For example, demographic effects might be expected for a pair of cryptic species (species that are difficult to distinguish based on phenotype, yet are unable to interbreed) that diverged in isolation but are intermingling in secondary contact. Reproductive barriers would minimize evolutionary consequences of this secondary contact but mate choice confusion or competition for resources could occur. Discrepancies in the opposite direction might be more common. if there are no reproductive barriers and low rates of exchange ($1 < mN_e < 10$) between two patches, demographic correlations might be weak despite a potent evolutionary homogenizing force countering differentiation by genetic drift.

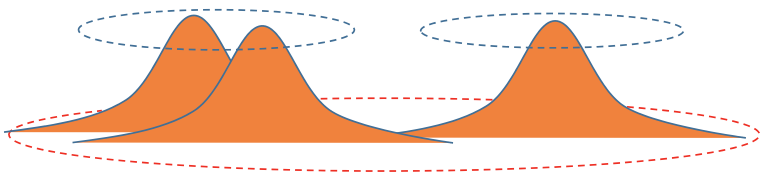

Fig. 1 Orange distributions represent dispersal kernels, the distribution of dispersal distances from a central point. The kernels are centered on adjacent habitat patches. Overlap between kernels depicts demographic connection. More overlap contributes to demographic correlations (left, one encompassing dashed circle). Less overlap may maintain a connection but promote demographic independence (separate dashed circle at right). The red dashed circle represents evolutionary processes and the larger spatial scale at which evolutionary exchangeability is maintained because fewer effective migrants are sufficient to counter differentiation by genetic drift.

Waples and Gaggiotti (2006) in their excellent simulation-based examination of population distinctness concluded that typical high resolution genetic studies can reliably discern allele frequency differentiation due to genetic drift, even with number of migrants as high as 25 per generation. This would be consistent with 10% exchange ($m = 0.1$) among constant size subpopulations with $N_e = 250$, implying that under some conditions genetics can resolve fine scale differentiation among "populations" that are likely to be demographically correlated. The prospects for management applications are high if high-resolution genetic data, when coupled with a careful spatial sampling design, can be used to estimate both contemporary m (the migration rate at the time of sampling, including both "effective" and non-effective migrants) and a long-term average effective migration (mN_e, Cayuela et al., 2018). In the remainder of this chapter we give some examples of populations and compare demographic and evolutionary population paradigms.

Simple populations – A collection of individuals in a defined space

A population can consist of a collection of individuals that are both demographically and evolutionary distinct. For such populations, there are no issues with different definitions based on demography and ecology versus genetics and evolution. Some populations even consist mostly of individuals with the same genotype. Examples include several macrophytes that reproduce vegetatively and where a large number of individuals within a lake may be part of the same clone (e.g. common reed *Phragmites* and eelgrass *Vallisneria*). Other groups such as cladoceran and rotifers may also have populations consisting of a limited number of clones. These zooplankton species reproduce parthenogenetically during most of the year and only produce males and reproduce sexually at the end of the growing season. Such populations consist of several coexisting clones that dominate at different times, representing evolutionary changes in the population. This can lead to eco-evolutionary feedbacks (De Meester et al., 2019). For example, early spring clones reduce phytoplankton abundance during the spring clear water phase, resulting in improved conditions for less edible cyanobacteria which in turn lead to changes in the *Daphnia* population toward clones that are able to feed on cyanobacteria (Schaffner et al., 2019).

Standard population dynamics equations describe how the number of individuals in a population are related to birth and death rates and the effect of population size on these rates (Fig. 2A). These standard equations for logistic population growth are fundamental to population dynamics theory and described in all standard ecological textbooks (e.g. Gotelli, 2008). Attributed to Malthus, Lotka and Volterra, these equations show how a single population that is not resource-limited initially increases exponentially. As the population size increases resources per individual decline, birth rates decline, and the population eventually cease to increase (birth rates = death rates) at its carrying capacity. This population growth model works well to describe population size response after colonization of a new habitat. As an example, the quagga mussel (*Dreissena rostriformis bugensis*), like its congener the zebra mussel (*Dreissena polymorpha*), are considered aggressive invaders in aquatic systems, each capable of changing the physical structure of the lakes they colonize (Higgins and Vander Zanden, 2010; Karatayev et al., 2015). Quagga mussels were first detected in Oneida Lake, New York USA in a marina in 2005 and 4 years later, the species reached densities of 5800 m^{-2}, or over 1 trillion individuals in the 207 km^2 lake (Hetherington et al., 2019). This tremendous population increase is partly due to the large number of free-swimming larvae (veligers) produced by these mussels; one female mussel may produce 1 million larvae in a year. At the same time, zebra mussels declined from 5800 m^{-2} in 2007 to 400 m^{-2} in 2011, showing an almost complete replacement of one invader by a new invader (Hetherington et al., 2019). Zebra mussel density ranged from 2600 to 7600 m^{-2} from 1995 through 2008, suggesting that ~6000 m^{-2} represents the carrying capacity of these mussel in Oneida Lake. The observed increase of the quagga mussel population was well described by a logistic growth equation with an intrinsic rate of growth (r) of 3.0 and a carrying capacity K of 6000 m^{-2} (Fig. 3A). The carrying capacity varied somewhat among three areas of the lake (example from hard bottoms in Fig. 3B) which may be related to different bottom structure and bathymetry in different parts of the lake. Even so, the similarity in the population growth trajectory throughout the lake suggests that the quagga mussels in Oneida Lake can be considered one population.

These standard population dynamics equations are the basis not only for predicting population development, but also for predator-prey interactions, competition, and harvest management (Gotelli, 2008). Of interest to inland waters is the large body of theory developed in fisheries (Beverton and Holt, 1957; Quinn and Deriso, 1999; Walters and Martell, 2004) in parallel with the development of theory in population ecology. The fisheries-based theory led to concepts such as stock-recruitment functions, surplus production models, and maximum sustainable yield, the latter predicting the maximum harvest rates possible without decreasing the population size (Fig. 2B). This occurs at the highest rate of increase in the logistic growth curve, often at a population size about half the density of an unfished population at carrying capacity.

This theory of population dynamics assumes that the individuals within the population can be considered equivalent. This is of course a simplification. For starters, a population consists of individuals of different age, and age may be related to size and fecundity. For fish, larger females produce more eggs, but also potentially eggs of higher quality (Chambers and Leggett, 1996). Many aquatic animals have juvenile and adult stages that differ in habitat use and diets. For example, the mussels discussed above have free swimming larvae (veligers) that live in the open water and are transported by currents whereas the adults are benthic and often attached to substrates. In addition to age, individual size is important. Fish larvae are orders of magnitude smaller than the adults and have dramatically different interactions with their environments, including being prey for their larger conspecifics (Fuiman and Werner, 2002). Cannibalism can be the most important source of mortality of young fish, leading to population cycles (Parker-Stetter et al., 2007; De Roos and Persson, 2013). Therefore, population dynamics depends on size structure, and

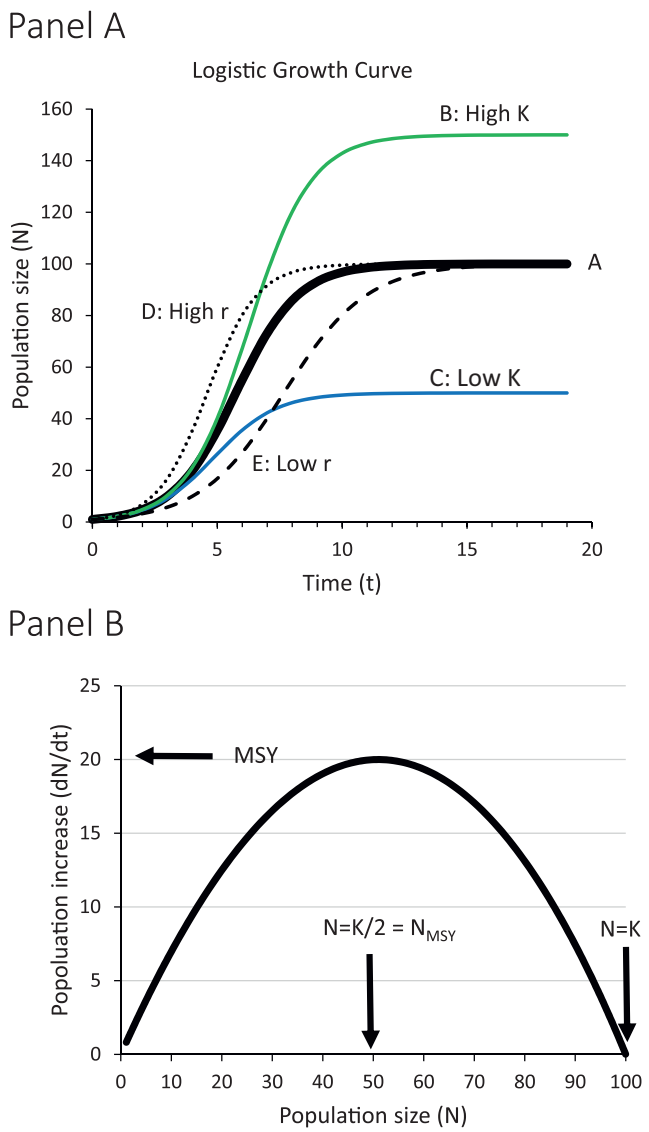

Fig. 2 Population growth according to the logistic growth equation: $N_t = K/(1 + [K\text{-}N_0)/N_0]e^{-rt})$. N_t is the population size at time t, K is carrying capacity, N_0 is the population at time 0, r is the intrinsic rate of increase. Panel A depicts the population increase for different carrying capacity (K) and intrinsic growth rate (r). Curve A has K = 100 and $r = 0.80$. Curve B and C show the effect of increasing K to 150 (curve B) and decreasing K to 50 (curve C). Curves D and E shows the effect of increasing r to 1.00 (curve D) and decreasing r to 0.60 (curve E). Panel B shows the rate of increase of the population (dN/dt) as a function of population size for curve A in panel A. dN/dt = rN (1-N/K). Maximum rate of population increase occurs when the population size is half of the carrying capacity (N = K/2 = 50 in this model). This maximum population increase at half the unfished population size is the maximum rate at which this population can be harvested without declines in the population (maximum sustainable yield, MSY).

incorporating such structure in population models has been an active area of research for some time (DeAngelis and Gross, 1992; De Roos and Persson, 2013).

Populations are also collections of individuals that differ along some trait continuum even at the same size and age. Some of these differences are due to genetics, others arise from the plasticity of individual form when residing in different environments. For example, Eurasian perch (*Perca fluviatilis*) are known to develop different morphology depending on whether these fish are in the littoral or pelagic zone of a lake. Littoral perch have a deeper body and larger fins and mouth than the more slender perch caught in the pelagic zone (Svanbäck and Eklöv, 2002). The more streamlined pelagic fish have more zooplankton in their diet than the littoral deeper bodied individuals. Interestingly, common garden experiments showed that most of these morphological differences in Eurasian perch were due to phenotypic plasticity and not genetic differences (Svanbäck and Eklöv, 2006), although genetics does influence the capacity to express environment-specific forms and this capacity may differ among sexes and individuals (Höök et al., 2021). Thus, the perch population should be considered one population that consist of individuals with forms representing a continuum of a given trait (here body depth and gape size). Individual differences in diet choice and ability to grow on different food resources has also been observed in other fish species such as roach (*Rutilus rutilus*, Faulks et al., 2015), yellow perch (*Perca*

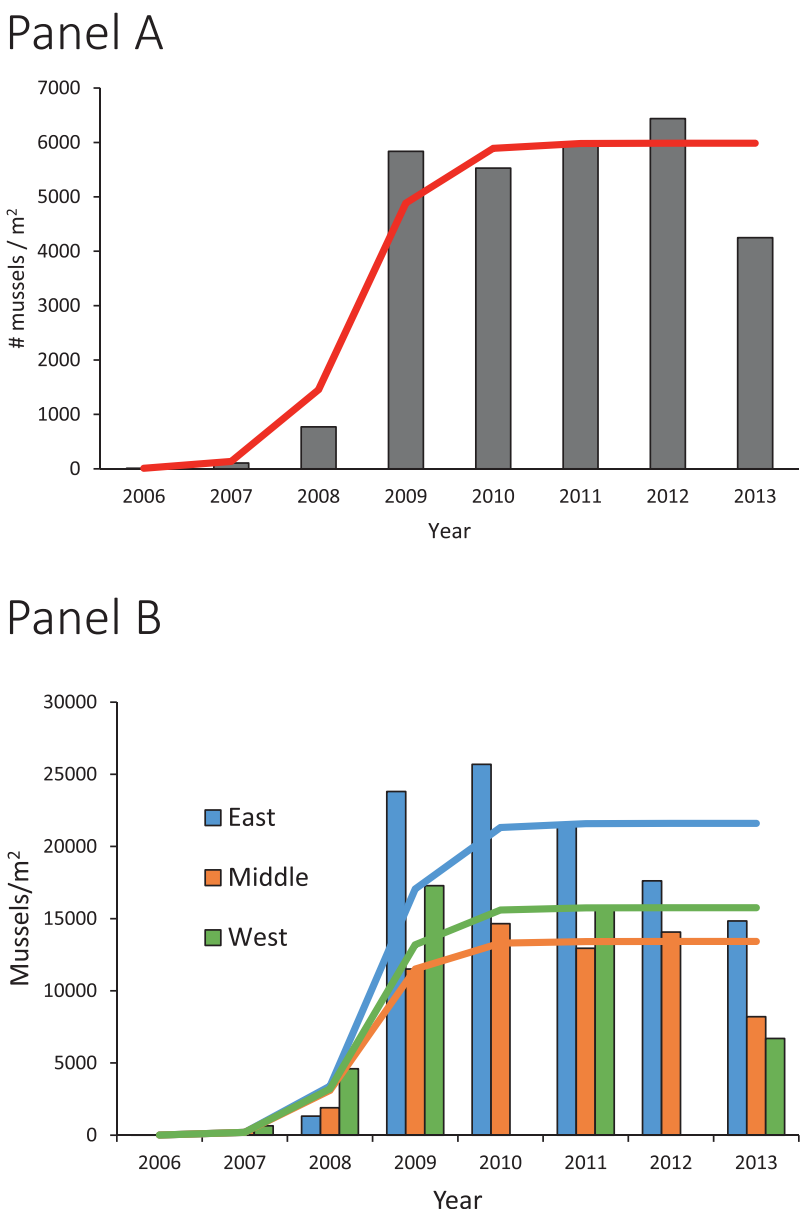

Fig. 3 Population increase of quagga mussels (*Dreissena rostriformis bugensis*) in Oneida Lake, New York follows a logistic growth curve with an intrinsic annual rate of increase of 2.6 and a carrying capacity of 6000 ind/m^2 (Panel A). Quagga mussels were first detected in Oneida Lake in 2005, and increased to between 10,000 and 25,000 ind/m^2 by 2009, an increase from a few individuals in 2005 to one trillion (1.2×10^{12}) individuals in the lake by 2009, 4 years later, exemplifying the population explosion possible in highly fecund organisms. Carrying capacity varied somewhat in different sections of the lake. The intrinsic rate of increase on hard substrate was 3.0, and the regional carrying capacity was 21,500 ind/m^2 in the eastern part of the lake, 13,400 ind/m^2 in the middle part, and 13,800 ind/m^2 in the western part (Panel B). The differences in carrying capacity likely reflect differences in substrate, although the samples depicted here are all from bottom with rocks and stones. Densities on other substrates were lower. The similarity in the increase in numbers in the different parts of this 207 km^2 suggest that the quagga mussels in this lake can be considered one population. In deeper, stratified lakes, the quagga mussels residing in deep water have a different morphotype with longer siphons and slower growth rates than the quagga mussels in shallow water leading to different population growth rates in these habitats (Karatayev et al., 2018). Oneida Lake data from Hetherington et al. (2019).

flavescens, Fetzer et al., 2015) and largemouth bass (*Micropterus salmoides*, Post, 1993) as well as in *Daphnia* (Schaffner et al., 2019), frogs and gastropods (Bolnick et al., 2003). Indeed, increased niche breadth in generalist species following release of interspecific competition may be due to increased difference between individuals rather than increased niche breadth of each individual (Bolnick et al., 2007). Thus, both populations dynamics and food web interaction models based on an average individual may not be sufficient to describe the dynamics of a heterogeneous population (Bolnick et al., 2003; Persson and DeRoos, 2003). The need to account for individual differences in population models led to the development of individual-based models that could account for a range of individual traits within populations (DeAngelis and Gross, 1992). At the extreme, within population differences between

morphotypes can lead to the development of distinct subpopulations and likely speciation over time. A classic example is the divergence of morphotypes of artic charr (*Salvelinus alpinus*) in Lake Thingvallavatn, Iceland into a benthic dwarf form, a benthivore, an open water planktivore and an open water piscivore (Sandlund et al., 1992).

A complex population – The brook charr

The brook charr (*Salvelinus fontinalis*) is a broadly distributed species that shows population distinctions at many spatial scales. The term "population" might reasonably be used at any of these hierarchical levels. The species inhabits cold water streams and lakes from the southern Appalachian Mountains of the U.S. to the watersheds of Labrador, Canada. The first order pattern of population subdivision, detected with genetic markers, coincides with regional river basins that likely differed in their post-Pleistocene recolonization timing and/or source. Allozyme data were used to distinguish Brook charr from the Allegheny, Hudson & Delaware, and St. Lawrence River basins (Perkins et al., 1993). Similarly, microsatellite markers revealed a broad regional pattern of subdivision among Labrador Brook charr consistent with hypothesized distinct Pleistocene refugial sources (Pilgrim et al., 2012). These studies illustrate how phylogeographic patterns across major portions of a species range can be used to infer historical processes shaping the distribution of genetic variation, sometimes revealing deep intraspecific genetic disjunctions that are not apparent phenotypically.

In brook charr, life history distinctions are a good example of trait-based population differentiation driven by natural selection and/or plastic responses to environmental variation. Across its geographic range, brook charr either live and breed in lakes, live and breed in streams, or are born in streams but migrate into a lake or ocean for a portion of the life cycle before returning to a stream for reproduction (anadromy). These life history traits, often associated with distinct morphologies, are a reasonable basis for distinguishing "populations," but the relative importance of trait inheritance vs phenotypically plastic responses to environment is typically ambiguous without intensive research. This is why understanding ecological and evolutionary exchangeability between these life history populations is challenging. For example, nonmigratory and migratory populations are sometimes sympatric, with a difficult to distinguish combination of genetic and environmental factors triggering one strategy or the other in individuals (Thériault and Dodson, 2003). The morphological variation associated with these life histories is moderately heritable (Varian and Nichols, 2010), meaning that both genetic and environmental factors contribute to population variation in the trait, and natural selection can induce an adaptive response. Thus, situations likely occur where demographic exchange is substantial between life history populations, but immigrants have maladaptive traits relative to locals and little of the exchange is evolutionarily effective (i.e., immigrants typically transmit no genes).

One of the fascinating aspects of brook charr population structure is that it extends down to extremely local levels in some continuous habitats where no dispersal barriers are known. Genetic drift theory applied across a continuous species range generates expectations for the amount of evolutionary independence to expect across different geographic distances. At spatial scales smaller than a certain limit, determined by population density and the distribution of dispersal distances, genetic variation will be spatially homogeneous (panmixia). At spatial scales above single generation average dispersal distances, and after an equilibrium is established between gene flow homogenization and genetic drift differentiation, pairwise levels of genetic differentiation will be positively correlated with geographic distance. The panmictic scale is sometimes referred to as a genetic neighborhood (Wright, 1946) whereas the broader pattern fits an 'isolation by distance' model in which the slope of the relationship between spatial separation and differentiation is steeper when average dispersal distances are shorter. Isolation by distance is a very common pattern to find in species that have not had major colonization, population expansion, bottleneck or fragmentation events over the last 100s to 1000s generations (thus having reached an approximate equilibrium between dispersal and genetic drift). In freshwater systems, panmictic genetic neighborhoods might be found at the level of tributaries, as is the case for brook charr, or entire watersheds, depending on the historical and contemporary levels of gene flow. Practical management decisions are simplified if the population genetic pattern coincides with a larger landscape feature (watershed). In this case a watershed population boundary suitably reflects both demographic and evolutionary processes and there is little controversy. In brook charr, where there is a dire need to manage population viability in response to the synergistic stressors of degraded water quality, introduced competitors, and climate change (Hudy et al., 2008), their population biology in streams often leads to very fine scale evolutionary differentiation of breeding populations at the level of single tributaries despite some demographic interdependence among adjacent tributary and mainstem reaches.

Several detailed studies have revealed these tributary distinctions in stream-dwelling brook charr (Kanno et al., 2014; Kazyak et al., 2016) using both demographic and genetic methods for estimating population sizes and connectivity. In a study of brook charr in two tributaries and the interconnecting mainstem reach, methods of detecting fish movements revealed symmetric exchanges between mainstem and tributaries by close to a third of individuals. In contrast, genetic sibship data revealed substantial movements of mainstem fish into tributaries to breed but gene flow in the reverse direction and between tributaries was rare (Kanno et al., 2014). Later genetic analyses capable of inferring the long-term realized impact of gene flow on allele frequency differentiation indicated that gene flow was sufficient to homogenize the mainstem with one of the tributaries but not the other, and revealed higher levels of differentiation ("cryptic" metapopulation structure) among these very closely spaced tributaries (Whiteley et al., 2017). Levels of genetic differentiation were surprisingly high given the amount and pattern of detected exchange, suggesting some combination of movements unrelated to reproduction, natal homing, and reduced reproductive success in non-natal fish relative to local residents.

Because brook charr have exchange rates seemingly sufficient to generate correlated demography, yet the genetic differentiation among tributaries conclusively demonstrates evolutionary independence, this species provides an excellent case study for comparing these two paradigms. Perhaps unsurprisingly, what brook charr studies reveal is the inadequacy of a population paradigm focused on spatially correlated demography or ecological exchangeability when habitat heterogeneities significantly impact vital rates in age-, season- and site-specific ways. For example, variation in stream flow rate and temperature were found to differentially affect brook charr vital rates in mainstem vs. tributary habitats, and these dynamic differences in habitat quality are not independent of movement patterns (Letcher et al., 2015). Also, system-wide tests of association among habitat features and genetic connectivity (riverscape genetics) can reveal spatial variation in population exchange that informs a more functional understanding than would a classification system defining populations (White et al., 2020). The typical genetic differentiation of brook charr at the tributary level in many areas frustrates management planning premised on identifying and prioritizing distinctiveness because it focuses on the isolation implied by genetic differences and the population viability risks inherent in isolation. In this species there is an underlying metapopulation structure - meaning an interconnected network of populations - with spatial and life cycle components that respond to environmental fluctuations differently such that the entire system is more resilient than the local evolutionary isolation implies. Ultimately, metapopulation theory may provide a more productive framework for managing species such as brook charr than trying to identify and manage discrete populations.

Knowledge gaps/future work

- For conservation and management of populations there are increasingly diverse ways of assessing population relationships from both a demographic and evolutionary perspective. For example, genetic parentage analysis on wild samples can provide inferences similar to mark and recapture methods of abundance estimation, but also contribute to landscape scale assessments of long term gene flow.
- Genomics can be used to survey the spatial patterns of genetic variation within and among populations and to identify genes that are responding to environmental stressors. Although this chapter focused on non-adaptive processes defining populations, genomics provides an important lens focused on local adaptation, the capacity for evolutionary responses, and the eco-evolutionary feedbacks shaping those responses.
- Geneflow, migration, and adaptative traits of individuals need to be better integrated into our understanding of population dynamics.
- Despite powerful ways that genetics informs conservation and management, it remains a mostly academic venture with less application than is warranted.

See Also: Emerging methods and topics: Environmental DNA Advancing Our Understanding and Conservation of Inland Waters; Fundamental concepts and theories: Metapopulations in Inland Waters; The Ecological Niche in Aquatic Ecosystems; Human pressures and management of Inland Waters: Inland Fisheries Management - Exploitation and Livelihoods; Structures and functions of Inland Waters - Lakes: Fish Populations; Structures and functions of Inland Waters - Rivers: Aquatic Food Webs In Rivers; Dispersal in Stream Networks: Meta-populations and Meta-communities

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Metapopulations in Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Assisted gene flow Physically moving individuals among populations/patches to increase and maintain genetic diversity.
Demographic rescue Moving individuals from one population to another population to increase population size and buffer against demographic stochasticity.
Dispersal Movement of individuals to different patches outside of their home and migratory range.
Emigration Permanent dispersal of individuals out of a patch.
Extirpation/local extinction A species that no longer exists within a specific location (e.g., a patch) but still exists elsewhere.
Genetic rescue Moving genetic diversity from one population to another population to increase the fitness of the receiving population.
Immigration Dispersal and establishment of individuals into a new patch.
Inbreeding depression Loss of fitness due to reproduction/breeding between closely related individuals.
Iteroparity Ability to have multiple reproductive events over the course of an individual's lifetime.
Lentic Standing waterbodies (e.g., lakes and ponds).
Lotic Moving water (e.g., streams and rivers).
Matrix The unsuitable habitat that surrounds the mosaic of patches.
Metapopulation Spatially structured populations with asynchronous dynamics connected by dispersal.
Mosaic A collection of habitat patches across the landscape that comprise the metapopulation.
Occupancy Presence of a species within a patch.
Patch Discrete, suitable habitat for a self-sustaining population.
Recolonization Immigration of individuals into an uninhabited patch that was previously extirpated.
Rescue effect Extirpation of population is prevented due to immigration from outside individuals.
Sink An unproductive patch or population that is dependent on immigration to persist.
Source A productive patch or population that is self-sustaining and produces individuals that disperse to other patches.
Stochasticity Fluctuations due to chance. Stochasticity (chance) exists in the environment and in a population's demographics. Environmental stochasticity is the unpredictability in environmental conditions, whereas demographic stochasticity are random fluctuations in population size due to birth and death rate dynamics.
Stock Many harvested fish populations are characterized by stock structure, that is, sub-species structure where component units are defined for purposes of management and often correspond to a population or subpopulation.

Introduction

Many populations of species occur in dynamic environments that vary over time, where demographic and environmental stochasticity can affect population dynamics (May, 1974). Often demographic information is studied for individual species and sites, but the study of a population in isolation may lead to only a partial understanding of its ecology. Early attempts at understanding population dynamics often used simple models that assumed population closure, where emigration and immigration are not considered. The role of dispersal was later acknowledged to influence population dynamics where the movement of

individuals among populations was important for persistence of nearby local populations (Brown and Kodric-Brown, 1977). A collection of multiple, interacting populations is termed a "metapopulation," in which local extinction and recolonization depend on the dispersal of individuals among discrete habitat patches, i.e., suitable areas surrounded by a matrix of unsuitable habitat (Levins, 1969). In other words, a metapopulation is an assemblage of many local populations where ecological processes take place at two scales, both local and regional.

There are several origins of the idea that natural populations in larger regions consist of discrete local populations connected by dispersal and that species persistence depends on a balance between local extinctions and recolonizations. While Levins (1969) is credited with coining the term "metapopulation theory," he wasn't the first to consider local extinctions and recolonizations of extirpated or vacant habitats. The earliest known concept of metapopulation processes is attributed to Nicholson and Bailey (1935) who noted the importance of local extinctions and recolonizations to maintaining parasite-host dynamics (Hastings and Harrison, 1994). Biologists like Sewall Wright (1940) considered the evolutionary implications of discrete patch structure. Andrewartha and Birch, (1954) emphasized the importance of local extinctions and recolonizations to the distribution and abundance of species. Around the same time as Levins' metapopulation theory appeared, MacArthur and Wilson (1967) published the theory of island-biogeography to predict species richness of vacant island habitats that were recolonized by dispersal from a mainland.

Levins' metapopulation model assumed identical populations where local habitat patches were the same size and quality, and equally connected to one another. However, real-world examples are often more complex, and Levins' theory proved too simplistic to accurately capture metapopulation dynamics (Hanski, 1989, 1991, 2001). Later both theoretical and empirical studies recognized the importance of differences among populations and further investigated the underlying ecology and evolutionary biology of these dynamics. Indeed, it is now well-appreciated that metapopulations are dependent on the spatial complexity of both local and regional dynamics where the size, arrangement, number, and distance among patches can influence population dynamics (Campbell Grant, 2011). Moreover, metapopulation dynamics do not remain static; population demographics and habitat can change over time.

For a classic metapopulation, Hanski et al. (1995) outlined four criteria that must be met. The first is that populations within a metapopulation occur in discrete patches that are separated from each other by unsuitable habitat (i.e., the matrix). Separation from neighboring populations allows for each population to act independently. The second criteria is that there must be some asynchrony in dynamics among populations. A complex of populations with asynchronous dynamics is less likely to experience simultaneous population declines and local extinction events. Third, there must be some dispersal of individuals to other patches so populations within a metapopulation are connected. Dispersal is critical to the existence of a metapopulation because it allows for unoccupied patches to be recolonized and for declining populations to be rescued from extirpation due to a demographic subsidy, a phenomenon known as the rescue effect (Brown and Kodric-Brown, 1977). Lastly, local populations are not large enough to persist on their own (or else they could be considered single populations). While Hanski outlined these criteria for classic metapopulations, other metapopulation types have been described with slight variations on these assumptions. For example, in mainland-island and source-sink metapopulations, a given local population may be highly persistent (Harrison and Taylor, 1997).

Despite the popularity of metapopulation theory in the literature, it continues to be challenging to empirically document given the amount of labor required for the long-term monitoring of multiple populations. Metapopulation theory first focused on terrestrial systems (Levins, 1969) and later expanded to marine and freshwater systems. Given that freshwater habitats are embedded within the terrestrial landscape, species' populations within a region are often spatially structured (Falke and Fausch, 2010; Erõs and Campbell Grant, 2015; McCullough et al., 2019), suggesting the potential for metapopulation dynamics to emerge.

Overview of freshwater metapopulations

The spatial discreteness of freshwater habitats in combination with environmental variability and disturbance regimes leads to spatially structured populations that can be characterized by metapopulation theory (Falke and Fausch, 2010). Lentic systems can align with the classical conception of metapopulation patches as islands, where discrete populations can exist in individual lakes, ponds, and wetlands which can be insular with populations isolated from each other by land (Fig. 1A), or occur in whole networks connected by streams and wetland habitats (Fig. 1B) (Meerbeek and Weber, 2020). Metapopulations can also arise within a single lake when species exhibit philopatric behavior (i.e., returning to natal habitat for reproduction) which can contribute to spatial structuring of local populations (Hayden et al., 2011). Discrete populations can also occur in streams, which are arranged in hierarchical dendritic patterns where the network topology of river and stream systems creates habitat and matrix patches with distinct abiotic characteristics (Erõs and Campbell Grant, 2015). The presence of natural and anthropogenic barriers can limit movement among habitats within this branching network, also contributing to spatial structure. Metapopulation structure occurs at different spatial scales within stream networks. For larger and more motile species, discrete populations may be distributed across tributaries of a watershed (Fig. 1C), whereas the metapopulation structure for sessile and small-bodied species may exist within reaches of a stream (Fig. 1D).

Freshwater species take advantage of numerous connectivity types among freshwater habitat patches (Fig. 1) and many species use a diversity of habitats across their life histories at various spatial and temporal scales (Schofield et al., 2018). Strictly aquatic species such as fish can move along stream corridors to access different tributaries within a watershed. Ephemeral and perennial wetlands and streams can connect lakes and ponds and act as corridors for aquatic species (Daniels et al., 2008; King et al., 2019). Semi-aquatic species (e.g., invertebrates, amphibians) may use both aquatic and terrestrial connections (McCullough et al., 2019).

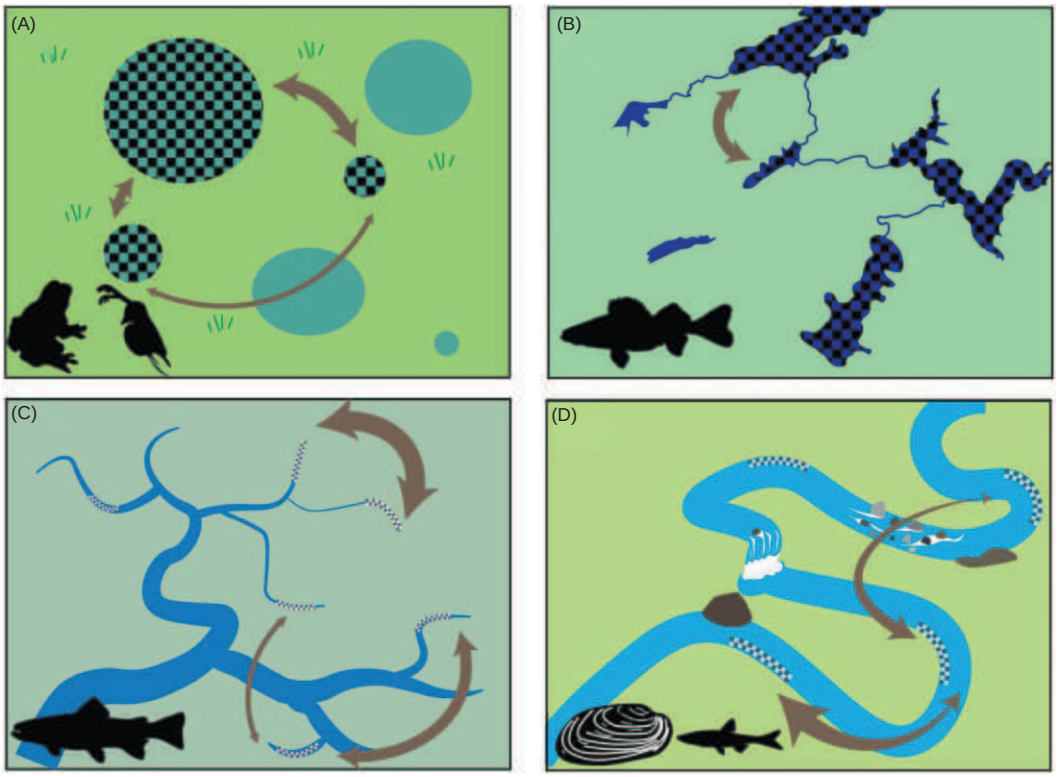

Fig. 1 Examples of spatial structure and degree of dispersal in various aquatic metapopulations. Metapopulation dynamics can exist between (A) insular ponds for semi-aquatic species, (B) lakes connected by inflows and outflows, (C) tributaries of a watershed, and (D) reaches of a single stream. Checkered areas indicate occupied patches. Arrows indicate dispersal, with arrowhead size signifying the dispersal rate between populations.

Many invertebrates and amphibians use freshwater habitats for breeding and juvenile rearing, with adults dispersing among patches overland or aerially (Bohonak and Jenkins, 2003; Semlitsch, 2008).

Thus, aquatic habitats can be characterized by discrete patches with varying degrees of connectivity, suggesting the potential for metapopulation dynamics to emerge. Unclear, however, is whether metapopulation dynamics are common among freshwater taxa. Syntheses are helpful for addressing this question. For example, a review of >50 journal articles and theses on amphibian metapopulations by Smith and Green (2005) revealed that the majority of studies (74%) did not test the key assumptions necessary to demonstrate the existence of classical metapopulation structure as outlined by Hanski (i.e., habitat patches support local breeding populations, patches are not too isolated to prevent recolonization via dispersal, local dynamics are sufficiently asynchronous to make simultaneous collapse unlikely, and no single population is large enough to ensure long-term survival). Even so, the review did identify some cases of pond-breeding amphibians functioning as metapopulations.

For example, a study by Sjögren (1991) explored local extinction and recolonization dynamics along an isolation gradient for pool frogs (*Rana lessonae*). In this system, reproduction is confined to distinct water bodies, which allowed researchers to closely monitor population size, survival, and dispersal rates. Local extinctions were likely to first occur at patches greater than 1 km from breeding populations. Neighboring ponds within 300 m of breeding populations were more likely to receive immigrating individuals and had a decreased risk of extirpation due to a rescue effect.

As an example from riverine systems, Koizumi (2011) summarized nearly a decade of research on a Dolly Varden (*Salvelinus malma*) metapopulation in the Sorachi River basin, Japan. While a few self-sustaining Dolly Varden populations were found within large tributaries, the majority of populations were small with fewer breeding individuals. They found that populations were largely independent and observed asynchronous dynamics across tributaries. The author concluded that these local populations should persist as long as some degree of connectivity was maintained among the tributaries to allow dispersal and recolonization.

Other syntheses also recognized critical next steps in addressing metapopulation dynamics in freshwater habitats. For example, Falke and Fausch (2010) reviewed 31 riverine fish papers published from 1995 to 2008 that investigated metapopulation dynamics. They noted that while authors framed their paper in the context of metapopulation theory, only the simplest of models were applied. Few papers included in their review incorporated the realisms of freshwater ecosystems in their models. As was recognized in early terrestrial metapopulation studies, spatial and temporal dynamics can also play an important role in the structuring of metapopulation dynamics in freshwater ecosystems. The following sections describe more realistic considerations of both spatial and temporal processes in freshwater ecosystems when applying metapopulation theory.

Local and regional dynamics in freshwater metapopulations

Local

Habitat size, quality, and heterogeneity can all influence local dynamics and extinction risk. In general, larger habitats are associated with larger populations and lower local extinction risk. However, habitat quality can greatly influence dynamics. For example, Suhonen et al. (2010) explored local extinction risk of dragonfly and damselfly populations in Finnish streams, ponds, and lakes and found that local extinction risk is generally elevated in low-quality habitats relative to high-quality habitats, consistent with source-sink theory. Moreover, species with narrow geographic ranges were more likely to go locally extinct in local patches compared to widely distributed species. Briers and Warren (2000) also noted that habitat quality can influence reproductive success and populations can have patch-specific probabilities of persistence in their study of breeding amphibians. Habitat quality and heterogeneity also influenced a wetland metapopulation of round-tailed muskrats (*Neofiber alleni*) in a study by Schooley and Branch (2007). The authors found that differences in the presence and density of the muskrat's food source, maidencane grass (*Panicum hemitomon*), resulted in spatially autocorrelated "neighborhoods" of high-quality and low-quality patches across the wetland.

Regional

The arrangement of patches relative to each other influences the amount of dispersal, a process necessary for recolonization, demographic rescue, and gene flow. The distance between patches and the degree of connectivity through the matrix are key factors that shape a metapopulation's regional dynamics (Hanski and Gaggiotti, 2004). For example, Sjögren's (1991) metapopulation study of pool frogs (*Rana lessonae*) inhabiting ponds at the northern edge of the species range in Sweden demonstrated how the distance between ponds was an important factor influencing extinction and occupancy. Fagan (2002) demonstrated how altered connectivity and fragmentation in dendritic stream networks can decrease metapopulation persistence given the diversity of fragmentation that can take place (e.g., both natural and anthropogenic).

Beyond distance and degree of connectivity, larger patch networks (e.g., those with a greater number of patches) are more likely to persist longer compared to smaller networks (Campbell Grant, 2011). Additionally, the position of patches within the network can lead to some patches being disproportionately important to metapopulation dynamics relative to others. For example, species in streams and rivers with limited dispersal capabilities may only disperse downstream through drift (Mari et al., 2014). In this common scenario in rivers, upstream habitat patches can be important sources for recolonization of downstream patches. For example, Sousa-Santos et al. (2014) found that for a threatened cyprinid metapopulation, (*Anaecypris hispanica*) recolonization primarily occurred in a downstream direction due to this fish's limited dispersal ability. The authors emphasized that if connectivity to the upstream patches became lost or if the upstream populations were extirpated, it could be detrimental to the long-term persistence of the metapopulation. The arrangement of patches can also impact metapopulation dynamics in lentic habitats. To explore the importance of patch position in pond habitats, Holmes et al. (2020) excavated experimental ponds, where a subset of these ponds were stocked with zooplankton (*Daphnia pulex*), and explored how the location of the stocked ponds influenced metapopulation dynamics. The authors found that centrally located ponds acted as a stepping stone for surrounding neighboring patches. Removal of these central ponds increased the risk of metapopulation extinction.

Temporal aspects of metapopulations

While advances were made in accounting for the importance of spatial patterns for metapopulation functioning, earlier models assumed that these patterns were stationary over time. In reality, just as populations experience temporal turnover due to local extinctions and recolonizations, the same is true of habitat patches and the uninhabitable matrix. Both habitat patches and the surrounding matrix can experience environmental variability, disturbances, habitat loss, and succession (Stelter et al., 1997; Keymer et al., 2000; Amarasekare and Possingham, 2001) which can vary in their timing, duration, and frequency.

Patch number and quality can also vary among years, and this shifting mosaic of habitat can influence local dynamics and extinction risk (Reigada et al., 2015). For example, Briers and Warren (2000) found that temporal variation in habitat (e.g., mud percentage cover) influenced the local extinction risk of notonectid backswimmers in small, artificial ponds in the United Kingdom. Directional habitat change can also influence occupancy and local extinction risk. For example, Skelly et al. (1999) studied a community of pond-breeding amphibians in Michigan, United States, which had been surveyed earlier between 1967 and 1974. The authors reported that forest succession negatively impacted breeding amphibians, through its effect on pond hydroperiod and canopy cover. Many ponds that supported pond-breeding amphibians in the early survey period were ponds that dried in summer during the later survey period, limiting their potential for all but those with the most rapid development.

Additionally, temporal variability can connect and disconnect habitat patches over time. Freshwater habitats have varying degrees of permanence, where some streams are perennial and flow year long, others are temporary and periodically go dry. Lentic habitats can also be ephemeral or temporary where ponds are wetted for only a portion of the year. Mediterranean-type rivers are characterized by a flow regime of fall-winter floods and summer droughts. These seasonal fluctuations can result in streams reduced to a series of disconnected pools where surface flows often cease entirely. Drought periods can be responsible for population

fragmentation and extirpation, and the movement of individuals during periods of connectivity allows extirpated regions to be recolonized. Similar disturbance dynamics are observed in dryland rivers in Australia that have low and unpredictable annual rainfall where metapopulation patches are prone to frequent extirpation due to drying. Huey et al. (2011) found that persistence of metapopulation structure depended on dispersal events during periods of connectivity for two species of fish (*Macquaria ambigua* and *Tandanus tandanus*) and a crustacean (*Macrobrachium australiense*). These dispersal events were critical to maintaining gene flow and genetic integrity due to the high frequency of extirpations and bottleneck events that isolate populations during dry periods.

Temporal macroscale interactions can occur where regional climate and weather patterns (e.g., temperature and precipitation) interact with local habitat to affect metapopulation dynamics. Griffiths et al. (2010) noted that inter-annual variation in rainfall can interact with local hydrology and influence the hydroperiod of temporary ponds. Fluctuations in rainfall can result in the water level of nearby ponds to vary asynchronously and affect the survival of amphibians such as crested newts (*Triturus cristatus*). Crested newts hibernate in terrestrial soil in winters and breed in temporary ponds in spring. Adult survival ranged from 25% to 80% over the 12 year study period, where low adult survival was associated with mild winters that resulted in warmer temperatures and more rainfall. The authors speculated that the changes in precipitation altered the local habitat to the point of affecting the crested newts' physiological needs. Warmer winter temperatures potentially disrupted winter hibernation causing individuals to use more energy. Since newts respire both across their skin and using lungs, wetter soils during hibernation could have also negatively impacted respiration, further contributing to lower survival and reproductive failure. The majority of patches experienced reproductive failure across most years—but a single successful patch with asynchronous dynamics relative to the other patches served as a source patch which allowed the metapopulation to persist.

Whether or not species' metapopulations persist ultimately depends on how their timing of dispersal and reproduction events correspond with landscape temporal structure (Reigada et al., 2015). The next section explores how species traits can be suited to these spatially and temporally variable environments.

Metapopulation persistence across space and time—species traits

In order for metapopulations to persist, species must be able to cope with both spatial and temporal variability. Spatial dispersal that connects populations within a larger metapopulation is a critical feature of metapopulation functioning, serving to rescue populations and reduce global extinction risk. Life history variation within populations—such as iteroparity or age complexity and overlapping generations—can also influence metapopulation functioning by generating asynchronous dynamics and reducing the probability of synchronous collapse.

In fact, many spatially structured populations have life history traits that spread extirpation risk across time and space (Buoro and Carlson, 2014). As an example, many harvested fish species are composed of multiple populations that differ in their dynamics. Such population diversity has consequences for resource flows to fishing communities via the portfolio effect, wherein the variability in the dynamics of the complex is lower than the variability in constituent populations, as exhibited in Bristol Bay sockeye salmon (*Oncorhynchus nerka*) (Schindler et al., 2010). Maintaining multiple populations that differ in their dynamics buffers the fishing community against stock fluctuations due to environmental variation and change (Hilborn et al., 2003; Schindler et al., 2010). Life history diversity that contributes to asynchronous dynamics could reflect local adaptations to environmental conditions (e.g., variation in spawn timing that reflects temperature variation, Lisi et al., 2013) or plasticity. Regardless, this population diversity reduces local extinction risk and stabilizes resource flows to consumers like fishers and predators (e.g., bears).

Environmental stochasticity can be an important driver of life-history evolution where iteroparous species may skip a breeding season if environmental conditions are unfavorable. Recent research has found this true in an amphibian metapopulation where among-year variability in pond characteristics resulted in life history variation in yellow-bellied toad (*Bombina variegata*) populations (Cayuela et al., 2019). The probability to skip breeding was higher in ponds with more variable hydroperiods. Similarly, a diversity of freshwater invertebrate species (including zooplankton, and odonates) can experience diapause, where development in offspring embryos is suspended during periods of unsuitable environmental conditions, such as drought (Bohonak and Jenkins, 2003). Long-lived and iteroparous freshwater fish species can also spread risk across multiple generations. Species that use multiple habitat types across their life histories, such as in diadromous species like salmonids, face multiple sources of risk across both time and space. Multiple cohorts in the ocean stage can compensate for reproductive failure in the freshwater stage. Spreading risk through space and time contributes to the resilience of a metapopulation and its ability to persist through disturbance and changes in the environment to some extent.

Anthropogenic impacts and conservation implications

To the extent that a particular freshwater taxon exists as a population of populations connected by dispersal, metapopulation theory has relevance for its management and conservation. Humans have dramatically changed landscapes in ways that have implications for metapopulation processes.

Habitat quality, size, and connectivity can all be altered by human disturbance, affecting metapopulation dynamics both at the local and regional scale (Fig. 2). Elimination or degradation of patches reduces connectivity and potentially persistence of whole metapopulations. Increased water use, sedimentation, and pollution can lower the quality of or eliminate patches, leading to a

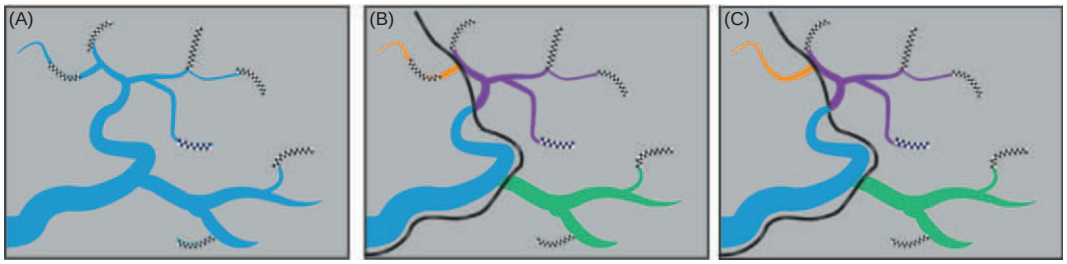

Fig. 2 Human disturbance can alter habitat quality, size, and connectivity and put metapopulation patches at increased risk of extirpation. For example, panel (A) shows a metapopulation within an intact watershed, with checkered areas signifying occupied patches (e.g., fish). In panel (B), a road (black line) is constructed across the watershed that blocks passage for fish between tributaries. The metapopulation patches are now fragmented into three regions (orange, purple, and green), resulting in some patches becoming extirpated (orange patch in panel (C)). Figure adapted from webinar by Jackson S (2006) *Ecological Considerations for Road Design at River and Stream Crossings [Webinar]*. US Forest Service. http://www.fsl.orst.edu/geowater/PEP/PEP_eco_consider.html (Accessed on 22 January, 2021).

reduction in capacity and a greater separation of populations by unsuitable habitat spaces. For example, historic strip mining and impoundments increased sedimentation and created large bodies of lentic waters, respectively in the Warrior River Basin, Alabama (Dodd, 1990). These human uses of the landscape led to large stretches of unsuitable habitat for stream-dwelling species such as the threatened flattened musk turtle (*Sternotherus depressus*), not only reducing available habitat but also increasing the distance of separation for remaining populations.

Barriers in rivers such as dams and culverts fragment populations and block dispersal between populations (Morita and Yamamoto, 2002). Individuals in isolated and small fragments have higher risks of extirpation because of disturbances, genetic drift, and environmental and demographic stochasticity (Shaffer, 1981). Anthropogenic alterations (e.g., dams) can lead to the permanent isolation of habitat patches and populations, which in turn has consequences for metapopulation persistence. Sink populations that typically inhabit smaller patches and are dependent on immigrants are especially vulnerable to extirpation from reduced connectivity (e.g., after a barrier is created). For example, in Hokkaido, Japan, white-spotted char (*Salvelinus leucomaenis*, resident and anadromous) were extirpated from upstream habitats after dams blocked connectivity, suggesting upstream populations are sink habitats that rely on immigrants to persist (Morita and Yamamoto, 2002). Although small sink populations are most dramatically affected by barriers, source populations and the metapopulation as a whole are also placed at greater risk of local extinction due to the lack of gene flow and the decreased potential for genetic and population rescue (Letcher et al., 2007).

Taken together, these anthropogenic impacts increase the risk of local extinction and often conservation intervention is needed to restore natural metapopulation processes. Restoring habitat patches and/or restoring connectivity among existing patches are strategies for reducing local extinction risk. Local habitat restoration in streams and rivers such as setting-back levees to expand floodplain patches and adding wood to re-configuring channels to create high quality pool habitats all hold potential for increasing the number and/or quality of habitat patches. Similar efforts within wetland ecosystems involve restoring existing wetland habitats (e.g., via dredging to improve drainage or removal of invasive vegetation to improve habitat quality) or creating new wetlands to mitigate pervasive wetland degradation and destruction. A synthesis by Brown et al. (2012) suggests that the restoration and creation of wetlands can be effective tools for increasing amphibian species richness and abundance, and that restored and created sites are as suitable as reference wetlands for supporting a suite of amphibians. A study by Lehtinen and Galatowitsch (2001) highlights that recently restored wetlands are rapidly colonized by amphibians, and that wetland size and spatial isolation were important predictors of species occupancy.

In addition to restoring or creating new habitat patches, enhancing connectivity can be an effective method of maintaining persistence of metapopulations if dispersal and/or gene flow are limiting. For example, restoring the natural hydrology and patterns of inundation and draining can influence connectivity and seasonal patterns of use by wetland-dependent species (Poff et al., 1997; Merenlender and Matella, 2013). More generally, restoration designs focused on connectivity vary by landscape and species of interest. Dams that inhibit connectivity can be circumvented by fish ladders and side-channels or be completely removed depending on their current function (Kondolf et al., 2006). Culverts that were previously designed to maximize hydraulic efficiency can be redesigned to facilitate movement of fishes between suitable habitats (Franklin and Bartels, 2012). A restoration design will no doubt affect the connectivity for species differently depending on life history, swimming ability, and spatial distribution (Wilkes et al., 2019). It is therefore critical for restorationists to understand the ecology of the species of interest and have defined targets/goals to help restoration designs achieve their desired outcome and to evaluate the success of those designs through post-project monitoring.

While restoring connectivity is the ideal outcome, often this may not be feasible due to logistics and/or costs. In instances where barriers to connectivity cannot be reversed, creative solutions must be applied if natural dispersal is not possible, given that artificial barriers can impact the genetic structure of a metapopulation. Permanent isolation can lead to the cessation of gene flow, resulting in a decrease in genetic diversity and an increase in inbreeding. These changes can lead to reduced fitness of the population and a greater risk of local extinction. Assisted gene flow in the form of translocations can help prevent the local extinction of small populations and can rescue populations from inbreeding depression and increase adaptive potential (Pavlova et al., 2015).

Translocations can rescue a population from local extinction by either increasing its size through demographic rescue or increasing population fitness by genetic rescue (Hufbauer et al., 2015; Whiteley et al., 2015). While demographic rescue can buffer against extirpation from stochastic events by increasing the number of individuals, genetic rescue can increase population fitness by reducing inbreeding.

The metapopulation approach is useful to conservation biology as it addresses restoring multi-scale processes to preserve dispersal and recolonization dynamics to minimize local extinction risk. Restoration and management efforts should focus on restoring and maintaining suitable habitat patches as well as connectivity among those patches. Careful consideration should also be given to maintaining habitat quality to increase survival of local populations. Moreover, maintenance of connectivity (or restoring connectivity) allows for dispersal and rescue effects to increase persistence of local populations and the metapopulation system as a whole.

Summary

In summary, it is evident that a diversity of freshwater systems can support spatially structured populations. The studies featured in this chapter highlight the importance of considering both spatial and temporal aspects of the environment when modeling metapopulation dynamics. Further synthesis efforts such as the one conducted by Smith and Green (2005) and Falke and Fausch (2010) are needed to better quantify the types and prevalence of metapopulation dynamics in freshwater habitats. Metapopulation theory has grown in relevance given the degree of habitat fragmentation and degradation observed in freshwater habitats that leads to human-induced spatially structured populations. In addition to understanding what regulates presence-absence and abundance of freshwater taxa, knowledge of dispersal, colonization, and extirpation rates is also required for successful conservation of spatially structured metapopulations.

Acknowledgments

This work was completed on the traditional homelands of the Ohlone people. K.C. Pregler was supported by a UC Berkeley Chancellor's Fellowship and E.K. Chen was supported by a California Sea Grant Fellowship during this work. We thank W.H. Satterthwaite for feedback on an earlier version of this manuscript.

See Also: Structures and functions of Inland Waters - Rivers: Dispersal in Stream Networks: Meta-populations and Meta-communities

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The Ecological Niche in Aquatic Ecosystems

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This is an update of W.M. Lewis, The Ecological Niche in Aquatic Ecosystems, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00204-0

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Competitive exclusion Elimination of one species population by another species population at a given location caused by competition between the two species.
Fundamental niche An ecological niche for a given species that is not restricted by competition with other species.
Niche All combinations of physical, chemical, and biological environmental attributes that are consistent with the sustained presence of a given species.
Niche overlap Components of an ecological niche for one species that are shared with those of another species.
Realized niche An ecological niche for a given species that is smaller than the fundamental niche because of competition from one or more other species.

Introduction

Niche, in everyday English usage, means a place or situation that is especially well suited to an individual or inanimate object. No doubt the word was used in this general way by ecologists before they began adapting its meaning to a more specific purpose, through the concept of ecological niche. Niche, defined ecologically, can be pronounced as a rhyme either with "rich" or "quiche."

J. Grinnell (1877–1939) was first to convert the niche in its generic sense to the niche as defined ecologically. Grinnell's ecological niche grew out of his observation, shared with other ecologists, that species are associated with specific ranges of environmental conditions that correspond to their spatial distribution in nature. Thus, Grinnell's niche was drawn from the idea that the persistence or success of a species in a given place is determined by a suite of environmental variables associated with that place.

Grinnell also explained that the distribution of a species within the range of environmental variables favorable to it is affected by the presence of other species. He drew the analogy of soap bubbles: a single bubble takes a symmetrical shape, but multiple bubbles are distorted as they press one upon the other. Thus, Grinnell foresaw the relevance of the ecological niche concept to the study of interspecific competition. In his classic book, *Principles of Animal Ecology* (1927), Charles Elton (1900–91) defined the ecological niche somewhat differently than Grinnell had (Elton 1927). He stated that the niche of an organism should be defined on the basis of processes rather than features of habitat. This was probably Elton's way of setting ecology apart from the dominant fields of taxonomy and natural history, which had emerged much earlier than ecology. Ecologists, according to Elton, want to understand the functions of organisms in relation to their environment and each other.

Ecological niche could have been a minor concept had it not been for the importance of interspecific competition in the development of ecology. In his studies of interspecific competition, G.F. Gause (1910–86), following the mathematically based predictions of V. Volterra (1860–1940), conducted experiments that demonstrated what became known as the "competitive exclusion principle." An example from Gause's work consists of an experiment in which two species of protozoan were held in a laboratory medium with a suspended food source (bacteria). Often one species declined to extinction, and thus was excluded from the habitat provided by the laboratory vessel. In some cases, two species coexisted because they showed reduced competition through differing adaptations. For example, one experimental contest of two protozoan species ended in coexistence because one species was adapted to feed on bacteria that had settled to the bottom of the vessel, whereas the other fed only on suspended bacteria. The general conclusion was that competition can exclude a competitor, but also coexistence of species can occur if competition involves the expression of differing requirements, i.e., differing fundamental niche dimensions.

Decades later, Hardin (1960) attacked the concept of competitive exclusion as a tautology, i.e., a self-evident truth. If so, the principle, while correct, would have little application to nature. It became increasingly clear as the study of competition progressed that different species, even if similar, do not occupy the same niche because they have different suites of adaptations; that environmental conditions change constantly, thus reversing competitive advantages from one species to another; and that environments in nature are heterogeneous spatially in a way that allows species appearing to be very similar to coexist indefinitely.

Ecologists now think in terms of niche overlap; the underlying scientific problem is to determine the degree of overlap that can produce strong competition. By wondering whether there may be empty niches in nature, Grinnell forecast modern thinking on the packing of apparently similar species together in a common environment such as the pelagic zone of a lake. Studies of population dynamics, viewed in large part through biological succession, also influenced the ecological concept of niche. In a famous paper entitled *Homage to Santa Rosalia*, G.E. Hutchinson (1903–91) pointed out that the pelagic zone of a lake or ocean is filled with dozens of species that have similar functions (e.g., all phytoplankton species in a given lake, or all herbivorous zooplankton species in a given lake, Hutchinson 1959). While the open water of a lake may seem similar to Gause's laboratory vessel, it is not. As Hutchinson pointed out, environmental conditions including temperature, nutrient availability, turbulence, and solar irradiance vary from week to week, allowing first one group of species to have an advantage, and then another. Competition in such a community does not go to completion because conditions are not stable.

Quantification of the ecological niche

The concept of ecological niche was modernized in 1957 by G.E. Hutchinson. One of Hutchinson's many gifts to the ecological sciences was his consistent use of quantitative tools in the formulation of ecological concepts. Such an approach opened new potential for old ideas, many of which had stalled in argumentation based on field observations and experiments. In essence, Hutchinson added a touch of something like physics to the rich mixture of taxonomy, natural history, population sampling, and field experiments that made up the bedrock of ecology in the first half of the twentieth century.

Hutchinson's idea of niche was that ecological space is defined by all environmental variables that have any influence on the welfare of a given kind of organism, including physical and chemical features as well as predation, parasitism, competition, and other biotic variables. Because more than three influential variables usually can be named for any kind of organism, the ecological niche space cannot be shown as a diagram or physical model; it has numerous ("*n*") dimensions, where *n* might not be known exactly but would be greater than 2 or 3. Hutchinson called the ecological niche defined in this way as an "*n*-dimensional hypervolume." The idea of dimensions exceeding three was unusual but not bothersome in 1957, by which time physicists had already conveyed at least to the science community that not only the three dimensions of space, but also time, a fourth dimension, define physical realities of the universe. Thus, conceptually, we may think of the ecological niche of a species as a hypervolume that has any number of dimensions, and all important factors affecting a particular species of organism are accounted for by it. With the *n*-dimensional hypervolume, Hutchinson generalized the idea of the ecological niche so that it would fit all species, regardless of the numbers or types of dimensions that might describe its requirements for persistence.

Elaborating on the *n*-dimensional niche concept, Hutchinson pointed out that there are actually two kinds of niches. The "fundamental niche," according to Hutchinson, is the *n*-dimensional hypervolume that could be occupied indefinitely by a species (Fig. 1). The "realized niche," in contrast, is the portion of the fundamental niche that can be occupied in the presence of other species that, by competition, allow the species to occupy only a portion of the fundamental niche.

It follows from Hutchinson's thinking that the realized niche is never greater than the fundamental niche and typically is smaller. Furthermore, the realized niche is site-specific. The realized niche of a weak competitor at a location with little or no competition could be quite large. On the other hand, the realized niche of the same species in a place with fierce competition could be small, even leading to the extirpation of the species population at that site.

It is clear from these examples that Hutchinson's redefinition of the niche offers many more possibilities than the earlier, simpler definitions. Like Grinnell's original concept, it invites a biogeographic interpretation and is based jointly on environmental variables and competition.

Current controversies surrounding the ecological niche concept

Analysis of competition and niche has moved in new directions over the last few decades (Hubbell 2001). Some ecologists have concluded that the niche has been overestimated as a determinant of community composition. S. Hubbell, for example, has proposed a "neutral theory of biodiversity and biogeography," one component of which is denial of the significance of niche for understanding the relative importance of a species at a given location. Hubbell's reasoning is that even species with very similar ecological requirements are sufficiently different to have offsetting advantages and disadvantages during competition. Thus, according to Hubbell, the distribution of species in relation to each other is much more a matter of chance than it is a reflection of the outcome of competition.

Modern analysis of the ecological niche has returned to some concepts that originated with C.S. Elton in the early twentieth century. As explained by Leibold (1995), the Hutchinsonian niche has as its basis the amount of environmental space that can be occupied by a species either with or without competition. In contrast, the earlier and simpler Eltonian concept is based conceptually

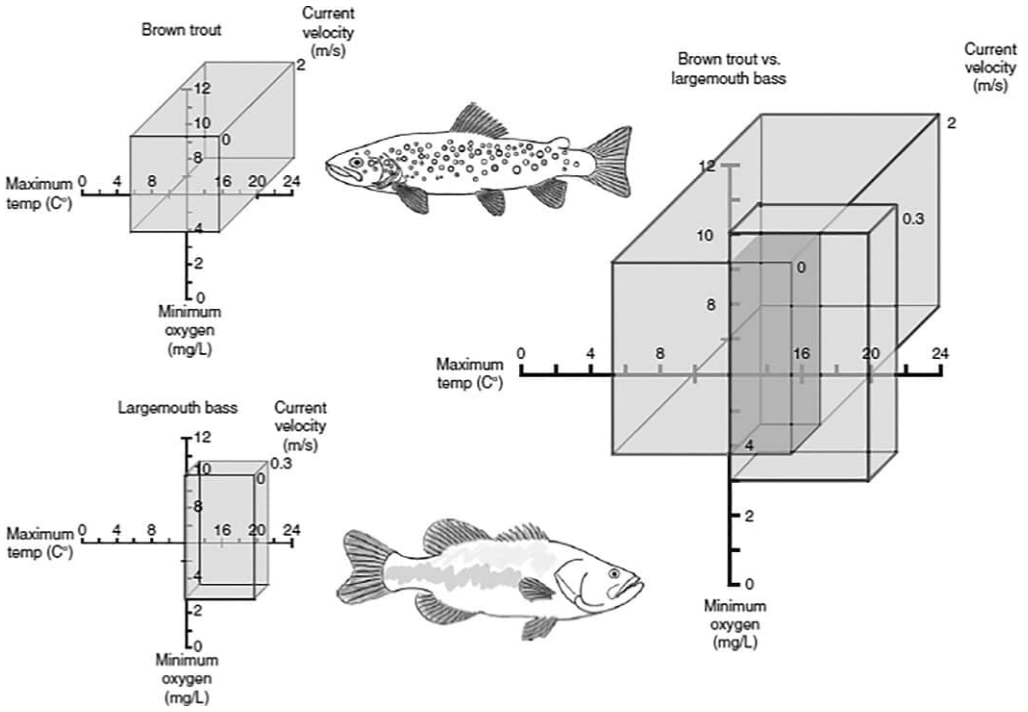

Fig. 1 A simplified depiction of niche space defined by three important environmental variables for a coldwater predator (brown trout, *Salmo trutta*) and a warmwater predator (largemouth bass, *Micropterus salmoides*). The fundamental niches are shown on the left, and their overlap is shown as the darkly shaded area on the right. More exact information on niche boundaries would most likely show the niche spaces as rounded and somewhat irregular rather than rectangular. The overlap shown on the right could lead to reduction of space (corresponding to the realized niche) for one or both species as a result of competition in a given ecosystem where the two species could occur together.

on the per capita effect (impact) that a given species has on the environment. The two concepts are related, but Leibold argues that a niche concept based on per capita effect leads to mechanistic (quantitative) analysis that is more realistic and therefore more productive.

Some ecologists also believe that the niche is a valuable determinant of species composition in communities of a given place, but they fault the original notions of niche for being overly vague about the means by which competition occurs. Chase and Leibold (2003) argue, as Hutchinson (1957) speculated, that the possibility of n dimensions for a niche is eclipsed by the likelihood that the distribution of a species is most likely defined by only two or three of the n dimensions. This re-examination of the Hutchinsonian model opens new possibilities for analysis because it presents the outcome of competition as a byproduct of a relatively small number of interaction types.

One further change in treatment of the ecological niche has been an increase in connectivity of the niche concept with other ecological concepts. Disturbance is one example; temporal changes at the ecosystem and community level explain why many species that might not coexist in a stable environment persist in an environment that is subject to constant change. Yet another example is the relationship between stability of an ecosystem or community and its number of species (species richness). The multiplicity of species occupying overlapping niches is viewed as a collective shock absorber that stabilizes ecosystems against externally induced change. Connection of the niche concept to a mechanistic understanding of ecosystems and communities insures that niche will continue to be a useful concept.

Aquatic ecological niches

Ecological niches are found in all types of ecosystems. At the level of concept or definition, there is no distinction between aquatic niches and terrestrial niches. Even so, aquatic environments are distinctive in that some (but not all) of the niche axes most likely to be important differ from those of terrestrial environments. Important dimensions of the ecological niche for aquatic organisms include temperature, dissolved oxygen, habitat structure, predation, and plant nutrients.

The range of temperature for aquatic ecosystems is much narrower than the range for terrestrial ecosystems because liquid water has a minimum temperature of 0 °C. Thermal thresholds are weak for phytoplankton and zooplankton, as shown by the distribution of species across wide ranges of latitude and elevation. Thermal thresholds are more important for large invertebrates and especially for fishes. For example, the family Salmonidae (salmon and trout) contains many species that are intolerant of waters

exceeding 15–20 °C. Similarly, perennially cool waters, such as montane or subarctic lakes, cannot sustain populations of many kinds of warmwater fishes, such as most species of the sunfish family (Centrarchidae).

Water holds only approximately 10 mg/L of oxygen at low temperatures and 6–7 mg/L at high temperatures. Thus, respiration can make water anoxic if it is not offset by photosynthetically produced oxygen or by contact of water with the atmosphere. High rates of respiration in water that is in contact with sediment, for example, can remove all oxygen from water in a matter of a few days.

Some aquatic environments are much more subject to oxygen depletion than others. Mountain streams of high gradient with low amounts of respiration are on one end of the spectrum, in that they have very little potential for oxygen depletion, whereas fertile lakes or wetlands, where there is much respiration and less efficient gas exchange with the atmosphere, show a much higher probability of oxygen depletion.

The distribution of organisms reflects in part their ability to tolerate oxygen depletion. Fishes, for example, show a wide range of tolerance to oxygen depletion. On one extreme are fishes that can obtain oxygen from the atmosphere (e.g., the tropical labyrinth fishes such as the betta, *Betta*) and fishes that have a small, upturned mouth capable of drawing oxygen from the top 1–2 mm of water in contact with the atmosphere (cyprinodont fishes, including the mosquito fish, *Gambusia*). Intermediate in tolerance are fishes that have no special means of obtaining oxygen, but have high physiological resistance to oxygen depletion (some catfishes, such as the bullhead, an ictalurid, *Ameiurus*, and the common carp, a cyprinid, *Cyprinus*). In contrast, other fishes are moderately or highly sensitive to oxygen depletion: trout and salmon, as well as largemouth bass (*Micropterus*), bluegill (*Lepomis*) and other sunfishes, and many others. Thus, the fish fauna of a particular waterbody reflects the likelihood of oxygen depletion. Invertebrates follow similar patterns. Aquatic larvae of midge species, for example, vary in oxygen tolerance, which explains their contrasting distributions in aquatic environments.

Habitat structure (cover) is a consistent component of most terrestrial environments; it is provided to a large extent by vegetation, which appears on all but the driest surfaces or on ice sheets. In contrast, the pelagic (open-water) environment of lakes provides no structure. Thus, organisms living in pelagic zones are specialized for living in an environment that lacks spatial stability and offers no refuge from predation. Variation in cover, ranging from the open waters of lakes and sandbed streams to richly vegetated littoral zones, vegetated wetlands, and rocky streams, offer a very wide range of possibilities for the niche axes that relate to habitat.

Limnologists and aquatic ecologists have shown repeatedly that predation has strong effects on the species composition of inland waters. Top predators are especially important in that they often remove or greatly suppress the abundance of their prey. Visual predators of lakes in particular may be much more efficient in eliminating their prey than would be the case in most other environments. In fact, some large invertebrates are unable to inhabit aquatic ecosystems that contain fishes. Small fishless lakes, for example, contain a rich abundance of large invertebrates that are not found in similar lakes that are stocked with fish. Thus, the niche dimension related to predation is critical to the distribution of many invertebrates.

Aquatic environments show an exceptional range of potential for producing autotroph biomass. Waters that have very low concentrations of nitrogen and phosphorus have production potential that falls well below that of any soil-based environment where moisture is present. In contrast, aquatic ecosystems with high concentrations of phosphorus and nitrogen have production potential for autotrophs that may be 1000 times higher than the least productive waters. Competition for nutrients is paramount in unproductive waters, which contain species having very high affinity for phosphorus and nitrogen. The most productive aquatic environments also support specialized taxa, but with different kinds of adaptations. Balance of nutrients may also be an important determinant of niche. For example, the nitrogen-fixing blue-green algae (heterocystous cyanobacteria) are, unlike other algae, capable of converting gaseous N2 to ammonia that can be used in making amino acids. When inorganic nitrogen is in short supply, these organisms are capable of continuing growth when other autotrophs cannot.

Conclusion

The ecological niche concept applies to all environments and should be seen as means of understanding the distribution and functional roles of species. Thus, ecological niche is a root concept for analysis of biodiversity, species distribution, ecosystem stability, and all other concepts that relate to the composition of communities. Critical niche dimensions of aquatic ecosystems provide some contrasts with terrestrial environments, and set the stage for comparison of aquatic ecosystems with other ecosystem types.

See Also: Structures and functions of Inland Waters - Wetlands: Boreal and Temperate River Wetlands; Riparian Vegetation of Gravel-bed Rivers - A Global Review

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Predation

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Attack efficiency The number of successful attacks divided by the total number of (successful plus unsuccessful) attacks.
Encounter rate The number of encounters between a predator and an individual prey per unit of time. An encounter is thereby defined as the arrival of the prey in the space where the predator is in principle able to detect it (Jeschke et al., 2002).
Functional response The functional relationship between (on the y axis) the number of prey that a predator consumes per unit of time (i.e., consumption rate) and (on the x axis) the abundance or density of its prey (Holling, 1959a).
Inducible prey defenses A prey defense (as defined below) that is phenotypically plastic. Such a defense is only expressed if a cue for the presence of predators is present, such as a chemical signal.
Invasive species Species that have successfully completed the invasion process, i.e., they have been (i) intentionally or unintentionally transported by human action from their native range to a new range, have been (ii) released there or escaped into the wild, have (iii) established one or more self-sustaining populations there, and have (iv) spread substantially beyond their point(s) of release or escape (Blackburn et al., 2011; Jeschke et al., 2013).
Permanent prey defenses A prey defense (as defined below) that is constitutive. Such a defense is always expressed, even if no cue for the presence of predators is present.
Predation cycle The process that a predator consecutively goes through when successfully hunting prey, consisting of the following steps: search, encounter, detection, attack, capture; if the predator is hungry again, the next cycle starts, beginning with search, encounter etc. (Jeschke et al., 2008).
Predator An organism that consumes other organisms (the prey) in part or completely, with the following conditions: (i) the organisms it attacks are alive (difference to detritivory), and (ii) it consumes many organisms during its lifetime (difference to parasitism). Predators can be categorized into: true predators, which typically kill their prey, and grazers, which remove parts of their prey but do not usually kill them (modified after Begon et al., 2005).
Predator confusion effect If a predator confronted with a swarm of its prey is limited by its neuronal abilities, resulting in a reduced attack efficiency (Krause and Ruxton, 2002; Jeschke and Tollrian, 2007). Predator confusion is a special type of swarming effect.
Prey An organism that is consumed by a predator (as defined above).

Prey defense Behavioral, morphological, physiological or life-history adaptation leading to a reduced likelihood that prey is killed or otherwise harmed by a predator.
Swarming effect If a predator confronted with a swarm of its prey is less successful at one or more steps of the predation cycle as compared to when being confronted with individual prey. Predator confusion is an example of a swarming effect.

Introduction

Predation is a classic species interaction that has been investigated for a very long time. Conceptually, predation is a +/− interaction that benefits one side, the predator, and harms the other side, the prey. In brutal reality, of course, prey is often not just "harmed" but killed. That depends on the type of predator: True predators are those that typically kill their prey, whereas grazers remove parts of their prey but do not usually kill them (modified after Begon et al., 2005). Species that first come to mind when imagining a "predator" are true predators, for example piscivorous fish species such as northern pike (*Esox lucius*) or zander (*Sander lucioperca*). However, fish and invertebrate predators that consume zooplankton (e.g., three-spined sticklebacks *Gasterosteus aculeatus* or tadpole shrimp *Triops cancriformis*) are, as defined here, true predators as well, and so are some herbivores (e.g., waterfleas *Daphnia* spp. consuming algae). Examples of grazers, as defined here, are in the terrestrial realm cattle and sheep; in fresh waters, examples include ducks, geese and swans that partly consume macrophytes.

Parasitism is a +/− interaction as well, where the parasite benefits from the interaction and harms the host organism. So how do parasites differ from predators? First, parasites have a much closer relationship to their host than predators have to their prey. Second, while predators feed on many organisms during their lifetime, parasites only have a limited number of hosts during their life. And finally, parasites do not usually kill their host; this last point is only a differentiation from true predators, not from grazers.

This chapter provides an overview of key concepts related to predator-prey interactions and illustrates them with examples: (1) the predation cycle and its stages search, encounter, detection, attack and capture; (2) prey defenses and how they can be classified based on the predation cycle, thereby also comparing inducible with permanent prey defenses, looking at aggregation as a defense and prey responses against specific vs. multiple predators; (3) predator offenses; and (4) predator functional responses with a focus on classic mathematical predator-prey models. In the chapter's final section, we turn to more applied questions related to predation in the Anthropocene, outlining how (5) predator-prey interactions are affected by anthropogenic stressors as well as novel predators and novel prey organisms.

The predation cycle

The predation cycle is a conceptualization of the consecutive steps that a predator goes through when successfully hunting prey (Fig. 1). First, the predator searches for prey. That means for cruising predators like a zander or crayfish that they are actively moving around to find prey. For ambushing predators like northern pike or *Chaoborus* (phantom midge) larvae, "searching" means waiting for suitable prey to swim by: fish for the pike, zooplankton for *Chaoborus* spp.

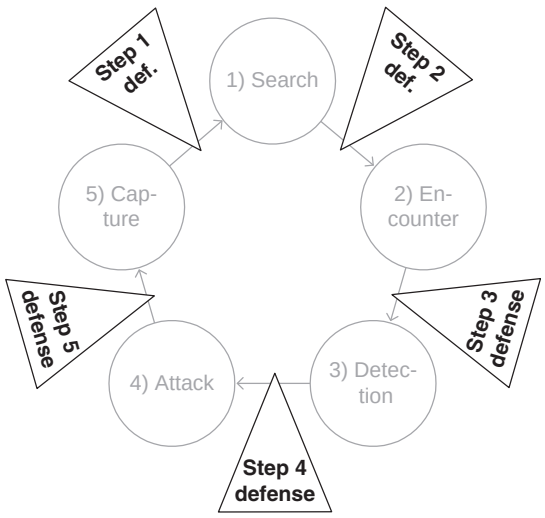

Fig. 1 The predation cycle consisting of the five steps search, encounter, detection, attack and capture. Prey defenses can be categorized according to the steps they interrupt.

Second, the predator encounters prey; that is, a prey item arrives in the space where the predator is, in principle, able to detect it (Jeschke et al., 2002). Again, such an encounter can be due to the active movement of a cruising predator and/or the movement of the prey, and strongly depends on the speed with which predator and prey move (Gerritsen and Strickler, 1977; Giguère et al., 1982). If the prey is immobile, e.g., a macrophyte, the predator obviously needs to move by itself in order to encounter prey.

Third, the predator detects prey. Predator species have different senses for prey detection. Many fish species, for instance, primarily rely on their eyes to detect their prey. They therefore hunt when and where light is sufficiently available. Other species, such as *Chaoborus* larvae, are mainly tactile predators that detect their prey, e.g., waterfleas, through their movement, leading to pressure gradients in the water. Chemical cues can also be very important for detecting prey, for example in catfish such as *Ictalurus punctatus*, which are sometimes called "swimming tongues" (Caprio et al., 1993).

Fourth, the predator attacks prey. Amazing organs and capabilities of predators have evolved, so that they can successfully transition through the predation cycle. At the same time, prey have evolved defense strategies to reduce the likelihood that they become a predator's next meal. Examples of such prey defenses and predator offenses are provided in the following two sections, so we only want to briefly mention here that well-known prey defenses reducing the likelihood of a predator attack are warning signals, such as bright coloration indicating toxicity.

Fifth and finally, the predator captures its prey. If it is still hungry or once it is hungry again, a new predation cycle starts.

Prey defenses

Prey defenses can be categorized according to different schemes. Here we outline (1) a classification based on the predation cycle, (2) inducible vs. permanent prey defenses, (3) aggregation as a defense and (4) responses against specific vs. multiple predators.

Classification based on predation cycle

Defenses are often classified according to the step of the predation cycle that they interrupt (Fig. 1). We outline such a classification in the following sub-sections, from step 1 to step 5 defenses, following Jeschke (2006) and Jeschke et al. (2008).

Step 1 defenses prevent search

Prey can prevent predators from searching, or increase the time period between a predator's last meal and its next search by way of: (A) Hardly digestible or toxic substances that increase predator digestion time and thus reduce the motivation to search for the next meal. In extreme cases, predators become sick or even die due to toxic prey substances. (B) Prey armor, weapons and flight behavior: they increase predator handling time, i.e., the time needed to attack, capture, and consume a prey individual.

Note that step 1 defenses are not advantageous for the consumed prey organisms themselves if they are killed by the predator. However, for prey of grazers (which only partly consume their prey), they can be beneficial on the individual level; macrophytes are a good example. Further, step 1 defenses can be evolutionarily adaptive in clonal prey such as *Daphnia* spp. (Fig. 2), or result from kin selection. Nonetheless, step 1B defenses are simultaneously and usually primarily step 5 defenses (see below).

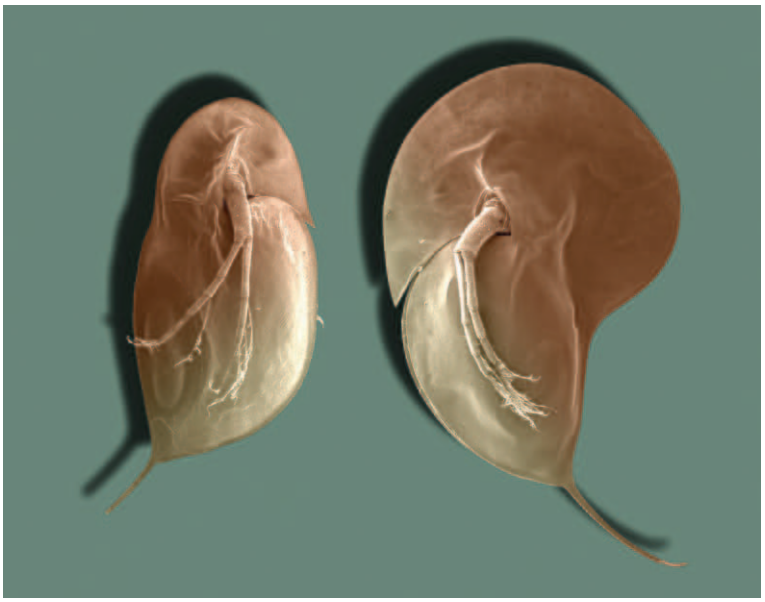

Fig. 2 *Daphnia longicephala* develop a large crest as an inducible step 1B, 5 defense which increases the handling time and reduces the attack efficiency of invertebrate predators (left: undefended morph, right: defended morph). © C. Laforsch.

Step 1 defenses are especially advantageous at intermediate prey densities: their effect is small at low densities, when predation rate is limited by other factors than handling or digestion time (namely by the encounter rate between predators and prey, the probability to detect and attack prey, and the probability that an attack is successful); at high prey densities, on the other hand, predation rate is limited by handling or digestion time, even if the prey are undefended (Jeschke, 2006). In other words, safety-in-numbers (also called the dilution effect, Hamilton, 1971) overrides the effect of step 1 defenses at high prey densities, making them unnecessary there.

Step 2 defenses prevent encounter

Defenses in this class prevent encounters with predators, i.e., prey are not within a predator's detection range. Examples are predator-avoidance strategies, such as hiding in refuges or diel vertical migration. The latter is performed by many aquatic invertebrates including *Daphnia* (Fig. 3): since visually hunting fish need light to successfully capture prey, they forage in the upper layers of the water body during the day. *Daphnia* can avoid them by spending the daytime in the lower layers of the water body and foraging for algae in the upper layers at night, when the fish are no danger due to the lack of light.

If prey move slowly or not at all, they also reduce the encounter rate with predators, especially when those predators move slowly or not at all themselves; the latter is true for ambush predators like northern pike or *Chaoborus* larvae (Gerritsen and Strickler, 1977; Giguère et al., 1982). A number of animals have evolved the ability to produce resting stages, e.g., *Daphnia* can produce resting eggs under unfavorable conditions. Although it might not be the foremost function of such resting stages, they can also serve as life-history defenses that avoid encounters with predators during periods of high predation risk.

Step 2 defenses are especially beneficial at low prey densities because the above mentioned dilution effect becomes stronger with increasing density and makes these defenses less advantageous under crowded conditions. The same is true for step 3, 4, and 5 defenses. Thus, defenses affecting the steps 2–5 are generally more beneficial at low than at high prey densities (Jeschke, 2006).

Step 3 defenses prevent detection

When being within the detection range of a predator, a prey individual can reduce the probability of actually being detected in several ways. Camouflage is the best known example of such a step 3 defense and is found in a vast number of animals, e.g., in mayfly, dragonfly or damselfly larvae (Ephemeroptera, Odonata). Freezing reduces the detection probability as well, and so does slow movement or sleeping—the latter is also a step 2 defense (see above).

Step 4 defenses prevent attack

Detected prey can avoid an attack by way of warning signals (aposematism), e.g., bright coloration as a sign of toxicity. Such warning signals are basically the opposite of camouflage, but are also widespread. Poison dart frogs (Dendrobatidae) and fire salamanders (*Salamandra salamandra*) are well-known examples. Aposematisms are often similar across prey species, so-called Müllerian mimicry, which increases recognition and avoidance by predators. Yet, warning signals offer opportunities for "cheating"

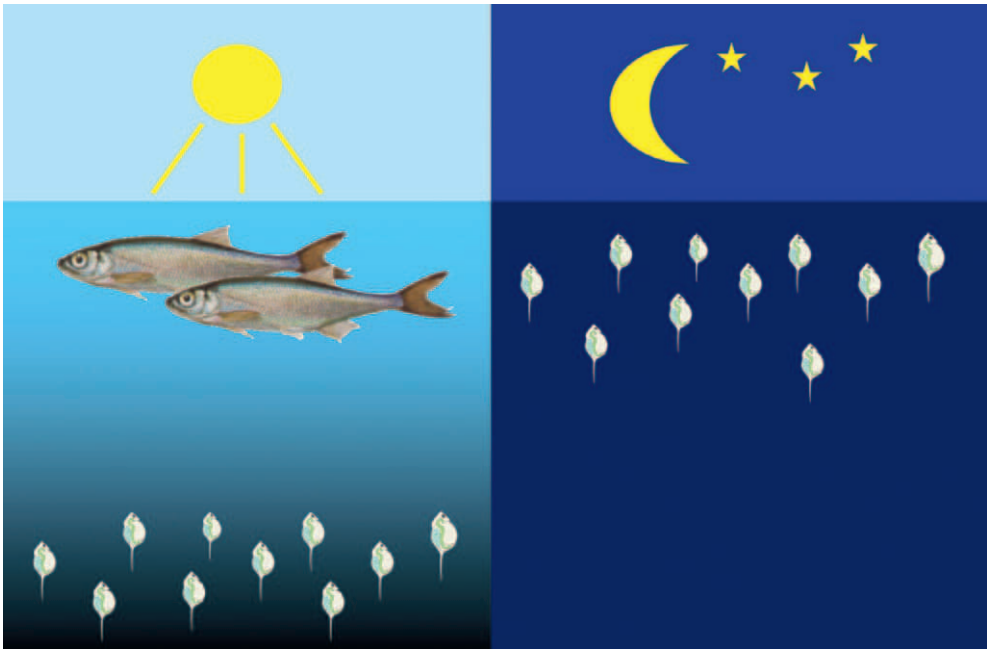

Fig. 3 *Daphnia* and many other planktonic species show diel vertical migration. During daylight hours (left side), they avoid the upper layers of the water body if they are populated by planktivorous fish during that time. At night (right side), the fish do not hunt due to the lack of light, so the *Daphnia* can migrate to the upper layers of the water body and forage for algae. Diel vertical migration avoids encounters with predators; it is an example of an inducible step 2 defense. © R. Tollrian.

species which are not poisonous but show the same appearance, so-called Batesian mimicry. A well-known example for insects are the black-and-yellow stripes of harmless hover flies (Syrphidae) resembling those of wasps and bees. An example for fish species is the appearance and behavior of juvenile grunt (*Pomadasys ramosus*) mimicking venomous juvenile leatherjacket (*Oligoplites palmeta*; Sazima, 2002). Finally, some prey species also warn acoustically. For instance, the tub gurnard (*Chelidonichthys lucerna*) produces sounds that resemble "grunts" when being confronted with a predator. These sounds are accompanied with visual warning signals—"raising of dorsal fin and spreading large and brightly colored pectoral fins" (p. 989 in Kasumyan, 2009).

Step 5 defenses prevent consumption

Defenses of this final category reduce predator attack efficiency, i.e., the probability that a predator attack is successful. Typical examples are flight behavior (most prey do that, unless they are immobile), armor (as in mussels, crayfish or *Daphnia*, Fig. 2), weapons (such as cnidocytes in cnidarians, Fig. 4; Tardent, 1995) and fighting. The latter is especially effective for grouped prey—for example, some fish species such as bluegill sunfish (*Lepomis macrochirus*) aggregate to mob predators away (Smith, 1992). Aggregated prey may also benefit from other swarming effects, as we further outline below.

Many aquatic predators are gape-limited and thus cannot mechanically handle prey beyond a certain size. For example, northern pike cannot ingest fish that exceed a certain height or breadth. Crucian carp (*Carassius carassius*) with a deep body are therefore effectively defended against this piscivore (Petersson and Brönmark, 1997). Similarly, *Daphnia* can allocate energy to growth instead of reproduction in order to outgrow the prey-size spectrum of *Chaoborus* larvae (Fig. 5), *Leptodora kindtii* and other gape-limited invertebrate predators. This energy-allocation strategy is also an example of a life-history defense (Fig. 6).

Step 5 defenses could in principle be further classified into defenses that prevent capture (e.g., flight) and those that prevent consumption (e.g., armor), but this distinction is often unclear. Recall that step 5 defenses also increase predator handling time, so they are also step 1B defenses.

Other classifications of defenses based on the predation cycle

Different authors have used different classification schemes of defenses based on the predation cycle, but they are largely similar. As in the above classification, defenses often fall into more than one category. This can be seen as a disadvantage, but it also expresses that many defenses function in several ways. Some classifications do not include defenses that prevent predators from searching (step 1 defenses according to the above terminology). For example, Edmunds (1974) divided defenses into primary and secondary ones, where primary defenses involve step 2, step 3 and step 4 defenses according to the above classification, and where secondary defenses equal step 5 defenses. Primary and secondary defenses have also been called pre- and post-contact defenses, respectively (Swift, 1992). Endler (1991) used the following categories: encounter defenses (= step 2 defenses); detection defenses (=step 3 defenses); identification defenses (= step 4 defenses); approach defenses and subjugation defenses (both together form the group of step 5 defenses); consumption defenses (similar to step 1 defenses).

Fig. 4 Charged and discharged cnidocytes. In addition to their offensive function as weapons for prey capture, they also defend cnidarians from being captured by predators and exemplify permanent step 5 defenses. © C. Laforsch.

Fig. 5 Phantom midge larvae (*Chaoborus* spp.) are gape-limited predators. © C. Laforsch.

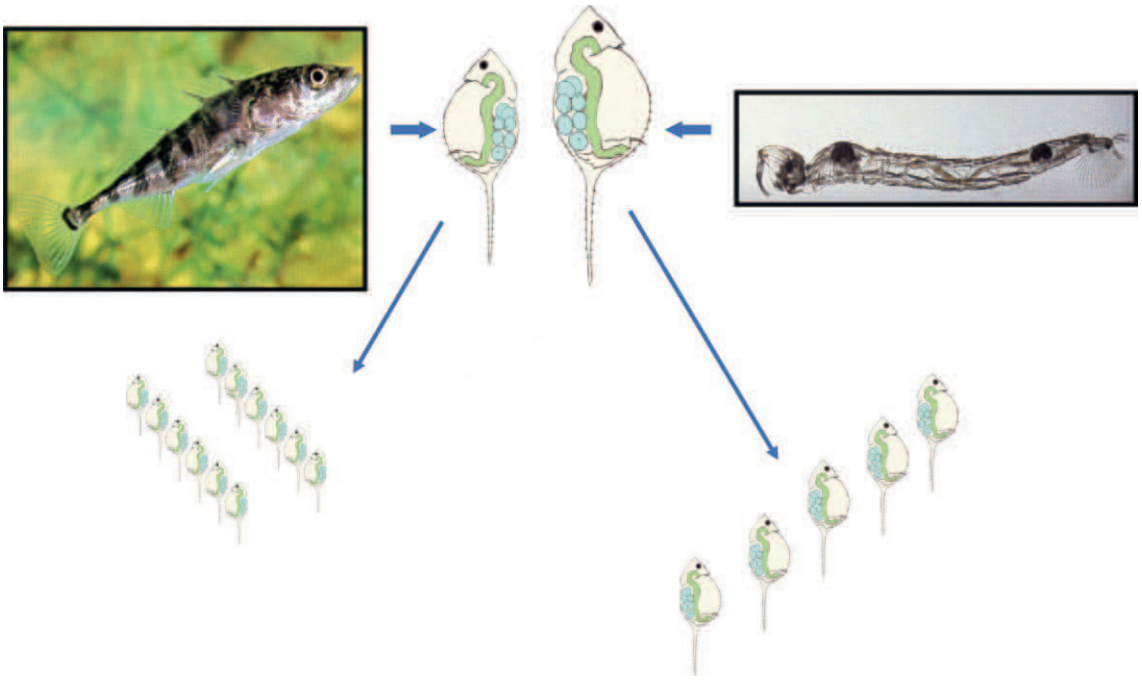

Fig. 6 *Daphnia* adaptively change their resource allocation between somatic growth and reproduction in response to cues from fish and gape-limited invertebrate predators (Stibor and Lüning, 1994). Fish consume larger size classes, so *Daphnia* invest less energy in somatic growth and more in reproduction if fish predation dominates. On the other hand, gape-limited invertebrate predators consume smaller *Daphnia*, so outgrowing their prey-size spectrum by investing much energy in somatic growth is an effective defense if invertebrate predation dominates. This resource-allocation shift is an example of an inducible step 5 defense that affects the prey's life history. © R. Tollrian.

Inducible vs. permanent prey defenses

Defenses can be permanent (i.e., constitutive) or inducible. The phenotypically plastic expression of defensive traits, i.e., inducible defenses, enables prey organisms to express a particular defense only if a reliable cue for a future attack is present (Tollrian and Harvell, 1999). Thereby, the organisms can minimize costs affiliated with the formation or maintenance of a defense when predation risk is low. Inducible defenses are an appropriate mechanism to cope with the variable hazard of a frequently changing predator spectrum. In the animal kingdom, inducible defenses are covering a taxonomic range from protozoans to vertebrates. The defensive traits range from behavior, morphology and life-history adaptations to the activation of the specific immune system of vertebrates. *Daphnia* show prominent examples of morphological plasticity triggered by chemical cues, so-called kairomones, released by predatory invertebrates and fish (reviewed by Tollrian and Harvell, 1999; Weiss and Tollrian, 2018; Diel et al., 2020). For example, elongated helmets, tail spines or crests have been shown to reduce predator-caused mortality (Fig. 2). Another example of inducible defenses is a deeper body shape of fishes, which is often an effective strategy against (gape-limited) piscivorous fish species (Petersson and Brönmark, 1997; Price et al., 2015).

Several factors have been identified that favor the evolution of inducible as opposed to permanent defenses: (1) the attacker has to have a variable but sometimes relevant impact; (2) the defense must be effective within a relatively short time, so lag phases can be avoided; (3) a reliable cue has to indicate the danger; and (4) costs have to outweigh the benefit of the defense during relevant periods of time (Tollrian and Harvell, 1999; Diel et al., 2020).

Aggregation as a prey defense

Aggregation can have several benefits. It can, for example, provide energetic benefits when swimming in a swarm as compared to swimming alone. It can also reduce the individual risk of being killed by a predator, simply because of "safety in numbers" (Hamilton, 1971). Such a dilution effect does not reduce the kill rate of the predator, but it is nonetheless a prey defense, as it reduces the likelihood that individual prey is killed or otherwise harmed by a predator.

There are also defenses where the kill rate of the predator is reduced. Such defenses are caused by swarming effects; here, a predator confronted with a swarm of its prey is less successful at one or more steps of the predation cycle as compared to when being confronted with individual prey. The following swarming effects can be discriminated:

- Early-warning or many-eyes effect: approaching predators are detected either with a higher probability or earlier by a prey swarm than by a single prey item (Pulliam, 1973; Godin et al., 1988).
- Encounter effect: the encounter rate with the predator is lower for aggregated than for individual prey (Englund and Harms, 2001).
- Confusion effect: a predator confronted with a swarm of its prey is limited by its neuronal abilities, resulting in a reduced attack efficiency (Krause and Ruxton, 2002; Jeschke and Tollrian, 2007). Empirical studies reviewed by Jeschke and Tollrian (2007) suggest that tactile predators and those visual predators that hunt highly agile prey frequently show a confusion effect, whereas visually hunting predators that focus on other prey do not usually have a reduced attack efficiency when being confronted with a swarm of their prey.
- Active defense effect: aggregated prey can defend themselves better actively than individual prey (Bertram, 1978).
- Clogging effect: if the filters of filter feeders clog in case of highly abundant food particles (Harbison et al., 1986).
- Toxin accumulation effect: predators suffer from an accumulation of prey-specific toxins (Halbach and Halbach-Keup, 1974).

All of these effects can lead to a reduced foraging success of the predator when prey aggregate. It is important to realize, however, that some predators can also benefit from prey aggregations. In particular, filter feeders such as *Daphnia* spp., silver carp (*Hypophthalmichthys molitrix*) or flamingos typically have a higher foraging success when encountering prey swarms (unless their filters clog), as their foraging strategy is optimized for prey aggregations.

Responses against specific vs. multiple predators

At first glance, some of the above-described defenses seem to be general defenses against predators per se. For example, the just mentioned swarming behavior will work against a large number of predators, not only one predator species. Similarly, some genera such as *Daphnia* enlarge their body size or the length of their appendages in the presence of many predation threats (Tollrian and Harvell, 1999; Weiss and Tollrian, 2018; Diel et al., 2020). A detailed look, however, reveals that this is only a rough approximation.

In many cases, defenses are evolutionarily tailored towards specific predators. Just recently, Kruppert et al. (2017) unraveled the mechanisms behind such a specific response in *Daphnia pulex* and *D. longicephala*: both species alter their carapace in the presence of their main predator, *Chaoborus* spp. and backswimmer *Notonecta* spp., respectively. While the former crushes its prey with its mandibles and needs to force it through the mouth opening (Schremmer, 1950; Kruppert et al., 2019), the latter pierces its prey's carapace and imbibes the externally digested, liquified innards (Dahm, 1972). While *D. longicephala* enhances the lamination of the layers of chitin fibrils forming its carapace cuticle, resulting in enhanced puncture resistance against *Notonecta*'s proboscis, *D. pulex* enhances lamination as well as carapace thickness, resulting in enhanced puncture and bending resistance, which complicates crushing and ingestion by *Chaoborus* spp.

Nevertheless, a variable impact is key for the evolution of inducible prey defenses, as mentioned above. Otherwise, the defense would evolve permanently. Such a variable impact does not necessarily result from fluctuations in one predator's abundance. More likely in nature are predator successions or varying predator regimes accompanied by fluctuating selectivity for different prey morphs.

Therefore, one-on-one interactions with a single threat are possibly rare in nature. Most of the time, the life of prey organisms may be jeopardized by a multitude of predaceous species, or predators in different life stages (Scharf et al., 2000). Such multipredator-prey-systems can be categorized as either functionally equivalent, functionally inverse or functionally diverse (Herzog and Laforsch, 2013). Depending on the system, a behavior, life history or morphology that is advantageous against one threat may be disadvantageous against another. Defenses that evolved via diffuse coevolution and function as a multitool against different predators are accordingly extremely useful. Again in *Daphnia*, we find two very impressive examples of such multitool defenses: *D. cucullata*'s helmet provides efficient defense against *Cyclops*, *Chaoborus* and *Leptodora* predation, acting on different ontogenetic stages and via different mechanisms (Laforsch and Tollrian, 2004), while the helmet formation in *D. lumholtzi* reduces predation rate in the presence of fish as well as *Chaoborus* (Engel et al., 2014). Interestingly, even seemingly very different morphological defenses can have a shared benefit, as for example in *D. barbata* (Herzog and Laforsch, 2013). This species is able to form different morphotypes against different predators, the tadpole shrimp *Triops* and backswimmer *Notonecta*. The defense against *Notonecta* was shown to be as advantageous against *Triops* as the specific defense, but not vice versa, even though there was still a small benefit compared to undefended individuals. Apart from the obvious costs of e.g., delayed reproduction, material investment into morphological structures or altered locomotion speed, the costs of being defended against the "wrong threat" are reduced through multitool-defenses.

Similarly, a defense against predators may have an additional benefit. For example, diel vertical migration (see above) in zooplankton is regarded as an avoidance strategy against visually hunting predators during daytime. However, it has been shown that an additional benefit in several *Daphnia* species is the avoidance of damage imposed by UV-radiation (Leech and Williamson, 2001; Rhode et al., 2001). A defense adjusted to the main threat(s) with an efficacy also against co-occurring dangers should therefore lead to the highest gain in fitness.

Predator offenses

While defenses are important for prey to protect themselves against predators, offenses are important for predators to avoid starvation. Similarly to prey defenses, predator offenses can be classified according to the steps of the predation cycle they affect (Jeschke, 2006).

Step 1 offenses reduce the time between the end of one predation cycle and the beginning of the next one, i.e., when the predator starts searching for its next meal. Examples of such offenses are physiological adaptations that reduce predator digestion time, or morphological adaptations that reduce handling time. Extreme cases are some filter feeders, such as *Daphnia*, with a morphology that allows them to simultaneously handle and search for (i.e., filter) food.

The benefit that a predator has from such step 1 offenses in terms of an increased consumption rate is particularly high at high prey densities (Jeschke, 2006). On the other hand, step 2–5 offenses, which are outlined in the following paragraphs, have a maximum effect at intermediate prey densities; this is because their effect is overridden at very high prey densities, where consumption rate is mainly determined by digestion time or, depending on the predator, handling time (Jeschke, 2006; see also the following section on predator functional responses).

Step 2 offenses increase the encounter rate with prey, for instance by means of an increased foraging speed or an enlarged encounter volume. Cruising predators, such as zander, benefit from such an offense. Long-distance senses are another example.

Step 3 offenses increase the probability that a predator detects prey it has encountered. Senses with high spatial resolution, such as sharp eyes or elaborated mechanosensillae as in *Notonecta* (Mail et al., 2018) are good examples of such an offense.

Step 4 offenses increase the probability that a predator attacks prey it has detected. This is particularly relevant in connection with aggressive, toxic or in other ways dangerous prey: if the predator is at least partly protected against such prey, it is more likely to take the risk and attack it.

Finally, step 5 offenses increase the likelihood that a predator attack is successful. Attack efficiency can, for example, be increased by a high acceleration when prey is attacked: northern pike have been reported to have an astonishing strike acceleration of 55 m/s^2 (Schriefer and Hale, 2004). Another good example is the explosive discharge of cnidocytes in cnidarians (Fig. 4; Tardent, 1995).

Predator functional responses

The functional response of a predator describes the relationship between the number of prey it consumes per unit of time and the abundance or density of its prey (Solomon, 1949; Holling, 1959a). This is another classic concept related to predation and highly important for several fields of research, for example for behavioral, physiological and evolutionary ecology, as functional responses and corresponding models capture key elements of foraging ecology (cf. Stephens and Krebs, 1986), digestion and fitness-related factors (e.g., the survival of prey). Given that functional responses epitomize the density-dependence of trophic relationships, they

are also highly important for predicting population dynamics whenever two or more trophic levels are present in a food web, which is of course almost always the case under natural conditions.

What do functional responses graphically look like? While predator consumption rate typically shows a monotonic increase with prey density, the exact shape of this increase varies and has been categorized into three main types (Fig. 7; Holling, 1959a; Jeschke et al., 2004): in type II functional responses, consumption rate shows a curvilinear increase; in type III functional responses, the increase is sigmoid; and in type I functional responses, the increase is linear until a threshold prey density is reached, beyond which consumption rate remains constant. For each of these three types, a dome-shaped variant is possible where consumption rate does not monotonically increase with prey density, but instead declines at high densities (Fig. 7; type II dome-shaped, type III dome-shaped, type I dome-shaped; Jeschke et al., 2004).

The most frequently observed type of functional response is the type II. This is particularly true for non-filter feeders. Reviewing 814 individual functional responses measured in 235 empirical studies, Jeschke et al. (2004) found for non-filter feeders (n = 449 studies) a frequency of 77% for type II, 13% for type III, 8% for dome-shaped functional responses and 3% for type I. For filter feeders, though (n = 365 studies), the type I was most frequent with 37% of the functional responses, followed by type II with 29%, type III with 25% and dome-shaped functional responses with 13%.

Functional responses have not only been measured for several decades, there also exist quite a number of functional response models (reviewed in Jeschke et al., 2002). The most influential model has been Holling's (1959b) classic disc equation:

$$y = \frac{a \cdot x}{1 + a \cdot b \cdot x}, \tag{1}$$

where y is consumption rate, a is predator success rate, x is prey density and b is predator handling time (Holling used a slightly different notation). Predator success rate a can be derived from the predation cycle, as it is the product of (i) encounter rate, (ii) the probability that the predator detects prey it has encountered, (iii) the probability that the predator attacks prey it has detected and (iv) attack efficiency. Similarly, predator handling time b is the sum of the time needed (1) to capture a prey item (including time wasted for unsuccessful attacks) and (2) to consume a prey item (Jeschke et al., 2002).

Predator consumption rate is at low prey densities mainly determined by predator success rate—and thus, by its components representing the different transitions in the predation cycle. At high densities, however, it is mainly determined by digestion time and handling time, more specifically by the longer of the two processes (digestion or handling), at least under circumstances where predator satiation and thus digestion are relevant. Most predators need more time to digest than to handle their prey (Jeschke et al., 2002), thus their long-term maximum consumption rate depends on their physiological digestion capacity. Short-term maximum consumption rates, where satiation does not kick in, can be higher—these are usually determined (in other words: limited) by handling time.

Handling and digestion time are also the reason why a type II functional response has a curvilinear shape: with increasing prey density, the predator spends an increasing amount of time handling and digesting prey; thus, the curve increasingly flattens. A key point here is that predators showing type II functional responses can typically either search for or handle prey, but they cannot do both simultaneously; this is also an assumption underlying Holling's disc equation. Other predators, which can search for and handle prey simultaneously (e.g., filter feeders such as *Daphnia* spp.) frequently show a type I functional response which does not flatten with an increase in prey density; here, consumption rate increases linearly to a certain point at which satiation kicks in and abruptly limits consumption rate. Type III functional responses result from a density-dependent effect. For example, if a given prey

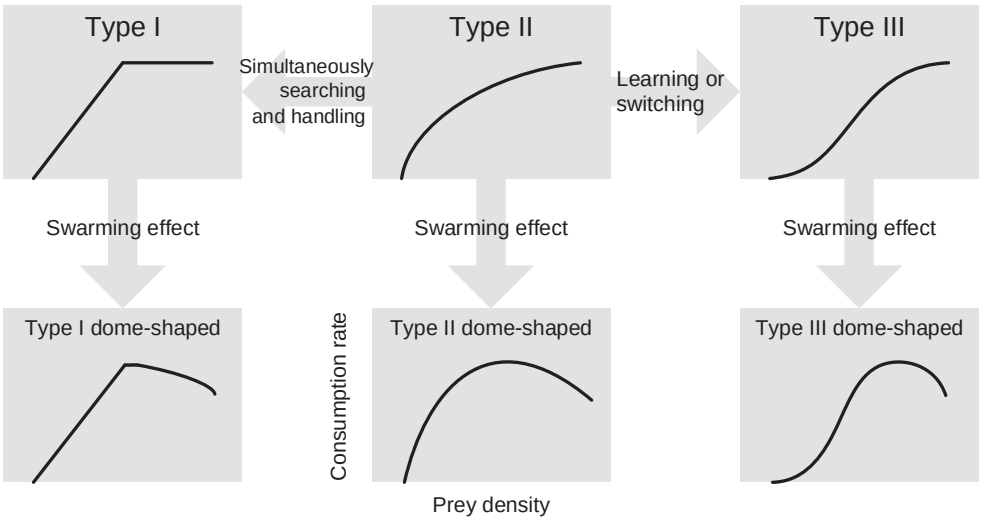

Fig. 7 Different types of functional response. Modified after Jeschke, J. M., Kopp, M., Tollrian, R., 2004. Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biological Reviews 79, 337–349.

species reaches a high density and predators learn to better detect (e.g., through developing a search image) or more efficiently attack this prey, then success rate *a* increases with prey density; this, in turn, leads to a sigmoid shape. Similarly, some predators switch from a sit-and-wait to a cruising foraging tactic when prey density increases (reviewed by Helfman, 1990), which also leads to a type III functional response. Finally, dome-shaped functional responses result from swarming effects, which are characterized by a reduced success rate at high prey densities (see above).

Predator-prey interactions in the Anthropocene

How anthropogenic stressors affect predators and prey

At least since the industrial revolution, anthropogenic activities (see Fig. 8) have massively impacted freshwater ecosystems and predator-prey interactions within those systems. Due to space limitation, we can only highlight some of these anthropogenic stressors here.

Private and industrial disposal of pharmaceuticals and personal care products (PPCP) (number 1 in Fig. 8) combined with the inability of sewage plants to remove all these compounds have been found to lead to residues of these often water-soluble chemicals in waterbodies, where they can affect freshwater organisms (Kreke and Dietrich, 2008; Hedgespeth et al., 2014). For example, drugs can mimic infochemicals, disrupt signal production/transduction pathways or interfere in other ways with the chemical communication of predator and prey organisms (Van Donk et al., 2016). Specifically, the antidepressants fluoxetine, venlaflaxine and bupropion, which are selective serotonin reuptake inhibitors (SSRIs), were found to slow down the escape behavior of larval fathead minnows (*Pimephales promelas*) (Painter et al., 2009). Sertraline, another SSRI, was found to decrease the feeding rates of Eurasian perch (*Perca fluviatilis*) consuming *Daphnia magna* (Hedgespeth et al., 2014).

Anthropogenic stressors derived from intensive agriculture (number 2 in Fig. 8), such as pesticides and nutrient input, can impact freshwater predator and prey organisms even more strongly. The rotifer *Brachionus calyciflorus* was found to express increased transgenerational costs, i.e., a reduced population growth rate, for its morphological defenses against its predator, the rotifer *Asplanchna girodi*, when exposed to the pesticide Methamidophos (Heine-Fuster et al., 2017). The indicated study further showed that pesticides might even affect future generations. A pesticide-related increase of the costs for predator-induced defenses was also found in *D. magna* preyed on by the brown trout (*Salmo trutta*) during exposure to Imidacloprid (Pestana et al., 2010). Furthermore, the authors detected that the pesticide compromised the predator-induced life-history defenses of the daphnids. The functional

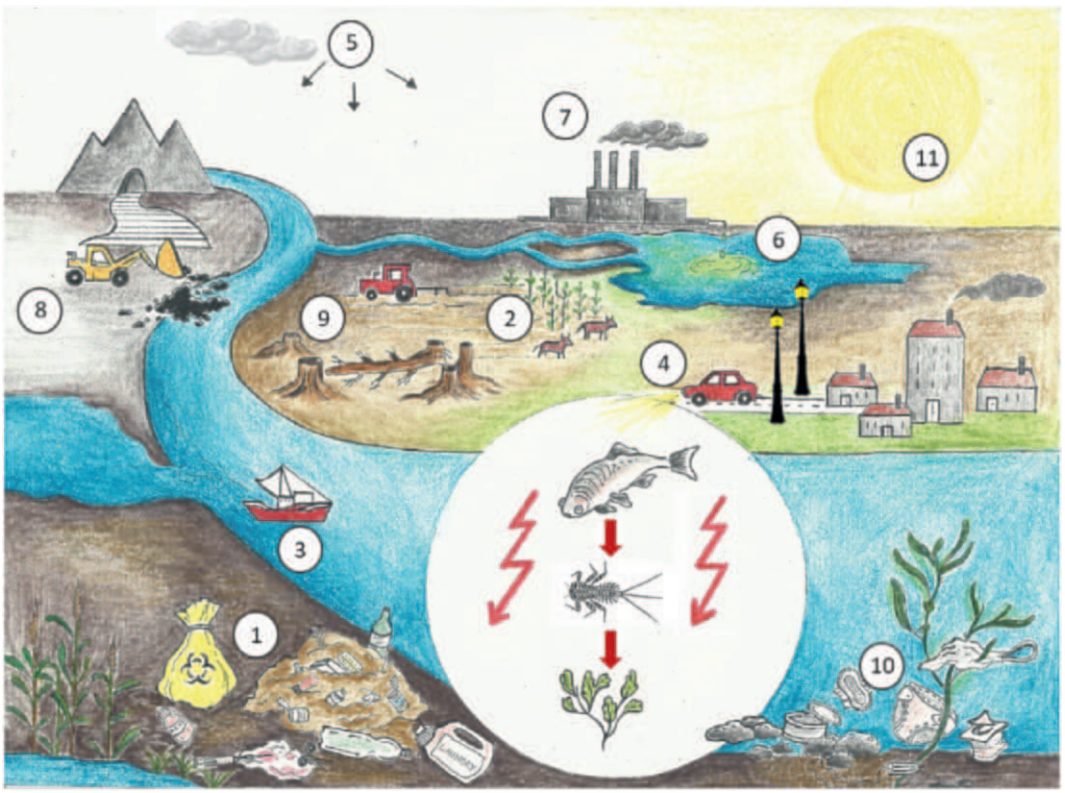

Fig. 8 Examples of anthropogenic stressors for freshwater bodies: (1) pharmaceuticals and personal care products, (2) intensive agriculture, (3 + 4) transportation, (5) acidification, (6) artificial light at night, (7) industrial manufacturing, (8) mining, (9) logging, (10) particulate contaminants, (11) climate change. Details on each stressor are provided in the main text, where we also outline the important, yet insufficiently understood, integrated effects of multiple stressors.

mechanism behind the pesticide-related changes is supposedly the inhibition of acetylcholinesterase, leading to an increased duration and strength of neurotransmission (Heine-Fuster et al., 2017). This changes the activity of the affected animal and also likely leads to life-history changes. Additionally, this effect can be transferred onto coming generations by the inhibition of acetylcholinesterase in the developing oocytes. Especially since *Daphnia* is a keystone genus in a multitude of freshwater bodies, this reaction to pesticides potentially leads to negative consequences for the communities in these ecosystems.

Further, there are a number of stressors related to transportation, for instance via waterways (number 3 in Fig. 8) or roads (number 4). Enhanced levels of salinity, which can be caused by road salt, were found to weaken life-history defenses of *D. pulex* against *Chaoborus americanus* (Liu and Steiner, 2017). Road salt can also cause a mobilization of heavy metals from roadside soils (Schuler and Relyea, 2018). When the combination of these chemicals arrives in adjacent water bodies, e.g., through precipitation, the toxicity of heavy metals is likely to rise as well, and trophic interactions can be strongly compromised. Another example for a transportation-related stress factor is noise. The European minnow (*Poxinus phoxinus*) reduces its attack rate and shows specific stress-related behavior when confronted with motorboat noise (Hanache et al., 2020). Resulting from the combination of aerial pollution through transportation, e.g., via cars, and industrial burning of fossil fuels, acidification (number 5 in Fig. 8) can impair predator-prey interactions as well. For instance, rainbow trout (*Oncorhynchus mykiss*) and brook charr (*Salvelinus fontinalis*) were found to have a reduced detection capability and responsiveness to conspecific alarm cues in reaction to small amounts of sulfuric acid, which is a known chemical substance associated with acidic rain (Leduc et al., 2004). The effect of acidification on freshwater fish may be related to a chemical change in the alarm cue and/or the inhibition of the chemosensory pathway (Leduc et al., 2013). In addition, transportation often requires artificial lighting (number 6 in Fig. 8), which can distort diel rhythms of organisms. Becker et al. (2013) also indicate that light pollution is in some areas likely to induce top-down trophic pressure on freshwater communities, through attracting prey organisms at night, which in turn allows predatory fish to hunt at night. Of course, transportation is not the only reason for artificial light at night—others are, for example, an increased security, or aesthetic or commercial reasons. Finally, transportation can lead to the arrival of invasive species that affect resident predator and prey organisms (see below for details).

Industrial manufacturing (number 7 in Fig. 8) and mining (number 8) can also affect predator-prey interactions, particularly due to an increase in the concentration of heavy metals in aquatic systems. For example, copper was found to affect the neckteeth induction in *Daphnia pulex*, possibly due to an inhibited kairomone reception pathway or an impaired neckteeth induction (Hunter and Pyle, 2004). Clements et al. (1989) found copper to increase the predation risk of caddisflies under predation pressure by the stonefly *Paragnetina media*. The authors attributed this partly to a suspected behavioral change of the prey organisms. A further chemical anthropogenic stressor for some freshwater predator-prey interactions is acid mine drainage. Hogsden and Harding (2012) highlighted fundamental alterations in the food-web composition and interactions in affected streams. They outlined that the reduced primary production in these water bodies is followed by an absence of herbivores, making invertebrates the top predators of these communities' food webs, as fish are rather lost due to acidification.

Logging (including removing trees including their roots, which is called whole-tree harvesting, WTH; number 9 in Fig. 8) can also affect predator-prey interactions in freshwater bodies. Trees act, in combination with base cation pools in the ground, as chemical buffers in many ecosystems. Through WTH, base cations are withdrawn from the soil, which can lead to a critical reduction in cation input into nearby water bodies (Watmough et al., 2003; Cox et al., 2018). When faced with reduced calcium concentrations, *D. pulex* are less capable of morphologically defending themselves against *Chaoborus* spp. (Riessen et al., 2012). Logging can also increase sediment input and turbidity, impeding fish and other visually oriented predators and prey. For example, increased turbidity was found to reduce the reactive distance of foraging rainbow trout (*Oncorhynchus mykiss*, Barrett et al., 1992) and coho salmon (*Oncorhynchus kisutch*, Berg and Northcote, 2011).

Some of the above-mentioned activities (numbers 1, 2, 3, 4, 7 in Fig. 8) additionally produce particulate contaminants (number 10), such as nanoparticles or plastic debris, as a novel suite of environmental stressors. Trotter et al. (2019) found plastic waste to negatively impact induced morphological and life-history defenses of *D. longicephala* against the predatory backswimmer *Notonecta glauca*. The plastic waste seems to adsorb kairomones emitted by *N. glauca*, thus reducing the amount of detectable infochemicals for *D. longicephala*. Any misperception of predator composition or density can have consequences on the population level and may even affect the whole food web.

The final stressor we are highlighting here is climate change (number 11 in Fig. 8), which is caused by a multitude of anthropogenic activities including those mentioned above. Grigaltchik et al. (2012) found that warm-acclimated Australian bass (*Macquaria novemaculeata*) interacting with eastern mosquitofish (*Gambusia holbrooki*) as prey launch more attacks and have a higher overall hunting success than cold-adapted individuals. However, the speed and number of attacks declined at very high temperatures, whereas the escape speed of mosquitofish increased, leading to an advantage of the prey at high temperatures. Solely rising pCO_2 levels without changing temperatures was also shown to have the potential to disrupt predator-prey-interactions, e.g., in *Daphnia* (Weiss et al., 2018). This variation in species reactions to temperature and rising pCO_2 levels illustrates how predator-prey interactions can be affected by climate change.

It is even more complicated when integrating the above anthropogenic activities and resulting stressors, plus those we did not outline here. This is a pressing task for science, as the diversity and magnitude of stressors has rapidly increased in the Anthropocene (Steffen et al., 2015; Waters et al., 2016). Moreover, while real ecosystems are faced with many anthropogenic stressors simultaneously, studies combining them are rare (Mazor et al., 2018). Based on a functional response approach and focusing on the copepod *Lovenula raynerae* preying on mosquito larvae (*Culex pipiens*), Cuthbert et al. (2019) found interacting effects of salinization

and warming on predator-prey interactions. Even more integrative studies are needed to better understand the combined effects that multiple stressors have on freshwater systems.

Novel predators and novel prey

Novel organisms are those organisms that have either been introduced by humans beyond their native range (non-native species, also called alien species), have expanded or shifted their range due to climate change (range-expanding species, also called neonatives, Essl et al., 2019), have recently emerged as new pathogens (emerging pathogens), have been modified genetically (GMOs) or even been created synthetically (synthetic organisms), typically by building their genomes with short DNA sequences called "BioBricks" (Jeschke et al., 2013). Novel organisms can heavily affect freshwater (and other) systems (e.g., Pyšek et al., 2020), and we here focus on the impacts of non-native predators and prey on resident prey and predators, respectively.

First, non-native predators can affect native prey species in various ways. Such impacts are often particularly strong if the prey species is evolutionarily naïve to the archetype represented by the predator—in other words, if the prey species lacks eco-evolutionary experience (Saul and Jeschke, 2015). Some prey species cannot detect cues from non-native predators (Carthey et al., 2017). For example, when exposed to the invasive red-eared slider turtle (*Trachemys scripta* elegans), three out of four European tadpole species did not reduce their swimming speed. They did, however, swim more slowly when exposed to native predatory turtles (Polo-Cavia et al., 2010). Furthermore, prey species can be poorly defended against novel predators (Weis, 2011). The introduction of the predatory spiny water flea (*Bythotrephes longimanus*) led to a decrease in many cladoceran species, because it preys on small instars of daphnids, whereas the native predator *Leptodora kindtii* preys only on later instars (Branstrator, 1995; Barbiero and Tuchman, 2004). Another invasive invertebrate predator is the freshwater amphipod *Dikerogammarus villosus*, called the "killer shrimp." Compared to native species, *D. villosus* consumes more prey (approximately one-third of their body weight per day) and feeds on other amphipod species as well as on fish larvae, which can lead to cascading effects in the food web (Krisp and Maier, 2005; Casellato et al., 2007).

Second, non-native prey have been shown to defend themselves against native predators in various ways, e.g., by way of habitat change, novel secondary metabolites or morphological defense structures (Bollache et al., 2006; Schultz and Dibble, 2012; Engel et al., 2014). These defenses can have strong impacts on resident predators, especially if they are novel for the community, so that the resident predators lack eco-evolutionary experience in interacting with such prey (Saul and Jeschke, 2015). For example, the invasive amphipod *Gammarus roeseli* has spines on the back, whereas the native *Gammarus pulex* shows no such morphological defenses (Bollache et al., 2006; Copilaș-Ciocianu et al., 2020). Another example is the invasive waterflea *D. lumholtzi*, which is known for its unique head and tail spines that serve as effective protection against both invertebrate and vertebrate predators (Kolar and Wahl, 1998; Engel et al., 2014).

These direct impacts of non-native predator and prey species often lead to indirect effects on other organisms and can restructure entire food webs (David et al., 2017). Continuing with the example of *D. lumholtzi*, if fish species cannot feed on these heavily armored daphnids, they may preferentially consume and thus reduce the density of native zooplankton species (Kolar and Wahl, 1998). It is also possible that biological invasions lead to new trophic interactions in already disturbed ecosystems. The invasive zebra mussel (*Dreissena polymorpha*), for instance, is a prey species of the invasive round goby (*Neogobius melanostomus*; Ray and Corkum, 1997). In Lake Erie, the round goby is in turn consumed by the native water snake *Nerodia sipedon insularum* (King et al., 2006). While this is as such beneficial for this endemic and threatened snake species, the gobies form a more contaminated diet than the snake's previous prey species (Fernie et al., 2008).

Conclusions

Predation is a classic topic for researchers investigating the ecology of freshwater organisms. Accordingly, countless studies have been published on predator-prey interactions in inland waters. In this chapter, we provided an overview of important long-standing concepts related to predators and their prey. We also outlined how predator-prey interactions are affected by the multitude of human actions in the current era, as this is a research topic where many pressing questions lack adequate answers. Work that is currently being done in this context draws on classic predation studies. A good example is the concept of predator functional responses and corresponding mathematical models (see above). This work, which was initiated in the mid-20th century (Solomon, 1949; Holling, 1959a,b), is the foundation of a fruitful line of research that is now investigating biological invaders and their interactions and impacts in the ecosystems where they were introduced (e.g., Dick et al., 2014; Cuthbert et al., 2019; Dickey et al., 2020; Linzmaier and Jeschke, 2020).

Knowledge gaps

- Many aspects of predation are better investigated in terrestrial than in aquatic systems.
- Carnivorous plants, such as *Utricularia* and *Aldrovanda*, can be quite important freshwater predators (Poppinga et al., 2017; Horstmann et al., 2019), but so far fly under the radar of most freshwater ecologists.

- Predator-prey-interactions are rarely mechanistically understood, which impairs our capability to make adequate predictions for their future dynamics, especially when being faced with anthropogenic stressors.
- Many anthropogenic stressors (e.g., most synthetic chemicals; Bernhardt et al., 2017) are rarely or not at all investigated. This is partly due to some of the stressors' novelty, but also due to topical research biases (cf. Jeschke et al., 2019).
- Our understanding of multi-stressor effects has remained even more limited.
- Similarly, there is a lack of knowledge about the impacts of non-native species in freshwater systems and how they change through time.
- There is even less knowledge about the impacts of other novel organisms (particularly genetically modified and synthetic organisms, see Jeschke et al., 2013) on predator-prey interactions and food webs in inland waters.

Acknowledgments

Some text and figures of this chapter were taken from Jeschke et al. (2008); these parts (text mainly in sections "Classification based on predation cycle" and "Inducible vs. permanent prey defenses", and Figs. 1–6) were revised and updated where appropriate. The other parts of the current chapter were freshly written and created. We thank Lars Rudstam and Thomas Mehner for the invitation to contribute this chapter and for helpful comments and suggestions. JGPD acknowledges financial support from the German Environmental Foundation (DBU; AZ 20017/509).

See Also: Fundamental concepts and theories: Bioenergetics; Structures and functions of Inland Waters - Groundwater: "Importance of the Micro-scale for the Macro-scale—What Can We Learn From Groundwater Ecosystems?"; Structures and functions of Inland Waters - Lakes: Predation on Zooplankton; Lake Food Webs; Structures and functions of Inland Waters - Rivers: Ecological and Evolutionary Consequences of Disturbance in Freshwater Ecosystems

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Earth's Freshwater—National Geographic: https://www.nationalgeographic.org/media/earths-fresh-water/?utm_source=BibblioRCM_Row
Food web: concept and applications: www.nature.com/scitable/knowledge/library/food-web-concept-and-applications-84077181
High speed footage of *Chaoborus* larvae preying upon defended and undefended *Daphnia pulex*: https://figshare.com/articles/High-speed-video_footage_chaoborus_larva_attacking_Dpulex/7355282
How fish behave: www.howfishbehave.ca
NOAAaquatic food webs. http://www.noaa.gov/education/resource-collections/marine-life/aquatic-food-webs.

Parasites in Aquatic Food Webs: How and Why Environmental Gradients Influence Epidemics and Their Implications

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

"Health herds" Reduction of disease prevalence by predators of hosts.
Clearance rate The proportion of habitat from which food resources are removed by a consumer-host (foraging sense) or the rate at which infected or exposed hosts are returned to the susceptible class due to immune-mediated killing of parasites (immunological sense).
Dilution Reduction of parasite prevalence by another host species via "encounter reduction" or "host regulation" mechanisms.
Epidemic An outbreak marked by a rapid increase of the number (or proportion) of hosts infected with a parasite.
Exposure Contact of susceptible hosts with a parasite; a first stage of disease transmission.
Host A species (victim) in or on which a parasite (enemy) grows.
Parasite A species that grows in or on its host (victim). They attack one host per life stage.
Predator A species (enemy) that attacks more than one prey (victim) in its life stage.
Propagules Infectious particles produced by a parasite, often distributed environmentally.
Reproductive ratio, R_0 The number of new infected hosts produced by a given infected host. It is a ratio of gains to losses of the life stages of the parasite. When $R_0 > 1$ the number of infected hosts increases over time in the population leading to an epidemic.
Susceptibility The probability that host becomes infected (or "exposed") given contact with infectious hosts or propagules.
Transmission Transfer of parasites to a new susceptible host.
Virulence Depression of a fitness component (fecundity, survival) of a host due to infection.

Introduction

Textbooks for aquatic ecologists often skip over or skimp on diseases of aquatic organisms and host-parasite interactions. This omission seems strange. After all, over the decades, aquatic ecologists have produced and perfected some of the finest models of species interactions in all of community ecology. For instance, lake biologists have championed concepts such as trophic cascades, resource competition and limitation, trophic heterogeneity, ontogenetic niche shifts, stage-structure and biomass overcompensation, density- and trait-mediated indirect effects, ecological stoichiometry, cryptic eco-evolutionary dynamics, and the like (Mittelbach and McGill, 2018). Furthermore, aquatic ecologists have developed and tested these models, with experiments and field observations, yielding great successes. Yet, those models have rarely been extended to include aquatic parasites (Johnson and Paull, 2011; Okamura and Feist, 2011) even though outbreaks in aquatic ecosystems can spread quickly and become very large (i.e., become an "epidemic") and profoundly influence host populations. In addition, parasites infect hosts embedded in food webs that aquatic ecologist so expertly characterize. Hence, one might imagine a future in which parasites become more integrated into our theories for aquatic ecosystems. Such a future would address questions such as: what are the core components of disease spread in aquatic ecosystems? What habitat and ecological factors influence when epidemics start and how big they get? How does disease alter community and ecosystem outcomes? What are the major sources of heterogeneity governing these outcomes?

In this article, I hope to encourage such integration via two steps. First, the integration must focus on the relevant natural history (Lafferty and Kuris, 2002). That natural history must identify the key sources of heterogeneity that influence disease epidemics

(Poulin, 2007). I consider three key sources here: variation of the parasite's life history (epidemiological); intra-specific variation in hosts themselves (stoichiometric, genetic, and stage-structured); and variation in the food web players (competitors, predators, and resources) that influence host-parasite dynamics. I discuss 12 examples centered on the host-resource interaction (a key difference from generic models of diseases of humans). I make this choice because aquatic organisms often strongly influence their resources (Shurin et al., 2002), and the subsequent feedbacks involving resources then reverberate into host-parasite dynamics.

Second, I focus on the environmental gradients and traits influencing disease spread using a case study of disease in the plankton (Hall et al., 2010b). I take the system, abstract some sources of heterogeneity (for the sake of brevity here), and translate its natural history into the language of equations. The payoff yields an organized inventory of the traits governing the gains and losses of parasites, in both propagule and infected host forms, that determines the size of epidemics. In particular, I use the net reproductive ratio, R_0, which determines the start of an epidemic ($R_0 > 1$) and often correlates with epidemic size (e.g., maximal prevalence of infection [proportion infected]). With that framework, I link environmental gradients to those traits (Lafferty and Holt, 2003). For instance, some environmental gradients (like resource quality and quantity, other non-dynamic resources, and toxins) can influence propagule production, therefore epidemic size. Others (like temperature) influence transmission (Shocket et al., 2018a). I propose that environment-trait connections can be captured using models of energy (and material) flow through individual hosts (i.e., using dynamic energy budget models: Cressler et al., 2014; Hall et al., 2009b). Then, I connect two more environmental gradients (dissolved organic carbon and refuge size) to losses of parasites. Those losses can emerge directly (by reducing damage from solar radiation: Overholt et al., 2012; Shaw et al., 2020) or indirectly (by governing density of the food web players that themselves influence epidemics). Finally, I illustrate how parasites themselves influence the traits of hosts, and those traits then shape epidemics. Specifically, I show three cases (foraging depression, fecundity-transmission tradeoffs, and allocation to males) that then alter the density, genetic composition, and sexual makeup of host populations.

Combined, this case study provides one potential roadmap for aquatic ecologists in the future. Using mathematical models, it shows how one might connect key parts of natural history and environmental gradients to the traits that determine the causes and consequences of disease epidemics. Such frameworks should prove extremely useful when looking to explain and predict how aquatic ecosystems will change in the future.

Some types of host-parasite systems (via 12 modules)

Before commencing, some definitions and illustrations seem mandatory. First, a parasite (enemy) infects one host (a victim) during a particular life stage (following Lafferty and Kuris, 2002): in contrast, predators attack more than one victim. Then, different forms of parasites exert varying effects on host fitness. Important aquatic microparasites (e.g., viruses, bacteria, fungi, and protists) include *Plasmodium* which causes malaria in birds, the VHS virus (Viral Hemorrhagic Septicemia, infecting fishes), and the oomycete *Aphanomyces astaci* (the devastating plague of crayfish worldwide: Martín-Torrijos et al., 2021). Important macroparasites include the trematodes causing schistosomiasis in humans and limb deformities in frogs (*Ribeiroia*). Some of these parasites use multiple hosts (like blood flukes [Echinostomatids] that move between snails and vertebrates, and the cnidarian parasite that uses oligochaetes before causing whirling disease in salmonids). Others spread by propagules that swim (e.g., chytrids that infect phytoplankton: (Kagami et al., 2007); the *Vibrio* bacterium that causes cholera in humans) or are simply passive particles in the water (viruses that infect phytoplankton: Biggs et al., 2021). Many of these examples—and a whole array of others not touched on here—pose important concern to aquaculture, conservation of species (e.g., chytridiomycosis in amphibians), and human health alike (see Tables 1 and 2 of Johnson and Paull, 2011 for an excellent overview).

To sample just a bit of diversity of host-parasite interactions in aquatic systems, I consider 12 different "modules" (simple compartment) models. These 12 models exemplify how host-parasite interactions in aquatic systems occur within food webs by considering the interactions with other species. These highly simplified representations capture the sometimes strong interactions that influence disease spread and community ecology alike. They have a long tradition in both community and disease ecology (Hudson et al., 2002), and they provide a template with which to evaluate individual host-parasite systems of interest in freshwater systems.

To start, let us focus on a baseline model of a susceptible host (S), an infected host (I), and a resource (A; Fig. 1A). Interactions of just these three players fuse the central role of hosts as participants in disease spread (leading to new infections) and as consumers of resources (and therefore influencing production, partitioning of biomass among trophic levels, nutrient cycling, etc.). To that template, I then layer on (at least) three forms of relevant heterogeneity.

- *Epidemiological heterogeneity* (Fig. 1B–F): For instance, one can add more realistic host-parasite epidemiology, illustrated via five examples. A parasite may produce exposed but not yet infectious classes, but others could spread via environmentally-transmitted propagules, trophic transmission (i.e., as one host consumes another infected hosts), and production of propagules from dead hosts. Multiple parasites may also compete for hosts, possibly yielding coinfection.
- *Intraspecific heterogeneity of hosts* (Fig. 1G–I): Then, intraspecific variation of hosts themselves provides a second important form of heterogeneity. Hosts and their resources can vary in their body composition (stoichiometry), in stage structure (e.g., juvenile vs. adults which may compete for a resource), and in genotype. Because transmission can vary with composition, stage, and genotype, each of these sources of intraspecific heterogeneity can strongly influence disease dynamics and spread.

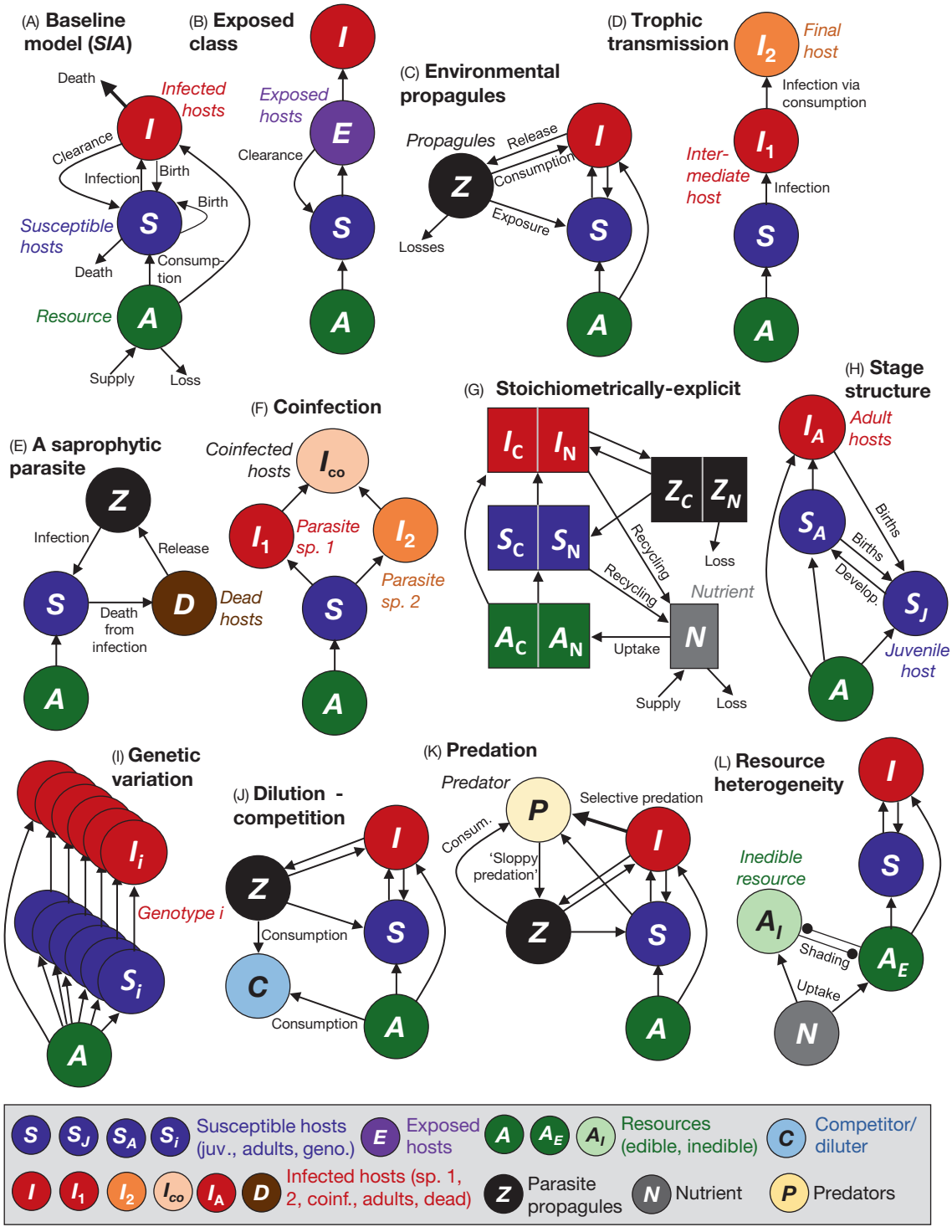


Fig. 1 Some types of host-parasite interactions in aquatic food webs—an illustration with 12 different modules. (A) *Baseline SIA model:* A baseline susceptible-infected model, with flows in an out of these host compartments labeled explicitly (see text; some of these flows are dropped in diagrams that follow). An explicit resource is added. *Five variations with epidemiological heterogeneity.* (B) *Exposed class*: Addition of an exposed class, where immune systems of the host can clear infection before hosts become infectious (i.e., able to spread parasites to new hosts). (C) *Environmental propagules*: Addition of a propagule class, where infectious hosts either shed propagules in the aquatic environment continuously or upon death. (D) *Trophic transmission,* where parasites move from intermediate hosts to final hosts via trophic (feeding) interactions. (E) *A "saprophytic" parasite*: Saphrophyte-like parasites first kill hosts very quickly, then consume corpses to release propagules. (F) *Co-infection*: Some aquatic parasites can coinfect their hosts, but exclusion or priority effects (alternative stable states) are also possible. *Three forms of intraspecific heterogeneity of hosts*: (G) *Stoichiometric composition*: Aquatics hosts and their resources and parasites can vary in their stoichiometric body composition (e.g., carbon:nutrient ratio), enabling tracking of nutrient recycling and losses. (H) *Stage structure*: Many aquatic hosts progress through ontogenetic life stages (e.g., juvenile to adult). Parasites can differentially infect those stages (e.g., only adults). (I) *Genetic variation:* Both hosts and parasites can vary genetically in traits governing epidemics. *Three forms of food web heterogeneity: (J) Dilution-competition:* Other host species can consume propagules ("encounter reduction") and shared resources ("host regulation"). (K) *Predation*: Predations can selectively prey upon infected hosts, release propagules via "sloppy predation," and directly consume propagules. (L) *Resource heterogeneity*: Inedible resources and epidemics can interact via shared nutrient pools.

- *Food web heterogeneity* (Fig. 1J–L): Finally, host-parasite interactions exist embedded within food webs. For instance, host species vary in resistance to parasites, predation can alter epidemiology, and disease might alter competition among heterogeneous resource species.

These three forms of food web heterogeneity combine into a suite of interactions that influence and are shaped by epidemics in aquatic systems.

Baseline (SIA) model: Direct transmission with a resource (Fig. 1A)

In a baseline model of disease in aquatic systems, susceptible hosts (S) consume resources (A), following their foraging biology (i.e., functional responses and assimilation efficiency). Without disease, they convert that consumed food into (susceptible) offspring, and they die at some background rate. But, when susceptible hosts contact infected hosts (I), they become infected themselves. If transmission is horizontal (i.e., no mother to offspring [vertical] transmission), infected hosts produce susceptible offspring (perhaps at a reduced rate). Immune systems might successfully clear infection and an infected host revert back to a susceptible host. But if the infections are not cleared, the host likely die at some enhanced rate. Hence, infection can exact virulent effects on fecundity (including up to complete castration by e.g., brood parasites or via physiological manipulation causing gigantism) and/or survival (by increasing death rate). Note that resources are also supplied and lost via production ecology familiar to freshwater ecologists.

This seemingly simple three dimensional (S, I, A) view of aquatic disease can capture a diverse array of dynamical properties (Anderson and May, 1991). For instance, it can delimit environmental conditions, via controls on nutrient supplies, that bound the fundamental niche of a parasite. For instance, for directly transmitted parasites, a minimal threshold host density, S_i^*, might be needed to ensure that an epidemic can start. If the resource-host (A-S) system provides sufficiently high host density [e.g., this "boundary" density, S_b^*, exceeds S_i^*], then an initial infected host could yield more than one new infection (i.e., $R_0 > 1$). If host density is too low, perhaps in an oligotrophic system, epidemics may not be possible. Once an epidemic starts, the *SIA* system can capture a diverse array of dynamics. For instance, prevalence of disease and density of infected hosts could increase along eutrophication gradients (if eutrophication increased carrying capacity of the resource: Johnson et al., 2007). Both resource density and infection status could alter key traits (feeding, fecundity, mortality). Via those traits, the disease epidemic could then cause a trophic cascade (higher resources, fewer hosts: Buck and Ripple, 2017). Alternatively, it could unleash a hydra effect (yielding higher resources and more hosts, named for the mythical beast: Penczykowski et al., 2022; Schroder et al., 2014). Both possibilities seem more likely in aquatic systems, where hosts can strongly depress resources. Higher resource density could then interact with (parasite modified) functional responses of the grazer (type II or type III [as in *Daphnia:* Uszko et al., 2015]) to stabilize or destabilize host-resource interactions (Hurtado et al., 2014). Hence, while simple, the *SIA* baseline model captures a rich array of dynamical possibilities. Furthermore, it helps explain fundamental issues of production, allocation of biomass among trophic levels, and dynamics of freshwater systems.

Epidemiological heterogeneity #1: An exposed class, E (Fig. 1B)

Many freshwater parasites (e.g., flatworms, nematodes, fungi, bacteria) undergo different life stages within their host. Such life history prompts addition of an exposed host class (E) that retains the ability to clear infection. However, eventually those exposed hosts can become infectious (e.g., by producing a terminal stage propagule). At this stage, immune systems may or may not succeed in clearing infection (as shown in the diagram: Stewart Merrill et al., 2021). For instance, once *Daphnia* produce infectious propagules of the focal fungus (described below), infection is irreversible, and the host will die from infection.

Epidemiological heterogeneity #2: Environmentally distributed propagules, Z (Fig. 1C)

A highly relevant class of parasites produce infectious propagules within the bodies of infected hosts. Then, those propagules are released continually (e.g., by shedding from guts) or upon host death (i.e., "obligate killers" or parasitoids: Lafferty and Kuris, 2002). Some infected hosts release massive numbers of propagules following physiological manipulation by parasites that redirect energy away from reproduction (castration) and towards growth (gigantism, e.g., in fish, snails, water fleas: Hall et al., 2007a; Cressler et al., 2014). While in the water column, these propagules can actively swim to contact hosts (often by penetrating the host body) or become consumed by foraging hosts. In that latter case, exposure to parasites interweaves intimately with foraging biology (i.e., it can become proportional to "clearance rate" [in the foraging rate rather than immunological sense]: Hall et al., 2007c). Once consumed, those propagules successfully infect with some susceptibility (infectivity) probability. However, while inhabiting the free-living water column, those propagules can suffer very high loss rates from various environmental factors (such as solar radiation and sinking: see below) while infected hosts (and other species) may consume them. Simultaneously, production of propagules can depend strongly on resource density (e.g., many hosts produce more propagules when feeding on richer resource quality; Cressler et al., 2014). As a result, this *SIZA* system creates additional mechanisms by which aquatic environments and resources shape disease spread.

Epidemiological heterogeneity #3: Trophic transmission & complex life cycles (Fig. 1D)

Once they infect their first host, certain parasites with complex lifecycles can then move into other hosts. In the example illustrated, parasites infect a first intermediate host (I_1). Often, these parasites reproduce to large numbers asexually before they become consumed by a second host. That consumption may be mediated by a morphological or behavioral modification that enhances consumption (mortality) of the intermediary host or hosts. Once they enter their final host (here, I_2), those parasites typically

engage in sexual reproduction to complete their life cycle (Johnson and Paull, 2011). Combinations of environmental stages and multiple hosts might best describe these complex life cycles. For instance, in a typical three-host life cycle of a trematode worm, an initial snail hosts might consume worm eggs. Those eggs hatch, undergo several life stages asexually within the host, and then exit via a swimming stage (cercariae). This stage then infects the second intermediary host (e.g., a frog) and produces a life stage that encysts (metacercariae). Once a final host (bird) consumes that host, eggs are produced by sexual reproduction, completing the life cycle.

Epidemiological heterogeneity #4: Production of propagules from carcasses (Fig. 1E)

Some aquatic parasites (e.g., oomycete parasites of *Daphnia*) quickly kill their hosts (Wolinska et al., 2008). Hence they exact extremely high virulence. Then, they produce propagules from the body of the dead host. These parasites act differently than mere saprotrophes (i.e., organisms that feed on decaying matter)—they do indeed infect and kill their hosts. However, because they kill so quickly, they can defy easy detection in nature. Instead, they might act as stealthier, unnoticed sources of mortality for aquatic hosts.

Epidemiological heterogeneity #5: Competition and coinfection (Fig. 1F)

Multiple aquatic parasites can disperse in the environment, and they can potentially co-infect hosts. For instance, a host infected with parasite species 1 (I_1) could become infected with parasite species 2 after contact with an individual hosting that parasite (I_2), yielding co-infection (Clay et al., 2020). Co-infected hosts, in turn, can suffer higher virulent effects. That interaction could also lead to competitive exclusion or alternative stable states (priority effects). In the latter case, parasites successfully invading first can gain an advantage that prevents invasion of other parasites into hosts.

Intraspecific host heterogeneity #1: Stoichiometric body composition (Fig. 1G)

Although such theory remains quite underdeveloped, a fully stoichiometric disease model might prove quite illuminating. Imagine that the resource (A) is an autotroph that uptakes a nutrient (N) for growth. It might have flexible stoichiometric content (i.e., plastic carbon:nutrient, or C:N ratio in its tissues), driven by environmental resource supply (e.g., incident light, nutrients, depth) and losses (from dilution, grazing sinking, etc.: Hall et al., 2007b; Sterner and Elser, 2002). Variation in such content can influence assimilation efficiency of susceptible hosts, thereby modulating density of hosts and disease transmission. Once infected, parasites could shift the C:N content and/or assimilation efficiency of hosts, potentially altering (speeding up, slowing down, altering ratio) of nutrients recycled relative to susceptible hosts (Frost et al., 2008; Narr and Frost, 2016). Furthermore, production of propagules (having their own C:N content) could depend upon quantity but also stoichiometric quality of resources. For instance, some propagules (e.g., viruses, bacteria) might demand higher nutrient supply (due to higher C:N content). Yet, propagule release from dead hosts could speed up nutrient recycling (e.g., in algal-virus systems). Alternatively, loss of propagules of parasites from the water column could yield a nutrient sink during epidemics. Hence, a fully stoichiometric model reveals how parasites could modify sources and sinks of nutrients in aquatic systems. They may also alter classical limnological relationships (like ratios of total phosphorus to chlorophyll *a* of algal autotrophs) in underappreciated ways.

Intraspecific host heterogeneity #2: Stage structure (Fig. 1H)

Many hosts in aquatic systems develop through distinct and even intricate life stages (de Roos and Persson, 2013). In this simplest case, host offspring first move through a juvenile stage, then mature into adults. Adults, in turn, produce offspring that enter the juvenile class. Through that ontogeny, hosts increase in body size and may even shift habitat. Yet, juveniles and adults may compete for resources. In that latter case, the parasite may target one life stage solely or preferentially (the example drawn illustrates attack solely on adults). Such ontogenetic asymmetry in infection, via virulence on mortality, feeding, and maintenance, could introduce or magnify asymmetry in energetics. If true, parasites could shift stage structure of hosts (i.e., partitioning of individual or biomass among stages) and even trigger counter-intuitive phenomenon like biomass overcompensation (when the stage infected increases in biomass: de Roos and Persson, 2013; Preston and Sauer, 2020). Such fusion of stage-structured resource theory with disease lies at a largely unexplored conceptual frontier, yet likely applies to many aquatic disease systems.

Intraspecific host heterogeneity #3: Genetic variation (Fig. 1I)

Aquatic hosts and their parasites often vary genetically in key epidemiological traits. For instance, the genetics of successful infection may require particular combinations of host and parasite genotypes (i.e., the "matching alleles" patterns famously shown in *Daphnia*-bacteria (Luijckx et al., 2013) and snail-trematode systems (Koskella and Lively, 2009)). Additionally, hosts may vary in other defensive traits that confer differential resistance to infection (via e.g., lower exposure while feeding, gut defenses) and clearance of infection (via variation in immune killing). Furthermore, those same traits granting resistance advantages may come with costs to fitness via other traits. For instance, some hosts become exposed to propagules while acquiring resources for growth and reproduction (Hall et al., 2007c). In those cases, traits granting higher fecundity (e.g., faster feeding rate) may also yield lower resistance (due to higher exposure: Hall et al., 2010a). As a result, the combination of parasite and resource densities could determine selection pressure upon hosts (as they influence the benefits and costs of resistance, respectively). That selection pressure can act quite strongly on hosts that reproduce clonally (asexually)—but, due to tradeoffs, natural selection might favor higher or lower resistance. The subsequent response of natural selection, in turn, can influence the size of epidemics (i.e., prevalence of

infection and density of infected hosts) and shape the fate of the density hit that populations face during epidemics. Indeed, rapid evolution could even alleviate severe density suppression endured by hosts during large epidemics (via "cryptic dynamics": Yoshida et al., 2007).

Food web heterogeneity #1: Dilution-competition (Fig. 1J)

Hosts in aquatic ecosystems inevitably interact with other species that share resources and/or interact with the parasite. Consider first a species, *C*, that only competes for the resource that also fuels the disease epidemic (in the *SIZA* system). Two interacting features emerge. First, disease that targets a superior competitor (i.e., one having a lower minimal resource requirement, A^*) could open realized niche space that allows an otherwise inferior competitor to persist (because disease increases the A^* of the system past the minimal requirement of the competitor). In this way, parasites could facilitate coexistence of the two consumers (Grover, 1997). Yet, once they enter, these competitors can suppress density of hosts. That 'host regulation' mechanism can reduce size of epidemics (Strauss et al., 2018). As a result, these competitors act as disease "diluters." Alternatively, disease could undermine coexistence of the competitors, exacerbating the harm to hosts caused by the competitors. In yet another variation, other host species might only consume, remove, or otherwise provide a sink for parasite propagules (Johnson et al., 2013). If they strongly resist infection, such consumption elicits the "encounter reduction" mechanism of disease dilution. However, if they can become infected, these other species may experience epidemics themselves via a process called "disease spillover." In aquatic systems with generalist, unselective feeders (e.g., mussels, snails, *Daphnia*) as host, these two mechanisms can become intertwined. In these cases, the net interaction of encounter reduction and host regulation can prove helpful to hosts (via disease dilution). Alternatively, it can end disastrously (where competitors fail to control epidemics but still exert strong competitive harm: Strauss et al., 2015). Hence, dilution-competition systems can truly explain a wide range of dynamics.

Food web heterogeneity #2: Predation (Fig. 1K)

Predators can also strongly shape disease dynamics. Consider four possibilities. First, predators may prey selectively upon infected hosts. That possibility seems particularly likely when infection transforms hosts into more obvious prey to visually-oriented predators (like fishes) or changes behavior or habitat use. In these cases, predators can reduce disease via "healthy" herd mechanisms (Duffy et al., 2005; Hall et al., 2005). Second, predators may disperse propagules of parasites via "sloppy feeding" (i.e., *Chaoborus* larvae feeding upon *Daphnia*). This mechanism might particularly benefit parasites that otherwise face a habitat trap if dead, infected hosts sink away before releasing propagules (Cáceres et al., 2009). Third, predation upon hosts might trigger trophic cascades. Those cascades can reduce disease epidemics (via lower host density) or amplify them (if higher resources enhance propagule production via "cascade fueling": Smith et al., 2015). Fourth, predators might directly consume free-living propagules of parasites (thereby acting as diluters via "encounter reduction": Orlofske et al., 2015). Hence, depending on the foraging biology of the predators (selective, sloppy, on propagules or hosts) and the response of resources (fueling), predators could reduce or catalyze disease spread in aquatic systems. And of course, as aquatic ecologists know well, predators can exert non-consumptive effects on host behavior, physiology, and habitat use (Peacor and Werner, 2001). All of those factors might also shape disease epidemics (e.g., Decaestecker et al., 2002). Hence, in aquatic systems, predators can strongly influence aquatic communities and disease epidemics alike.

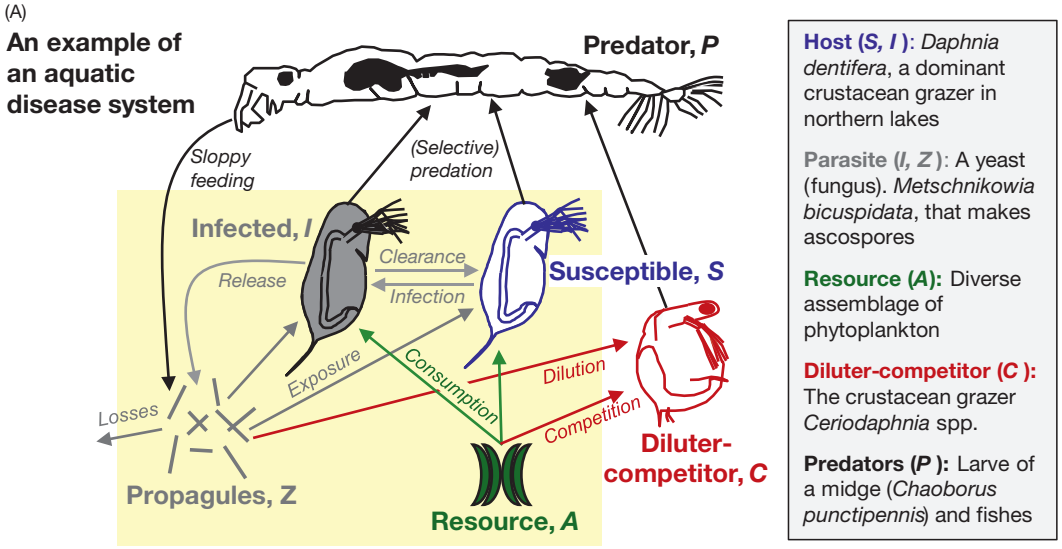
Food web heterogeneity #3: Resource heterogeneity (Fig. 1L)

In a final example, we could imagine disease epidemics altering competition among resource species. For instance, an edible autotroph resource (A_E) might compete superiorly for a nutrient with an inedible resource (A_I: Grover, 1997). By controlling density of autotrophs, grazing by hosts could enable coexistence between hosts (by indirectly meeting the nutrient needs of inedible species). However, in one scenario, a disease epidemic could reduce this control of grazers over the superior resource competitor. In this case, epidemics would reduce freely available resources, shrinking realized niche space for the inedible species. Such a scenario might influence the probability or magnitude of blooms of inedible autotrophs. Of course, parasites of inedible autotrophs might regulate or even end such blooms (not illustrated here, but famously shown in a diatom-chytrid system: Kagami et al., 2007). Hence, disease might directly or indirectly influence the likelihood of algal blooms. Much theory remains to be developed at this interface of basic and applied aquatic disease ecology.

Dynamics of epidemics in aquatic systems: A case study of environmental gradients, traits, and outcomes in the plankton

Overview: For a given host-parasite system, how can aquatic ecologists understand the drivers of epidemics? How can they connect environmental gradients, habitat structure, and food web players to the start, magnitude, and consequences of those outbreaks? A case study of disease spread in plankton illustrates a useful path forward (Fig. 2). To make this case, we first must meet the system, both conceptually and dynamically (in the language of a model). That model organizes several sources of heterogeneity that influence the components of disease spread. It also provides an index (R_0) that nicely highlights both the gains and losses of parasites. With that tool, we can then see how environmental gradients enhance components of gains, by influencing transmission rate and propagule production (Fig. 3A). Furthermore, those drivers of gain focus on energetics of hosts (as part of a "host condition" hypothesis). We can envision such connections using a dynamic energy budget model (Fig. 3B). Then, other (possibly correlated) environmental gradients can shape losses of parasites, directly (via mortality on propagules) or indirectly (by shaping

(A)



(B)

Example of a mathematical model for that disease system

Susceptible: $dS/dt = [\, e\, f_S(A)\, A - (\, d_S + f_P\, P\,) - u\, f_S(A)\, Z\,]\, S + (\, \rho\, e\, f_I(A)\, A + c\,)\, I$ (1.A)

Births; Deaths; Infection; Births and recovery; Foraging; Predation; Exposure; Clearance; Conversion; Background; Susceptibility; Fecundity reduction; Foraging reduction

Infecteds: $dI/dt = u\, f(A)\, Z\, S - (\, d_s + v + c + \theta\, f_P\, P\,)\, I$ (1.B)

Infection; Losses; Virulence; Clearance; Selective predation

Propagules: $dZ/dt = \sigma(A)\, (d_s + v + \gamma\, \theta\, f_P\, P)\, I - (\, f_S(A)\, S + f_I(A)\, I + f_C(A)\, C + d_z)\, Z$ (1.C)

Propagule release; Losses – consumption and environmental; Yield; Sloppy feeding; Consumption by hosts; Dilution; Sinking, radiation

Resource: $dA/dt = [\, r(A) - (\, f_S(A)\, S + f_I(A)\, I + f_C(A)\, C\,]\, A$ (1.D)

Production; Consumption; By hosts; By diluter-competitor (competition)

(C)

An index of disease spread: R_0, the reproductive ratio $R_0 > 1 \rightarrow$ epidemic

Can the parasite invade?

$$R_0 = \left(\frac{\sigma(A)\, (d_s + v + \gamma\, \theta\, f_P\, P)}{(\, f_S(A)\, S + f_I(A)\, I + f_C(A)\, C + d_z)} \right) \left(\frac{u\, f(A)\, Z\, S}{(\, d_s + v + c + \theta\, f_P\, P\,)} \right)$$ (2)

Release of propagules / *Loss of propagules*; *New infections* / *Losses of infecteds*

S and A in their disease free state

Fig. 2 *A model for a planktonic disease system: a case study.* Links between environmental gradients in aquatic ecosystems, traits that govern disease spread, and the outcome of epidemics can be illustrated with a pelagic example in freshwater lakes. (A) *Natural history, simplified:* The freshwater grazer *Daphnia dentifera* hosts the virulent fungus *Metschnikowia bicuspidata* while competing with other zooplankton (e.g., *Ceriodaphnia* sp.) for phytoplankton resources and while falling prey to predators such as larvae of the phantom midge (*Chaoborus* sp., shown) and fishes (not show). (B) *A mathematical model for that disease system*: It tracks gains and losses of susceptible (*S*) and infected (*I*) hosts, propagules of the fungus (*Z*), and the resource (*A*). For simplicity, density of the predator and diluter-competitors are fixed parameters. (C) *An index of disease spread: R_0, the reproductive ratio*: The mathematical model predicts key aspects of the epidemic such as R_0. When R_0 exceeds 1, epidemics can begin in a disease-free system. This index is a ratio of gains to losses of both the propagule class (yellow shading) and the infected class (orange shading).

predation and host composition: Fig. 4). Finally, parasites themselves can alter traits of hosts (such as foraging rate, tradeoff structure among genotypes, and allocation to sex (Fig. 5). Via these traits, parasites can then influence density, trait evolution, and sexual dynamics of their host.

*A model for planktonic disease system—A case study (*Fig. 2*)*

A well-studied example of planktonic disease illustrates how drivers of environmental gradients, community composition, and heterogeneity of disease traits all collide to modulate the size of disease epidemics. This intersection happens in the open waters (pelagia) of small, north-temperate, dimictic (stratified) lakes during autumn in the Midwestern United States (Hall et al., 2010b). The focal host is the grazer *Daphnia dentifera*, a crustacean waterflea (S). This host is famous for at least three ecological roles: it can strongly graze edible forms of phytoplankton resources (A) and compete with other species (C) for those resources; it provides an important food source for fishes and invertebrate predators, particularly larvae of the phantom midge *Chaoborus punctipennis* (P); and it recycles nutrients. While it reproduces asexually during most of the summer and autumn seasons, the host creates a sexual diapausing egg (after producing males) that create temporal dispersal. It also serves as host to a fungus (the yeast *Metschnikowia bicuspidata*). Hosts become exposed to the parasite while eating propagules (ascospores) distributed in the water column. If the fungus successfully penetrates the gut of the host, it undergoes several life stages (which, in principle, could be cleared by the immune system). However, once these exposed hosts produce propagules, these hosts are irreversibly infected (I: Stewart Merrill et al., 2021). For simplicity, we collapse the E into the I stage here. Upon host death (sped up by infection), bodies of infected hosts can release up to 100,000 or more propagules (Hall et al., 2009a,b). If they enter the water column, those propagules then continue the epidemic.

A relatively simplistic mathematical model of this system can pinpoint the key traits underlying disease spread. An example model described below tracks dynamics of susceptible (S) and infected (I) hosts, both of which consume a resource (A) that fuel production of parasite propagules (Z). The predator (P) and diluter-competitor (C) are simply treated here as parameters (but could be modeled more explicitly and dynamically).

Production of susceptible hosts and the infection process—dS/dt

To start an epidemic, the parasite requires enough hosts to infect and produce parasites. Hence, the ecological factors shaping host and resource density apply. Density depends on per capita births, $e\ fs(A)\ A$, where e is conversion efficiency (governed by, e.g., digestion resistance, stoichiometry, etc.) and $fs(A)$ is "clearance" in the foraging rather than immunological sense (governed by, e.g., *Daphnia*'s type III functional response—so a function of resource density, body size, and traits like maximal feeding rate that can itself vary among genotypes and depend upon chemical cues from other species, temperature, etc.). These hosts then die, at some background rate (d_S) and predation (where predators, P, feed at linear rate f_P here). On top of that ecology, we can then layer in the epidemiology: these hosts also become infected at a transmission rate determined by both exposure and susceptibility. Hosts contact propagules, Z, proportional to their foraging clearance rate. Once exposed, hosts become infected with some susceptibility, u. This parameter has a quantitative genetic component. It also likely depends on a variety of other factors (e.g., gut thickness, rearing [maternal effects], Shocket et al., 2018b; Stewart Merrill et al., 2021). Finally, infected hosts can contribute to susceptible hosts via birth, assuming horizontal transmission (from propagule to susceptible host), and recovery from infection (following immune clearance parameter c). Births depend on foraging rate of infected hosts, which itself can be diminished ($f_I < f_S$), and any further fecundity depression due to virulence (where $\rho = 1$ means no additional depression while $\rho = 0$ indicates complete castration [as for the bacterium *Pasteuria*]). In the particular case study, horizontal infection slows feeding but does not depress fecundity too much ($\rho \approx 0.8$).

Production of infected hosts and parasite propagules, dI/dt and dZ/dt

To continue with an epidemic, parasites must grow and produce propagules that re-enter the environment. Hence, production of infected hosts (dI/dt; Eq. 1.B, Fig. 2B) follows the increase from new infections, $u\ f(A)\ Z\ S$, and losses at a rate elevated from background by virulence of the parasite ($d_S + v$), immune clearance (c), and predation (where $\theta > 1$ indicates selectivity on infected hosts). Then, in the propagule production equation (dZ/dt; Eq. 1.C; Fig. 2B), spores are released at a yield times a rate. The yield is $\sigma(A)$, a function of resource density in the environment, A. In the focal system, this function increases monotonically: hosts with higher (edible) resource density (but especially higher resource quality) produce more propagules. Then, that yield is released when hosts die due to virulence ($d_S + v$). Predators, P, with "sloppy feeding" can also release a proportion of propagules (γ) when preying (at rate $\theta\ f_P$). In the planktonic example, sunfish predators release some viable spores that likely do not return to the water column (so $\gamma \approx 0$: Duffy, 2009) while phantom midge large release about half into the epilimnion (upper water column) at night (Cáceres et al., 2009).

Then, losses of propagules stem from both biotic and abiotic sources. First, susceptible hosts, S, consume them (given their foraging clearance rate, $f_S(A)$). That route leads to exposure and possible successful infection. However, infected hosts, I, also consume them (at clearance rate $f_I(I)$). Quite importantly, other more resistant or completely resistant hosts, C, also remove them (at their own foraging clearance rate $f_C(C)$). Via this consumption, these hosts (such as *Ceriodaphnia* sp. and *Daphnia pulicaria*) enact the "encounter reduction" mechanism of dilution (Strauss et al., 2018). Finally, here, the other courses are lumped into a d_Z rate. This term can capture much germane abiotic biology. For instance, solar radiation (ultraviolet [UV] but even photosynthetically active [PAR] light) can damage propagules quite significantly (Overholt et al., 2012; Shaw et al., 2020). Furthermore, if mixing is limited, propagules that cannot swim may sink out of the water column. Hence, factors shaping penetration of solar radiation

(incident levels, dissolved organic carbon [DOC], background turbidity, phytoplankton density, water column depth) and physical mixing in the water column (wind shear, night-time cooling, stratification strength, depth)—all key limnological factors—could influence this vital loss rate of parasites.

Production of resources, the fuel of epidemics, dA/dt

To finish out this model, we must not forget phytoplankton resources, the fuel of epidemics (dA/dt; Eq. 1D; Fig. 2B). Resources power production of both hosts and their competitors but also of parasites. Primary production, $r(A)\,A$, is presented here as some generic function, but one which aquatic ecologists have spent decades describing (i.e., as functions of nutrient supply, uptake kinetics, internal nutrient storage, light intensity, sinking, etc.). Indeed, a more detailed model might include flexible nutrient content, plastic defenses (like digestion resistance), etc. Then, both susceptible, S, and infected, I, hosts consume those resources. Diluter-competitors also can share this resource (particularly when hosts are generalist filter feeders). Through this indirect exploitative mechanism, these diluter-competitors can reduce disease prevalence (through a "host regulation" mechanism). On the other hand, the epidemic can disadvantage hosts in the competition (by increasing their minimal resource requirement). Hence, this resource competition dimension complicates the role of diluter-competitors: they might reduce disease prevalence but also severely depress host density during epidemics (as can happen in the focal system). Yet, these interactions almost certainly abound in aquatic systems (e.g., with other plankton, snails, mussels, tadpoles, etc.).

Pulling the pieces together: An index of disease spread, R_0 (the reproductive ratio, Eq. 2)

With production of all players described, the model can predict dynamics of epidemics in aquatic systems. An overview of all such dynamics exceeds the scope of this article, but some immediate insights flow from an expression the net reproductive ratio, R_0 (Eq. 2, Fig. 2C). This quantity governs the success ($R_0 > 1$) or failure ($R_0 < 1$) of an epidemic to start. In the focal plankton system, that start date falls somewhere in the late summer to late autumn months. The R_0 quantity often (but not always) increases with disease prevalence (proportion infected). It can be derived using mathematical techniques well-known to epidemiologists (i.e., the Next Generation Matrix method: Diekmann et al., 2010). Helpfully, following this calculation, R_0 can be written as a ratio of gains (numerator) to losses of propagules (yellow shading) and infected hosts (orange shading; Fig. 2C). Hence, factors enhancing release of propagules and transmission rate catalyze disease spread; those strengthening losses undermine it. Furthermore, tension can arise between components of spread. For instance, predation might reduce host density (S) before epidemics begin. All else equal, lower density suppresses disease spread (lowers R_0). However, through a trophic cascade (indirect release of resources), release of propagules could increase, thereby catalyzing it (higher R_0). Fortunately, parameterized equations provide the machinery needed to mediate a tug of war among factors. Furthermore, they provide the opportunity to map environmental factors to traits to disease spread. To illustrate, we can focus on environmental drivers driving gains and losses.

*Tension between gain components and the host condition hypothesis (*Fig. 3*)*

The focal planktonic system reveals how environmental drivers of disease spread can operate through traits linked to gains for the parasite. Those gains appear in the numerator of the R_0 expression. However, environmental gradients can pull these traits in opposing directions. To illustrate, consider three environmental drivers: quality and quantity of a dynamic resource (phytoplankton: Civitello et al., 2015; Hall et al., 2009a), a non-dynamic resource (potassium: Civitello et al., 2013), and sublethal doses of a toxin (copper; Fig. 3, top three rows: Civitello et al., 2012). Higher resource quantity/quality can reduce transmission rate (through contact/foraging clearance mechanisms) but increase both host growth and propagule production within infected hosts. In experiments and in the field (among lakes), the net result is larger epidemics with richer resource environments. Hence, the response of parasite production matters most (top row). This framework recapitulates with the non-dynamic resource potassium (second row). In experiments, potassium enrichment has no effect on exposure but does stimulate host growth. In mesocosms and the field, higher potassium levels led to higher propagule production and large epidemics. In contrast, sublethal doses of copper increased feeding rate (hence transmission) but depressed host growth and parasite production. In mesocosms, copper reduced epidemics (third row). Integrating among all three stories, the links between gradient and parasite production, mediated through host growth, reigned supreme. Yet, a thermal example provides a counterpoint. Specifically, warmer temperatures (from 15 °C to 25 °C) speed up transmission rate, via both faster feeding (exposure) but also a rearing effect (i.e., propagules produced in warmer conditions infect more readily: Shocket et al., 2018b). Meanwhile, production of propagules responds unimodally yet fairly flatly to temperature (despite that host growth increases considerably with warming). The net result: because warmer temperatures enhance the transmission rate, "warmer is sicker" (Shocket et al., 2018a).

An energetic framework can likely capture key components of this tug-of-war between traits governing gains (Fig. 3B). Consider, for instance, the dynamic energy budget (DEB) model. In this model of an individual host, food is consumed, and via assimilation, converted into an energy reserve (with recycling of waste). This reserve, in the typical model, is then allocated (utilized) to growth of structure (body mass and length) and production of offspring with payment of associated metabolic costs. Because DEB models hinge on body size, the rate of maximal resource consumption increases with size. While initially developed with *Daphnia* in mind, this model successfully captures growth and fecundity of a variety of organisms, using one currency (e.g., energy) or multiple ones (e.g., adding in phosphorus). Parasites then intercept this flow of energy at some point: as shown, parasites take from the reserve before it is utilized (Hall et al., 2009b). Through this energy theft, parasites can exact virulent costs on growth and fecundity and shorten lifespan (e.g., by starving hosts internally). Additional features added to the model could capture other life history. For instance, parasites can reduce foraging rate beyond mere stunting of growth (through "anorexia": Strauss et al., 2019). They can also

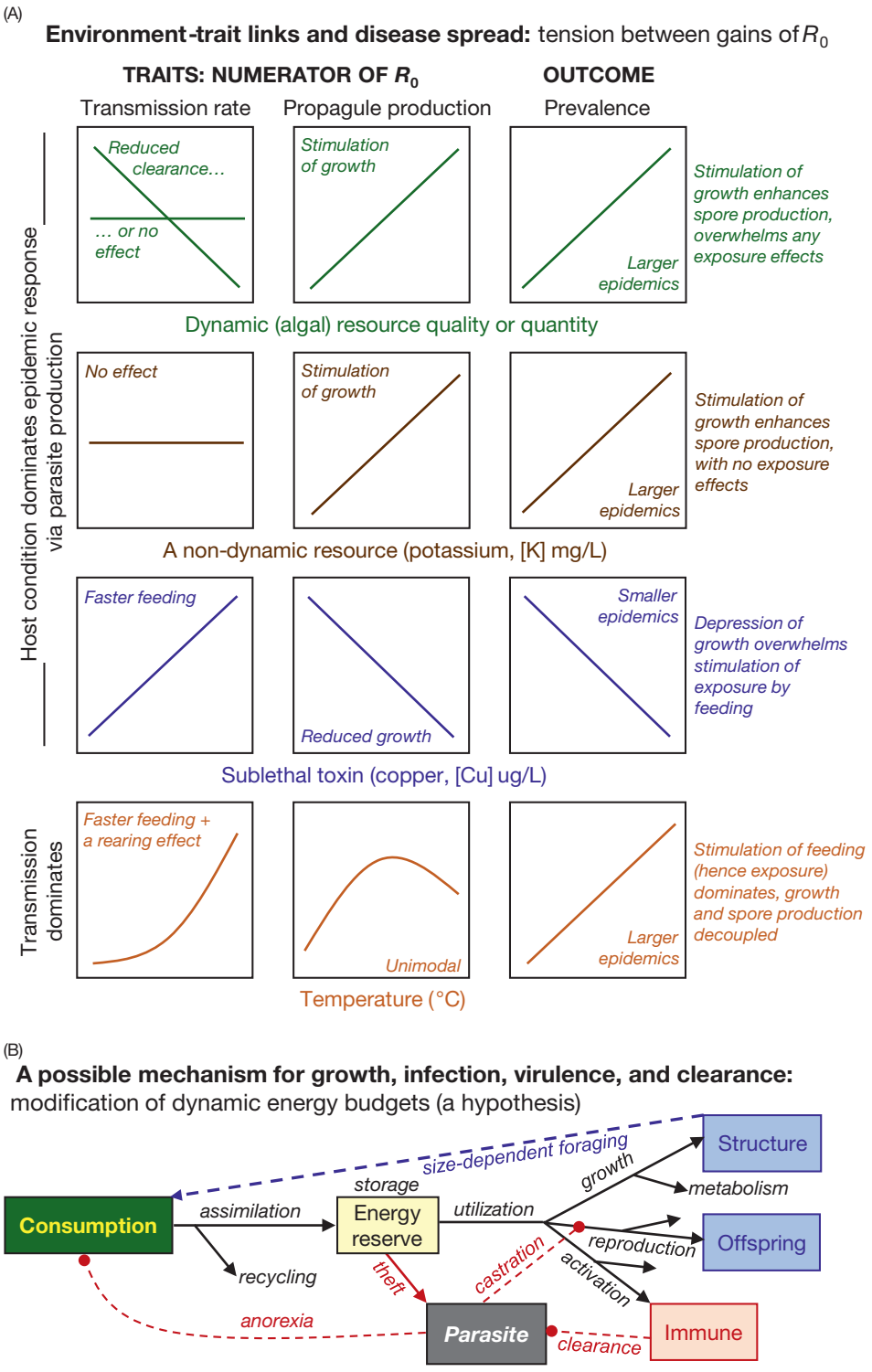


Fig. 3 *Tension between components of disease spread and the host condition hypothesis.* (A) *Environmental-trait links to disease spread and tension between gains of R_0.* Three examples—a dynamic resource, a non-dynamic resource (potassium), and a sublethal toxin—illustrate how these environmental factors can influence both transmission rate and/or production of parasite propagules, perhaps even in opposition. All three highlight the supremacy of the propagule production trait—epidemics increase or decrease in size depending on how the environmental factor affects this trait. However, the thermal example provides a counter-point: warmer temperatures lead to larger epidemics ("warmer is sicker") by strongly increasing the transmission rate trait. (B) *A possible mechanism for growth, infection, virulence, and clearance: modification of dynamic energy budgets (the host condition hypothesis).* These environment-trait-outcome connections can be captured by models of energy and nutrient flow within individual hosts. Here, in a typical dynamic energy budget model, consumed energy is assimilated into an energy reserve, then utilized for growth of structure, production of offspring, and payment of associated maintenance and other metabolic costs. Then, parasites can steal energy, reduce feeding (through "anorexia"), and alter allocation away from reproduction (causing castration and possibly gigantism).

alter allocation of utilized energy reserve away from reproduction and towards growth (producing [possibly transient] gigantism: Hall et al., 2007a). Finally, some representation of immune function (such as hemocyte cells) could be layered in, enabling clearance (via killing) but also present an energetic loss (Cressler et al., 2014).

This framework becomes pertinent to the focal planktonic examples because it provides a mechanism for the "host condition hypothesis." Any factor increasing energy flow into hosts (e.g., better phytoplankton resources, more potassium) can increase both energy reserve and host growth. Hence, this fungal parasite has a larger body to fill with propagules, and that large body provides energy at faster rates (through faster feeding). Alternatively, any toxin (like copper) that increases metabolic costs (e.g., for detoxification) would decrease size, hence energy input and space to pack parasites. Additionally, a thermally explicit version of this model might explain decoupling of host growth and production of propagules with warmer temperatures (particularly if thermal scaling of the traits governing energy acquisition and use differ between host and parasite). Finally, the model could help predict transmission rate, particularly once realistic forms of immune clearance are added. Other factors, like digestion resistance via gut passage time mechanisms can enhance realism for both resource quality and infection dimensions (Hall et al., 2012). Yet, much work remains on such frameworks.

*Environmental gradients and abiotic and biotic losses of parasites (*Fig. 4*)*

The focal planktonic system also illustrates how environmental gradients can influence losses of parasites, both in the free-living propagule and infected host stages. Through these effects, they also influence epidemic size (Fig. 4A). These factors feature in the denominator of R_0. The example gradients here, dissolved organic carbon (DOC) and refuge size (i.e., oxygenated waters below the thermocline) shape both abiotic and biotic losses. For instance, solar radiation proves highly damaging to propagules distributed in the water column. As a result, propagule loss rate (m_Z) increases in lakes with lower concentration of dissolved organic carbon (Fig. 4B, panel (i)). Hence, epidemics tend to start earlier in the autumnal season (more incident UV) and can become larger in browner lakes (i.e., "browner is sicker"). Additionally, lakes with higher dissolved organic carbon have more midge predators (ii).

Furthermore, deeper lakes with larger thermal refuges (that last longer when stratified) also have more midges (iii) and sometimes have higher density of a diluter-competitor (*D. pulicaria*). Typically, this species has left the water column before epidemics commence (hence is not drawn here: but see Penczykowski et al., 2014). Conversely, lakes with smaller thermal refuges tend to have higher realized predation intensity from visually oriented sunfishes (like sunfish: (iii); all of below from Strauss et al., 2016). Those visually oriented predators increase frequency of smaller-bodied species (esp. *Ceriodaphnia* sp). that act as diluter-competitors by consuming spores (iv). These fishes tend to selectively prey upon infected hosts ($\theta \gg 1$) since infection turns ordinarily translucent hosts more opaque (v)) but release few if any viable propagules into the water column ($\gamma \approx 0$). As a result, they act like "healthy herds" predators: higher realized predation intensity by fishes leads to smaller epidemics. Conversely, midge predators feed differently (by mechano-sensory mechanisms), often in the epilimnion at night. As a result, they are not selective upon infected hosts ($\theta \approx 1$) but do release propagules into habitat that where they can readily contact new hosts to infect ($\gamma > 0.5$). If that release occurs in darker lakes (lower loss rate) and avoids sink-out of infected hosts before propagule release, these 'predator spreaders' can increase epidemic size.

The case studies then illustrate two general points that should apply broadly across aquatic disease systems. First, some environmental gradients will facilitate epidemics by reducing abiotic losses (from damage, sinking, flushing, etc.) Second, those same or other environmental gradients can change community composition of the suite of predators and diluter-competitors with which hosts interact. Depending on foraging biology of the predators (e.g., degree of selectivity on infected hosts and diluters, release of propagules, etc.), increases in their density may lower disease ("health herds") or increase it ("predator spreaders"). Then, third, note how densities of these factors influence losses can also indirectly shift components of the gains. For instances, trophic cascades caused by predators could increase resource density (hence propagule production)—but, then again diluter-competitors may control resources and prevent the cascade. Finally, predators can influence other components of host biology that also shape disease spread. For instance, selective predation on juveniles can shift populations towards adults. If parasites more easily infect adults, they may help spread disease via shifts in stage structure. Hence, environment gradients that influence losses can act in straightforward but also in more intricate ways interwoven within food webs.

*Some other connections between traits and epidemic outcomes (*Fig. 5*)*

The focal parasite itself can change key traits that then influence the density or composition (genetic or stage) of its host. Three examples illustrate this point.

(i) *Foraging depression and cascades* vs. *hydras*: In this first case, parasite propagules in the environment depress foraging of hosts (Fig. 5A). This sensitivity to propagules can depend upon host genotype (i.e., some respond more sensitively than others: Strauss et al., 2019). However, this plasticity of foraging can create a trait-mediated indirect effect that leads to higher host density during epidemics of virulent epidemics (via a "hydra effect"; Fig. 5B; Penczykowski et al., 2022). The causal chain starts with an increase in resource density caused by the epidemic. That increase can boost production of the resource (if the host strongly controlled it). Then, both foraging depression and mortality influence per capita resource consumption at equilibrium. Since host density hinges on a ratio of production to per capita consumption (at equilibrium), models predict parasite-driven trophic cascades (more resources, less hosts) at low carrying capacity of the resource (e.g., more oligotrophic systems). However, the potential for hydras (more resource, more hosts) arises in more eutrophic conditions (Penczykowski et al., 2022). Hence, the parasites can initiate trait-mediated indirect effects that then influence allocation of biomass among trophic levels.

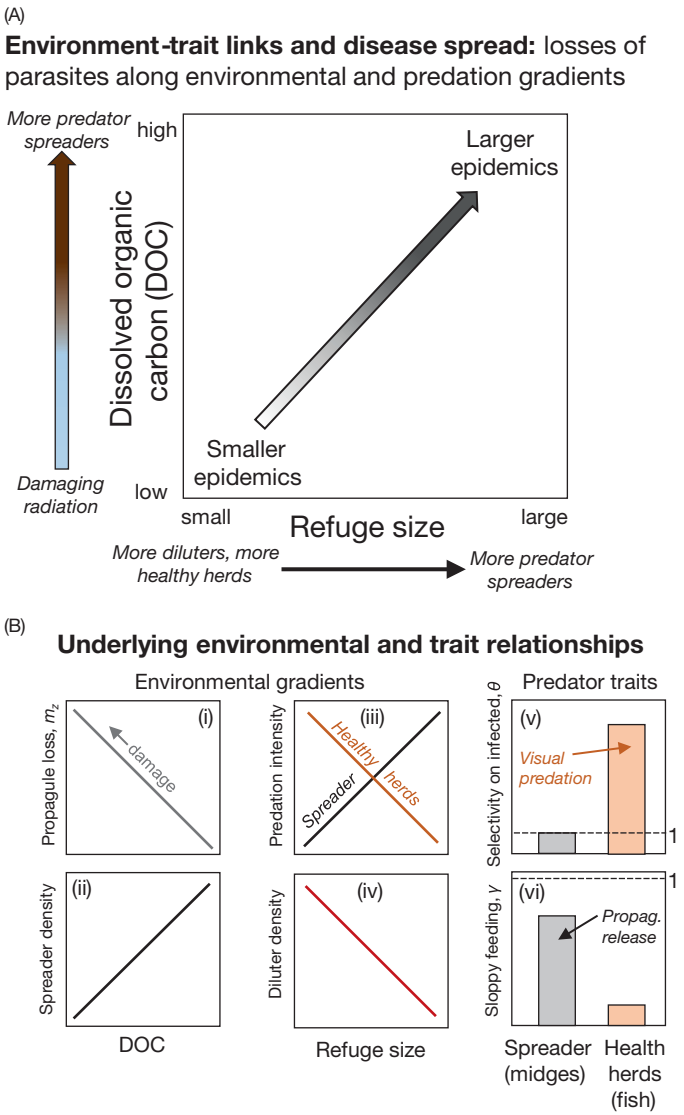


Fig. 4 *Environmental factors influencing losses of parasites.* (A) *Environment-trait links and disease spread: losses of parasites along environmental and predation gradients.* In the focal plankton system, two environmental gradients (dissolved organic carbon [DOC] and refuge size) influence losses of parasites both directly and indirectly. Therefore, both modulate the size of epidemics. (B) *Underlying environmental and trait relationships.* (i) Higher DOC protects propagules from damaging solar radiation, but (ii) also correlates with higher density of midges that spread disease. Then, larger size of thermal refuge (i.e., thickness of oxygenated water column below the thermocline) creates gradients of predators with different traits and diluter-host composition that influence epidemics indirectly. The two major predators, in turn, vary in two key traits. Fishes act like "healthy herds" predators (reducing disease) because they (iii) selectively prey upon infected hosts but (iv) release few propagules back to the water column. Midges, in contrast, do not selectively consume infected hosts (v) but release half or more of the propagules back into the epilimnion at night (vi).

(ii) *Fecundity-transmission tradeoffs and evolution of resistance:* In a second example, clonal genotypes of the host can trade off fecundity and transmission rate. In this relationship, more fecund genotypes resist infection less while less fecund ones better resist infection (Fig. 5C; Hall et al., 2010a). Such a relationship arises in the focal system because both traits depend on feeding rate (i.e., fast feeders consume more propagules while consuming more phytoplankton resources). This covariance of traits then influences evolution of resistance and feeding rate traits during epidemics (Fig. 5D; Duffy et al., 2012). Under certain conditions, hosts rapidly evolve higher resistance to the virulent fungus. In others, hosts can rapidly evolve higher susceptibility (because fast feeding becomes the fittest strategy during epidemics). In this later situation, such an evolutionary response can paradoxically trigger large declines of host density during epidemics. Hence, connections between traits that influence epidemics and consumer-resource interactions can shift trait distributions and host abundance.

(iii) *Allocation decisions and the stage and sexual structure of host populations—the example of males*: In the third example, disease epidemics can shift allocation of a host population towards production of males (Hite et al., 2017). In the focal host-parasite

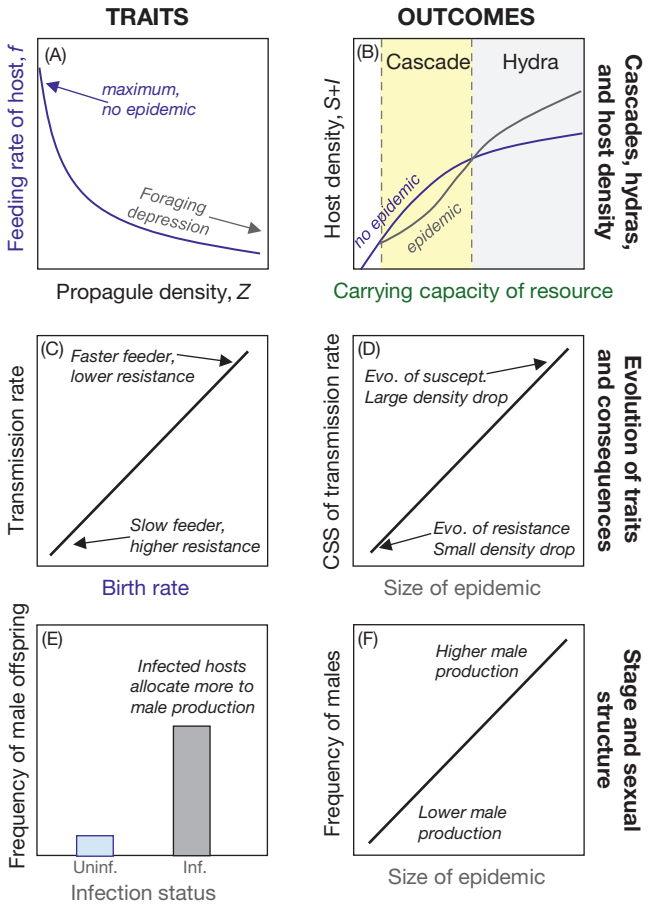


Fig. 5 *Three other connections between parasites, host traits, and the outcomes of epidemics. Foraging depression and the cascade-hydra gradient*: (A) Propagules reduce foraging rate of hosts. (B) Through that trait, epidemics can cause trophic cascades (more resources, fewer hosts: more likely at lower carrying capacity of resources). They can also trigger "hydra effects" (more resources, more hosts: higher carrying capacity). *Fecundity-transmissions tradeoffs and the evolution of hosts during epidemics*: (C) Through connections to the feeding rate trait, hosts with high fecundity (while uninfected) tend to have less resistance to infection. The tradeoff strongly influences (D) whether hosts (often rapidly) evolve more resistance to infection or lower resistance. The eco-evolutionary outcome can reduce or magnify depression of host density during epidemics. *Allocation to males and stage/sex structure of host population*: (E) Infected hosts allocate more reproduction to males. (F) Subsequently, during larger epidemics, the frequency of males in the host population increases.

system, individual infected females produced more male offspring. (These males were not more resistant to infection). As a result, lakes (and mesocosms) with larger epidemics become composed of a higher percentage of males during late autumn. Hence, parasites can influence allocation of host populations to production of males (sex) during epidemics.

Conclusions

Despite what textbooks may lead us to believe, parasites feature prominently in aquatic food webs. Once we embrace this interesting dimension of aquatic ecosystems, how can we characterize them, understand the factors that modulate epidemic size, predict the consequences for host populations, and link them to the food webs? This article proposes a two-part approach. First, we must understand the natural history of the host-parasite interaction. Epidemiological books teach us some of the basics—for instance, transmission as the transfer of infection upon contact between host and parasite. But then, the biology of the organisms themselves can require modeling of more details. Indeed, three categories of heterogeneity almost certainly must be considered (e.g., epidemiological, intraspecific, and food web architecture). Hence, in order to characterize the community ecology of an aquatic disease we must embrace these forms heterogeneity. With this focus, we can model disease spread.

The second part of the approach connects that model to environmental gradients that so profoundly shape aquatic communities. A planktonic host-parasite case study illustrates some examples. First, a mathematical model can capture the gain-loss processes that influence the start, magnitude, and implications of fungal epidemics in zooplankton hosts. Then, that model connects environmental gradients to these traits influencing gains and losses. Some environmental gradients (e.g., resources, toxins, temperature) more strongly influence gains of parasites, either by influencing transmission rate (especially via exposure [feeding rate]) or production of parasite propagules. Then, other environmental gradients most strongly influence the losses of

parasites, either directly or via species that themselves strongly shape the size of epidemics. Of course, parasites themselves can influence traits of hosts that then determine the magnitude and scope of epidemics in aquatic ecosystems. Three examples (foraging depression, fecundity-transmission tradeoffs, and allocation to males) illustrate how aquatic parasites can alter density, genetic composition, and sexual/stage structure of host populations.

Once we identify and characterize the important host-parasite interactions, we then can predict how they influence inland waters in a changing climate. For instance, perhaps a "browner world is a sicker world" in lakes: increased concentration of dissolved organic carbon into otherwise clearer lakes may remove direct constraints on parasites and/or facilitate interactions with species that spread them. Additionally, warmer conditions may exacerbate epidemics ("warmer is sicker") if they more strongly influence traits governing disease spread (like transmission rate) than enhance the food web factors that constrain epidemics (like "healthy herds"-type predators: Hall et al., 2006). These and other similar questions remain tractable for aquatic ecologists once they embrace relevant heterogeneity inherent in the host-parasite system, then link (changing) environmental gradients to those sources of heterogeneity. Though these steps, aquatic ecologists can create predictive theories for disease epidemics within aquatic food webs in a changing world.

Research gaps

Looking to the future, several directions arise. In freshwater aquatic communities:

1. What are the major drivers of the start of disease epidemics? What combination of physical, environmental, immunological, and ecological factors trigger their start ($R_0 > 1$), and which of them inhibit epidemics ($R_0 < 1$)?
2. How will climate change alter these factors? For instance, will enhanced browning or warmer lead to larger disease epidemics? Could more variable climatic conditions trigger them? Does pollution with nutrients and/or chemicals further modify conditions for epidemics?
3. Once they begin, in what (understudied and likely underappreciated) ways do parasites alter the ecology of their aquatic hosts? How do they shift stage structure, genetic diversity, sexual characteristics, density and production, etc., of their hosts?
4. Then, beyond the host, to what extent do disease epidemics influence freshwater ecosystems? To what extent do they alter primary production, cause trophic cascades or hydras, modify nutrient cycling (as sources or sinks), interact with algal blooms, shift community composition, and/or influence energy and material flow up food webs?

These questions and more await future discovery in the study of freshwater systems.

Acknowledgments

SRH was funded by NSF DEB 1655656 (United States).

See Also: Fundamental concepts and theories: Ultraviolet Radiation; Structures and functions of Inland Waters - Lakes: Fungi and Chytrids

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Light as an Ecological Resource☆

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This is an update of D.M. Leech, S. Johnsen, Light, Biological Receptors, in Encyclopedia of Inland Waters, Edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00073-9.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Brownification An increase in the yellow-brown color of inland waters, caused mainly by inputs of dissolved humic matter of terrestrial and wetland origin, which absorbs solar radiation strongly in the short wavelength part of the visible spectrum.
Chromophore A molecule that absorbs light. As a component of photoreceptors, the chromophore is often retinal (i.e., vitamin A1 or A2).
Eutrophication The process by which a body of water becomes enriched in dissolved nutrients, such as phosphates, that stimulate the growth of aquatic plant and bacterial life, usually resulting in the depletion of dissolved oxygen.
Opsins A group of proteins made light-sensitive through their chemical bond with a chromophore. The amino acid sequence of an opsin protein, combined with the type of chromophore, determines the absorption spectrum of a visual pigment.
Photopigment A chromophore bound to an opsin protein. Photopigments are classified by their wavelength of maximum absorbance.
Photoreceptor A sensory neuron that contains chromophores bound to opsin proteins within their membranes and thus responds to light. Examples include rod and cone cells in the eyes of vertebrates.
Spectral tuning Adaptive shifts in the absorption spectra of photopigments, aligning peak spectral sensitivity with the predominant wavelengths available in a particular environment.

☆*Change History*: October 2021. DM Leech and S Johnsen as requested, Leech and Johnsen have rewritten the chapter from a broader perspective to discuss all wavelengths of light, not just UV radiation. References are included. Further reading has been revised to match updated text. Relevant websites have been updated. Tables 1 and 2 are new to this edition. Figs. 1, 2, and 6 were retained from the previous chapter. Figs. 3–5 & 7–10 have been added.

Introduction

Light energy has bathed the Earth since its formation ~4.5 billion years ago, even at depth in underwater environments. It is therefore unsurprising that most species have evolved the ability to capture light and utilize it as an ecological resource. Beyond its conversion into chemical energy by primary producers, light—via photoreception— enhances the fitness of organisms in numerous ways, ranging from habitat selection, foraging, and mate choice to the setting of biological clocks. What is somewhat surprising is that the basic mechanism of light capture, or photoreception, is similar across all three domains of life: Bacteria, Archaea, and Eukarya. This suggests that photoreception is an evolutionarily old trait. Often, with only small modifications at the molecular level, species adapt, or spectrally tune, to light in their environment. Nevertheless, benefits of photoreception must be balanced with potential costs, such as exposure to damaging solar radiation. In the present chapter, we briefly describe the properties of light in freshwater environments and the structure and function of photoreceptors used to capture light. We discuss the visual and non-visual uses of photoreception by a wide diversity of taxa as well as possible tradeoffs. We further highlight how recent, human-induced alterations in the underwater light environment, including eutrophication, brownification, and artificial lighting (or light pollution), affect inland waters. We conclude with knowledge gaps that require future research.

The underwater light environment

Light in freshwater ecosystems primarily originates from the Sun and is both absorbed and scattered as it penetrates through water. As a result, downwelling irradiance decreases with depth, with shorter and longer wavelengths attenuating more rapidly than the wavelength of peak transmission (generally between 470 nm (blue light) and 550 nm (green light)). In clear, oceanic water, absorption by the water itself is the primary source of light attenuation. However, particulate and dissolved organic matter are typically the dominant contributors to light attenuation in freshwater ecosystems. Increased phytoplankton biomass attenuates light as a result of both scattering and absorption, particularly in the visible range (400–700 nm). In systems with moderate-to-high dissolved organic carbon (DOC) (>3 mg L^{-1}), UV and blue wavelengths (<450 nm) are attenuated rapidly, and the underwater light field shifts towards longer wavelengths (>550 nm), while in systems with low DOC (<3 mg L^{-1}), shorter wavelength radiation penetrates farther, and UV and blue wavelengths are more prevalent. In 1996, 25% of the lakes in North America were estimated to have 1% attenuation depths (the depth to which 1% of surface irradiance remains) greater than 4 m for 320 nm UV-B radiation and greater than 10 m for 380 nm UV-A radiation (Williamson et al., 1996). However, more recent data from the United States Environmental Protection Agency's National Lakes Assessment Program suggest that the percentage of clear, blue lakes in the US is declining (i.e., 46% of lakes in 2007 to 28% in 2012) while the percentage of murky lakes is increasing (i.e., 24% of lakes in 2007 to 35% in 2012), due to continued inputs of nutrients and organic matter from the terrestrial watershed (Leech et al., 2018). In turn, these changes in water color dramatically affect light penetration depth, intensity, and spectral characteristics (Levine and MacNichol, 1982; Fig. 1).

Additionally, solar elevation, cloud cover, and turbidity influence light availability at depth by affecting either surface light or the depth to which surface light can penetrate (Kirk, 2010). In shallow, relatively clear waters, the reflectance of bottom substrates can have a significant effect on the light environment. For rivers and streams, canopy cover and riverbed topology must also be considered (Julian et al., 2008; Heaston et al., 2017).

Together, these differences in light intensity and spectral composition create potential "light niches." For example, relative quantities of UV radiation can be greater during crepuscular periods (i.e., dawn and dusk) compared to daylight hours due to the increasing proportion of high-UV skylight in the total irradiance (Fig. 2). Twilight hours may therefore provide a temporal niche for predators with UV vision, enhancing target–background contrast and potentially silhouetting prey (Cronin and Bok, 2016), while clear waters near the surface may provide a spatial niche, with relatively more available UV radiation compared to deeper depths. The relative abundance of UV radiation, compared to visible light, is highest in the horizontal and downward lines of sight, representing up to 40% of the total photons in clear oceanic surface waters (Johnsen, 2012). In both cases, UV radiation can serve as a short-range private communication channel for organisms with UV vision because it is absorbed and scattered more than most visible wavelengths.

While bioluminescence is an important source of light in the ocean, it is extremely rare in fresh waters. Only one genus of adult freshwater bioluminescent animal has been identified, the freshwater limpet-like snail *Latia*. It consists of four species that reside in clean, fast flowing streams in New Zealand (Shimomura et al., 1972; Ohmiya et al., 2005). In contrast, bioluminescence has been widely observed in marine taxa, from bacteria to sharks (Widder, 2010; Johnsen, 2012). The reason for the lack of bioluminescence in fresh waters remains unknown.

Biological photoreceptors

Structure and function

Photoreceptor proteins have been observed in all domains of life, including rhodopsins, phytochromes, xanthopsins, cryptochromes, phototropins, and BLUF or "sensors for blue-light using FAD" proteins. In archaea, bacteria, and eukaryotes, photoreceptors often consist of a chromophore bound to an opsin protein, and together, they are referred to as a rhodopsin, photopigment,

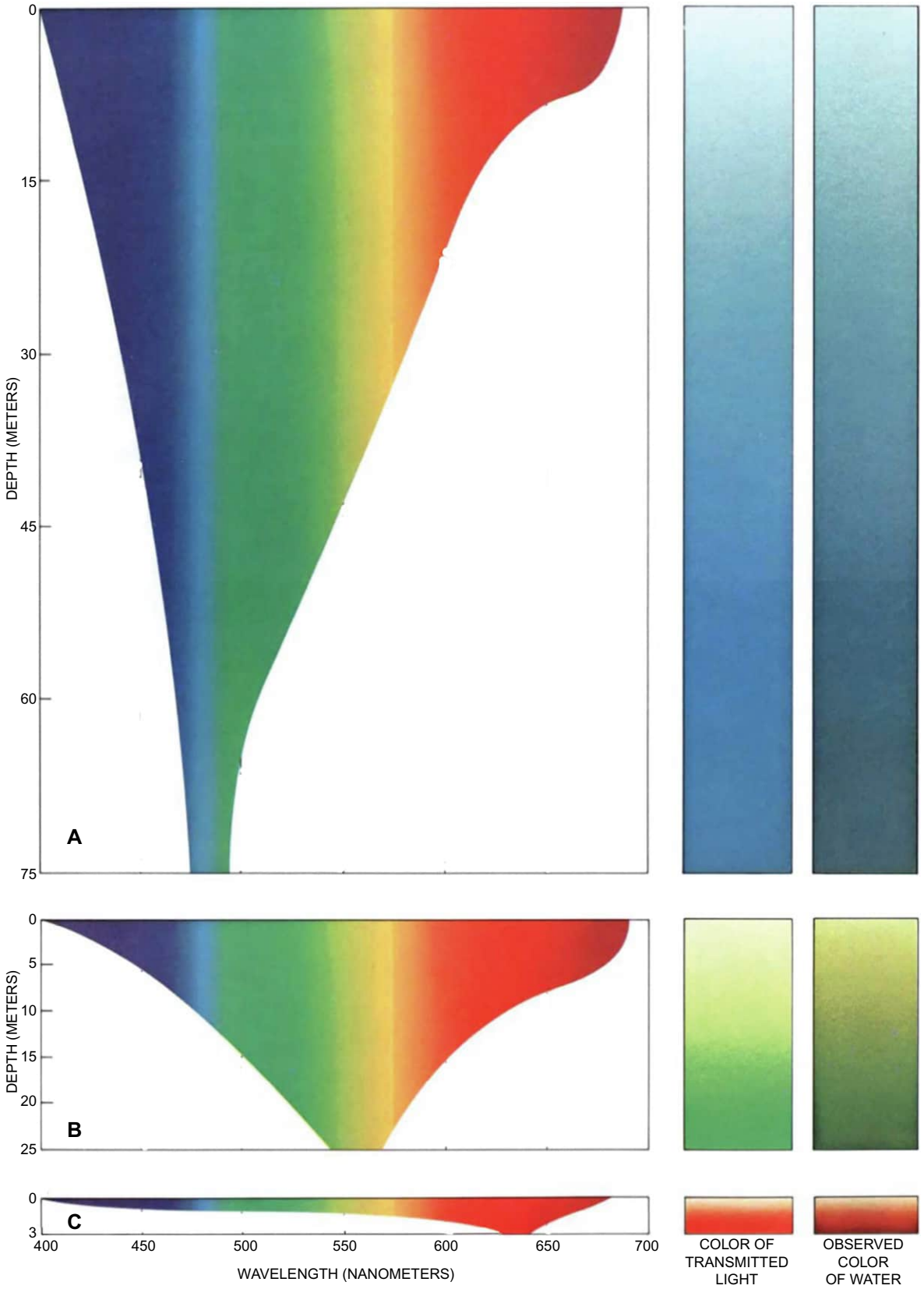

Fig. 1 Transmission of light by water is dependent on the color or wavelength of the light. In clear oceans and lakes (A) the light becomes increasingly monochromatic and blue as its path length increases. In fresh water that carries green organic matter (B) light at all wavelengths is absorbed more quickly than it is in clear water, but the light becomes greener with path length. In rivers, swamps and marshes that carry large amounts of the products of plant and animal decay (C) absorption is rapid and the spectral distribution of the light shifts to the red. Such waters are called black because the human eye is relatively insensitive to light at long wavelengths; a less anthropomorphic name would be infrared water. The depths given for the maximum penetration of light are typical, but they vary widely. Reproduced with permission from Levine J and MacNichol E (1982). Color vision in fishes. *Scientific American* 246: 140–149.

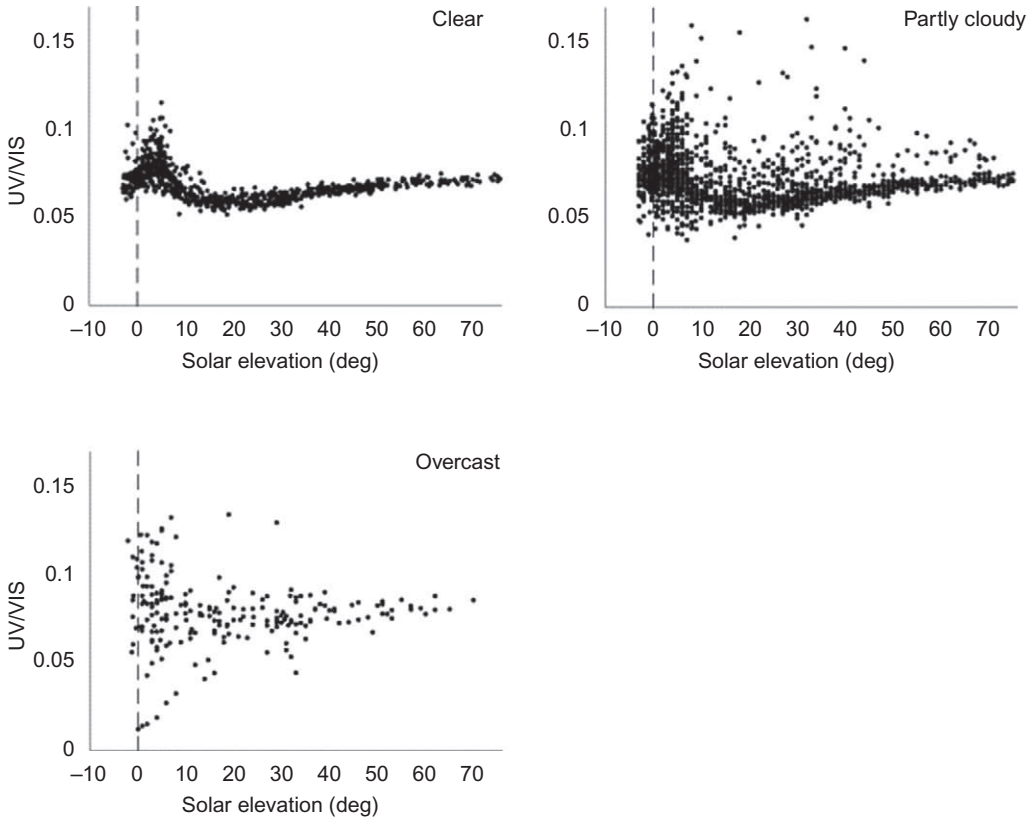

Fig. 2 Ratio of UV (300–380 nm) to visible light (380–780 nm) as a function of solar angle under clear, partly cloudy, and overcast conditions. A total of 2600 spectra were measured from the roof of the University of Granada's Science Faculty (Granada, Spain, 37_110N 3_350W, elevation 680 m) from February 1996 to February 1998 using a LI-1800 spectroradiometer (LI-COR Bioscience, Lincoln, NE, United States) fitted with a cosine-corrected receptor. Measurements were taken at all solar elevations greater than -4^{o} and in all weather except for rain or snowfall. Data were collected at 5 nm intervals from 300 to 1100 nm. Data are courtesy of Dr. Javier Hernandez-Andres at the University of Granada in Spain.

or visual pigment (Fig. 3). Each photopigment absorbs light most efficiently at a specific wavelength based on the amino acid sequence of the opsin protein and its interaction with the chromophore. Most often the chromophore is either 11-cis-retinal (A1) or 11-cis-dehydroretinal (A2) although other chromophores have been identified. Opsin proteins are more diverse and are divided into two major groups: Type I opsins, or microbial opsins, found in archaea, bacteria, algae, and fungi, and Type II opsins, or animal opsins, found only in metazoans (Table 1).

Both microbial- and animal-opsins are seven-transmembrane-helix receptor proteins (Ernst et al., 2014). Yet interestingly, despite their similarity in protein tertiary structure, Type I and II opsins are believed to have evolved through convergent evolution, given the lack of homology in their amino acid sequences (Ernst et al., 2014). Organisms often possess multiple opsin genes that allow them to measure and compare light intensity across a broader spectrum (Fig. 3). For example, five general families of opsins are observed across a diversity of aquatic taxa, including the rod opsin RH (blue-green sensitive, 460–530 nm) and four cone opsins: SWS-1 (ultraviolet sensitive, 355–450 nm), SWS-2 (shortwave sensitive, 415–480 nm), MWS (mid-wavelength sensitive, 470–530 nm), and LWS (long-wavelength sensitive, 495–570 nm) (Table 2).

For single-celled organisms, photoreceptors most often occur as simple cell membrane receptors; however, advanced ocular structures are found in some species. For example, warnowiid dinoflagellates have a light-sensitive ocelloid that is similar to the camera-like eyes of multicellular organisms (Hayakawa et al., 2015), and cells of the freshwater cyanobacterium *Synechocystis* act like lenses, focusing light to a single point inside the cell (Schuergers et al., 2016). In animals, photoreceptors are often associated with eyes, which can allow for color vision and detailed image formation. However, extraocular photoreceptors are commonly found throughout the body (e.g., pineal gland, brain, nerves, and skin), serving important non-visual functions (Cronin and Johnsen, 2016).

Eyes and color vision

Eyes are unique to animals and vary in complexity from simple eyespots that can only detect shadows to camera-like and compound eyes with detailed color vision. The evolution of eye complexity generally correlates with a species' visually guided behaviors

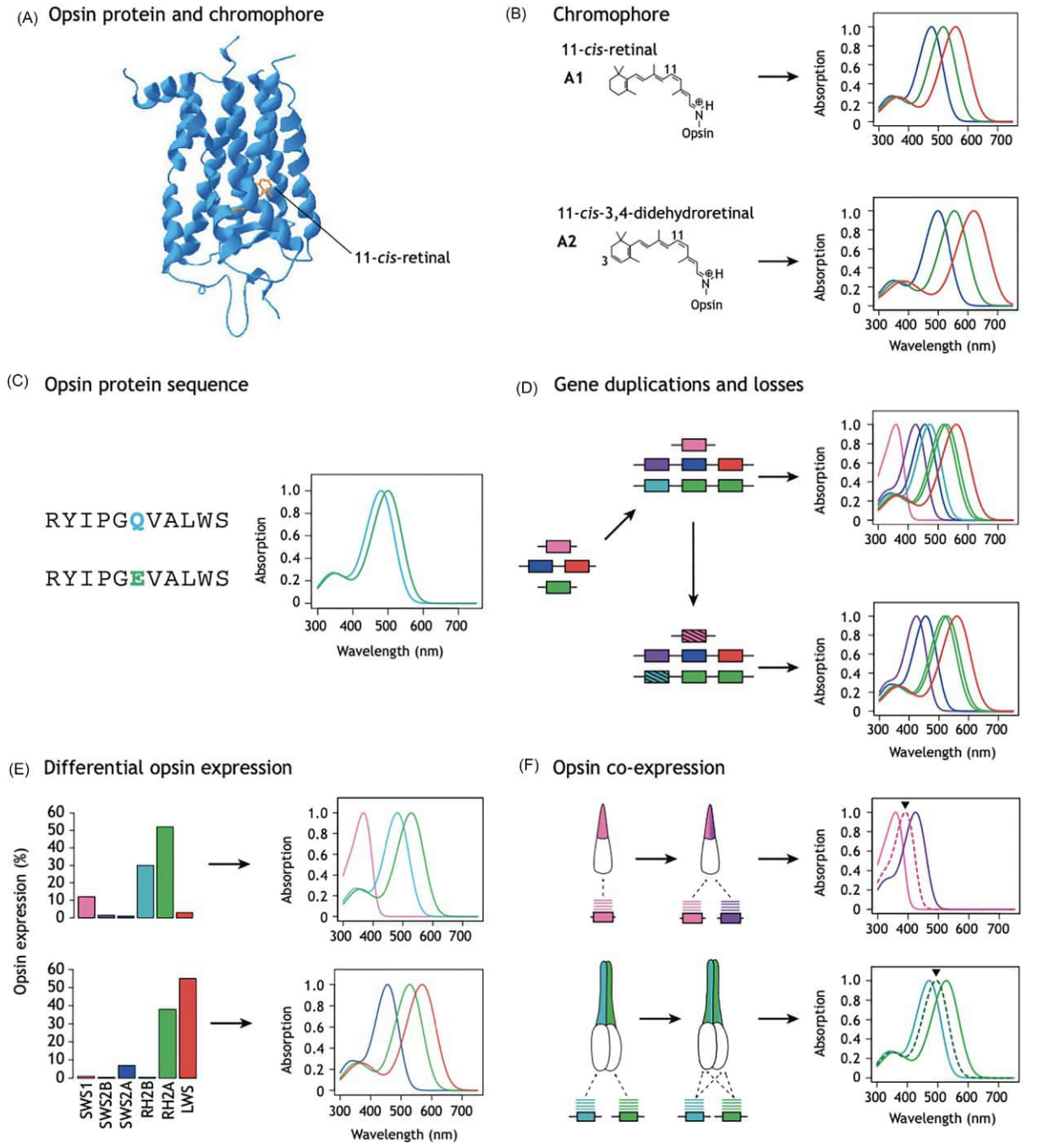

Fig. 3 Mechanisms affecting visual pigment sensitivities, including changes to opsin genes and the retinal chromophore. (A) Photoreceptor sensitivities are set by visual pigments, which are composed of chromophores (yellow) and opsin proteins (blue). Several different mechanisms can alter sensitivities (shown by absorption spectra for each visual pigment) including: (B) shifts between vitamin A1- and A2-derived chromophores; (C) changes to opsin amino acid residues; (D) opsin gene duplications and losses, with duplicate genes acquiring new function (e.g., violet versus blue) and some duplicates subsequently being lost (shaded); (E) differential opsin expression (shown as % total cone opsin); and (F) co-expression of multiple opsins with co-expression possible both in single cones (top) and double cones (bottom). Opsin genes are color coded as SWS1 (pink), SWS2B (violet), SWS2A (blue), RH2 (blue-green to green) and LWS (red). From Carleton KL, Escobar-Camacho D, Stieb SM, Cortesi F and Marshall NJ (2020) Seeing the rainbow: mechanisms underlying spectral sensitivity in teleost fishes. *Journal of Experimental Biology* 223: jeb193334.

(Land and Nilsson, 2012; Nilsson, 2013). Non-directional photoreception, such as monitoring ambient light intensity as a depth gage or to set a circadian clock, requires simple light sensing structures while high resolution vision, needed to detect, pursue, and communicate with others at relatively long distances, requires more complex structures (Fig. 4). In vertebrates, eyes consist of a cornea and lens to collect and focus light combined with a retina of photoreceptors that absorb and thus detect light. These retinal photoreceptors include rods, which aid in low-light vision, and cones, which permit color vision.

Table 1 Summary table of common Type I and Type II opsins and their general location and function.

Opsins	*Location*	*Known functional roles*
Type I: present in archaea, bacteria, and algae		
Bacteriorhodopsin	Cell membrane	Photosynthesis; proton pump
Bacterial sensory rhodopsins	Cell membrane	Ion-pump; proton-pump; phototaxis
Channelrhodopsins	Cell membrane	Ion channel; phototaxis
Halorhodopsin	Cell membrane	Chloride pump; phototaxis
Proteorhodopsin	Cell membrane	Ion and proton pumps
Type II: present in animals (excluding sponges)		
C-opsins (Ciliary)	Eye, brain, skin, pineal organ, sperm, heart, kidney, liver, blood vessels, placenta	Vertebrate vision, ranging from non-directional light sensors to high resolution image formation and color vision; entraining circadian rhythms; body color change; photorelaxation of blood vessels
Cnidops (Cnidarian opsins)	Eye, neuropil (jellyfish)	Entraining circadian rhythms; gamete release
R-opsins (Rhabdomeric)	Eye, brain, skin, pineal, blood vessels, sperm	Invertebrate vision; entraining circadian rhythms
Go/RGR	Eye, brain, spinal cord, pineal, skin, sperm, tube feet	Photoisomerases; regulate retinoid traffic

Not an all-inclusive list. Based on information from Ernst et al. (2014) and Leung and Montell (2017).
New functional roles continue to be discovered.

Animals must express multiple opsins with varying wavelengths of peak absorption in order to see color. Some have simple color vision with only two types of cone photoreceptors (dichromacy) while others see a broader color spectrum as tri- or tetra-chromats; the latter of which generally possess UV vision (Cronin and Bok, 2016). Invertebrates are generally dichromats or trichromats, often with one UV sensitive photopigment (Land and Nilsson, 2012). Among vertebrates, fishes show the greatest diversity for detecting color, with more colorful fishes displaying increased chromacy (Marshall and Vorobyev, 2003). That said, many freshwater, predatory fishes are dichromatic, with color vision centered on red and green wavelengths, such as adult largemouth bass *Micropterus salmoides* (Lythgoe, 1979; Mitchem et al., 2019).

Spectral tuning

The ability to adjust to spectral changes in the optical environment is advantageous. This spectral tuning is accomplished in several ways, over both short- and long-time scales (i.e., days to generations). Natural selection acts on opsin genes that vary in amino acid sequence to allow for light absorption across the visible solar spectrum, from the ultraviolet to near-infrared. Interestingly, even single amino acid changes may cause up to 75 nm shifts in spectral sensitivity, depending on the location and proximity/interaction with the chromophore (Carleton et al., 2020). In addition, switching the chromophore from vitamin A1 (retinol) to A2 (3,4-didehydroretinol) shifts peak absorbance to longer wavelengths. This is often seen in amphibians, crustaceans, fishes, and insects on a behavioral and/or seasonal basis as the dominant wavelengths of their light environment change (Fig. 5; Enright et al., 2015). Interestingly, the adult American bullfrog has A1-based photopigments in the lower portion of the retina and a mixture of A1- and A2-based pigments in the upper portion, corresponding to its time spent at the air-water interface (Enright et al., 2015). The fact that sea lamprey display A1 to A2 chromophore shifts suggests that this trait may have evolved during the Cambrian period, approximately 500 Mya (Morshedian et al., 2017). In animal eyes, changes in the shape and pigmentation of the lens can also affect the wavelength of peak light absorbance. For instance, retinal UV sensitivity is only possible if the ocular media are UV transparent and UV- and blue-sensitive photoreceptors are present (Cronin and Bok, 2016).

With the increasing use of molecular techniques in visual ecology, we have learned that species can down- and up-regulate opsin genes within their genome based on environmental conditions. For example, African cichlids possess seven opsin genes in their genome but generally only express three to four (Carleton et al., 2020). Gene expression differs among cichlid species inhabiting surface versus benthic habitats, clear versus turbid lakes, as well as at different life history stages within a species (Fig. 6). More recently, regulation of opsin gene expression has been demonstrated on finer time scales. Killifish (*Lucania goodei*) transferred from clear to tannin-stained waters, and vice versa, were shown to spectrally tune by altering opsin gene expression within 1–3 days (Fuller and Claricoates, 2011). This suggests that spectral sensitivity and tuning are more plastic than previously thought. Differential expression of opsin genes within a species' genome is hypothesized to permit expansion into varied habitats, as seen in the highly invasive western mosquitofish *Gambusia affinis*. This species also possesses seven cone opsin genes (i.e., one *sws1*, two *sws2*, one *rh2*, and three *lws*), with gene expression for short-wavelength *sws1* and *sws2* being higher in larval stages compared to adults (Chang et al., 2020). More information is needed to understand the role of spectral tuning in invertebrates. The water flea *Daphnia pulex* contains the largest number of opsin genes reported thus far, with 46 opsin genes encoded in its genome. Based on molecular phylogeny, 27 of these genes are related to vision; however, their functional role, including possible involvement in spectral tuning, is unknown (Colbourne et al., 2011).

Table 2 Representative peak absorbances for short-wavelength (sws1, sws2), mid-wavelength (MWS), long-wavelength (LWS), and rod photoreceptors among aquatic taxa.

Species	*Collection site*	*Life history stage*	*SWS1*	*SWS2*	*MWS*	*LWS*	*Rod*	*Method*	*References*
Zooplankton									
Asplanchna brightwelli, Rotifer	Freshwater	Adult	*	*	*	*	NR	Behavior	Clément and Wurdak (1984)
Asplanchna girodi, Rotifer	Freshwater	Adult	–	–	*	–	NR	Behavior	
Asplanchna priodonta, Rotifer	Freshwater	Adult	*	*	*	*	NR	Behavior	
Brachionus calyciflorus, Rotifer	Freshwater	Adult	*	–	*	*	NR	Behavior	
Filinia longiseta, rotifer	Freshwater	Adult	*	*	*	–	NR	Behavior	
Daphnia magna, Water flea	Freshwater	Adult	348	434	525	608	NR	MSP	Smith and Macagno, (1990)
Daphnia pulex, Water flea	Freshwater	Adult	*	*	*	*	*	RNA seq	Database Colbourne et al. (2011)
Eucyclops serrulatus, Copepod	Freshwater	Unknown	–	–	*	–	*	RNA seq	Database Porter et al. (2017)
Lernaea cyprinacea, Copepod	Freshwater	Unknown	*	–	*	–	*	RNA seq	Database Porter et al. (2017)
Unionicola aculeata, water mite	Mussel symbiont	Adult	–	*	*	560	NR	Behavior	Dimock and Davids (1985)
Unionicola bonzi, water mite	Mussel symbiont	Adult	–	*	*	560	NR	Behavior	Dimock and Davids (1985)
Unionicola ypsilophora, water mite	Obligate Mussel symbiont	Adult	–	*	*	600	NR	Behavior	Dimock and Davids (1985)
Triops longicaudatus, Tadpole Shrimp	Ephemeral pools	Adult	362	415	500	606	NR	ERG	Lessios et al. (2018)
Strptocephalus mackini, Fairy Shrimp	Ephemeral pools	Adult	360	430	550	586 600	NR	ERG	Lessios et al. (2018)
Decapods									
Orconectes immunis	Freshwater	Adult	–	425	–	565	NR	ERG	Goldsmith and Fernandez (1968)
Orconectes virilis	Freshwater	Adult	–	425	–	565	NR	ERG	Goldsmith and Fernandez (1968)
Procambarus clarkii, crayfish	Freshwater	Adult	–	–	–	570	530	ERG	Kennedy and Bruno (1961)
P. clarkii, crayfish	Freshwater	Adult	–	440	530	–	NR	MSP	Cummins and Goldsmith (1981)
Fishes									
Cottus kessleri	Lake Baikal, 2–5 m	Adult	–	449	525	–	515	MSP	Bowmaker et al. (1994)
Paracottus kneri	Lake Baikal, 2–5 m	Adult	–	450	522	–	516	MSP	Bowmaker et al. (1994)
Batrachocottus baicalensis	Lake Baikal, 1–120 m	Adult	–	450	521	–	509	MSP	Bowmaker et al. (1994)
Batrachocottus nicolskii	Lake Baikal, 300–1000 m	Adult	–	428	511	–	488	MSP	Bowmaker et al. (1994)
Cottocomephorus inermis	Lake Baikal, 50–450 m	Adult	–	450	520	–	495	MSP	Bowmaker et al. (1994)
Cottocomephorus grewingki	Lake Baikal, 1–300 m	Adult	–	449	523	–	503	MSP	Bowmaker et al. (1994)
Asprocottus intermedius	Lake Baikal, 100–500 m	Adult	–	–	512	–	488	MSP	Bowmaker et al. (1994)
Limnocottus eurystomus	Lake Baikal, 100–500 m	Adult	–	428	515	–	490	MSP	Bowmaker et al. (1994)

(*Continued*)

Table 2 (Continued)

Species	*Collection site*	*Life history stage*	*SWS1*	*SWS2*	*MWS*	*LWS*	*Rod*	*Method*	*References*
Limnocottus pallidus	Lake Baikal, 100–1000 m	Adult	–	–	500	–	488	MSP	Bowmaker et al. (1994)
Cottinella boulengeri	Lake Baikal, 100–1000 m	Adult	–	–	496	–	482	MSP	Bowmaker et al. (1994)
Abyssocottus korotneffi	Lake Baikal, 400–1500 m	Adult	–	–	494	–	481	MSP	Bowmaker et al. (1994)
Comephorus dybowskii	Lake Baikal, 200–1500 m	Adult	–	–	–	–	498	MSP	Bowmaker et al. (1994)
Salmo trutta, Brown Trout	Freshwater	Young-of-the Year	355	440	535	600	NR	MSP	Bowmaker and Kunz (1987)
Ictalurus punctatus, Channel catfish	Aquaculture	Larvae & Adult	–	–	535	608	541	MSP	Sillman et al. (1993)
I. catus, White Catfish	Freshwater	Adult	–	–	536	605	541	MSP	Sillman et al. (1993)
Ictalurus melas, Black Bullhead Catfish	Freshwater	Adult	–	–	536	607	541	MSP	Sillman et al. (1993)
Ictalurus nebulosus, Brown Bullhead Catfish	Freshwater	Adult	–	–	–	530	541	MSP	Sillman et al. (1993)
Kryptopterus bicirrhis, Glass Catfish	Aquaculture	Juveniles	–	–	–	607	540	MSP	Douglas and Wagner (1984)
Lepomis macrochirus, Bluegill Sunfish	Freshwater	Adult	–	–	536	620	NR	MSP	Hawryshyn et al. (1988)
Lepomis cyanellis, Green Sunfish	Freshwater	Adult	–	–	525	621	525	ERG	Dearry and Barlow. (1987)
Micropterus salmoides, Largemouth bass	Freshwater	Adult	–	–	535	614	528	MSP Behavior	Mitchem et al. (2019)
Carassius auratus, Goldfish	Freshwater	Adult	356	447	537	623		SPE	Palacios et al. (1998)
Danio rerio, Zebrafish	Freshwater	Adult	360	400	500	580	NR	ERG	Hughes et al. (1998)
Scardinius erythrophthalmus, Rudd	Freshwater	Adult	355–360	405–415	505–515	565–610	534	MSP/ERG	Whitmore and Bowmaker (1989)
Amphibians									
Xenopus sp., African clawed frog	Freshwater	Adult	>400	434 440	–	611	440 523		Röhlich and Szél (2000)
Pleurodeles waltl, Ribbed newt	Unknown	Adult	360 377	489	–	611	503,529	MSP	Korenyak and Govardovskii (2013)
Lissotriton vulgaris, Common Newt	Unknown	Adult	340	470	–	609	499,523	MSP	Korenyak and Govardovskii (2013)
Cynops orientalis, Red-bellied Newt	Unknown	Adult	350	466 477	–	547	496,519	MSP	Korenyak and Govardovskii (2013)
Reptiles									
Alligator mississippiensis, Mississippi Alligator	Freshwater	Juveniles	–	443	535	566	500	MSP	Sillman et al. (1991)
Caiman crocodilus, Caiman	Freshwater	Juveniles	–	430	535		506	MSP	Govardovskii et al. (1988)
Crocodylus johnstoni, Freshwater crocodile	Freshwater	Juveniles	–	426	510	554	510	MSP	Nagloo et al. (2016)
Trachemys scripta elegans, Red Eared Turtle	Herp Dealer Freshwater	Adult	372	458	515	617	518	MSP	Loew and Govardovskii (2001)

Methodology includes behavioral assays, electroretinogram (ERG), microspectrophotometry (MSP), suction pipette electrodes (SPE), and identification of RNA sequences in genetic databases. Dashed lines indicate the absence of a particular group of photoreceptors. The asterisks indicate that a photoreceptor is present, but the peak absorbance was not reported because photoreception was determined by behavior experiments or molecular evidence from genetic sequence databases. In some cases, sources focused on cone photoreceptors and not rods. We indicate these with NR for not reported. Based on our survey, fishes are extensively studied but more research is needed to identify specific peak absorbances for invertebrate photoreceptors.

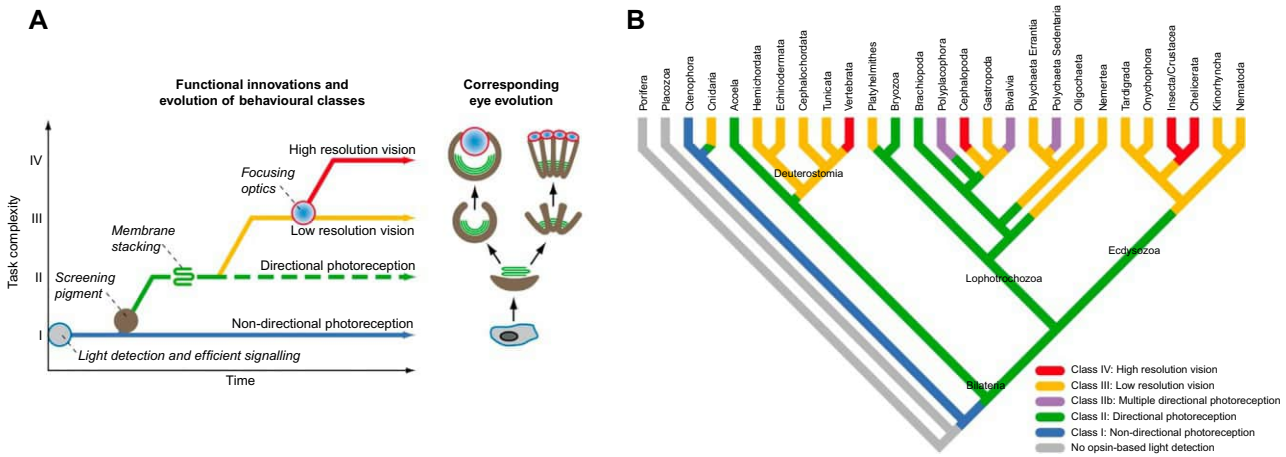

Fig. 4 Behavior and the evolution of the eye. (A) Schematic illustration of the evolution of photoreceptive behaviors on a vertical scale of task complexity, with the position of major functional innovations indicated. The line for directional photoreception is dashed to indicate that class II tasks may become superfluous by the evolution of class III tasks, whereas the other classes remain relevant after a higher class has evolved. Eyes capable of class IV tasks can still handle class III tasks. The corresponding receptor/eye morphologies are shown to the right. Note that compound and single chambered eyes are principally different solutions, suggesting independent transitions from class II to class III. (B) The classes of photoreceptive tasks plotted on a metazoan phylogeny. Reproduced from Nilsson DE (2013) Eye evolution and its functional basis. *Visual Neuroscience* 30: 5–20.

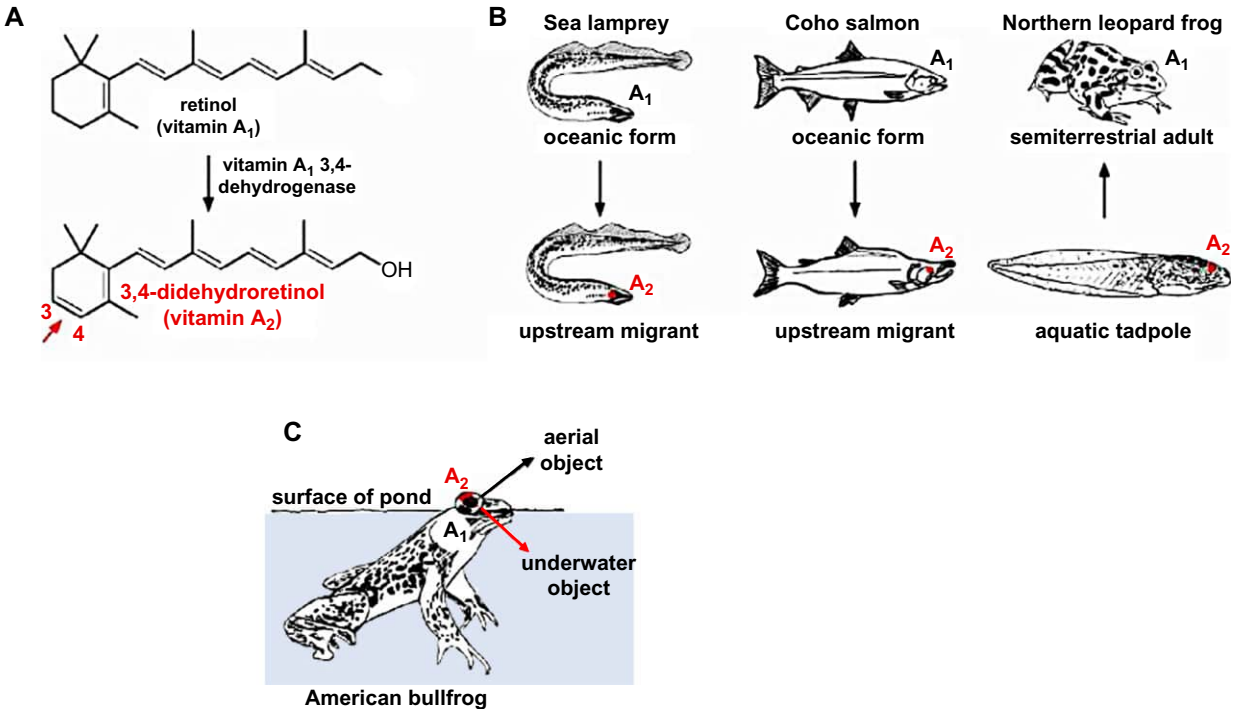

Fig. 5 Examples of chromophore switching. (A) The conversion of retinol (vitamin A1) to 3,4-didehydroretinol (vitamin A2) underlies the rhodopsin-to-porphyropsin switch. (B) This vitamin A1 to A2 switch is widely used by a variety of vertebrates and can be deployed at key stages of the life cycle: e.g., during upstream migration in sea lamprey (*Petromyzon marinus*) and Coho salmon (*Oncorhynchus kisutch*) and upon metamorphosis in amphibians such as the Northern leopard frog (*Lithobates pipiens*). (C) The American bullfrog (*Lithobates catesbeianus*) often sits at the water's surface and possesses exclusively A1-based visual pigments in the ventral retina and a mixture of A1- and A2-based visual pigments in the dorsal retina, possibly facilitating downward vision into murky, red-shifted water. Modified from Enright JM, Toomey MB, Sato SY, Temple SE, Allen JR, Fujiwara R, Kramlinger VM, Nagy LD, Johnson KM, Xiao Y, How MJ, Johnson SL, Roberts NW, Kefalov VJ, Guengerich FP and Corbo JC (2015). Cyp27c1 red-shifts the spectral sensitivity of photoreceptors by converting vitamin A1 into A2. *Current Biology* 25: 3048–57.

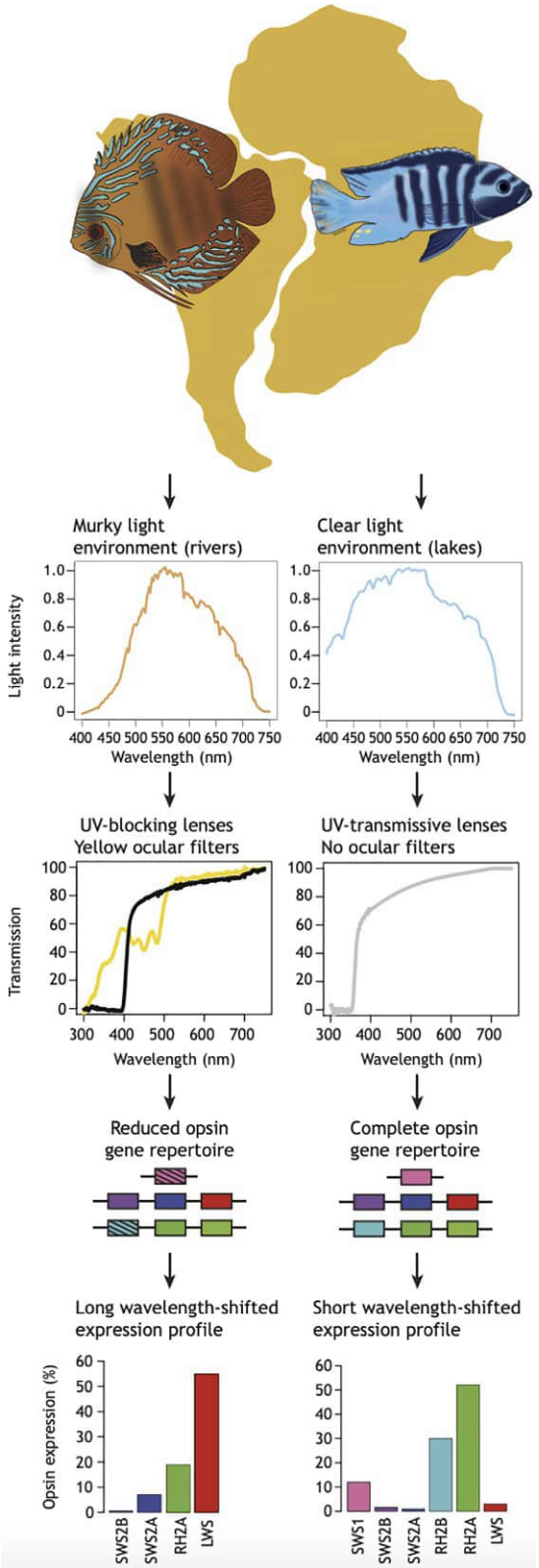

Fig. 6 Visual system divergence in cichlids. Cichlids have adapted to different rivers and lakes on different continents. African rivers and lakes may be quite clear, leading to a diverse array of opsin genes that detect a broad spectrum of light. South American waters are often murkier, such that cichlids have lost a number of shorter wavelength opsins. South American cichlids have also acquired yellow cornea and lens filters, perhaps to reduce the transmission of scattered light in the murkier waters. References cited within text. From Carleton KL, Escobar-Camacho D, Stieb SM, Cortesi F and Marshall NJ (2020) Seeing the rainbow: mechanisms underlying spectral sensitivity in teleost fishes. *Journal of Experimental Biology* 223: jeb193334.

Adaptive significance of photoreception

The conversion of light to chemical energy by primary producers is arguably the most important example of light as an ecological resource. However, light perception also conveys valuable spatial and temporal information that can enhance an organism's fitness. Visually, light helps organisms to select optimal habitats and mates, find food, and avoid predators. Non-visually, light aids in setting biological clocks as well as regulating other physiological functions, like proton and ion pumps in microbes. Here, we briefly describe the adaptive significance of photoreception in a wide diversity of freshwater taxa.

Visual functions

Diel vertical migration

In aquatic ecosystems, an organism's position in the water column can mean life or death. Light works as an effective depth gage, varying in intensity and spectral quality as it travels downward through the water column. By comparing differences in the quantity and quality of light with depth, species respond with positive or negative phototaxis. One of the most interesting behavioral responses to sunlight is the phenomenon of diel vertical migration (DVM). Large zooplankton, like the cladoceran *Daphnia* spp., the cyclopoid *Mesocyclops* spp., and the phantom midge larvae *Chaoborus* spp., often exhibit deep migrations during the day to darker depths in the water column (Lampert, 1989; Hayes, 2003). In turn, smaller zooplankton, including rotifers and copepod nauplii, remain in the surface waters during daylight and migrate to the deeper waters at night to avoid predation or competition with larger zooplankton. Many factors, including temperature and food availability, have been proposed to explain these patterns in fresh waters; however, predation by visually feeding fish is typically identified as the primary factor inducing DVM (Lampert, 1989; Hayes, 2003). Nevertheless, in high-UV systems, ultraviolet radiation may induce downward, diel vertical migrations in freshwater zooplankton, even in the absence of predators (Leech and Williamson, 2001; Williamson et al., 2011; Fischer et al., 2015).

Avoidance of damaging solar radiation

A wide diversity of aquatic taxa display avoidance behaviors to damaging solar radiation, particularly UV radiation and short wavelength blue light. In algae, exposure to high intensities of sunlight can bleach pigments critical to photosynthesis. Negative phototactic responses have been detected in protists, like the freshwater ciliate *Blepharisma japonicum*, which swims away from wavelengths of UV-B but swims towards yellow light (580 nm) (Lenci et al., 1997). Within filamentous cyanobacterial mats, individual cells of *Microcoleus chthonoplastes* were shown to migrate to greater depths in response to increased UV-B exposure (Bebout and Garcia-Pichel, 1995). Interestingly, in the cyanobacterium *Chlorogloeopsis*, a UV-B photoreceptor regulates the production of shinorine, a photoprotective compound (Portwich and Garcia-Pichel, 2000; Singh et al., 2008).

The zooplankter *Daphnia magna* is positively phototactic to wavelengths of visible light (421–600 nm) and negatively phototactic to UV radiation (260–380 nm), with maximal sensitivity at 340 nm (Smith and Macagno, 1990). Field experiments in high-UV lakes have also demonstrated a strong negative phototactic response to UV radiation in *Daphnia* as well as calanoid

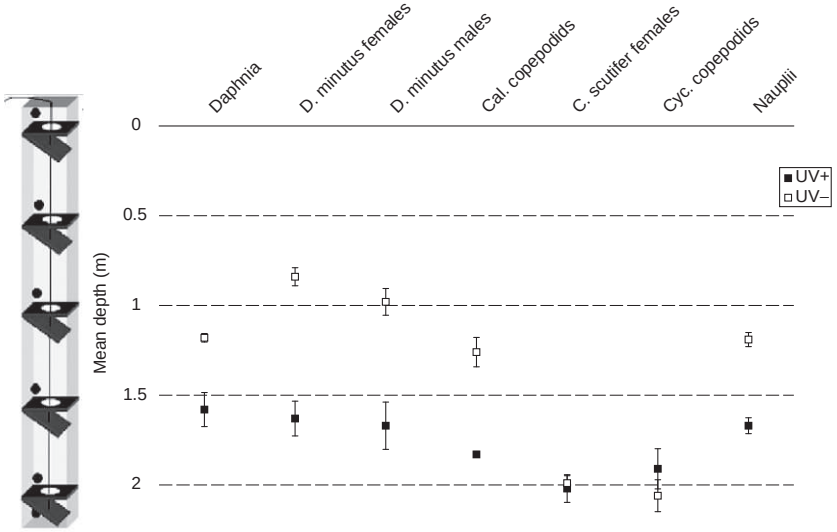

Fig. 7 Mean depths of zooplankton in the presence and absence of UVR at the surface of Lake Giles, Pocono Mountains, PA, United States. Error bars represent standard errors. Zooplankton were placed in 2.2 m long acrylic columns that were either UV-transparent or UV-blocking columns (shown to the left). Columns were suspended from 0 to 2 m between 9:00 p.m. on 20 June to 10.30 a.m. on 21 June 2001. At the end of the experiment, the trap doors were closed and the number of species in each section was counted. Species included the cladoceran *Daphnia catawba*, the calanoid copepod *Diaptomus minutus*, and the cyclopoid copepod *Cyclops scutifer*. Copepod nauplii represent both calanoids and cyclopids. Note the deeper distribution of the Daphnia and calanoid copepods in the presence of UVR. *C. scutifer* is a cold-water species that typically inhabits the deeper waters of Lake Giles during both the day and night. Therefore, their deep distribution in both the UV+ and UV− treatments is expected.

copepods (Fig. 7; Leech et al., 2009; Fischer et al., 2015). Zooplankton with increased photoprotective compounds, such as carotenoids, melanin, and mycosporine amino acids, are often less responsive to shorter-wavelength radiation (Rautio and Tartarotti, 2010). More recently, negative phototactic behaviors in response to UV exposure have been observed in benthic species, such as the planarian *Schmidtea mediterranea* (Paskin et al., 2014) and the leech *Hirudo* spp. (Jellies, 2014). Little or no behavioral responses were observed when exposed to visible light (Jellies, 2014; Paskin et al., 2014).

Differences in the spawning depths of yellow perch (*Perca flavescens*) in a high-versus a low-UV lake suggest that they also avoid exposure to UV radiation (Williamson et al., 1997; Huff et al., 2004). Comparable results have been reported for nest building in bluegill sunfish *Lepomis macrochirus* (Olson et al., 2006). This is particularly interesting because adult perch and sunfish lack UV-sensitive cones, unlike larval stages. Vertical distribution patterns differ for larval vendace (*Coregonus albula*) occupying the surface waters of clear versus brown Finnish lakes (Ylönen et al., 2005). Larvae in clear lakes were deeper on sunny days compared to cloudy days. Laboratory experiments with larval zebrafish have linked retinal UV photoreceptors in larval zebrafish to UV avoidance behaviors (Guggiana-Nilo and Engert, 2016). In contrast, zebrafish larvae swim towards light with wavelengths >400 nm (Guggiana-Nilo and Engert, 2016).

Predator avoidance

As described above, exposure to visible light serves as a proximate cue for zooplankton to move deeper, which ultimately aids in avoiding visual predators. Similar behaviors are seen in streams, whereby macroinvertebrates drift downstream during twilight or dark hours to presumably avoid visual predators while searching for improved habitat conditions (Nanam et al., 2015). In both cases, invertebrates are required to distinguish changes in light due to time of day from changes due to variations in canopy- or cloud cover (Ringelberg, 1999; Schloss and Haney, 2006). Vertical and horizontal migrations in response to light levels are dampened in the absence of predator cues, such as kairomones, suggesting an integration of light and olfactory stimuli to properly execute the behavior (Ringelberg, 1999).

Light can also help prey avoid direct contact with predators. "Shadow responses" are associated with rapid changes in behavior, such as altered swimming speed/direction or body contraction, due to sudden reductions in light intensity. In larval zebrafish, shadow responses appear early in development (i.e., ~70 h post hatch), supporting its importance to survival (Easter and Nicola, 1996). Sessile or sedentary organisms also exhibit shadow responses. For example, the oligochaete *Lumbriculus variegates* resides in the littoral zone of ponds with its tail segments positioned above the sediment and horizontal at the air-water interface to facilitate gas exchange. Rapid escape responses are exhibited when exposed to moving shadows or abrupt decreases in light intensity (Drewes and Fourtner, 1989). In planktonic organisms, shadow responses appear to be more common in marine zooplankton compared to freshwater (Buskey et al., 1987). However, ectoparasitic copepods are an exception, which rather than predator avoidance, use shadow responses as a means to locate their fish hosts swimming overhead (Poulin et al., 1991).

Foraging

Simultaneously, adequate light levels are required for visual predators to locate and strike at prey. In aquatic ecosystems, fish are most often the top predators, preying on zooplankton, macroinvertebrates, and/or other fishes. The eyes of visually feeding fishes are adapted to both the environment as well as prey type (Caves et al., 2017; Fig. 8). Fishes that inhabit darker waters have a higher portion of rod photoreceptors and depend on differences in light intensity to locate and capture prey while fishes inhabiting brighter waters often possess 2–5 cone photoreceptor types in addition to their rod cells, permitting color vision and higher visual acuity, or the ability to resolve spatial detail. In teleost fishes, visual pigments within the cone cells often correspond to the background illumination, with blue-shifted pigments in fishes inhabiting clear waters and red-shifted pigments in those inhabiting tannin stained blackwaters (Lythgoe, 1979; Carleton et al., 2020). Objects at depth that differ in spectral reflectance from the illumination spectrum will thus appear darker than the background (Fig. 9).

UV photoreceptors are also thought to enhance prey contrast for visual foragers. Zooplankton prey, such as *Daphnia* and *Leptodiaptomus*, often contain compounds that absorb UV-A and short-wavelength blue light (e.g., carotenoids, melanin, and mycosporine-like amino acids (MAAs)). While these compounds block UV radiation, they may also make zooplankters appear darker than the background (Cronin and Bok, 2016). In addition, zooplankton also scatter light and may appear lighter or darker depending on the direction of illumination as well as the organism's shape and refractive index. Scattering and absorption of UV radiation in tissues is often higher than that of longer-wavelength visible light, giving predators with UV vision a possible advantage in certain viewing geometries. In laboratory experiments, larval fish within the genera *Lepomis*, *Micropterus*, *Perca*, and *Oncorhynchus* caught more prey and had longer pursuit distances in the presence of UV radiation (Loew et al., 1993; Browman et al. 1994; Leech et al., 2009; Novales Flamarique, 2016). In some cases, fish fed better under UV-A alone than under visible light at the same energy. Predation rates of African cichlids *Metriaclima* spp. feeding on *Artemia* spp. were greater for species with UV sensitivity than those without, suggesting that UV vision can provide an adaptive advantage (Jordan et al., 2004).

Nevertheless, other studies have detected no effect of UV radiation on foraging, including laboratory experiments with the guppy *P. reticulata* (White et al. 2005; Zukoshi et al., 2018), juvenile bluegill L. *macrochirus* (Leech and Johnsen, 2006), and freshwater three-spine sticklebacks *Gasterosteus aculeatus* (Rick et al., 2012). In field experiments conducted in Patagonia, Argentina with rainbow trout (*Oncorhynchus mykiss*), the removal of UV wavelengths from solar radiation had no effect on the number of prey eaten or on prey preference (Rocco et al., 2002).

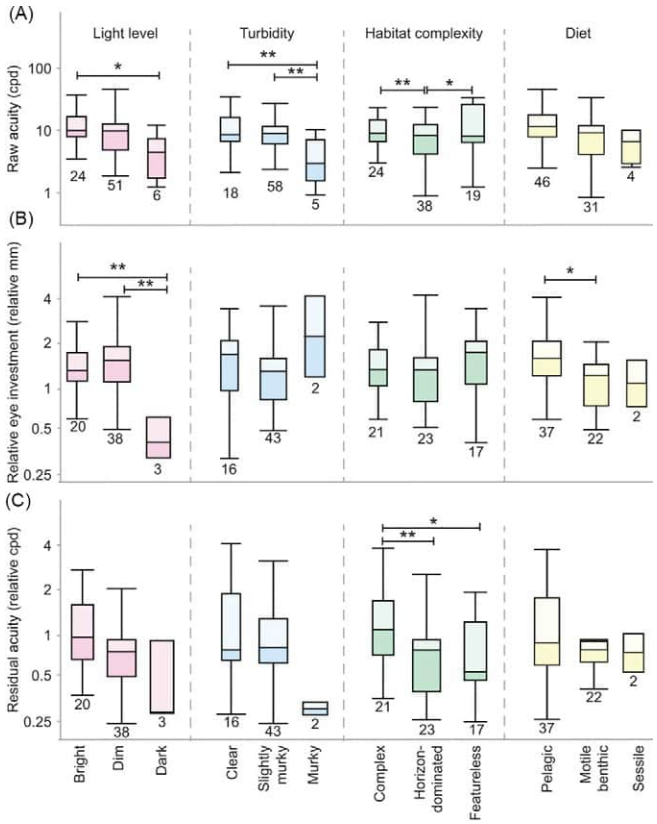

Fig. 8 Acuity and eye investment across ecological categories in ray-finned fishes. (A) Raw acuity (uncorrected for morphology or phylogeny), (B) relative eye investment, and (C) residual acuity across light level (pink), turbidity (blue), habitat spatial complexity (green) and diet (yellow) categories. Sample sizes are presented below each box. Statistics are from pairwise Student's *t*-tests ($^{*}0.02 > P > .01$; $^{**}P < .01$). Only comparisons with $P \leq .02$ are shown, which is the Bonferroni-corrected significance level for three pairwise comparisons. In B and C, the y-axis has been translated from log space into either relative eye investment (mm) or relative acuity (cpd). This means that, for example, a residual acuity of two in C indicates a species that has acuity twice as high as the mean of species with the same relative eye investment. Species with positive relative eye investment have larger eyes relative to their body size than expected, and species with negative relative eye investment have smaller eyes relative to their body size than expected. Reproduced with permission from Caves EM, Sutton TT and Johnsen S (2017) Visual acuity in ray-finned fishes correlates with eye size and habitat. *Journal of Experimental Biology* 220: 1586–1596.

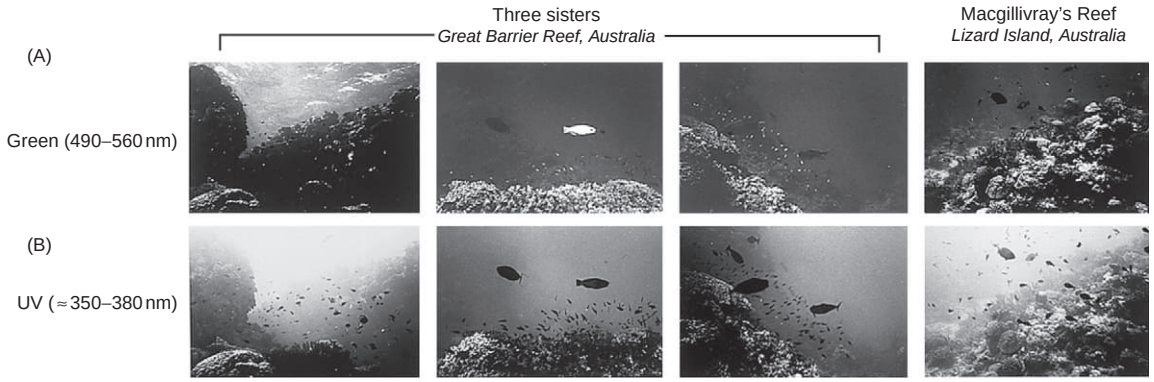

Fig. 9 Simultaneous images taken at (A) green (490–560 nm) and (B) ultraviolet (350–380 nm) wavelengths. Note the bright background in the UV image that silhouettes fish strongly, even against the reef. Also note that distant items in the UV images have lower contrast than in the visible images. Images courtesy of Dr. Thomas Cronin at the University of Maryland, Baltimore Campus.

Communication

Light also conveys important information about conspecifics with respect to schooling behavior, mate choice, and territory displays. Schooling animals are continually evaluating whether to join, stay, or a leave a group. While living in groups reduces predation risk, it does have certain costs, such as increased competition for food as well as susceptibility to disease. Selecting a group to join is therefore an important decision for an individual. In addition to the lateral line, light is believed to be essential for school behavior,

with fishes dispersing under dark conditions (Appenzeller and Leggett, 1992; Brodeur and Wilson, 1996). Three-spined sticklebacks (*G. aculeatus*) prefer to join schools seen under high UV conditions (Hiermes et al., 2015); however, wavelengths within the visible spectrum are also important (Pavlov and Kasumyan, 2000). Body coloration, including contrast stripes, spots, or other patterns, facilitates the recognition of conspecifics and aids in schooling coordination and orientation (Pavlov and Kasumyan, 2000), with the light environment critical to how these patterns are viewed and interpreted.

Colorful patterns are also important to mate choice and territorial displays, both playing an important role in sexual selection. Again, UV radiation may play an important role, such as in courtship behaviors of three-spined stickleback (Boulcott et al., 2005), the northern swordtail *Xiphophorus* (Cummings et al., 2003), and the guppy *Poecilia reticulata* (Smith et al., 2002; Sandkam et al., 2017). In the case of the latter, guppies mate primarily at dawn and dusk when short-wavelength violet and blue light dominate over middle and longer wavelength green to red light. In species inhabiting murkier waters, longer-wavelength red light is more vital to conspecific recognition, such as Amazonian cichlids (Escobar-Camacho et al., 2017).

Navigation

For anadromous fishes, which migrate between inland waters and the ocean throughout their life history, light provides both temporal and spatial information. In some species of salmonids (i.e., *Oncorhynchus nerka*, *O. tshawytscha*, and *O. keta*), UV photoreceptors are arranged in the retina such that animals can detect the polarization pattern of skylight (Kamermans and Hawryshyn, 2011). This is believed to assist salmonids in navigating to their natal streams for spawning. UV photoreceptors are expressed in larvae and early juveniles but disappear from the retina during a metamorphosis that prepares fish for deeper, marine waters. Subsequently, UV photoreceptors reappear 5–6 years later, with the onset of sexual maturation and the initiation of their return migration. Experiments have shown that polarized light is only detected in the UV range in these fish, with remarkable discrimination between small differences in the angle of the e-vector of skylight (Kamermans and Hawryshyn, 2011). As adult salmonids move from the ocean into riverine habitats, their vision shifts to longer wavelengths by switching the chromophore from A1 to A2 (Beatty, 1966; Temple et al., 2006). Enright et al. (2015) recently demonstrated an enzyme encoded by the gene *Cyp27c1* is critical to the switch as fish with mutated versions of the gene cannot make the transformation.

Non-visual functions

Circadian rhythms

Sunlight is a primary factor in setting and regulating biological clocks and circadian rhythms (~24 h) in all living organisms (Beale et al., 2016). Varying with latitude and season, day and night cycles have been a predictable environmental cue throughout the evolutionary history of life on Earth (Beale et al., 2016). Changes in photoperiod are correlated with changes in temperature, oxygen availability, threat of predation, availability of prey, and reproductive activity. In mammals, light perception through eyes is necessary to set circadian rhythms (Yerushalmi and Green, 2009). However, in fishes and other aquatic organisms, non-ocular photoreceptors are also important (Whitmore et al., 2000; Fernandes et al., 2013). Light perception regulates positive and negative feedback loops for the transcription of genes involved in the controls of physiological and behavioral processes. For example, the production of melatonin, the "time-keeper hormone," is linked to photoreception in bacteria, unicellular eukaryotes, macroalgae, fungi, plants, and animals (Vivien-Roels and Pévet, 1993; Zhao et al., 2019). Melatonin not only plays a role in sleep-wake cycles, it can also affect an individual's metabolism, immune responses, and behavior (Esteban et al., 2013; Zhao et al., 2019).

Physiological and behavioral functions in microbes

Both phototrophic and chemotrophic prokaryotes possess a diversity of photosensitive proteins, including bacteriorhodopsins, phytochromes, xanthopsins, cryptochromes/photolyases, phototropins, and flavoproteins that span the visible to near infrared spectrum (380–750 nm; Ernst et al., 2014). These photosensitive proteins are responsible for a number of non-visual functions. For example, bacteriorhodopsin helps move protons into the cells of bacteria and archaea, supplying energy for ATP synthesis (Ernst et al., 2014) while ion-pumping rhodopsins help to move chloride and sodium ions into and out of cells (Ernst et al., 2014). The freshwater bacterium *Caulobacter crescentus*, which primarily inhabits oligotrophic environments, uses flavoproteins sensitive to blue light to regulate its own attachment to suspended particles (Purcell et al., 2007). It is hypothesized that since nutrient concentrations in oligotrophic systems are lower in the surface waters compared to the benthic sediments, light may serve as a signal to surface-dwelling cells to quickly attach to a particle to aid in sinking (Purcell et al., 2007). Similarly, light has been shown to influence whether microbes remain in a motile single-cellular state or join a multicellular surface-attached community (i.e., biofilm) (Gomelsky and Hoff, 2011).

Potential fitness tradeoffs

While light perception is beneficial, it is not without fitness costs. Arguably, the greatest tradeoff is exposure to damaging ultraviolet radiation. In clear, high UV systems, particularly those in alpine regions, damaging levels of UV-A and UV-B radiation may travel deeply into the water column, affecting all life forms, from bacteria to higher vertebrates (Häder et al., 2015; Peng et al., 2017; Williamson et al., 2019). A recent meta-analysis determined that marine organisms in the northern hemisphere tend to be more

susceptible to UV damage compared to those in the southern hemisphere, due to higher levels of UV-absorbing stratospheric ozone in the former (Agustí et al., 2015). However, similar comparisons are not known for inland waters.

Reductions in growth, impaired development, changes in behavior, suppression of the immune system, reduction of disease resistance, DNA damage as well as metabolic and physiological stresses have been observed in a wide variety of aquatic species exposed to UV radiation (Häder et al., 2015; Peng et al., 2017; Williamson et al., 2019). Like humans, aquatic organisms can become sunburned with increased exposure to damaging sunlight (Häder et al., 2015). Similarly, fish eyes develop cataracts, corneal epithelium/stoma damage, thickening of the cornea, or "doughnut" opacities in the lens (Alves and Agustí, 2020), all of which reduce visual acuity. Early life history stages appear to be most vulnerable, but later stages are also susceptible to damaging affects (Häder et al., 2015; Peng et al., 2017; Williamson et al., 2019; Alves and Agustí, 2020).

To protect themselves, aquatic organisms have evolved several photoprotective strategies, including behavioral avoidance, production or dietary acquisition of photoprotective compounds (e.g., melanin, carotenoids, and mycosporine amino acids), and photorepair mechanisms for DNA and protein damage (Alves and Agustí, 2020; Häder et al., 2015; Peng et al., 2017; Williamson et al., 2019). Organisms may exhibit multiple photoprotective strategies, such as *Daphnia* spp. that possess melanin pigmentation, DNA photorepair, and behavioral avoidance. Animals are generally believed to acquire photoprotective compounds from their diets or symbionts; however, recent studies have shown that fishes and amphibians produce their own sunscreens (i.e., gadusol compounds) (Osborn et al., 2015). Undoubtedly, photoprotective adaptations come at a fitness cost to growth and reproduction, but little information is currently provided in the primary literature.

Alterations to underwater light and ecological consequences

Inland waters are modified by a complexity of human-induced environmental stressors, from local to global in scale (e.g., watershed development to global climate change). In terms of underwater light, variations in intensity and spectral characteristics are linked to changes in climate as well as land use/land cover, given their effects on nutrient and organic matter runoff. New sources of light have also been introduced during natural periods of darkness as shoreline development increases. Ultimately, these changes in light have complex ecological consequences, such as altered behavior and species interactions that subsequently affect biodiversity and ecosystem productivity.

Eutrophication and brownification

Eutrophication, or the "greening" of waters due to algal blooms fed by nutrient pollution, continues to be a global, systemic problem (Wurtsbaugh et al., 2019). More recently, many fresh waters in the northern hemisphere have also shown signs of "browning" due to increased runoff of chromophoric dissolved organic matter, and in some cases dissolved iron, from the terrestrial watershed (Solomon et al., 2015; Leech et al., 2018; Kritzberg et al., 2020). In both cases, light penetration is reduced, and the spectrum is shifted towards longer wavelength red light (Lythgoe, 1979; Kirk, 2010).

These changes to the photic environment influence aquatic systems from the organismal to ecosystem level. For example, cyanobacteria have a competitive advantage over green algae in red-dominated environments because of their suite of photopigments (i.e., phycobilisome-based versus chlorophyll-based pigments, respectively) (Luimstra et al., 2020). This may serve as a positive feedback loop for harmful algal bloom development in systems affected by eutrophication and brownification. As water transparency declines, visual predators (e.g., planktivorous fish) can be replaced with tactile predators (e.g., chironomids). Migration behaviors are often damped or halted in systems receiving increased nutrients and organic matter (Solomon et al., 2015), further altering species interactions and predator-prey overlap. Conspecifics may have increased difficulty finding mates, as is seen in African cichlids in eutrophic Lake Victoria (Seehausen et al., 1997). This led to increased interbreeding and an overall loss in diversity (Seehausen et al., 1997). Shifts towards longer wavelengths with eutrophication and brownification may particularly affect organisms using UV vision to find food and mates or avoid predators.

At the ecosystem level, alterations in species composition and food web dynamics may lead to decreases in productivity, particularly at higher trophic levels. Hyper-eutrophication and brownification can have negative effects on fisheries. For example, Craig et al. (2017) found that bluegill in lakes of increasing brown color were smaller in size and had lower fecundity compared to those living in lakes with less color. Taipale et al. (2018) noted that zooplankton and fish had poorer nutritional quality in browner systems because the phytoplankton on which they fed had lower concentrations of essential fatty acids, proteins, lipids, and carbohydrates. Consequently, changes in the underwater light environment may have cascading effects on fisheries, reducing recruitment strength, sustainable yields, and food web stability in systems affected by browning.

Artificial lighting and light pollution

In recent decades, artificial lighting (or light pollution) produced by urban, industrial, recreational, and roadway sources has dramatically altered the nighttime, underwater landscape. Electric lighting has the capacity to generate light intensities visible at night to satellites orbiting the Earth. Spectra produced by artificial lighting can be narrow- or broadband, as shown for low- and high-pressure sodium, light-emitting diode (LED), and metal halide lamps (Fig. 10). LEDs in particular produce broad spectrum white light that permits color vision at night (Zapata et al., 2019).

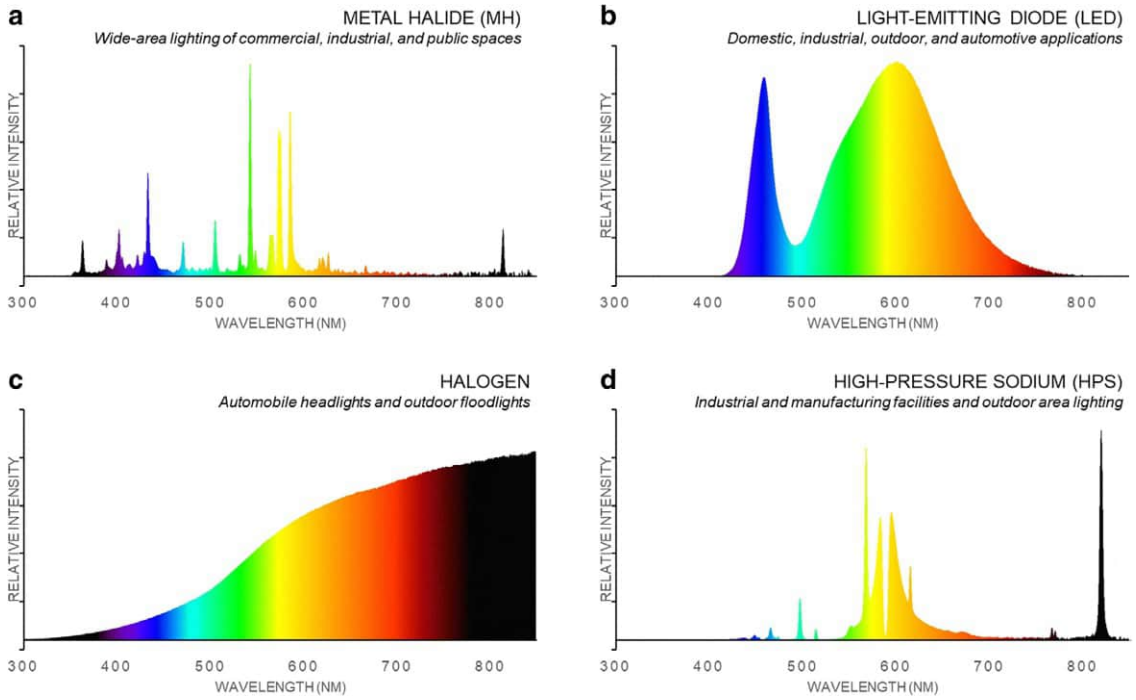

Fig. 10 Emission spectra of four artificial lighting types including metal halide, light-emitting diode, halogen, and high-pressure sodium lamps (spectra from Lamp Spectral Power Distribution Database 2017). From Zapata MJ, Sullivan SMP and Gray SM (2019) Artificial lighting at night in estuaries—Implications from individuals to ecosystems. *Estuaries and Coasts* 42: 309–330.

As a result of nighttime lighting, circadian rhythms can be disrupted. For example, even at fairly low levels of broad spectrum white light (~1 Lux: about the level of mid-nautical twilight), melatonin production was inhibited in Eurasian perch (*Perca fluviatilis*), resulting in increased nighttime activity (Brüning et al., 2015). Perch also displayed differences in the reproductive hormone gonadotropin, which the authors hypothesize may reduce fecundity and fitness (Brüning et al., 2015). Artificial lighting can also extend diurnal or crepuscular behaviors, such as vertical migration. In zooplankton, upward migrations into warmer, food rich surface waters at night can be inhibited by artificial lighting (Moore et al., 2000). Exposure to artificial lighting along estuarine migratory routes affects recruitment of salmonids to natal upstream habitats (Mueller and Simmons, 2008). At the community and ecosystem level, white LEDs have the potential to alter phytoplankton community composition, with varied effects on biomass (Grubisic, 2018). Aquatic insect biomass is often higher in artificially illuminated streams, potentially because the adult flying insects are drawn to the short wavelengths of LED lights and then deposit their eggs nearby (Manfrin et al., 2017). While beneficial to the immediate area, this attraction of insects has the potential to modify connections between terrestrial and aquatic ecosystems, reducing aquatic resources to consumers in terrestrial ecosystems (Manfrin et al., 2017).

Conclusions

Inland waters widely vary in their light environment, depending on the particulate and dissolved constituents within a system. Over time aquatic organisms have adapted to these varied conditions, both in terms of their light capturing abilities (e.g., eye structure, size) and spectral sensitivity (e.g., opsin gene selection). Light is an invaluable ecological resource used for numerous visual and non-visual tasks vital to an individual's fitness, such as foraging, mate choice, circadian rhythms, and cellular energy transport. Yet, executing these tasks may become increasingly more difficult as inland waters are degraded by climate change, land use alterations, and urbanization. Questions remain as to whether populations can evolve at a rate sufficient to keep up with human-induced environmental change. If not, similar to other environmental stressors, alterations in the underwater light environment may lead to reductions in biodiversity and ecosystem function.

Knowledge gaps

Studies linking every level of biological inquiry (i.e., genetic, biochemical, cellular, neurobiological, ecological, behavioral and evolutionary aspects) are needed: While great strides have been made in the fields of bio-optics and visual ecology, particularly with advances in

molecular biology, few studies explicitly link processes at the molecular and cellular level to behavior, ecology, and evolution. While hypothesized, questions remain regarding the quantitative effect of spectral tuning on fitness as well as cascading effects on species interactions and ecosystem productivity.

Studies examining other sensory mechanisms are needed: While light is an important ecological resource, it is not the only source of information in an individual's environment. As visual creatures, humans are often biased towards the importance of light and vision. Yet, to other species, particularly those in aquatic habitats, auditory, olfactory, electrical, or mechanical cues could be equally or more important. In comparison to vision, these senses are dramatically understudied (Cummings and Endler, 2018). Consequently, a greater understanding of alternate sensory drives is needed, particularly given declines in water transparency with continued eutrophication and brownification.

See Also: Fundamental concepts and theories: Diel Vertical Migration; Ecosystem Engineers in Freshwater Ecosystems; Optical Properties of Water; Structures and functions of Inland Waters - Groundwater: Biogeochemical Cycling of Carbon and Nitrogen in Groundwater—Key Processes and Microbial Drivers; Structures and functions of Inland Waters - Lakes: Benthic Algae in Lake Littoral Habitats; Biophysical Interactions in Phytoplankton; Lakes as Recorders of Earth Surface Dynamics From Yearly to Plurimillennial Time-Scales; Measurement and Variability of Lake Metabolism; Structures and functions of Inland Waters - Rivers: Algae and Primary Production of Streams and Rivers Ecosystems

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Temperature as a Driving Factor in Aquatic Ecosystems

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This is an update of BT De Stasio, T Golemgeski, DM Livingstone, Temperature as a Driving Factor in Aquatic Ecosystems, In *Encyclopedia of Inland Waters*, Edited by GE Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00074-0.

This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editor Lars Rudstam.

Glossary

Arrhenius relationship A form of relationship that uses a curvilinear formula to describe the influence of temperature on biological processes. These relationships are typically described by the amount of change in a given process for a 10 °C change in temperature. This parameter is referred to as the Q_{10} value.

Benthic An adjective describing organisms or habitats associated with the bottom of aquatic systems. The group of organisms associated with aquatic bottom areas is referred to as the benthos.

Evapotranspiration The process in which plants release water vapor through transpiration. This process is driven by evaporation of water from the surface of leaves, and is affected strongly by temperature and wind speed.

Latent heat The amount of heat energy released or absorbed by a substance during a change of phase; for instance, from liquid water to water vapor (latent heat of evaporation) or from water vapor to liquid water (latent heat of condensation).

Metabolism The sum of biological processes in an aquatic ecosystem that transform energy and materials. Such processes include photosynthetic, chemosynthetic, and respiratory reactions that affect the concentrations of oxygen and carbon dioxide in lakes.

Mixis The time period when vertical mixing of water in a lake occurs. Also referred to as the period of turnover in a lake. The number of mixing periods in a lake is often used to categorize lake dynamics.

Planktonic An adjective used to describe organisms or habitats found in the open water region of lakes and rivers. The plankton is the group of organisms that live suspended in the open water and that cannot move appreciably against water currents.

Poikilotherm An organism whose body temperature conforms to the temperature of the environment. These organisms are often called 'cold blooded' but their body temperature can be quite warm if the surrounding water is warm. Many poikilothermic animals can control their body temperature by selecting habitats with different temperatures. This process, called behavioral thermoregulation, is common for fish in lakes and rivers.

Productivity The construction of new biological material by organisms in an ecosystem. This is typically defined as the amount of material produced per unit time. Productivity can be determined for each separate component of an ecosystem or can be assessed as the sum of the separate rates.

Sensible heat The amount of heat energy released or absorbed by a substance that is accompanied by a change in its temperature, but not by a change of phase. In the case of lakes, when the lake water temperature is warmer than the atmospheric temperature, sensible heat will be transferred to the air. When air temperature increases above water temperature, heat energy will be transferred from the air to the water.
Stratification The situation where water with lower density is "floating" on a layer of water with higher density. During summer thermal stratification of lakes, warmer water occurs above colder water. In the winter, under ice cover, inverse stratification occurs where water between 0 °C and 4 °C is found above water that is warmer than 4 °C because it is less dense than the warmer water.
Thermal guild A grouping of organisms according to their preference for habitats with distinct temperatures. In lakes, the thermal guild concept has been used to distinguish between cold water, cool water, and warm water thermal guilds of fish.

Introduction

The distribution of heat is one of the most influential drivers of physical habitats and biological processes in freshwater ecosystems (Wetzel, 2001). Temperature is the main factor determining water density, and consequently establishes heterogeneity in the physical environments of lakes, rivers, and wetlands (Imberger and Patterson, 1990). Temperature also directly controls the rates of chemical reactions, and is therefore the major determinant of metabolic processes in inland aquatic ecosystems (Stumm and Morgan, 1995). Essentially all aquatic organisms in freshwater systems are poikilotherms (aside from a few types of birds and mammals), meaning that temperature has a direct effect on the rate of key processes such as photosynthesis, nitrogen fixation, growth, development, respiration, and excretion.

Temperature and heat

Heat balance in lakes

The heat balance of a water body, and hence its mean temperature, is determined by five main processes (Fig. 1): (1) the absorption of infrared radiation emitted by the atmosphere; (2) the emission of infrared radiation by the water body to the atmosphere; (3) the absorption of direct and diffuse short-wave solar radiation; (4) the exchange of latent heat of evaporation and condensation between the water body and the atmosphere; and (5) the exchange of sensible heat between the water body and the atmosphere by convection in the atmosphere immediately above the water surface (Imberger and Patterson, 1990).

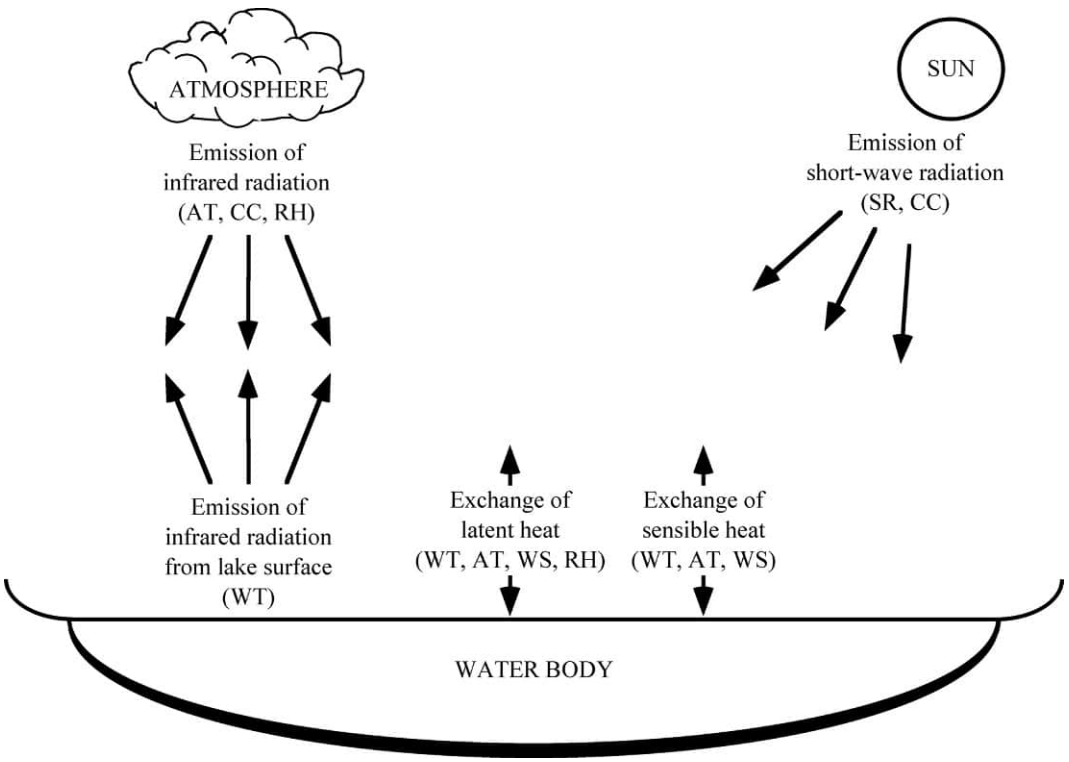

Fig. 1 The five major heat-exchange processes governing the heat balance of a water body. These processes involve the surface temperature of the water body (WT), ambient air temperature (AT), clear-sky solar radiation (SR), cloud cover (CC), wind speed (WS), and relative humidity (RH).

Temperature structure

In shallow bodies of water, such as wetlands and rivers, water temperatures are usually highly correlated with air temperature (Mohseni and Stefan, 1999). In deeper bodies of water such as lakes, mixing by wind energy at the surface in spring results in an isothermal surface layer that extends well into, or below, the photic zone (Fig. 2). As this surface layer continues to warm through spring and into summer, separate strata of isothermal water develop. A warm, well-mixed surface layer, or epilimnion, is separated from the colder, deeper water, or hypolimnion, by a vertical gradient in temperature (and hence in density) in the transition region, which is known as the metalimnion. The existence of the density gradient in the metalimnion results in extremely limited mixing between the epilimnion and hypolimnion in summer because of high relative thermal resistance to mixing. Because heat fluxes mainly occur at the surface, the epilimnion will continue to increase in temperature throughout the summer while the temperature of the hypolimnion is driven mainly by the water temperature in the spring when stratification is established. The hypolimnetic temperature generally remains cold throughout summer and early fall, except in some lakes that experience hypolimnetic heating during the summer by direct solar radiation (i.e., very clear lakes), turbulent transfer of energy across the metalimnion, or by seiche activity when the hypolimnion moves close to the surface during oscillations (Wetzel, 2001; Mortimer, 2003). As surface temperature decreases in the fall with decreased solar radiation and lower air temperatures, the thermal resistance to mixing also decreases. Fall mixis, or turnover, occurs when convection currents of cooled surface water and wind-driven circulation of the epilimnion exceed the resistance to mixing and the lake becomes homothermal at all depths. Lake waters continue to cool and circulate as air temperatures decline. If air temperatures decrease below the freezing point, and wind energy does not prevent ice cover, the lake will become capped with ice. Inverse stratification occurs when water just below the ice at the surface is colder than the temperature of maximum density (4 °C) and floats above deeper, slightly warmer water.

Patterns of stratification

Annual cycles of solar radiation, wind patterns, and atmospheric temperature changes primarily determine the stratification and mixing pattern observed in a given lake. Such mixing patterns have a large effect on biological processes, including metabolism, ecological interactions, and nutrient dynamics. Lakes have been classified into six basic groups according to annual mixing patterns

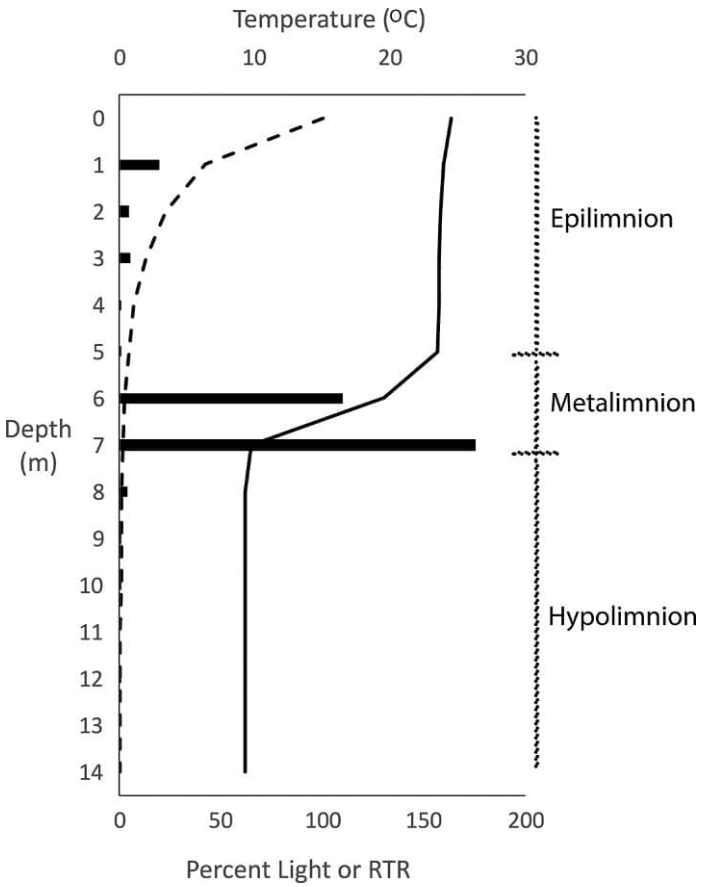

Fig. 2 Vertical depth profiles of light penetration (dashed line), temperature (solid line), and relative thermal resistance to mixing (solid bars) in Green Bay, WI, United States in August 2006. Depth region names based on thermal stratification are indicated (epilimnion, metalimnion, hypolimnion).

(Wetzel, 2001). Most lakes studied in the past have exhibited the annual cycle described above with two periods of mixing (spring and fall turnover), and are called dimictic lakes. Permanently frozen lakes never mix completely and are called amictic, while lakes that mix only once each year are called monomictic. Cold monomictic lakes mix in the summer during the ice-free period, while warm monomictic lakes mix from fall through spring and never freeze. Lakes that are stratified most of the year but which undergo cooling and circulation at irregular intervals are classified as oligomictic. Some lakes experience frequent or continuous mixing. These lakes are considered polymictic.

Temperature and biological processes

Metabolism and temperature

The overall metabolism of a lake ecosystem is largely driven by temperature, but many other factors can control overall metabolism depending on the group of organisms examined. In the most simplistic manner, ecosystem metabolism can be separated into carbon fixation processes (e.g., gross primary production via photosynthetic and chemosynthetic processes) and biological carbon oxidation processes typically termed as ecosystem respiration; (e.g., del Giorgio and le Williams, 2005; Staehr et al., 2010; Winslow et al., 2016). Phytoplankton productivity shows clear, direct temperature dependence, but also exhibits strong responses to other factors such as light intensity and nutrient concentration (Falkowski and Raven, 2013). In general, algal photosynthetic rate varies in a unimodal response pattern to temperature change, with taxa exhibiting various optima (Wetzel, 2001; Fig. 3). Because of the simultaneous changes in water temperature and light intensity in lakes at different times of the year, associations of algae tend to be dominated in some seasons by one or a few taxonomic categories. Diatoms tend to dominate in cold waters while cyanobacteria do well in warm waters in the late summer in many lakes. However, individual species within a given taxon can vary in their temperature optima over a wide range, a fact that is useful for recreating past environmental conditions using paleolimnological methods (Weckström and Korhola, 2001; Smol, 2019; Fig. 4). Diatom remains preserve well in sediments, and because many diatom species are good indicators of water temperature, examination of changes in diatom remains in various layers of sediments can provide evidence of past temperature changes in lakes.

Both chemosynthesis and respiration are also highly temperature dependent (Brown et al., 2004; Yvon-Durocher et al., 2012; Scharfenberger et al., 2019). In general, these processes have been described with the Arrhenius relationship and the van't Hoff rule, where change in the metabolic rate over a 10 degrees change in absolute temperature is expressed as a Q_{10} value. Respiration rates of planktonic and benthic organisms, measured over the range of 10–20 °C, typically have Q_{10} values in the range of 2.1–2.3 (Reynolds, 1984; Wetzel, 2001). The relative rate of change of respiration rates per degree Celsius is also temperature dependent, with higher relative rates of change at lower temperatures (Pace and Prairie, 2005; Fig. 5). This indicates that a given temperature change in the hypolimnion of a lake will result in a larger change in respiration rates than will a corresponding temperature change in the warmer epilimnion.

Growth rates

Growth rates of zooplankton and fish are heavily dependent on temperature due to the temperature dependence of feeding, respiration, and development rates. Zooplankton feeding rates exhibit optima over a wide range of temperatures from 5 °C to over 25 °C (Wetzel, 2001). Embryonic development time shortens as temperature increases for zooplankton such as rotifers and planktonic crustaceans (Bottrell et al., 1976), resulting in increased growth rates, faster development, and faster population generation time. Therefore, increasing temperatures increase the potential population growth rates of these groups. However, because growth rates of zooplankton are often strongly controlled by other factors such as food and nutrient limitation, direct relationships between temperature and zooplankton growth rates are rare. For fish, most metabolic processes increase with

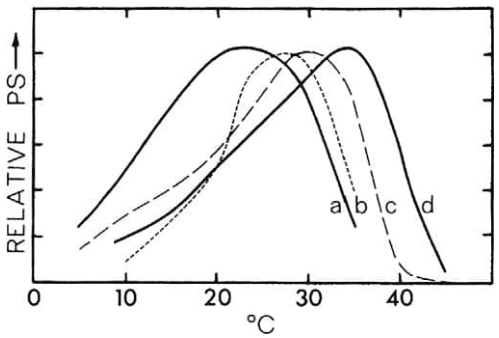

Fig. 3 Photosynthetic rate as a function of temperature for various algae: (A) *Synedra* (diatom), (B) *Anabaena* (cyanobacteria), (C) *Chlorella* (green algae), and (D) *Scenedesmus* (green algae). Reproduced from Fig. 15–23 in Wetzel RG (2001) *Limnology: Lake and River Ecosystems*, 3rd edn. San Diego, CA: Academic Press, with permission from Elsevier.

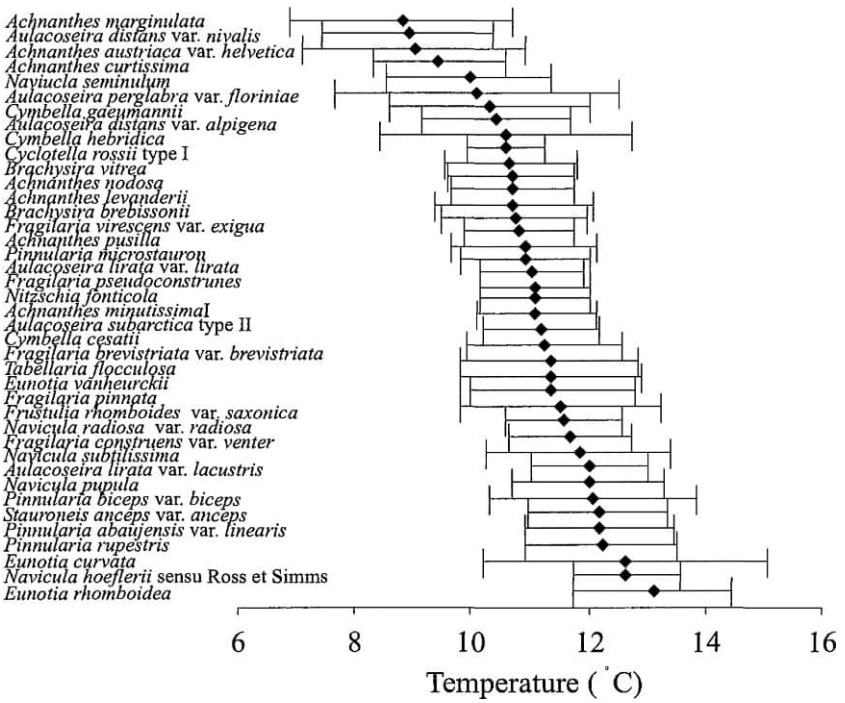

Fig. 4 Temperature optima (weighted average and tolerance) of diatoms from 64 lakes in Arctic Lapland. Reproduced from Fig. 7 in Weckström J and Korhola A (2001) Patterns in the distribution, composition and diversity of diatom assemblages in relation to ecoclimatic factors in arctic Lapland. *Journal of Biogeography* **28**: 31–45, with permission from Blackwell Publishing, Ltd.

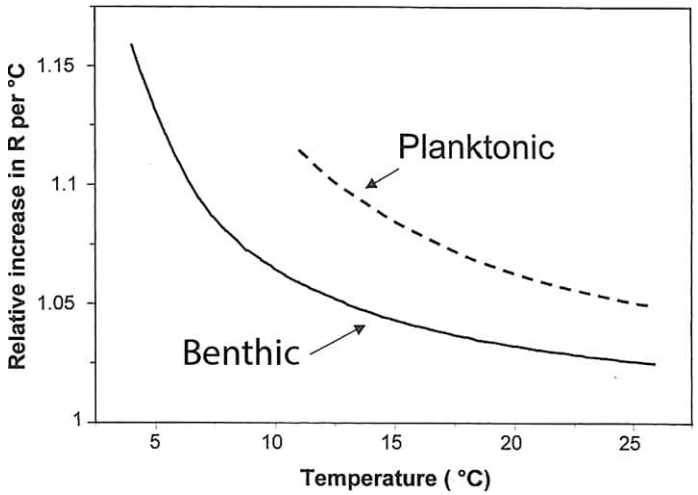

Fig. 5 Relation of relative change in respiration rate per degree Celsius and temperature for planktonic and benthic communities of organisms. Reproduced from Fig. 7.4 in Pace ML and Prairie YT (2005) Respiration in lakes. In: del Giorgio PA and le Williams PJB (eds.), *Respiration in Aquatic Ecosystems*, pp. 103–121. Oxford: Oxford University Press, with permission from Oxford University Press.

temperature up to a maximum rate, after which growth rates decline (Kitchell et al., 1977; Hanson et al., 1997; Essington et al., 2001; Fig. 6). This means that the specific growth rate of fish is directly determined by the water temperature experienced. The temperature at which the maximum growth rate occurs differs for different thermal guilds, as defined by F.E.J. Fry in the late 1940s (Fry, 1971). Fry defined the thermal niche of fish based on lethal, controlling, and directive temperature ranges. Fish in the warm water thermal guild have higher temperature optima for growth rates, and can generally tolerate a wider range of temperatures. Fish in each guild will also seek out water that is near the optimum temperature for growth (Magnuson et al., 1979), but in many lakes and rivers, water of the desired temperature is not always available, thereby limiting annual fish growth (Magnuson and De Stasio, 1996; Eaton and Scheller, 1996; Fig. 7).

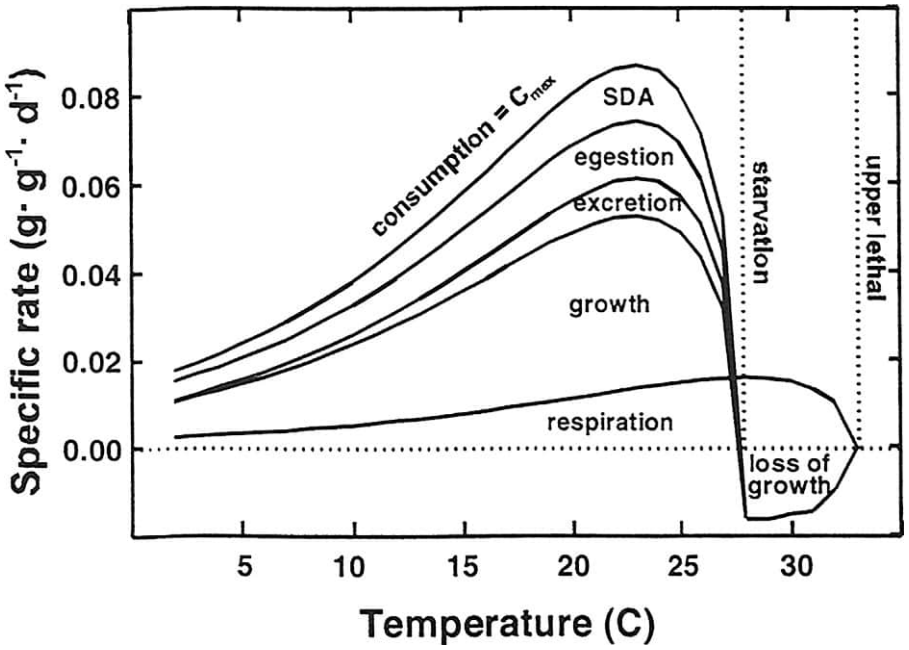

Fig. 6 Predicted specific physiological rates as a function of temperature for the yellow perch, *Perca flavescens*, using a fish bioenergetics model. Energy not used for specific dynamic action (SDA—cost of processing food), egestion, excretion and respiration can be used for growth. Reproduced from Fig. 1 in Hanson PC, Johnson TB, Schindler DE and Kitchell JF (1997) *Fish Bioenergetics 3.0*. Madison, WI: University of Wisconsin Sea Grant College Program, with permission from University of Wisconsin Sea Grant Institute.

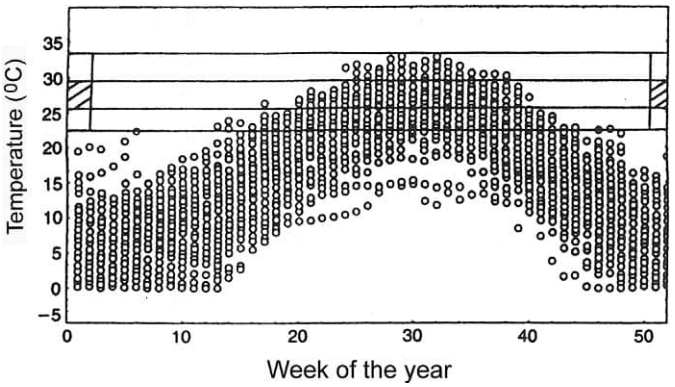

Fig. 7 Observed thermal distribution of largemouth bass in streams of the United States from January to December. Optimum temperature for growth (27.5 °C) is found in the center of the cross-hatched region representing the 4 °C-wide thermal niche range, with the 10 °C-wide range also indicated. Reproduced from Fig. 8 in Magnuson JJ and De Stasio BT (1996) Thermal niche of fishes and global warming. In: Wood CM and McDonald DG (eds.), *Global Warming: Implications for Freshwater and Marine Fish*, pp. 377–408. Cambridge: Cambridge University Press, with permission from Cambridge University Press.

Effects of climate change

Effects on lake physics and mixing

The current consensus of informed scientific opinion is that a long-term change in the global radiative heat balance, resulting primarily from human activities, is causing climate change on global and regional scales and will continue to do so into the foreseeable future (Intergovernmental Panel on Climate Change (IPCC), 2014). Climate change is already having an impact on temperatures not only in the atmosphere and oceans, but also in inland water bodies (Adrian et al., 2009; O'Reilly et al., 2015). Increasing concentrations of greenhouse gases in the atmosphere is increasing temperatures in rivers and surface waters of lakes and affecting mixing.

Air temperature effects on surface waters

All of the heat balance processes listed earlier are expected to be affected by climate change (Boucher et al., 2013). Most importantly, rising air temperatures result in an increased downward emission of infrared radiation from the atmosphere, and hence in an

increase in the amount of infrared radiation impinging on, and absorbed at, the water surface, leading directly to higher surface water temperatures. Rising air temperatures also affect the exchange of latent heat and sensible heat; however, the direction of the long-term change in heat flux that occurs because of these two processes depends on the long-term change in the temperature difference across the air-water interface and not on the long-term change in the ambient air temperature alone (Boucher et al., 2013). Thus, depending on whether the surface water temperature or surface air temperature rises faster, these two processes can either strengthen or weaken the increasing trend in water temperature.

Effects of clouds and aerosols on surface waters

Recent studies have linked the importance of climate change to changes in cloud cover dynamics and the phenomena of global dimming and global brightening. Clouds have powerful updrafts that contain aerosol particulate matter. These aerosol particles (both natural and anthropogenic) directly interact with cloud particles which lead to increased cloud cover causing global dimming (Boucher et al., 2013). Global dimming leads to a reflection of sunlight and a predominant decline in surface solar radiation and has a cooling effect on earth's surface temperature. Conversely, global brightening is the reversal of the trends seen in global dimming. There is an increase in total surface radiation and decreases in total Earth cloud cover due to fewer light-absorbing compounds (Wild, 2012). Noted instances of global dimming and brightening have been documented and used to understand the effects of these phenomena. Global dimming was documented during the 1950s–1980s whereas global brightening was observed during the 1980s–1990s. Data on global dimming/brightening trends after 2000 are mixed, showing both global dimming and brightening (Hatzianastassiou et al., 2020). These phenomena will affect the amounts of both atmospheric and solar radiation impinging on water bodies. Climate change and global dimming and brightening will also involve shifts in relative humidity and wind speed, but these shifts are likely to be geographically more heterogeneous than in the case of air temperature (Boucher et al., 2013). A shift in either of these variables would affect the exchange of latent heat across the air-water interface, and a shift in wind speed would additionally affect the exchange of sensible heat.

Effects on surface water temperature structure

In lakes, a long-term change in meteorological forcing is likely to lead not only to a change in the mean lake temperature, but also result in changes in the vertical temperature distribution and intensity and timing of vertical mixing (e.g., De Stasio et al., 1996, 2016; Livingstone, 2003; Fang and Stefan, 2009). This will alter the surface water temperature, thus indirectly affecting the heat flux associated with the emission of long-wave radiation from the lake surface, and the heat flux associated with the exchange of latent and sensible heat. Since climate change is not confined to air temperature, but involves several interdependent but geographically heterogeneous meteorological variables, the effect of climate change on lake temperature profiles in general is not easy to predict.

Lake modeling studies

Many modeling studies have been conducted to estimate the response of lake temperatures to future climatic change (e.g., De Stasio et al., 1996, 2016; Fang and Stefan, 2009; Peeters et al., 2002; Woolway and Merchant, 2019; Woolway et al., 2021). The studies consistently indicate increased lake surface temperatures. In addition, models indicate an increase in the intensity and duration of "heat waves" where surface temperatures exceed the 90th percentile of average historical baseline temperatures (Woolway et al., 2021). Most of these studies have been on strictly dimictic lakes, which freeze over each winter and in which lake temperatures are reset each spring to 4 °C, the temperature of maximum density. In such a lake, assuming winters do not become sufficiently warm to prevent ice cover, model studies predict that the mean lake temperature during the open-water period will undergo a long-term increase (Peeters et al., 2002). However, water temperatures are not predicted to increase at all depths. Within the epilimnion, a long-term increase in temperature is expected, but in the hypolimnion temperatures are predicted either to increase only slightly, or not at all, or even to decrease, implying an increase in the thermal stability of the water column (e.g., De Stasio et al., 1996, 2016; Peeters et al., 2002). This is because warm periods tend to be associated with stable water column stratification and little downward mixing of heat, whereas during cold periods such mixing tends to be enhanced.

Modeling studies on lakes that are not strictly dimictic—many of which do not freeze over in winter—are fewer. However, these studies reveal the necessity of including the heat carried over through winter in any predictive calculations for such lakes (e.g., De Stasio et al., 2016; Woolway and Merchant, 2019; Caramatti et al., 2020). If a lake does not freeze over during winter, it will generally not mix at the temperature of maximum density in spring. It will either mix at some higher temperature or will remain stratified to some extent during the entire year and will not turnover at all (Peeters et al., 2002). The meteorological conditions pertaining during the winter will then determine the amount of heat carried over from autumn to the following spring. In warm winters, more heat will be carried over than during cold winters, with the result that the effect of future warmer summers will be compounded by the effect of future warmer winters. In lakes in which heat is carried over from autumn to spring in this manner, deep-water temperatures can undergo long periods of gradual increase, owing to the continual downward mixing of heat from the lower metalimnion by turbulent diffusion. However, these periods of gradual increase are always brought to a sudden end when the deep-water temperature has risen far enough to allow deep, penetrative mixing to take place (Peeters et al., 2002). This usually occurs during a winter that is somewhat colder than normal, causing an extremely rapid fall in the deep-water temperature. If cold winters become rare, however, then these events may not occur. In the long term, the result of this process is a deep-water temperature time-series that exhibits an irregular sawtooth structure. The effect of climate change is thus not necessarily a continual, long-term increase in deep-water temperature, but rather an increase in the frequency of occurrence of longer-term sawtooth events.

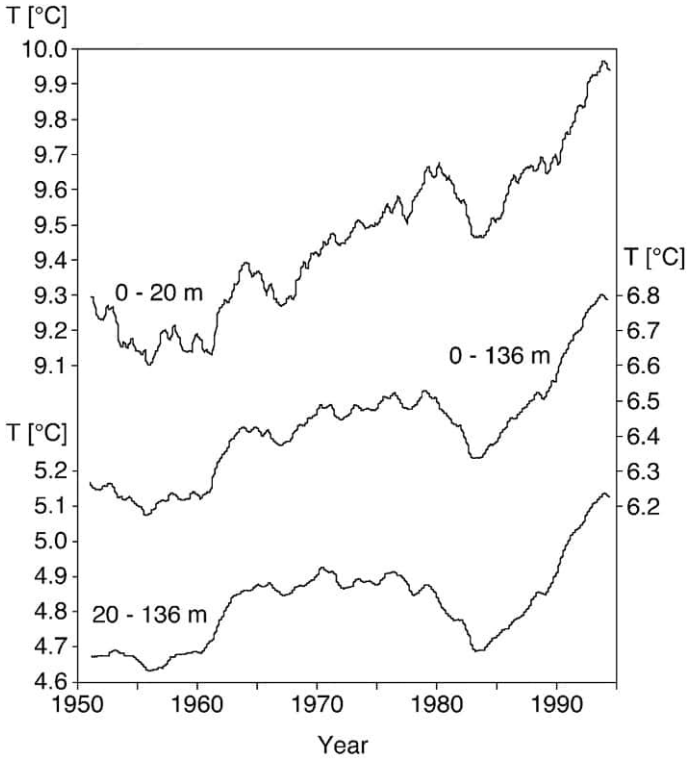

Fig. 8 Long-term increase in the water temperature of Zürichsee, Switzerland, in 0–20 m (epilimnion and metalimnion, left axis), 20–136 m (hypolimnion, left axis), and 0–136 m (the entire lake, right axis). Data (shown as centered decadal running means) from Wasserversorgung Zürich.

Averaged over several years, however, deep-water temperatures do exhibit a long-term increase (Fig. 8), since an increase in the frequency of sawtooth events implies a decrease in the frequency of complete turnover events.

Observed changes

Long-term monitoring data from lakes essentially confirm the results of the modeling studies. Summer surface water temperature data for a globally distributed lake dataset showed a mean temperature rise of 0.34 °C per decade from 1985 to 2009 (O'Reilly et al., 2015). These data indicated that seasonal ice-covered lakes (0.72 °C decade^{-1}) had greater temperature increases than ice-free lakes (0.53 °C decade^{-1}). Differences among lakes were related to both climatic and geomorphic factors, more than regional geographic aspects (O'Reilly et al., 2015). For shallower and smaller lakes, surface water temperatures are closely related to air temperature (Austin and Colman, 2007; Toffolon et al., 2014; O'Reilly et al., 2015). For larger and deeper lakes, a shorter ice cover duration and increasing air temperature resulted in earlier summer stratification leading to faster increases in surface water temperature than air temperature. Changes in stratification patterns have also been observed in other studies of globally distributed lakes, with generally deeper thermoclines and more stable stratification over the period 1970–2010 (Kraemer et al., 2015). In contrast to surface waters, effects of climate change on deeper water temperatures are more variable. In a study of 102 lakes distributed globally, summer surface water temperatures increased significantly but temperatures in the hypolimnion were more variable and did not change significantly (Pilla et al., 2020). There was higher variability in responses among lakes, with some exhibiting increased bottom temperatures but others decreasing over the period 1970–2009. In a separate study of 139 globally distributed lakes, 77% of the lakes showed increased mean temperatures from 1978 to 2013, and there were changes in thermal habitats zones (both increases and decreases) in almost 20% of lakes (Kraemer et al., 2021).

Decreases in temperature of hypolimnetic water typically occurred in lakes where conditions result in stratification being established when water temperatures are lower followed by stratification that persists longer, as indicated by modeling studies. Cooling trends for hypolimnetic water are therefore associated with smaller surface areas, location and higher dissolved organic carbon concentration (Pilla et al., 2020). In larger, deeper lakes with greater transparency, earlier thermal stratification and a prolongation of the summer stratification period reduces the period of homeothermy. For instance, the duration of the stratification period in Zürichsee increased by 2–3 weeks from the 1950s to the 1990s (Peeters et al., 2002; Fig. 8). During this stratification the effect of warmer summers on lakes will be stronger in the epilimnion than in the hypolimnion (O'Reilly et al., 2015; Pilla et al., 2020). The effect of warm winters on lake temperature profiles is significantly different from that of warm summers. As an example, in Zürichsee because the hypolimnion is shielded from meteorological forcing to a large degree during summer, its temperature

during summer is determined to a large extent by meteorological forcing during the previous winter, when large-scale vertical mixing can occur (Livingstone, 2003). Thus, the signature left in the water column by warm winters tends to persist throughout the following stratification period in the hypolimnion, but not in the epilimnion.

Due to changes in the winter and spring air temperatures over the past 150 years, dates of first ice formation on lakes and streams of the Northern Hemisphere are occurring later, with an average of more than 11 days later per 100 years (Magnuson et al., 2000; Sharma et al., 2019; Woolway et al., 2020; Fig. 9). At the same time, dates of ice breakup have been occurring earlier on average, leading to shorter durations of ice cover by 19 days per century (Woolway et al., 2020). These trends of decreased duration of ice cover on lakes and streams have contributed to changes in heat balance of lakes as indicated above through longer stratification periods and longer potential growing seasons for many organisms.

Effects on biological processes

While the effects of a warmer climate on temperature structure have now been observed clearly in a large number of lakes and rivers, the direct effects of climate change on metabolism and ecological interactions have been more difficult to document (e.g., Havens and Jeppesen, 2018). This is due in large part to the complex nature of the ecology of lakes, and the various time scales over which processes respond to climate forcing. As noted above, increased duration of the ice-free season has been observed in many lakes, resulting in longer growing seasons for phytoplankton, zooplankton, macrophytes, and fish.

Effects on primary production and algae

Increases in overall primary productivity have occurred in some ecosystems, but increases in total biomass of phytoplankton have not been observed in the same systems. Warmer conditions in spring have led to earlier increases in phytoplankton population

Fig. 9 Trends of (A) ice freeze and (B) breakup dates from lakes across the globe. Modified from Fig. 2 in Woolway RI, Kraemer BM, Lenters JD et al. (2020) Global lake responses to climate change. *Nature Reviews Earth & Environment* **1**: 388–403, by permission from Springer Nature.

abundance, especially for diatoms (Rühland et al., 2015). There have also been increases for groups with higher temperature optima, like cyanobacteria. Increased abundance and dominance of lake phytoplankton communities by cyanobacteria related to warming waters and longer duration of stratification has been observed repeatedly (e.g., Davis et al., 2009; Wagner and Adrian, 2009; Winder, 2012; Smol, 2019). However, warmer conditions do not always lead to an increase in phytoplankton populations. In fact, population abundance can vary under different circumstances, especially in shallow lakes where a more complex set of mechanisms (i.e., changes in wind speed, ice cover, stability of stratification, etc.) can result in shifts of phytoplankton species. In addition, a shift to larger sized benthic organisms and smaller sized planktonic diatoms has been documented during recent warming periods, in part because smaller species are favored by a more pronounced stratification regime (Przytulska et al., 2017). These clear trends related to temperature are even more striking considering the importance of other factors known to control populations of algae such as light intensity, nutrient availability, and losses due to grazing.

High-latitude arctic and sub-arctic lakes are often considered to be less susceptible to human influences because the ecosystems are relatively far away from the population centers; however, high-latitude regions are especially sensitive to environmental stressors (Smol, 2016). Changes in air temperatures have caused increased runoff of sediment and associated nutrients into arctic streams and lakes via a number of mechanisms (Hobbie et al., 1999; MacIntyre et al., 2009; Daniels et al., 2015). For instance, changes in permafrost characteristics have resulted in thawing of surface layers that causes slumping and increased sheer flow over underlying frozen layers (Mesquita et al., 2010). Moreover, terrestrial landscape changes resulting from permafrost thaw can influence carbon accumulation and mercury deposition in nearby shallow lake systems (Korosi et al., 2015). Consequently, increases in the sediment load to streams and receiving lakes have been observed. Similar eutrophication of rivers and lakes may also result from increased evapotranspiration relative to water supply rates, causing increases in concentrations of solutes like nutrients and trace metals (Smith et al., 2005). Such trends are especially prevalent in the abundant shallow lakes and ponds found throughout the higher latitudes of North America (Smol, 2016).

Effects on zooplankton

Similar to the patterns observed for algae, the seasonality of zooplankton populations has been observed to shift to earlier spring population increases, but zooplankton communities have not shown increases in overall abundance (Vadadi-Fülöp et al., 2012). Increases in *Daphnia* occur earlier in the spring of warmer years, but summer and fall dynamics do not appear to be driven strongly by climatic change (Adrian et al., 1999). Overall, abundance of zooplankton is likely to stay the same in warmer years, or perhaps even decrease. Studies show that zooplankton evolve to have different behavioral responses to temperature changes in their environment (Vadadi-Fülöp et al., 2012). Zooplankton can select habitats to offset changes in temperature and are able to migrate vertically to avoid predation and other harsh habitat conditions. Stratification and temperature changes in lakes can change abundance and spatial distribution of food for zooplankton (Wang et al., 2020). Large-bodied grazing zooplankton, like *Daphnia*, can respond to increases in phytoplankton abundance with improved and altered feeding mechanics, but are affected by antipredation adaptations like toxin production, growth in colonies or mucus capsule formation as occurs with cyanobacteria (e.g., Lampert, 1987; Trabeau et al., 2004). As indicated above, warmer water temperatures have a direct correlation with cyanobacterial blooms in lakes, potentially limiting *Daphnia* populations, but *Daphnia* are able to develop a cyanobacterial toxin resistance and select an alternate food source so that their population abundance does not always decrease in the presence of cyanobacteria blooms (Krzton and Kosiba, 2020). In addition, a shift to dominance by smaller-bodied species is expected under warmer conditions because zooplankton assemblages in warmer lakes have been observed to contain a higher percentage of smaller-bodied forms (Moore et al., 1996).

Effects on fish

The effects of climate warming are expected to differ for the different thermal guilds of fish (De Stasio et al., 1996; Magnuson and De Stasio, 1996; Stefan et al., 2001; Hansen et al., 2017). Because much of the water in large, northern lakes is colder than the temperature optima of most fish, warming of hypolimnetic waters may increase fish growth for cold-water fish, such as salmon, in the Laurentian Great Lakes (Magnuson et al., 1990). In smaller lakes, the data indicate that thermal guilds of warm and coolwater fish should experience increases in availability of preferred thermal habitats, and that growing seasons and overall growth rate potential will increase as well (De Stasio et al., 1996; Stefan et al., 2001). However, a few aspects may lead to decreases in fish populations. First, warming of shallow lakes that do not stratify may lead to temperatures beyond the lethal limits of some fish, especially cold-water species. Secondly, because earlier stratification can result in colder hypolimnetic temperatures and more stable stratification, overlap of fish with their prey may decrease if prey can find cold refugia in the hypolimnion (De Stasio et al., 1996; Pilla et al., 2020). Third, increased duration of stratification may lead to more severe depletion of hypolimnetic oxygen and restriction of suitable habitat for fish (Fang and Stefan, 2009). Finally, changes in biogeographic limits are likely to occur, essentially moving fish ranges northward and to higher elevations (Lynch et al., 2016; Hansen et al., 2017). Changes in elevation ranges may be especially troublesome for coldwater fish because habitat fragmentation may result as lower order streams begin to warm significantly and isolate cold and cool water fish in small headwaters of river systems (Rahel et al., 1996).

Conclusions

Direct effects of climate change on river, lake, and wetland ecosystems have clearly been documented over the past few decades. Based on numerous studies it is clear that mean lake temperatures have been increasing in response to warmer meteorological conditions and duration of the ice-free season has been increasing in both rivers and lakes. However, exact predictions of all lake temperature responses are difficult because of the complex interactions between aquatic environments and the atmosphere. Data indicate that in some cases there may have also been direct responses of ecosystem function to climate warming, including primary productivity, nutrient dynamics, seasonality of plankton, and habitat use and growth of fish. Challenges for the future include modeling such responses at the individual lake and population level to illuminate effects at the whole ecosystem scale.

Knowledge gaps

- Interactive effects of atmospheric and landscape changes on surface waters.
- Direct and indirect effects of temperature on whole ecosystem metabolism.
- Modeling lake-level responses within the context of ecosystem-scale changes.
- Understanding changes in lake temperature structure and effects on limnological and ecological dynamics.
- Relative effects of changes in trophic interactions vs. climate warming.

See Also: **Fundamental concepts and theories**: Physical Properties of Water; **Human pressures and management of Inland Waters**: Implications of Climate Change for Freshwater Fisheries; **Structures and functions of Inland Waters - Groundwater**: The Ecology of Aquatic Cave Environments; **Structures and functions of Inland Waters - Lakes**: Surface Mixed Layers in Lakes; **Structures and functions of Inland Waters - Rivers**: High Latitude Rivers: Ecosystems Shaped by Environmental Extremes; Secondary Production in Streams

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Relevant websites

http://www.amap.no—Arctic Monitoring and Assessment Programme.
https://gleon.org/—Global Lake Ecological Observatory Network.
http://www.ipcc.ch—Intergovernmental Panel on Climate Change.
https://climate.nasa.gov/—NASA Global Climate Change.
http://lter.limnology.wisc.edu—North Temperate Lakes Long Term Ecological Research Program.
http://www.ucsusa.org—Union of Concerned Scientists.
https://www.un.org/en/climatechange/—United Nations Climate Action.
https://www.unep.org/—United Nations Environment Programme.
http://www.globalchange.gov/—US Global Change Research Program.

Bioenergetics

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Absolute rate A physiological rate expressed per unit time. For example, metabolic rate for a fish expressed as mg O_2 day^{-1}.
Allometry Relationships describing how biological processes scale with body size.
Assimilation efficiency The proportion of consumed food, nutrient or contaminant that is assimilated and retained by a consumer.
Ectotherm An organism whose regulation of body temperature is dependent on external sources such as water temperature or sunlight.
Egestion The process of voiding or discharging non-assimilated (undigested) food as feces.
Excretion In fish and other aquatic organisms, the process of eliminating assimilated energy as waste in the form of ammonia.
Gonadal growth Change in mass of reproductive organs that include testes in males and ovary in females.
Hypoxic Conditions characterized by water with low dissolved oxygen concentrations below 2 mg O_2 L^{-1} or less than 30% O_2 saturation.
Normoxic Conditions characterized by water with normal dissolved oxygen concentrations greater than 2 mg O_2 L^{-1} or between 30% and 100% O_2 saturation.
Somatic growth Change in mass of body tissue and organs, excluding gonads.
Specific dynamic action The amount of energy expenditure above resting metabolism due to the cost of processing food.
Specific rate A physiological rate expressed per unit weight per time. For example, metabolic rate for a fish expressed as mg O_2 g^{-1} day^{-1}.
Standard metabolism (poikilotherms) Minimum aerobic metabolic rate at a specific temperature.

Introduction

Development and application of bioenergetics modeling has increased in recent years owing to the complexity of issues being faced by aquatic scientists. Bioenergetics models provide a sound, theoretical approach for estimating energy allocation in animals by partitioning consumed energy into three basic components that include (1) metabolism, (2) wastes, and (3) growth. Because the models are based on an energy balance, they are often used to estimate growth or food consumption given information on other variables. Bioenergetics models are particularly attractive for estimating food consumption by free-ranging ectotherms given the

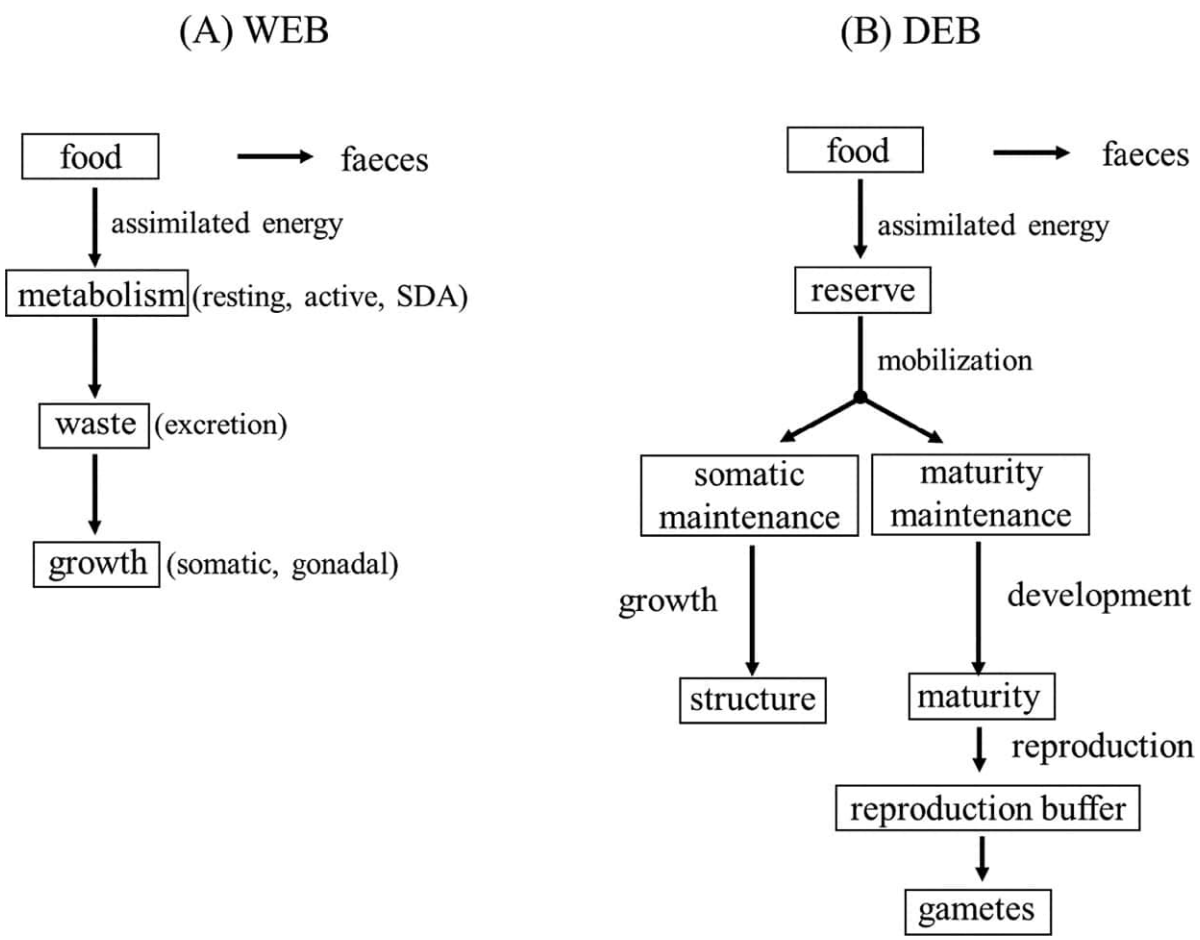

Fig. 1 Conceptual overview of (A) the Wisconsin Energy Budget (WEB) and (B) the Dynamic Energy Budget (DEB). The WEB approach is generally species-specific and is structured as a hierarchal model where food energy is first apportioned to metabolic costs, then waste loss, and finally to somatic and gonadal growth depending on maturity. The DEB approach can integrate intra- or interspecific information as well as life-stage specific data from a variety of studies during the parameterization process, thus providing a full-life-cycle approach to energy acquisition and allocation. DEB adapted from Kooijman SALM (2010) *Dynamic Energy Budget Theory for Metabolic Organization*, 3rd edn. Cambridge, UK: Cambridge University Press.

time and effort required of traditional approaches such as continuous feeding models or chronology-of-feeding methods (Adams and Breck, 1990). Today, bioenergetics models are widely used for a myriad of animals, ranging from zooplankton to whales, to address issues related to climate change, invasive species, sportfish management, and endangered species—just to mention a few.

Two modeling approaches are generally used in bioenergetics analyses. Traditional models based on the Wisconsin Energy Budget (WEB, Kitchell et al., 1977; Hanson et al., 1997) use a hierarchical approach to resolve energy allocation by an individual organism (Fig. 1). The wide-scale application of WEB modeling has benefited from the availability of user-friendly software first introduced in 1987 (Hewett and Johnson, 1987). The most recent version, *Fish Bioenergetics 4.0*, includes bioenergetics models for 73 species (Deslauriers et al., 2017). A more generalized, albeit abstract approach to bioenergetics modeling is based on the Dynamic Energy Budget (DEB) theory (Kooijman, 2010). Although conceptually similar to the data driven WEB approach, DEB modeling is a theory driven approach where an animal's biomass can be defined as the sum of three compartments: structure, reserve, and (adult) reproductive buffer (Nisbet et al., 2012; Fig. 1). DEB models can be parameterized to include full-life-cycle features, providing a robust platform for integrating available information from studies of specific life stages, habitats and processes (Nisbet et al., 2012).

Like other mathematical models, bioenergetics modeling approaches are simplifications of reality. How well they describe or predict actual conditions depends on appropriate measurement of model parameters and the input data used to drive them. Fortunately, as development and application of bioenergetics models have increased, so too have methods for parameterizing model input and evaluating model output, with the goal of reducing uncertainty in bioenergetics models (Chipps and Wahl, 2008). As our late colleague Dr. James Kitchell once noted, "The model cannot be wrong because it is based on a budget that must be right. It will improve in proportion to our ability to estimate the physiological parameters that regulate growth and the errors or bias of data employed as inputs."

Wisconsin energy budget: Core processes

Bioenergetics models are based on an energy budget that is driven by the second law of thermodynamics, where consumed energy is balanced by energy expenditures that ultimately lead to increased entropy. Conceptually, an energy budget can be expressed as,

$$\text{consumption} = \text{metabolism} + \text{wastes} + \text{growth}$$

where consumed energy is partitioned into three major processes that include metabolism, waste, and growth. We can refine each term on the right side of the equation to account for different aspects of consumed energy (C) as,

$$C = (R + A + SDA) + (U + F) + (SG + GG) \quad (1)$$

where metabolism includes standard metabolic rate (R), energy expended due to swimming activity (A), and specific dynamic action (SDA), the latter representing the energy required to digest and assimilate food. Similarly, consumed energy that is lost as waste is accounted for by excretion (U) and egestion (F) processes. Energy not partitioned to metabolism or waste is available for somatic (SG) and(or) gonadal growth (GG) depending on maturity. Relatedly, knowledge of any seven components above, allows us to estimate the eighth. Somatic growth, for example, can be derived by re-arranging the conceptual model above as,

$$SG = C - (R + A + SDA + F + U + GG) \quad (2)$$

The hierarchical partitioning of consumed energy in WEB models has been likened to an account balance, where the *living costs* paid to rent or mortgage are equated to metabolism. Similarly, *taxes*, which are proportional to income (i.e., consumed energy), are paid as waste losses (Hanson et al., 1997). Any *income* left over can be added to *savings* as individual growth (SG) or *invested* in the future in the form of gonads (GG). Generally speaking, the energy budget of a typical predatory fish, when represented simply as metabolism, waste, and growth, corresponds to about 44%, 27%, and 29% of consumed energy, respectively. Similarly, for herbivorous fishes, metabolism, waste, and growth correspond to about 37%, 43%, and 20% of consumed energy (Brett and Groves, 1979). Lower growth efficiency and greater waste loss among herbivorous fishes is likely due to eating foods with a greater proportion of indigestible material and lower energy content. Growth efficiency of fish is greater than that reported for mammals and birds, although the variation around estimates reported above can be high (±20% of the mean; Hanson et al., 1997).

Other processes that are commonly incorporated as sub-models in WEBs include nutrient regeneration and contaminant uptake. The excretion process in fish and aquatic invertebrates represents the primary loss of soluble nitrogen and phosphorus that is readily available for uptake by primary producers (e.g., algae). When information on P (or N) content of predators and their prey are known, phosphorus excretion (U_p) can be easily incorporated into bioenergetics models as,

$$U_p = (AE_p \cdot C_p) - G_p \quad (3)$$

where AE_p represents assimilation efficiency, or the proportion of P that is taken up by the predator (~0.7), C_p is the mass of P consumed by the predator, derived as prey consumed (g) multiplied by P concentration in the prey (g P/g wet weight), and G_p equals the mass of P (g) allocated to growth. In a similar fashion, contaminant uptake by target organisms can be evaluated using bioenergetics models when information on predator and prey contaminant levels are known.

Converting our conceptual bioenergetics model in equation 1 to a mathematical model requires that parameters be expressed in the same units; for the WEB, the standard unit of measure is the Joule (1 J = 0.239 cal). Physiological processes are typically measured in a laboratory setting under controlled conditions where precise measurements can be made. Body size and water temperature are the primary factors affecting physiological rates of ectotherms and must be accounted for in parameter estimation. Respiration rate (R), which is used as an estimate of standard metabolic rate, is an important component of the energy budget and is often expressed as a power function,

$$R\ (g\ O_2\ g^{-1}\ day^{-1}) = aW^{-b} \cdot f(T) \quad (4)$$

where W represents fish wet weight (in g), a and b are regression coefficients, and $f(T)$ is a temperature-dependent function. Oxygen consumption (g O_2 day^{-1}) and fish mass (g wet weight) are converted to J using an oxycaloric equivalent (13,560 J g^{-1} O_2) and information on fish energy density (J g^{-1} wet weight), respectively. Note that R can then be expressed as a specific rate relating to J of oxygen consumed per J of fish per day (J J^{-1} day^{-1}). In this context, energy allocation and scope for growth can be easily related to water temperature for a given size fish. As one might expect, the potential scope for growth of a fish is maximized when they feed in optimal water temperatures at their maximum feeding rate (Fig. 2).

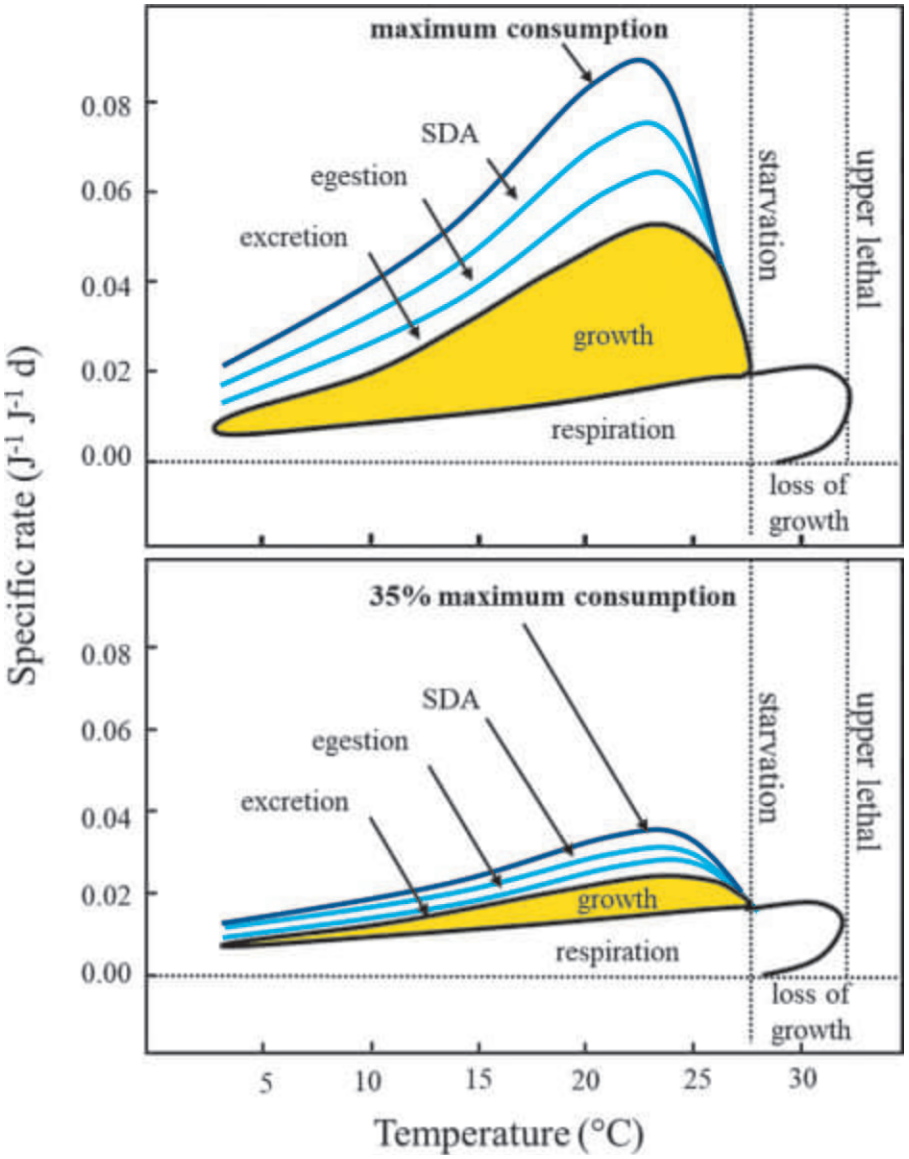

Fig. 2 Generalized Wisconsin energy budget (WEB) as a function of water temperature. The top panel depicts energy use and resultant growth for an ectotherm (e.g., fish) feeding at its maximum feeding rate (maximum consumption, $C_{max} = 100\%$). The bottom panel depicts similar energy allocation, but for a fish feeding at 35% of its maximum consumption rate. Adapted from Fig. 1 in Hanson PC, Johnson TB, Schindler DE, and Kitchell JF (1997) Fish Bioenergetics 3.0 Madison, WI: University of Wisconsin Sea Grant Program, with permission from University of Wisconsin Sea Grant Institute.

Specific rates also point out the importance of allometry on energy budget components that at first glance can appear contradictory. Consider R plotted as a function of fish weight at a fixed water temperature (Fig. 3). In this case, the absolute rate of standard metabolism (J day^{-1}) is positively related to fish size and thus greater for larger fish than for smaller fish—as would be expected. However, when expressed as a specific rate (J J^{-1} day^{-1}), standard metabolism is negatively related to fish size (i.e., –b coefficient) and is greater for smaller fish due to greater oxygen demand per unit of body mass. Similar allometric responses are observed in other physiological rates including feeding (C) and growth (SG) rate.

Once parameterized, bioenergetics models can be used to address a variety of applied or ecological questions. Because growth integrates how well a fish resolved its energy budget, it can relay important information about environmental conditions and(or) food availability that can be addressed by bioenergetics modeling. Moreover, bioenergetics models can be used to explore a variety of hypotheses related to food availability, habitat quality, species interactions, climate change, nutrient regeneration and contaminant uptake. Below, we highlight several areas where bioenergetics modeling has been used to address important questions in fisheries management and ecology.

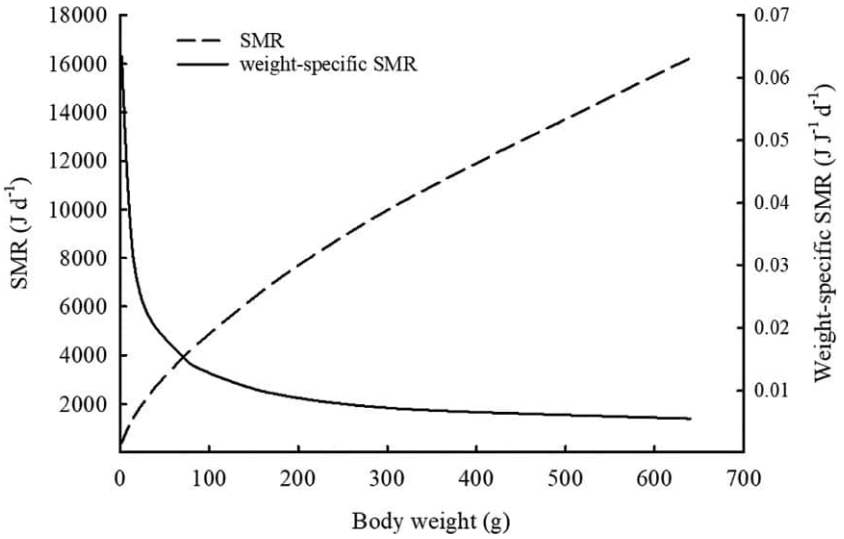

Fig. 3 Comparison of standard metabolic rate (SMR, dashed line) and weight-specific SMR (solid line) for 2–640 g largemouth bass (*Micropterus salmoides*) at 25 °C.

Modeling applications

Predator-prey dynamics

An often-cited example of a fish bioenergetics model application being used to guide fishery management decisions is the predator-prey modeling of the salmonine and alewife (*Alosa pseudoharengus*) populations in Lake Michigan (United States). Salmonines, including Chinook salmon (*Oncorhynchus tshawytscha*), lake trout (*Salvelinus namaycush*), rainbow trout (*O. mykiss*), coho salmon (*O. kisutch*), and brown trout (*Salmo trutta*), have fed primarily on alewives in Lake Michigan since the 1960s. Researchers at the University of Wisconsin Center for Limnology (CFL) applied bioenergetics models to salmonine populations in Lake Michigan during the 1970s and 1980s, and they determined that their estimates of annual consumption of alewives by salmonines were equal to 33% of the estimated annual biomass production of alewives in the lake in some years during the 1970s and early 1980s (Stewart et al., 1981). CFL researchers warned fishery managers that the high degree of predation exerted by salmonines would eventually result in a drastic decline in alewife abundance in Lake Michigan. During the 1980s, fishery managers in three of the four states bordering Lake Michigan heeded this warning by reducing the stocking rates of Chinook salmon into the lake. During the late 1990s and 2000s, researchers at Michigan State University developed a predator-prey model (PPM) for the salmonine and alewife populations in Lake Michigan by coupling salmonine bioenergetics models with age-based population models for the salmonines and alewives (Tsehaye et al., 2014). In their simulation model, annual consumption of alewives by salmonines was estimated, and the corresponding mortality on the alewife population is calculated and applied toward modeling alewife population size in the lake. For each year of the simulation, the PPM generates age-specific estimates of lakewide population sizes, population biomasses, and mortality rates for salmonines and alewives. Every year, fishery managers review the PPM output to make decisions on the stocking rates of salmonines, primarily Chinook salmon. Stocking rate of Chinook salmon into Lake Michigan has been reduced five times during 1990–2020. These decisions appear to have been effective, because the alewife population has not undergone a complete collapse and the Chinook salmon fishery has persisted since the 1960s. Clearly, bioenergetics modeling has been a keystone to effective management of the salmonine fisheries in Lake Michigan since the 1980s.

Endangered species

Bioenergetics models provide an important tool for understanding habitat-related energetic requirements of endangered species that can aid in conservation planning. However, empirical data can be limited for endangered species and they are often not readily available for experimentation due to their precarious status. Alternative approaches of developing bioenergetics models for endangered species are often needed to meet conservation objectives. A number of approaches exist to deal with this lack of information. A bioenergetics model for the humpback chub (*Gila cypha*), an endangered species of minnow inhabiting the Upper Colorado River Basin (United States), was developed using parameter bounds for other *Gila* spp. and fit to observed growth for humpback chub (Petersen and Paukert, 2005; Petersen et al., 2008). Similarly, field-based approaches that make use of mark-recapture and water temperature data have been used to estimate bioenergetics parameters for a number of endangered species including white sturgeon (*Acipenser transmontanus*) in the Upper Columbia River (Canada; van Poorten and McAdam, 2010). These models can then be used to predict growth rates and evaluate habitat quality.

The Dynamic Energy Budget (DEB; Nisbet et al., 2012) approach also offers the opportunity to estimate bioenergetics model parameters without directly having access to animals. This approach uses available laboratory and field data from the literature to estimate the parameters using a mathematical calibration technique. Such a model can then be used to recreate the life history of a species and evaluate the impacts of food limitation and elevated temperatures as has been done for early life stages of green sturgeon (*Acipenser medirostris*) in the Sacramento River, California (United States; Hamda et al., 2019), where this subpopulation of the species has been considered threatened since 2006.

Once a bioenergetics model has been developed using one of the approaches mentioned above it then becomes possible to apply it spatially to take advantage of often existing datasets describing water temperature and prey availability attributes that can be used as inputs in bioenergetics modeling. In systems that have been highly impacted by human activities, such as the Chesapeake Bay, a spatially-explicit bioenergetics approach can be used to identify areas for conservation and recovery efforts (Dalyander and Cerco, 2010) for species such as the Atlantic sturgeon (*Acipenser oxyrinchus*; Niklitschek and Secor, 2009) and Atlantic salmon (*Salmo salar*; Nislow et al., 2000). Bioenergetics modeling can also be used to evaluate the carrying capacity of a system (Eastern Oyster, *Crassostrea virginica*; Filgueira et al., 2014) to assess if conservation stocking practices might lead to a population collapse due to a high number of fish being stocked in a system where limited food resources exist to support growth as has been noted for endangered sturgeon species including the pallid sturgeon (*Scaphirhynchus albus*; Steffensen et al., 2019).

Extending bioenergetics modeling further, individual organisms within a population can be modeled independently allowing them to interact with their environment and generating population characteristics that provide unique insight about the system under study (Grimm et al., 2016). These models, termed Individual/Agent-Based Models (IBM/ABM) are becoming increasingly popular as a way to simulate ecological, biological, and physiological dynamics under a spatially-explicit framework. The main advantage of integrating an IBM/ABM framework within a virtual spatial environment is that individuals are allowed to move, thus recreating behaviors that will seek to optimize growth and survival. A few examples exist in the literature that have applied this approach in the context of endangered species conservation. In one study, experimental data on the physiology and behavior of pallid sturgeon were combined with empirical information on prey density, water temperature and velocity from the Missouri River (United States) to create a virtual environment in which the impact of habitat heterogeneity on the growth rates of larval fish could be assessed (Deslauriers et al., 2018). Results from this type of computer simulation can be used to identify favorable nursery areas for the pallid sturgeon, and then fishery and environmental managers can work together to protect these important areas of the river to better conserve the species. The use of an IBM/ABM approach allows for multiple sources of information to be combined and thus provides a valuable tool for the conservation and management of endangered species.

Trophic interactions

Trophic interactions involving the widely introduced opossum shrimp (*Mysis diluviana*), kokanee salmon (*O. nerka*), and lake trout have been well documented in North American lakes. Diel vertical migration exhibited by *Mysis* plays an important role in limiting their exposure to planktivorous fish predation, particularly among populations that were introduced into non-native environments. Following the establishment of introduced *Mysis* populations in large, western North American lakes, early research showed significant changes in zooplankton abundance and concomitant declines in kokanee salmon. As studies progressed, the application of bioenergetics modeling became an important tool in enabling researchers to evaluate trophic interactions among *Mysis*, kokanee and lake trout. Studies in Lake Pend Oreille, Idaho (United States) revealed that annual zooplankton consumption by *Mysis* was over four times greater than that by the kokanee population, accounting for 5–70% of the daily cladoceran zooplankton biomass (Chipps and Bennett, 2000). Bioenergetics modeling also revealed that annual phosphorus excretion by *Mysis* was over three times greater than that by the kokanee population, although much of the phosphorus recycling by *Mysis* was constrained to deeper strata where they spend a considerable portion of their day.

The establishment of non-native *Mysis* populations also influenced lake trout populations that in most cases, represented another introduced species in many lakes of northwestern North America. Because *Mysis* represent an important prey for young lake trout, many lake trout populations expanded following *Mysis* introductions. In Colorado reservoirs, bioenergetics modeling showed that the management of trophy lake trout fisheries led to an imbalance between lake trout consumption and their available prey base (i.e., kokanee), placing additional constraints on the kokanee population (Johnson and Martinez, 2000). It is now recognized that kokanee production is largely constrained by the degree of competition with *Mysis* that ultimately determines the magnitude of sustainable predation by lake trout (Corsi et al., 2019; Fig. 4).

Contaminant accumulation

Fish bioenergetics modeling has provided key insights into the processes regulating contaminant accumulation in fish. For example, during the 1960s and 1970s, direct uptake of polychlorinated biphenyls (PCBs) from the water into the fish's body via the gills was believed to be the predominant pathway of entry of these environmental contaminants into the bodies of free-ranging fish in lakes, rivers, and oceans. As discussed above, if the growth rates of free-ranging fish are known, then bioenergetics modeling can be used to estimate the amount of food consumption needed to attain the observed growth. In turn, the quantity of PCBs entering the fish's body via dietary uptake can be estimated. Computer simulation models, including a bioenergetics model subcomponent but also including a subcomponent for direct uptake of PCBs from the water via the gills, were developed and applied to populations of free-ranging fish during the late 1970s and 1980s. Results clearly revealed that the bulk (>95% in some cases) of PCBs accumulated

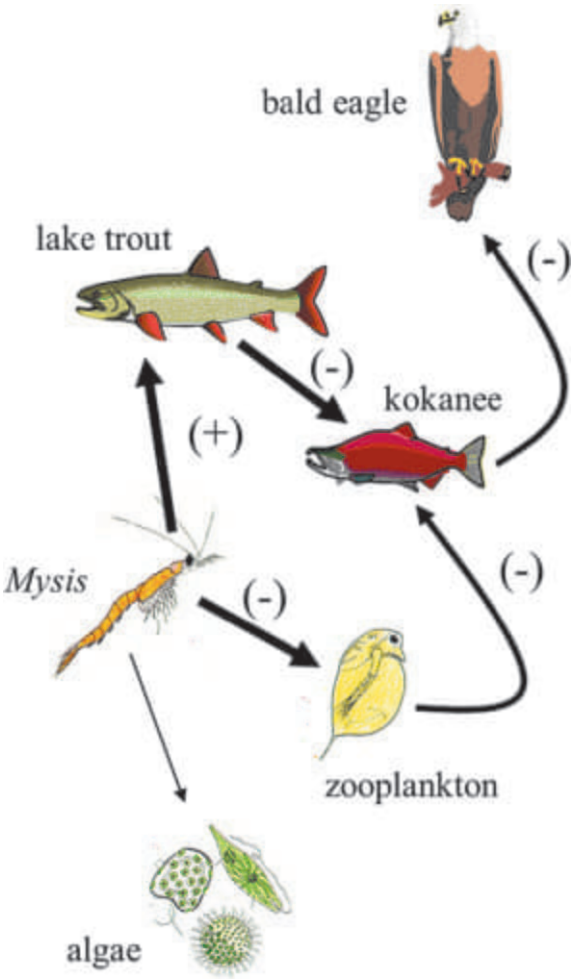

Fig. 4 Food web interactions in lakes containing non-native *Mysis diluviana* and lake trout. The width of the arrows corresponds to the relative strength of species interactions and the (+) or (–) signs indicate the direct or indirect effects of opossum shrimp and lake trout on kokanee salmon and bald eagles. Adapted from Fig. 13.1 in Chipps SR and Graeb BDS (2010) Ecology and management of lake food webs. in: Hubert W and Quist M, (eds.) *Inland Fisheries Management in North America*, (3rd edn.) Bethesda, Maryland: American Fisheries Society, pp. 395-424.

by fish entered via food consumption rather than direct uptake from water (Weininger, 1978). Bioenergetics modeling can also be used to quantify the growth dilution effect. The growth dilution effect refers to the phenomenon of lower contaminant concentrations in faster-growing fish compared with slower-growing fish, when all other factors are equivalent. Essentially, the contaminant concentration is "diluted" over the greater body mass of the faster-growing fish. Results from bioenergetics modeling have shown that the growth dilution effect can usually account for a modest (<20%) difference in contaminant concentrations between individual fish, but the growth dilution effect cannot explain relatively large (twofold or greater) differences in contaminant concentrations between individual fish (Madenjian et al., 2016). When incorporated into computer simulation models, bioenergetics modeling continues to be indispensable in predicting contaminant concentrations in fish under various scenarios of future environmental dynamics, such as climate change, changes in fishing mortality, and changes in the rates of discharge of contaminants into the environment.

Climate change

Bioenergetics models provide a powerful tool to address effects of climate change on feeding and growth dynamics of aquatic animals. Bioenergetics modeling is well suited to address organismal responses to changing climate conditions because it is grounded in a mass-balance model driven by physiological responses to water temperature. Metabolic rate represents an important component of the physiological response to climate change because it accounts for an appreciable part of the energy budget and has a non-linear response to increased water temperature. Consider, for example, a species at its southern and northern range where mean, summer water temperatures vary between populations. Because of the non-linear relationship between metabolism and

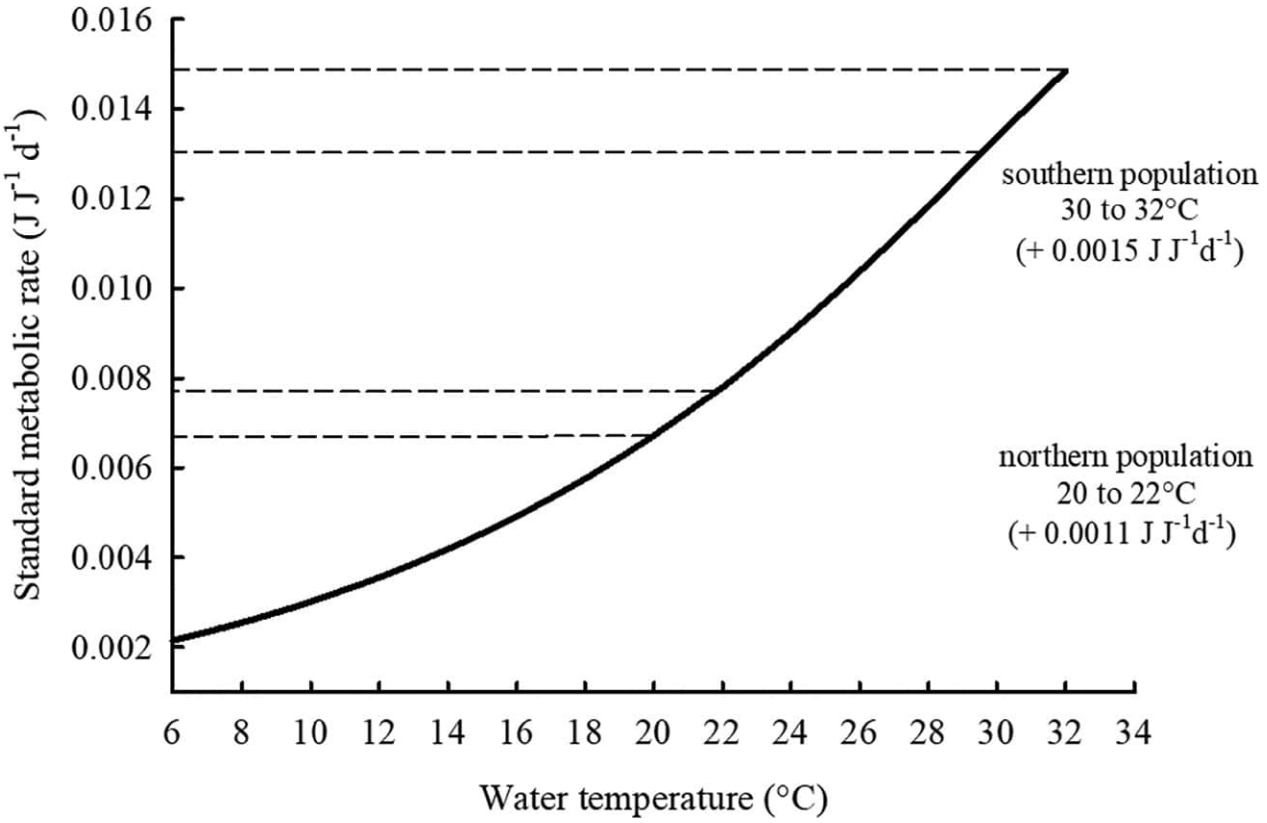

Fig. 5 Standard metabolic rate of an adult, 300 g bluegill sunfish (*Lepomis macrochirus*) at water temperatures ranging from 6 °C to 32 °C. Dashed lines correspond to a 2 °C increase in water temperature for simulated populations at the northern or southern edge of their range. Note that for the southern population, a 2 °C increase in water temperature (30–32 °C) results in a greater change in daily metabolic rate compared to the northern population (20–22 °C) due to the non-linear increase in metabolism.

water temperature, a 2 °C increase in water temperature results in greater metabolic cost to individuals from southern populations compared to those from cooler, northern climates (Fig. 5). And while much focus is directed to climate change in the mid- to high latitudes of the Northern Hemisphere where climate warming is occurring more rapidly, scientists have raised concerns that impacts of climate warming should be considered on a global scale that includes tropical regions (Dillon et al., 2010).

Climate change has become an important research focus in aquatic science. The degree to which global warming affects species distribution, aquatic food web interactions, fish production, and species extinction are topics receiving considerable attention. One example of how bioenergetics modeling is being applied to address climate change involves food web interactions in large reservoirs. Because many large reservoirs are managed for warm and coolwater sportfishes, questions arise as to the relative impacts of future warming trends on both groups of fishes. Lake Sharpe, a large, Missouri River reservoir in central South Dakota United States, contains both smallmouth bass (*Micropterus dolomieu*) and walleye (*Sander vitreus*). While walleye are native to the upper Missouri River, smallmouth bass were introduced to Missouri River reservoirs to provide increased angling opportunities. Bioenergetics modeling has shown that based on future climate predictions, warmer water temperatures could enhance growth potential for smallmouth bass that feed on gizzard shad (*Dorosoma cepedianum*)—a warmwater forage fish. At the same time, warmer water temperatures would reduce growth potential of walleye and threaten rainbow smelt (*Osmerus mordax*), an important coolwater forage fish for walleye (Wuellner et al., 2010).

Sex and life stage variation

Energy budgets have been developed for various species of fish, although they have not yet been developed for sexes within a fish species. For many bioenergetics model applications, including a level of detail such that differences between males and females are taken into account is not necessary to achieve the objectives of the modeling exercise. However, in some instances, sex-specific fish bioenergetics models may be useful. With continued research, sex-specific fish bioenergetics models will eventually become available.

A body of evidence has recently emerged that indicates that adult male fish expend energy at a higher rate than adult female fish (Madenjian et al., 2016). The higher energy expenditure rate in males stems from a higher standard metabolic rate and greater swimming activity by males. For a given size of fish, it has been estimated that energy expenditure rate of mature males may exceed that of mature females by up to 20% or more (Madenjian, 2020). Interestingly, the characteristics of higher resting metabolic rate and higher activity in males compared with females is shared by other vertebrates, including humans (Madenjian et al., 2016; Madenjian, 2020).

Extrapolation of the metabolic component of a fish bioenergetics model to the larval stage may result in inaccurate estimation of food consumption by fish larvae, because metabolism has an isometric relationship with weight when fish are larvae but an allometric relationship with weight in juvenile and adult fish (Post, 1990; Klumb et al., 2003). Typically, a bioenergetics model for a given fish species is based on respiration rate determinations for older juvenile and adult fish, but not on determinations for larval fish. Specific respiration rate is usually expressed in units of grams of oxygen consumed per gram of fish per day. Extrapolation of the respiration rate model based on respiration rate determinations for older juvenile and adult fish to fish larvae may lead to serious error in food consumption estimates for fish larvae (Post, 1990; Klumb et al., 2003). Of the fish species for which bioenergetics models are available, the models are appropriate for application to older juveniles and adults, but not to fish larvae in most cases. Because the physiological responses of larval fish are different from those of larger fish, bioenergetics models have been developed specifically for the larval stage and these models are available for several fish species.

Modeling limitations

All mathematical models of biological processes have some kind of limitation to their applicability, and bioenergetics models are not an exception to this general rule. As with any model, the reliability of output from bioenergetics modeling is strongly dependent on appropriate parameterization and the accuracy of the input data used to drive them. Because WEB-based models tend to be parameter-rich, corroboration of model output is an important step in the model development phase. Unfortunately, not all models are created equal as evidenced by field and(or) laboratory evaluations of bioenergetics models (Chipps and Wahl, 2008). In recent years, efforts to corroborate bioenergetics models have led to improvements to existing models and new insights affecting the accuracy of model output. Accounting for factors such as life-stage, sex, feeding rate and environmental adaptations in bioenergetics models can lead to refinement of species-specific models and improved understanding of fish physiology.

A case study of a muskellunge (*Esox masquinongy*) bioenergetics model demonstrates how field/laboratory evaluations led to improvements in the model and increased our understanding of muskellunge biology. Early studies showed poor agreement between field estimates of food consumption and those predicted by a bioenergetics model for juvenile muskellunge (Wahl and Stein, 1991). Field-derived estimates of food consumption were 39–53% lower than those predicted by the bioenergetics model. Subsequent studies using laboratory-derived estimates of food consumption revealed similar findings in that food consumption was 30–75% lower than that predicted by the model. Moreover, in winter months (<10 °C), the model overestimated food consumption by 113–328% (Chipps et al., 2000a). An evaluation of seasonal variation in juvenile muskellunge metabolism showed that respiration rate varied among seasons and was lower in winter months at temperatures of 5–25 °C (Fig. 6). After accounting for seasonal, metabolic compensation by juvenile muskellunge, the bioenergetics model generated food consumption estimates similar to those observed in independent feeding and growth trials.

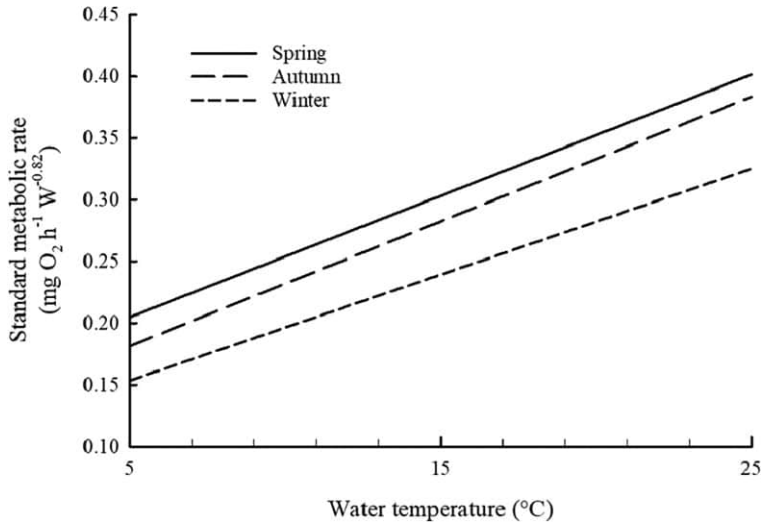

Fig. 6 Weight-adjusted, standard metabolism of age-0 muskellunge measured in spring, autumn, or winter at 5 °C, 15 °C, and 25 °C. Fish weight (W) is in grams. Adapted from Chipps SR, Clapp DF and Wahl DH (2000b) Variation in routine metabolism of juvenile muskellunge: evidence for seasonal metabolic compensation in fishes. *Journal of Fish Biology* 56:311-318.

Conclusions

Bioenergetics modeling offers a powerful tool to address contemporary issues in fisheries management and ecology. Increasingly, bioenergetics models are being used to address questions related to climate change, habitat quality, prey availability, and species interactions. In many cases, bioenergetics modeling provides insight into factors affecting fish growth and(or) food consumption. In other cases, quantitative predictions from bioenergetics modeling can be used to generate point estimates for setting harvest goals, stocking quotas, or balancing predator-prey demand, although such applications should be reserved for corroborated models. As we've seen with the example for Lake Michigan salmonines, the application of corroborated bioenergetics models can be a robust tool to successfully guide fisheries management in large ecosystems.

Future research/Knowledge gaps

- Efforts to integrate DEB theory with traditional WEB models should benefit both modeling approaches. Linking DEB theory with WEB modeling may reveal oversimplified assumptions for some applications but in other instances should prove useful in filling knowledge gaps in WEB models.
- Continued development of new, species-specific WEB models using traditional or new approaches will reduce "species borrowing" of parameters and expand the application of bioenergetics modeling.
- Field and laboratory evaluation of WEB models is an important aspect of the modeling process that can lead to refinement of WEB models for specific life-stages, sexes and(or) environments. The development of new methods to evaluate field performance of WEB models will be useful in advancing bioenergetics modeling.
- The application of new technologies (e.g., physiological telemetry) to better quantify swimming activity and associated energy expenditure of free-ranging fish will lead to more accurate modeling for both the DEB and WEB approaches.
- Otolith microchemistry, which can track trace elements and stable isotope fluctuations over the life cycle of fish, is an emerging technology being pursued in the development and application of bioenergetics models.

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http://www.debtheory.org/wiki/index.php?title=Main_Page—Dynamic Energy Budget theory.

Diel Vertical Migration☆

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This is an update of L.De Meester, Diel Vertical Migration, in Encyclopedia of Inland Waters, edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00151-4.
This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Introduction

Diel vertical migration (DVM) is a conspicuous and widespread behavior in planktonic organisms in both inland waters and marine environments. The first scientific studies on this behavior date from more than 100 years ago (Bandara et al., 2021), and DVM has been observed in a wide variety of habitats worldwide. DVM has attracted a lot of attention from researchers for several reasons: (1) it is a spectacular behavior, (2) its causes have remained enigmatic for a long time, and (3) the behavior has important ecological consequences.

DVM in its various forms

DVM is often associated with zooplankton, and zooplankton ecologists have indeed devoted great attention to the phenomenon. However, it should be mentioned that other organisms too have been shown to perform DVM, including fish, aquatic insects, and phytoplankton. Figs. 1–3 provide illustrations of DVM in zooplankton, chosen because they reveal several key aspects of the behavior and its variation. Fig. 1 (Hart, 1976) illustrates the migration pattern of a calanoid copepod in a subtropical lake. It shows the classical pattern of a "standard" migration: the animals reside higher in the water column during the night than during the day. During the day, they stay in deep water layers, whereas at night, they distribute themselves more evenly in the water column. The copepods move toward the surface water layers just after sunset, and they return to deeper waters before dawn. The migration is over a long distance relative to their body size. Indeed, the animals move 30–40 m twice every day, which is $>40 \times 10^3$ times their own body length (to human standards, this would translate into a traveling distance of >60 km a day). This illustrates why DVM is considered a spectacular behavior. Finally, the figure also illustrates another common feature: there is a clear tendency for more individuals to be caught during the night than during the day. This phenomenon is called the 'daytime deficit,' and is often observed in studies on zooplankton populations showing extensive DVM patterns. In the study system shown in Fig. 1, it was shown that a fraction of the copepod population actually moves into the sediments during the day. Although net avoidance by zooplankton during the light of day can contribute to this daytime deficit, in many more shallow lakes the daytime deficit is likely caused by the fact that the zooplankton is either residing so close to the sediments during the day that it cannot be sampled by traditional sampling gear or is even moving into the surface layers of the sediment. This is striking, as the sediment is a harsh environment for a zooplankton individual to reside in during part of the day. In many systems that show a strong oxycline, during the day the zooplankton resides at depths that are characterized by very low oxygen levels. Fig. 2 even shows a population of calanoid copepods that resides part of the day in the anaerobic monimolimnion of a meromictic lake (De Meester and Vyverman, 1997). In this coastal lake, there is no oxygen below 5 m depth. Fig. 2 also shows the pattern of changes in vertical distribution around sunset and illustrates that different life stages may differ in their daytime distribution and migration pattern. Indeed, it is clear from this

☆*Change History*: December 2021. L De Meester, T Mehner, and A Scofield were involved in the update. Updates involve smaller edits and the addition of recent references throughout the text, a paragraph on new methods and a new figure (Fig. 4) in the "DVM in its various forms section", and the addition of "DVM in fish" section.

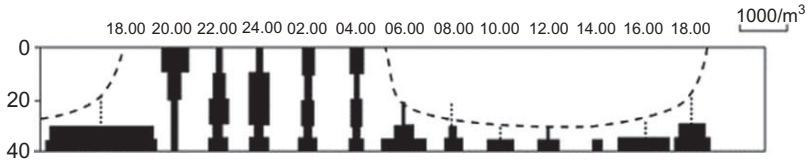

Fig. 1 Diel vertical migration of adult females of the calanoid copepod *Pseudodiaptomus hessei* in Lake Sibaya (March 1972). The broken line indicates a light intensity isocline (1 lux). X-axis: time of day; Y-axis: depth (m); thickness of bars indicates number of animals (see scale bar). Reproduced from Hart RC (1976). The substrate bin—A new sampling device for studying diel vertical migratory movements to and off lake sediments. *Freshwater Biology* 6: 155–159, with permission from Blackwell Publishing.

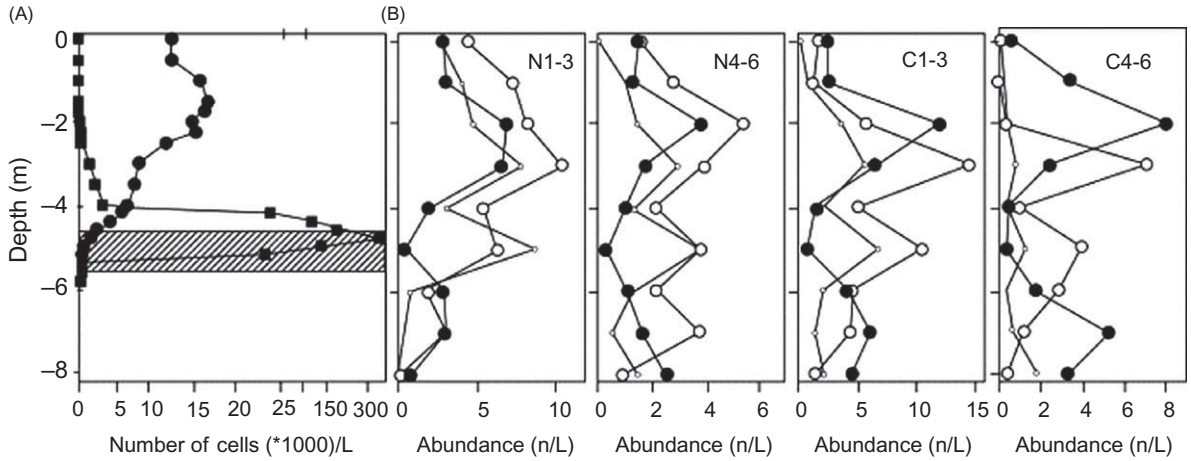

Fig. 2 Vertical distribution of calanoid copepods in meromictic coastal Lake Nagada (Papua New Guinea); the lake has a brackish mixolimnion and has no oxygen below 4.5 m (cf. accumulation of hydrogen sulfide by anaerobic metabolism). (A) Vertical distribution of algae in a mid-lake station, June 4, 1992. Filled circles: diatoms and flagellates; filled squares: cyanobacteria (*Oscillatoria*); shaded area: bacterial plate. (B) Vertical distribution of different ontogenetic stages (small nauplii: N1–3; larger nauplii: N4–6; young copepodites: C1–3; larger copepodites: C4–6) of *Acartia tonsa* 1 h before sunset (17.00; small empty symbols), at sunset (18.00; larger empty symbols) and 1 h after sunset (19.00; filled symbols) at a mid-lake station, May 30, 1992. Reproduced from De Meester L and Vyverman W (1997). Diurnal residence of the larger stages of the calanoid copepod Acartia tonsa in the anoxic monimolimnion of a tropical meromictic lake in New Guinea. *Journal of Plankton Research* 19: 425–434, with permission from Oxford University Press.

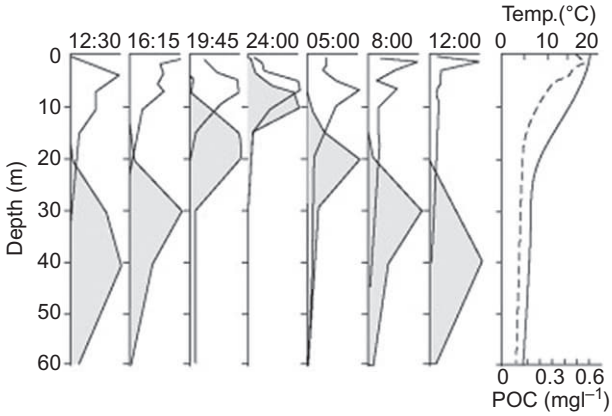

Fig. 3 Vertical migration patterns of *Daphnia galeata* (plain) and *D. hyalina* (shaded) during summer in Lake Constance. The right panel shows depth profiles of temperature (solid line) and particulate carbon (broken line) (particles <35 mm, i.e., potential food for *Daphnia*). Reproduced from Lampert W and Sommer U (2007) *Limnoecology: The Ecology of Lakes and Streams.* 2nd edn. Oxford: Oxford University Press, with permission.

figure that the youngest life stages tend to be distributed similarly to their food during the day, whereas most (sub)adult animals reside in the monimolimnion (depths that do not mix with the surface water) during the day and rapidly ascend to the mixolimnion (surface layer that mix vertically) after sunset. Fig. 3 illustrates strongly different DVM patterns among two congeneric species in the same habitat (Stich and Lampert, 1981). This same study also reported seasonal changes in DVM, with *Daphnia hyalina* migrating only vertically during the summer season. This pattern has been reported for many deep lakes in temperate regions (Ringelberg et al., 1991).

Our understanding of the diversity of forms DVM can take has also expanded with increased use of technological approaches to monitoring zooplankton distributions within the water column, such as hydro-acoustics methods and optical plankton counters (Stockwell et al., 2002; Finlay et al., 2007; Watkins et al., 2017; Scofield et al., 2020). These tools allow researchers to study in situ zooplankton distributions on much finer depth scales, as well as over much larger horizontal scales, than can be accomplished with traditional approaches like stratified net tows. For example, both stationary and towed acoustics transducers have been used to track DVM of *Mysis diluviana* in large deep lakes. This extremely light-sensitive omnivorous zooplankton species typically migrates from the hypolimnion to the metalimnion at night, remaining below the thermocline even at night (Euclide et al., 2017; Jensen et al., 2009). Laser optical plankton counter (LOCP) technology has shown that at times, zooplankton is concentrated in narrow thin layers of extremely high density within the metalimnion, especially during the day; zooplankton biomass within this layer may be an order of magnitude greater than the surrounding waters (Fig. 4; Vanderploeg et al., 2015; Scofield et al., 2020). Furthermore, extremely fine-scale differences in the distributions of different size groups of zooplankton can be observed using tools such as the LOCP, potentially shedding light on niche partitioning and/or predator-prey dynamics that may occur within the zooplankton.

Summarizing, DVM involves changes in depth distribution over a diel cycle, can take extreme forms, and shows tremendous variation through time as well as among life stages, species, and lakes. All four examples illustrated by the figures represent the most commonly observed pattern of migration, with the animals residing deeper in the water column during the day than during the night ("standard migration"). However, it should be mentioned that many natural zooplankton populations exhibit a clear-cut depth distribution that does not change over a diel cycle, and there are also observations of a range of non-standard migration behaviors, including partial migrations (Bayly, 1986; Ogonowski et al., 2013; Euclide et al., 2017) and "reverse migrations"—deeper during the night than during the day (Hairston, 1980; Ohman et al., 1983). The reverse pattern of DVM is less common, but it is nevertheless observed in several, often small-bodied species, such as rotifers (Dumont, 1968).

In the face of this overwhelming diversity in DVM patterns among species and populations, it is important to develop a broad perspective that allows structuring the observed variation. DVM can be considered a habitat selection behavior. More specifically, it is a depth selection behavior that consists of several elements that can vary among habitats, species, and populations: the depth at which the animals reside during the day, the depth at which they reside during the night, and the timing and speed of the migration from one depth to the other. This approach has proved productive in framing the observed variation in DVM patterns. For instance, it allows the viewing of the many observations of strong but constant depth preference during day and night as a DVM phenotype that may be selected for if the optimal depth is the same during the day and night, e.g., because it is only determined by the distribution of food. The ubiquity of standard migration would then reflect the fact that under a wide variety of circumstances it is adaptive to stay deeper in the water column during the day than during the night. It is revealing that DVM, viewed as a habitat selection behavior, is essentially very similar to twilight activity as reported for many small mammals, or the migration of aquatic macroinvertebrates in rivers to the underside of stones during the day. Furthermore, as a habitat selection behavior, DVM can also be considered an alternative to diel horizontal migration (DHM). DHM has been observed in many zooplankton species in shallow lakes with a well-developed littoral zone (Kvam and Kleiven, 1995; Burks et al., 2002). In a typical DHM migration, the zooplankton resides in the macrophyte vegetation in the littoral zone during the day and moves into the open water during the night. DHM shows many parallels to DVM: it exhibits similar diel dynamics, with the main movements being associated with dawn and dusk, and in both cases, the zooplankton moves to rather marginal habitats during the day.

Causes of DVM

What causes zooplankton to migrate vertically in a diel cycle? It is important to make a distinction between the proximate and ultimate factors leading to DVM in nature.

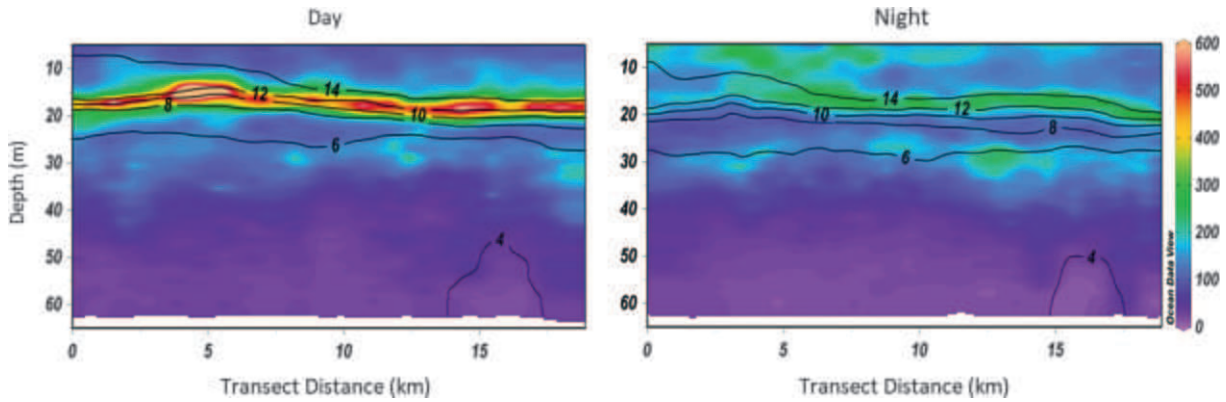

Fig. 4 Distribution of total zooplankton biomass at a transect in the open waters of Lake Michigan during the day (left) and night (right), based on laser optical plankton counter (LOPC). Data were collected offshore from Saugatuck, Michigan, U.S. on July 10–11, 2015. The transect distance is from east to west. The color scale indicates zooplankton biomass (μg dry weight/m^3), and the contour lines with labels show isotherms to visualize the thermocline. Redrawn from Scofield AE, Watkins JM and Rudstam LG (2020). Heterogeneity in zooplankton distributions and vertical migrations: Application of a laser optical plankton counter in offshore Lake Michigan. *Journal of Great Lakes Research* 46: 780–797.

Proximate causes

Proximate causes are the stimuli from the immediate environment of the individual organism that trigger the animal to move downwards or upwards. These stimuli–response processes relate to the physiology of the organism and translate environmental cues into the selection of a specific day- or nighttime depth as well as into a particular timing and speed of migration. It has been convincingly shown that zooplankton DVM is a response to relative changes in light intensity. Elegant laboratory experiments have revealed that a decrease in light intensity that surpasses a specific threshold elicits an upward movement, whereas an increase in light intensity above a specific threshold elicits a downward movement (Ringelberg, 1964, 1999). These responses have been called "secondary phototaxis"—in contrast to "primary phototaxis" that involves a response to a constant light intensity. Most detailed experiments have been carried out with the water-flea *Daphnia* and have shown that changes in light intensity result in eye rotations, which then translate in a change in body orientation and an upward or downward swimming behavior. These simple secondary phototaxis responses may allow for the prediction of day and night time depths as well as the timing and speed of migration. Moreover, several modifying factors affecting zooplankton migration behavior have been identified. For instance, the presence of fish kairomones (i.e., chemicals produced by fish that are recognized by zooplankton as indicating risk of predation) has been shown to increase the sensitivity to changes in light intensity, which translates into an increase in DVM amplitude in the presence of fish (De Meester et al., 1999). In contrast, both a strong temperature gradient and the absence of food may reduce the responsiveness of zooplankton to relative changes in light intensity, thus altering DVM behavior under different environmental conditions (Dini and Carpenter, 1992).

Ultimate factors

To the question why the zooplankton engages in DVM, one can also answer with reference to the ultimate factors causing DVM, i.e., its adaptive significance (Lampert, 1989). For a long time, the adaptive significance of DVM remained enigmatic, as researchers were puzzled by the fact that the zooplankton resided in deep, cold water layers that are characterized by low food concentrations during a large part of the diel cycle. Initially, many authors were convinced that DVM was a side-product of the visual system (Ringelberg, 1964). Others believed that there were metabolic advantages associated with residing part of the time at a lower temperature (Enright, 1977). These hypotheses were, however, at odds with empirical observations and are unsatisfactory with respect to the synchronized timing of DVM. The currently most widely accepted explanation for DVM in zooplankton is that it acts primarily as a predator-avoidance mechanism (Gliwicz, 1986a; Bollens et al., 1992; Stich and Lampert, 1981; Lampert, 1989; De Meester et al., 1999), driven by complex trade-offs between predation risk and optimal environmental conditions for feeding and growth (Lampert et al., 2003). The animals move into the deeper and darker water layers during the day to avoid predation by fish or visually-oriented predatory zooplankton (Bourdeau et al., 2011), returning to preferred habitat with warmer temperatures and higher food concentrations during the cover of night. When in oligotrophic lakes phytoplankton resources are concentrated in deep chlorophyll maxima, the cause of migration to the surface may be less apparent (Williamson et al., 1996; Winder et al., 2003).

There are many lines of evidence pointing to the importance of predator-avoidance in DVM, most of them being related to the observation that variation in DVM can often be explained by variation in predation risk:

- First, the hypothesis is logical: fish need light to detect their prey efficiently, and by hiding in the darker water layers, the zooplankton can reduce mortality by visually hunting fishes. During the night, the zooplankton moves to the upper water layers to feed on algae that remain in the epilimnion because they need sufficient light for photosynthesis. Thus, the hypothesis can explain both the day- and nighttime depth distributions, as well as the timing of the upward and downward migrations.
- Overall, there is a tendency for larger zooplankton species to migrate more or with more amplitude than smaller species. For instance, large *Daphnia* species migrate to deeper water layers than smaller crustacean zooplankton, whereas rotifers often do not migrate at all.
- Smaller life stages often migrate with less amplitude or do not migrate at all (e.g., Fig. 2).
- Individuals that are more conspicuous, such as egg-bearing females, often migrate with more amplitude (Vuorinen et al., 1983).
- It has been reported repeatedly that also within a population, there is a tendency for a correlation between body size and daytime residence depth within a given lake (De Meester and Vyverman, 1997) and in experimental settings (De Meester et al., 1995).
- Among-population variation in DVM amplitude can sometimes be related to differences in predation risk by fish (Fig. 5; Dini and Carpenter, 1991) This is illustrated by the absence of migration in many fishless lakes (e.g., Gliwicz, 1986a).
- Many populations show seasonal variation in DVM amplitude that can be explained by seasonal variation in predation risk by fish (highest in summer when the young-of-the-year are roaming through the pelagial; e.g., Fig. 6; Ringelberg et al., 1991; Bollens et al., 1992).
- Very direct evidence for the predator-avoidance hypothesis is provided by the many experimental studies that have shown that DVM behavior can be induced by the presence of predator-specific (fish and invertebrate predators) chemicals (kairomones; Fig. 7; Loose, 1993; De Meester et al., 1999).
- Several mathematical models have shown that DVM behavior can indeed be adaptive as a predator-avoidance strategy, i.e., that the benefits outweigh the costs of staying at low food and temperature during part of the diel cycle (Fiksen, 1997; Liu et al., 2003).

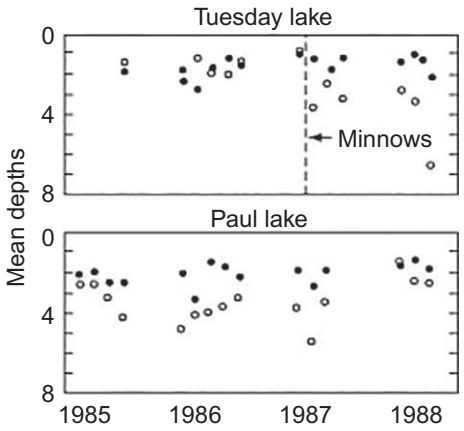

Fig. 5 Impact of fish on DVM: field data from Tuesday and Paul Lake, two kettle lakes at the University of Notre Dame Environmental Research Center. Shown are night (solid symbols) and day (empty symbols) average depth of the *Daphnia* assemblage in the two lakes as determined from vertical profiles taken during several sampling campaigns across four summers. In 1985 and 1986, Tuesday Lake was biomanipulated, resulting in a strong reduction in fish predation pressure; in 1987, fish were reintroduced to the lake, resulting in quite high minnow densities. DVM amplitude of the *Daphnia* assemblage is associated with the presence of planktivores. Paul Lake was not biomanipulated, and harbored planktivorous fish during the whole period. Reproduced from Dini ML and Carpenter SR (1991) The effect of whole-lake fish community manipulation on Daphnia migratory behavior. *Limnology and Oceanography* 36: 370–377, with permission from American Society of Limnology and Oceanography.

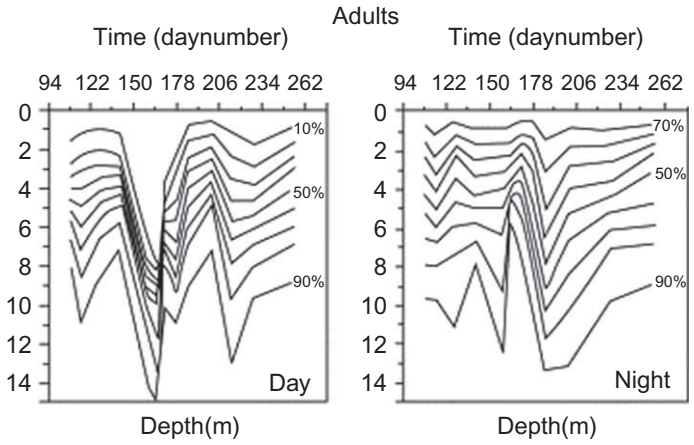

Fig. 6 The changes in day (left) and night (right) depth of adult *Daphnia hyalina x galeata* hybrids in Lake Maarsseveen during the course of the growing season (April 18—September 141,989). The dip in the bundle of lines indicates the period of strong DVM. This period corresponds with the massive appearance of juvenile perch in the pelagial of the lake. Reproduced from Ringelberg J, Flik BJG, Lindenaar D and Royackers K (1991). Diel vertical migration of Daphnia hyalina (sensu latiori) in Lake Maarsseveen: Part 1. Aspects of seasonal and daily timing. *Archiv für Hydrobiologie* 121: 129–145, with permission from E. Schweizerbart'sche Verlagsbuchhandlung.

- Evolution of DVM behavior linked to changes in predation pressure within a single lake (Cousyn et al., 2001; Stoks et al., 2016) or in experimental settings also provides strong evidence for predation being an important selection factor driving DVM.

The evidence for the predator-avoidance hypothesis is overwhelming. Yet, predator avoidance need not be the sole adaptive value of DVM. Indeed, some cases of day depth distribution or DVM cannot be satisfactorily explained by the predator avoidance hypothesis. Recently, evidence has accumulated that an important adaptive value of DVM may lie in the avoidance of damage caused by UV-radiation, or more generally, by high light intensity (Fischer et al., 2015; Urmy et al., 2016; Williamson et al., 2011). Especially in transparent high-altitude lakes, the presence of fish may not be the only or even the main reason for DVM behavior to develop. UV-avoidance can also explain the pattern and timing of typical normal DVM behavior. Moreover, there is an intrinsic interaction between UV- and predator-avoidance, as animals have two mechanisms to avoid photodamage: they may accumulate protective pigments, or they may migrate vertically. In the absence of predators, protective pigments may be the more beneficial option, but in the presence of predators, DVM may be the better alternative because pigmentation bears a high cost of increased predation risk (Hansson et al., 2007). It is often observed in alpine lakes that copepods are pigmented, whereas cladoceran zooplankton are not and migrate vertically (Hairston, 1980). What drives this difference is insufficiently understood, but it

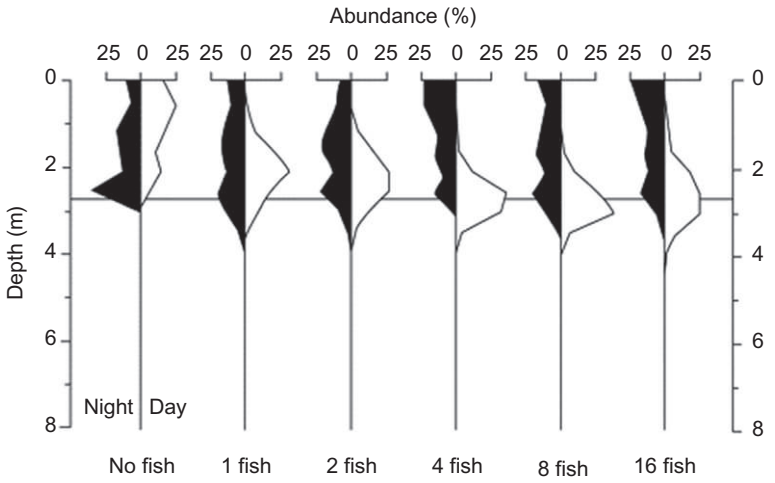

Fig. 7 Induction of DVM by fish kairomone in a clonal population of *Daphnia galeata x hyalina* hybrids in an experiment using the Plankton Towers at the Max Planck Institut for Limnology, Plön. The experiment was started without fish. Then, the upper 3 m of the tank received water that was conditioned by one fish (*Leucaspius delineatus*, 5 cm body length). After 4 days of adaptation, the vertical profile was recorded again at night and during the day. Subsequently, the number of fish was doubled, and the same procedure was continued three more times (cf. up to 16 fish). Reproduced from Loose CJ (1993) Daphnia diel vertical migration behavior: Response to vertebrate predator abundance. *Archiv fur Hydrobiologie-Beiheft Ergebnisse der Limnologie* 39: 29–36, with permission from E. Schweizerbart'sche Verlagsbuchhandlung.

might be related to the fact that most copepods are relatively small and better swimmers than water fleas. Alternatively, it may be that copepods have better capacity to accumulate photoprotective pigments from their food.

A third ultimate reason to exhibit a typical depth distribution or DVM may be avoidance of competition. This has been shown experimentally in rotifers (Dumont, 1968), and it is a likely reason for depth selection of small zooplankton, which may avoid depths at which larger bodied zooplankton accumulate. It should be noted, however, that this mechanism can only operate in a situation where the competitively superior species is restricted to its depth distribution by additional factors. If competitively dominant large bodied water fleas are forced to hide in the deeper water layers by predation risk or UV radiation, then this may open a window for coexistence of smaller species that occupy the upper water layers during the day. During the night, these smaller species may avoid the upper water layers to reduce interference competition with the large bodied species. The result is a reverse migration. A reverse migration may also be associated with the avoidance of invertebrate predation (Ohman et al., 1983; Gilbert and Hampton, 2001). Small bodied species are more vulnerable to invertebrate predators, and as these may be forced to hide in deeper waters during the day because of predation risk by fish or larger invertebrate predators such as notonectids, the small bodied species may increase their fitness by residing in the upper water layers during the day and then spread over the water column during the night, when the invertebrate predators move up into the open water to search for prey (Gilbert and Hampton, 2001).

Costs

Viewing DVM as a habitat selection behavior provides a flexible approach to the overwhelming variation in DVM patterns, as the observed day and night time depth distribution as well as timing and speed of migration can be considered to be selected because they provide a high benefit to cost ratio. The benefits of DVM are, as mentioned, often related to reduced mortality by predation, but also reduced damage from high light intensities, and in some cases, reduced competition. The costs are largely cast in terms of reduced food intake, reduced food quality, increased competition (when several competing taxa are migrating to the same refuge), and metabolic costs associated with residing at a lower temperature. In addition, there may be costs associated with residing in truly marginal habitats, such as near-anoxic conditions or being buried in sediments. Residing at or near the sediments can also increase the risk of infection by increasing the likelihood of taking up infective parasite spores, as has been shown in the water flea *Daphnia* (Decaestecker et al., 2002). The costs associated with the movement from one depth layer to the other has, however, been shown to be relatively low or even negligible (Vlymen, 1970; Dawidowicz and Loose, 1992). This is because the animals in general must actively swim to keep their position in the water column anyway, coupled with the observation that the descent is often passive. During the descent, the animals become less active, and they become more active during the ascending phase. In simple wording: if a water flea shows its typical hop–sink–hop–sink swimming behavior to keep its vertical position, descending is accomplished by hop–sink–sink–hop–sink–sink and ascending by hop–hop–hop–sink behavior. One can imagine that the energy lost during the ascending phase matches more or less the energy gained during the descending phase.

Linking proximate and ultimate factors in DVM

The previous paragraphs picture a situation in which the most advantageous DVM behavior may strongly differ from lake to lake. The question then arises as to how this is matched with the response to proximate stimuli. How do the physiological responses of the animals lead to the right vertical distribution during the day and night and the right timing and speed of the ascent and descent? There are two possible mechanisms that are not mutually exclusive, and both of which are supported by experimental evidence. On the one hand, part of the variation in DVM behavior can be accomplished by phenotypic plasticity, through a change in behavior at the level of the individual. It has, for instance, been shown that predator kairomones and hunger influence the sensitivity of zooplankton individuals to relative changes in light intensity, resulting in a modification of DVM behavior (Van Gool and Ringelberg, 1995; De Meester et al., 1999). Populations may thus adjust their DVM behavior by showing the appropriate phenotypic plasticity in response to changes in environmental conditions. At the same time, it has been shown that there is ample genetic variation for DVM behavior, among others through laboratory quantitative genetic analyzes of the variation in response to a light gradient (Fig. 8; De Meester et al., 1995) and, to a lesser extent, changes in light intensity. Moreover, it has been shown that there is also genetic variation in phenotypic plasticity for DVM, at least in the water flea *Daphnia* (De Meester, 1993). This sketches a picture of very high flexibility: populations can adjust their DVM behavior by phenotypic plasticity of the individuals as well as by changes in genetic composition with respect to DVM. It has indeed been shown that populations show local genetic adaptation for DVM in relation to predation risk (De Meester, 1996). Furthermore, reconstruction of microevolution in DVM behavior on laboratory populations hatched from dormant egg banks that were isolated from a dated sediment core has shown that local populations can genetically track changes in fish predation pressure over a period of less than a decade (Cousyn et al., 2001; Stoks et al., 2016).

The picture that emerges is that DVM is an important component of an antipredator strategy in many populations of zooplankton. It should be emphasized that DVM should not be seen in isolation from other antipredator traits (Stoks et al., 2016). It has, for instance, been shown that there is often a relationship between size at maturity and day-depth, with larger animals residing in deeper water layers than smaller ones (De Meester et al., 1995). Different genotypes and species may thus differ in the antipredator strategy they employ. This is nicely illustrated in the differences in migration pattern of *D. galeata* and *D. hyalina* in Lake Constance (Fig. 3; Stich and Lampert, 1981). The strategy of *D. galeata* involves a high predation risk associated with continuous residence at higher temperatures and under good food conditions. This results in high birth and death rates. The strategy of *D. hyalina* is to reduce mortality rates and bear the cost of having lower birth rates. The fact that both species can co-occur in the lake

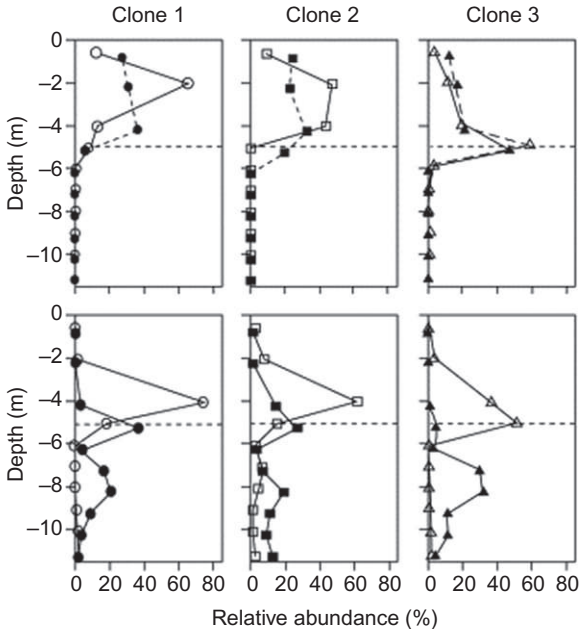

Fig. 8 Vertical distribution of three *Daphnia hyalina x galeata* hybrid clones isolated from the same population (Schöhsee, Germany) in the Plankton Towers of the Max Planck Institute for Limnology (Plön), showing genotypic differences in DVM behavior. Top: Average vertical distribution of adult females during the day (open symbols) and night (solid symbols) in the absence of fish chemicals or fish; bottom: daytime distribution in the presence of fish chemicals (open symbols) and fish (solid symbols). The dotted line indicates the thermocline. The experiment involved mixed populations of the three clones, and individuals were identified using allozyme markers. Clone 3 has a clearly different vertical distribution from clones 1 and 2. Reproduced from De Meester L, Weider LJ, and Tollrian R (1995) Alternative anti- predator defences and genetic polymorphism in a pelagic predator–prey system. *Nature* 378: 483–485, with permission from Nature Publishing.

illustrates that both strategies may have similar fitness. Part of this relationship is also observed at the genotypic level, with larger bodied genotypes showing a stronger response to light gradients (De Meester et al., 1995). Similarly, DVM behavior and pigmentation are both photoprotection strategies, of which the relative importance may be strongly influenced by predation risk. Both pigmentation and DVM have a cost, but the cost of pigmentation is strongly dependent on predation risk (Hansson et al., 2007).

Consequences of DVM

DVM has important consequences, as it strongly influences the top–down impact in lake food webs (Lampert and Taylor, 1985; Lampert and Sommer, 2007). DVM reduces the direct impact of fish predation on zooplankton. A more subtle consequence of DVM is that populations of large bodied zooplankton may survive longer in the lake, which thus extends the time during which this food resource remains available for the fish to feed on. In this sense, DVM can be expected to strongly buffer predator–prey interactions between fish and zooplankton. With respect to the zooplankton–algae interaction, DVM has been shown to strongly affect the grazing impact of zooplankton on algae (Lampert and Taylor, 1985; Reichwaldt and Stibor, 2005; Haupt et al., 2009). Here again, however, this has two aspects to it. On the one hand, grazing impact would be higher in the absence of fish-induced DVM, because DVM reduces the time during which zooplankton resides in the epilimnion to feed on algae. On the other hand, DVM may allow large bodied zooplankton to survive in lakes that harbor fish. Given that large bodied zooplankton are more efficient phytoplankton grazers than small bodied zooplankton (Gianuca et al., 2016), DVM may thus indirectly promote the grazing impact of zooplankton on algae, as it allows large-bodied zooplankton to graze on phytoplankton during at least part of the day. In lakes in which the zooplankton exhibits a strong DVM, the algae are indeed fed on by large and efficiently grazing zooplankton during the night. The impacts of DVM on population dynamics of zooplankton and algae and on predator–prey interactions are thus very pervasive. A nice illustration of the impact of DVM on population dynamics is given by the observation of a lunar cycle in zooplankton densities in Lake Kariba (Gliwicz, 1986b). The population densities of zooplankton species in this lake have been reported to show cyclic changes associated with increased predation success of fish on zooplankton during moonlit nights at full moon. In the tropics, sunset and moonrise occur quite fast, and at full moon, the zooplankton is trapped in the surficial water layers by the suddenly rising full moon, providing a feast for the fish.

An interesting avenue of thought in this context is the impact of predator-induced plasticity in DVM on predator–prey interactions and top–down control in lakes. As DVM has strong impacts on top–down control, it should be recognized that part of the impact of predators is actually mediated by induced avoidance behavior rather than by direct predation itself (Haupt et al., 2009).

Reverse migrations

We have focused on the DVM behavior of herbivorous zooplankton (mainly cladocerans, copepods, and rotifers). Omnivorous and predatory zooplankton may, however, also strongly engage in DVM. A good example is the fish-induced DVM behavior of phantom midge larvae (*Chaoborus*) (Dawidowicz et al., 1990). *Chaoborus* species that inhabit fishless habitats do not migrate vertically, but in fish lakes, the animals often migrate to the sediments during the day and appear in the water column at night (e.g., Oda and Hanazato, 2008). This is believed to be a strong structuring force on the zooplankton in lakes. During the day, large-bodied zooplankton, including *Chaoborus* larvae, hide in the deep water layers as a refuge from fish predation. By doing so, they provide enemy-free space to small-bodied zooplankton. The small-bodied zooplankton may, however, move out of the high food upper water layers during the night, as these layers are then invaded by efficiently grazing large-bodied zooplankton and gape-limited invertebrate predators that hunt for the small-bodied zooplankton. The resulting pattern is a strong standard migration for larger zooplankton and *Chaoborus* and a reverse migration for smaller zooplankton (Lagergren et al., 2008).

There is an interesting parallel in large, motile phytoplankton. Algae often perform a "reverse" DVM, residing deeper in the water column during the night than during the day. There is much less literature on DVM in algae, but here too, it is a useful approach to consider it a habitat selection behavior (Cullen, 1985; Heaney and Eppley, 1981; Ralston et al., 2007). There are two main reasons for DVM in algae. First, it may be a strategy to combine efficient photosynthesis during the day with a reduction of mortality by zooplankton grazing during the night. Alternatively, DVM of algae may also be a strategy to increase nutrient uptake. By migrating to deeper and nutrient-rich layers during the night, the phytoplankton may increase nutrient availability for photosynthesis during the day, thus reducing the impact of nutrient depletion in the epilimnion (Baek et al., 2009; Heaney and Eppley, 1981).

DVM in fish

Fish have also been reported to migrate vertically. They may do so for two reasons—to follow their prey, and to avoid their predators. Even though it is much less efficient to hunt in deeper water layers, it may still be more profitable for fish to follow their food in suboptimal conditions, rather than remaining in a habitat that is devoid of any food. It has been shown that fish may even venture for short dives into the near-anoxic conditions to hunt for zooplankton that use these inhospitable layers as a refuge (Rahel

and Nutzman, 1994). This may explain why zooplankton often migrate deeper than the border zone of the refuge. In turn, fish might migrate to avoid their own predators. By avoiding the surface waters during the day, they may reduce their mortality from both fish-eating birds and fish. Many fish populations have been reported to either change their vertical or horizontal distribution. In the latter case, they hide in the littoral zone during the day and migrate to the pelagial during the night (Bohl, 1980). Given that studies often show that both fish and zooplankton avoid the surficial layers of the pelagial zone during the day, one may wonder why the zooplankton does not simply reinvade the food-rich upper water layers. There are several explanations for this. First, it should be acknowledged that in zooplankton populations that show a very strong DVM behavior, intensive sampling of the superficial water layers often reveals some individuals residing there at very low densities. Secondly, it is easy to imagine that, if densities in the superficial layers would become higher, the fish would also rapidly start exploring this food source. Given that hunting at high light intensities is so efficient, even short excursions of the fish to these water layers would decimate the zooplankton. So, one expects densities of larger bodied zooplankton to be very low in the epilimnion in such lakes, which is the pattern that is observed.

It is intriguing that the vast majority of fish DVM is performed by species that can be classified as belonging to the cold-water thermal guilds. These species have thermal optima and preferences for water temperatures that are typical for the hypolimnion of stratified lakes (~4–12 °C). Accordingly, the standard DVM is characterized by a switch between deep and very cold hypolimnetic layers during daytime and shallower and warmer layers close to the thermocline during night-time. DVM patterns by which fish migrate from the hypolimnion through the thermocline up to the surface during the lake stratification phases have been rarely observed, while fish more often migrate into very shallow layers during the mixing phases when lakes are isothermal. Fishes of the warm-water guild seem to migrate dominantly horizontally between littoral (daytime) and pelagic (night-time) habitats within the epilimnion (Bohl, 1980), similar to the DHM of zooplankton.

The main proximate cue of fish DVM is the diurnal change in illumination strength, inducing migrations upwards in the water column during dusk and downwards during dawn for the standard DVM (Appenzeller and Leggett, 1995, Scheuerell and Schindler, 2003). There are several empirical observations that DVM stops when the vertical light gradient is strongly weakened, for example during the polar summer or if lakes are covered by thick ice and snow layers (Gjelland et al., 2009, Jurvelius and Marjomäki, 2008). However, the triggering of migrations by light intensity is superimposed by a small-scale orientation along vertical temperature gradients, which causes seasonal changes in night-time depths and hence migration amplitudes (Levy, 1990). If vertical depth and extension of the thermocline change over the months, fish likewise change their night-time depths to always being located in layers with their metabolically optimum temperatures (Mehner et al., 2010).

Ultimate explanations for fish DVM include feeding opportunities and predator avoidance, similar to the reasoning for the DVM of zooplankton. This creates the fascinating situation that zooplankton in stratified lakes are squeezed between warm-water planktivorous predators enforcing a standard DVM in zooplankton, and cold-water planktivores against which a reversed zooplankton DVM would be the best strategy. Under these conditions, amplitudes of standard zooplankton DVM are often small and spatially confined to the epilimnion and the upper part of the thermocline. Evidence that either feeding efficiency or predator avoidance alone explains fish DVM is rarely found. For example, planktivorous fish do not follow zooplankton DVM to maximize feeding efficiency. And fish DVM is often found also in systems where the predator density is very low, such that predator avoidance is unlikely to be the sole ultimate explanation. A third ultimate explanation for fish DVM is referred to as bioenergetics efficiency, for example by a "hunt warm—rest cool" strategy. Here, it is assumed that the temperature optimum for hunting and feeding differs from that optimal for digestion. Empirical evidence for fish DVM solely be explained by bioenergetics efficiency is likewise equivocal, at best (Neverman and Wurtsbaugh, 1994; Mehner et al., 2011).

Accordingly, a multi-factor ultimate explanation may be more suitable to understand fish DVM. One example is the "anti-predation window," based on the observation that the visual ranges of fish predators and their fish prey differ substantially (Scheuerell and Schindler, 2003). Planktivorous fish (the prey) can feed at lower light intensity than their predators (piscivorous fish) and hence may find a refuge under darker conditions. Therefore, prey fish actively seek layers characterized by this low illumination and continue feeding during the day but because of high light at the surface, these layers are relatively low in the water column. The layer with the optimal illumination moves upwards at dusk and downwards at dawn. Prey fish can move within this anti-predation window and therefore feed along the zooplankton gradient while ascending and descending. In this way, prey fish minimize the ratio between predation risk and feeding gain or growth (Scheuerell and Schindler, 2003). This concept can be expanded by also including bioenergetics efficiency. Predator avoidance causes the fish to stay in deep layers by day. Feeding opportunities drive the migration within the anti-predation window. Bioenergetics efficiency is enhanced when fish seek layers of optimum temperature at night. Therefore, DVM often reflects a three-way compromise between the three ultimate hypotheses on fish DVM—feeding efficiency, predator avoidance, and bioenergetics efficiency (Mehner, 2012).

Multi-factor ultimate explanations also reflect that DVM is an ecological trade-off for fitness optimization. Prey density, temperature, and light level affect feeding and hence growth rates, whereas predator density and illumination strength affect predation risk. It is expected that the costs of DVM incurred by residing in water layers that are suboptimal with respect to feeding are balanced by the benefits to minimize predation risk. An additional and almost unexplored cost in fish DVM is the energy needed for the movement itself. Most of the fish species possess a swim bladder, and hence the vertical movements during crepuscular phases induce changes in the compression of the swim bladder at the differing depths. It is likely that pressure compensation is not fast enough to keep neutral buoyancy of fish at all depths during the migration, hence indicating that fish must swim actively against the negative or positive lift resulting from non-optimal swimbladder volumes, at least for some time during vertical migrations (Fleischer and TeWinkel, 1998; TeWinkel and Fleischer, 1998; Clemens and Stevens, 2007). Fish without swimbladders and

most invertebrates do not have this problem. The contribution of migration costs to the cost-benefit ratio of fish DVM is currently unresolved.

Most of the empirical studies of fish DVM have focused on population behaviors. However, it has to be considered that the adaptive value of behaviors is related to individuals. Deciphering ultimate causes and proximate causes for a population is, therefore, only correct if all individuals of a population would be equal in the traits relevant for the cost-benefit ratio. However, individuals of a population always differ, for example with respect to size or life-history stages. The growth of fish during their ontogeny is substantial, and hence most fish populations are strongly size-structured. Size is decisive with respect to prey selectivity, feeding efficiency and predation risk because the intensity of predator-prey interactions in aquatic systems depends on the size ratios between predators and prey. Furthermore, differing phases of the life history, for example the switch from the immature individual to one that is reproducing, may modify the relative importance of having fast growth versus being safe from predation because fast growth in length has less priority when fish start reproducing. The typically recorded fish DVM at the population level is the average of individual DVMs. Few studies have focused on individuality of DVM patterns. However, the documentation of partial DVM by which fish populations split into migrants and residents supports the predictions that the cost-benefit ratio of a DVM strategy differs between individuals. The recent technological development of acoustic devices, for example scientific echosounders or acoustic telemetry arrays (Guzzo et al., 2018), has facilitated more in-depth studies on the individuality of DVM patterns and potential biotic and abiotic correlates (Gutowsky et al., 2013).

See Also: Fundamental concepts and theories: Light as an Ecological Resource; Pressure

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Models of Animal Distributions in Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Biotelemetry The method uses different type of tags (active and passive) to track movement of animals or gathering information about animal environment (e.g., temperature, depth).
Diel vertical migration Very common phenomenon in both marine and freshwater ecosystems when different taxa (most typical fish and zooplankton) perform regular day night depth changes. More common for migrating organisms to be deeper during the day and shallower at night but the opposite does occur as well.
Ecology of fear Concept studying the total impact of predators on prey populations and communities. Beside direct effect of predator (prey is killed) there is strong indirect cost of predation for prey. Cost of avoiding predation ("fear") may induce prey source avoidance and thus reduce prey fitness. This indirect predation effect can have higher impact on populations than the direct effect of predation mortality.
Evolutionary stable strategies Behavioral strategy (or set of strategies) that, if adopted by all individuals in a population, cannot be replaced or invaded by any alternative strategy.
Give-up-density The quantity of food remaining in a patch when an animal leaves that patch. It is often used to measure the effect of predation on optimal patch use (predation risk cause a substantial increase in give-up-density).
Handling time The time taken to move toward and consume a food item.
Lentic and lotic environment Lotic is related to running fresh waters, lentic to stagnant, still waters.
Predation-prey cycles Predator and prey populations cycle through time. Numerous predators decrease numbers of prey and lack of prey in turn decrease predator abundance which allows prey to increase again, thereby repeating the cycle.
Reaction distances The distance in which a predator can detect a prey, usually determined as the distance an animal would travel in a straight line directly toward a food item.
Remote sensing Is the process of detecting and monitoring the physical or biological characteristics (e.g., chlorophyll concentration) of an area by measurements from satellites or aircrafts.
Trophic cascades Cascades are defined as reciprocal predator–prey effects that alter the abundance, biomass or productivity of a population, community or trophic level across more than one link in a food web.

Background and significance of distribution modeling

Who is where, when, how and why? These are the fundamental questions of ecological modeling of distribution. Where are animals? When and how do they change their distribution? Why are they at specific sites? Why do they move somewhere else? The answers to these simple questions allow us to understand interactions between animals and their environment and gain insight into

 https://doi.org/10.1016/B978-0-12-819166-8.00065-7

how spatial distributions can affect ecosystem structure and function. Distribution models also contribute to theory development and inform applied issues associated with conserving and managing natural resources.

Distribution models (DM) are tools for describing and predicting distribution of animals under variable conditions. These models use several statistical approaches to predict the location of an animal in space and time. Hence, DM require an understanding of a species basic habitat requirements, such as physical structure, depth, or temperature. The field also developed numerous frameworks and mechanistic models for understanding drivers of habitat selections. By providing mathematical descriptions of the influence of factors such as food source, quality, predation, and competition on spatial distributions, the field of DM has enabled the development of testable hypotheses that can inform ecological theory. Models based on mechanistic understanding can be used for prediction and simulation of individual, population, or ecosystem behavior under altered conditions.

In this article, the focus is given to DM based on distribution of an individual animal rather than whole species. Modeling distribution of whole species derived from habitat or niche environmental parameters represents entire field of models covering approaches such as habitat suitability and species distribution models (environmental/ecological niche modeling). Here, we briefly summarize important parameters, influential concepts and tools used in modeling distribution of animals within inland aquatic environments.

Habitat and fitness definition

Animals are not distributed randomly. Their distribution is a result of their responses to biotic, abiotic and internal factors. A habitat is defined as a location with distinct abiotic and biotic factors where animals stay, and which provide food, shelter or mates (e.g., open water, bottom sediment or littoral structured habitats; Begon and Townsend, 2006). DM are often descriptions of an animal's habitat selection or habitat selection rules.

Animals usually change habitats during their lifetime. This change may occur within a lake, between marine and freshwater environments, or between aquatic and terrestrial ecosystems. Even sessile animals may have a highly mobile dispersal stage, such as gametes, seeds, or eggs. These movements depend on external or internal factors and can be of various spatial (e.g., a few centimeters or thousands of kilometers) and temporal (lifetime, year, seasons, diel cycle, etc.) scales. These changes should increase an animal's fitness as defined by its contribution to the gene pool of the next generation (Begon and Townsend, 2006). However, fitness is affected by a combination of variables (prey, predators, mates, abiotic factors) and the importance of these variables will change through the lifespan of an animal. Given the complexity of factors driving fitness, a key challenge for DM is selecting a measurable indicator (or proxy) for fitness. In DM, maximization of fitness or one of its components (feeding rate, growth, fecundity, predation risk, mortality) is usually used for finding the best strategy for habitat selection or movement among habitats (Giske et al., 1998).

Time scale and animal unit

Animals may change their distribution on hourly, daily, seasonal or even longer time scales depending on the species. DM need to operate on a time scale relevant to the animals and movements in question. Therefore, models are constructed to operate at different time scales, from hours (e.g., models of patch selection according to food resource quality), to diel cycle (e.g., diel habitat switch such as vertical migrations in lakes), to seasons (long-distance migrations), and to years (whole life cycle migrations).

DM also need to specify the animal units to be modeled, again given the questions the model intends to answer. Even within a species, spatial distribution may differ between individuals, certain personality types, ecospecies (e.g., individual sex, larvae, adults, cohorts, etc.), and different populations. Selection of an animal unit influences model complexity. The more complex the animal unit, the greater is the uncertainty in the model structure and parameters. Individual models can reflect specific individual behavior and variation, while ecosystem models often omit individual interactions and work instead with functional groups or whole species.

Abiotic factors

The key abiotic factors considered by spatial models in aquatic environments are temperature, depth, oxygen, light and current (Fig. 1, Giske et al., 1998). Temperature drives the rate of metabolic processes for nearly all freshwater animals (except water birds and mammals) and limits the occurrence of animals to the temperature ranges to which the animals are adapted (e.g., Hofmann and Fischer, 2002; Riha et al., 2017). In lakes and reservoirs (lentic systems), temperature is tightly correlated with depth and both are typically considered when modeling depth distributions. In temperate stratified waters, available temperatures can range from 4 °C at the bottom or even almost 0 °C close to ice to over 30 °C at the surface during the summer. Thus, depth preference is driven by species-specific temperature requirements and by metabolic advantages of being in cold or warm temperatures (Wurtsbaugh and Neverman, 1988; Lampert, 2005; Mehner, 2012).

Similarly, oxygen is a key element for most animals. Oxygen concentrations have to be included in DM when oxygen can be depleted, as is the case of hypolimnion of many eutrophic stratified lakes in the summer (Hanke et al., 2014).

Another important factor is light. Light availability largely determines how predator and prey can detect each other as well as the distribution of primary producers. Light is used in calculating reaction distances, an important part of predator-prey models and

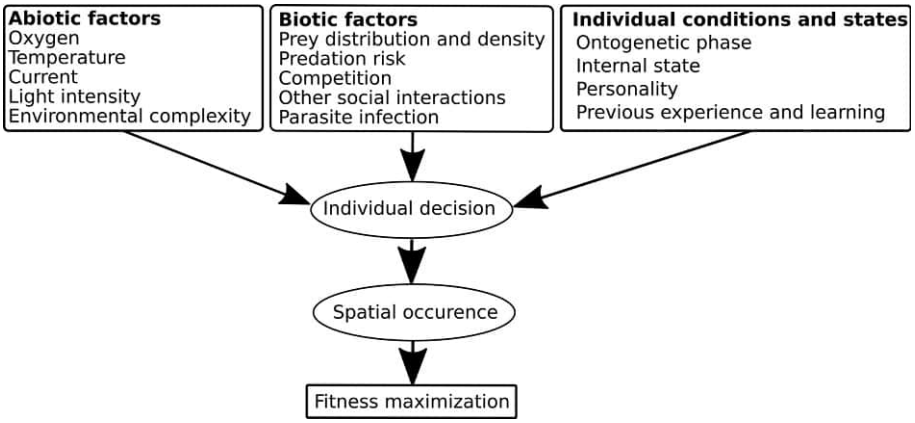

Fig. 1 Schematic overview of external and internal drivers influencing individual decision for spatiotemporal presence.

defined as the visual range in which the animal can detect prey (Vogel and Beauchamp, 1999). Light is also a factor in describing an animal perception of predation risk (Boscarino et al., 2010) and is used to understand the distribution of primary producers that are food sources for animals (Scofield et al., 2020).

In rivers and streams (lotic systems), water flow causes drag that requires additional energy for the animal to hold position or move upstream. How water flow affects habitat selection or migration pathway is often considered in river habitat selection models and in models predicting movement pathways through river or river obstacles such as weirs or fish passes (McElroy et al., 2012).

Biotic factors

The most important biotic factors considered in DM are food source (quality and distribution) and effect of inter- and intra-species interactions, especially predation and competition (Fig. 1). The effects of food source, predation and competition have been intensively studied over the last 30 years, yielding several important concepts for understanding distribution dynamics (see below). Other biotic interactions, such as parasitism (Barber et al., 2000; Poulin, 2013), diseases (Lefcort and Blaustein, 1995), and positive interactions such as cooperation, mutualism, symbiosis, and commensalism (Silknetter et al., 2020) can also influence spatial distributions. However, effects of these other interactions on spatial distribution in inland waters have received comparatively little attention to date (Silknetter et al., 2020).

Intrinsic individual conditions and states, such as neurobiological, developmental, or reproductive stage, can also be considered as biological drivers and some DM consider how habitat selection depends on these intrinsic factors. Juveniles and adult can differ in their need for food resources and in the risk of predation (Werner and Hall, 1974), hungry individuals likely tolerate higher predation risk (Moran et al., 2020), and learning may affect spatial distributions (Krebs and Inman, 1992). Recent research is also considering the effect of personality on the spatial distribution of animals with some individual being more risk prone and others more risk averse (Sih et al., 2015).

Model concepts and application

Next, we introduce several approaches and concepts widely used in modeling of animal distributions. These concepts are described approximately in the order they were introduced to the academic audience, as some were derived from previously developed concepts while others are more independent.

Optimal foraging theory

Optimal foraging theory (OFT) focuses on the effects of habitat quality and diet choice on the spatial distribution and movement of animals. This theory addresses the question of how long a forager should spend exploiting one food source before switching to another (Emlen, 1966; MacArthur and Pianka, 1966). A central assumption of OFT is that an animal will increase its fitness by minimizing the time and energy required to acquire the maximum amount of energy from food (Ritvo, 2018). Optimal forager should consider the quality of the food source and invest handling time for a food item only if, on average, it cannot maximize its food intake rate by passing up this food item to continue foraging and find a more valuable food item (Pyke and Stephens, 2019).

The original theory was developed in the 1970s and received considerable attention in the scientific community. Early empirical studies of this theory supported its prediction on patch and diet choice. The time spent by an animal in a food patch increased with increasing travel time between patches and decreased with increasing average patch quality (Stephens and Krebs, 1986). Werner and

Hall (1974) showed a good match of selection in size of consumed *Daphnia* (a common water flea) by bluegill (*Lepomis macrochirus*) in laboratory conditions. Ringler (1979) found that the size preference of prey for brown trout (*Salmo trutta)* in small streams was predicted by OFT. Milinski and Heller (1978) were able to predict optimal feeding strategies of stickleback (*Gasterosteus aculeatus)* while under risk of predation by kingfishers. Further examples of classical OFT studies on fish are given in Townsend and Winfield (1985).

However, quantitative comparisons between observed and expected residence times per patch have often found significant discrepancies, with foragers typically spending more time in patches than predicted by the model (Nonacs, 2001; Pyke and Stephens, 2019). The early OFT studies were found to be too simplistic and ignoring other important factors such as predation risk, competition, individual state, need for other nutrients than just calories, temporal environment dynamics, and incomplete food-source information (Gould and Lewontin, 1979; Pierce and Ollason, 1987). Therefore, the OFT framework was expanded to include these other factors. The influence of competitors on distribution was developed within ideal free distribution theory (Fretwell and Lucas, 1970), the effects of predation risk and cost of movement among source patches were developed in concepts of ecology of fear (Stephens et al., 2007) and landscape of energy (Wilson et al., 2012) and the importance of additional food resources in optimal diet theory (Sih and Christensen, 2001).

Foraging theory

Foraging theory (FT) is a result of merging OFT and Life history theory (LHT). Developed in parallel to OFT, Life history theory (LHT) is also based on optimization of various individual adaptations to maximize fitness. However, LHT considers the optimum strategies to maximize life-time fitness, whereas OFT makes the assumption that optimization of the immediate energy intake per unit time is proportional to individual fitness. Using life-time fitness maximization as a target function, it has been possible to analyze optimal lifetime reproductive patterns, energy allocation rules, phenology, and willingness to take risk (Giske et al., 1998). LHT has traditionally been concerned with questions such as the age at which an animal should first reproduce and whether it should breed once or repeatedly (MacNamara and Houston, 1996; Giske et al., 1998).

An approach that can be considered as a combination of OFT and LHT was proposed by Gilliam (1982) and Werner and Gilliam (1984). Because an animal should minimize predation risk ($\boldsymbol{\mu}$) and maximize foraging gain (growth, g), their suggestion was to use the ratio of $\boldsymbol{\mu}$/g as a measure of habitat profitability related to ontogenetic habitat shifts for pre-reproductive animals (or $\boldsymbol{\mu}$/f if we consider growth to be proportional to feeding rate, f). Studies of Mittelbach (1981) and Werner et al. (1983) showed that the presence of a piscivore (largemouth bass *Micropterus salmoides*) induced habitat segregation by size in their prey (bluegill). Such segregation resulted in increased individual growth rates for large (less vulnerable) individuals who selected open areas, and decreased growth rates for smaller (more vulnerable) individuals staying in safer, yet energetically poorer, vegetated areas. Other authors developed this approach by showing that this ratio can change with the timing of reproduction (the ratio differs when reproduction is timed to occur with seasonal events, such as increased water temperature and food production; Aksnes and Giske, 1990) or the state of the individual (Ludwig and Rowe, 1990). Further development of this approach includes attention to the physiological state of the animal as well at its condition and personality (Clark, 1994; Moran et al., 2020; Sih et al., 2015).

As the field developed, LHT and OFT were merged in Foraging Theory, which considered the effects of both short-term decisions and long-term strategies on fitness (Mangel and Clark, 1986; Giske et al., 1998). In turn, FT has spurred a large number of studies comparing predation risk, habitat use, and growth in many different aquatic taxa (Leibold and Tessier, 1997; Grossman, 2014). Persson and Greenberg (1990) studied perch (*Perca fluviatilis*) as they shifted from pelagic to benthic habitats. Brönmark et al. (2008) looked at the migration of cyprinids from a lake to winter refuge. Mehner (2012) studied the diurnal vertical migration phenomenon of fish in general.

Ideal free distribution

Ideal free distribution (IFD) theory builds on the OFT framework and offers an important baseline for predicting how foragers are distributed across resource patches and select habitat (Matsumura et al., 2010). Fretwell and Lucas (1970) put forth a continuous-input model which has become classic in the field of IFD theory. This model assumes that food items arrive randomly at different rates in different patches and that foragers consume food items immediately, with each getting an equal share of resources on the patch (Parker and Sutherland, 1986). If these assumptions are met, the distribution of foragers reaches an equilibrium when no forager can improve its intake rate by switching habitats. If two patches differ in quality, foragers move toward the point of ideal foraging density, which occurs when the density is proportional to the prey input rate in all patches (called input matching). Milinski (1979) provided a simple example of IFD distribution by conducting a tank experiment where a different number of prey (*Daphnia magna*) were offered at different rates in two sides of an aquaria containing sticklebacks. The number of sticklebacks feeding on each side reflected the ratio of patch profitability—more prey more sticklebacks; less prey, fewer sticklebacks. The distribution of sticklebacks balanced resource gains and resulted in the same amount of resources for all competitors. IFD has also been proposed as an explanation for habitat use of northern pike *Esox lucius* (Haugen et al., 2006) and vertical distribution of zooplankton (Lampert, 2005).

Early experimental studies in laboratory conditions found relatively good support for the predictions of the IFD in aquatic animals (Kennedy and Gray, 1993). However, not all studies found a distributional pattern following the model. These discrepancies between the expected and observed patterns suggest that some of the model assumptions were violated. Hence, subsequent

IFD studies attempted to include factors that might explain discrepancies, such as the effect of unequal competitors (Parker and Sutherland, 1986; Grand and Dill, 1997), predation risk (Grand and Dill, 1999), interferences (interference IFD, Parker and Sutherland, 1986), defense of territory (ideal despotic distribution, Brown, 1969; Pulliam and Danielson, 1991), and cost of travel time (Abrahams and Labelle, 2020). Ideal despotic distribution explained the distribution of salmonids during spawning (Purchase and Hutchings, 2008).

Game theory

In previous concepts (OFT, LHT, IFD), the effects of predation or competition are considered to be fixed. However, predators and competitors in the real world are often mobile and can react in real time to distribution of their prey or other competitors.

Imagine a situation where resources, foragers and their predators are distributed in patches. Foragers should consider patch quality and number of competitors, and then distribute themselves among patches according to IFD principles. When the use of some patches becomes risky (presence of a predator), foragers should redistribute according to the $\boldsymbol{\mu}/\mathbf{g}$ ratio. However, static models, such as OFT and IFD, use predation risk as a constant parameter and do not account for predators directly affecting the distribution of prey (Hugie and Dill, 1994). In the real world, mobile predators, are expected to go where prey are denser, and prey are expected to simultaneously avoid areas where there are more predators (Lima, 2002).

The framework used to explain these interactions is called game theory (GT). GT studies situations where there is a conflict of interest between two or more players (Owen, 2001). The goal of the theory is to find an equilibrium distribution where neither player, in our case animals, improves their fitness by shifting to another patch (evolutionary stable strategies EES; Hammond et al., 2007). In the predator-prey case, both predator and prey have options that can potentially thwart the other, but the consequences of these options are not intuitively obvious (Lima, 2002). For example, a predator-prey distribution model based on GT developed by Hugie and Dill (1994) predicts that prey would prefer safer habitats and that the predator, but not the prey, would be distributed according to IFD. However, a predator's IFD is not related to the density of its main prey, but to the feeding rates (production) of the prey. Such a situation is called a three trophic level IFD model, as the predator redistributes according to the abundance of the food of their prey. This model also suggests that the prey distribution may not respond to an experimental manipulation of its food resources when the predator is present. Several studies have provided empirical examples from aquatic environments supporting these GT predictions (Heithaus and Dill, 2002; Hammond et al., 2007; Luttbeg et al., 2009; Vijayan et al., 2018) and the model was further extended by Sih (1998). Beside predator-prey interactions, GT has been used to explain diel vertical migration (e.g., Iwasa, 1982; Thygesen and Patterson, 2019) and IFD (Křivan et al., 2008).

The GT approach, however, is still not fully utilized in DM of predator-prey interactions within the aquatic environment due to a lack of information about key components, such as predator behavior and spatial interactions with prey, and anti-predator behavior in a multi-predator environment (Lima, 2002).

Landscape of energy and fear

Landscape of energy (LE) and Landscape of fear (LF) are two novel approaches that attempt to model predation risk and cost of movement. Their development is mostly driven by our increased ability to precisely measure both movement of animals and quality of the environment and merging them together (Gallagher et al., 2017). These approaches are derived from OFT, but, unlike OFT, consider the importance of energy loss or exposure to predation risk during movement in real heterogeneous landscapes, riverscapes or lakescapes (Laundré et al., 2001; Wilson et al., 2012). These real-life conditions include not only profitability of habitat, but also physical barriers, structural complexity, shelters, or the presence of predators.

LE calculates required energy for transport in real conditions. It predicts that animals will move to optimize their access to resource patches and will spend as little energy as possible to move (Wilson et al., 2012). In a simple OFT model, cost of transport is usually considered as energy required to linearly move from point A to point B under constant speed. However, such an assumption is a simplification of reality. Many physical obstructions determine movement cost in aquatic ecosystems, such as currents, debris, depth, temperature, or oxygen availability. Calculating the cost of transport in each location of the real landscape creates a landscape of energy, with peaks of high cost and valleys of low cost. Projections of real trajectories of moving animals (usually obtained from tracking devices) show the energy cost to move across the landscape and whether the movement follows an optimal trajectory (where the sum costs of moving along the chosen trajectory across the different energy landscapes are minimized). These projections can also show that the optimal trajectory of getting from point A to point B can be far from linear in real-life conditions (Gallagher et al., 2017).

In freshwater environments, this concept was used mostly to find optimal pathways during fish migration through river or fish passages. For example, McElroy et al. (2012) found that Pallid sturgeon (*Scaphirhynchus albus*) selected a pathway to minimize energy expenditure during the river upstream migration. Lindberg et al. (2016) tested usage of the optimal pathway for Atlantic salmons (*Salmo salar*) within fish passages and, ultimately, informed fish passage design. Hanke et al. (2014) modeled optimal pathways to determine if silver perch (*Bairdiella chrysoura*) could escape hypoxic lake spaces.

The concept of the landscape of fear (LF) was introduced in 2001 (Laundré et al., 2001) and belongs to a broader concept called ecology of fear (Stephens et al., 2007). LF describes spatial variation of predation risk, risk perception, and prey response in a real landscape. The LF theory is based on the assumption that predators elicit a fear of being killed in their prey (so called predator-induced resource avoidance). This predator-prey interaction dynamic affect how both groups navigate through their landscapes (Power, 1984; Gaynor et al., 2019).

The visual presentation of LF is similar to LE, where the peaks represent high risk regions and valleys represent low risk regions. Thus far, LF has been largely used for visualization of predator-mediated space use. However, LF concepts are rapidly developing, and researchers have suggested ways to calculate predator-mediated energy loss for prey (e.g., effect to give-up-density or optimal movement trajectory) and further consequences for an ecosystem (Gaynor et al., 2019). The LF concept has been applied more in the terrestrial ecology, but several studies using the LF concept were recently published for coral reef fishes in marine environments (e.g., Mitchell and Harborne, 2020). Further, several recent LF studies have been done in freshwater environments (Detmer and Wahl, 2020; Manenti and Barzaghi, 2020).

Foraging arena theory

Foraging arena theory (FAT) is not an approach to predict habitat selection. Rather, this theory is a quantitative model for calculating predator-prey consumption. Unlike traditional models used to predict consumption (such as functional response models), FAT models incorporate spatiotemporal dynamics in overlap between predator and prey (Ahrens et al., 2012). FAT is based on research of behavioral interactions between predator and prey (Werner et al., 1983; Walters and Juanes, 1993; Walters et al., 1997). The basic assumption of FAT is that spatial and temporal restrictions in predator and prey activities result in the division of prey into vulnerable vs. invulnerable animals. Invulnerable prey are hidden perhaps in a refuge (close to structures, in dark or anoxic water, or burrowed in bottom sediments), and not available for predators. Only vulnerable prey share space with predators within the foraging arena and can be consumed. Predation rates are then limited by exchange rates between vulnerable and invulnerable individuals within the prey population. The foraging arena could be defined by time when a large portion of the prey are available, for example during crepuscular migration to surface or the periodic drift of benthic animals in small streams (Ahrens et al., 2012).

The FAT framework helps to explain some common features of predator-prey interactions, such as the lower-consumption rates of predators in the field compared to predictions based on laboratory experiments, the stability of predation-prey cycles, the common occurrence of trophic cascades, and the common observations that multiple predators share one prey (predators utilizing prey in different forage arenas; Ahrens et al., 2012). FAT is part of the Ecosim and Ecopath modeling software and used as the background theory for predicting the impacts of changing trophic interactions in multispecies fisheries and whole aquatic food webs.

Individual based models

Recent decades have seen increased used of Individual or Agent Based Models (IBM) as scientist need to account for individual variation when predicting at the population, community, and ecosystem levels (DeAngelis and Mooij, 2005). Spatially explicit IBM are used to investigate how local interactions and movements of animals manifest themselves in population-level consequences, in other words, investigate the collective behavior emerging from the behavior of individuals obeying simple rules. Individuals (also called agents) can vary by trophic position (predator & prey), state (juvenile & adult) or personality (shy & bold; DeAngelis and Mooij, 2005). It is also possible to incorporate learning or adaptation by individuals through time (Railsback, 2001). In spatially explicit IBM, individuals apply assigned response rules to conditions at their locations, their internal state, and their performance in previous steps (adaptive component) to achieve the best performance (fitness, growth, or other currency that should be maximized).

The most common IBM approach used in ecology is Pattern-Oriented Modeling (POM). Researchers using POM build models of an observed pattern found in a real system, pose hypotheses explaining this pattern, and derive testable predictions from these hypotheses. These models are structurally realistic and can be verified and validated (Grimm and Railsback, 2006). DeAngelis and Grimm (2014) divided IBM according to their application as either paradigmatic or pragmatic models. Paradigmatic models help to gain a better understanding of the underlying causes of ecological phenomena, while pragmatic models construct simulations for specific situations (ecosystem or communities) usually with a management goal.

Railsback and Harvey (2002) present a POM-IBM designed to test whether they could reproduce six patterns of habitat selection by three trout species (*Oncorhynchus clarki*, *Salmo trutta*, *Oncorhynchus mykiss*) by contrasting three alternative habitat-selection objectives: maximizing actual growth rate, current survival probability, or expected maturity. They compared model predictions with field observation to deduce the habitat selection mechanisms operating in these trout species. Their POM-IBM appeared successful especially when expected maturity is used as it provides reasonable trade-offs between growth and mortality risks. Similarly, DiNuzzo and Griffen (2020) tested the effect of animal personality on IFD distribution and suggested that a prevalence of inactive personality types lead to lower predictability of the IFD. An example of a pragmatic use of IBM is a model developed by Phang et al. (2016) predicting the growth and distribution of juvenile Atlantic salmon and brown trout in response to changes in summer flow in rivers.

Currently, spatial ecology is going through a transformation by elevating the importance of the role of individuals in driving ecological processes. IBM is a very fitting tool for addressing these challenges.

Applications of spatial models

Knowledge of where, when and why a particular animal is present is not only important for mechanistic understanding of behavioral rules, but also for the management of inland waters. Distribution models are used for understanding the effect of

fishing on harvested population densities and life traits (e.g., Jørgensen et al., 2008; Claireaux et al., 2018). The foraging arena theory that is an implicit distribution model is an important assumption in the widely used Ecopath with Ecosim models of whole ecosystem dynamics and explorations of management applications (Christensen and Walters, 2004). Spatially explicit individual-based models are used for simulating targeted species responses to environmental and biological changes. For example, Railsback and Harvey's trout IBM (Railsback and Harvey, 2002) was used to further develop inStream software used for simulation of trout population responses to environmental changes. These models can also contribute to the design of appropriate sampling schemes for reliable estimates of species densities and communities (Oberdorff et al., 2001). Finally, spatial models are important for the design of protected areas, thus far, mostly in marine environments (Botsford et al., 2003). There are many more examples and examples in this article represent only a small sample of the modeling approaches currently in use.

Conclusions and future directions

Models of animal distribution have brought both empirical knowledge and theoretical concepts to our understanding of how and why animals are distributed across geographic space (Fig. 2). Classical concepts (such as OTF, LHT and IFD) consider how animals optimize their foraging strategies based on all relevant environmental factors (such as the amount of prey, predation risk, and number of conspecifics) and their internal physiological states to choose the behavior that maximizes the animal's individual fitness and future reproduction (Giske et al., 1998). But individuals never have complete knowledge of their environment, have imperfect ability to analyze information and foresee consequences of alternative behavioral options, and process this information in relation to their internal state and personality (Andersen et al., 2016). This realization has led to the incorporation of individual abilities in distribution models. More attention is paid to the role of how individual decisions are made and how these decisions regulate behavior (Nathan et al., 2008; Andersen et al., 2016). Mechanistic models of behavior and distribution of animals now include a broader range of individual traits, such as the genome, physiology, hormonal system, perception, emotions, motivation, and cognition (Budaev et al., 2019).

The field has also moved toward a deeper understanding of the proximate causes of animal distribution, a development which has been enabled by the rapid development of automatic high resolution sampling tools, such as biotelemetry (Baktoft et al., 2015), fast zooplankton samplers (Watkins et al., 2017; Bochinski et al., 2019) and remote sensing (Shuchman et al., 2013). These technological advancements are contributing significantly to the development of spatial data which allow us to describe animal distribution in new and better ways. Further, technological development is tightly linked with the rapid increase of computational power and with the development of artificial intelligence capable of complex pattern recognition (Christin et al., 2019). We believe this process will stimulate a rapid development of current and novel frameworks and models for predicting spatial distributions.

Distribution models have and will continue to greatly contribute to our understanding of the distribution and movement of animals in inland waters. They help us to unravel the rules behind animal movement dynamics, which will enhance our ability to predict distributions, even under novel conditions. However, all models, even extremely sophisticated and complex ones, are a simplification of nature and as such the results have to be interpreted consciously.

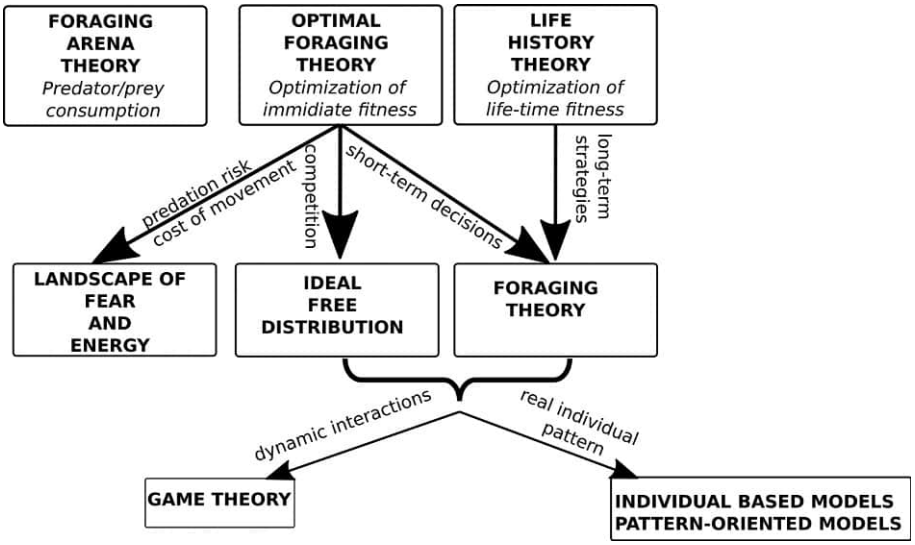

Fig. 2 Schematic overview of links between spatial modeling frameworks.

Further reading

Further reading about forage theory in Stephens et al. (2007) and Pyke and Stephens (2019). Ahrens et al. (2012) provide a review with detail description of forage arena theory. More details on the concept of landscapes of fear are in Gaynor et al. (2019). DeAngelis and Grimm (2014) provide a summary of progress in individual based models during last decades.

See Also: Emerging methods and topics: Electronic Tagging and Tracking of Animals in Inland Waters; Fundamental concepts and theories: Diel Vertical Migration; Structures and functions of Inland Waters - Lakes: Fish Populations; Structures and functions of Inland Waters - Wetlands: Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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Relevant websites

https://nowosad.github.io/presentations/—Handy basic tutorials for starting with spatial data in R.
https://cran.r-project.org/web/views/Spatial.html—List of available R packages for spatial analyses.
https://github.com/r-spatialecology—List of available R packages for landscape ecology.
https://ecomodel.humboldt.edu/instream-and-insalmo-overview—IBM instream software, Humbolt State University (CA, USA).

Eco-Evolutionary Dynamics in Freshwater Systems

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Adaptive evolution A genetic change in a species' trait in response to its environment that results in an increased fitness in that environment.

Common garden experiment An experiment in which trait values of individuals from different populations are quantified in a single (i.e., 'common') environment. Common garden experiments often involve multiple generations of culture in a similar environment, and are typically used in quantitative genetics to determine the degree to which differences in trait values among populations have a genetic basis.

Common gardening experiment An experiment in which one places individuals or populations that differ in trait values in the same environment ('common garden') to then quantify how they differentially influence the garden. Common gardening experiments are a well-established approach to quantify the impact of evolutionary trait change on ecological processes.

Eco-evolutionary dynamics Simultaneous occurrence of reciprocal interactions between ecological and evolutionary processes, each influencing the outcome of the other.

Evolution Any change in gene frequencies in a population of a species.

Evolving metacommunity A framework that integrates evolutionary processes in metacommunity ecology and thus considers how evolution and community assembly interact in space. Environmental gradients, dispersal and stochasticity are key processes structuring both landscape genetics and metacommunity structure, which leads both to parallel processes and opportunities for eco-evolutionary dynamics.

Metacommunity A set of spatially distinct local communities linked by dispersal of multiple interacting species

Transplant experiment An experiment in which individuals from populations originating from different experimental or natural environmental conditions are (reciprocally) transplanted between these conditions or natural sites, and their trait values measured after one or more generations.

Introduction

Eco-evolutionary dynamics refers to the simultaneous occurrence of reciprocal interactions between ecological and evolutionary processes, each influencing the outcome of the other. Ecological processes encompass any aspect of an organism's interaction with its environment, while evolution is defined as any change in gene frequencies in a population of a species. Evolution can be adaptive if it involves a genetic change in a species' traits in response to its environment that results in an increased fitness in that environment. The classic view of ecological and evolutionary dynamics has been that they are largely independent, occurring on different time scales. There are, however, two pathways that connect both. The first, long recognized in biology, is an eco-to-evo pathway in which the environment imposes pressures on populations, which may influence evolutionary trajectories through evolution by natural selection. The second, an evo-to-eco pathway, only became fully appreciated during the 1990s and 2000s (Pianka, 2000), and depends on the changing trait distributions that result from contemporary evolution immediately altering ecological interactions. Recognition of the importance of the evo-to-eco pathway has been mainly inspired by accumulating studies demonstrating that evolution can be rapid, occurring within a few generations. As a result, evolution can occur on similar time scales as the ecological processes it affects, resulting in a continuous feedback between ecological changes altering evolutionary trajectories (Fig. 1). This dynamical view of rapid evolution influencing ecological interactions, makes eco-evolutionary dynamics different from the more traditional field of 'evolutionary ecology' (Orians, 1962; Pianka, 2000), which has been more focused on whether the expression of organism traits can be understood as adaptations to particular environments (e.g., optimal foraging, body size, life history, etc.), and how trait expression in nature can influence ecological interactions.

It is the combination of rapid evolution (often in response to a changing environment) combined with the effects of the evolving traits on the strength of ecological interactions that is central to eco-evolutionary dynamics. For example, when a predator population increases in abundance, a prey species may evolve to increase its defenses against predation (Fig. 1). That is a case of contemporary evolution or evolution that occurs in the same time frame as ecological processes. If that trait evolution in prey defense results in a decline of the predator population, those combined events reflect eco-evolutionary dynamics. The importance of these dynamics is that many interactions that were hitherto considered to be ecological might reflect the combined action of both ecological and evolutionary processes.

In freshwater systems, evidence of rapid evolution started to accumulate in the early 1980s. An important milestone is the work of John A. Endler on male coloration in wild guppy populations from different predation environments (Endler, 1980). Using a transplant experiment, he showed rapid evolution to brighter male coloration. Brightly colored males are highly attractive to females but are also easily seen by predators. When predators are present, male colors are less bright. When predators are absent, female preferences dominate, and males tend to be more brightly colored. This work was followed by David N. Reznick's study showing rapid evolution of the life history traits of the guppies transferred from high-predation to predator-free sites (Reznick and Endler, 1982).

Another example involves the demonstration of rapid evolution of diapause in the copepod *Onychodiaptomus sanguineus* by Nelson G. Hairston Jr. and William E. Walton (1986). During a severe drought event, the shallower of two natural forest ponds

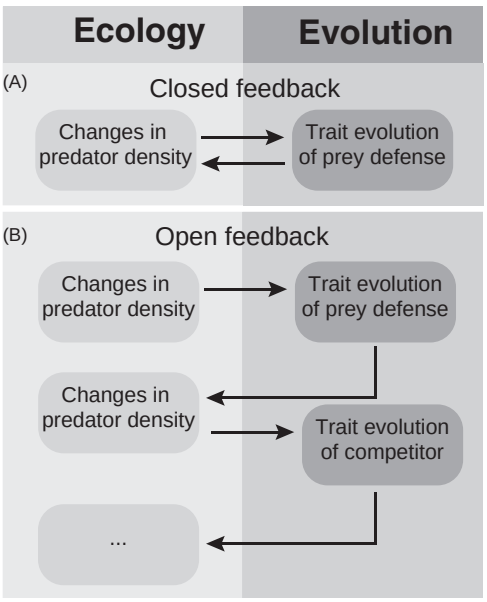

Fig. 1 Example of a (A) closed and (B) open eco-evolutionary feedback loop, in which ecological and evolutionary processes recurrently influence one another. Figure inspired from Fig. 4 from De Meester L, Brans KI, Govaert L, Souffreau C, Mukherjee S, Vanvelk H, Korzeniowski K, Kilsdonk L, Decaestecker E, Stoks R, and Urban MC (2019) Analysing eco-evolutionary dynamics—The challenging complexity of the real world. *Functional Ecology* 33: 43–59.

containing fish dried out completely killing all the fish, while the deeper pond did not dry and had no fish kill. Before the drought, the copepod populations in both ponds entered diapause on nearly the same date in spring as an adaptation to avoid summer-time intense fish predation. Hairston and Walton (1986) found that 2 years after the drought the copepods in the pond that lost its fish had evolved an onset of diapause nearly a month later in the year, demonstrating rapid evolution. This study and Reznick's in 1982 were among the first to demonstrate, for freshwater organisms in nature, that traits closely related to fitness can harbor large genetic variation upon which selection can act.

The accruing evidence of rapid phenotypic evolution in natural systems showcases that strong selection and heritable variation in adaptive traits are more common in nature than previously recognized. This contrasts with the 'standard model' in the field of population genetics, which has assumed random genetic drift as the dominant force in genetic change, with nearly all evolution being stabilizing, i.e., removing deleterious mutations, but with rare exceptions of selective sweeps (Messer et al., 2016). In this model, genetic variation is primarily maintained by selection-mutation balance and is mostly non-adaptive. Examples of eco-evolutionary dynamics, in contrast, often involve fluctuating selection tracked by rapid trait evolution frequently reversing direction in response to environmental change, and with the result that adaptive genetic variation is maintained. Under such circumstances, the net effect of evolution might be small or even negligible over longer time periods, but evolutionary rates can be fast on short time scales, and the resulting trait changes can have important implications for ecological dynamics. Given that evolution occurs on the same time scale as ecological processes, it is the fast genetic tracking of environmental change that is important in eco-evolutionary dynamics.

For eco-evolutionary interactions and feedbacks to occur, one needs (1) sufficiently strong natural selection, (2) genetic variation for the trait under selection, leading to (3) a genetic change in trait value, and (4) a feedback of that evolutionary trait change on one or more ecological processes (e.g., population dynamics, species interactions, ecosystem fluxes). This feedback loop can be 'closed' if the changed ecological interaction then alters the strength and/or direction of natural selection on the original trait which then affects the original ecological interaction, and so on. Alternatively, the loop may be 'open' if the evolving trait change alters some different ecological process, which in turn alters evolution of some different trait (Fig. 1). Eco-evolutionary feedbacks result in a fundamental change in the dynamics of ecological entities, because of the iterative interplay between ecological and evolutionary responses.

Experimental approaches for detecting eco-evolutionary dynamics

Eco-evolutionary dynamics have been shown in a diversity of freshwater systems, and involve population evolution affecting feedback loops at different levels of ecological organization (population, community, ecosystem) (Palkovacs and Hendry 2010) (Fig. 2). Because phenotypic traits often determine the strength and quality of ecological interactions, from population processes (birth and death rates) to community and ecosystem properties, eco-evolutionary dynamics are governed by the traits of organisms. This makes phenotypic traits the 'common currency' between ecology and evolution (De Meester et al., 2019). Phenotypic traits consist of a genetic and an environmental component (Lynch and Walsh, 1998). The latter component, often referred to as phenotypic plasticity, is the ability of a single genotype to produce multiple phenotypes under different environmental conditions. Eco-evolutionary dynamics requires evolutionary change, and thus one needs to separate evolutionary trait change from phenotypic plasticity, with the recognition that there can also be evolution of plasticity (Pigliucci, 2001).

Approaches to studying eco-evolutionary dynamics have varied from measuring ecological and evolutionary changes over time and inferring how changes in ecology have influenced evolution, and vice versa, to comparing dynamics of systems that have the

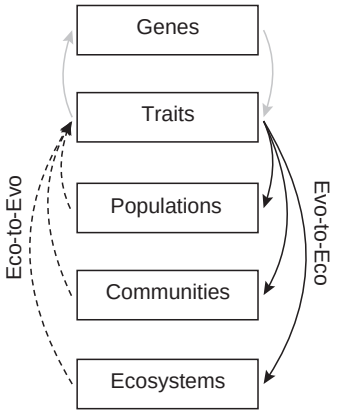

Fig. 2 Conceptual scheme illustrating eco-evolutionary dynamics, in which changes in population, communities and ecosystem dynamics influence phenotypic traits and their underlying genes (eco-to-evo pathway; dashed black arrows), and evolutionary trait changes in turn feedback to influence populations, communities and ecosystem dynamics (evo-to-eco; solid black arrows). Figure is modified from Fig. 1 from Palkovacs EP and Hendry AP (2010) Eco-evolutionary dynamics: Intertwining ecological and evolutionary processes in contemporary time. *F1000 Biology Reports* 2.

potential for eco-evolutionary feedbacks with those that do not (De Meester et al., 2019). In both cases, experiments are quite complex, because one needs to show both that evolution (i.e., genetic differentiation) has occurred, and that this influences an ecological process. Experiments on eco-evolutionary dynamics can often be distinguished in two sets, aligned with the eco-to-evo and the evo-to-eco pathways outlined above.

Demonstrating (past) evolution: Common garden and transplant experiments

In the first pathway—the eco-to-evo pathway—evolutionary response to an ecological condition is assessed. One way to quantify evolution is to introduce a set of individuals with the same distribution of genotypes into experimental units with different ecological conditions, and determine whether these different ecological conditions results in different evolutionary responses. At the end of the experiment, to distinguish evolved genetic differences between the populations from phenotypic plasticity, 'common garden' experiments are often used in which trait values of individuals from different populations are quantified in a single (i.e., 'common') environment. In such experiments, it is important to reduce interference from common environmental effects, including (grand)maternal effects (Lynch and Walsh, 1998). If trait values of individuals from different populations continue to differ in a common garden experiment, this then indicates that genetic differences have evolved as a result of exposure to the different environments. If in addition, trait expression is assessed in two or more distinct environments (two or more 'common gardens'), then phenotypic plasticity, as well as genetic differences in the extent of that plasticity among the populations, can be measured.

Such common garden experiments can also be used with individuals directly collected from natural populations, either at different time points to investigate a population responding to changing environmental conditions or from locations that differ in ecological conditions. Evaluating the traits of those individuals originating from settings exposed to different environmental conditions in a common environment, allows an assessment of genetic differences and quantification of adaptation to their respective environments. For example, a study by Cousyn et al. (2001) demonstrated adaptation to fish predation for the trait phototactic behavior (i.e., vertical migration of zooplankton; see Further Reading) in a population of the zooplankton species *Daphnia magna*. The study used a common garden experiment involving individuals hatched from dormant eggs collected from three different layers of a sediment core corresponding to distinct time periods in the pond where they lived that varied in fish predation intensity. In the laboratory, *Daphnia* from these different sediment ages were exposed to two treatments, with and without fish kairomones (i.e., a chemical cue detectable by *Daphnia*), and exhibited distinct levels of predator avoidance behavior by different levels of vertical migration through the water column. The study thus showed that the population was able to rapidly evolve a reduction in phototactic behavior in response to an increase in fish predation demonstrating the eco-to-evo pathway (see Further Reading).

As an alternative to common garden experiments, one can also use transplant experiments, in which individuals from populations originating from different experimental or natural environmental conditions are (reciprocally) transplanted between these conditions or natural sites, and their trait values measured after one or more generations. For example, Reznick and Endler (1982) studying natural populations of guppies used a transplant approach to detect whether predation influenced life-history traits of these fish (Fig. 3). They transplanted guppies from high-predation sites to low-predation sites, and vice versa, and found that the shift in predation regime affected both guppy densities (an ecological response) and life history traits (an adaptive evolutionary response). Specifically, guppies transferred from high-predation to low-predation sites evolved a later age at maturity, larger size at maturity, and produce larger and fewer offspring compared with guppies that stayed in the high-predation communities (Fig. 3B–D; Reznick et al., 1997). This study, and an increasing number of others, thus quantify how ecological differences impact evolutionary trajectories and rates, and in this way demonstrate the eco-to-evo pathway.

Demonstrating the evo-to-eco feedback: Common gardening experiments and partitioning metrics

In the second pathway—the evo-to-eco pathway—one tests whether evolved trait changes have implications for ecological dynamics. This is often done via 'common gardening' experiments, an experimental design rooted in community genetics (Crutsinger et al., 2006). In a common gardening experiment, one introduces different genotypes, or genetically-differentiated populations, into experimental units with identical ecological conditions. One then assesses whether the genetic differences among individuals or populations result in the development of different ecological properties and dynamics in the experimental units, i.e., one checks whether the different genotypes differentially influence the 'garden'. In one example, Pantel et al. (2015) quantified the impact of evolution on community assembly in zooplankton. A genetically variable *Daphnia magna* population was allowed to adapt genetically (evolve) to different ecological conditions (i.e., a full-factorial design of presence and absence of fish and macrophytes). Then in a second experiment, the investigators quantified whether the evolved populations impacted zooplankton community assembly differently from the original, non-evolved *D. magna* population. They found that the effect of *D. magna*'s adaptation to the different environmental conditions was equally large in driving zooplankton community structure as the differences in environmental conditions (i.e., presence of fish and macrophytes). There is an increasing number of studies that show that eco-evolutionary feedbacks indeed often have an important impact on ecological processes (Hendry, 2017).

Many studies only quantify either the eco-to-evo or evo-to-eco pathway, but in a complete investigation of eco-evolutionary dynamics ideally both pathways are integrated into a single study (as in, e.g., Pantel et al., 2015). As an alternative to using genetically differentiated populations in the common gardening approach, one can also manipulate the potential for evolution by using non-evolving versus evolving systems. This can be done by using a mono-clonal population or one with low genetic variation

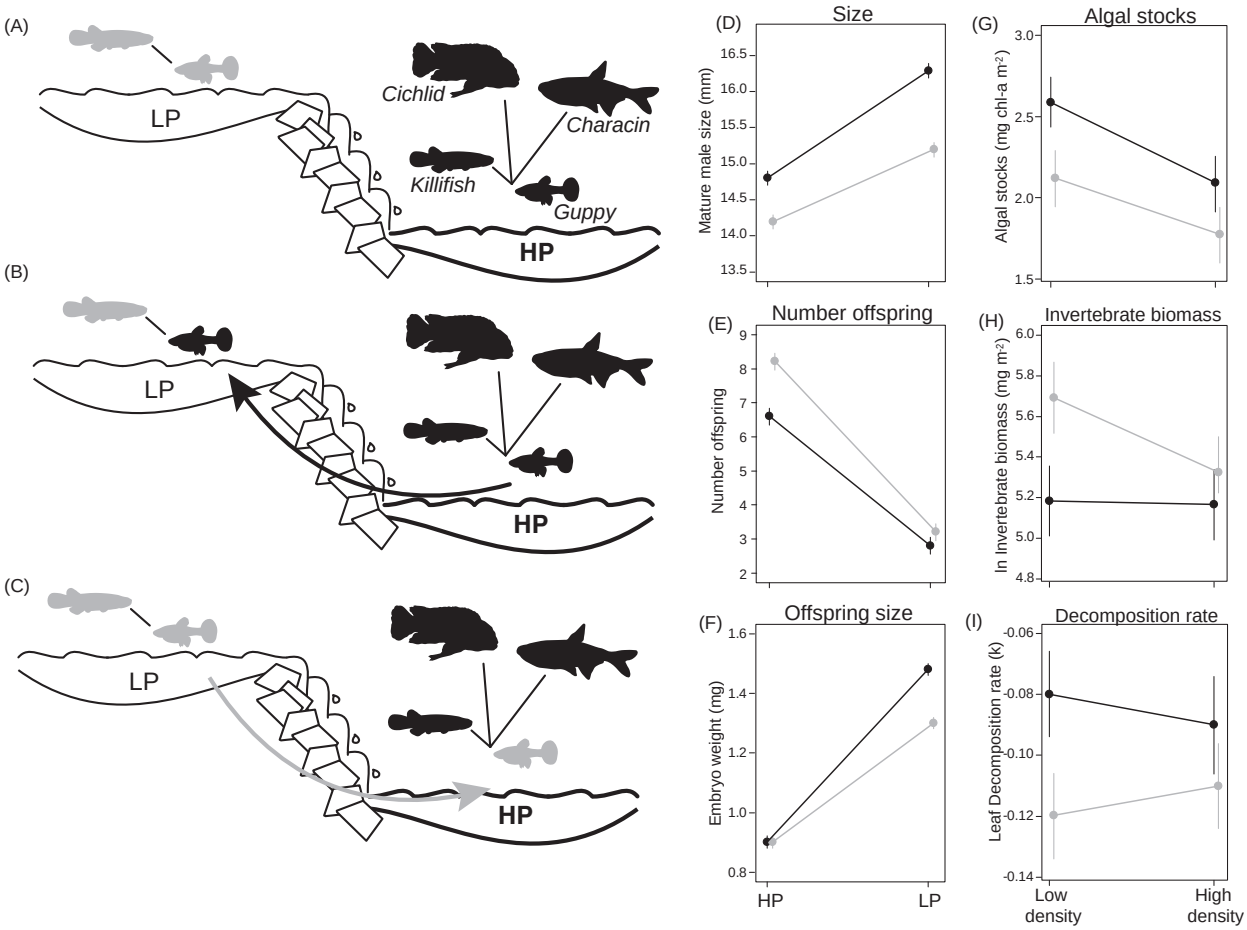

Fig. 3 (A) Representation of food web composition in the High-Predation (HP; below waterfall; depicted in black) and Low-Predation (LP; above waterfall; depicted in grey) environment inhabited by Trinidadian guppies. (B and C) Representation of the transplant experiment in which guppies from (B) a HP environment are transplanted to a LP environment (depicted by the black filled guppy in LP), and from (C) a LP environment are transplanted to a HP environment (depicted by the grey filled guppy in HP). Trait values of (D) mature male size, (E) number of offspring per female and (F) embryo weight (i.e., dry weight of developing offspring) from the HP and LP population in the High-Predation (HP) and Low-Predation (LP) sites. Experimental measures of (G) algal standing stocks, (H) invertebrate biomass, and (I) leaf decomposition rate from common gardening experiment when using LP guppies (black circles), and HP guppies (grey circles) in low and high guppy density. Data in (B–D) are obtained from Fig. 3 in Reznick DN, Ghalambor CK, and Crooks K (2008) Experimental studies of evolution in guppies: A model for understanding the evolutionary consequences of predator removal in natural communities. *Molecular Ecology* 17: 97–107. Data in (G–I) are obtained from Fig. 1 in Bassar RD, Marshall MC, López-Sepulcre A, Zandonà E, Auer SK, Travis J, et al. (2010) Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences* 107: 3616–3621.

for the non-evolving system (in the absence of genetic variation, there can be no evolution even if there is strong selection) and a multi-clonal or genetically diverse population for the evolving system (see e.g., Yoshida et al., 2003).

The data obtained from experiments or field studies can be used to parametrize mathematical eco-evolutionary models. In these models, one can then manipulate evolutionary potential, strength of selection, and ecological context (e.g., community context). Modeling different scenarios can provide further insight into how ecological and evolutionary dynamics interact, and influence each other (Jones et al., 2009; Cortez, 2016).

The data of common gardening experiments and models can be used to quantify the impact of evolution on ecological dynamics. Eco-evolutionary partitioning metrics have been developed (Hairston et al., 2005; Ellner et al., 2011; Govaert et al., 2016) that enable quantification of the relative importance of evolution (i.e., of traits important to interactions with other species) and ecology (e.g., environmental variation, differences in population densities) on population dynamics, community assembly and ecosystem properties. This allows comparative analyses across systems, species and at particular time points in natural and experimental systems. Such studies have shown that the effect of evolution on ecological properties of the system (e.g., community composition, species diversity) can be similar in magnitude to the effect of ecological drivers (e.g., temperature, predation). However, in most of these studies, the effect of evolution on the population, community or ecosystem features was in the opposite direction from the effect of ecology. As a result, evolutionary changes reduce the impact of ecology rather than augmenting it.

Freshwater environments as model systems for eco-evolutionary dynamics

Freshwater systems, especially ponds and lakes, are ideal for studying eco-evolutionary dynamics as these systems often have distinct boundaries (i.e., the water's edge) so that interactions among organisms, and between organisms and their physical and chemical environment, are naturally confined, and often intense. They provide excellent model systems to explore patterns across spatial and temporal scales, including seasonality and spatial patterns in the landscape in response to a geographic mosaic of stressors. Ponds and lakes represent patches in the landscapes that are each inhabited by local communities that are composed of species that may show evolutionary dynamics and that can be linked to one another via dispersal of species (i.e., movement of individuals from one place to another) and gene flow (i.e., exchange of genetic material from one population to another, changing the genetic composition of the receiving population). The set of communities inhabiting such patches and connected via dispersal is also referred to as a metacommunity (Leibold et al., 2004). The concept of 'evolving metacommunities', also considers evolutionary dynamics in addition to integrating spatial and community dynamics, and thus provides a strong conceptual framework to study how eco-evolutionary dynamics play out in a multiple species context and in space (Urban and Skelly, 2006; Urban et al., 2008). Eco-evolutionary dynamics can play a role at both local and regional scales in shaping community patterns and dynamics.

Eco-evolutionary dynamics are likely to affect aquatic trophic webs through multiple routes. In many freshwater systems, organisms at the lower trophic levels are often characterized by very short generation times, providing the opportunity for rapid evolution to be detected within the duration of a typical study, and providing a high potential for observing eco-evolutionary dynamics. At the same time, rapid evolution has also repeatedly been reported in fish. Given that aquatic systems are often characterized by important top-down cascading effects, evolutionary trait change in fish has the potential to have strong impacts on the dynamics of lower trophic levels.

Key freshwater examples of eco-evolutionary dynamics

Eco-evolutionary dynamics have been demonstrated using (a) laboratory experiments where the environment and interacting organisms can be highly controlled, (b) field experiments where tight control is more difficult, but which can come much closer to including natural environmental variation, and (c) in unconfined nature where the processes of interest play out against the full background of natural complexity. Below, we develop five well-documented examples of eco-evolutionary dynamics in freshwater environments. Three of the five examples include studies using *Daphnia* (water fleas), small crustaceans of the order Cladocera, as a model system. *Daphnia* is frequently used as model organism to address ecological and evolutionary questions due to its short generation time, its reproduction mode and its ease of maintenance in the laboratory. In section '*Daphnia* as model system for eco-evolutionary dynamics', we explicitly focus on the breadth of interactions for which questions at the interface of ecology and evolution have been addressed using *Daphnia* as a model organism.

Rotifer-algal predator-prey cycling: Eco-evolutionary dynamics in highly controlled laboratory microcosms

A clear example of eco-evolutionary dynamics involves rapid prey evolution in response to oscillating predator density, which has been both mathematically modelled and demonstrated in highly controlled experimental laboratory microcosms (called chemostats) using the freshwater alga, *Chlorella vulgaris*, and its planktonic consumer, the rotifer *Brachionus calyciflorus*. Both taxa are common in many lakes. Fussmann et al. (2000), investigating joint predator-prey dynamics in populations of these two species, found unexpectedly that instead of exhibiting the quarter-period phase lag between *Chlorella* and *Brachionus* peak densities predicted by consumer-resource theory (Bulmer, 1976), the dynamics displayed anti-phase cycles with peak rotifer density occurring at the minimum in algal density and the minimum in rotifer density occurring at peak algal density. An exploration of alternative possible explanations using mathematical modeling found that the most compatible model incorporated algal evolution in response to predator density (Shertzer et al., 2002). This hypothesis was then experimentally tested by Yoshida et al. (2003) who manipulated genetic variability in the algal prey population. They found that rotifer-algal dynamics exhibited typical quarter-period phase lags when single-clone algal populations lacking genetic variability were used, i.e., in the absence of prey evolution (Fig. 4A), but anti-phase cycles occurred when the algal population was comprised of multiple clones, and so could evolve (Fig. 4B). The anti-phase cycles could be explained as the shift in relative abundances of defended versus undefended clonal genotypes in response to changing predator density. This shift in clonal frequencies was governed by a trade-off between defended and undefended algal clones. Defended clones survive passage through rotifer guts (Meyer et al., 2006) and so provide no sustenance to the consumers, but are poor competitors for limiting nutrients when predators are scarce. The undefended clones, which do not survive gut passage, instead are good food for rotifers. However, undefended clones are also superior competitors for limiting nutrients. Thus, when rotifer densities are high, defended algal clones have an advantage compared with undefended ones, and increase in abundance. This dominance by defended clones causes rotifer densities to decline. Low densities of the predator give undefended but superior competitor algal clones an advantage over defended clones, which results in an increase in the frequency of undefended clones, which allows rotifer densities to increase once more, starting the cycle all over again. The resulting anti-phase predator-prey cycles are thus an example of eco-evolutionary dynamics in which rapid evolution radically alters classic ecological predator-prey dynamics, as previously shown theoretically by Abrams and Matsuda (1997).

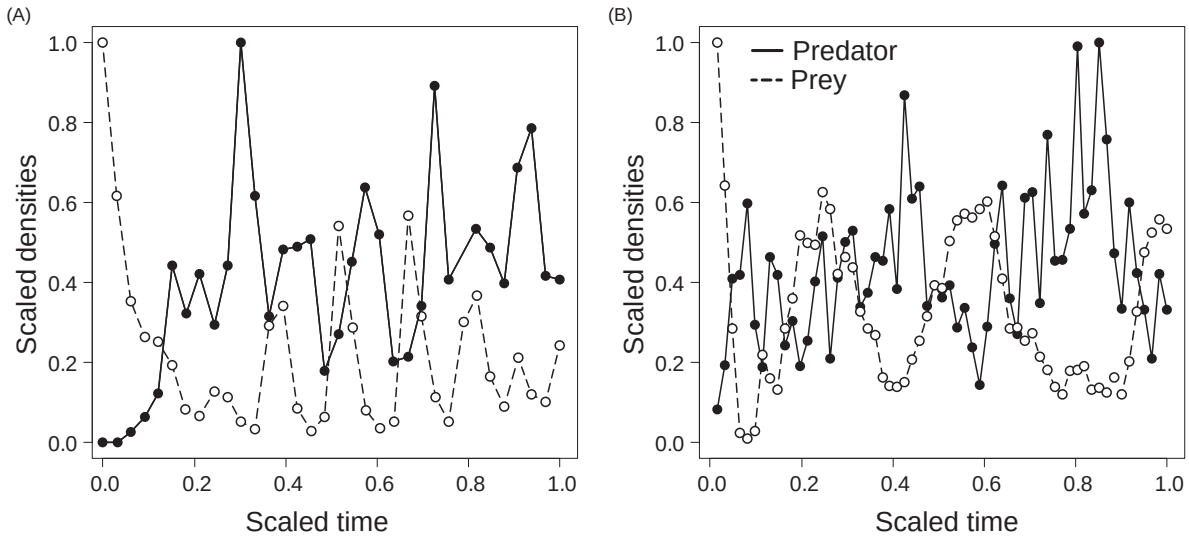

Fig. 4 Experimental predator-prey rotifer-algal dynamics for (A) single-clone algal population and (B) multiple-clone algal population. Figure is modified from Fig. 2 from Yoshida T, Jones LE, Ellner SP, Fussmann GF, and Hairston NG (2003) Rapid evolution drives ecological dynamics in a predator–prey system. *Nature* 424: 303–306. Panels (A) and (B) in this figure refers to panels (B) and (G) of Fig. 2, respectively.

Daphnia evolution structures zooplankton community structure: Evolution and its feedback in outdoor mesocosms

In a study by Pantel et al. (2015), outdoor mesocosms were used to evaluate the evolutionary response of *Daphnia magna* to two key ecological gradients structuring lake and pond zooplankton communities—the presence/absence of fish and the presence/absence of macrophytes (Fig. 5A–C). In a full-factorial design, the authors started from a random sample of the genetic variation present in the dormant egg bank of a natural population of *D. magna* inhabiting a shallow pond (Fig. 5A), and allowed the resulting genetically diverse populations to evolve and adapt to the four environmental conditions during a selection experiment (Fig. 5B). This resulted in sets of populations that differed in their selection background. At the end of a two-month selection experiment, 20 clonal lineages were isolated from each of the experimental units. These isolates were then used in a subsequent community assembly experiment (Fig. 5C). Specifically, the authors re-created the four environmental conditions in mesocosms (i.e., full factorial design of presence/absence of fish and presence/absence of macrophytes), and inoculated each of these environments with the same number of *D. magna* individuals, but obtained from populations that were allowed to adapt to that environmental condition (obtained from the selection experiment) or with individuals from the original, non-adapted population. After 1 week, a standardized and species diverse cladoceran non-*D. magna* community inoculum was added to all mesocosms. This community sample was obtained by collecting zooplankton from multiple ponds chosen such that no *D. magna* was present. One month later, the resulting zooplankton community was sampled.

From the community assembly experiment, it was found that the two-months of evolution in response to the divergent environmental conditions had far-reaching effects. First, the *D. magna* densities were on average higher when using the adapted versus non-adapted genetic lineages (Fig. 5D), showing that 2 months of adaptation resulted in significantly higher performance in the respective habitats. Second, adaptation of *D. magna* had a significant effect on the composition of the cladoceran community. Strikingly, even though the presence of fish and macrophytes are known to be key environmental gradients driving zooplankton community structure, Pantel et al. (2015) found that the effect size of *D. magna* evolution, in response to the presence of fish and macrophytes, on zooplankton community structure was similar to the effect size of the presence of fish and macrophytes themselves (Fig. 5E). However, *D. magna* evolution resulted in a shift in community structure in the opposite direction of the shifts in community structure resulting from exposure to fish and macrophytes (Fig. 5E). The direction of the effect of evolution was thus opposite to the direction of the effects of the environmental gradients. Finally, the evolution of *D. magna* had distinct effects on different cladoceran taxa. For instance, whereas chydorids generally were suppressed in the presence of adapted-compared with non-adapted-*D. magna*, the effect of evolution of *D. magna* on the densities of *Simocephalus* depended on whether or not fish were present. This study thus demonstrates rapid evolution of *D. magna* in response to key ecological factors feeding back to altering the zooplankton community structure.

Alewives, sticklebacks and zooplankton: Eco-evolutionary dynamics in field mesocosms

Beginning with the classic study by Brooks and Dodson (1965) it has been well accepted that size-selective predators can change the zooplankton community of lakes. A study by Palkovacs and Post (2009) demonstrated that predation by two genetically distinct

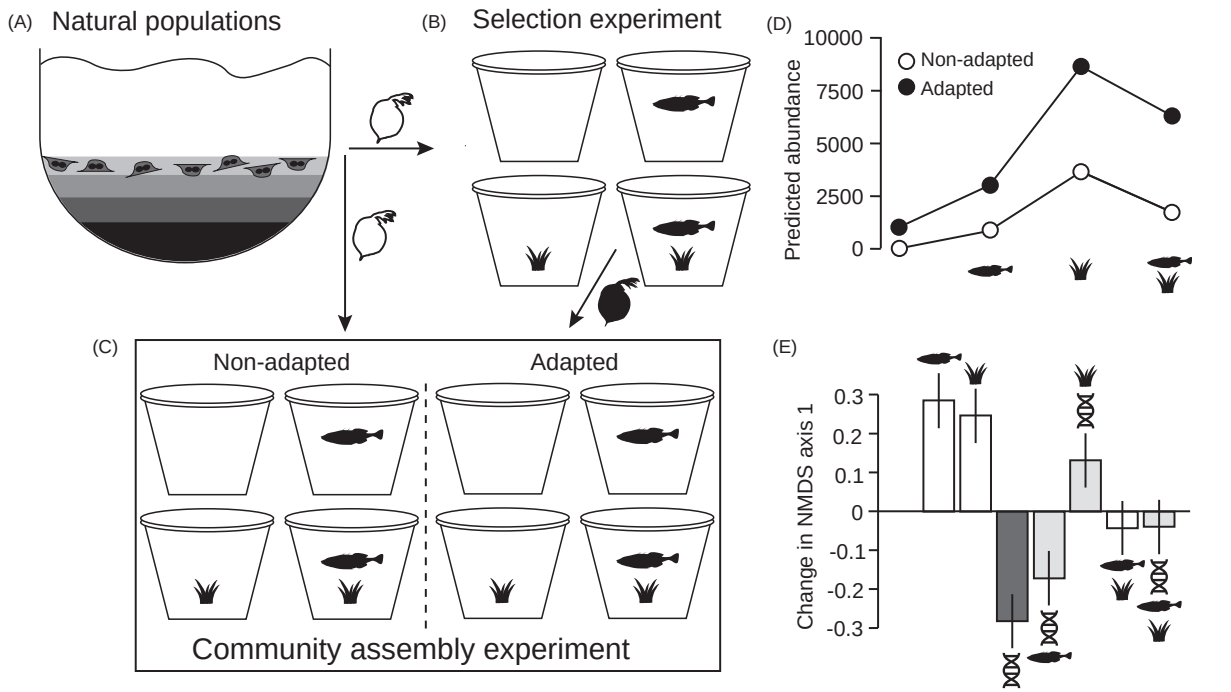

Fig. 5 Representation of the experimental design in which Pantel et al. (2015) started with (A) a random sample of *D. magna* clonal lineages obtained from dormant eggs in (B) a selection experiment consisting of a full-factorial design combining presence/absence of fish with presence/absence of macrophytes followed by (C) a community assembly experiment in which adapted and non-adapted clonal lineages were exposed to the full-factorial design of presence/absence of fish and the presence/absence of macrophytes. (D) Predicted *D. magna* abundances of non-adapted *D. magna* (empty circles) and adapted *D. magna* (filled circles). (E) Effect sizes of ecological factors (fish and macrophytes depicted with respective symbols) and *D. magna* local adaptation (depicted with helix) and their two- and three-way interactions on community structure (as quantified by the main axis of variation in a multidimensional plot, i.e., score for NMDS axis 1). Pure ecological effects are indicated with white bars, pure evolutionary effects are indicated with dark grey bars, and eco-evolutionary interactions are indicated with light grey bars. Data in (D) and (E) is obtained from Fig. 2 and Fig. 5A in Pantel JH, Duvivier C, and De Meester L (2015) Rapid local adaptation mediates zooplankton community assembly in experimental mesocosms. *Ecology Letters* 18: 992–1000, respectively.

types of alewives (zooplanktivorous fish) structures lake zooplankton prey communities differentially. Anadromous fish (seasonally migrating from the ocean to lakes) and non-migrating 'land-locked' alewives differ morphologically (Fig. 6A). In addition to a large difference in adult body size, anadromous populations have larger mouth gapes and wider spacing between their gill rakers (i.e., a kind of internal sieve that retains ingested prey) compared with land-locked populations (Fig. 6B–C). As a result, anadromous alewives tend to feed selectively on larger bodied zooplankton than do land-locked alewives. Genetic data show that these phenotypic differences among alewife populations have evolved repeatedly in independent land-locked lake populations. Further, as land-locked alewives are continuously present in their lake ecosystems, while anadromous alewives are only present part of the year, this difference in presence, in addition to differences in feeding morphology, also determines the predation intensity on zooplankton communities resulting in lower zooplankton biomass and dominance of smaller zooplankton species in lakes with anadromous alewives.

Palkovacs and Post (2009) explicitly tested the hypothesis that evolved phenotypic divergence of alewife morphology caused a difference in zooplankton community structure using experimental mesocosms suspended in a lake, with treatments of no alewives, 15 land-locked alewives, or 15 anadromous alewives. Treatments with anadromous fish showed a steeper reduction in zooplankton biomass, a greater decline in average zooplankton body size, and lower zooplankton species diversity (Fig. 6D–F). Predation by size-selective anadromous alewives eliminated large-bodied zooplankton species, and reduced the biomass of medium-bodied species, while predation by land-locked alewives did not eliminate large-bodied zooplankton species. The evolution of trait differences between these fish populations thus resulted in a different prey zooplankton community, and a common gardening experiment in which genetic differences in a key species were manipulated produced an ecological pattern consistent with the zooplankton community differences observed in the field.

Eco-evolutionary dynamics in this example reach further than evolution of fish impacting zooplankton communities. First, in a follow-up study, Walsh et al. (2012) used a common gardening experiment to show that *Daphnia ambigua* clones originating from lakes containing either land-locked, anadromous or no alewives had distinct effects on algal biomass. Algal densities declined faster in mesocosms with *Daphnia* from lakes with anadromous alewives than they did with *Daphnia* from lakes with land-locked or no alewives. This result stems from the fact that *Daphnia* populations had evolved different adult body sizes in these different lake

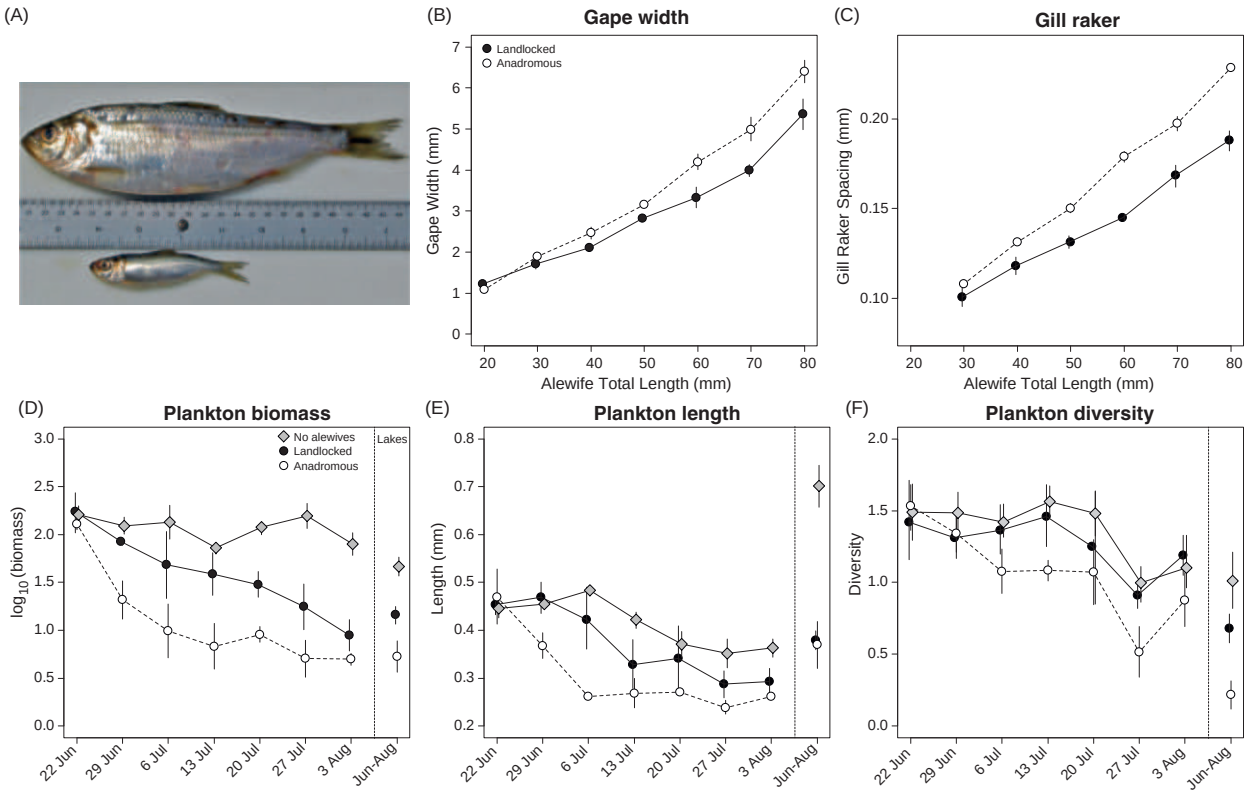

Fig. 6 (A) Anadromous (top) and land-locked (bottom) alewife (photo by D. M. Post). (B) Mean gape width and (C) gill raker spacing for wild anadromous (empty symbols) and land-locked (filled symbols) alewife populations calculated across a range of size classes. Weekly experimental measures of (D) log-transformed biomass, (E) body length and (F) species diversity calculated as Shannon's diversity of crustacean zooplankton assessed in three treatments: no alewives (grey diamonds), land-locked alewives (filled circles), and anadromous alewives (empty circles). Values right of the dashed line represent mean trait values obtained from lake samples (detailed in Palkovacs and Post, 2009). Error bars represent standard errors around the mean. Data in (B and C) are obtained from Fig. 2 in Palkovacs EP, and Post DM (2008) Eco-evolutionary interactions between predators and prey: Can predator-induced changes to prey communities feed back to shape predator foraging traits? *Evolutionary Ecology Research* 10: 699–720. Data in (D–F) are obtained from Fig. 2 in Palkovacs EP, and Post DM (2009). Experimental evidence that phenotypic divergence in predators drives community divergence in prey. *Ecology* 90: 300–305.

types, and body size is important in determining feeding rate. In this system, the combination of studies thus suggests that evolution of fish, along with differences in fish densities, induced evolution in *Daphnia*, and that this evolution in turn impacts top-down control of algae. Moreover, Palkovacs and Post (2008) also showed that the observed difference between zooplankton communities intensified the selection on the feeding morphology of the alewives, resulting in subsequent further evolution of fish feeding traits. This creates a direct closed eco-evolutionary feedback from evolved fish morphology to prey community structure and back to selection and evolution of fish morphology.

Evolutionary divergence in predatory fish morphology and its effects on prey communities has also been shown for sticklebacks (Matthews et al., 2016), where recent adaptive divergence of lake and stream populations of these fish resulted in lower zooplankton biomass and richness in the presence of stream compared to lake populations.

Guppies in Trinidad: A field transplant experiment followed by a field mesocosm study

In Trinidad, guppy populations live in streams often interrupted by waterfalls due to the steep-sided ravines. These waterfalls result in a barrier for the upstream dispersal of some fish species, such as the predatory cichlids and characins. Thus, upstream and downstream fish communities are often very different, even when these habitats are immediately adjacent to each other and connected by water flow. As these types of communities can be found in multiple drainages, they represent natural replicates. Guppies are present both down- and up-stream. However, the presence of multiple predators downstream of the waterfalls exerts strong predation pressures on the guppies found in these downstream communities (further referred to as 'high-predation'). In the upstream habitats, guppies co-occur with only an omnivorous species of killifish (further referred to as 'low-predation'). The presence of predators has a strong ecological effect on the guppy population density: in the high-predation communities, guppy population density is four to five times lower compared with low-predation communities. Using transplants followed by a common-garden experiment, Reznick et al. (1997) found that guppies transferred from high-predation to low-predation

communities evolved towards a later age at maturity and larger size at maturity, and produced larger and fewer offspring compared with guppies that stayed in the high-predation communities (Fig. 3D–F) (see also Reznick et al., 1990; Reznick et al., 2008; Reznick et al., 2012).

This classic study of rapid evolution in response to an ecological change (i.e., showing the eco-to-evo link) was followed up by a large field mesocosm common gardening experiment (in this study artificial rivers established in the natural habitat of guppies were used) in which it was shown that guppies from low-predation and high-predation environments differentially influence ecosystem functioning (Bassar et al., 2010; Palkovacs et al., 2009). Guppies from the high-predation environment increased algal biomass, and displayed greater food selectivity by consuming more invertebrates and less algae and detritus compared with guppies from the low-predation environment. Moreover, mesocosms with guppies from the high-predation environment had lower primary productivity and leaf decomposition rates (Fig. 3G–I). The study also tested for and revealed important interactions between the ecological effect (different densities) and the evolutionary effect (different guppy types) of guppies in these two contrasting but neighboring habitats. The effect sizes of differential evolution of guppies were large. This study therefore shows a strong evo-to-eco link, where the phenotypic differences between guppies locally adapted to different predation environments has strong impacts on the structure and the functioning of the whole stream ecosystem.

Daphnia-algal consumer-resource dynamics: Eco-evolutionary dynamics in unconfined nature

Daphnia plays a major role in the top-down control of algal biomass and species composition, influencing seasonal phytoplankton dynamics. In many lakes, there is a seasonal shift from dominance by edible algae in spring (diatoms, chlorophytes, cryptophytes) to relatively inedible phytoplankton (especially cyanobacteria) in summer (Fig. 7A). Schaffner et al. (2019) showed that in a large shallow lake *Daphnia mendotae* evolved increasing tolerance to dietary cyanobacteria as spring 'good food' progressed to summer 'bad food' (an eco-to-evo pathway). In spring the *Daphnia* population was dominated by clones not resistant to dietary cyanobacteria (Fig. 7B): in laboratory feeding trials they exhibited a steep decline in the growth rate of juveniles when fed a diet containing 50% cyanobacteria and 50% edible chlorophyte algae (Fig. 7C). By late summer, clones resistant to cyanobacteria became dominant in the population (Fig. 7D). These were the clones that showed little or no depression in juvenile growth rate on the diet with 50% cyanobacteria (Fig. 7C). The rapid evolution of increased tolerance to dietary cyanobacteria led to an evo-to-eco pathway, influencing the per capita population growth rate of *Daphnia* in the lake (Fig. 7E).

Daphnia as model system for eco-evolutionary dynamics

Three of the examples developed previously (sections '*Daphnia* evolution structures zooplankton community structure: Evolution and its feedback in outdoor mesocosms', 'Alewives, sticklebacks and zooplankton: Eco-evolutionary dynamics in field mesocosms', and '*Daphnia*-algal consumer-resource dynamics: Eco-evolutionary dynamics in unconfined nature') involved studies using the water flea *Daphnia* as a model system to study eco-evolutionary dynamics. Because *Daphnia* is a well-known model organism in ecology and evolution, it is no surprise that it also serves as a good model for exploring dynamics at the interface of ecology and evolution. In this section, we highlight the advantages of *Daphnia* as a model system and showcase the ubiquity of eco-evolutionary dynamics in which *Daphnia* might be involved. The latter is intended to illustrate that it is worthwhile to investigate eco-evolutionary dynamics in a wide variety of contexts and interactions.

Daphnia are small crustaceans in the order Cladocera that reproduce by cyclical parthenogenesis: during their growing season they reproduce asexually, while at the end of the growing season they reproduce sexually. During asexual (i.e., clonal) reproduction, female *Daphnia* produce offspring genetically identical to themselves, which makes them especially useful in studies of traits that may be either genetically determined, phenotypically plastic, or both. In addition, clonal reproduction implies that *Daphnia* can be easily kept in a laboratory environment as pure genetic lineages for many years.

Daphnia is an example of a 'strong interactor' as it is a highly efficient grazer on phytoplankton, a major recycler of nutrients and a preferred prey item for planktivorous fish and other predators (Fig. 8) (e.g., Miner et al., 2012). Its strong ecological interactions depend in part on its plastic and variable morphological, physiological and behavioral traits. Those traits may evolve in response to environmental changes, including changes in the interactions with other organisms. For example, large-bodied *Daphnia* graze phytoplankton more efficiently compared with smaller-bodied zooplankton taxa including other cladocerans, copepods and rotifers. In addition, due to their higher filtration rates and broader food size spectrum, large *Daphnia* excrete nutrients at a higher rate than smaller *Daphnia*. Furthermore, because of their high growth and reproduction rates, large *Daphnia* require and retain from their diet larger amounts of phosphorus compared with other nutrients, resulting in lower excretion rates of phosphorus, altering the availability of nutrients for phytoplankton (Sterner and Elser, 2002). *Daphnia* with large body size are also more visible to predatory fish than are smaller *Daphnia*. Thus, evolution in *Daphnia* body size (e.g., in response to urbanization, as in Brans and De Meester, 2018) will have both top-down consequences for phytoplankton communities as well as bottom-up consequences for its predators. Changes in ecological properties of *Daphnia*'s environment can thus, through changes in selection patterns or changes in drift and gene flow, alter its evolution (eco-to-evo pathway), and this evolution in *Daphnia* can feed back onto one or more

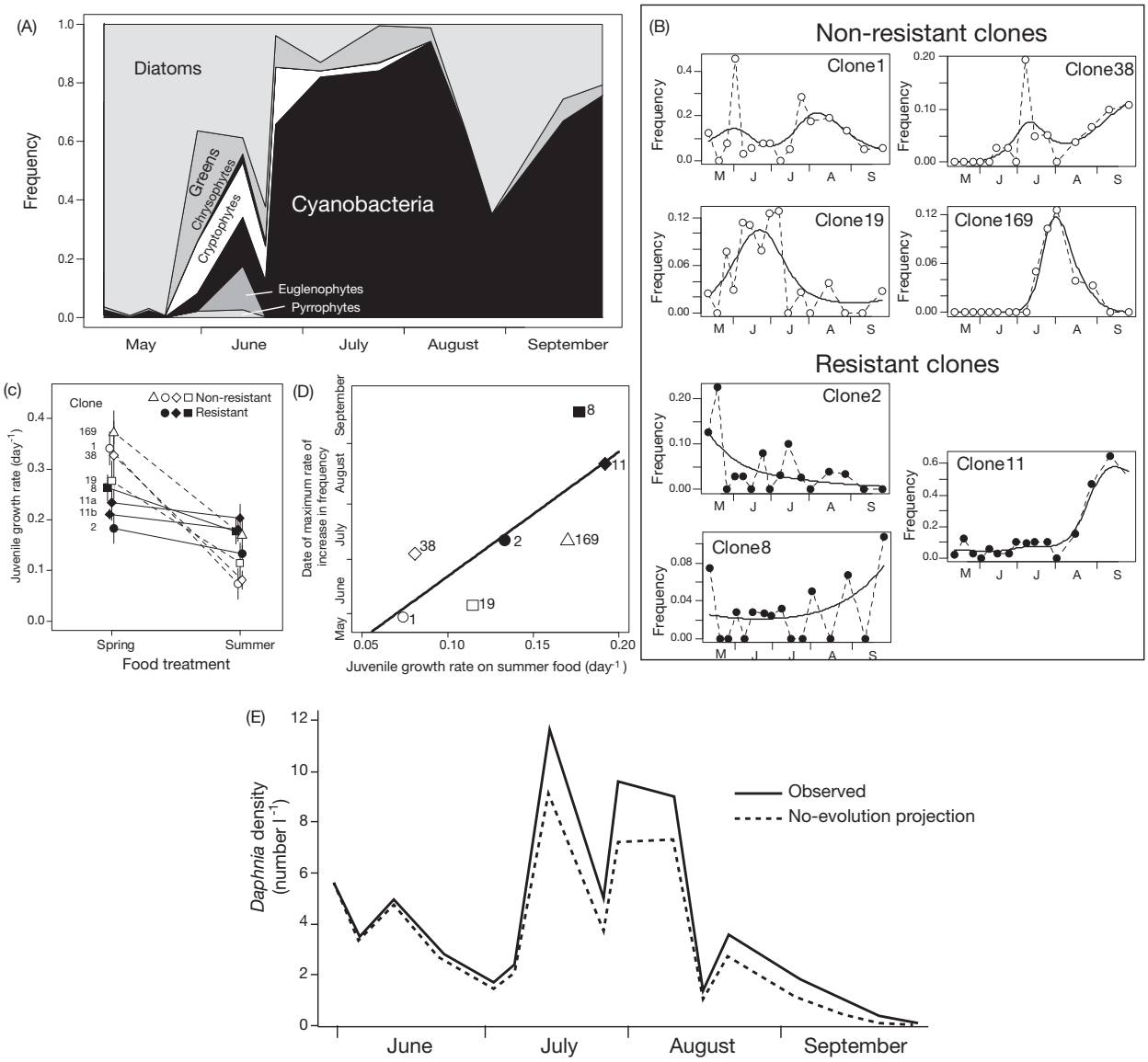

Fig. 7 (A) Frequency of phytoplankton phyla over the course of the season showing a succession from a spring bloom dominated by edible algae to a summer bloom of inedible cyanobacteria. (B) Frequencies of the seven *Daphnia mendotae* clones used in the laboratory common garden experiment during the season. (C) Reaction norms of juvenile growth rate of the seven clones measured in a spring and summer food treatment. Unfilled (resp. filled) symbols reflect non-resistant (resp. resistant) clones. Clone 11 was represented by two independent clonal isolates. (D) Regression of the time point at which each clone had its maximum rate of frequency increase and its juvenile growth rate on cyanobacteria-rich summer food. (D) The observed and projected density of *Daphnia* population. Projected densities were calculated based on no change in clonal frequencies across the season. Data are obtained from Fig. 1C, 2, 3, and 5A in Schaffner LR, Govaert L, De Meester L, Ellner SP, Fairchild E, Miner BE, Rudstam LG, Spaak P, and Hairston NG (2019) Consumer-resource dynamics is an eco-evolutionary process in a natural plankton community. *Nature Ecology & Evolution* 3: 1351–1358.

ecological properties (evo-to-eco pathway). The central role of *Daphnia* in the aquatic food web (Fig. 8), its ability to evolve rapidly in response to changing ecological conditions, and its long-standing role as a model system in ecology and evolution makes it an ideal model system to study eco-evolutionary dynamics. We next highlight with some examples ways in which evolution of *Daphnia* can affect its interactions with other organisms, influencing food web structure and the structure and functioning of aquatic ecosystems. We cannot be exhaustive in our examples; rather the following paragraphs are intended to show the breadth of potential eco-evolutionary dynamics, and stimulate readers to explore them.

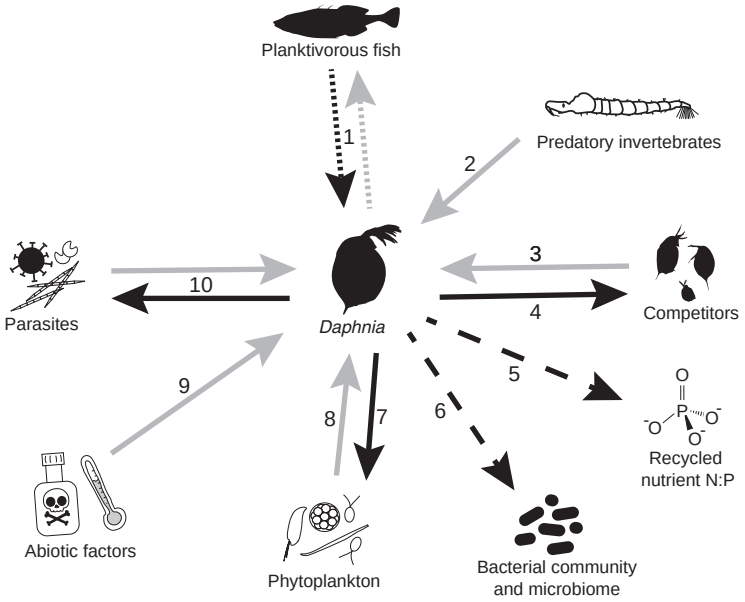

Fig. 8 Illustration of evolutionary and ecological interactions of *Daphnia* in freshwater ecosystems. The arrows refer to interactions reported in the literature (indicated by number); likely other interactions exist, but these have not yet been studied. Solid black arrows indicate evolution of *Daphnia* influencing ecological dynamics. Dashed black arrows indicate the potential of *Daphnia* evolution to influence these ecological properties. Dotted black arrow indicates evolution of fish influencing ecological *Daphnia* dynamics. Solid grey arrows indicate changes in ecological conditions inducing evolutionary change in *Daphnia*. Dotted grey arrow indicates ecological changes in *Daphnia* enforcing evolutionary changes in fish. Settings in which both arrows are present offer opportunities for direct eco-evolutionary feedbacks. Numbers refer to the following studies: 1—Palkovacs and Post (2008), 2—De Block et al. (2013), 3—Steiner et al. (2007), 4—Pantel et al. (2015), 5—Sterner and Elser (2002), 6—Degans et al. (2002) and Callens et al. (2020); 7—Chislock et al. (2013), 8—Schaffner et al. (2019), 9—Brans et al. (2017) and Ward and Robinson (2005), 10—Decaestecker et al. (2007). Figure modified from Miner BE, De Meester L, Phrender ME, Lampert W, and Hairston NG Jr. (2012) Linking genes to communities and ecosystems: Daphnia as an ecogenomic model. *Proceedings of the Royal Society B* 279: 1873–1882.

Eco-evolutionary dynamics in *Daphnia* and its predators

Fish generally exert a strong top-down effect on zooplankton, and impose strong selection pressures on zooplankton populations (Stoks et al., 2016). Evolution of predation-defense traits in zooplankton such as smaller body size and more safe habitat selection in the water column (cf. diel and horizontal migration), will then likely affect feeding rates of fish and can thus alter predator-prey interaction strengths, although we know of no studies that explicitly quantified this. Similarly, *Daphnia* also shows among-population genetic variation in predator-induced defenses against *Chaoborus* predation, involving changes in body size and the development of neck spines (Spitze, 1991). Reger et al. (2018) similarly showed genetic variation in predator-induced defenses among *Daphnia* populations isolated from habitats that vary in the type of predators present. Several studies have shown that predator-induced defenses in *Daphnia* are effective in reducing predation rates by *Chaoborus* (Tollrian, 1995; Laforsch and Tollrian, 2004), but we know of no study showing a clear effect of local adaptation on predation rates.

De Block et al. (2013), in a space-for-time approach on adaptation to warming lake temperatures, showed that *Daphnia* survival when predated upon by damselfly larvae depended upon the interplay of temperature and the latitude of the predator, consistent with a scenario of local thermal adaptation. Specifically, a common garden experiment was performed exposing *Daphnia* clones from southern, central and northern latitude European populations to predation by damselfly larvae from these same latitudes, at both 20 and 24 °C. Relative survival of *Daphnia* was higher at 24 °C than at 20 °C in southern *Daphnia*, while the reverse was found for northern *Daphnia*. However, this thermal advantage disappeared when *Daphnia* were predated by damselfly larvae of the same latitude. This study thus shows that both evolution of *Daphnia* and of its damselfly predator can impact interactions strengths, and differentially so at different temperatures.

Eco-evolutionary dynamics in *Daphnia* and its prey

The study by Schaffner et al. (2019) demonstrated an eco-evolutionary feedback, where *Daphnia* evolution of tolerance to nutritionally poor food affects *Daphnia* population growth during the growing season. It is likely that this might also impact the changes in phytoplankton abundance and composition during the season, but this was not quantified by Schaffner et al. (2019). Chislock et al. (2013), however, did show that different genotypes of *Daphnia pulicaria* can differ strongly in the strength of top-down control of phytoplankton. Different *Daphnia* clones varying in genotype-specific differences in tolerance to toxic phytoplankton had distinct effects on phytoplankton biomass. Tolerant *Daphnia* genotypes had a larger effect on phytoplankton biomass compared with toxic-sensitive genotypes. There is thus a clear potential for strong feedbacks.

In addition to food-induced evolution impacting top-down control of phytoplankton, there are several studies demonstrating that evolution in response to other selection factors can impact top-down control of phytoplankton. As mentioned previously, Walsh et al. (2012) showed that alewife-induced evolution in *Daphnia* results in a faster suppression of algal growth in *Daphnia* isolated from lakes with anadromous alewives compared to *Daphnia* isolated from lakes with land-locked alewives. Similarly, Goitom et al. (2018) showed, in a mesocosm experiment using *Daphnia* subpopulations that are differentially adapted to fish predation pressure, that these differ in their capacity to control phytoplankton. They inoculated mesocosms with *Daphnia* subpopulations derived from hatching dormant eggs from different times in the past that had evolved in response to changes in fish predation pressure (Stoks et al., 2016) and then quantified changes in both *Daphnia* densities and phytoplankton biomass. In this study, similar to that of Walsh et al. (2012), the differential suppression of algal growth was linked to the influence of trait evolution on *Daphnia* population development. In a selection experiment in outdoor mesocosms combined with common garden experiments, Vanhamel et al. (n.d.) show that eutrophication and warming can directly lead to evolution of differential grazing pressure in *D. magna*. In a follow-up transplant experiment, they then show that this differential evolution also impacts phytoplankton biomass development in outdoor settings.

These studies demonstrate the breadth of eco-evolutionary pathways, in which evolutionary changes in *Daphnia* induced by different ecological factors such as changes in food quality (Schaffner et al., 2019), changes in predation (Walsh et al., 2012; Goitom et al., 2018) and via global change (Vanhamel et al., n.d.) can all impact top-down control of phytoplankton.

Eco-evolutionary dynamics in *Daphnia* and its competitors

Steiner et al. (2007) showed evidence of evolution of competitive ability in *Daphnia ambigua*. They hatched clones of *D. ambigua* from long-lived dormant eggs deposited in lake sediments at different times in the past and used them to test for heritable changes in population traits over an interval when the environment changed—a research discipline called 'resurrection ecology' (see Further Reading). They used clones from two time periods: one before *Daphnia dentifera*, a competitor of *D. ambigua*, had been introduced to the lake, and the other after *D. dentifera* became present. Steiner and colleagues then tested the outcome of competition between the two species and found that *D. ambigua* clones present before the introduction of *D. dentifera* performed poorly in competition, whereas clones from after the introduction were able to persist in the competition trials. Because this study focused on an interaction trait through quantifying competitive ability, it also illustrates an eco-to-evo link.

For competition, one may also expect eco-evolutionary impacts of selection by abiotic stressors: if a focal species succeed to adapt to a given stressor (e.g., pesticides, warming) then it may increase their competitive performance towards other species that fail to do so. This, however, will also depend on trade-offs, given that adaptation to a stressor might come at a cost of reduced competitive strength. The earlier highlighted study by Pantel et al. (2015) in which adaptation by the *D. magna* to the combined absence or presence of fish predation and submerged vegetation altered zooplankton community composition is an example of a study in which the capacity of a key interactor to adapt to specific stressors impacts it competitive interactions, resulting in an eco-evolutionary feedback.

Eco-evolutionary dynamics in *Daphnia* and its parasites

Host-parasite interactions can exhibit closed loops of eco-evolutionary dynamics. When there is genetic variation in both *Daphnia* resistance to parasites and parasite virulence, the two antagonists can co-evolve and in this way impact performance and population densities of each other (Thompson, 2005). As a result, many studies on host-parasite co-evolution and its consequences provide evidence for eco-evolutionary feedbacks (Duffy and Hall, 2008). In one example, Decaestecker et al. (2007) hatched *Daphnia magna* clones from dormant eggs obtained from different sediment layers, together with populations of its parasite, the bacterium *Pasteuria ramosa*. In a laboratory experiment, *Daphnia* clones from the different sediment layers were exposed to parasites obtained from the immediately previous time period, as well as from the same and subsequent time periods, thus exposing the *Daphnia* host to parasites from 'the past', 'the present', and 'the future'. They found that infectivity was higher when *Daphnia* were exposed to parasites of the present, than to parasites from the past or future. This study shows that parasites rapidly evolved to track the evolving defenses of common host clones, but also that the host population rapidly evolved in response to the parasites. Because this study quantified infectivity as the proportion of hosts that were infected, it also measured the effect of this co-evolution on prevalence of the parasite in the host population.

Eco-evolutionary dynamics in *Daphnia* and its microbiome

Recently, there has been an upsurge in host-microbiome research using *Daphnia* as a model system. Here too, we may expect strong eco-evolutionary feedbacks, given that the results of several studies point to the fact that *Daphnia* genotype may significantly affect microbiome composition (Callens et al., 2020), and that microbiome composition may be a key component in some ecological interactions and responses to the environment, including the degree to which *Daphnia* genotypes are resistant to toxic cyanobacteria (Macke et al., 2017). In future research, it will be important to disentangle trait changes mediated by evolution, by changes in the microbiome, or by the interaction of genotype and microbiome when quantifying the consequences of trait change on ecological responses and ecosystem functioning.

Overall, while eco-evolutionary dynamics have been reported for an ever-widening scope of ecological dynamics, we are only at the start of quantifying the impact of evolutionary trait change on ecological processes in natural settings. The previous examples address how ecological changes at different trophic levels can influence evolution in *Daphnia*, and how this evolution in turn can influence ecological interactions at various trophic levels. Other ways in which evolution of *Daphnia* can impact ecosystem functioning are likely through the impact *Daphnia* can have on the bacterial community (Degans et al., 2002; Macke et al., 2020) as well as on the availability of nutrients for phytoplankton (Sterner and Elser, 2002).

Conclusion

Anthropogenic processes are rapidly changing the Earth's environments altering the strengths and kinds of ecological interactions. There are many examples of rapid adaptive evolutionary responses of organisms to these changes. If this rapid evolution occurs in traits that determine the nature or strength of interactions among organisms or between organisms and their environment or ecosystem, there is the potential to alter ecological processes with further consequences for evolution, resulting in eco-evolutionary dynamics and feedbacks. Although we have discussed here the ubiquity of such rapid evolution and its eco-evolutionary dynamics in inland waters, examples also exist across a variety of other taxa and model systems (see Hendry, 2017). Understanding when and how such dynamics and feedbacks occur in natural systems is important as they change the predicted outcome of evolution, ecology and their interplay. The demonstration of such feedbacks in these and other natural systems raises the question of how prevalent eco-evolutionary dynamics are in nature, and how they affect responses of populations, communities and ecosystems to human-induced global change.

See Also: Structures and functions of Inland Waters - Lakes: A Diversity of Primary Producers in Lakes; Structures and functions of Inland Waters - Rivers: Ecological and Evolutionary Consequences of Disturbance in Freshwater Ecosystems

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Further reading

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Egg Banks, Bet-Hedging and Resurrection Ecology☆

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This is an update of N.G. Hairston, J.A. Fox, Egg Banks, Editor(s): Gene E. Likens, Encyclopedia of Inland Waters, Academic Press, 2009, Pages 659-666, ISBN 9780123706263, https://doi.org/10.1016/B978-012370626-3.00152-6.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Bet-hedging strategy An evolved life history that maximizes long-term fitness in variable environments. Bet-hedging organisms may have a lower than maximum possible fitness under good environmental conditions but also never have zero fitness under poor conditions.

Bioturbation The mixing of sediments by organisms, living in or on the lake bottom, due to their burrowing, filtering, ingestion, or defecation.

Eco-evolutionary dynamics The feedback between evolutionary changes and ecological processes. Rapid evolutionary changes impact the strength and direction of ecological interactions, which alters natural selection, which in turn causes further evolutionary change.

Dormant egg, embryo, cyst, propagule and spore Life-history stages of animals, algae, bacteria and other organisms that facilitate dispersal in space or time through prolonged dormancy. They are typically resistant to environmental conditions that would kill an active individual, and are often encased (encysted) in a protective coating.

Life history strategy The pattern of timing of life stage events determined by the allocation of resources to growth, maintenance, reproduction and survival so as to maximize fitness.

Paleolimnology The study of the history of lake organisms and ecosystems using physical, biological, and chemical properties of lake sediments deposited in historical order, often used to reconstruct past climate or environmental changes.

Prolonged dormancy Dormancy that persists longer than to the next annual growing season.

Red Queen dynamics The proposition that a population must constantly evolve in order to survive and reproduce successfully in the presence of natural enemy species (competitors, predators or parasites) that are themselves continuously evolving to overcome their competitors, prey or hosts.

Sediment focusing The tendency for sediments to accumulate in the deepest part of a lake basin because sediment resuspension processes are greatest near shore resulting in net sediment movement from shallow to deep.

Introduction

"Egg bank" is both a specific term describing the accumulation of diapausing eggs of zooplankton within the sediments at the bottom of a lake or pond, and a more general term describing the sediment accumulation of a diversity of dormant life-history

☆*Change History*: September 2020. NG Hairston Jr. and JA Fox (1) modified title to include "Resurrection Ecology" as desired by editor Lars Rudstam, (2) updated text, (3) added more section subheadings, (4) replaced Fig. 6, (5) added literature citations within the text and updated referenced.

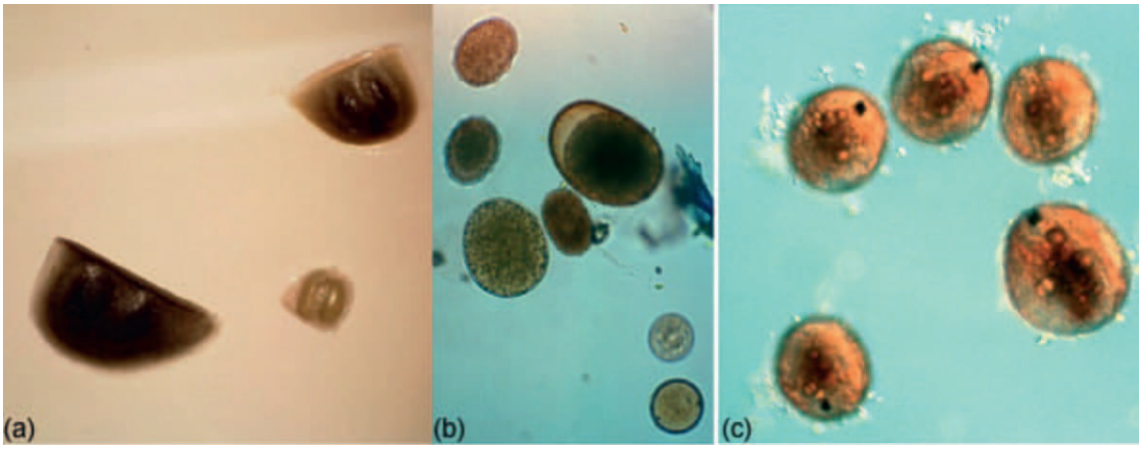

Fig. 1 Diapausing eggs of freshwater planktonic crustaceans: (A) ephippial egg cases of three cladoceran species of the genus *Daphnia*, each case contains two eggs; (B) resting eggs of seven rotifer species; (C) the copepod genus *Onychodiaptomus*, one at the gastrula stage, the rest at the eyed-embryo stage. Photos by JA Fox (A) and CM Kearns (B and C).

stages made by a variety of aquatic organisms. These stages, known collectively as "dormant propagules," include embryos of invertebrates (Fig. 1), encysted gametes of protists and algae, and spores of bacteria and cyanobacteria. Many of these stages have the ability to remain dormant for long periods of years, decades, and in some cases more than a century while retaining the capacity to emerge from dormancy to become metabolically and ecologically active in lake ecosystems (Hairston Jr., 1996). This "prolonged dormancy" (i.e., dormancy that lasts longer than from one growing season to the next) leads to the formation of an egg bank as on average more dormant propagules are deposited each year on the lake bottom than the number that emerge. As will be explained below, the adaptation of prolonged dormancy that leads to the formation of egg banks (life-history bet-hedging) has important implications for the maintenance of biological diversity in lakes and ponds, while the existence of egg banks provides a resource for the study of evolution in response to changing environments (resurrection ecology).

Dormant propagules typically possess traits that permit them to survive harsh conditions that would be lethal to individuals in the active stage; these harsh conditions include, but are not limited to, temperatures that are too warm or too cold, freezing, low dissolved oxygen, desiccation, low food availability, and high predator or pathogen densities. Prolonged dormancy permits otherwise short-lived organisms to persist in environments that vary in how hospitable they are from one growing season to the next (i.e., occasional occurrence of a harsh season). In a temporally unreliable environment, a parent organism that produces multiple dormant propagules, some of which emerge the following growing season and some of which remain in dormancy for longer periods, increases the chance that its descendants will persist in the long term. A single season that is so harsh that individuals not in dormancy fail either to reproduce or to survive would quickly cause population extinction if it were not for the fact that some individuals survive through the harsh season as dormant propagules. A life history in which some of the offspring of an individual emerge to try out one growing season while others wait to try out other growing seasons is called a "temporal bet-hedging strategy" (Seger and Brockmann, 1987).

Because dormant propagules are resistant to harsh conditions, they can also provide a means for individuals to disperse from one lake to another. Dormant eggs, cysts, or spores may become attached to the fur, feathers or integument of vertebrates or insects that visit first one lake or pond and then another. Propagules disperse spatially if they attach to the visitors in one lake and then fall off in another (Simonis and Ellis, 2014). Some dormant propagules, consumed by a predator, can survive gut passage and can disperse between lakes if they are ingested in one lake and defecated in another (Mellors, 1975). Other dormant propagules may be dispersed by wind when floating eggs or spores accumulate against the shore from which they can be lifted by a breeze (Pinceel et al., 2016; Sirianni, 2017). Still other dormant propagules may be transported by water flows from one water body to another (Pellow-Wagstaff and Simonis, 2014). The dispersal of dormant propagules to numerous lakes, each with a different environmental condition can result in spatial bet-hedging, which is similar conceptually to the temporal bet-hedging already described.

Egg banks are important in lake ecosystems in three ways.

(1) They are a means by which populations survive through periods of stressful or uninhabitable conditions in a lake, whether those harsh conditions are natural in origin or are caused by human activity. Species or genotypes produced in the past, but absent from the water column in the present, can emerge from dormancy and reinvade rapidly in response to a change in the environment. Reinvasion by hatching from an egg bank provides a mechanism for the long-term maintenance of biological diversity in a lake.

(2) Species or genotypes that establish large water-column populations after a period of absence by reinvading from an egg bank can affect how the lake ecosystem functions and how lakes respond to environmental change. For example, when a keystone taxon, such as the dominant phytoplankton grazer, *Daphnia*, appears from the egg bank after some years of absence, the abundance and composition of phytoplankton and other suspended particles can be dramatically altered by their feeding

(Effler et al., 2015). If distinct assemblages of *Daphnia* genotypes emerge from diapause in different years, those genetic differences may likewise affect consumer-resource dynamics (Hairston Jr. et al., 2001; Schaffner et al., 2019).

(3) The sediments of lakes typically accumulate year by year, with the most recent sediments at the surface and older sediments occurring progressively at greater depths. Buried eggs, cysts, and spores provide a historical record of the species, genotypes, and phenotypes that existed in the past. Hatching or germinating these propagules from different sediment depths (*i.e.*, times in the past) provides a means to study how populations have evolved qualitatively and quantitatively in response to changing environments. This relatively new field is called "resurrection ecology."

Prolonged dormancy as an adaptive life history strategy

Dormancy and diapause defined

Dormancy is any state of reduced metabolic activity; either a temporary loss of the ability of cells to divide (in single-celled organisms such as bacteria, algae, and protists), or the suppression of growth, development, and reproduction (in complex organisms such as rotifers and crustaceans). Many dormant life-history stages also possess a resistant covering that aids survival in harsh conditions. Nondiapause dormancy is seasonal quiescence—a reversible state of suppressed metabolism directly imposed by exposure to harsh conditions (e.g., low temperature, low dissolved oxygen). Diapause-dormancy is induced by environmental factors that do not directly reduce metabolic rate but which act as a signal to the organism that conditions will soon deteriorate (e.g., day-length, temperature, food concentration, population density, and presence of predators or pathogens) (Tauber et al., 1986). Life history stages in "prolonged dormancy" do not all emerge at the first return of favorable conditions in the lake; it is these long-lived dormant stages that accumulate in sediments to produce an egg bank (De Stasio, 1989).

Egg and cyst viability

Dormant propagules can remain viable for amazingly long time periods. Eggs of cladocerans and copepods have been found to remain viable in lake sediments for as long as several centuries (Fig. 2) (Hairston Jr. et al., 1995; Frisch et al., 2014). Egg and cyst viability of several decades is common (Hairston Jr. and Cáceres, 1996). At least some eggs and cysts reduce their metabolic rate in dormancy to undetectable levels. The physiological mechanisms maintaining prolonged embryonic diapause and hence egg banks include accumulation of sugars, carotenoid pigments, and heat-shock proteins that inhibit physical–chemical damage during dormancy (Clegg, 2001).

Very short time scales (2–3 years) seem to have little effect on the ability of diapausing eggs to hatch. Over longer time periods, from a few years to several decades, viability generally decreases with age. Reduced viability is evidenced by decreased hatching rates, and by both the increased time to hatch of older eggs and the decreased health of the individuals that do hatch (Fig. 3; Fox, 2007).

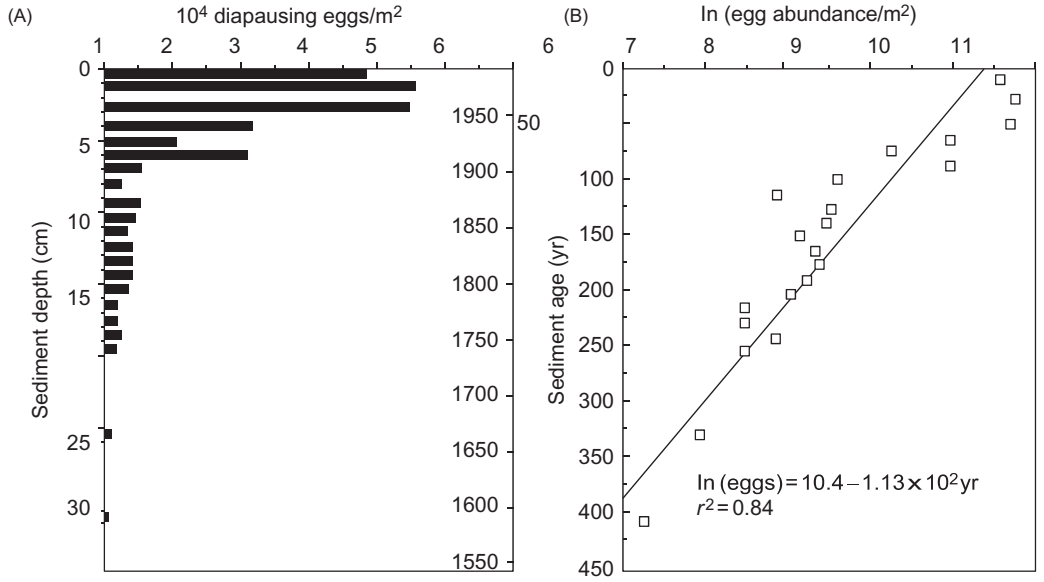

Fig. 2 (A) The density of diapausing eggs of the copepod *Onychodiaptomus sanguineus* in the sediments of Bullhead Pond, RI, as a function of sediment depth and sediment age; (B) The slope of the relationship between the natural logarithm of viable-egg density and sediment age is the mortality rate of the eggs, which in this case is 1.13% per year. From Hairston NG Jr., Van Brunt RA, Kearns CM and Engstrom DR (1995) Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* 76: 1706–1711.

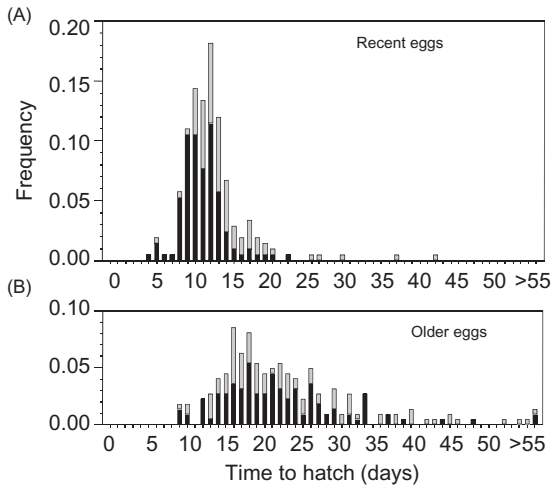

Fig. 3 The time to hatch and incidence of inviable hatchlings. (gray portion of bars) for diapausing eggs of *Daphnia mendotae* taken from sediments less than 5 years old (A) and 15–20 years old (B) in Onondaga Lake, NY. Hatchlings were considered inviable if they had obvious physical deformities or survived less than 7 days in culture. Adapted from Fox JA (2007) Hatching timing of *Daphnia mendotae* diapausing eggs of different ages. *Fundamental and Applied Limnology* 168: 19–26.

Temporal migration, temporal dispersal, and temporal bet-hedging

Many environments vary seasonally. In the temperate zone and higher latitudes, winter conditions are harsh for organisms. In tropical regions and elsewhere, the dry season can be stressful in naturally shallow ponds. Mobile organisms avoid these physiologically challenging periods by migrating to a region where conditions are more benign. Organisms of limited mobility, including the plankton of lakes, lack the ability for long-distance directional movement from one favorable habitat to another. For them dormancy and diapause provide a capacity for "temporal migration" when spatial migration is not possible (Brendonck and De Meester, 2003). For example, cladoceran crustaceans in a pond that dries every summer can produce diapausing eggs that are able to survive in the pond sediments in the absence of standing water. When the pond refills the following spring the eggs hatch, transiting the organisms from one favorable period to another.

One way for organisms to survive in an unpredictable and spatially patchy environment is to disperse their eggs (or their offspring) randomly (similar to spatial seed dispersal in plants). Some individuals will land on unfavorable habitat patches but others will land on good sites and can grow and reproduce to disperse again. The dormant propagules of lake organisms may be dispersed to other lakes by more mobile organisms or by wind or overflows, as described earlier. Long-lived dormant propagules, however, also possess the capacity for "temporal dispersal" in which the propagules stay in one place, but emerge from dormancy in different years. For example, a copepod crustacean may produce a clutch of 20 diapausing eggs in a temporary pond. In some years when the pond refills, predator densities may be so great that any individual hatching has little or no chance of survival. In other years, however, predator density may be low and individuals hatching can mature and produce diapausing eggs of their own. Temporal dispersal occurs when the hatching of diapausing eggs from a single clutch hatch is spread out over multiple years, some of which are favorable and some of which are not.

In a temporally varying environment, years differ in their suitability for the survival and reproduction of an organism. The fraction of propagules that should theoretically emerge from the egg bank in any given year depends upon the likelihood of a year being either good or bad and the ability of the diapausing propagule to survive to subsequent years. The greater the probability of any year being good, the greater the optimal hatching fraction. This optimal emergence (or hatching) fraction is called a "bet-hedging strategy" and can be calculated based upon the probability of a good year occurring. It is probable, however, that year suitability will not simply be either good or bad; mediocre years can also occur in which survival and reproduction is not zero but is less than in good years. Again, an optimal hatching fraction can be calculated depending upon the probability of the occurrence of particular year types. Finally, environments may or may not become uninhabitable (e.g., a pond may or may not dry depending upon the amount of rainfall in a given year). Organisms may make some eggs that hatch immediately and some that enter diapause, and again, an optimal allocation of reproduction to diapausing and nondiapausing eggs can be calculated as a bet-hedging strategy.

Structure of egg banks

Egg bank formation and dynamics

An egg bank represents the summation of the allocation to prolonged dormancy by the organisms living in a particular lake or pond. Dormant propagules accumulate in lake sediments both because long-lived propagules settle to the lake bottom when they are released and because sediment processes cause them to become buried (Fig. 4) (Cáceres and Hairston, 1998). Only those

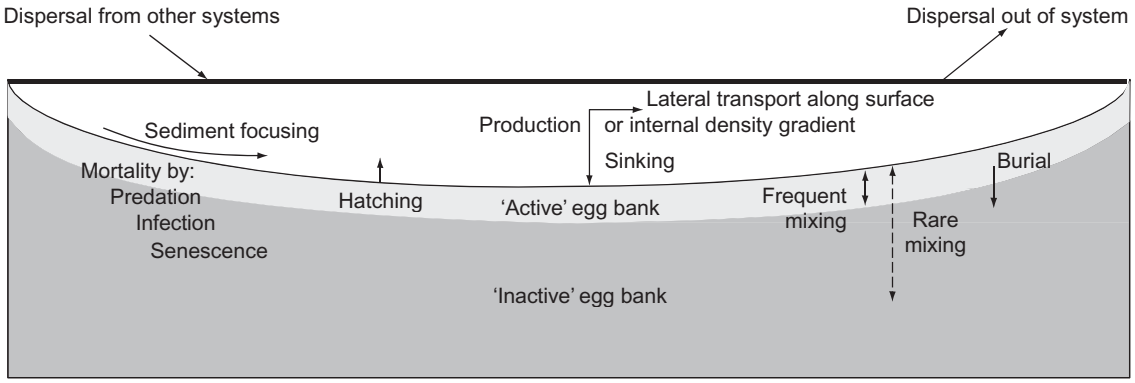

Fig. 4 Side-view schematic diagram of a lake and its sediments depicting the distribution of dormant propagules within the egg bank. Because deeply buried propagules are viable but unlikely to hatch, the egg bank consists of "active" and "inactive" compartments. The active fraction receives the new propagules from the water column and is defined as the depth to which propagules can receive the cue to exit from dormancy and emerge successfully, most likely less than 1 cm into the sediment. Although propagules in the inactive compartment may remain viable for many years, they cannot emerge from dormancy unless some localized disturbance returns them to the active compartment. Adapted from Cáceres CE and Hairston NG Jr. (1998) Benthic-pelagic coupling in freshwater zooplankton: The role of the benthos. *Archiv für Hydrobiologie – Advances in Limnology* 52: 163–174.

propagules within the top few millimeters of the sediment surface can successfully emerge (Hairston Jr. and Kearns, 2002). Propagules that become buried below this depth may remain viable for decades or more, but they cannot emerge unless brought to the surface by a dramatic event such as burrowing by a vertebrate or sediment disturbance by a boat anchor.

Sediment deposition buries propagules at rates varying between less than a millimeter to greater than a centimeter per year, depending on lake and watershed conditions. Sedimentation rates also vary spatially within a lake. Sediment focusing—the tendency for sediments to accumulate in the deepest portion of a lake basin—makes it likely that eggs deposited in the deepest portion will be buried more quickly, and so will be less likely to hatch, than those near shore. Sediment mixing by insects and worms living in the mud at the bottom of lakes (called "bioturbation"), transports propagules near the sediment surface deeper into the mud, while propagules at depth may be transported to the surface from which they can emerge (Kearns et al., 1996). Bioturbation typically mixes only the top few centimeters of lake sediments. Physical disturbance (e.g., wave action, currents, fluctuations in water depth) is typically greater for shallow near-shore sediments. Macrophytes also influence egg movement by stabilizing sediments and channeling movement of benthic invertebrates (Hairston Jr. and Kearns, 2002).

Lake size influences the relative importance of biological and physical disturbance of sediments. In larger lakes physical mixing, particularly in shallow, near-shore areas where wind action is greatest and near inlets where currents are strongest, may play an important role in mixing sediments. Smaller bodies of water are often more protected from wind action and have a greater proportion of shallow, near-shore regions where bioturbation may be more important. Egg density is typically greatest in deep-water sediments and lowest in near-shore areas (Table 1); however, the probability of receiving a hatching cue is greatest in shallow-water sediments. Thus, different regions of the same lake play different roles in the egg bank dynamics. Hatching from near-shore sediments may act as an important contribution to ongoing population processes while long-term storage in deeper sediments serves as an archive of population history in a lake.

Number versus depth

The density of dormant propagules or eggs in sediments varies widely by lake and species, with densities of 10^3 to 10^6 m^{-2} typical for algae, rotifers, copepods, and cladocerans (Table 1). The vertical distribution of eggs within the sediments is not uniform. The abundance of eggs at a given depth below the sediment surface is a function of the history of the rates of production, mortality, and emergence, as well as sedimentation rate and disturbance (Brendonck and De Meester, 2003). The number of eggs typically decreases with depth in the sediments, often with a peak in abundance just below the actively mixed sediment layer near the sediment–water interface (Fig. 2). The distribution of eggs in the sediments may show gaps or breaks, corresponding to periods of time when the species was absent from the water column or present in smaller numbers (Fig. 5).

Evidence of lake recolonization from the egg bank

Resistant diapausing eggs play an important role in facilitating colonization of new environments and recolonization of temporarily unsuitable water bodies. An egg bank allows species to persist years after no adults survived to reproduce. Several experiments monitoring emergence of hatchlings from sediments have shown that copepods and cladocerans hatched from the egg bank years after no adults were present in the water column. Two studies of lakes, in which newly stocked fish eliminated water-column populations of zooplankton, showed that after the fish were removed, both copepods and *Daphnia* returned to the water column of

Table 1 The densities of zooplankton diapausing eggs in central deep sediments compared with shallow near-shore sediments in lakes and the ratio of densities in deep compared with shallow sediments.

Taxon	Lake	Egg densities (no. m^{-2}) and depth (m)			Source
		Deep	Shallow	D/S	
Cladocera					
Holopedium[a]	Windgfällweiher	2.5×10^6 (4.7)	$<1.0 \times 10^5$ (0–2)	25	1
Ceriodaphnia[a]	Piburger See	$>3.0 \times 10^5$ (>20)	$<1.0 \times 10^5$ (<5)	3	2
Bosmina[a]	Piburger See	$1–6 \times 10^5$ (>5)	$<5.0 \times 10^4$ (<5)	2	2
Daphnia[b]	Schöhsee	7.2×10^4 (21–25)	1.1×10^4 (5–10)	6.5	3
Daphnia[b]	Kellersee	1.2×10^5 (21–25)	3.8×10^4 (5–15)	3.2	3
Daphnia[a]	Oneida Lake	$>1.0 \times 10^5$ (12)	$<3.5 \times 10^3$ (3)	28	4
Copepoda					
Diaptomidae[a]	Oneida Lake	$>1.0 \times 10^6$ (10)	$<6.0 \times 10^5$ (3)	1.7	5
Onychodiaptomus[a]	Bullhead Pond	$>2.0 \times 10^5$ (4)	$<2.0 \times 10^4$ (1)	10	6, 7

D/S is the ratio of deep to shallow egg densities.

[a]Total density of diapausing eggs.

[b]Total diapausing egg-case densities.

Lampert W and Krause I (1976) Zur Biologie der Cladocere Holopedium gibberum Zaddach im Windgfä llweiher (Schwarzwald). *Archiv für Hydrobiologie Supplement* 48: 262–286; Moritz C (1988) Die Verteilung der Ephippien von Bosmina longirostris und Ceriodaphina pulchella im Sediment des Piburger Sees (Ö tztal, Tirol) (Cladocera, Crustacea). *Berichte des Naturwissenschaftlich-medizinischen Vereins in Innsbruck* 75: 91–107; Carvalho GR and Wolf HG (1989) Resting eggs of lake-Daphnia: I. Distribution, abundance and hatching of eggs collected from various depths in lake sediments. *Freshwater Biology* 22: 459–470; Cáceres CE (1998) Interspecific variation in the abundance, production and emergence of Daphnia diapausing eggs. *Ecology* 79: 1699–1710; Hairston NG Jr. and Van Brundt RA (1994) Diapause dynamics of two diaptomid copepod species in a large lake. *Hydrobiologia* 292/293: 209–218; De Stasio BT Jr. (1989) The seed bank of a freshwater crustacean: Copepodology for the plant ecologist. *Ecology* 70: 1377–1389; Hairston NG Jr., Van Brundt RA, Kearns CM, and Engstrom DR (1995) Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* 76: 1706–1711; Hairston NG Jr. and Kearns CM (2002) Temporal dispersal: Ecological and evolutionary aspects of zooplankton egg banks and the role of sediment mixing. *Integrative and Comparative Biology* 42: 481–491.

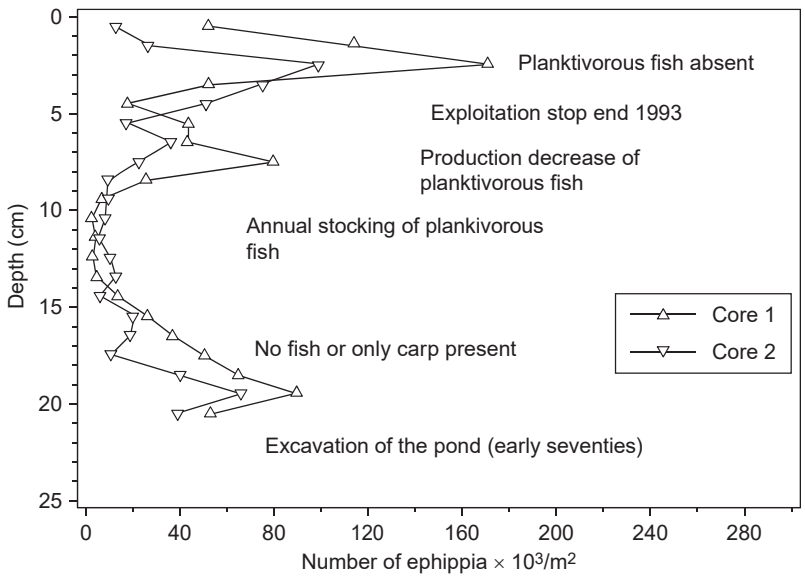

Fig. 5 The depth distribution of dormant egg cases (ephippia) of *Daphnia magna* in two sediment cores taken from an artificial pond created in Belgium in the 1970s. Noted on the figure are periods of high and low abundance of fish that consume *Daphnia*. Adapted from Cousyn C and De Meester L (1998) The vertical profile of resting egg banks in natural populations of the pond-dwelling cladoceran Daphnia magna Straus. *Archiv für Hydrobiologie – Special Issues Advances in Limnology* 52: 127–139.

lakes that had a large sediment egg bank, but did not return in a lake that had no egg bank because the eggs had been consumed by a large population of predatory benthic invertebrates (Parker et al., 1996; Knapp and Sarnelle, 2008).

Studies of the genetic structure of populations provide indirect evidence of recolonization from the resting egg bank. For example, using population genetic analyses of diapausing eggs obtained from different sediment ages, a population of *Daphnia* in a Kenyan lake was shown to recolonize that water body after a 50-year period absence (Mergeay et al., 2007). A bryozoan population

showed the same genetic composition before and after a significant demographic bottleneck, suggesting recolonization from the dormant propagule bank rather than from neighboring populations that are genetically distinct (Freeland et al., 2001).

In most species examined, hatchlings from the egg bank exhibit tremendous genetic diversity, which is often greater than the diversity of the planktonic population at the end of the season (Freeland et al., 2001; Schaffner et al., 2019).

The role of egg banks and the storage effect in the maintenance of lake biodiversity

Temporal bet-hedging by long-lived dormant propagules present in egg banks can play an important role in maintaining species diversity in lakes. This occurs when the environment in a lake varies from year to year and species differ in the environmental conditions under which they do best. Without an egg bank, two species with similar ecological requirements may not be able to coexist due to competition. Even when the environment varies and species differ in the environmental condition that is favorable to them, on average one species will be better at using the available resources and over time will eliminate the other. If, however, individuals emerge each year from an egg bank into a varying environment, newly emerging individuals will have high reproductive success in years that are favorable and low success in unfavorable years. In favorable years, the individuals can build up a large population, produce a large number of new dormant propagules, and restock the egg bank before the end of the season. If each species is successful in survival, reproduction, and ultimately restocking its egg bank under environmental conditions when the other does poorly, then conditions exist for the two species to coexist over the long term. This mechanism, by which biological diversity is maintained, is called the "storage effect" and makes it possible for many species to coexist (Chesson, 2000). In one study (Cáceres, 1997), *Daphnia pulicaria* and *Daphnia mendotae* were shown to coexist for several decades even though the former species was the superior competitor in most years. The latter had a more substantial egg bank that it was able to restock in years when high fish predation (to which it is less vulnerable) gave it a fitness advantage.

The egg banks and the storage effect also serve to maintain genetic diversity within a species if genotypes differ in the environmental conditions under which they do best (Ellner and Hairston, 1994). In a population of the copepod *Onychodiaptomus sanguineus*, genetic variation for a trait that influences their ability to survive predation by fish is apparently maintained *via* the storage effect in the presence of year-to-year variation in predation intensity (Ellner et al., 1999).

Egg banks as historical archives and resurrection ecology

Dormant propagules buried in lake sediments provide a paleolimnological record of the changes in a population over years, decades, or centuries. Several different approaches are used, often together, to reconstruct the history of populations using egg banks: (1) determining the distribution and relative abundance of species and genotypes within species through time, (2) performing genetic analyses on the dormant propagules, and (3) hatching individuals from eggs of different ages to compare phenotypes. These methods provide insights into the evolutionary history of the species being examined as well as community and ecosystem processes.

The abundance of dormant eggs in the sediments is correlated with population size at the end of the season in which the eggs were produced. Therefore, in the absence of significant disturbance of the sediments, changes in egg density throughout the sediments can be used to estimate the size of past populations. Egg banks have been used extensively to document the impact of human-induced changes on zooplankton community structure. Changes in cladoceran community structure over two centuries in Lake Naivasha, Kenya (Mergeay et al., 2004) showed that the introduction of exotic fish played a key role in determining which species were most abundant, with large-bodied species being absent during periods of intense fish predation. In addition, increased erosion from agricultural lands caused increased turbidity and decreased the abundance of submerged aquatic plants, which in turn led to a decline of smaller species that are found in macrophyte beds. Conversely, changes in the abundance of macrophyte-associated species in an egg bank may indicate past vegetation or other ecosystem changes. The effects of heavy metal pollution on zooplankton populations in lakes in Europe and North America have been recorded in the egg banks of these lakes. For example, analysis of the zooplankton egg bank in a Canadian lake recovering from acidification reveals a species shift associated with changes in the lakes' acidity levels interacting with the effects of drought (Arnot and Yan, 2002) and the *Daphnia* egg bank and *Bosmina* microfossils show declines in abundance during periods of peak industrial activity in a small lake near Lake Superior (Kerfoot et al., 1999).

Studies of egg banks have led to greater understanding of the processes of colonization and the relative importance of population re-establishment from the egg bank and from external sources. For example, the historical species record in the egg bank revealed that the establishment of a particular *Daphnia* species in lakes recovering from acidification must be from external sources, despite the existence of a large bank of viable eggs of other *Daphnia* species.

Egg banks also register unusual past events, such as the invasion of exotic species. In Onondaga Lake, NY, the presence of two salt-tolerant exotic *Daphnia* species during periods of high industrial pollutant salt-loading into the lake were documented by the presence of large numbers of diapausing eggs in the sediments (Hairston et al., 2005). These species had been undetected or misidentified in samples taken during those years, and were later identified through a combination of morphological, hatching, and genetic analyses of ephippia and eggs stored in the sediments. Genetic analyses revealed that the population of one of these species was established by the introduction of only one or two individuals into the lake, a reminder of the tremendous dispersal and establishment capabilities of these dormant stages.

Evolution can also be studied using molecular genetic techniques applied to dormant propagules from lake sediments. The approach has enabled genetic analyses directly on diapausing eggs, without introducing the potential bias of examining only those individuals capable of hatching. DNA has been successfully extracted, amplified and genotyped from diapausing eggs hundreds to over a thousand years old (Ellegaard et al., 2020). Genotyping, though not able to provide insight into functional trait evolution, nevertheless has been used to document changes in clonal, species and hybrid composition. This approach has been used to demonstrate changes in genetic structure corresponding to alterations of the environment for a variety of taxa including rotifer response to changing water level (Epp et al., 2010) and *Daphnia* response to lake eutrophication (Brede et al., 2009; Frisch et al., 2014). Methods for whole genome sequencing of single diapausing eggs have been reported (Lack et al., 2018), providing potential for analysis of evolution in even greater detail once sequences are assigned to functional traits.

Resurrection ecology

Dormant propagules produced at different times in the past can be hatched or germinated and then grown in the laboratory to investigate how population physiological, morphological and behavioral phenotypes have changed in response to environmental change. This research approach, named "resurrection ecology" by Kerfoot et al. (1999), is an extension of classic paleolimnology that provides a powerful method for investigating the trajectories and rates of evolution.

A study of the 17-year history of changes in size-selective predation by fish on *Daphnia magna* was recorded by observing changes in the size and density of the cladoceran ephippia in the sediments of a fish pond (Fig. 5) (Cousyn et al., 2001). Then, studies of the predator avoidance behavior of clonal genotypes hatched from different time periods demonstrated that the species evolved rapidly in response to changes in fish predation pressures (Fig. 6).

Eutrophication of Lake Constance caused an increase of cyanobacteria in the water column, a phytoplankton group known to be of poor food quality to *Daphnia*. Experiments on *Daphnia* hatched from sediments corresponding to times after a decade of eutrophication show that they are more resistant to toxic cyanobacteria than are *Daphnia* hatched from sediments deposited before eutrophication, when cyanobacteria levels were much lower. This rapid evolution of phenotypes is associated with a change in molecular genetic frequencies over the same time period (Hairston Jr. et al., 2001).

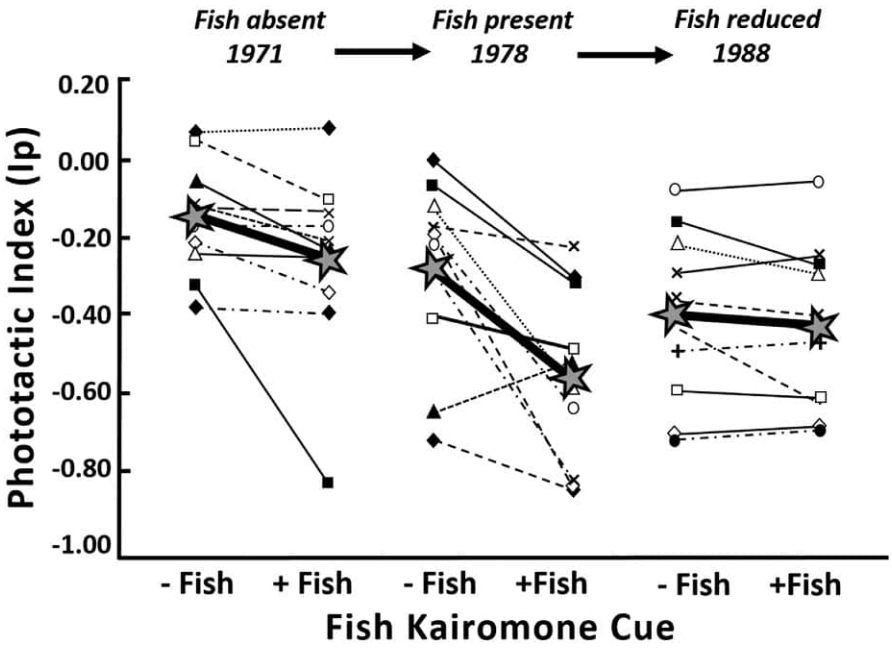

Fig. 6 Evolution of *Daphnia magna* predatory-fish avoidance behavior when fish were present in a Belgian fish pond, and loss of that avoidance behavior when fish were absent or rare. The predator-avoidance behavior was determined for *Daphnia* hatched from diapausing eggs collected from three different sediment depths. The 1988 and 1971 sediments are from time periods when *Daphnia*-eating fish were either rare or absent; the 1978 sediments are from a time when these fish were abundant (see Fig. 5). For each time period, the vertical distribution of *Daphnia* was determined in an illuminated cylinder of water ("phototactic index") for each of 10 different *Daphnia* clones (each clone descended from a single diapausing egg) in water without (– Fish) or with (+ Fish) fish kairomone cue. *Daphnia* sensitive to fish have a low phototactic index (lp) because they swim away from illuminated water (in a pond that would be to a depth where fish cannot see them). The sloping lines show the lp for each clone in the absence or presence of the fish kairomone cue. Sensitive clones have a strong response to the kairomone and so a steep slope; insensitive clones have lines with little or no slope. The average sensitivity, shown with stars connected by a thick solid line, is greatest during the period when fish were present. Original data from Cousyn CL, De Meester L, Colbourne JK, Brendonck L, Verschuren D and Vlockaert F (2001) Rapid, local adaptation of zooplankton behavior to changes in predation pressure in the absence of neutral genetic changes. *Proceedings of the National Academy of Sciences USA* 98: 5256–6260; figure redrawn from Hairston NG Jr. and De Meester L (2008) Daphnia paleogenetics and environmental change: Deconstructing the evolution of plasticity. *International Review of Hydrobiology* 93: 578–592.

Decaestecker et al. (2007) used a resurrection ecology approach to show the co-evolutionary interplay between host sensitivity to its pathogens and pathogen virulence over the course of three decades. Both *Daphnia* diapausing eggs and spores of *Daphnia*'s bacterial pathogen, *Pasteuria*, were hatched or germinated from a series of sediment ages and the susceptibility of the host was assayed for pathogens present before, during and after each time period from which the *Daphnia* were obtained. The study showed that, evolutionarily, pathogen infectivity rapidly tracked host resistance: a clear example of so called "Red Queen" dynamics.

It is furthermore possible from these resurrection ecology studies to delve deeper into the evolutionary process by exploring the rates of evolution and the evolution of plasticity (Hairston Jr. and Meester, 2008), comparing the rates of molecular and phenotypic evolution (Cousyn et al., 2001; Frisch et al., 2014), defining the constraints placed by trait covariance on evolutionary response (Ellner, 2013), and quantifying the reciprocal effects of ecological change on the evolution of traits and influence the strength of ecological interactions, which then in turn affect further evolution (Ellner et al., 2011), in a process called eco-evolutionary dynamics (Hendry, 2017).

Conclusions

Egg banks collect dormant propagules of many aquatic organisms in lake sediments. These propagules allow populations to move in time in the sense that their genetic descendants can emerge many years after the propagules were deposited on the lake bottom. Long-term dormancy allows species to "bet hedge" and survive in temporally-varying environments, escape competitive exclusion, minimize the negative effects of predators and pathogens, and recolonize after periods of environmental change. Lake size and shape influences both where dormant propagules accumulate and the likelihood that they will receive hatching cues, and can therefore influence the dynamics of populations that rely on egg banks for persistence.

Egg banks can be used to better understand evolutionary and ecological processes. The history of a lake or pond population can be reconstructed by examining its egg bank. Past population sizes and genetic diversity, as well as community composition can be explored using egg banks. We can also directly assess rates of evolution and or responses to environmental change in past populations by hatching individuals from different time periods to measure their phenotypes.

See Also: Fundamental concepts and theories: Parasites in Aquatic Food Webs: How and Why Environmental Gradients Influence Epidemics and Their Implications; Structures and functions of Inland Waters - Rivers: Invasive Species in Streams and Rivers

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Trophic Dynamics and Food Webs in Aquatic Ecosystems☆

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This is an update of U. Gaedke, Trophic Dynamics in Aquatic Ecosystems, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00208-8

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Detrital food chain Food-web components that begin with particulate organic matter (detritus) or dissolved organic matter, and pass through bacteria to other consumers.
Ecological stoichiometry Study of element ratios within biomass in relation to element ratios within food or in the surrounding environment.
Food web A diagram or model that shows the feeding connections between all major groups of organisms in an ecosystem.
Grazer food chain Components of a food web that begin with photoautotrophs (in pelagic systems: cyanobacteria, algae, aquatic vascular plants) and pass through herbivores to carnivores.
Trophic guild A group of organisms that share common food sources and common predators.
Trophic level A group of organisms that obtain their food from sources of equal distance from the original source. Autotrophs equal level 1, herbivores equal level 2, primary carnivores equal level 3, and secondary carnivores equal level 4. Species feeding from more than one level may be assigned a fractional trophic level called trophic position based on their diet composition.
Trophic transfer efficiency The fraction of total production at a given trophic level that is converted to production at the next trophic level.

Introduction

An understanding of the role of individual species within an ecosystem and the functioning of ecosystems in their entirety is only possible by considering the multitude of simultaneous interactions among all species present. Feeding relationships have proven to be an essential part to bridge the gap between populations and ecosystems. Early studies of this type involved pyramidal diagrams of feeding levels (trophic levels) in an ecosystem (Fig. 1). Such a diagram begins with photoautotrophs (level 1) such as phytoplankton and higher plants, which live by using inorganic substances and solar energy to synthesize biomass. Photoautotrophs are consumed by herbivores, which are the first level of consumers. Herbivores in turn are consumed by carnivores of the first level, which are consumed by carnivores of the second level. When the organisms are arranged by trophic level, they can be shown as a vertical stack of boxes that comprises a feeding pyramid (or trophic pyramid), or they can be shown in more detail as a diagram with separated compartments connected by lines indicating the feeding pathways (Fig. 2).

Because there are numerous kinds of organisms at any given trophic level, a feeding diagram takes the form of a web, which gives rise to the term "food web". A diagrammatic analysis of a food web may be relatively simple if it aggregates all species into only a few compartments. However, it is typically more realistic to differentiate more precisely between the different properties of the component organisms and explicitly include the subdominant members as well, yielding a higher number of compartments.

A purely qualitative diagram is informative in respect to who eats whom, but a quantification of the amount of energy or materials passing through the food web produces considerably more insight into ecosystem functioning as the quantitative importance of the fluxes varies by orders of magnitude (Fig. 2). Quantitative studies of feeding relationships at the ecosystem level may be referred to as "food-web analysis" or "trophic dynamics."

☆*Change History:* December 2020. U. Gaedke updated entire text and added Fig. 4 for extra explanation.

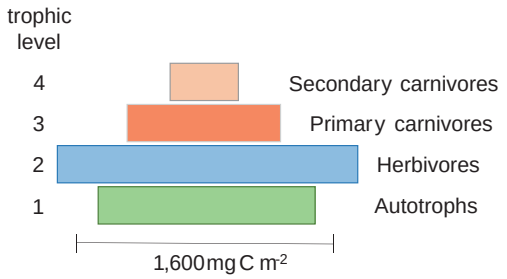

Fig. 1 A pyramid of the annual biomass of organisms arranged by trophic level from the pelagic zone (open water) of Lake Constance, adjacent to Germany, Switzerland, and Austria (grazing chain only). The biomass at the third and at the fourth trophic level, in particular, are reduced by severe fishing pressure (Gaedke et al., 2002).

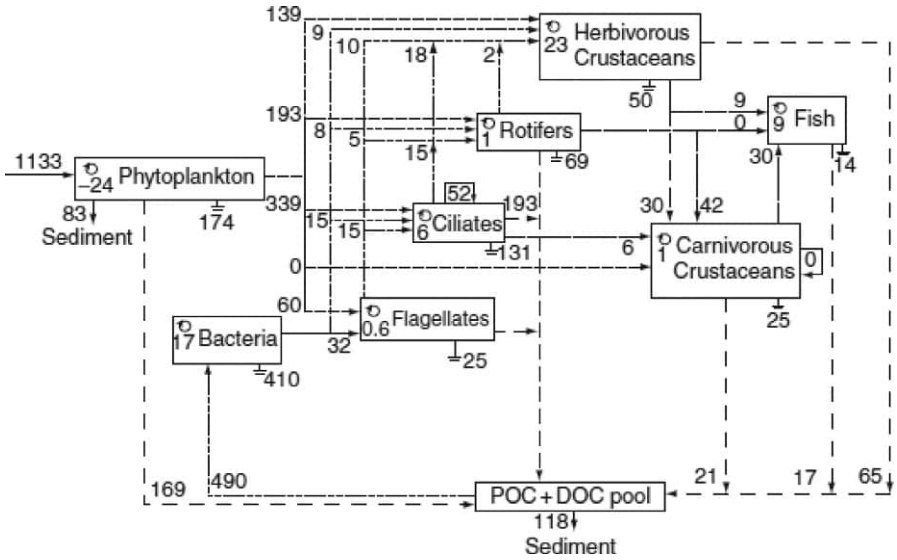

Fig. 2 A modern food-web diagram for the pelagic zone (open water) of Lake Constance. Fluxes are given as mg C m^{-2} d^{-1}. Circles within the compartments symbolize biomass changes during the investigation period and the symbol with two horizontal bars the losses by respiration. Gaedke U, Hochstädter S, and Straile D (2002) Interplay between energy limitation and nutritional deficiency: Empirical data and food web models. *Ecological Monographs* 72: 251–270.

Feeding relationships as portrayed in a food web may be quantified by any of several commodities, according to their relevance to understand the food web dynamics. For example, the amount of biomass passing from the prey to the predators may be quantified in units of fresh weight, dry weight or carbon. The energy equivalent per unit mass is fairly constant among most organism if the biomass is measured in units of carbon (or ash-free dry weight which can typically be converted to carbon by multiplying by 0.5 approximately). Hence, it provides also a quantification of energy flows, which can be connected to the metabolism of the groups of organisms.

It is also possible to study food webs quantitatively in terms of the passage of an element or even a class of compounds through the food web. In addition to carbon, representing a surrogate for food quantity and energy, fluxes are often quantified additionally in units of phosphorus, nitrogen and/or silicate, representing potentially limiting inorganic nutrients for autotrophic and for herbivore growth. Using nutrient fluxes enables studies of the importance of nutrient recycling within food webs. To further account for food quality it is also possible to include the flow of other essential organic substances such as polyunsaturated fatty acids or cholesterol through food webs. Thus, food webs can be quantified in various ways to answer a large variety of questions.

Trophic levels and trophic positions

Modern food-web analysis grew from the concept of the trophic pyramid (Fig. 1), which was used by the British ecologist Charles Elton (1900–91) and other founders of modern ecology to summarize information on the roles of organisms in ecosystems. When based on biomass, such a diagram takes a pyramidal shape for terrestrial environments whereas it resembles more a column for pelagic ecosystems at least for the lower trophic levels. That is, the laws of nature do not require the pyramidal shape, and a higher trophic level may have the same or even more biomass than a lower trophic level adjacent to it (for details see below).

The concept of the trophic pyramid was advanced significantly toward modern food-web analysis by Raymond Lindeman (1915–42) who, working with Evelyn Hutchinson (1903–91), introduced the concept of trophic dynamics. The linkages between trophic levels, when portrayed as energy flows, provide a view of the ecosystem that is linked to the solar energy source and to the metabolism of individual organisms. Furthermore, an analysis of trophic relationships based on energy leads to the calculation of the efficiency to transfer energy from lower to higher trophic levels.

The early concept of trophic levels contained several important flaws, the solution of which has produced a number of innovations. The first and most obvious flaw is that individual organisms often cannot be assigned to a single trophic level. For example, an omnivorous organism, such as a crayfish, is able to derive nourishment from both plant and animal matter, and therefore cannot be assigned either to the level of herbivores or to the level of carnivores. It is especially common for high-level carnivores to feed at multiple lower levels, including herbivores and lesser carnivores, at the same time. But also photoautotrophs, such as pitcher plants and numerous phytoplankter, may supplement their gain of energy and inorganic nutrients by consuming heterotrophic organisms such as insects or bacteria. In the case of phytoplankton, they are called mixotrophs as they combine an autotrophic and heterotrophic life style.

Hence, the modern view is that species must be assigned to fractional trophic levels, called trophic positions that reflect their diet. For example, an omnivore (e.g., a bear or a crayfish) feeding 50% on level 1 (e.g., autotrophs) and 50% on level 2 (e.g., herbivores) would be assigned a trophic position of $2^{*}0.5 + 3^{*}0.5 = 2.5$. Thus, models can take into account proportionate differences in the diet composition.

A second problem arises from organisms that use particulate organic matter (POM, detritus, also designated as particulate organic carbon POC) or dissolved organic matter (DOM; also designated dissolved organic carbon, DOC) as food. Modern food-web analysis views such feeding relationships as a "detrital food chain", which is an important complement to the more traditionally recognized "grazing food chain" that is based exclusively on photoautotrophs passing organic matter to herbivores and subsequently carnivores. The detrital food chain, like the grazer food chain, contains multiple levels (Fig. 3).

Inclusion of the detrital food chain leads to a more realistic view of bacteria in ecosystems. Heterotrophic bacteria are often the direct consumers of detritus (which they dissolve prior to consuming) and dissolved organic matter. Even though they create biomass at the base of the detrital food chain, they cannot do so through use of sunlight, as in the case of production of photoautotrophs, such as algae and vascular plants at the base of the grazing food chain. The realities of the detrital food chain must be incorporated into quantitative models because detritus and dissolved organic matter are abundant in all ecosystems. Detritivores such as bacteria are now commonly assigned to the first trophic level.

The increasingly realistic view of food webs leads away from the traditional pyramid or four-step energy diagram (Fig. 1) and more toward diagrams that show various groups of organisms occupying non-integer positions in the grazing food chain, and connected to the detrital food chain, which incorporates bacteria as first-level producers of biomass (Fig. 2) (Gaedke et al., 2002).

Use of trophic guilds to analyze the trophic structure of food webs

A trophic guild consists of all organisms within a food web that have similar food sources and predators (e.g., the compartments shown in Fig. 2). In most cases, trophic guilds defined in this way would consist of multiple species, all of which would occupy similar positions in the trophic diagram or food-web model. Thus, application of the concept of guilds simplifies analysis and modeling of food webs.

The use of trophic guilds also enables us to handle the complication that species may change their feeding habits during their ontogenetic development. For example, piscivorous fish typically feed on zooplankton when they are small but feed on other fish

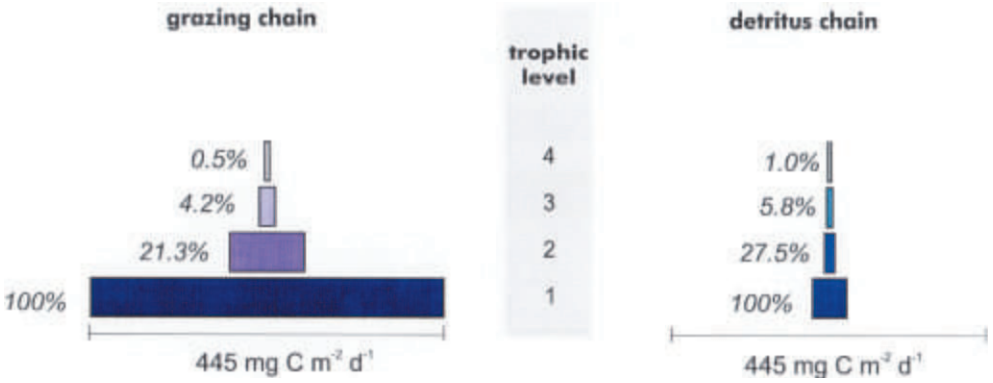

Fig. 3 Trophic pyramids for the grazing chain and the detritus chain of Lake Constance, shown is the daily production averaged across years. That is, values are higher in spring and lower in winter. Gaedke U, Hochstädter S, and Straile D (2002) Interplay between energy limitation and nutritional deficiency: Empirical data and food web models. *Ecological Monographs* 72: 251–270.

when they are large. In such cases, the younger stages of a certain species are assigned to a different guild than the older individuals of the same species.

Fig. 2 shows the structure of a food-web model of the open waters of Lake Constance, which adjoins Germany, Switzerland, and Austria. The model is based on compartments corresponding to guilds of organisms as well as a pool of DOM and POM. Carbon comes into the food web through this DOM and POM pool or through a photosynthetic guild (in this case, phytoplankton) and leaves the food web either as sedimentation of POM to the bottom of the lake or release of CO_2 gas to the water as a by-product of respiration. Circles within each of the compartments indicate biomass changes (in this case expressed as mg C m^{-2} d^{-1}). Arrows passing from one compartment toward another indicate consumption, and arrows passing out of each compartment going to the POC + DOC pool indicate fecal output. Further losses of C and energy occur via respiration. The numbers indicate fluxes (biomass per unit time for a given unit area of the lake, here mg C m^{-2} d^{-1}). Establishing such mass-balanced quantitative food web models demands appropriate computer programs, which assure that the energy entering each compartment via, for example, ingestion equals the sum of all loss factors (e.g., excretion, respiration, predation and changes in biomass).

A quantitative model such as the one shown in Fig. 2 is either an average for a considerable period of time or snapshot of a short period of time (Gaedke et al., 2002). The flow of mass from one compartment to another can be expected to change substantially from season to season and even week to week in a lake. Thus, modeling that encompasses changes occurring over any substantial period of time (e.g., a year) can require a great deal of information. It results in a web that likely never exists at any distinct moment in time. Nevertheless, it is informative by revealing average conditions of the main fluxes that account for ecosystem metabolism and the efficiency of transfer of mass or energy through the food web.

Trophic transfer efficiency

The trophic structure of a food web is affected greatly by loss of energy that occurs when transferring energy from one trophic level to the next. It amounts to at least 70% but is often higher (90% or more, see below) (Fig. 3) (Gaedke and Straile, 1994). The second law of thermodynamics, when applied to trophic transfers, requires that dissipation of energy as heat will be a substantial loss even for the most efficient transfers. For example, the growth efficiency of individual cells seldom exceeds 40%, even when non-metabolic losses are disregarded (Straile, 1997). Ecological factors introduce additional non-metabolic inefficiencies related to non-grazing mortality, export of organic matter from the system (outflow or sedimentation), and excretion/egestion (urine and fecal output, hereafter referred to as excretion). That is, biomass produced at a distinct trophic level is either not consumed but dies prior to consumption and is thus channeled to the detritus chain, or ingested by the next higher trophic level (Fig. 4). The ingested food is either excreted because it cannot be digested, or it is assimilated. The assimilated substances are either used to cover the respiratory needs or converted into new consumer biomass (including somatic growth and reproduction).

Losses by excretion are typically high for organisms feeding on organic sources that are difficult to digest. This is particularly the case for herbivores consuming vascular plant tissue, which is rich in chemically complex substances that are difficult to digest such as lignin.

All organisms must respire in order to live. Respiration involves the release of chemical energy from organic matter. The energy gain is used either for synthesis of new biomass (including somatic growth and reproduction), or to maintain the integrity of basic metabolic functions that sustain life. This basal respiration is relatively low for unicellulars and invertebrates, increases for ectothermal vertebrates such as fish, amphibians and reptiles, and is very high for endotherms like birds and mammals.

A further loss factor is non-grazing mortality, which can occur when organisms are exposed to lethal physical or chemical conditions, physiological death related to age, or inadequate nutrition. It diverts biomass and energy from the transfer process that

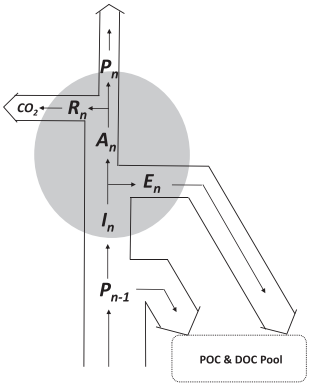

Fig. 4 Bioass produced at the trophic level n–1, P_{n-1}, either dies prior to consumption and fuels the pool of dead particulate or dissolved organic carbon (POC and DOC), or it is ingested by the next trophic level, I_n, i.e., it is taken up by a consumer, here symbolized by the shaded circle. The ingested food is either excreted, E_n and channeled to the POC + DOC pool, or assimilated, A_n. An often substantial fraction of A_n is respired, R_n, and the remaining part can be used for new production, P_n.

connects one trophic level to the next. Both, non-grazing mortality and excretion pass energy and mass to the POC + DOC pool and thus the detrital food chain (Fig. 4).

The various modes by which energy and mass can be lost are the basis for quantifying several kinds of ecological efficiencies that are used in food-web analysis. The ratio of biomass production to biomass ingested, P_n/I_n, as food is symbolized by $K1$, the gross growth efficiency (which corresponds to the trophic transfer efficiency discussed earlier if all prey production is consumed). $K1$ rarely exceeds 0.30 under natural conditions, and often is considerably lower. The net growth efficiency of an organism ($K2$) is defined as the ratio of new biomass produced to the amount of biomass that is assimilated (i.e., passing through the gut wall into the body of the organism), P_n/A_n. This efficiency has a maximum value of ca. 50% for small organisms but is much lower for large organisms (e.g., fish or mammals) (Straile, 1997). Finally, the consumption efficiency represents the ratio between the amount of matter and energy ingested by the upper trophic level divided by the total production at the next lower level, I_n/P_{n-1}. Thus, it accounts for the non-grazing mortality. This efficiency is low if the material produced is hard to ingest or digest (e.g., wood) or if there are few consumers which can exploit the prey production at that time and location. This may be because the consumer level is itself strongly depressed by its predators, or because the prey grows much faster than the consumers and can build up high biomasses before predator abundances increase. This happens for example during the phytoplankton spring bloom.

Finally, the trophic transfer efficiency is the ratio of biomass production at one trophic level to the biomass production of the next lower level, P_n/P_{n-1}. Thus, it is the product of the consumption efficiency and the gross growth efficiency. In plankton food webs, trophic transfer efficiencies may be high (0.15–0.30) (Fig. 3) when compared with webs dominated by a transfer from vascular plants to herbivores or strongly involving birds or mammals. Temporal variability of the trophic transfer efficiency is high, even within a given ecosystem, because of the instability of the numerous factors that can affect it. For example, the trophic transfer efficiency is strongly reduced when inedible algae (such as cyanobacteria) dominate or when animals with high respiratory needs (such as vertebrates and especially birds and mammals) prevail.

Food quality and quantity

Heterotrophs (consumers, including bacteria) live by consumption of biomass or nonliving organic matter. Due to the chemical composition of biomass (disregarding skeletal material or support structures) across all heterotrophs falls within a relatively narrow range, carnivores that feed on other heterotrophs are assimilating approximately the same mixture of elements that they will need in order to synthesize their own biomass (skeletal material and support structure typically pass through the gut unassimilated). Hence, their food quality is high. Detritivores also benefit from this carryover of elemental mixtures from one kind of organism to another, although detritus is more likely to show some selective loss of elements such as nutrients that would alter the balance typical of living biomass.

Unlike heterotrophs, photoautotrophs assimilate elements separately from water or, if they are rooted vascular plants, from sediments. For example, carbon is derived from H_2CO_3 and related inorganic carbon forms dissolved in water, and phosphorus is taken up separately as phosphoric acid that is dissolved in water. Large imbalances may develop when some essential components are much more abundant than others because the inorganic substances required to synthesize biomass are taken up separately. For example, phytoplankton has a high carbon:nutrient ratio under nutrient-depleted conditions. Thus, autotrophs face greater challenges than carnivores in assembling the necessary ratios of elements to synthesize biomass, but also herbivores (and bacteria) can experience imbalances of elements.

The approximate ratios of elements that are characteristic of autotrophic biomass have been extensively studied. Characteristic ratios of carbon to nitrogen and phosphorus are often the greatest focus of analysis. Because carbon is the feedstock for photosynthesis and phosphorus and nitrogen are the two additional elements that are often in short supply for conversion of photosynthetic products (carbohydrates) to other molecule types that are needed for the synthesis of protoplasm (e.g., amino acids which are rich in N, or RNA which is rich in P). The importance of C:N:P ratios in aquatic organisms was first brought out by Alfred Redfield (1890–1983), who discovered that healthy oceanic phytoplankton show a characteristic molar C:N:P ratio of about 106:16:1. Thus, the nutrient status of a phytoplankton community can be judged to some degree from the elemental ratios. For example, a phytoplankton community suffering phosphorus deficiency may show a C:P ratio of 500:1 rather than 106:1, as predicted by the Redfield Ratio for well-nourished phytoplankton. The analysis of elemental ratios for diagnosis of elemental imbalances is termed “ecological stoichiometry” (Sterner and Elser, 2002).

Imbalances in elemental ratios in one trophic level can create imbalances in the diet and thus an inefficient transfer of energy to the next trophic level. This is particularly true between primary producers and herbivores. For example, plants suffering phosphorus scarcity may pass biomass with a high C:P ratio to their grazers. The grazers must then consume extra food in order to obtain the correct balance for the synthesis of their own biomass because of an imbalance of elements in the food. Similarly, an especially low C:P ratio (e.g., 50:1) will provide an oversupply of phosphorus (e.g., when bacteria are consumed), a large part of which is released to the environment without generating any biomass.

Another strategy that herbivores may employ in improving the elemental balance of food intake is to consume heterotrophs in addition to autotrophs (omnivory, which is feeding at multiple trophic levels) as animals and bacteria are generally more nutrient rich than autotrophs. Thus, combining the consumption of a phosphorus-rich food (high quality) with a carbon-rich food (often available in high quantity, e.g., grass), enables a more efficient use of ingested mass than a single food type.

Trophic structure of food webs in open water, near shore and wetlands

In the open water of a lake or the ocean at some distance from the shore (i.e., in the pelagic zone), the dominant autotrophs are phytoplankton, which live as individual cells or colonies of small cells suspended in the water. Some groups of phytoplankton (e.g., filamentous cyanobacteria) are rejected by most grazers because they are difficult to ingest or digest due to their toxicity. Algae of low palatability may become quite abundant when grazing pressure is high under highly eutrophic conditions. Overall, however, phytoplankton often is composed of a high proportion of edible and digestible species. Thus, a large proportion enters the grazing chain. Rooted vascular plants, which can only grow in shallow waters, offer a less useful food supply because the digestible component of their biomass is embedded in complex carbohydrates that maintain the shape of the plant. This is particularly valid for emergent growth forms like reed. For this reason, much of their biomass that develops during a growing season dies and decomposes rather than being eaten while alive. The detrital food chain benefits from the biomass that was left uneaten by the grazer food chain. This pattern strongly resembles terrestrial ecosystems.

Macrophytes may account for most of the autotroph biomass in a littoral zone, but attached algae colonize macrophytes and all other surfaces that are illuminated. Given their high food quality, edibility and growth rate, these attached autotrophs (periphyton) are an important food for herbivores in the littoral zone despite their low biomass compared to the macrophytes.

The trophic structure in the pelagic zone often is dominated by four significant trophic levels (or even more in the ocean) (Andersen et al., 2016). The top predator guild, which may consist of multiple fish species, is not exposed to substantial predation pressure because of its size and mobility. It therefore builds up biomass until it is limited by scarcity of appropriate food. This type of limitation is called a "bottom up" limitation because the trophic level below is restricting the increase in biomass of the trophic level above. The prey of the top predator, in turn, is controlled from the top down. "Top down" control in this situation involves suppression of the biomass of the trophic level that serves as food for a bottom-up controlled level which heavily exploits its food sources. Thus, top-down and bottom-up control alternate along a food chain.

In a four-level food web, the third level consists of first level carnivores. When top predators are abundant, these intermediate predators (e.g., fish that eat herbivorous zooplankton) are suppressed, which relieves predation pressure on herbivores. Therefore, herbivores may become abundant and increase in biomass. This, in turn, will impose a strong grazing pressure on autotrophs like phytoplankton, which can cause a decline in their biomass, yielding a higher water transparency. Thus, water clarity may be enhanced by stocking large predatory fish. This technique is called biomanipulation. However, its success is often limited due to the usually web-like structure of pelagic food webs.

Physical factors may affect the structure of food webs as well. For example, the absence of any solid attachment points in the pelagic zone requires that all autotrophs are small. This is partly because large cells have a lower surface-to-volume ratio making them less competitive than small cells in taking up nutrients from the water. In addition, large cells may sink faster out of the illuminated surface layer. Thus, the pelagic food web must be based on herbivores capable of harvesting large numbers of small autotrophs. The grazers that can do this work have to be small, which implies that generally only small carnivores can efficiently exploit the (small) herbivores (unless they are, for example, very efficient filter feeders that can rely on spatial subsidy effects like some whales). This leaves the opportunity for a top carnivore level that feeds on the small carnivores but cannot use the herbivores efficiently as they are too small compared to its own body size. Thus, the food chain cannot be shortened by having the top predator feeding directly on the more abundant herbivores. Hence, we find a distinct relationship between trophic position and body size in pelagic ecosystems (Gaedke and Kamjunke, 2006; Andersen et al., 2016). This stands in contrast to terrestrial systems where autotrophs, herbivores and carnivores of almost every size occur and the food chains often comprise only three significant trophic levels as the top predator can hunt large herbivores. This shortens the food chain.

Food webs of the littoral zone in lakes are more similar to those of terrestrial environments or wetlands than to those of pelagic food webs if their production is dominated by vascular plants. Under these conditions often tall plants can attain more light and are thus more competitive. Grazers (herbivores) may then have a larger body size because larger plants are available. Thus, top carnivores may feed directly on herbivores rather than on intermediate carnivores and body size and trophic level are not as strongly correlated as in pelagic food webs. In this case, the herbivores come under top-down control, and the efficiency of energy transfer from plants to herbivores is reduced because there are not enough herbivores to consume the total plant production. Thus, the length of the food chain influences the amount of biomass present at each trophic level (Oksanen et al., 1981), often referred to as the trophic cascade (Carpenter et al., 1985).

The fact that in pelagic ecosystems all autotrophs are small and that the following trophic levels are increasingly larger in body size explains why we find a biomass column rather than a biomass pyramid in pelagic systems (cf. Fig. 1 and Gaedke, 1992). The weight-specific metabolic activity declines with increasing size, e.g., a kilogram of mice is metabolically more active than a kilogram of elephants. This so-called allometric relationship holds for all organisms and implies that small organisms consume and produce more per unit biomass than larger ones.

Hence, even with similar biomasses at each trophic level the autotroph production exceeds that of the herbivores which, in turn, is higher than that of the carnivores. Obviously, a lower production implies that also the food demands are lower at higher trophic levels. In other words, a certain biomass of autotrophs (herbivores) can sustain a similar biomass of herbivores (carnivores) because the losses occurring at each trophic transfer may be compensated by the higher weight-specific production of lower trophic levels comprising smaller organisms (Gaedke, 1992). This holds in particular if the non-grazing mortality is low and unicellular organisms or invertebrates dominate, having a high growth efficiency due to relatively low respiratory needs. Both conditions are typically fulfilled in unpolluted pelagic systems but not in terrestrial ones where often a large proportion of the primary production

is not consumed by herbivores. In contrast to pelagic systems, these herbivores may be birds or mammals which build up relative little biomass compared to their food intake given their high respiratory needs. However, in every ecosystem there is always a pyramid for the production as a substantial amount of energy is lost during each trophic transfer due to losses by non-grazing mortality, excretion and respiration (Fig. 3).

Transfer efficiency along the size gradient in pelagic food webs

In pelagic food webs, all autotrophs are small and predators exceed the size of their prey. Thus, matter and energy flow from small to progressively larger organisms. The entire food web's transfer efficiency along the size gradient of organisms reflects each of the trophic linkages and the number of trophic levels in the web (Gaedke et al., 1996). For example, the efficiency of fish production in oligotrophic lakes is lower than in eutrophic lakes when expressed as a proportion of the total amount of photosynthesis.

In oligotrophic lakes, food is more strongly dispersed, and has to be gathered by consumers that search for their prey and handle it individually. Consumers that locate their prey by searching usually are closer in size to their prey than filter-feeding consumers that can take up a large number of particles simultaneously. This feeding mode is successful under eutrophic conditions where prey densities are higher. When consumers are very close in size to their food source, the transfer of energy and materials along the size gradient up to large fish is less efficient because it requires more trophic transfers to reach a given size. Thus, there is a theoretical explanation for the lower transfer efficiency along the size gradient in oligotrophic lakes. This is an example of the use of food-web analysis to explain observations about productivity and efficiency in pelagic ecosystems.

Conclusion

Quantitative studies of food webs greatly magnify the value of information on individual populations. Analysis of linkages in the food web provide explanations for the efficiency of energy or mass transfer to various points in the food web and the controlling influences that either enhance or suppress production at a given trophic level. Thus, quantitative food-web studies support the understanding of mechanisms that govern the functioning of ecosystems.

See Also: Fundamental concepts and theories: Nutrient Stoichiometry in Aquatic Ecosystems; Human pressures and management of Inland Waters: Agricultural Pressures on Inland Waters; Structures and functions of Inland Waters - Groundwater: Biogeochemical Cycling of Carbon and Nitrogen in Groundwater—Key Processes and Microbial Drivers; Trophic Interactions in Subterranean Environments; Structures and functions of Inland Waters - Lakes: Lake Food Webs; Phytoplankton Growth and Nutrients; Phytoplankton Productivity; Structures and functions of Inland Waters - Rivers: High Latitude Rivers: Ecosystems Shaped by Environmental Extremes; Intermittent Rivers and Ephemeral Streams; Structures and functions of Inland Waters - Wetlands: Wetlands Under Global Change

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Lakes as Ecosystems☆

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This is an update of W.M. Lewis, Lakes as Ecosystems☒, Reference Module in Earth Systems and Environmental Sciences, Elsevier, 2014, ISBN 9780124095489, https://doi.org/10.1016/B978-0-12-409548-9.09055-2.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Biogeochemistry Scientific study of the mass flux of any element, compound, or group of compounds within or across the boundaries of an ecosystem or any other spatial component of the environment. Mass flux within an ecosystem is often designated as nutrient cycling or element cycling.
Cycling A biogeochemical term referring to the movement of elements or compounds within an ecosystem or any other bounded environmental system.
Ecosystem Any portion of the earth's surface that shows strong and constant interaction among its resident organisms and between those organisms and the abiotic environment.
Lake trophic state Fertility of a lake, as measured either by its concentrations of key plant nutrients (especially phosphorus and nitrogen) or the annual production of plant biomass (aquatic vascular plants and algae). Trophic-state categories include oligotrophic (weakly nourished), mesotrophic (nutrition of intermediate status), and eutrophic (richly nourished).
Mass flux Movement of mass per unit time, often in ecosystem studies expressed as mass per area per time.
Stable isotope Any isotope of an element that does not decay spontaneously.
Trophic dynamics Fluxes of energy or mass caused by feeding relationships, including rates of grazing by herbivores on plant matter, rates of predation by carnivores on other animals, or rates of decomposition of organic matter by microbes.

Introduction of the ecosystem concept

Scientific studies of lakes began as early as the seventeenth century, but at first were descriptive rather than analytical. Toward the end of the nineteenth century, measurements and observations on lakes became more directed. For example, the thermal layering of lakes was attributed to specific physical causes, and such phenomena as the movement of plankton in the water column were the subject of hypotheses that were tested with specific kinds of data (Kalff, 2002).

Comprehensive studies of lakes began with the work of Alphonse Forel (1841–1912) on Lac Léman (Lake Geneva), Switzerland, as well as other Swiss lakes. In a three-volume monograph (*Le Léman*: 1892, 1895, 1904), Forel presented data on a wide variety of subjects including sediments and bottom-dwelling organisms, fishes and fisheries, bacteria, water movement, transparency and color, temperature, and others. Thus Forel, who introduced the term 'limnology' (originally the study of lakes, but later expanded to include other inland waters), demonstrated the holistic approach for understanding a lake as an environmental entity, but without application of an explicit ecosystem concept (Vincent and Bertola, 2012).

The conceptual basis for studying lakes as ecosystems was first clearly given by Stephen Forbes (1844–1930; Fig. 1) through a short essay, *The Lake as a Microcosm* (1887). Forbes was professor of biology at the University of Illinois in Champaign, IL, USA, and director of the Illinois Natural History Laboratory (subsequently the Illinois Natural History Survey), which was charged with describing and analyzing the flora and fauna of Illinois. Forbes realized that it was not possible to achieve a full understanding of a lake or, by implication, of any other environmental system such as a stream or forest, simply from knowledge of the resident species. Forbes proposed that the species in a particular environment, when interacting with each other and with the nonliving components of the environment, show collective (system) properties. The microcosm that Forbes described today would be called an ecosystem,

☆*Change History:* July 2021. WM Lewis updated synopsis for clarity, added new paragraph and Table 1 in Introduction, edited Metabolism in Lakes section for clarity, edited Community Organization section for clarity, and added a new reference.

Fig. 1 Stephen A. Forbes. Reproduced from the Illinois Natural History Survey website, with permission from the Illinois Natural History Survey.

although this term did not come into use until 48 years later through the work of the British botanist A. G. Tansley. By current usage, an ecosystem is any portion of the Earth's surface that shows strong and constant interactions among its resident organisms and between these organisms and the abiotic environment (Golley, 1993).

Forbes not only described accurately the modern ecosystem concept, but also identified ways in which critical properties of ecosystems could be measured and analyzed (Table 1). In contrast to his fellow natural historians and ecologists, he was numerically oriented in that he emphasized the quantitative measurement of abundance and comparative abundance for species in an ecosystem or across ecosystems. He also recognized that ecosystem science best reveals the interface between human actions and the natural function of ecosystems; he characterized adverse human effects on ecosystems as comparable to the effects of disease on humans. He was probably the first ecologist to make specific use of statistics in testing ideas about relationships between different kinds of organisms. Overall, Forbes brought extraordinary intellectual vitality to the new science of ecology.

Although the essay by Forbes now is considered a classic in limnology and in ecology generally, it caused no immediate change in the practices of limnologists or ecologists. Like many important discoveries in science, it was a seed that required considerable time to germinate.

In studies of Cedar Bog Lake, Minnesota, for his Ph.D. at the University of Minnesota, Raymond Lindeman (1915–1942; Fig. 2) gave limnologists the clearest early modern example of the study of lakes as ecosystems. Rather than focusing on a particular type of organism or group of organisms, which would have been quite typical for his era, Lindeman decided that he would attempt to analyze all of the feeding relationships ('trophic' relationships) among organisms in Cedar Bog Lake. Thus, his Ph.D. work extended from algae and aquatic vascular plants to herbivorous invertebrates, and then to carnivores, and conceptually even to bacteria,

Table 1 Examples of innovative concepts that Forbes brought to ecology and limnology.

Concept	*Implication or outcome*
A key unit of nature is the ecosystem	Ecology requires the study of ecosystems
Ecosystems are integrated and self-regulated	Ecosystems show the balance of nature
Humans damage ecosystem functions	Ecosystem science has applications
Quantitative study of nature is essential	Descriptive or lab studies are insufficient
Statistics can be used in studying interactions	Ecosystem science needs quantitative tools
Competition takes several forms	Interactions require careful analysis
River ecology is important	Established first river lab (Illinois River)

Fig. 2 R. L. Lindeman and his famous study site, Cedar Bog Lake, MN. Reproduced from People of Cedar Creek website, with permission from Cedar Creek Natural History Area.

although there were no methods for quantifying bacterial abundance accurately at that time. Lindeman's descriptions of feeding relationships were voluminous but straightforward to write up and publish, but he sought some more general conclusions for which he needed a new concept.

Lindeman took a postdoctoral position with G. Evelyn Hutchinson at Yale University in 1942. Hutchinson had become a limnologist of note through his quantitatively oriented studies of plankton and biogeochemical processes in the small kettle lakes near New Haven. He would in subsequent decades become the world's most influential limnologist, and part of his reputation grew out of his contributions to the field of biogeochemistry, an important tool of ecosystem science (Sterner, 2012).

Hutchinson encouraged Lindeman's work on a groundbreaking paper, *The Trophic Dynamic Aspect of Ecology* (1942, published in the journal *Ecology*), which now is recognized as a landmark in limnology and in ecology generally. Lindeman proposed a way of converting the tremendous mass of highly specific information for Cedar Bog Lake into a format that would allow comparisons with any other lake or even with other kinds of ecosystems. Building on the work of the German limnologist August Thienemann and the British ecologist Charles Elton, Lindeman organized the feeding relationships as a feeding hierarchy within which each kind of organism was assigned to a specific feeding level (trophic level). He then proposed that the feeding relationship represented by any given link in the food web be quantified as an energy flow. Thus, the total energy flow from level 1 (plants) to level 2 (herbivores) could be quantified as the summation of energy flows between all pairs of plants and herbivores; a similar estimate could be made for all other adjacent pairs of trophic levels. In this way, the flow of energy across the levels of the food web could be expressed in quantitative terms.

The first important conclusion from Lindeman's energy-based approach was that each transfer of energy between trophic levels is governed by the second law of thermodynamics, which requires that significant energy loss must occur each time energy is transferred. Thus, Lindeman demonstrated why food webs have relatively few trophic levels: progressive dissipation of energy as it passes through the food web from the bottom (plants) to the upper levels (upper-level carnivores) ultimately provides insufficient energy for expansion of the food web to further levels. Also, analysis of a food web in this way sets the stage for calculating efficiencies of energy transfer, comparison of efficiencies across different ecosystem types, and the identification and analysis of bottlenecks restricting the flow of energy within the food web.

The contributions of G. Evelyn Hutchinson in the 1940s on the biogeochemistry of carbon in lakes also must be counted as landmarks in the development of ecosystem science. Even so, ecosystem science was scarcely represented in the research agenda of ecologists or in the academic curriculum as late as 1950. Penetration of ecosystem thinking into research, teaching, and public awareness occurred first through the publication of a textbook, *Fundamentals of Ecology* (1953), written by Eugene P. Odum, and especially through the second edition of the same book (1959), written by E. P. Odum and Howard T. Odum. The Odums visualized ecology as best viewed from the top down, with ecosystems as a point of departure and studies of ecosystem components as infrastructure for the understanding of ecosystems.

The ecosystem perspective has not displaced the more specialized branches of ecology that deal with particular kinds of organisms or specific kinds of physical phenomena, such as studies of water movement, optics, or heat exchange. Rather, ecosystem science has had a unifying effect on studies of ecosystem components (Fig. 3). Study of a specific ecosystem component produces not only a better understanding of that component, but also a better understanding of the ecosystem, which is a final objective for the science of an ecosystem type, such as lakes.

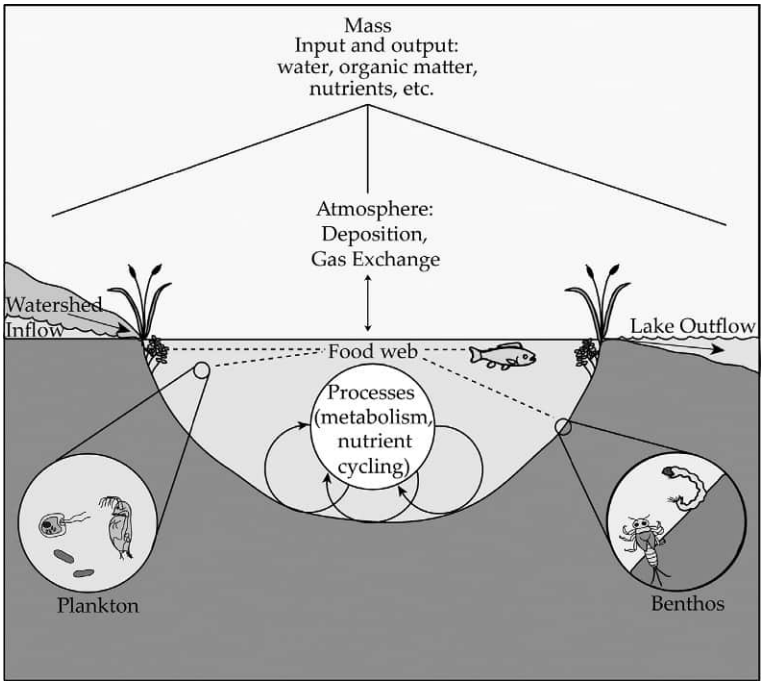

Fig. 3 Ecosystem diagram of a lake.

Metabolism in lakes

The dominant anabolic component of metabolism in lakes is photosynthesis based on carbon dioxide and water plus solar irradiance as an energy source. The dominant catabolic component is aerobic respiration based on the oxidation of organic matter with oxygen as an electron acceptor. Conversion of solar energy to stored chemical energy in the form of biomass seldom reaches 1% efficiency in lakes because of losses inherent in the wavelengths that can be intercepted by photosynthetic pigments, inefficiency in the interception process, and thermodynamic losses in the conversions leading to the production of biomass. Respiration also involves thermodynamic losses. Therefore, the solar energy source greatly exceeds photosynthetic output, and cellular capture of the energy released from organic matter by respiration greatly exceeds the energy stored in the organic matter. Aerobic photosynthesis is characteristic of the aquatic vascular plants, attached algae, and phytoplankton of lakes and occurs wherever light and oxygen are present. Aerobic respiration is characteristic of aerobic autotrophs as well as invertebrate and vertebrate consumers and bacteria; it occurs wherever oxygen is present (Table 2). Other categories of metabolism occur under either of two more restrictive conditions: (1) where light penetrates into an anaerobic zone, and (2) where there is an interface or mixing between oxidizing and reducing conditions, as is common near a sediment–water interface or between water layers of differing oxidation states.

A study of whole-ecosystem metabolism would require consideration of all of the metabolic categories listed in Table 2. The dominance of aerobic photosynthesis and aerobic respiration, however, often allows ecosystem studies to focus on these two metabolic components. In open water, photosynthesis and respiration are often measured with a vertical series of paired transparent and darkened incubation bottles filled with lake water; rate of decline of oxygen in the dark bottles indicates respiration rate, and rate increase of oxygen in the transparent bottles indicates net photosynthesis. In unproductive lakes, uptake of ^{14}C-labeled CO_2 can be used as an even more sensitive indicator of photosynthesis. Where macrophytes or attached algae are important, as is often the

Table 2 Summary of metabolic processes in lake ecosystems (note that aerobic respiration extends to animal consumer respiration in addition).

Metabolic process	*Energy source*	*Capabilities*			*Occurrence conditions in lakes*
		Eukaryotic plants	*Cyanobacteria*	*Other bacteria*	
Aerobic photosynthesis	Solar	Yes	Yes	No	Universal, photic, oxic
Anaerobic photosynthesis	Solar	No	No	Specialists	Occasional, photic, anoxic
Aerobic chemosynthesis	Inorganic oxidation	No	No	Specialists	Common, oxic/anoxic interfaces
Aerobic respiration	Organic oxidation	Yes	Yes	Yes	Universal, oxic
Anaerobic respiration	Inorganic or organic reduction	No	No	Yes	Common, oxic/anoxic interfaces

case in small lakes, separate measurements must be made of their photosynthesis, typically by the use of enclosures. The metabolic rates of microbes in deepwater sediments can be inferred from the rate of oxygen loss from the hypolimnion of a stratified lake, or can be measured with enclosures.

Annual rate of photosynthesis and respiration per unit area (typically given as mg C m^{-2} $year^{-1}$) is the most commonly used metabolic statistic for lakes. A complete metabolic accounting would also include processing of organic matter entering a lake from the surrounding terrestrial environment, primarily through stream flow and groundwater inflow.

Total annual net production of autotrophs (production in excess of respiration) is a measure of the capacity for a lake to generate biomass at higher trophic levels (Fig. 4).

Also, the time-course of production, which shows seasonal and nonseasonal variation, is often a useful point of departure for the analysis of mechanisms that control biotic functions in a lake. Factors that may suppress production include deep mixing of the water column, exhaustion of key nutrients, grazing, and hydraulic removal of biomass. Photosynthesis and respiration often respond differently to a specific physical or chemical change.

Food-web analysis

Modern food-web analysis follows the example given by Lindeman. The sophistication of the analysis is much greater today than it was in 1942, however, and the methods of food-web analysis have diversified as well (Belgrano et al., 2006; Carpenter, 2003).

At the base of the food web is organic matter generated within a lake or coming to a lake from its watershed and atmosphere above (Fig. 5). All of these sources of organic matter can be quantified, as explained in the preceding section, but require the application of several methods and must take into account both spatial and temporal variability in the synthesis or transport of organic matter.

Quantification of linkages in the food web begins with feeding relationships between autotrophs (primary producers) and herbivores (primary consumers). Analysis of gut contents is one method for establishing the linkage between a specific kind of consumer and one or more plant foods. A linkage measured in this way has two disadvantages, however: (1) it is not quantitative because consumed food items often cannot be identified fully, and (2) it is subject to errors of interpretation caused by the ingestion of foods that are not assimilated or only partially assimilated through the gut wall of a consumer. The first problem can be overcome either by the use of feeding experiments or by the quantification of growth rate of the consumer, supported by empirically-based knowledge of growth efficiency of the consumer. The second problem can be resolved by experimental use of tissue labels (typically radioisotopes) or, more efficiently, by the use of stable isotopes as passive tracers (i.e., relying on the natural abundance of stable isotopes to infer food sources). For example, because primary producers of different categories may differ substantially in their

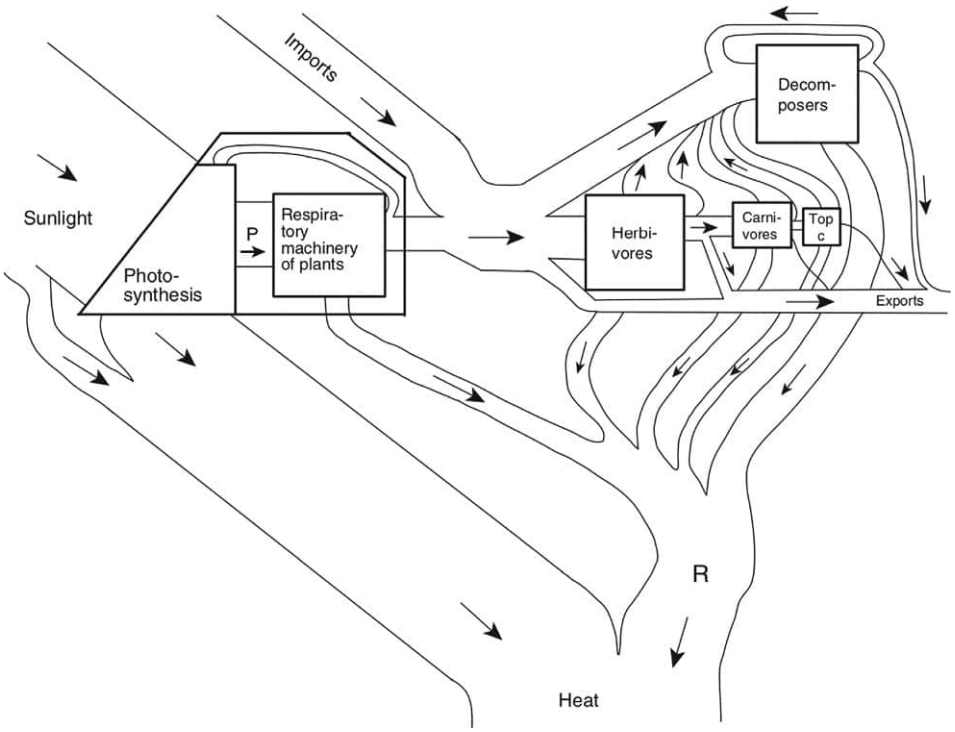

Fig. 4 Example of an early metabolic (energy-flow) diagram for an aquatic ecosystem. Reproduced from Odum HT (1956) *Limnology and Oceanography* 1: 102–118, with permission from the Association for the Sciences of Limnology and Oceanography (ASLO).

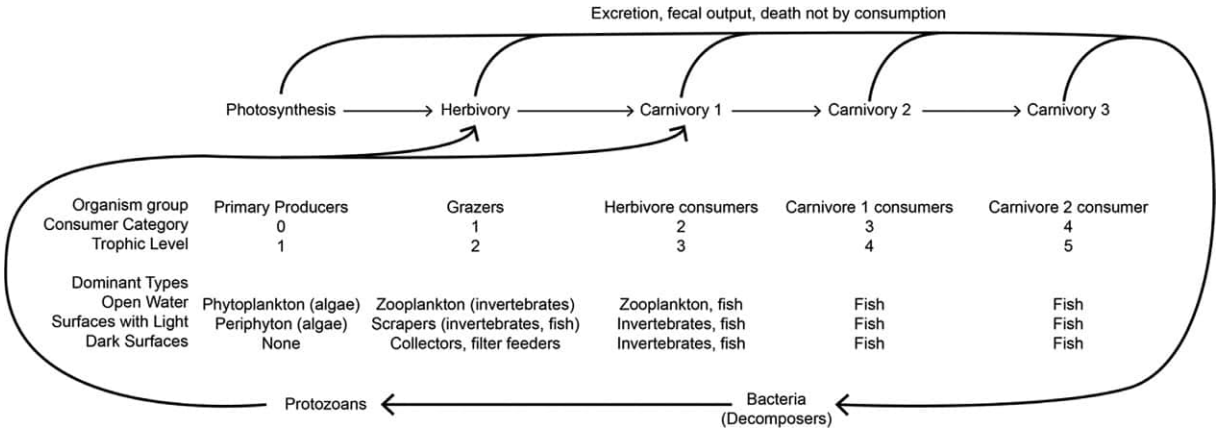

Fig. 5 Ecosystem foodweb components shown as flow of energy or biomass. Bacteria and protozoans, shown at the bottom of the figure, are abundant in all ecosystem components (open water, surfaces with light, dark surfaces, anaerobic synthesis omitted). Source: WM Lewis and JL Roberson, with permission.

concentration of the stable carbon isotope ^{13}C, analysis of ^{13}C content of protoplasm from a consumer may allow a quantitative estimation of the relative importance of several possible foods contributing to the synthesis of biomass by the consumer.

Above the level of primary consumers (herbivores) are carnivores that consume herbivores or other carnivores (third and fourth level consumers). Measurements of growth rate, along with gut-content analysis and use of passive or active tracers, can be applied to carnivores just as they are to herbivores. Within the carnivore trophic levels, however, the assignment of consumers to a specific trophic level may be difficult because carnivores often consume foods belonging to more than one trophic level. The stable nitrogen isotope ^{15}N is useful in assigning a species to a fractional position on the food web because ^{15}N shows increasing tissue enrichment from one trophic level to the next.

When completed, a food-web analysis shows the efficiency of energy transfer from one level to the next. Because of the thermodynamic limits on efficiency and inefficiency in capture and assimilation of food, a food-web analysis based on energy shows whether particular linkages are unusually weak or strong. Such observations in turn lead to hypotheses about mechanisms of control for energy transfer within the food web. For example, modern ecosystem theory includes the concept of 'trophic cascades' involving 'top-down' and 'bottom-up' effects on trophic dynamics, which is easily applicable to lakes. Change in one trophic level may be visible in other trophic levels, in the form of a cascade (Fig. 6). Top-down effects pass from any trophic level to the next trophic level below. For example, an unusual abundance of algal biomass in a lake could be traced to unusually efficient removal of herbivores through predation at such a rate as to leave algae mostly uneaten (a top-down effect).

Similarly, bottom-up control passes from any trophic level to the next level above. For example, the inability of an oligotrophic (nutrient-poor) lake to grow substantial amounts of algal biomass (phytoplankton) exerts a bottom-up effect on all higher trophic levels by restricting the amount of energy that is available at the base of the food chain.

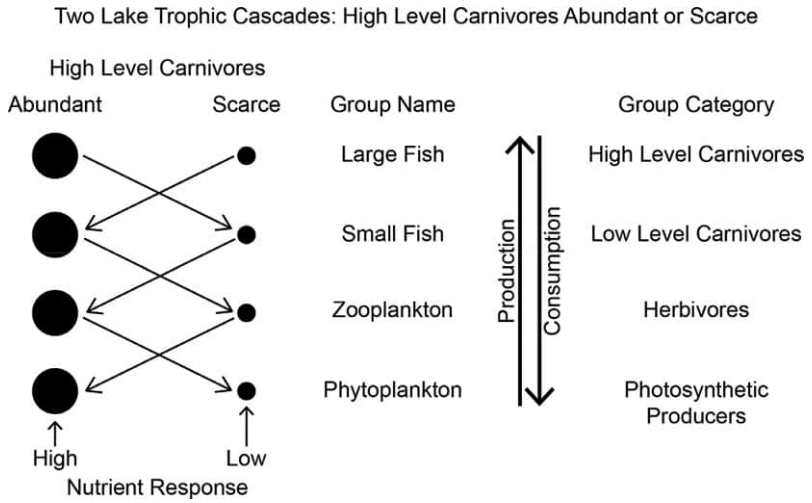

Fig. 6 Lakes with abundant large fish suppress (eat) populations of small fish, which then fail to remove zooplankton herbivores effectively; the abundant herbivores then suppress phytoplankton, even if stimulating nutrients are added; this is a trophic cascade. Where large fish are scarce, the cascade is reversed. Source: WM Lewis and JL Roberson, with permission.

Trophic-dynamic analysis also leads to other fundamental questions involving the structure of biotic communities. For example, food webs might or might not be more productive or more efficient with a high diversity of herbivores than with strong dominance from a very successful, specific type of herbivore. Such questions bear not only on the analysis of natural ecosystems, but also on ecosystem management.

Biogeochemistry

Many of the functional attributes of lake ecosystems can be analyzed through biogeochemical studies. While metabolism and trophic dynamics are viewed in terms of energy flux, biogeochemistry typically is viewed in terms of mass flux. As with energy analysis, the foundation is basic physics: mass is neither created nor destroyed under conditions that are compatible with the presence of life. The conservation of mass leads to the mass-balance equation, which can be given as follows for an ecosystem: $O = I + \Delta S$ where I is input of mass of a particular type (carbon or phosphorus, for example), O is output of mass, and ΔS is change in storage of mass. Input and output pathways for lakes are either hydrologic (flow) or atmospheric (deposition or gas exchange).

Over the short term, change in storage may involve changes in concentration of mass in the water column, but over the long term, change in storage mostly reflects accumulation of mass in sediments. Any element can be a target for biogeochemical studies, but the most frequently studied biogeochemical processes in aquatic ecosystems involve carbon, phosphorus, and nitrogen.

The mass-balance equation applies not only to the entire ecosystem, but also to compartments within the ecosystem (Fig. 7).

For example, carbon in the water column could be partitioned into compartments, each of which would have its own mass-balance equation. Some of these compartments would have a high turnover rate, while others would not. The dynamics of compartments explain restrictions on specific biological processes such as photosynthesis, and account for differences in individual lakes or categories of lakes, such as those that differ greatly in nutrient supply.

Studies of the carbon cycle are ideal complements to studies of lake metabolism and food webs. CO_2, which is the feedstock for photosynthesis, enters aquatic autotrophs from either free CO_2 ($CO_2 + H_2CO_3$) or bicarbonate (HCO_3^-). CO_2 is converted to organic matter by the reduction process of photosynthesis. Either within an autotroph or through consumption of autotroph or other biomass by consumers or decomposers, reduced carbon is reconverted to its oxidized form as CO_2 through aerobic respiration.

Organic carbon resides not only within organisms, but also in water or sediments in dissolved or nonliving particulate form. Dissolved organic carbon derives from the watershed, atmosphere, or organisms within the lake. Watershed contributions to dissolved organic carbon in lakes are composed to a large extent of humic and fulvic acids, which are the byproduct of the degradation of organic matter within soils. Humic and fulvic acids are refractory (resistant to breakdown), although they are slowly decomposed by microbes and can be broken down by ultraviolet light in a water column. Humic and fulvic acids are generally present in concentrations of 1–10 mg l^{-1} in lakes and, when present at concentrations above 5 mg l^{-1}, generally impart a brown or orange color to the water.

Organic compounds that are released to the water column of lakes by the resident organisms vary greatly in composition. All soluble organic compounds present in organisms can be found in the water column at measurable concentrations. Thus, a careful analysis of lake water would show a wide variety of amino acids, carbohydrates of varying complexity, and other metabolites of organisms. These compounds enter the water column through leakage (excretion), death, or the production of fecal matter. As might be expected, the turnover rate for metabolites is generally high because most of these compounds are labile (easily used by bacteria), in contrast to humic and fulvic acids.

	Inorganic	Organic
Dissolved	CO_2, H_2CO_3, HCO_3^-	Humic and fulvic acids from soils Protein, carbohydrate, and nucleic acid breakdown products from organisms
Particulate	$CaCO_3$	Nonliving debris, organisms

Fig. 7 Compartment matrix for analysis of carbon cycling in the water column of a lake.

Particulate organic matter present in a water column may be either living or nonliving. Frequently, these two compartments are physically joined, as all nonliving particulate organic matter in water is colonized by bacteria and, under some conditions, fungi. Most of the carbon attributable to living organisms is accounted for by phytoplankton and zooplankton; fish and bacteria make smaller contributions in the sense of mass but have important ecosystem effects. Carbon is continually stored in sediments, which accumulate at rates often about 1 mm per year, much of which is organic. As sediments become buried by additional sediments, their decomposition slows because of the lack of oxygen and chemically hostile conditions for active metabolism of bacteria. Thus, while some of the organic matter in sediments is remobilized into the water column, other organic matter in the sediments becomes long-term storage.

A study of mass flux and storage, when viewed in terms of ecosystem compartments and subcompartments, tells a story about the mechanisms by which a lake functions. For example, lakes may differ greatly in the terrestrial contribution to carbon processing and carbon storage, and also may differ greatly in speed of carbon turnover in specific living and nonliving compartments.

The cycling of phosphorus in lakes has been studied intensively, because phosphorus is one of the two elements (nitrogen is the other) most likely to be critically depleted by aquatic autotrophs. Thus, phosphorus at the ecosystem level is commonly viewed as an ecosystem regulator; lakes in which it is abundant (eutrophic lakes) have potential to produce high amounts of plant biomass (phytoplankton, attached algae, or aquatic vascular plants) and have water-quality characteristics that are often viewed as undesirable (low transparency, green color, potential for odor production, and severe loss of oxygen in deep water). In contrast, lakes having low supplies of phosphorus (oligotrophic lakes) may show constant suppression of plant growth through phosphorus scarcity. Such lakes have much lower amounts of carbon in the water, higher transparency, often appear blue, and retain oxygen in deep water consistent with the requirements of fish and other eukaryotes.

Because the phosphorus requirement of plants is only approximately 1% of dry biomass, scarcity of phosphorus can be offset by relatively modest increases in the phosphorus additions to a lake. Addition of 1 kg of phosphorus per unit volume or area, e.g., could easily generate 100 kg of dry mass or 500 kg of wet mass of autotrophs. Thus, mobilization of phosphorus by humans has the potential to change lakes and has done so throughout the world wherever human populations liberate phosphorus through waste disposal, agriculture, and disturbance of soil. For this reason, the study of trophic state (nutrient status) has received more attention than any other ecosystem feature of lakes. The practical application of modeling or analysis of trophic status in lakes arises through the desire to prevent changes in trophic state or to reverse changes in trophic state that have already occurred, which requires ecosystem-level understanding of the lake and particularly of its nutrient budgets.

Lakes may also be limited by low concentrations of the forms of inorganic nitrogen that are readily available to aquatic autotrophs (ammonium, nitrate). In this case, nitrogen limitation rather than phosphorus limitation may control plant growth. In fact, the two types of nutrient limitation may occur sequentially across seasons or across years in a single lake.

Nitrogen cycling in lakes is much more complicated than is phosphorus cycling because nitrogen has a gaseous atmospheric component that phosphorus lacks, and because nitrogen exists in seven stable oxidation states within a lake, which sets the stage for the use of nitrogen as a substrate for oxidation reduction reactions supporting microbial metabolism (Table 2). Like phosphorus, nitrogen enters lakes through the watershed and, in small amounts, with precipitation. Unlike phosphorus, nitrogen also enters lakes as a gas by diffusion at the air–water interface in the form of N2. N2 is so inert chemically that it cannot be used as a nitrogen source by most organisms. Certain prokaryotes have the ability to use N2 by converting it to ammonium, which then can be used in organic synthesis, provided that a substantial energy supply is available. This process is called nitrogen fixation, in that it converts the gaseous nitrogen to a solid that is soluble in water (ammonium). The dominant nitrogen fixers in lakes are the cyanobacteria. Not all cyanobacteria fix nitrogen, but certain taxa that have a specialized nitrogen-fixing cell (heterocyst) grow commonly in lakes that show nitrogen depletion.

Nitrogen fixers escape the limitation of growth associated with nitrogen depletion, thereby gaining an advantage over other autotrophs. Thus, lakes that are enriched with phosphorus but showing nitrogen depletion often have nuisance growths of nitrogen-fixing cyanobacteria, which produce all of the expected symptoms of nutrient enrichment, and sometimes also produce toxins. There is currently much interest in predicting and preventing the development of circumstances that lead to large and persistent blooms of nitrogen-fixing cyanobacteria.

Nitrogen is a multiplier element, just as phosphorus is. It constitutes approximately 5% of dry mass in plants. Therefore, when it is added to lakes, provided that phosphorus is added at the same time, it supports a 20-fold multiplication of dry plant biomass. A detailed documentation of the carbon, nitrogen, and phosphorus cycles for a lake produces an understanding of factors that regulate the metabolic rates of lakes and the accumulation of biomass of various kinds in lakes. These ecosystem phenomena have numerous practical applications, ranging from interest in biomass production (e.g., fish) to interest in constraining water quality within boundaries that are either natural or that favor human purposes.

Community organization

Ecosystems have a strong degree of spatial organization involving the arrangement of organisms according to abiotic constraints based on factors such as amount of irradiance, concentration of dissolved oxygen, or substrate characteristics. The requirement for irradiance is especially important because it dictates the distribution and growth potential for aquatic autotrophs. Phytoplankton grow strongly only within the euphotic zone, which corresponds approximately to water receiving at least 1% of the solar irradiance available at the water surface. Thus, vigorously growing phytoplanktons often are confined to the upper part of the water column

(epilimnion and sometimes metaliminon). The same principle applies to periphyton and rooted aquatic plants, which can occupy substrates only over portions of the sediment that are exposed to at least 1% surface irradiance. The gradient of irradiance is controlled by transparency of the water.

Spatial organization of animal communities and microbial communities is dictated partly by physical conditions and partly by the distribution of autotrophs. Crustacean zooplankton, e.g., may migrate large distances vertically in the water, hiding in deep water during the daytime but rising to feed within surface waters at night. The zooplankton of the littoral zone differs from that of open water, in that the littoral zone offers food types (periphyton especially) that are not available in open water. Distribution of fishes may be dictated in part by the presence of structure associated with littoral zone. The effect of structure may even be related to life history in that immature or small fish may seek the structure of the littoral zone for shelter from predation.

Because organisms conduct the business of an ecosystem, an understanding of their habitat requirements, reflected as spatial organization, leads to explanations of the total abundances of certain categories of organisms, the failure of certain organisms to fare well in one lake but not in another, and the consequences of habitat disturbances of natural or human origin.

Synthetic analysis of ecosystems

Synthetic analysis of ecosystems often involves the statistical study of empirical information, particularly if the objective is to test a particular hypothesis. A quantitative overview of multiple ecosystem functions or of the intricate detail for an ecosystem component typically involves modeling as a supplement to other types of quantitative analysis. When computers first became available, it was anticipated that ecosystem science would ultimately be driven almost entirely by mechanistic models that would predict ecosystem responses to natural or anthropogenic conditions. These expectations were not realized. Ecosystems, like other complex systems such as climate or economics, are moderately predictable from modeling that combines a modest number of well-quantified variables addressed to a specific question, but typically are unpredictable on the basis of large number of variables addressing more general questions. Even so, modeling of numerous variables in an ecosystem context can be useful in setting limits on expected outcomes or showing possible outcomes of multiple interactions that cannot be easily discerned from the study of individual variables. Therefore, modeling is useful in promoting the understanding of ecosystems.

Conclusion

Lakes first inspired the ecosystem concept, and have been a constant source of ideas about ecosystem structure and function. Ecosystem science, as applied to lakes, is supported by and is consistent with other kinds of ecological studies that are directed toward specific organisms, groups of organisms, or specific categories of abiotic phenomena in lakes. The strength of ecosystem science lies in its relevance to the understanding of all subordinate components in ecosystems, and to its often direct connection to human concerns in understanding and managing lakes.

See Also: **Fundamental concepts and theories**: Ecosystem Engineers in Freshwater Ecosystems; Invasive Species; **Human pressures and management of Inland Waters**: Measuring Impact, Overview and Reference Conditions; **Social/societal values of Inland waters**: Freshwater Governance and Resilience; **Structures and functions of Inland Waters - Groundwater**: Karst Groundwater Dependent Ecosystems—Typology, Vulnerability and Protection; **Structures and functions of Inland Waters - Lakes**: Ecological Consequences of Climate Extremes for Lakes; **Structures and functions of Inland Waters - Rivers**: Biodiversity Conservation of Aquatic Ecosystems; Ecological and Evolutionary Consequences of Disturbance in Freshwater Ecosystems; Ecosystem Services of River Systems – Irreplaceable, Undervalued, and at Risk; River Resilience; Succession in Streams; The River Continuum Concept; **Structures and functions of Inland Waters - Wetlands**: Structure and Function of Inland Waters-Wetlands: Classification Systems of Wetlands;

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Hydrologic Setting Affects Ecosystem Processes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Denitrification A microbially facilitated process where nitrate is reduced ($NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$) and ultimately produces molecular nitrogen (N_2); denitrification occurs in low oxygen environments and organic C is consumed in the process; incomplete denitrification can result in the emission of N_2O.
Emergent property An emergent property of an ecological unit is one that arises through interactions among smaller parts that alone do not exhibit such properties; properties or behaviors which only emerge when the parts interact with the wider whole.
Lake metabolism The collective term for the turnover of biomass and energy in a lake ecosystem through carbon fixation (gross primary production) and biological carbon oxidation (ecosystem respiration).
Nitrification A microbially facilitated processes where ammonia is oxidized to nitrite followed by the oxidation of the nitrite to nitrate.
Retention Fraction of the reactant input load that is held within the lake (1-output/input).
Source limitation When inputs of dissolved organic matter and nutrients are limited by the abundance, location, or production of the elements on the landscape, particularly in regions that are already subjected to high annual precipitation; an increase in discharge decreases the concentration of elemental inputs.
Transport limitation When inputs of dissolved organic matter and nutrients are limited by the amount or connectivity of inflowing water; an increase in discharge increases the concentration of elemental inputs.

Inland waters play an important role in global biogeochemical cycles. They collect, transform, store, and export to the atmosphere or to the oceans the organic and inorganic nutrients that wash in from terrestrial ecosystems. Carbon, and to some extent nitrogen, can also be taken up from the atmosphere to fuel aquatic primary production, which is then transformed and either stored or exported. The movement of water to and through aquatic ecosystems plays a major role in controlling rates and extents of biogeochemical transformations in those ecosystems via two mechanisms (Fig. 1). First, hydrologic loads deliver the carbon and nutrients that fuel microbial communities and geochemical processes. Second, hydrologic loads flush carbon, nutrients, and microbial communities downstream.

In this chapter, we start by discussing the complexity and heterogeneity of lake hydrology with a concept we term 'hydrologic setting.' We emphasize the role of hydrologic setting in influencing water and chemical residence time, a property of aquatic systems that ultimately controls many biogeochemical cycling rates. Next, we discuss the utility of models in helping us understand this complexity, and its implications for the biogeochemistry of lake ecosystems. We highlight what has been learned from empirical studies about the role of hydrology and residence time in the biogeochemical cycling of carbon (C), nitrogen (N), and phosphorus (P). Finally, we conclude by identifying knowledge gaps and highlight emerging research needs.

Hydrologic setting and its influences

Hydrologic setting is defined by a lake's size, shape, geographic location, geologic context, and climate which combine to dictate hydrologic flows to and from the lake (Fig. 2). Physical factors of hydrologic setting include lake and landscape morphology such as lake volume, watershed size, connectivity to surface and groundwater, and watershed land cover. These features ultimately set a template that interacts with climate to dictate supply of material to the lake and pace of processing of matter in the lake. Variation in

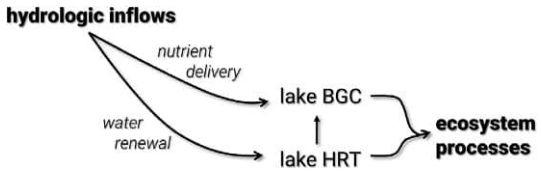


Fig. 1 Competing hydrologic drivers of aquatic biogeochemistry. As hydrologic inflows to a lake from its catchment increase, the amount of nutrients and carbon delivered increases, but the hydrologic residence time (HRT) decreases as a result of increased water renewal. As HRT decreases the fluvial export of solutes increases and time for lake biogeochemistry (BGC) decreases. The interaction between these two effects of hydrologic inflow have strong implications for carbon, nitrogen, and phosphorus fate in lake ecosystems.

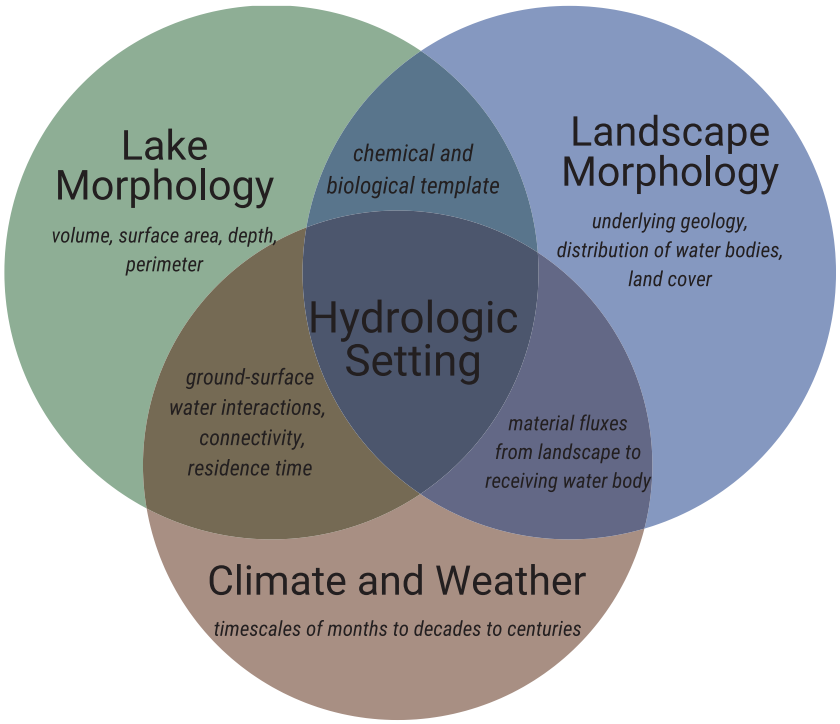


Fig. 2 A Venn diagram depicting how variation in lake morphology, landscape morphology, and climate describe the hydrologic setting of a waterbody. Points of intersection show emergent properties of hydrologic setting, which arise from interactions between two drivers. For example, variation in precipitation and lake volume result in variability in residence time. Climate and landscape characteristics interact to influence loads of material from the landscape. Together, lake morphometry and landcover interact to form the basic biogeochemical constraints within which lake ecosystem processes operate.

climate and weather exert temporal controls on lake morphology and hydrology (volume, hydrologic residence time) and landscape features at various timescales. For example, catchment land cover may change at short (e.g., seasonal succession) or long timescales (e.g., decadal drought cycles, land use change). Climate and weather will also influence the water sources to lakes and the overall hydrologic load (runoff, groundwater, direct precipitation) and interact with lake morphology (volume, surface area, depth) to determine input rates of organic and inorganic compounds for a given land use or land cover of the catchment. Hence, climate and lake and landscape morphology are inextricably linked in the concept of hydrologic setting.

The relative importance of different components of water budgets, and the concentrations of elements in those flowpaths, varies substantially but in some fairly systematic ways. Sources of hydrologic load include surface runoff and inflow streams, groundwater, and direct precipitation. The importance of surface water inputs is dependent on catchment area and slope. Hydrologic inputs to a lake with a large catchment are likely dominated by surface inflows, whereas hydrologic inputs to lakes with relatively small catchments will often rely on direct precipitation. Groundwater inputs and outputs will depend on landscape position and regional hydrogeology. Although sometimes overlooked, evaporation is an important hydrologic loss, especially in small lakes with small catchments and no outlets.

Surface inflows, groundwater inputs, and direct precipitation often differ in their relative contributions of water to a lake, but these flow paths also differ in concentrations of carbon, nitrogen, and phosphorus. Surface waters generally are much more concentrated in particulate and dissolved forms of carbon, nitrogen, and phosphorus when compared to groundwater or precipitation. Groundwater can be a meaningful source of dissolved constituents, but these flow paths do not contribute particulate

material to lakes. Finally, precipitation is dilute in its dissolved carbon, nitrogen, and phosphorus concentrations, but can be a meaningful source of particulate carbon. Notably, in some instances, direct precipitation can account for a substantial proportion of nutrient budget (e.g., sparsely vegetated mountainous areas subjected to elevated N deposition; Baron and Campbell, 1997). These are generalities, and the influence of hydrology on nutrient biogeochemistry will ultimately also depend on geographic location and catchment land cover and land use.

Distinct types of hydrologic setting arise from interrelationships among these landscape features but substantial variation also exists in space and time (Fig. 3). For example, steep, mountainous landscapes typically have little wetland cover and hydrologic flow paths dominated by surface runoff, direct precipitation, and relatively little groundwater influence. High-elevation and high latitude lakes are typically dominated by seasonal snowmelt. In contrast, flat and hydro-geomorphologically complex landscapes in boreal and north temperate regions may have high wetland cover and both surface and subsurface connectivity. In these types of landscapes, evaporation may play a particularly important role for lakes lacking surface water connections or for lakes perched above the regional groundwater table.

An important component of hydrologic setting is hydrologic residence time (HRT). The geographic context of a lake provides predictive power for HRT because the ratio of catchment area to lake area (the drainage ratio) is a useful predictor of HRT. However, lake volume or mean depth are important modifier of this relationship (Jones et al., 2018). The importance of evaporation as a hydrologic loss is influenced by drainage ratio and mean depth. Specifically, in shallow lakes with small drainage ratios, evaporation can be the main pathway for water loss. Interestingly, neither catchment size nor lake size alone are good predictors of drainage ratio or HRT (Hill et al., 2018).

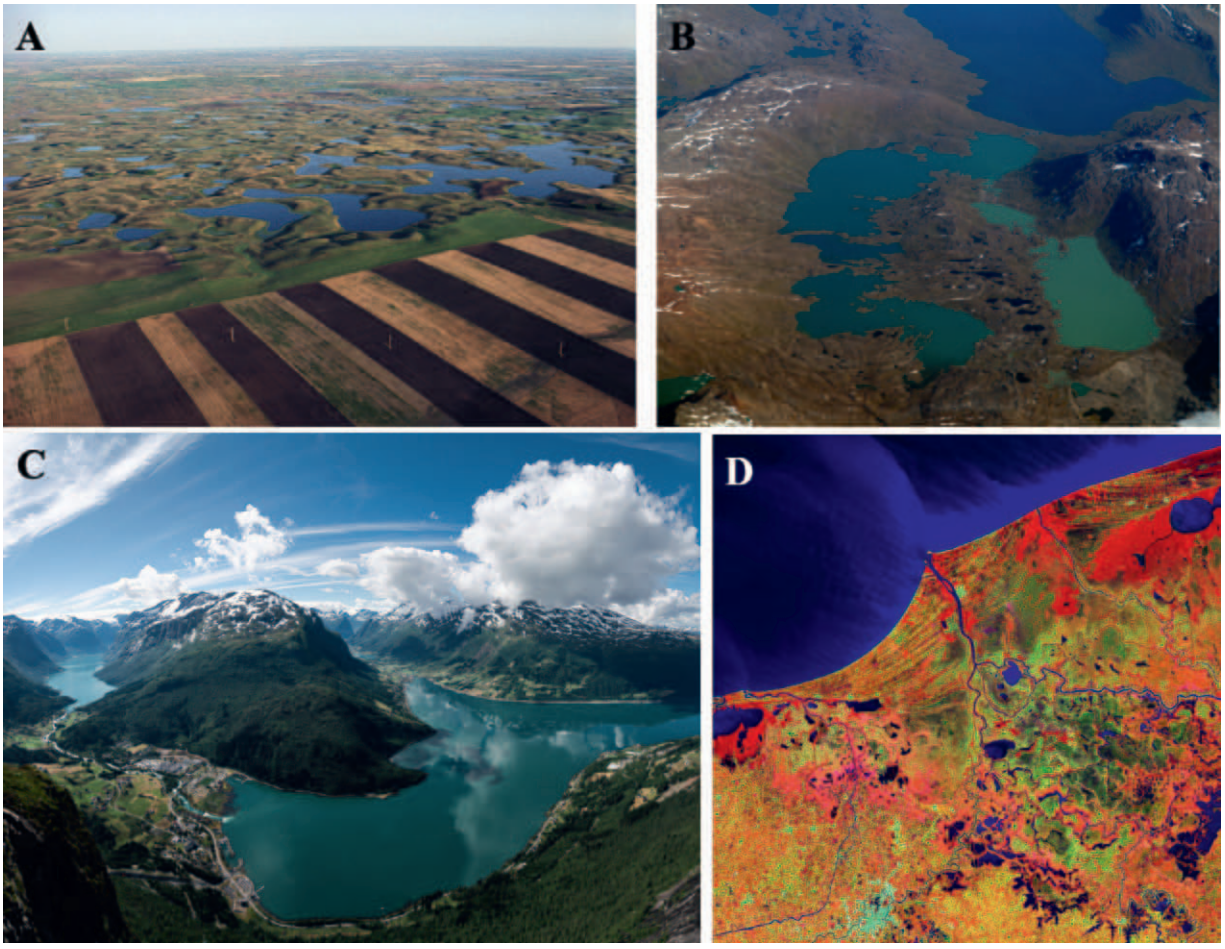


Fig. 3 Real world examples of various hydrologic setting archetypes. (A) Prairie pothole lakes in the upper midwestern United States and Canada have a high degree of groundwater connectivity, high wetland cover, long residence times, and high evaporative demand. Photo credit: Jim Brandenburg, Minden Pictures. (B) In northern Norway, slopes are steep, vegetation cover is low, and water clarity is determined by the influence of glacial till. A mosaic of lake sizes and surface water connections exist, and groundwater plays a relatively small role in hydrologic budgets. Photo credit Peter Prokosch, creative commons: (C) In the Alps mountain range of Europe, hydrology is dominated by seasonal snowmelt and surface water connectivity among valley lakes and streams is high. Photo credit: Lachlan Gowen creative commons. (D) Satellite imagery of Reserva de la Biosfera Pantanos de Centla, Frontera, Tabasco, Mexico illustrates the importance of scale in describing hydrologic settings. In reality, lakes exist in a landscape mosaic with continuous variation in landscape cover, surface water and groundwater connectivity. Photo credit: U.S. Geological Survey creative commons, where color represents different land cover types.

Regional hydrogeology is the primary determinant of the influence of groundwater on lake water budgets. In regions with the potential for groundwater-lake interactions, lake elevation or landscape position determine whether lakes exclusively lose water to the regional aquifer (seepage lakes) or gain appreciable amounts of groundwater (drainage lakes). Drainage lakes are also dominated by fluvial processes, thus large loads and short hydrologic residence times mean retention is low but instantaneous biogeochemical rates are high. In smaller seepage lakes, loads of water and matter are relatively low, which means instantaneous biogeochemical rates are low, but evaporation, which does not transport matter, becomes an important hydrologic loss (Brooks et al., 2014). As a result, chemical residence time is decoupled from hydrologic residence time in these systems and very high rates of retention are predicted and observed.

Research on nutrient dynamics and metabolism of aquatic ecosystems has demonstrated how considering water bodies along residence time gradients leads to insights into rates of key ecosystem processes and transformations of elements, especially carbon (Table 1). In the remainder of the chapter, we focus our discussion on lakes, but note that considering water bodies along residence time gradients allows scientists to make predictions in both lentic and lotic systems, which are usually studied separately (Hotchkiss et al., 2018). In the next section we outline general approaches to modeling lake hydrology and biogeochemistry and note how these models have evolved over time. We conclude the chapter by exploring the role of residence time in structuring spatiotemporal variability in carbon, nitrogen, and phosphorus cycling.

Modeling lake hydrology and biogeochemistry

Models help us gain an understanding of the mechanisms underpinning ecosystem processes. By necessity, models include assumptions and simplifications of systems, but in reality, we know that lakes are heterogeneous both within and across systems (Fig. 4). Simplified models negate many natural complexities of lakes by grouping or ignoring certain hydrologic flow paths and biogeochemical processes, assuming instantaneous and perfect mixing, and assuming static behavior and the existence of hydrologic and biogeochemical equilibria. For example, as a consequence of stratification, thermal and chemical gradients exist within many lakes that ultimately control rates of biogeochemical processes. Bathymetry, or the overall geometry of a lake, is also highly irregular and no two lakes are alike. That spatial complexity inherently structures the flow of water, energy, and materials into and out of lakes. As our understanding of lake ecosystem function grows, the mechanistic framework guiding predictions must include some gradients of heterogeneity. Even so, simplified models have guided and continue to improve our understanding of the role of hydrology in biogeochemical cycling in inland waters (Vollenweider, 1975 is a classic example).

We owe much of our current understanding of the interplay between lake hydrology and biogeochemistry to simple box models that rely on the mass balances of water and matter. Early versions of these models were likely derived from chemical and environmental engineering applications, including the completely mixed, flow reactor (CMFR) model. Interestingly, work in enzymology and microbiology gave rise to chemostat models that are also commonly used in aquatic ecology and have a very similar mathematical derivation (Fussmann et al., 2000). The strength of these models is their simplistic, but process-based representation of hydrologic inputs, biogeochemical rates, and their interaction (Box 1). Over the intervening decades, these models have been applied at lab to continental scales to consider a multitude of biogeochemical processes (primary production, decomposition, internal loading of phosphorus, and denitrification) and cycling of numerous elements (carbon, nitrogen, phosphorus, chloride, and more).

Although aquatic ecosystems are complex, chemostat and CMFR models capture many of the basic hydrologic and biogeochemical behaviors of lakes, which can be represented as naturally occurring reactors in the landscape (Fig. 4). From their earliest

Table 1 Gradients in metabolism from the extremes of small streams to large lakes and aquifers, and their respective roles in OC cycling over broad temporal and spatial scales, when viewed through the continuum lens of hydrologic residence time.

Low HRT (e.g., small streams)	← →	*High HRT (e.g., large lakes)*
Metabolic behavior dominated by loads		Metabolic behavior dominated by trophic state
Events are a dominant time-scale feature		Integration of longer time periods is the dominant time-scale feature
Allochthonous organic C (OC) pool is relatively young		Allochthonous OC pool is relatively old
Mineralization of allochthonous OC $\geq$ 0.1 days^{-1}		Mineralization of allochthonous OC $\sim$0.001 days^{-1}
Particulate OC can be a dominant constituent of the transformed OC pool, because of high energy		Particulate OC rarely a dominant constituent of the transformed OC pool, because of low energy
Large gradient in biologically reactive solute concentrations (e.g., carbon, nutrients) at landscape scale		Smaller gradient in biological reactive solute concentrations
Closely coupled with surrounding landscape		Loosely coupled with surrounding landscape
Allochthony is the dominant term in most metabolic budgets		Autochthony is the dominant term in metabolic budgets at decadal and longer timescales

Table originally appears in Hotchkiss ER, Sadro S, and Hanson PC (2018) Toward a more integrative perspective on carbon metabolism across lentic and lotic inland waters. *Limnology and Oceanography Letters* 3: 57–63.

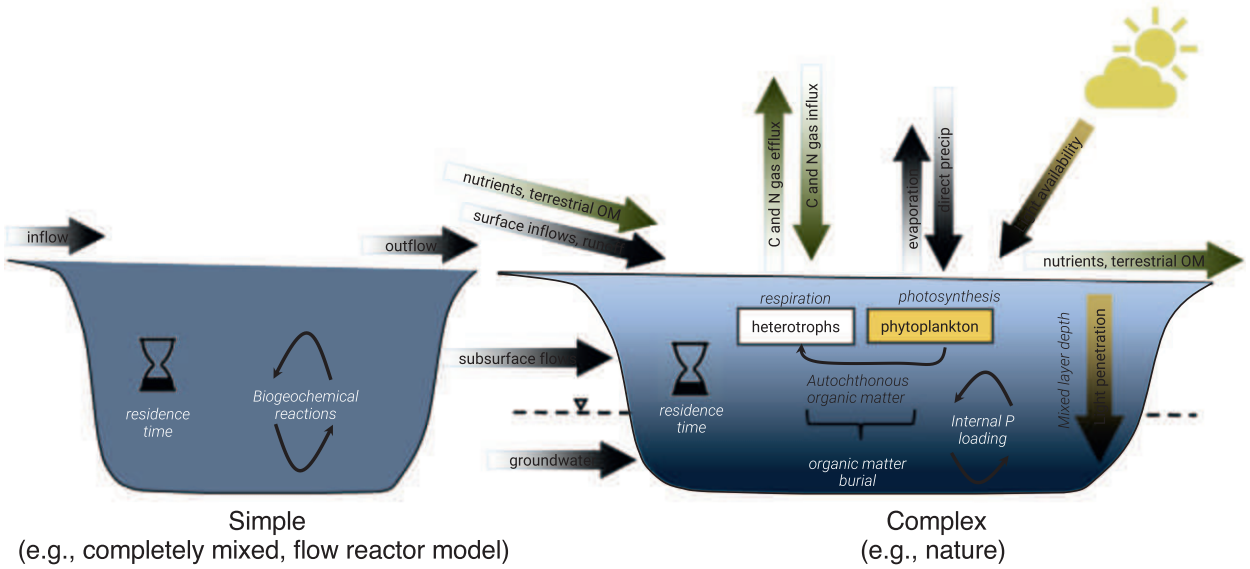


Fig. 4 Models versus reality. On the left, is a modeled lake that includes inflows and outflows of water and a chemical constituent and the resultant biogeochemical reactions within the system. On the right is a hypothetical "natural" lake with arrows depicting the myriad pathways for water and nutrient loss and gain within the system.

application, the limitations of these models have been recognized and refined. Early refinements of the Vollenweider model of phosphorus retention split the total phosphorus pool into dissolved and particulate forms and represented contrasting physical and biogeochemical environments of the epilimnion and hypolimnion of lakes. The physical complexity and treatment of internal lake hydrodynamics has been a major focus over the last decade or more (e.g., Dynamics Reservoir Simulation Model, Imberger et al., 1981; General Lake Model, Hipsey et al., 2019). Other work has sought to explore the importance of representing heterogeneity in the chemical availability of carbon, nitrogen, or phosphorus (reactivity continuum; internal loading of P). By adding multiple hydrologic flow paths into and out of a simple lake biogeochemistry model, our appreciation for the importance of hydrologic setting for lake biogeochemistry and retention of matter has expanded (Fig. 4).

Despite their simplicity, adoption of CMFR and chemostat models has generated adequate prediction for many systems and enabled transformative scientific inference. This work has been applied both within a single ecosystem and at broad spatial scales. Early application of these models provided important prediction and understanding of the process of eutrophication of lakes due to excess phosphorus supply (Vollenweider, 1975; see also "Further Reading"). Similar models have improved our understanding and prediction of the freshwater carbon cycle, including the fate of terrestrial carbon in freshwaters (Jones et al., 2018), ecosystem-scale aquatic primary production (Jäger and Diehl, 2014; Kelly et al., 2018), and the intricacies of predation and competition within the microbial loop (Thingstad and Lignell, 1997).

Residence time and biogeochemical cycling of C, N, P

In this section we discuss the relationships between hydrology and the import, processing, and export of C, N, and P in lakes. The cycles of these elements are important because of their implications for primary productivity and global climate, and they are relatively well-studied.

Import from land to lakes

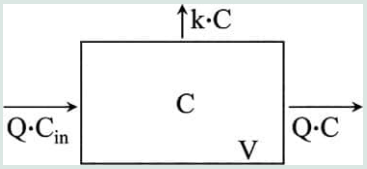
The total input of nutrients to a lake depends on the volume of water coming in via all flow paths, and on the concentrations of nutrients in those sources of water. The flow paths of water to the lake – including whether it has traveled over the surface, through shallow soils, or in deep groundwater – influence the concentration and composition of the dissolved and particulate C, N, and P that this water transports (Kaiser and Kalbitz, 2012). For instance, shallow subsurface flow paths often yield high concentrations of dissolved organic carbon, while surface flow paths have the highest concentrations of particulate organic carbon. The relative importance of different flow paths for the total hydrologic load to a lake depends on factors like topography, geology, and climate (Fig. 2).

Box 1 Mathematical representation of completely-mixed lake

Simple box models that rely on the mass balances of water and matter allow us to gain a process-based understanding of how hydrologic inputs and biogeochemical rates interact. Early versions of these models were derived from chemical and environmental engineering applications, including the completely mixed, flow reactor (CMFR) model for the concentration of a reactant, C (g L^{-1}).

The CMFR model assumes that the volume of the reactor, V (L), is constant. Consequently, inflows to the reactor at rate Q (L d^{-1}) are exactly balanced by outflows at the same rate. The concentration of reactant in the inflow is denoted by C_{in} (g L^{-1}). The model also assumes that the reactor is continuously and instantaneously mixed, which means that the output concentration is equal to the concentration in the reactor. The reactant decays in the reactor following a first-order reaction with rate k (d^{-1}).

This model can be represented with a box-and-arrow diagram:



Or, equivalently, with an equation that describes how the concentration of the reactant changes as a result of each of the inputs and outputs. Recall that flow multiplied by concentration gives mass, and dividing mass by volume gets back to concentration:

$$\frac{dC}{dt} = \frac{QC_{in}}{V} - \frac{QC}{V} - kC$$

Or further simplified:

$$\frac{dC}{dt} = \frac{Q}{V}(C_{in} - C) - kC$$

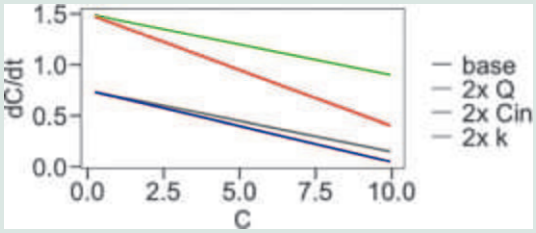
At steady state $\frac{dC}{dt} = 0$, therefore $kC = \frac{Q}{V}(C_{in} - C)$. Hydrologic residence time (θ) is defined as $\frac{V}{Q}$ in units of days. From there, we can define the reaction kC as:

$$kC = \frac{C_{in} - C}{\theta}$$

Ultimately, the equilibrium reactant concentration (C^*) is a function of input concentration, the reaction rate, and residence time:

$$C^* = \frac{C_{in}}{1 - k\theta}$$

Graphical exploration shows us that the rate of change in concentration in the chemostat (dC/dt) responds linearly to the concentration (C). Further, the slope and intercept of this linear response is influenced by any of the three parameters included in our model (Q, C_{in}, and k).



Where surface runoff is the dominant hydrologic input, variation in the amount of runoff into the lake is the primary driver of variation in element inputs. The volume and nutrient concentration of water tend to be positively correlated, because nutrient fluxes tend to be transport- rather than source-limited. For a given lake, discharge is the primary driver of variation in nutrient load, because it often varies over several orders of magnitude while concentration varies over a much narrower range. Localized loads of elements into a waterbody depend on landscape features such as land cover and the degree of hydrologic connectivity. Overall our best estimates of terrestrial loads to inland waters illustrate that loads of organic and inorganic C are several orders of magnitude higher than they are for N and P. Ultimately, these three elements are cycled and buried at different rates, resulting in shifts in C:P and C:N ratios along the freshwater continuum (Maranger et al., 2018).

Processing - production, consumption, and burial

The major biogeochemical elemental cycles (C, N, P) are tightly linked via key ecosystem functions such as primary production and ecosystem respiration. Within the lake, organic carbon is produced by photosynthesis and consumed by respiration. Nitrogen and phosphorus, though not directly involved in photosynthesis, play key roles in the structure of proteins and lipids synthesized by

primary producers, who compete directly with microbial heterotrophs for these same nutrients. In this section, we discuss how C, N, and P are produced, consumed, and buried in lake ecosystems, and how the rates of biogeochemical cycling are influenced by hydrologic residence time. While these elemental cycles are coupled, key distinctions in the transformations among these elements exist.

Rates of photosynthesis depend in large part on the availability of nutrients and light, both of which are dictated by hydrology. Hydrologic inputs bring inorganic nutrients and dissolved organic matter-bound N and P, which stimulate photosynthesis. They also bring dissolved organic matter and particulates, which can inhibit photosynthesis by reducing light penetration. The net effect of these opposing influences depends on the carbon-nutrient stoichiometry of the hydrologic inputs to the lake, how darkly colored the organic matter inputs are, and on other factors like lake size, which interacts with water color to determine mixed layer depth and thus the light climate experienced by phytoplankton.

Rates of ecosystem respiration are both directly and indirectly linked to hydrologic inputs. They depend directly on hydrologic inputs of organic carbon, which provide the predominant substrate for heterotrophic respiration in many lake ecosystems. When inputs of organic carbon are low, instantaneous rates of ecosystem respiration are also low, because the supply of relatively labile carbon compounds is only slowly renewed. At the same time, however, the proportion of the organic carbon input that is respired may be relatively high, because low hydrologic inputs mean a long residence time of water and solutes in the system. This is particularly true in lakes where evaporation is an important component of the water budget, lengthening the residence time of solutes like dissolved organic carbon relative to the residence time of the water itself, with potential for increased gaseous C emissions (see Section "Export"). Ecosystem respiration is also linked to rates of photosynthesis by the autotrophic respiration of phytoplankton and by heterotrophic respiration of organic carbon fixed by phytoplankton, and thus are indirectly linked to hydrologic inputs.

Hydrologic residence time (HRT) affects rates of flushing and sedimentation, ultimately influencing the retention of C, N, and P in lake ecosystems (Fig. 5). For example, instantaneous rates of P sedimentation may be higher in lakes with short HRT because these lakes often have greater inputs of particulate P bound to terrestrial organic matter. Despite faster rates of removal of P by sedimentation at short HRT, most lakes with short HRT retain less phosphorus than lakes with long HRT due to the competing influence of sedimentation and flushing on phosphorus retention. At long HRT, the sedimentation rate of P has a larger relative influence on phosphorus retention while flushing has a larger relative influence at short HRT. Similar patterns are observed for carbon, where rates of both dissolved organic carbon production and consumption can be predicted from hydrologic residence time. Extended residence times allow for greater mineralization of dissolved organic carbon, but also flocculation and settling of dissolved organic matter. In contrast, short residence time systems will not mineralize a large fraction of their dissolved organic carbon load, but are likely to receive higher loads of particulate organic carbon that is buried in lake sediments. Rapid rates of sediment accretion in man-made reservoirs are a good example of the importance of particulate load and burial in short residence time systems.

Denitrification, the primary biogeochemical process responsible for nitrogen removal, has three requirements to proceed: anoxic sediments, nitrate, and organic matter. Because of these three players, the rates and relative importance of denitrification are difficult to predict from HRT alone. Nitrogen loading impacts the magnitude of organic matter available for denitrification through its limitation of primary production. Depth impacts nitrate availability via the coupling of nitrification and denitrification processes

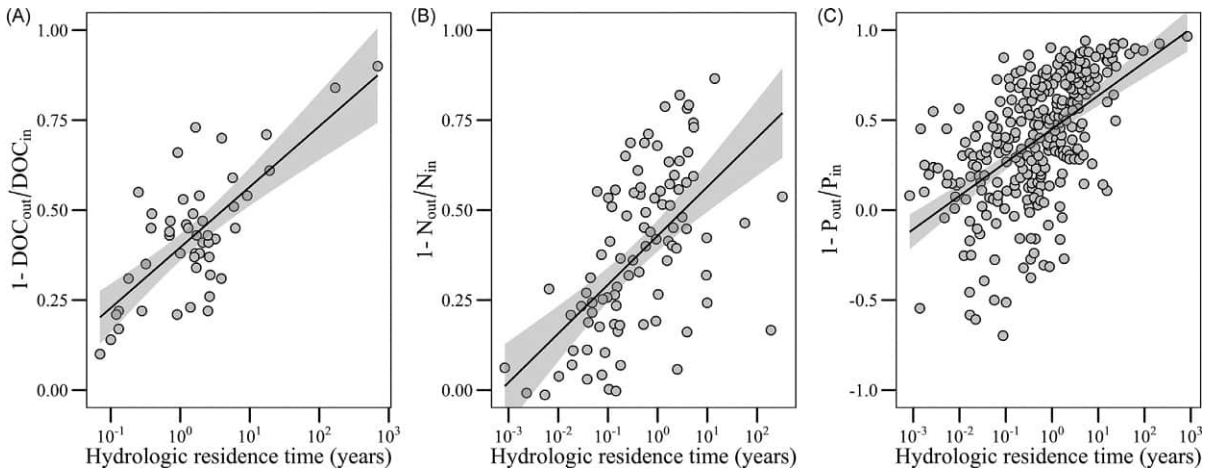


Fig. 5 Carbon (A), Nitrogen (B), and Phosphorus (C) removal efficiency as a function of hydrologic residence time. Note: in panel C, negative values on the y-axis indicate that lakes export more P than is received, possibly as a consequence of internal nutrient loading from sediment release. (A) Figure redrawn from Evans CD, Futter MN, Moldan F, Valinia S, Frogbrook Z, and Kothawala DN (2017) Variability in organic carbon reactivity across lake residence time and trophic gradients. *Nature Geoscience*, 10(11), 832–835., (B) Figure reprinted from Finlay JC, Small GE, and Sterner RW (2013) Human influences on nitrogen removal in lakes. *Science*, 342 (October): 247–250.); (C) Figure redrawn from Brett MT and Benjamin MM (2008) A review and reassessment of lake phosphorus retention and the nutrient loading concept. *Freshwater Biology*, 53(1): 194–211.

which is maximized at the sediment-water interface and dictates the probability that organic matter makes sediment contact via sedimentation. Finally, phosphorus availability may underly and limit nitrogen fate and processing rates because P often limits primary production. Despite these caveats, empirical work shows a similar relationship between retention and HRT for all three elements (C, N, and P; Fig. 5).

Export

Matter in lakes can be exported from the water column of a lake to one of three pools: the atmosphere, lake sediments, or downstream toward the ocean. Hydrologic residence time influences the instantaneous rates of export to each of these fates, and the importance of each fate relative to the others and to the inputs of organic matter from the watershed. Periods of high precipitation (at time scales ranging from individual storms to multi-year climate cycles or changes) can decrease the proportion of carbon exported to the atmosphere (as CO_2 or methane, CH_4) by increasing inputs and decreasing hydrologic residence time thereby increasing the relative importance of fluvial export.

When residence times are long, inputs of terrestrial organic matter are relatively small but they are exposed to degradation processes in the lake for a long time (see previous sections). This means that, proportionally, most of the incoming organic matter is exported to the atmosphere, but the instantaneous rate of export to the atmosphere is low. In oligotrophic systems with long residence times, only a small portion of the available organic carbon is exported downstream or buried in sediments. In more productive lakes, substantial *in-situ* production of organic carbon by photosynthesis may lead to larger downstream exports and burial.

One factor that sets the P cycle apart from C and N cycles is the lack of a gaseous loss. Elements or solutes that lack a gaseous phase can have decoupled residence times from water with implications for ecosystem function. Retention or permanent removal for such solutes is dependent on permanent burial in lake sediments or fluvial export from the system, respectively. Due to this dependence, lake hydrologic setting plays a key role in determining solute fate and a more nuanced understanding of hydrology, outside of hydrologic residence time, is crucial. For example, seepage lakes lack a fluvial outlet and water is primarily lost by evaporation. In this hydrologic setting, solutes without a gaseous phase are less likely to be exported from the system and may become more concentrated due to the decoupling between their residence time and water. Consequently, an increase in the elemental or solute residence time relative to hydrologic residence time introduces the potential for eutrophication particularly in systems with a strong anthropogenic presence. In contrast, drainage lakes, with comparatively shorter HRTs, have hydrologic budgets dominated by fluvial export rather than evaporation which increases the likelihood of fluvial solute export.

Knowledge gaps and opportunities for future research

Several ideas stand out as important topics for future work on the connections between hydrology and ecosystem processes. Questions remain in understanding how key aspects of hydrologic setting are related (e.g. correlations among topography, connection to network, flow path, residence time, etc.). What do these patterns mean for patterns of biogeochemical processing? In regard to modeling approaches, the coupling and interdependency of elemental cycles must be more fully embraced within the context of CMFR- and chemostat-style models (see Cheng and Basu, 2017). Many past and recent successful applications of these models focused on a single elemental cycle, but including a combination of hydrologic and stoichiometric constraints within these models will likely enhance what we can learn and predict.

While empirical studies have demonstrated that HRT influences N processing rates and retention (Finlay et al., 2013), the relationship is more context-dependent than for C and P due the mechanistic complexities of the N cycle. As with C and P, the fraction of N retained in a water body is positively correlated with HRT. This is likely due to more time for removal processes to occur such as primary production, sedimentation, and denitrification. Although fractional nitrogen retention is positively correlated with HRT, the rates and relative importance of the processes involved in nitrogen cycling do not demonstrate clear patterns. For example, studies have found both positive (Jansson et al., 1994) and negative correlations between denitrification rates and HRT (Harrison et al., 2009). This suggests that there are complex, non-linear interactions between HRT, lake depth, and N loading on the retention and transformation of N in aquatic ecosystems that deserve further investigation given the global perturbation of the N cycle.

Future work must consider the coupled roles of the three major elements that drive aquatic metabolism and incorporate hydrology in making predictions about ecosystem processes. As discussed above, the carbon, nitrogen, and phosphorus cycles are inherently linked to each other through aquatic ecosystem metabolism. Many unanswered questions remain such as: How do C, N, and P loads and HRT interact to impact the rate of primary production? How does the rate of primary production feed back into the rates and relative importance of sedimentation, flushing, and internal loading of phosphorus? How does temporal variability in weather or climate interact with lake hydrology to influence ecosystem processes? Addressing some of these questions may provide answers to some of the considerable scatter that is evident around the fit between C, N, and P retention and HRT of Fig. 5. Finally, our knowledge of coupled biogeochemical cycles are highly biased toward boreal and temperate waterbodies—future research is critically needed in humid tropics and other data-poor regions to deepen our understanding on the role of hydrology and residence time on aquatic ecosystem processes.

Conclusion

- Movement of water controls biogeochemical processes in aquatic ecosystems by delivering carbon and nutrients and by flushing those reactants and microbial communities downstream.
- Lake morphometry, climate, and the surrounding landscape define a "hydrologic setting" that determines how water and nutrients enter the lake, and in what quantities.
- Simple models have been useful for understanding the influences of hydrology on biogeochemical processes in lakes.
- Hydrologic residence time provides a simple description of the hydrologic cycle of a lake with considerable power for understanding how biogeochemical process rates vary in space and time.

See Also: Fundamental concepts and theories: Hydrological Cycle and Water Budgets; Structures and functions of Inland Waters - Groundwater: Groundwater Systems—A Hydrogeological Typology; Structures and functions of Inland Waters - Lakes: Lakes as Recorders of Earth Surface Dynamics From Yearly to Plurimillennial Time-Scales; Structures and functions of Inland Waters - Rivers: Hyporheic Zone and Processes; Inland Waters—Rivers: Land Use and Water Quality; Riparian Zones

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Regime Shifts and Tipping Points

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Allee effect Is a feature of small populations whereby low density limits population growth.
Alternative stable state Different (multiple) states (equilibria) of a system under the same environmental conditions. The state to which a system converges is path dependent (i.e., it depends on the initial conditions).
Basin of attraction Set of initial conditions that lead to a particular state (equilibrium).
Bifurcation A critical threshold in environmental conditions at which the qualitative behavior of a system changes.
Bistability The case where two alternative stable states exist.
Critical slowing down The phenomenon that the return time of a disturbance back to equilibrium increases close to a bifurcation.
Equilibrium The condition at which competing processes are balanced. At a stable equilibrium, a system returns to it upon a small perturbation. At an unstable equilibrium, a system moves away from it upon a small perturbation.
Hysteresis Is the dependence of state of a system on its history.
Positive and negative feedback A process through which a change has a respectively positive or negative effect on itself. Also referred to as self-enforcing and dampening feedback respectively.
Regime shift A sharp change from one regime (state) to a contrasting regime. A regime is a dynamic "state" of a system.
Threshold A point where the system is very sensitive to changing environmental conditions.
Tipping point A point where the system flips from its current state to another state.

Introduction

The terms regime shifts, ecological thresholds, and tipping points are often used in aquatic ecology to describe abrupt transitions ranging from population collapse to community reorganization, and even shifts at the whole ecosystem scale. A large range of examples of regime shifts have been described in the literature including the shift from healthy coral reefs to deteriorated corals (Hughes, 1994), shifts of tropical forests to savanna vegetation (Hirota et al., 2011) and historic and contemporary regime shifts in the Sahara and Sahel (Foley et al., 2003; Tierney et al., 2017), but perhaps one of the most illustrative examples is the rather sudden transition observed in shallow lakes going from clear water and dominated by submerged vegetation to turbid water and dominated by phytoplankton. This sudden transition can occur when a tipping point is surpassed. The two contrasting states—clear versus turbid water states—are often resilient to change, i.e., internal feedback mechanisms maintain the lake turbid and large changes are needed for the system to return back to the clear state. In this chapter we explain how this works. We explain (1) what regime shifts and tipping points are, (2) how they are manifested in inland waters, (3) how they are linked to ecosystem functioning and (4) if and how we can detect regime shifts in time to prevent an ecosystem from tipping.

Regime shifts and tipping points

An ecosystem can respond to changes in different ways. Some changes occur in a smooth, near-linear way (Fig. 1A). Imagine, for example, a fish pond from which benthic fish are harvested. The fish resuspend the sediment causing turbidity. Without an *Allee effect* and when internal feedback mechanisms are weak or absent (see below), a small—gradual—decrease in fish biomass may lead to a small—gradual—decrease in bioturbation which in turn reduces turbidity. Stronger shifts may occur when conditions change while the system is near a certain threshold (Fig. 1B). Imagine a vegetated stream receiving an increasing herbicide load. Initially, the herbicide concentration remains below the concentration at which effects occur. When the concentration increases to levels that surpass the tolerance of the stream vegetation, a massive death of the plants with an unvegetated stream as a result is expected.

The third type of system response is the focus of this chapter; it occurs when under the same conditions alternative states exist (Fig. 1C). Imagine a system where increased nutrient loading slowly increases periphyton and phytoplankton growth, resulting in decreased light availability for submerged plants. At low nutrient loading, the submerged plants still receive sufficient light to grow and plant coverage remains relatively stable. However, when a certain critical periphyton density or a critical turbidity level is surpassed the submerged plants do not receive enough light and the vegetation will wane. Although the external driver—here nutrient loading—changed gradually, the system reacts abruptly. The critical nutrient loading at which this shift from a clear water and vegetation dominated state to a phytoplankton dominated turbid state occurs is often referred to as an ecological threshold or tipping point. In mathematical theory, such tipping points are called catastrophic bifurcations, with the fold catastrophe (F1 and F2 in Fig. 1C) as the most prominent example. Close to a bifurcation point a small perturbation can flip the system into its alternative stable state, in other words "little things can make a big difference" (Gladwell, 2000). The reason for this is that a small perturbation leads to a self-propagating change that eventually causes the system to shift to a qualitatively new state. The self-propagated change caused by the existence of strong positive feedbacks determines the nature of an ecosystem response with hysteresis (see "Feedbacks and hysteresis" section). In practice, a transition across a threshold without alternative states (Fig. 1B) cannot be distinguished from a transition in a system with alternative states (Fig. 1C). In both cases, such transitions will appear as abrupt and persistent shifts over a gradient of environmental conditions. For this reason, they both can be characterized as regime shifts but it is only the latter (Fig. 1C) that is associated with the existence of a tipping point.

The concepts of tipping points and alternative stable states, also referred to as alternative regimes to underline that a system state is not fully static, can be explained using "stability landscapes" (Scheffer et al., 2015; Fig. 2). The ball in this "landscape" represents the state of an ecosystem and the valleys—or basins of attraction—the stable equilibria a system can be in. The hilltops represent the unstable equilibria. The stability landscape can have different shapes, depending on external conditions. Projecting the same example as above (Fig. 1C) on the stability landscape in Fig. 2, we can interpret the front most stability landscape as an oligotrophic shallow lake full of submerged plants. Nutrient loading is too low for algae to be able to outcompete the submerged plants. Hence there is only one valley, no alternative states exist and the lake belongs to the submerged plant dominated state. In the transition from oligotrophic to more eutrophic conditions (central 3 stability landscapes), a second valley appears, the ball can be in either one depending on the initial conditions. Going from oligotrophic to eutrophic conditions the ball will be in the valley on the left (in our example the submerged plant dominated state), while during the recovery from eutrophic conditions to oligotrophic conditions the ball will be in the valley on the right (the algal dominated state). When nutrient loading increases, the valley shrinks and the system becomes less resilient to external perturbations. This means that a small perturbation—e.g., removal of some of the vegetation—, can lead to a transition to the alternative algal dominated state. A catastrophic shift occurs when nutrient loading crosses the F2 threshold: higher than this point the valley on the left disappears, submerged plants cannot dominate the system, and a positive feedback causes a self-propagating increase in algal concentrations until the submerged plants disappear and the lake reaches the alternative turbid water state.

In short, the stability landscape visualizes that a system can tip in two different ways: either through change in conditions or through a large perturbation (van Nes et al., 2016). The first type of tipping is the result of the gradual decrease in stability of a stable

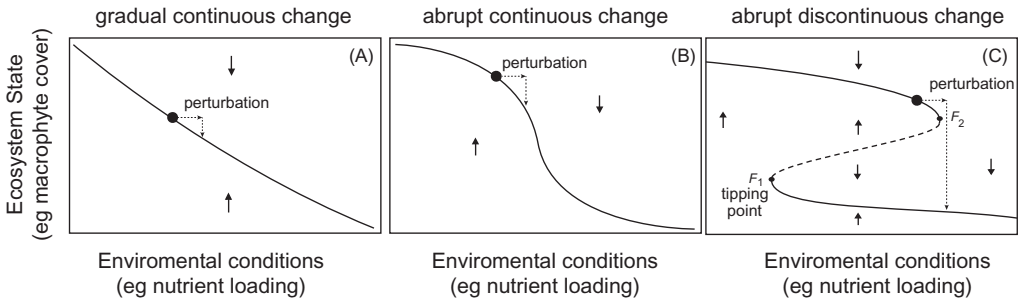

Fig. 1 Ecosystem response to changing conditions: near-linear response (A: small change in environmental conditions results in a small surprise); a non-linear response indicating a strong response around a certain threshold (B: a small change in conditions leads to a big but reversible surprise); a non-linear response indicating a strong response at a tipping point (F2, catastrophic (fold) bifurcation) (C: a small change in conditions leads to a big and hard-to-reverse surprise). In (C) F1 is the tipping point in the system where the system shifts back to the previous state. The range of conditions between the two tipping points (F1 and F2) marks the range of bistability in the system.

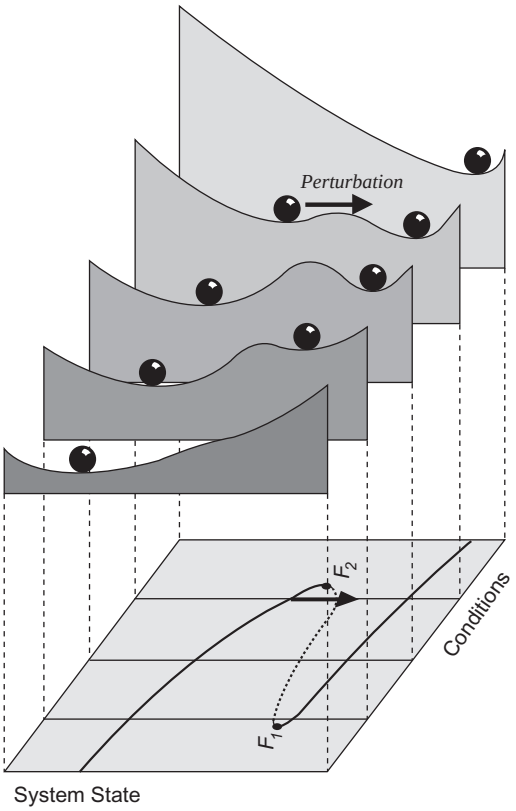

Fig. 2 Stability landscape illustrating the existence of alternative stable states, resilience and transitions. Bistability occurs in the three central landscapes. Scheffer M, Carpenter SR, Dakos V and van Nes EH (2015) Generic indicators of ecological resilience: Inferring the chance of a critical transition. *Annual Review of Ecology, Evolution, and Systematics* 46: 145–167.

state and can be anticipated using resilience indicators (see "Foreseeing regime shifts" section). The ability to remain in a stable state is defined as the systems "resilience." However, note that between scientific disciplines, there are numerous different concepts of resilience. In ecology, the most commonly used definition is the one postulated by Holling (1973);

"Resilience (. . .) is a measure of the ability of systems to absorb changes of state variables, driving variables, and parameters, and still persist (. . .). Stability, on the other hand, is the ability of a system to return to an equilibrium state after a temporary disturbance. The more rapidly it returns, and with the least fluctuation, the more stable it is."

Besides ecological (or Holling's) resilience, the *rate of recovery* after a disturbance is another measure of resilience, also referred to as *engineering resilience* (contrasting Holling's *ecological resilience*). Changes in recovery rate have been also used as a way of detecting regime shifts (see "Foreseeing regime shifts" section).

Another common regime shift in inland water is the shift between dominance of floating plants such as duckweed, water hyacinth or water lettuce, to alternative regimes consisting of either a submerged-plant dominated state (Strange et al., 2018), or a phytoplankton-dominated state (de Tezanos Pinto and O'Farrell, 2014). Besides shifts in the macro-ecological aspects of inland waters, regime shifts and hysteresis also occur in microbe-driven biogeochemical functioning. For instance, in deep, seasonally stratified lakes, shifts can occur between an oxic, cyanobacteria-dominated state and an anoxic state dominated by sulfate-reducing bacteria and phototrophic sulfur bacteria (Bush et al., 2017). Likely, this is a ubiquitous feature in stratified ecosystems, in which microbial feedback loops cause a rapid decline in oxygen levels which are not easily reversed (Bush et al., 2017).

Feedbacks and hysteresis

The stability of alternative ecosystem states as well as the accelerating change during a regime shift derive from internal feedbacks. Such feedbacks have been defined as "processes where changes in the state feed back to the input" (DeAngelis et al., 2012). Feedbacks can be either negative (stabilizing or dampening change), or positive (self-enforcing or magnifying change). Returning to the classic shallow lake example: submerged plants suppress algal growth—and thereby turbidity—by decreasing nutrient concentrations, as well as by secreting algal-repressing substances (Scheffer and Jeppesen, 1998; Fig. 3A and B). At the same time, low turbidity facilitates the establishment and growth of submerged plants, leading to a stabilizing positive feedback loop (Fig. 3D). However, if part of the submerged plants would be removed—leading to a change in system state-, or if nutrient loads would pass a

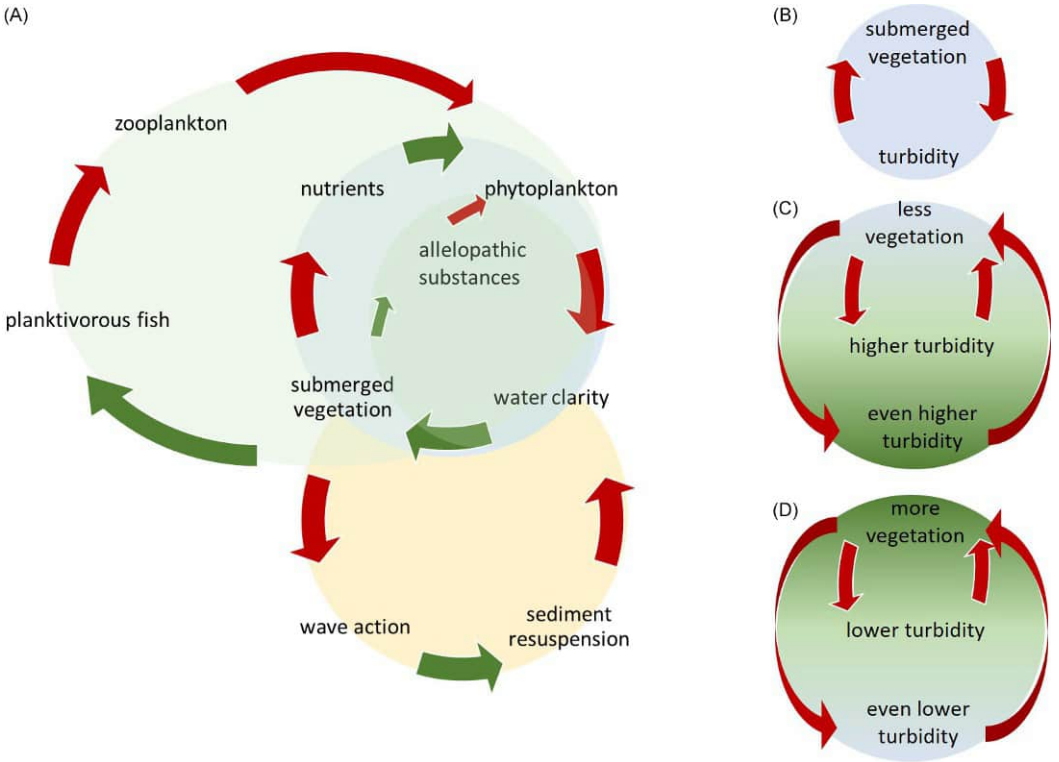

Fig. 3 Different self-enforcing feedback loops in a shallow lake, arising from positive (green arrows) and negative (red arrows) interactions in the network (A). Vegetation has a negative effect on turbidity (B and D), while turbidity has a negative effect on vegetation (C). Modified from Scheffer M and Jeppesen E (1998). Alternative stable states. In Jeppesen E, Søndergaard M, Søndergaard M and Kristoffersen K (eds.), *Structuring Role of Submerged Macrophytes in Lakes* vol. 131 ed., pp. 397–406. New York: Springer-Verlag and van Nes EH, Arani BM, Staal A, van der Bolt B, Flores BM, Bathiany S and Scheffer M (2016) What do you mean, 'tipping point'? *Trends in Ecology & Evolution* 31(12): 902–904.

critical threshold—leading to a change in external conditions-, stabilizing feedbacks are weakened and the system can be propelled into the turbid state, through self-enforced deterioration (Fig. 3C; van Nes et al. (2016)). Less submerged plants lead to less-efficient nutrient uptake, leading to algal growth, causing shading which further suppresses submerged plant growth. Once arrived in the new—turbid-state, a new stabilizing feedback is in place, where turbidity enhances turbidity.

To return to the clear water state, one cannot simply restore nutrient loads, but one must reduce these to a much lower level (represented by critical threshold F1 in Fig. 2). This is a defining property of systems in which alternative stable states exist. Here, due to stabilizing feedback loops, the road to recovery is much more difficult than tipping into a deteriorated state, a principle referred to as *hysteresis*. The first unambiguous proof of biological hysteresis was found in a phytoplankton population consisting of the cyanobacterium *Aphanizomenon flos-aqueae*, which was exposed to increasing light irradiance (Faassen et al., 2015, Fig. 4A). These cyanobacteria need light for growth, but too much light damages their cells. Even at low light levels, cells already profit from mutual shading, resulting in density-dependent growth due to an *Allee effect*. When light irradiance passes a critical threshold, too many cells are damaged, leading to loss of cells and thereby loss of the mutual shading underlying the *Allee effect*. The system is now propelled into extinction. To return to a high-biomass state, the light level has to be reduced to a much lower intensity than where the population went extinct, before a fresh inoculum will regrow to its original density.

Hysteresis in inland waters

Hysteretic effects have also been observed in inland waters. For example, Lake Veluwe, the Netherlands, went through several regime shifts over a period of 30 years (Meijer, 2000; Scheffer et al., 2001; Fig. 4B). Three alternative stable states occur in this lake: (1) a clear, submerged plant dominated state; (2) an intermediate state in which clear and turbid lake areas coexist, and turbidity is caused by sediment resuspension rather than phytoplankton blooms; (3) a turbid, phytoplankton dominated state arising from excess phosphorus (P) loads. In this lake, the road to recovery was considerably more difficult than the road to deterioration. Submerged plants disappeared at total phosphorus (TP) concentrations above 0.20 mg L^{-1}, whereas they only returned when TP was decreased to below 0.10 mg L^{-1} (Ibelings et al., 2007). After reducing P-loads, an intermediate state occurred where shallow areas of the lake were clear and recolonized by *Chara* spp., whereas deeper areas of the lake remained turbid through sediment

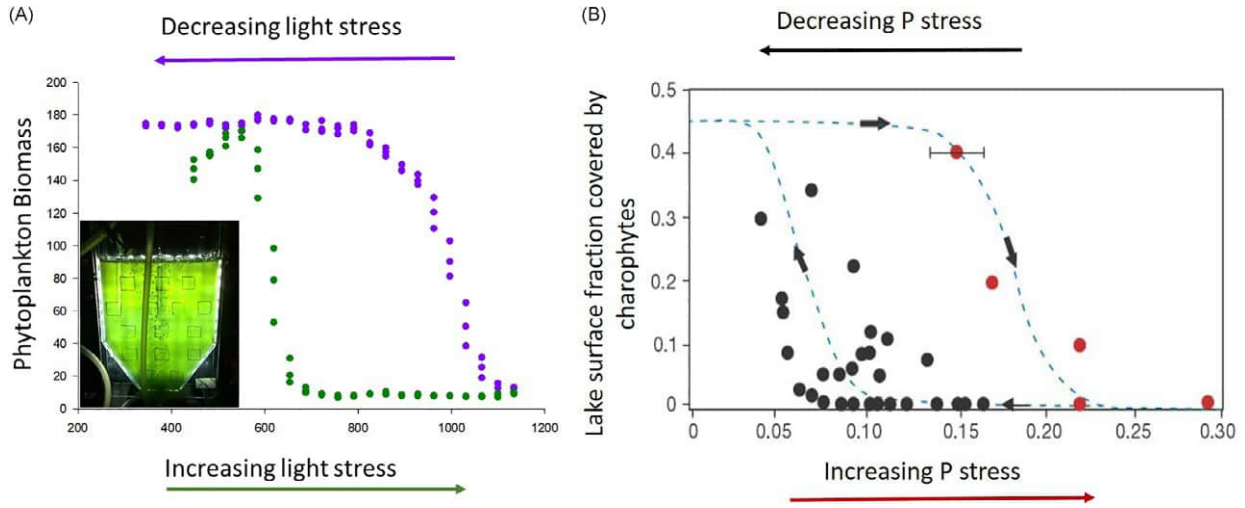

Fig. 4 (A) Hysteresis in an experimental phytoplankton population exposed to increasing and decreasing light stress (x-axis in μmol photons m^{-2} s^{-1}), the inset shows the experimental system. (B) Hysteresis in shallow lake Veluwe exposed to increasing and decreasing P-stress (x-axis, in mg L^{-1}). Adapted with permission (A) Faassen EJ, Veraart AJ, Van Nes EH, Dakos V, Lürling M and Scheffer M (2015) Hysteresis in an experimental phytoplankton population. *Oikos* 124(12): 1617–1623; (B) Meijer ML (2000) Biomanipulation in the Netherlands—15 Years of Experience. Wageningen University; Scheffer M, Carpenter SR, Foley JA, Folke C and Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413, 591–596.

resuspension by wind action and benthivorous fish. True lake-wide water clarity only occurred after substantially reducing numbers of benthivorous fish. This type of hysteretic behavior in which an intermediate recovery state or unstable clear state occurs is commonly observed in turbid, north-temperate shallow lakes on the road to recovery (Hilt et al., 2018). In those lakes, the stability and nature of the intermediate state depend on the type of restoration measures.

Overcoming hysteresis: Biomanipulation

Despite the lack of full insight into how ecosystem services change when a regime shift occurs (see "Foreseeing regime shifts" section), worldwide considerable effort is put into stimulating regime shifts, or in other words: to restore ecosystems to their original state. Lake Veluwe is just one of the many examples of inland waters where measures have been taken to reduce external and internal nutrient loading. Different measures and techniques are available (see e.g., Jilbert et al., 2020), but reaching a sufficiently low nutrient loading (i.e., below the value corresponding to tipping point F1 in Fig. 2) is often challenging and sometimes impossible. Biomanipulation may be used to "force" a shift to the desired state. Various biomanipulation techniques have been used to end a phytoplankton or floating plant dominated state and reestablish submerged vegetation. Well known examples are the removal of planktivorous fish to increase zooplankton grazing on phytoplankton, the introduction of piscivorous fish to achieve the same cascading effect, removal of benthivorous fish to reduce resuspension and uprooting of submerged vegetation, the introduction of filter feeders (fish or mussels) to remove phytoplankton and the introduction of submerged plants or the removal of floating plants (Jeppesen et al., 2012). Note that biomanipulation will only lead to the establishment of an alternative state when the environmental conditions are within the range that alternative states exist (i.e., between F1 and F2 in Fig. 2). Even then, biomanipulation is not always successful and sometimes repetitive actions are needed to keep the system in the desired state (Søndergaard et al., 2008).

Linking alternative states to ecosystem services

Regime shifts are large, persistent changes in the structure and function of ecological systems, with substantive impacts on the suite of ecosystem services provided by these systems (Folke, 2016). For aquatic systems the link between alternative regimes and ecosystem services are receiving increasing attention. It is clear that inland waters provide a wide range of ecosystem services, ranging from habitat provisioning for different types of organisms and nutrient retention to the provisioning of drinking water and recreational areas. Overview studies (Hilt et al., 2017; Janssen et al., 2019) indicate that alternative states differ in the services that they provide. Phytoplankton dominated systems, for instance, are much more suitable for navigation and different kinds of watersports, while engine propellers get stuck in aquatic plants. Aquatic plants (submerged and emergent) on the other hand stabilize the sediment with their roots, thereby protecting the shores or the bottom for erosion. The majority of studies report a higher biodiversity when a system is plant dominated as compared to systems that are dominated by phytoplankton, but notably

the opposite has also been found for instance for fish and phytoplankton communities. How regime shifts impact other ecosystem services, including greenhouse gas emission, carbon and nutrient retention, strongly depends on the system and so far no generalities can be distilled (see also knowledge gaps).

Foreseeing regime shifts

Foreseeing regime shifts ideally refers to identifying critical values in external conditions where a tipping point occurs. However, the identification of actual critical values is a daunting task. The alternative approach is to identify mechanisms and patterns that are related to the existence of alternative states and transitions between them (deYoung et al., 2008). These patterns can be used as criteria for detecting catastrophic regime shifts (Scheffer and Carpenter, 2003). Detecting regime shifts helps understanding their mechanisms and improves our ability to predict them. To achieve this, the most common approach is to identify discontinuities in time-series data using a breakpoint analysis (Andersen et al., 2009). Such identified breakpoints in long-term monitored aquatic systems are used to identify potential alternative states. Another approach is to infer the existence of alternative states from analyzing frequency distributions of state variables (Scheffer and Carpenter, 2003). A bimodal frequency distribution will flag the existence of alternative states and could even allow the reconstruction of stability landscapes (Fig. 2; Livina et al., 2010). However, both these approaches are performed post hoc meaning that a regime shift has already occurred.

To enable foreseeing tipping points and estimating the risk of an impending regime shift the use of different (or early warning signals) have been explored (Scheffer et al., 2009). The majority of these indicators stem from changes in the shape of the stability landscape of the system close and far from the tipping point (Scheffer et al., 2012; Fig. 5A and B), and they change in a consistent and predictable manner as the system is slowly approaching the tipping point. First, a system takes longer to recover back to equilibrium after a perturbation (Fig. 5C and E). Second, variability in the systems is rising (Fig. 5D and F), third the system states start to become more similar (autocorrelation increases Fig. 5G and I), and fourth the distribution of the system state becomes more skewed (Fig. 5 H and J). The prospects (Dakos et al., 2015) as well as the number (Clements and Ozgul, 2018) of resilience indicators have increased in recent years and there are complete statistical tools available for estimating such indicators in time series (Dakos et al., 2012) and in spatial datasets (Kefi et al., 2014). These tools have been applied using data from different types of

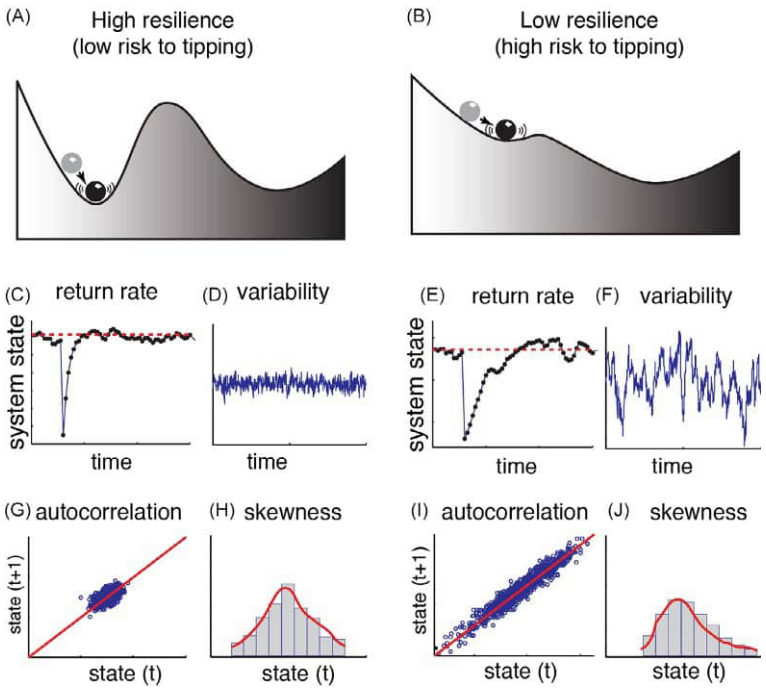

Fig. 5 Low resilience and high risk of tipping are fingerprinted by consistent changes in the dynamics of a system. Recovery rates upon perturbations (return rate, C and E) are slower when the basin of attraction is shallower (B) than when the basin of attraction is deeper (A). Increased slowness is reflected in stronger fluctuations in the state of the system measured as an increase in variability (compare D and F) as well as an increased temporal autocorrelation (G and I). Finally, the increasing asymmetry of the stability landscape close to the tipping point (B) leads to a skewed distribution towards values that reflect the direction of the future state of the system (H and J). Adapted from Scheffer M, Carpenter SR, Lenton TM, Bascompte J, Brock W, Dakos V, et al. (2012). Anticipating critical transitions. *Science* 338(6105): 344–348, with permission.

systems. Increased recovery rate has been manifested in a phytoplankton population prior to collapse in an experimental setup (Veraart et al., 2012), and rising variance and autocorrelation have been observed prior to trophic regime shifts in a whole lake manipulation (Carpenter et al., 2011). In addition, rising variance and skewness were found prior to eutrophication when analyzing sediment records in lake Erhai (Wang et al., 2012). However, estimating resilience indicators in five past well-documented regime shifts in aquatic systems showed divergent patterns among indicators (Gsell et al., 2016), highlighting that the practical application of resilience indicators for lake management is still challenging (Burthe et al., 2016).

Conclusion/Synthesis

Inland waters are facing numerous environmental stressors. In some situations, the resulting loss of ecological resilience causes small disturbances to trigger large shifts in the ecosystem state—a regime shift. When such shifted ecosystems are restored, hysteretic behavior triggered by new stabilizing feedback loops causes systems to shift back to their original state at much reduced levels of the original stressor. Therefore, successful restoration often consists of a combination of stressor reduction and biomanipulation—actively resetting dominant feedback loops. Regime shifts in inland waters strongly affect ecosystem functioning and the services associated with alternative regimes. Based on current insights, anticipating regime shifts remains a challenge.

Knowledge gaps

1. How to quantify resilience warnings that anticipate regime shifts and how to apply *them in order to take action before a shift occurs?* Whole-lake manipulation experiments and high-frequency continuous monitoring have demonstrated that resilience warnings could help to avert cyanobacteria blooms (e.g., Pace et al., 2017). Adoption of such approaches in lake management, however, remains a challenge.
2. *How to predict changes in ecosystem services related to alternative regimes*. Existing studies show contrasting results with respect to how ecosystem services, such as biodiversity provision and nutrient removal, change as a result of regime shifts (Hilt et al., 2017). A better mechanistic understanding is needed to predict changes in ecosystem services due to regime shifts.
3. *How to integrate spatial variation in resilience in our understanding of regime shifts*. First steps have been made in integrating spatial heterogeneity in models (e.g., Hilt et al., 2011 in streams; Janssen et al., 2017 in lakes), but further development of spatial ecosystem bifurcation analyzes and the validation and application in empirical studies are needed to, for instance, decide on spatially explicit restoration measures.
4. *How to apply knowledge on regime shifts and tipping points to inland waters other than shallow lakes*. Thus far, the main research focus has been on shallow lakes. However, we know little about regime shifts in other inland waters such as deep lakes, reservoirs, rivers and streams (Mesman et al., 2021).
5. *How to distinguish persistent regime shifts with alternative stable states from transient regime shifts with alternative unstable states?* Empirical work demonstrates that regime shifts may appear persistent, while in fact they are not. This is caused by slow ecological dynamics that lead in long-term transients following an abrupt change (e.g., Mushet et al., 2020). In a similar way, slowly responding systems may appear not shifting although in the long-run they would end up in a stable alternative state (e.g., Hughes et al., 2013). The theoretical and modeling framework of how persistent and transient regime shifts between alternative states occur is well-developed (Dakos et al., 2015), but identifying whether a regime shift will be persistent in practice remains a challenge.
6. *How to use knowledge on hysteretic behavior to optimize restoration?* Optimal restoration strategies need to take into hysteretic behavior into account as well as potential undesired new alternative states. Quantifying hysteretic effects, even when extensive system-specific knowledge is available, remains a challenge. In some cases, restoration does not result in the expected restored state (Chorus et al., 2020). For highly degraded systems, within-lake measures such as biomanipulation and geoengineering combined with stressor (nutrient) reduction show promise in restoration efficiency (Lürling and Mucci, 2020). Still, how to optimally design and execute restoration measures remains challenging as well.

Important case studies

A wide variety of studies has focused on alternative states in inland waters in different type of systems using different approaches with different foci. Below (Table 1) we mention several examples.

Table 1 Examples of case studies.

System	*Alternative states*	*Type of study*	*Main finding*	*References*
South African shallow lakes	Floating plants vs. invasive submerged plants	Field data	Biological control of floating invasive macrophytes can cause a regime shift between floating and submerged invasive plants	Strange et al. (2018)
Temperate, shallow lake (Lake Veluwe)	Clear, macrophyte dominated, turbid phytoplankton dominated and an intermediate state	Field data, long-term dataset	Clear hysteresis was observed during recovery from turbid-to clear in a shallow lake	Ibelings et al. (2007)
Shallow lakes in the Yangtze basin	Macrophyte vs. plankton dominated	Field data	Historic regime shifts were reconstructed using paleontological data and had different drivers in two different lakes	Xu et al. (2019)
Tropical shallow lake (Brazil)	Submerged vs. floating macrophytes	Field data	Phosphorus and light availability determine alternative state; floating plant dominance leads to a lower biodiversity	Moi et al. (2020)
Large shallow lakes	Submerged macrophyte vs. phytoplankton	Field data and modeling	Lake size, spatial heterogeneity and internal connectivity can explain the observed spatial presence of different states	Janssen et al. (2014)
Temperate, seasonally stratified lakes (Lake Vechten)	Oxic vs. anoxic—P dependent cyanobacteria-dominated vs. anaerobic microbial community with sulfur reducing bacteria and phototrophic sulfur bacteria	Field data and modeling	Feedbacks between biogeochemical processes and microbial-community dynamics drive shifts between oxic and anoxic states in seasonally stratified lakes	Bush et al. (2017)
Temperate Rivers and chains of lakes	Vegetated and clear vs. phytoplankton dominated and turbid	Modeling	Alternative stable states can only occur in systems with a high retention time and shift occurring upstream can propagate downstream	Hilt et al. (2011)
Shallow lakes in South America	Turbid vs. Clear	Field data and remote sensing	Turbidity is bimodally distributed in shallow lakes	Kosten et al. (2012)
Shallow lake (Gehu lake, China)	Turbid vs. Clear	Remote sensing	A regime shift from clear and macrophyte dominated to turbid was observed by remote sensing	Xu et al. (2020)
Large shallow lake (Lake Chaohu; China)	Submerged macrophyte vs. phytoplankton	Paleolimnology and modeling	Combined approaches showed interactive effect of two stressors (water level and nutrient loading) on regime shifts	Kong et al. (2017)

See Also: Structures and functions of Inland Waters - Lakes: Benthic Algae in Lake Littoral Habitats; Structures and functions of Inland Waters - Rivers: Riparian Zones

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Relevant Websites

http://www.early-warning-signals.org/—The Early Warning Signals Toolbox—For learning how understanding patterns can be used to quantify resilience based on dynamical system's theory.
https://www.regimeshifts.org/—The Regime Shifts DataBase provides examples of different types of regime shifts that have been documented in social-ecological systems. The database focuses specifically on regime shifts that have large impacts on ecosystem services, and therefore on human well-being.
https://www.oxfordbibliographies.com/view/document/obo-9780199363445/obo-9780199363445-0108.xml—Oxford bibliographies: "Ecological Transitions: Regime Shifts, Thresholds and Tipping Points".

Invasive Species☆

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This is an update of R.P. Keller, D.M. Lodge, Invasive Species, in *Encyclopedia of Inland Waters*, Edited by: Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00226-X.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Ballast water Large ships and other boats have tanks in their hulls which hold ballast water. These vessels take on and discharge ballast water to compensate for changes in the weight of cargo being carried.
Canal Human-created channels that usually connect freshwater ecosystems that were not previously connected. Canals are generally built for the movement of water (e.g., from relatively wet to relatively dry areas) and/or to facilitate boat movement.
Established A species that is successfully reproducing to maintain a population beyond its native range.
Introduced A species that has been transported and then released beyond its native range.
Invasive A species that has at least one population established beyond its native range that is causing harm to ecosystems, economies, and/or human health.
Laurentian Great Lakes This system of lakes is made up of five individual lakes; Superior, Michigan, Huron, Erie, and Ontario. These lakes hold ~20% of the world's surface freshwater.
Nonindigenous A species is considered nonindigenous when it is found in a region outside of its native range.
Propagule pressure A measure of the number of organisms of a species that are introduced to a given region. Propagule pressure is composed of both the number of times that individuals of the species are introduced, and the number of individuals released.

☆*Change History*: October 2021. RP Keller prepared the update. Text has been modified with minor edits throughout for clarity and to update with current knowledge. "Impacts on Human Welfare" section has been added. Text in the examples has been updated to reflect current state of these invasions. Further reading section has been updated with newer references, and several older references deleted.

Species traits Characteristics of a species. This includes many factors like a species' size, fecundity, diet, and its tolerances to environmental factors like temperature and salinity.
Vector A process or object that moves organisms. For example, the pet trade is considered a vector because it is responsible for the movement of many thousands of individual organisms. Likewise, the ballast water of ships is a vector because many organisms are inadvertently moved with it.

Introduction

The introduction of nonindigenous species occurs as a byproduct of globalization. As human societies, and thus the ecosystems where humans live, have become more connected through trade and travel, species transfers have increased. In freshwater ecosystems around the globe a large number of nonindigenous species are already established and in many systems the rate at which new species are becoming established is increasing exponentially. The impacts that these species have in their new ecosystems can be very high, and invasive species are likely to remain one of the greatest drivers of losses in freshwater biodiversity and ecosystem services for the foreseeable future. Thus, the future biodiversity, productivity, and ecosystem function of freshwaters is dependent on how societies manage current invaders and on whether the arrival of future invaders can be prevented.

Freshwater invasion biology involves the study of a diverse range of taxonomic groups in a diverse range of ecosystems. In this article, we first provide an overview of invasion biology, especially as it applies to freshwaters and the general management and policy options available. Second, we present three extended case-studies: (1) the history of multiple species invasions in the Laurentian Great Lakes basin; (2) the Nile perch (*Lates niloticus*) invasion of Lake Victoria; and (3) the history of invasions by water hyacinth (*Eichhornia crassipes*) in tropical and sub- tropical regions of the world. These case-studies are representative of the impacts of many more species in many more regions. The 'Further Reading' section directs readers to longer and more thorough analyses of many of the topics covered here, and these include analysis of many more individual invasions.

Invasion sequence

To become invasive, a species must pass through three steps (Lodge et al., 2006). First, to be introduced, it must be transported by a vector to a region beyond its native range. Second, the species is defined as established if reproducing populations are found beyond human cultivation. Finally, a species is defined as invasive if it spreads and causes undesirable impacts to the environment, economy, and/or human health. In the following section, we describe each step more thoroughly.

Introduction of nonindigenous freshwater species

The globalization of trade and travel has created many vectors that transport species short and long distances across the globe (Table 1; Lodge et al., 2006). Some of these vectors, such as the aquarium and live food trades, intentionally transport species; we refer to these vectors as commerce in living organisms. Other vectors, such as shipping, transport aquatic species as a side effect of other human activities; we refer to these as transportation-related vectors. Later, we examine some of the most important vectors listed in Table 1, but we emphasize here that the number and diversity of vectors is far greater than displayed in Table 1, especially for transportation-related vectors. Furthermore, we emphasize that vectors differ in importance in different parts of the world, vectors have fluctuated over time in terms of the number of species that they introduce, and vectors differ in importance for different taxonomic groups.

Table 1 Important vectors of transport for the introduction of non-native freshwater organisms.

Category	*Vector*
Transportation related	Ship's ballast water
	Fouling organisms on the outside of boats
	Movement of recreational boats (e.g., on trailers and motors, in live-wells)
	Hitch-hikers (e.g., snails on plants) moved unintentionally with trade organisms
	Angling equipment (e.g., waders, fishing tackle)
	Canals
Commerce in living organisms	Pet/aquarium trade
	Watergarden trade
	Bait trade
	Live food trade
	Aquaculture
	Stocking for recreational/commercial fisheries
	Biological control

Commerce in living organisms

Stocking for sport and food

Throughout history, humans have intentionally moved freshwater organisms in attempts to generate new food resources and/or opportunities for sport. The most commonly transported taxa have been fish, crayfish, and mollusks, with introductions occurring across the globe. In the United States alone, for example, 128 fish species that are non-native to the country are now established, and a further 323 species that are native to the United States have become established in regions of the country beyond their native range. Rainbow trout (*Oncorhynchus mykiss*), a popular angling fish and probably the single most introduced sportfish in the world, has been introduced to over 100 countries.

Stocking for sport and food has been carried out by government agencies as well as by private organizations and individuals. Growing awareness of the impacts of nonindigenous species has led to tighter regulations, and introductions of new species have dropped in many countries. Despite this, the economic and social value derived from desirable fishes means that while new introductions have declined there are still many species being stocked. For example, although no new fish species have been intentionally introduced to the North American Great Lakes Basin in recent decades there are still large government programs which annually release millions of non-native salmonids including brown trout (*Salmo trutta*), rainbow trout, Chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*).

The aquarium trade

Thousands of species of fish and other aquatic organisms are moved around the world for the aquarium trade, and hundreds of these have been released and become established. When the sheer number of organisms involved in this trade is considered, it is easy to see why it is an important vector for new invasions. In the United States, for example, the aquarium trade in the early 2000s was annually introducing over 172 million individual freshwater fish (Smith et al., 2008). The vast majority of these fish were not identified at the species level so the diversity of species being imported is unknown. Although the trade is presumably smaller in countries with smaller economies, it is still an important vector for introductions, with, for example, 22 out of a total of 34 established nonindigenous freshwater fish species in Australia originally introduced as aquarium pets. Globally, the aquarium trade is growing so introductions and harmful invasions are likely to increase. An additional concern is that a large diversity of freshwater organisms can now be ordered online and quickly delivered (Keller and Lodge, 2007). This makes it difficult to fully understand and assess the risk from the aquarium trade vector because species sales and transport are less likely to be recorded.

Aquaculture and the live food trade

Freshwater aquaculture, the captive propagation of freshwater organisms, is growing rapidly across the globe. Approximately 46% of all seafood (freshwater and marine) production globally came from aquaculture in 2018 (the most recent year for which statistics are available), and the largest portion (60%) of this is freshwater fish (FAO, 2020). Introduction and invasion often accompany these benefits because the aquaculture industry usually selects species that thrive in local conditions, that are tolerant of a wide range of environmental conditions, and that are fast growing. These qualities also predispose species to become invasive if they escape, and aquaculture has led to numerous invasions across the globe. Although the potential for invasions from this industry is now well known, few measures have been taken to prevent escapes. Several fish species, collectively known as tilapia species, for example, are being promoted to developing countries through international aid programs, despite the fact that many of these species have a long record of escape and harm to native species and ecosystems. In the United States, bighead (*Hypophthalmichthys nobilis*), silver (*Hypophthalmichthys molitrix*) and black (*Mylopharyngodon piceus*) carp have escaped from aquaculture facilities in the last three decades and have invaded the Mississippi River and tributaries. These species now threaten to invade the Laurentian Great Lakes via a canal that connects these waterways.

Transportation-related vectors

Canals

The construction of navigation canals has connected many isolated freshwater ecosystems and allowed many species to cross barriers that previously restricted their range. For example, the construction of the Rhine-Main canal means that there is now a navigable water connection from the Black Sea in Eastern Europe, along the Danube River and through to the Rhine River, which eventually flows into the North Sea. Similarly, in North America, the Chicago Sanitary and Ship Canal connects the Laurentian Great Lakes—St Lawrence River biogeographic region with the Mississippi River basin. As well as allowing species to expand their ranges through their own propulsion, canals facilitate the movement of species via ships and other transportation-related vectors.

Shipping: Ballast and hull fouling

Ships take on and discharge ballast water to compensate for changes in the mass of cargo carried. Organisms become entrained when water is taken on and can be released far from their native range when the ballast is discharged. Many other species, referred to as fouling organisms, are transported when they attach to the hulls of ships. Both ballast and hull fouling are important vectors of freshwater, as well as marine, organisms. Hull fouling is likely to be a strong vector especially for ships and barges that travel through freshwaters, but may also be significant for other voyages given the broad environmental tolerances of many species. Because global shipping is increasing rapidly, and because the movement of ships now effectively links all ports on earth, the number of invasive species moved by ships is likely to continue to increase.

Establishment of nonindigenous freshwater species

Three factors interact to determine establishment success for introduced freshwater species: propagule pressure, traits of the introduced species, and the suitability of the receiving habitat.

Propagule pressure

The number of organisms released into a new habitat, and the number of times that releases occur, is referred to as propagule pressure. Species are more likely to become established if many individuals are released simultaneously, and if multiple introductions occur over long periods of time. When propagule pressure is low, too few individuals may survive long enough to establish, and for sexually reproducing populations, this makes individuals unlikely to find mates. With multiple introductions during a year, conditions most favorable for survival and reproduction are more likely to be encountered by the species. Although propagule pressure is clearly important, records of the number of individuals and introduction events are rare. Hence, although it is known that propagule pressure is positively related to risk of establishment the exact relationship between these factors is not well known.

Species traits

The establishment success of a species also depends on the traits of that species. A good example is that a broad diet and fast growth rate increase the likelihood of an introduced fish species establishing in the Laurentian Great Lakes (Howeth et al., 2016). Similar relationships have been quantified for fishes introduced into California (Moyle and Marchetti, 2006), and for other taxonomic groups introduced to many freshwater regions of the world. Not surprisingly, the traits associated with establishment differ across species and across freshwater ecosystems.

Habitat suitability

Because each species can survive and reproduce under a limited range of environmental conditions, it is often straightforward to predict where and when certain introductions will fail to establish populations. Good examples come from fish in the aquarium trade, which are mostly of tropical or sub-tropical origins. In the temperate Laurentian Great Lakes basin, only two species from the aquarium trade have established. In contrast, Florida, a sub-tropical state in the Southern United States, has over 40 established fish species that were introduced for the aquarium trade. Habitat suitability includes the potential effects of native species which may increase (e.g., by serving as prey) or decrease (e.g., by preying upon) the probability that introduced species will become established.

Impacts of invasive freshwater species

The final step in the invasion sequence occurs when established species spread and cause negative impacts. It is notable that most established species do not cause any measurable harm. Despite this, the sheer number of species that are introduced and become established means that the number of species that do cause harm is very large. These species are referred to as invasive. The same factors associated with species passing from introduced to established are important at this step, with species whose traits are well matched to their receiving environment being more likely to reproduce rapidly and spread. Propagule pressure may remain important at this step if new propagules increase genetic diversity that enhances local adaptation to the new environment. Below we discuss some of the major impacts caused by invasive freshwater species. First, we describe the ways in which invasive species harm ecosystems and economies. Finally, we describe damages to human welfare which have only recently begun to receive more research and attention.

Impacts on ecosystems

Invasive species often have large impacts as predators, herbivores, competitors, and ecosystem engineers. Additionally, when an invasive species is closely related to native species, hybridization with the native species can cause a loss of native genetic diversity. Although these are the same mechanisms by which native species interact with each other, the impacts of invasive species are often very large because they either introduce a novel function to their recipient ecosystem, or they prove more capable of exploiting resources than native species.

Freshwater invasive species impacts can be particularly severe when the invader becomes established as a 'trophic dead-end.' For this to occur a species must consume a large portion of total ecosystem productivity but not be susceptible itself to high levels of predation. Thus, resources become concentrated in the invading species. An example is the New Zealand mudsnail (*Potamopyrgus antipodarum*) that is invasive in Australia, North America and Europe. In a study of a stream in Wyoming, United States, this species was found to consume 75% of gross primary production through its herbivory (Hall et al., 2003). The main predators of New Zealand mudsnail are fish, but other studies have shown that the snails can survive gut passage. Hence, a large portion of total system productivity has been lost to the native food web. In this example, the primary impact of the invasive species is through

herbivory (grazing on algae), but secondary impacts may spread throughout the food web and ecosystem. Similar impacts are caused by the invasion of North American and European waters by zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels, and by invasions by crayfish (e.g., red swamp crayfish *Procambarus clarkii*) in many parts of the world.

Competition between freshwater species is often difficult to demonstrate. Nevertheless, it is likely an important mechanism by which many invasive species impact biodiversity. Some well-known examples are invasive macrophytes, especially floating plants such as water lettuce (*Pistia stratiotes*) and water hyacinth (*Eichhornia crassipes*), many of which establish thick mats of vegetation on the water surface that deprive the native species below of light.

North America is recognized for a diverse freshwater biota. Many of these species are recently evolved under conditions of geographic isolation. The construction of canals, release of aquarium and bait organisms, and other mechanisms that overcome natural isolation have produced many opportunities for hybridization and subsequent loss of biodiversity (Perry et al., 2002). For example, rainbow trout were introduced extensively for decades in the Rocky Mountain region of the U.S. to establish populations for sport-fishing. In many areas these non-native rainbow trout hybridize with the native cutthroat trout (*Oncorhynchus clarkii*). The hybrids produced are fertile and introgression of rainbow trout genes into cutthroat trout genomes means that across much of its historical range the native species has been replaced by the invader and hybrids (Muhlfeld et al., 2017).

In addition to strong direct impacts on biodiversity via food web interactions, invasive freshwater species often change physical and chemical conditions in their recipient ecosystem. For example, invasive macrophytes can reduce light and oxygen levels in the water column, thus altering opportunities for other species. Invasive crayfishes (e.g., red swamp crayfish) can burrow into the substrate and cause increased erosion and water turbidity, and some invasive fishes (e.g., common carp *Cyprinus carpio*) cause similar impacts through their feeding activities.

Introduction of parasites and diseases

Parasites and diseases are often transported in association with nonindigenous species, and these may have large impacts when native organisms have little or no resistance. Because the introduction and impacts of parasites and diseases are difficult to recognize and study, it is reasonable to believe that they are more common and larger than available results suggest. One well-known example is crayfish plague (*Aphanomyces astaci*), a fungal disease endemic to North America that was transported to Europe with American crayfish introduced for aquaculture. European crayfish species have no resistance to the disease, and in both Scandinavia and the United Kingdom whole populations of the only native crayfish species (white-clawed crayfish *Austropotamobius pallipes*) have been eradicated by this disease.

Economic impacts

Loss of valuable species

Many of the highest profile invasive freshwater species achieved notoriety by harming species that humans exploit. Sea lamprey (*Petromyzon marinus*) has invaded the Laurentian Great Lakes and caused large declines in commercial fish stocks, and Nile perch (*L. niloticus*) has greatly reduced populations of endemic cichlids in Africa's Lake Victoria that were once captured for the aquarium trade (each of these examples is detailed further in the *Case-Study* section below). Other species have had similar impacts. For example, concern about the spread of the algae *Didymosphenia geminata* in New Zealand is largely focused on its potential to reduce food resources for trout, and thus to decrease the value of recreational fisheries.

Fouling of industrial systems

Many industries around the world are sited on lakes and rivers to provide easy access to water, and several species have become serious pests by fouling water intake structures. The highest profile of these are the zebra and quagga mussels. Each of these has a planktonic juvenile stage during which individuals can be entrained into pipes where they settle and grow, eventually restricting water flow through the pipe. In response, whole industrial systems, such as nuclear power stations, may need to cease operations to clean out their pipes on a regular basis. In the United States portion of the Great Lakes alone, it is estimated that zebra mussels caused losses of over $200 million annually during the early part of their invasion through direct costs for cleaning and lost production. Recent impacts may be lower as industrial facilities have altered equipment and practices to reduce the impacts of these species. Dreissenid mussels have similar impacts across much of Europe and the United Kingdom. While these impacts are costly, the filtering activity of dreissenid mussels has made water clearer in many lakes. Clearer water is considered more desirable by many people and in some cases this impact of mussels has been linked to higher property prices.

Impacts on human welfare

Most research on the impacts of invasive freshwater species has occurred in relatively wealthy countries and has focused on how ecosystems, industrial economies, and recreational opportunities are affected in those countries. Because these countries generally have good infrastructure the direct impacts of invasive species on human welfare—for example by reducing water supply to subsistence farmers—have largely been overlooked. Several recent studies have begun to address this and made clear that some invasions lead to very severe impacts for human welfare. For example, Wular Lake in Kashmir (India) was recently invaded by two floating aquatic plant species. These plants now cover much of the lake for much of the year and reduce access to fisheries and water. The human population in the area experiences high levels of poverty, low levels of education, and relies heavily upon resources

extracted from the lake. As those resources have been reduced by the invasive plants many people have had to leave their villages to seek work elsewhere (Keller et al., 2018). A similar example comes from South Africa where dense populations of invasive plants—including aquatic invasive plants—transpire more water than native plants and lead to reduced streamflow in regions that are already water-stressed. This leads to less water availability for municipal purposes and agriculture (van Wilgen and Wannenburgh, 2016). Because these and other impacts on human welfare have received relatively little attention it is likely that they are much greater and more widespread than is currently known.

Managing established freshwater invaders

Two things are generally true about the detection and management of invasive freshwater species. First, most species are well established by the time that they are detected, and second, established populations of aquatic species can rarely be controlled or eradicated without using broad spectrum poisons that cause large nontarget effects. For example, with rare exceptions (e.g., the sea lamprey example below) the best option for controlling invasive fish populations is to use the poison rotenone, which kills all fish in the waterbody. Likewise, efforts to control or eradicate macrophytes often rely upon broad spectrum herbicides that kill all aquatic plant life. Because of the unintended effects on native species these methods are most commonly used in heavily human altered ecosystems (e.g., impoundments, canals) where the value of native biota is generally considered to be lower than in more natural systems. In very large or flowing systems (e.g., large lakes, rivers) the use of poisons is usually impractical because they disperse too quickly. Thus, preventing introduction of species and preventing further spread once a species is established in a region are the most cost-effective management strategies.

Interactions with other mechanisms of global environment change

The number of established invasive species, as well as their impacts, are magnified by a host of other mechanisms of global environmental change (Kolar and Lodge, 2000). In many cases environmental changes favor nonindigenous species over native species adapted to the previous conditions. Regulation and impoundment of rivers, for example, favors lentic over lotic species. Similarly, eutrophication, a globally common environmental change, creates similar conditions across continents that facilitate establishment, spread, and impacts of the same invaders like common carp.

Global climate change is altering conditions in freshwater ecosystems across the globe, including flow rates and volumes in rivers and patterns of drought and flood. In many cases the resulting changes are reducing populations of native species and allowing non-native species to become established (Rahel and Olden, 2008). The situation in freshwaters is complicated, however, because although rivers and lakes may become warmer, there is usually no opportunity for invaders to naturally disperse over land among these systems. The exceptions are lakes that are large enough that some species can presently survive in some but not all parts, and rivers that flow on a north south orientation. Because humans continue to transport and introduce invasive species, however, invasive species ranges are likely to grow as species that would previously not have persisted where they are released will be able to establish under the new conditions.

Case study 1: Invasions of the Laurentian Great Lakes

Europeans settled the Laurentian Great Lakes basin in the early 1800s, and ever since the lakes have been a focus for navigation, commerce, and recreation. These activities have caused the establishment of at least 188 non-native species (Fig. 1; Ricciardi, 2006; Sturtevant et al., 2019). Many of the earliest species introduced to the Great Lakes were fish released by private individuals and government agencies with the aim of providing new commercial and recreational fisheries (Fig. 1). Records of these releases were not well kept, and because lake ecology was not well studied at the time, little is known about the impacts of these introductions.

The first nonindigenous species to attract widespread attention was the sea lamprey, which entered the Great Lakes through the Welland Canal. This canal was constructed in the 1830s to allow boats to bypass the Niagara Falls and directly access the upper Great Lakes. It has also allowed for biotic transfer between the two previously isolated ecosystems. Sea lamprey are a parasitic fish that feed off larger fish, including the native lake trout. At the time that sea lamprey arrived there was a large commercial fishery for lake trout and populations of lake trout were already declining due to over-fishing. Sea lamprey greatly accelerated this decline and many stocks of lake trout were completely lost, along with the commercial fishery and many jobs. Sea lamprey persists in the Great Lakes to this day, although it is effectively controlled by lampricide applications to its breeding streams (Fig. 2; Heinrich et al., 2003). These lampricides can be implemented with acceptable levels of non-target effects because lamprey are susceptible to poisons that are not toxic to other species, and because lamprey breeding streams have been identified so that general application of the lampricide is not needed.

As oceangoing ships have gotten larger and faster, ballast water has become the dominant source of new introductions, and is the likely vector for 65% of the approximately 70 species that have become established since the enlarged Welland Canal opened and oceanic shipping to the upper lakes began in 1959. As the number of established species has grown, so too have the total impacts of invaders. The invaders that have achieved the greatest notoriety are probably the closely related zebra and quagga mussels, which

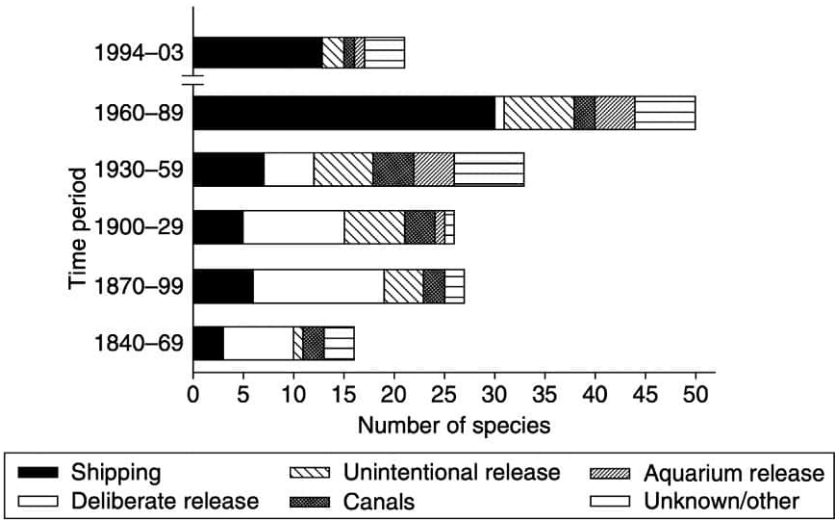

Fig. 1 Number of species introduced, and vectors of transport, for the Laurentian Great Lakes from 1840 to 2003. Reproduced from Ricciardi A (2006) Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions* **12**: 425–433.

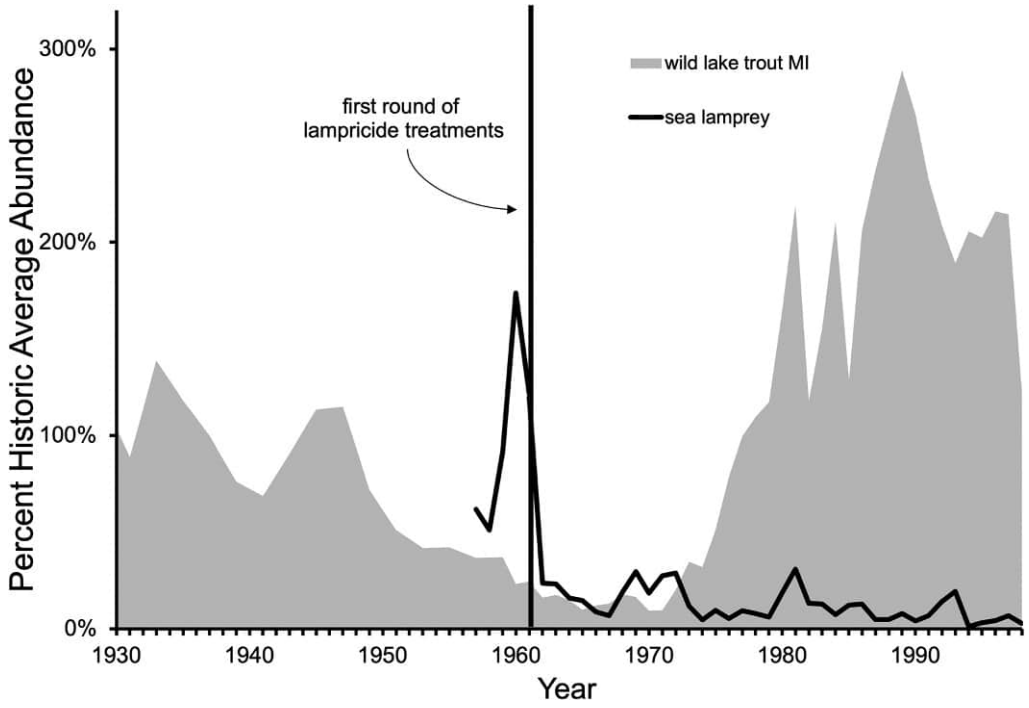

Fig. 2 Population fluctuations (expressed as relative abundance) of lake trout and sea Lamprey in the Michigan waters of Lake Superior from 1930 to 2000. Lake trout populations were already in decline due to overfishing when sea lamprey achieved high populations, and sea lamprey parasitism contributed to further lake trout population declines. Lake trout populations have since recovered, and sea lamprey populations are now kept down by applying a lampricide to their natal streams. Source: Great Lakes Fishery Commission.

were introduced in ballast water and discovered in the mid-1980s. Although the zebra mussel was initially dominant, it has largely been replaced in the five Great Lakes by the larger quagga mussel in recent years. Quagga mussel are larger and live across a greater range of depths, and they now consume a vast amount of the primary production of the lakes. Although one impact of zebra and quagga mussel establishment has been positive—its filter feeding has improved water clarity—these species have caused enormous economic damages and extensive ecological changes to the Great Lakes (Karatayev et al., 2015).

Efforts to reduce future impacts of Great Lakes invaders are focused on preventing the further spread of known invaders and the arrival of new invaders. Ships are now required to exchange ballast water in the open ocean before they can discharge it into the Great Lakes, and efforts are being made to address invasions from trades. A drop in the rate of new species discovery indicates that these efforts may be having some success (Sturtevant et al., 2019). Overall, however, further invasions should be expected through trade, shipping, and canals because many of these pathways and vectors remain active.

Case study 2: Nile Perch in Lake Victoria—Good intentions gone wrong

Perhaps the best-known example of biodiversity impacts from a freshwater invasive species is the introduction of Nile perch to Lake Victoria (Africa) in 1954 (Pringle, 2005). This introduction was intended to augment fisheries in the lake, and thus to provide an extra source of protein, jobs, and income for locals. For a number of years the species thrived, and to this day it supports a large, mainly export, fishery. Although the original intentions for introduction were initially met, they have come at a large cost to biodiversity and indigenous fisheries.

Lake Victoria is famous for its enormous diversity of endemic cichlid fish, which although never fully counted probably once numbered around 450 species. These cichlids were captured and reared for the aquarium trade, but it is estimated that approximately half of these species have been driven to extinction—or at least to undetectably low abundances—by Nile perch predation. Additionally, because many of these cichlid species were algae eaters, it is likely that the Nile perch introduction is at least partly responsible for an increased incidence of nuisance algal blooms in the lake. These algal blooms reduce visibility, which further interferes with mate recognition for the endemic cichlids and leads to hybridization and genetic introgression.

Nile perch support a valuable fishery in Lake Victoria, and even if the will existed it is unlikely that they could be eradicated. Indeed, most efforts to remove populations of invasive fish rely on general purpose fish poisons, so the consequences of such attempts would be unacceptable. Recent declines in the Nile perch population have, however, allowed for a recovery of some cichlid species. As these declines in Nile perch may be due to overfishing, the future of many of the remaining cichlid species may depend on future management of the Nile perch fishery.

Case study 3: Water hyacinth—An attractive invader

One of the most popular species in the global ornamental plants trade, and one of the most invasive, is water hyacinth. This species is native to Brazil, but is now widely established in tropical and subtropical regions around the world. Water hyacinth is popular for both aquarists and water gardeners because it is one of only a few floating aquatic plants, it reproduces extremely quickly (a population can double its biomass every 6–18 days), and because it produces large numbers of attractive purple flowers. It is also highly invasive and forms monospecific mats on invaded lakes and rivers (Fig. 3). This leads to a number of ecological impacts, including reduced light and oxygen levels in the water column, which in turn reduces native macrophyte diversity and can lead to fish kills, and to the loss of waterbird habitat. Water hyacinth populations have large negative impacts on human society by clogging lakes and waterways and impeding navigation and fishing, by providing breeding areas for mosquitoes and thus exacerbating vector-borne diseases, and by reducing opportunities for recreation. It is considered one of the world's most costly and damaging species.

As well as introducing water hyacinth beyond its native range, humans have altered the hydrology and chemistry of many tropical and subtropical freshwater ecosystems in at least two ways that encourage this species. First, the conversion of flowing rivers to impoundments has provided habitats ideal for this floating species. Second, eutrophication resulting from agricultural runoff leads to much higher water hyacinth growth rates, and subsequently much higher impacts.

Fig. 3 Water hyacinth (*Eichhornia crassipes*) infestation in Hawaii. Courtesy Forest and Kim Starr, Starr Environmental, Bugwood.org.

Although water hyacinth is a well-known invader, it remains valuable for trade and easy to purchase, creating an obvious tension with the large amounts of money spent to manage the species. In the United States, populations are often broken up with large, floating chopping machines. This method reduces the current size of an infestation, but does not eradicate the plant. It can also have the unintended consequence of encouraging further spread because the fragments created are relatively easy to inadvertently transport (e.g., on boat trailers) and may remain viable. In Africa, a number of infestations have been controlled through the release of insect species that preferentially feed on water hyacinth. Elsewhere, manual removal of infestations is favored because it reduces the possibilities of fragments founding new populations, and does not involve the risks from introducing new species. Despite the successes from these methods, however, water hyacinth will undoubtedly remain a serious invader across the globe for the foreseeable future. New populations are likely to become established as a result of further releases from the ornamental trades, and it is likely that climate change will enable the establishment of water hyacinth in regions where it was previously too cold for the species to survive.

See Also: **Emerging methods and topics**: Environmental DNA Advancing Our Understanding and Conservation of Inland Waters; **Human pressures and management of Inland Waters**: Biological Invasions: Case Studies; Biological Invasions: Impact and Management; Biological Invasions: Introduction, Establishment and Spread; **Structures and functions of Inland Waters - Lakes**: Benthic Algae in Lake Littoral Habitats; **Structures and functions of Inland Waters - Rivers**: Invasive Species in Streams and Rivers; **Structures and functions of Inland Waters - Wetlands**: Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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Relevant websites

www.fishbase.org—FishBase.
www.asiancarp.us/—Invasive Carp Regional Coordinating Committee (ICRCC).
http://nas.er.usgs.gov—United States Geological Survey (USGS).

Ecosystem Engineers in Freshwater Ecosystems

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Glossary

Allogenic engineers Organisms that modify the environment by transforming material (other than themselves).
Autogenic engineers Organisms that modify the environment by their own physical presence.
Bioturbator An organism that disturbs sediments.

Introduction

The term Ecosystem Engineer was first coined in to describe "organisms that modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and/or create habitat" (Jones et al., 1994). Prior to 1994, when the term's definition was published, researchers were studying cases of specific species that changed their environments, e.g., Darwin wrote extensively on soil formation by earthworms (Darwin, 1892) and beavers have long been known to alter streams (Naiman et al., 1988). However, the lack of a term for an idea makes it difficult to discuss. For example, consider trying to discuss "organisms that share the same function in the food chain and the same nutritional relationship to the primary sources of energy" (Oxford Languages) instead of discussing "trophic levels." Ecosystem engineering is a fundamental concept for understanding how organisms interact with and modify their environment. The citation rate of the term 'ecosystem engineer' has increased since 2010 (Emery-Butcher et al., 2020). Despite increasing citation of this term, many textbooks on ecology don't include the term in their table of contents (e.g., Begon and Townsend, 2020; Sher and Molles, 2022). It is true that the citation rate increase has been slower in freshwater than terrestrial and marine systems; this relative inattention to ecosystem engineering in freshwater research does not reflect the actual importance of ecosystem engineering in inland waters.

Types of ecosystem engineers

Ecosystem engineers were categorized as one of two primary types by Jones et al. (1994):

1. *Autogenic engineers* modify the environment by their own physical presence via their living or dead tissues. Note that habitat modification by an organism's body differs from the energy that their tissues may contribute to the food web. Examples include submerged aquatic vegetation (SAV) that define the littoral zone, or dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*) that create hard surfaces with many interstitial spaces.
2. *Allogenic engineers* transform living and nonliving material (other than themselves) from one physical state to another. Examples include beaver (*Castor canadensis*) which construct dams (Fig. 1) that can alter the flow of rivers, and phytoplankton which shade the water column and can outcompete SAV and benthic algae for light.

Ecosystem engineers in different freshwater habitat types

Open water: The open water zone lacks hard physical structures and therefore autogenic ecosystem engineering is not likely to be prominent in this habitat. However, spatial structure in open water zones is often be defined by gradients in temperature, oxygen, and light which can be influenced by allogenic ecosystem engineering.

Organisms that control light are a major category of ecosystem engineers (Berke, 2010). Phytoplankton frequently control water clarity, thereby regulating light penetration, and are consequently a common ecosystem engineer in the open water. Regulation of light penetration by phytoplankton can control the depth to which other primary production is possible. The depth of SAV is controlled by light availability (Duarte et al., 1986) although plants are adapted to different light conditions and therefore the actual

Fig. 1 Beaver family near entrance of their lodge at Old Woman Creek National Estuarine Research Reserve. Photo by E. Kuzmick.

depth limit is species-specific (Middleboe and Markager, 1997). Some phytoplankton such as *Microcystis* spp. control their buoyancy with gas vacuoles (Reynolds et al., 1987) and can therefore maintain their position near the water surface and shade light away from other phytoplankton species. Consequently, phytoplankton acting as light engineers may influence the distribution of all other primary producers in aquatic habitats.

Phytoplankton also produce oxygen as a byproduct of photosynthesis and therefore affect oxygen gradients, especially in lakes. Oxygen is required by all animal life and therefore defines where animals and aerobic microorganisms can live. Although physical mixing with the atmosphere also contributes oxygen, as one of the major producers of oxygen, phytoplankton are important ecosystem engineers controlling this essential element. The ancient marine ancestors of freshwater cyanobacteria evolved the ability to photosynthesize and released large amounts of molecular oxygen into the atmosphere early in Earth's history (Buick, 2008). The appearance of oxygen in the atmosphere literally changed the world and altered the course of the evolution of life. Therefore, the marine precursors of freshwater phytoplankton were the original, and global-scale ecosystem engineers.

Bottom: Submerged Aquatic Vegetation (SAV) provides a structured habitat to other organisms ranging from algae to fish. Algae, microbes, and small animal live on the surfaces of SAV stems and leaves. Many of these organisms can also live on inert substrates, but the presence of SAV vastly increases the amount of substrate available meaning that SAV acts as autogenic engineers. SAV may additionally supply attached algae with nutrients, especially in oligotrophic waters (Eminson and Moss, 2007) and consequently SAV can also function as allogenic engineers. Attached algae themselves may also be considered ecosystem engineers, albeit at a much smaller spatial scale than SAV because they form a structural matrix that is inhabited by microbes and small animals such as rotifers. At a larger spatial scale SAV provides habitat for littoral fish species, such as sunfish (family Centrarchidae). The presence of SAV transforms an aquatic area via autogenic engineering in the same way that trees transform a terrestrial area and define it as a forest. The cover created by SAV can modulate foodweb interactions (Carter et al., 2010) and SAV density can affect commercial fishery landings (Giacomazzo et al., 2020). The littoral zone, which is defined by growth of SAV is therefore an area that is highly impacted by both autogenic and allogenic engineering.

Bioturbators physically restructure sediment and act as allogenic ecosystem engineers in the same way that earthworms engineer terrestrial soils (Le Bayon et al., 2017). Even relatively small burrowing invertebrates such as chironomid larvae affect the physical properties of sediment (Baranov et al., 2016). Mayflies of the genus *Hexagenia* construct U-shaped burrows and maintain high oxygen concentrations in their area (Wang et al., 2001). *Hexagenia* burrowing activity can release phosphorus from sediment and contribute to internal loading (Chaffin and Kane, 2010). Large bivalves such as those of the Unionidae family may restructure sediment at a more bulk-scale than do insect larvae. Unionids physically alter sediment by increasing water content and homogenization and they may also alter carbon and other nutrient content via biodeposition of waste (Vaughn and Hakenkamp, 2001). Consequently, the effect of engineering by bioturbators depends on the species, and can affect the structure and chemistry of the sediment as well as the coupling between the benthic and open water habitats of inland waters.

In contrast to bioturbating bivalves which churn sediment, other bivalves cap sediment and form a hard substrate (autogenic ecosystem engineering), qualitatively altering the type of bottom present. Zebra (*D. polymorpha*) and quagga (*D. bugensis*) mussels, introduced and invasive ecosystem engineers (Karatayev et al., 2002), have restructured bottom habitats outside their native range. They grow in clusters (Fig. 2) with interstitial spaces that provide habitat for invertebrates, which can increase locally in density (Mayer et al., 2002; Stewart et al., 1998). In addition to autogenic engineering, where they create hard substrate, *Dreissena* are also allogenic engineers as filter feeders that clear the water column and modulate the availability of light to other organisms. *Dreissena* can sharply increase water quality and this effect occurs at a lake-wide spatial scale (Mayer et al., 2014). Alteration of the light environment connects directly to a number of trophic levels rather than being transmitted through a series of links as in a trophic cascade. Increased light increases the photosynthetic rate of plants and algae, and also directly alters the environment for visual

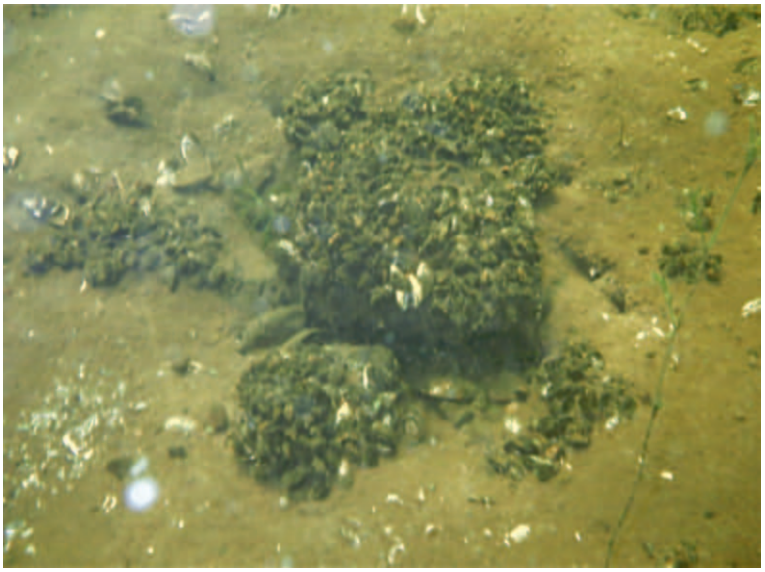

Fig. 2 Zebra mussels forming clusters surrounded by silty sediment in Oneida Lake. The largest cluster is formed on a rock. The smaller clusters are spreading out from smaller stones or other hard objects. Photo by K. Schulz, SUNY-ESF.

predators and prey. Additionally, *Dreissena* shift the spatial distribution of nutrients towards shallower areas where they are more abundant in large lakes, a process called the Near Shore Shunt (Hecky et al., 2004). The combination of multiple types of engineering coupled with large populations have made *Dreissena* a highly influential invasive ecosystem engineer.

Moving Water: In streams engineers also affect stream flow in addition to the effects on bottom structure and light penetration. This activity can dramatically change habitats. Beavers construct dams that make pools out of streams; probably the most well-known example of an ecosystem engineer (Jones et al., 1994). But other species also change stream flow. One of the most striking types of ecosystem engineering is gravel nest building. For example, fish of the genus *Nocomis* build mounds of gravel by transporting individual stones in their mouths (Frimpong, 2018) (Fig. 3). These nests often provide habitat used by nest associate species which benefit from spawning on the constructed nests (Johnston, 1994) and likely benefit the host species in a mutualistic association (Peoples and Frimpong, 2013). This form of allogenic ecosystem engineering is similar to dam construction by beavers in that both animals are purposefully moving materials to construct nests that happen to cause larger habitat modifications.

Applications to management and conservation

Invasive ecosystem engineers may disrupt ecosystems more than non-engineering invasive species because they modify habitat (Emery-Butcher et al., 2020). It is true that not all the impacts of invasive engineers are negative. For example the roots of an invasive species of SAV may stabilize sediment similarly to a native species (Emery-Butcher et al., 2020) and zebra mussels enhance habitat availability for native benthic invertebrates (Mayer et al., 2002). Nonetheless, status as an ecosystem engineer may be an important consideration in assessing the risk a potential invader poses. Conversely, for species that are managed for conservation, ecosystem engineer status may increase the perceived value of conservation since that species effect on the overall ecosystem via habitat modulation is likely to be great.

Knowledge gaps

One challenge in research on ecosystem engineers is that there is less basis for making predictions about the outcomes of interactions than there is when studying other processes such as predation or competition. In a predation event, there is a clear winner (predator) and loser (prey). In contrast, changing habitat may favor some organisms while disadvantaging others. For example, as *Dreissena* increase water clarity and light penetration fish species that forage efficiently in low light may experience a relative disadvantage, whereas some visually feeding species may forage more successfully. Consequently, focusing on approaches that describe and quantify the magnitude of interactions in addition to direction may help study of ecosystem engineering continue to move beyond case-studies.

Fig. 3 (A) Abandoned gravel spawning nest built by a *Nocomis* chub in central Tennessee, United States. (B) Spawning male redtail chub (*Nocomis effusus*) collecting and placing rock on a gravel spawning nest in the Duck River watershed, central Tennessee, United States. Photo by Mr. Lance Merry, (natureman187@yahoo.com).

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Nutrient Stoichiometry in Aquatic Ecosystems

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This is an update of RW Sterner, Nutrient Stoichiometry in Aquatic Ecosystems, In *Encyclopedia of Inland Waters*, edited by GE Likens, Elsevier Inc.,2009 https://doi.org/10.1016/B978-012370626-3.00113-7 with revisions made by the Editor.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Introduction

In chemistry, the term 'stoichiometry' refers to the number of atoms of elements on both sides of a reaction. Stoichiometry tells you how many different molecules of each type of reactant you need to generate a specific product or set of products. Ecologists and limnologists can use these same principles of stoichiometry to understand aquatic ecosystems because individual species, like molecules, have defined chemical composition. The elemental formula of an individual species is normally not as strictly defined as the kinds of molecules we are most accustomed to thinking about, those with specific, unvarying composition. However, stoichiometry can still be a very useful approximation. Stoichiometry has much to say about the linkage of cycling of different elements and about patterns of nutrient limitation in primary producers and other parts of food webs. It bridges studies on individual species with studies dealing with the flow of matter and energy in ecosystems.

In this article, we first consider some of the patterns in elemental content of particular aquatic organisms and then we consider the ecological consequences of those patterns.

Stoichiometric homeostasis

Homeostasis is one of the hallmarks of life. Homeostasis is a resistance to change. For example, homeothermic organisms maintain a constant body temperature in spite of fluctuating environmental temperature. There are many other examples of homeostasis in biology, like the pH of blood and the concentration of ATP in a cell. Homeostasis results from negative feedbacks. In ecological stoichiometry, we use this same term to refer to the tendency of an organism to maintain its chemical content in spite of variation in the chemical content of its resources (Fig. 1). The figure illustrates the general principle. Mathematically, stoichiometric homeostasis (H) is defined as

$$y = cx^{1/H}$$

where y = organismal elemental content (e.g., moles P per dry mass of animal), c = a constant, x = elemental content of resources (measured in the same units as 'y'), and H (the Greek letter 'eta') is the measure of homeostasis. If homeostasis is so strong that organismal content is constant no matter what the chemical content of the organism's food is, the stoichiometric coefficient H approaches infinity and we refer to that as a 'strict homeostasis'.

Not all species maintain stoichiometric homeostasis to the same degree, and within any given species not all resources are regulated equally. These differences will be elaborated upon later, but in terms of nutrients such as nitrogen and phosphorus, primary producers generally have more variable chemical content than animals. Algae and macrophytes, like other 'plants' and many microorganisms, can store nutrients by assimilating them at rates much larger than immediate requirements. Later, these organisms can then tap into these reserves for future growth. Animals have more limited capacity for nutrient storage. Differences in mean chemical content between plants and animals have also been suggested recently by analysis of selected proteomes (all of the proteins produced by a species) of these groups; animals had about 7% higher number of N atoms per amino acid side chain than did plants.

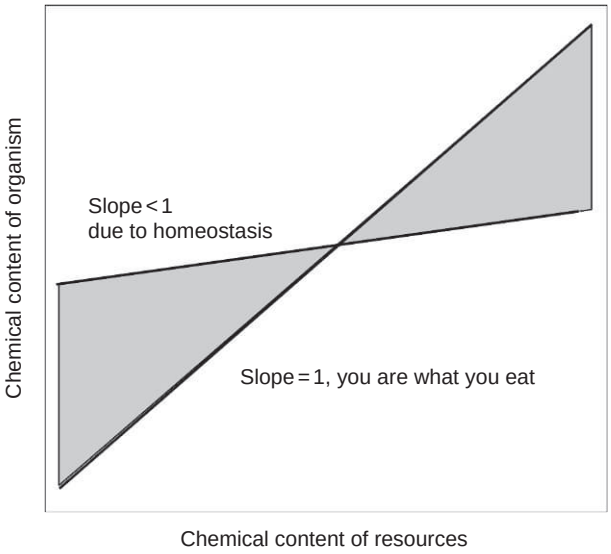

Fig. 1 Stoichiometric homeostasis deals with the question of whether organisms 'are what they eat'. Organisms have varying strengths of regulating their own content of different elements. If the chemical content of organisms passively reflects the resources they take in, their own chemistry would match the chemistry of their resources, and observations would lie along the 1:1 line marked 'you are what you eat'. This would be an absence of stoichiometric homeostasis. Stoichiometric homeostasis reduces the slope of the relationship below the 1:1 line (shaded regions). Different organisms and different chemical resources produce different degrees of homeostasis (see for example Table 1).

Table 1 Coefficients of variation (CV) of content of different elements (log10-transformed) measured over a season in a single pond.

Organism	*Content of elements*									
Amphipod	C	N	P	Cu	Zn	Se	As	Pb	Hg	Cd
	0.004	0.005	0.007	0.009	0.018	0.019	0.021	0.059	0.079	0.124
Damselflies	C	N	P	Cu	Se	Zn	As	Hb	Cd	Pb
	0.004	0.004	0.016	0.024	0.025	0.030	0.035	0.05	0.053	0.074
Snails	C	N	P	Se	Zn	As	Cu	Cd	Hb	Pb
	0.002	0.005	0.007	0.018	0.018	0.018	0.019	0.040	0.045	0.085
Zooplankton	C	P	N	Zn	Se	Pb	As	Cu	Cd	Hg
	0.003	0.003	0.006	0.007	0.017	0.02	0.026	0.035	0.041	0.059

Within an animal taxon, variation in element content is lowest for macronutrients, intermediate for essential micronutrients, and highest in nonessential metals (Table 1). Animals apparently regulate macro-elements most strictly and they regulate elements with definite biological function more than those elements that are incorporated into cells even though they are not essential for growth or survival.

There has been progress recently in defining patterns of homeostasis across elements and across organisms, but we are still a long way from a comprehensive understanding of all the potentially important patterns and contrasts. Homeostasis is an important concept in ecological stoichiometry because the stricter the homeostasis the closer the more an organism's chemical composition resembles a molecule with defined composition. Maintaining a given chemical content in spite of the composition of resources has some detrimental effects on fitness. As we will see later, homeostasis makes organism growth sensitive to the composition of the food that is eaten. Without homeostasis, organisms would 'be what they eat' and there would be no slowing of growth when an individual element becomes scarce. There must be substantial benefits to homeostasis to make up for the easily observed costs, but much less is known about the nature of these benefits.

Stoichiometry at the organism level

Let us now examine some of the stoichiometric patterns for particular aquatic organisms. Organisms vary in nutrient content for many reasons because there are many functions of different elements in biology. Several fundamental causes for organism-level variation in stoichiometry are phylogeny (closely related species are more likely to resemble each other in terms of stoichiometry as well as many other phenotypic traits), structure (especially for large organisms or those with major investments in support or

defense), allometry (effects of body size), and life histories (high rates of growth have a unique stoichiometric signature). In considering these factors, we will start at the base of the food chain, the primary producers.

Primary producers

As is apparent from many examples given throughout this article, stoichiometric variability is the hallmark of primary producers. This variability arises because nutrient uptake and biomass gain can be decoupled. For example, if one exposes a nutrient-limited algal cell suddenly to high concentrations of nutrients, within minutes it can replenish cellular nutrient stores. It then puts those stores to work over time scales of hours to days as the cell gains organic carbon via photosynthesis and eventually divides by fission or mitosis. Cells also may take up nutrients for more than any immediate growth needs, resulting in higher nutrient content than seen in long-term, high growth-rate situations. These cellular nutrient stores sometimes are in the form of specialized storage compounds such as polyphosphate (for P) or cyanophycin (for N). The autotroph cell can also divert resources among different functional pools, for example photosynthetic pigments are N-rich and often cells growing under low light and excess N will be very rich in these pigments. If that cell moves to a high light but low N environment, those pigments can be broken down and the N moved into different pools. In this way, photosynthetic pigments serve as an N reservoir, even though they are not storage compounds per se.

The general model used to describe the linkage between cellular stores and cell growth was proposed years ago by M.R. Droop. Droop's model applies under conditions of a single limiting chemical resource. Droop performed experiments with algae in continuous culture and suggested that growth rate was negatively and linearly related to ratio of biomass to nutrients within the cells (Fig. 2). The Droop relationship ties a stoichiometric quantity (C:P) to a dynamic variable (growth rate).

The higher the CV, the more variable is the element in the given organism relative to the element's mean concentration. Elements are arranged left to right by increasing CV. Macronutrients are unshaded. Essential micronutrients are lightly shaded. Non-essential trace elements are darkly shaded.

Aquatic primary producers come from deeply branched evolutionary lineages. Some of the stoichiometric variability across diverse algal forms was recently described. Two of the major lineages, the 'red superfamily' and the 'green superfamily' can be separated on the basis of their patterns in trace metal composition. Members of the red superfamily (e.g., diatoms) tend to be higher in Cd, Co, and Mn whereas members of the green superfamily (e.g., green algae) tend to be higher in Cu, Zn, and Fe. Quite possibly these differences reflect major geological events such as the relative concentration of ocean oxygen during the evolutionarily origin of these groups.

This straight-line model is normally written algebraically as:

$$\mu = \mu'(1 - (Q_{\min}/Q))$$

where μ = cellular growth rate (time^{-1}), $Q_{\min}$ = the cell quota at zero growth, and Q is cell quota (in this case, P:C or N:C). The term 'quota' refers to the nutrients per cell or per biomass in the cell, e.g., P:C or N:C. In the Figure, a is $1/Q_{\min}$ and b is μ'. The parameter μ' is a theoretical (high) growth rate that would be reached at infinite quota. The thick part of the line represents a range where one would expect to see actual observations. The narrow part of the line would be growth rates that were never observed.

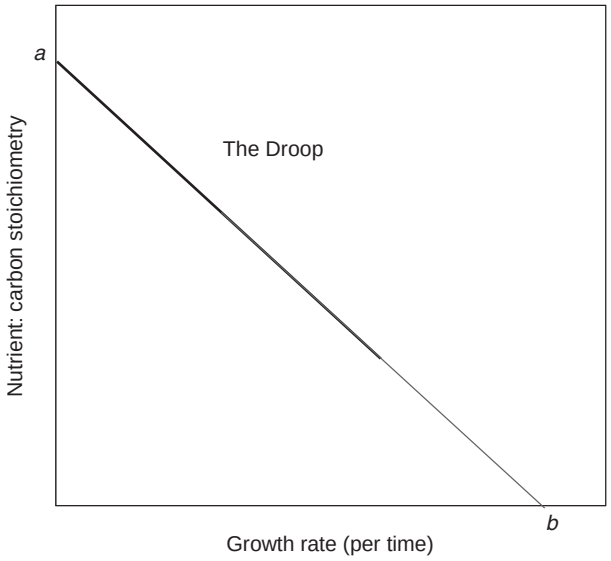

Fig. 2 The functional coupling between organismal stoichiometry (e.g., C:P or C:N, vertical axis) and growth (per capita rate, time-1) is often linear when one resource is limiting. Adapted from Karimi R and Folt CL (2006) Beyond macronutrients: Element variability and multielement stoichiometry in freshwater invertebrates. *Ecology Letters 9*: 1273–1283.

Freshwater algae attached to substrates include microscopic forms ('periphyton') living in close association with other microbes and nonliving organic materials, all collectively forming a biofilm. These biofilms are the main source of autochthonous production in streams and sometimes in nearshore lake habitats as well. Living algae are often a minor contributor to the total carbon within such biofilms. Especially in streams, the stoichiometry of the entire biofilm is made up by living and nonliving components. In order of decreasing N and P content, those include wood, leaf litter, green leaves, and both periphyton and fine particulate organic matter (Fig. 3). Stoichiometric variability at the base of stream food webs is probably more dependent on the relative contributions of these different components than it is on variation within any one component.

Zooplankton

Moving up the food chain from primary producers, we encounter a variety of herbivores. In water columns, these herbivores are members of the zooplankton. The freshwater zooplankton is not a particularly taxonomically diverse group; protozoans, rotifers, cladocerans and copepods as well as juvenile insects are common members. Cladocerans and copepods both belong to the Crustacea, and they plus the insects are all Arthropods. Though species from any number of these several major taxonomic groups may coexist, may have overlapping diets, and may share many other aspects of their ecology such as predators, they nevertheless can have divergent stoichiometries. In particular, some species, such as *Bosmina*, have low P content, whereas others, such as *Scapholeberis* or *Daphnia* have P content several times higher. All of these species, diverse from the standpoint of their elemental content, are members of the same taxonomic order. Homeostatic regulation of element content is highly variable, even within

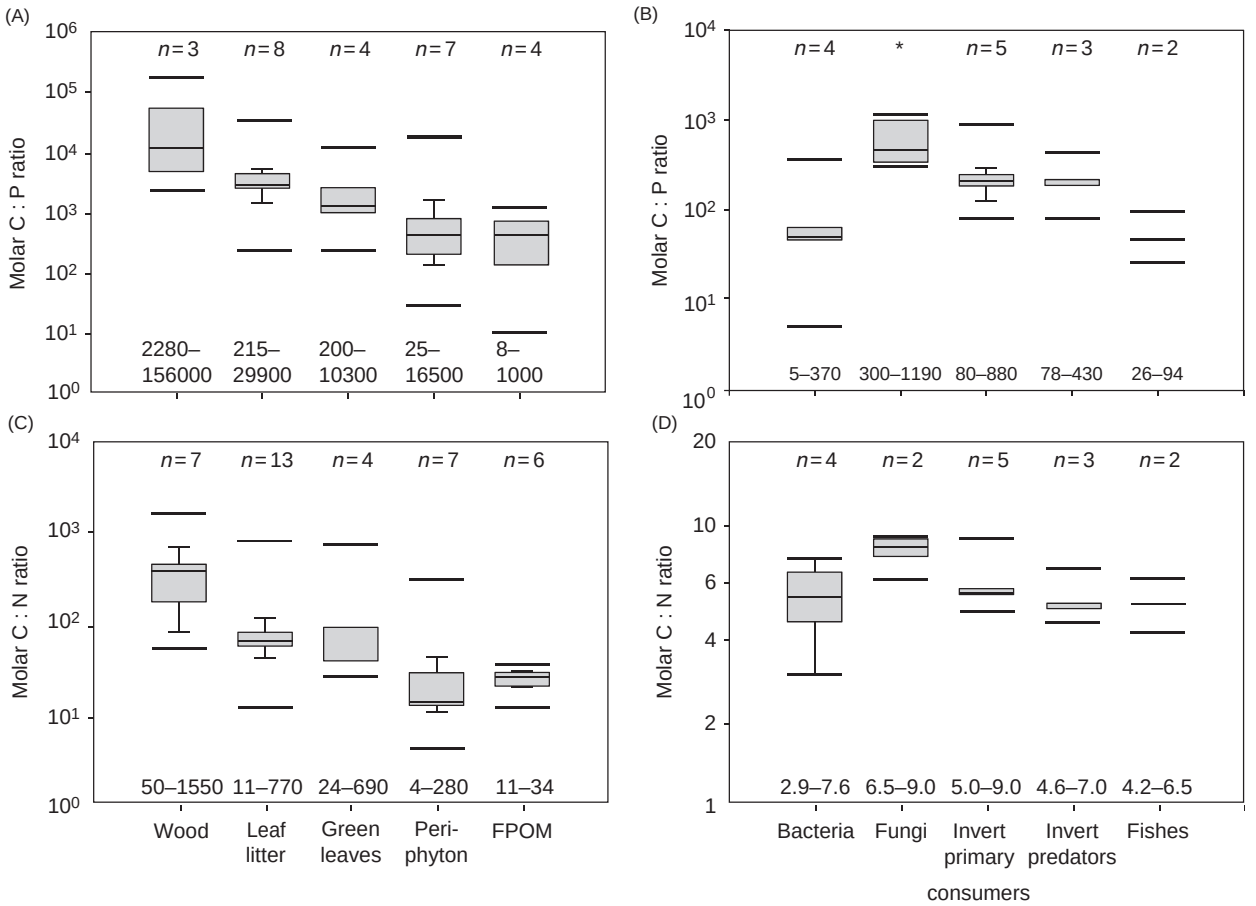

Fig. 3 Means and variability of C:N:P stoichiometry in common freshwater benthic resources and consumers. FPOM: fine particulate organic matter. Boxes and whiskers give the median, 10th, 25th, 7th, and 90th percentiles of the data within each category. Original sources of data include 49 literature studies. Ranges are given in text below the boxes. Reproduced from Fig. 1 in, Cross WF, Benstead JP, Frost PC, and Thomas SA (2005) Ecological stoichiometry in freshwater benthic systems: Recent progress and perspectives. *Freshwater Biology* 50: 1895–1912, with permission from Blackwell Publishing.

members of a single genus of zooplankton. Thus, stoichiometric patterns include not just average nutrient content but also the degree of variation within the taxon. We have made much progress in understanding the importance of average nutrient content, which will be apparent later in this article, but we have a very poor understanding of the ecological relevance of differences in homeostatic regulatory ability. Why some species are very homeostatic in element content and others are less tightly regulated is not at all understood yet.

Cross-species variability in average phosphorus content has been linked to life-history differences because biochemicals responsible for growth have a distinct elemental signature. Species with a potential for rapid biomass growth rates must contain large complements of P-rich biosynthetic machinery. This machinery is dominated by ribosomes, subcellular organelles involved in protein synthesis and which have distinctly high P content. The Growth Rate Hypothesis (GRH) proposes that elevated P demands caused by increased allocation to P-rich ribosomal RNA under rapid growth drives variation in whole-organism P content and thus whole-organism C:P and N:P ratios. Through the GRH, there may be very strong couplings between life histories and stoichiometry and therefore nutrient and energy flow. One example of couplings between growth and P content is given in Fig. 4. Note that the GRH coupling exists when overall food concentration is high. When food concentration is low, animals are likely mainly energy limited and couplings to nutrient content are muted or absent. Linkages among growth rate and stoichiometry seem to depend upon the nature of growth limitation, what resource is limiting at any given time.

Other aquatic invertebrates

The stoichiometry of stream and lake benthic invertebrates has been explored, and wide chemical variation among the diverse members of this group has been observed. In one such study, %P ranged from 0.2% to 1.5% and the N:P ratio ranged from <20 to >100. Trichoptera and Ephermeroptera were lower in %P and %N than Diptera, Odonata, and Plectoptera. When examined as a function of feeding group, predators were found to have higher P and N than other feeding groups. This is an impressive amount of stoichiometric variation. Not many studies have examined the consequences of this stoichiometric variation in streams, but perhaps some of the same processes we describe later relative to planktonic systems hold as well in streams.

Bacteria and protozoa

Heterotrophic microorganisms include bacteria and Protozoa. Not much work has been done yet on the stoichiometry of freshwater Protozoa. Freshwater bacteria are often found to have relatively high N and P content (low C:N and C:P) compared with other aquatic organisms. Studies suggest that bacterial N content is very homeostatic but P content varies with the availability of P for uptake as well as the growth rate of the bacteria. One study on *E. coli* that varied the chemistry of the growth substrate and the growth rate itself found a range in C:P from 40 to 75, a range in N:P from 11 to 18 and a very constant C:N of 4. At high growth rate, bacteria

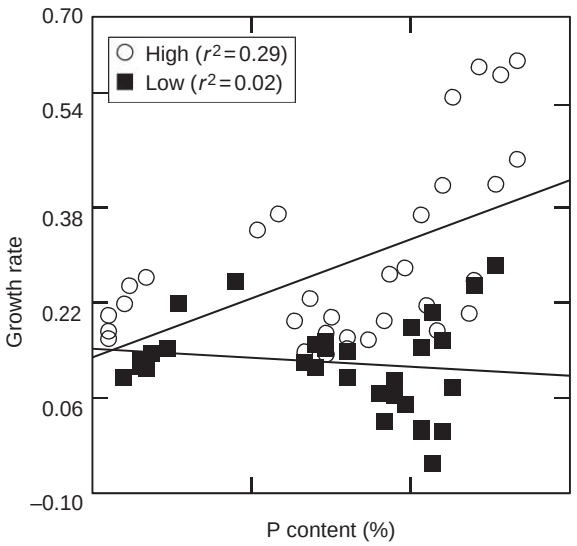

Fig. 4 In a laboratory bioassay study involving four species from three genera of cladocerans, growth rate and P content were positively related when food concentration was high (open circles) but not when it was low (closed squares). At low food concentration, animals were energy limited, but at high food concentration they were likely P limited so that growth was linked to P levels in the animals. Reproduced from Fig. 2 in Ferrão-Filho AS, Tessier AJ, and DeMott WR (2007) Sensitivity of herbivorous zooplankton to phosphorus-deficient diets: Testing stoichiometric theory and the growth rate hypothesis. *Limnology and Oceanography* 52: 407–415, with permission from American Society of Limnology and Oceanography.

had low C:P and elevated RNA content. In comparing the results for *E. coli* with literature findings, this same study suggested that individual bacterial strains were strongly homeostatic whereas in nature bulk bacterial communities varied much more widely, suggesting that varying dominance of individual strains may be responsible for much of the variation in bacterial C: N:P composition in the field. In this respect, stoichiometric patterns in the bacteria have a resemblance to other organisms, including freshwater zooplankton.

Fish

Fish are often the ecologically dominant vertebrates in aquatic ecosystems. Fish can be herbivores as well as carnivores or even detritivores or omnivores. Fish have numerous effects on aquatic ecosystems and at times they can be so abundant that they channel great quantities of nutrients in and out of their own biomass through feeding, excreting, etc.

This group too is characterized by wide stoichiometric variation and the ecological consequences of such a wide stoichiometric variability are just beginning to be understood. Phosphorus content of fish ranges from less than one to over 4%. Low-P fish include minnows in the Cyprinidae family. High-P fish occur in both temperate and tropical ecosystems; they are bony and are typical of the Percidae, Centrachidae and Loricariidae families. In fish, evolutionary patterns associated with structure (boniness) account for most of the stoichiometric variation. We see this in a very strong correlation between fish Ca and fish P (Fig. 5). Fish skeletons can account for from one to more than 5% of body mass. Bony skeletal material is made of a calcium phosphorus mineral called apatite with chemical formula $Ca_5F\ (PO_4)_3$ where other anions may replace F. This large quantity of mineral has a great effect on the stoichiometry of individual species of fish—the slope of the line in Fig. 5 is almost exactly as predicted from the stoichiometry of apatite mineral.

We will now consider the ecological ramifications on these stoichiometric properties of species.

Food quality

Consumers rely on organic food resources that may or may not closely match their own chemical requirements for survival and growth. The idea of a 'balanced' diet is familiar to everyone from the standpoint of human nutrition—it means that the chemical composition of food matches closely an ideal composition. Stoichiometry helps us understand how balanced vs. imbalanced a particular diet may be for any given aquatic consumer. Natural ecosystems often present highly imbalanced diets to consumers. Effects of many different nutritive substances such as vitamins, amino acids and fatty acids are known. Here, we will focus solely on individual chemical elements.

To help understand how different elements may limit consumer growth, we use a tool called a 'Threshold Element Ratio' (TER). A TER is the ratio of elements in an organism's resources where that organism is equally limited by both elements. When the ratio of elements (e.g., C:P) in the food exceeds the TER, the element in the denominator (P) limits consumer growth. Likewise, when the ratio is lower than the TER, the element in the numerator (C) limits growth. TERs are determined by two main things: the nutrient content of the consumer organism, which we considered earlier, and growth efficiency, which we will consider next.

Growth efficiency is defined as the amount an organism gains divided by the mass it ingests. Growth efficiencies based on carbon for aquatic consumers average around 0.3 with large variation around that average. Stoichiometry helps explain some of that

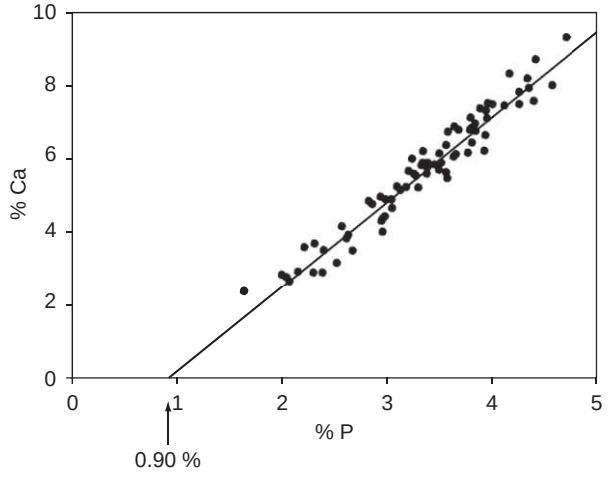

Fig. 5 Ca vs. P for 18 species of fish. The line has equation $y = 2.31x - 2.09$ ($r^2 = 0.95$). Reproduced from Fig. 4 in Hendrixson HA, Sterner RW, and Kay AD (2007) Elemental stoichiometry of freshwater fish in relation to phylogeny, allometry and ecology. *Journal of Fish Biology* 70: 121–140, with permission from Blackwell Publishing.

variation. The growth efficiency of a strongly homeostatic organism must adjust to the composition of the food, otherwise the consumer would not be able to maintain its homeostasis. There are many well studied examples where decreased growth efficiency on poor quality (low nutrient) foods has been observed in aquatic systems. A good example is heterotrophic bacteria where growth efficiency is typically well above 50% for growth on substrates with C:$N < 5$, but declines to 10% or less on substrates with C:N ratios >30. Because bacterial processing of organic carbon is often a very big part of the organic carbon cycle in lakes, these stoichiometric modulations of C shunted into cell growth versus loss as CO_2 or organic C can play a very large role in the biogeochemical cycling of carbon.

TERs have been calculated for many aquatic organisms (Fig. 6A). Fish have low C:P TERs (typically about 100–200), a reflection of their P-rich skeleton. The highest C:P TERs (about 500) are found for aquatic insects, which of course do not have bony skeletons but still require P for making RNA and other biomolecules. In fact, within the invertebrates, there is a statistically significant negative relationship between maximal potential growth rate and the C:P TER (Fig. 6B, open symbols). Here we see the elemental requirements for the machinery for growth affecting whole-organism ecology, consistent with the Growth Rate Hypothesis described earlier. There have been numerous studies on stoichiometric dimensions to food quality in zooplankton. One example comes from the study of a model organism in ecological stoichiometry, *Daphnia*, the water-flea. *Daphnia* are keystone herbivores in planktonic systems; they merit special attention because of the role they can play in decreasing algal biomass. Above, we discussed how *Daphnia* are generally high in P content. As one would therefore expect, *Daphnia* growth is sensitive to the P content of their food (Fig. 7). Algae with high C:P ratio (and thus low P content) dramatically lowers *Daphnia* growth rate, in this case lengthening by three-fold the time to double biomass. Other studies on zooplankton stoichiometry have shown: (a) low P zooplankton such as *Bosmina* are much less affected by the C:P of algal food than are high P zooplankton like *Daphnia*; and (b) particular life stages of some zooplankton may be particularly sensitive to C:P of food; thus, an overall effect on the animal may be determined most at specific points in its life cycle One recent study showed that hybrids of two *Daphnia* species performed better on high C:P food than the two parental species, suggesting that success in stoichiometrically imbalanced systems might be responsible for maintenance of hybrids in the ecosystem.

Stoichiometry predicts that consumers of high element content should be rare in environments where that element is scarce. A large Norwegian study showed a strong relationship between the abundance of *Daphnia* and seston C:P ratios (Fig. 8). In this study,

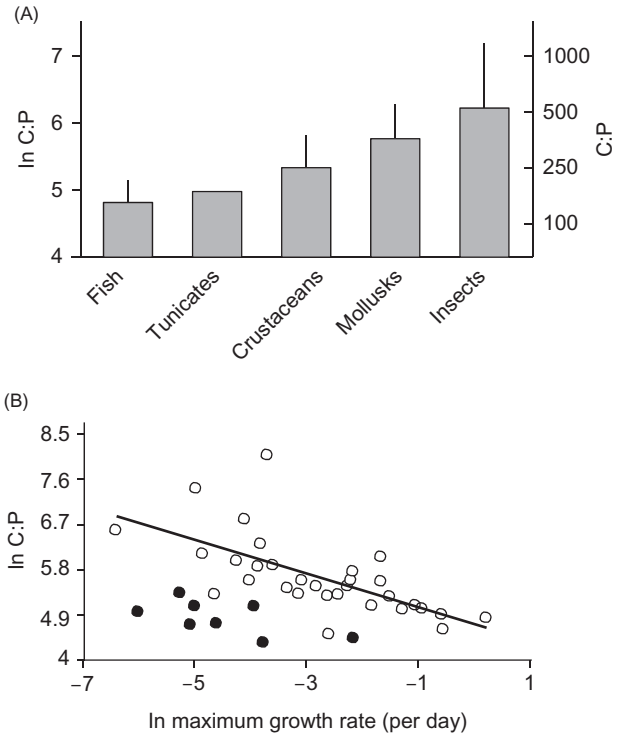

Fig. 6 Ratios of C:P (moles C per moles P), where different kinds of aquatic animals switch between growth limitation by carbon vs. growth limitation by phosphorus. When food C:P exceeds an animal's TER, the animal is limited by P and when food C:P is less than an animals's TER, carbon limits growth. (A) Their higher TERs (mean ± SD) indicate that less food P is required per unit food carbon for mollusks and insects relative to fish, tunicates, and crustaceans. (B) A higher growth rate depresses the C:P TER in invertebrates (open circles), a signal consistent with the growth rate hypothesis. Further, at any given growth rate, high P content depresses fish C:P TER (closed circles) below that observed for invertebrates. Adapted from Figs. 2 and 4 in Frost PC, Benstead JP, Cross WF, Hillebrand H, Larson GL, Xenopoulos MA, and Yoshida T (2006) Threshold elemental ratios of carbon and phosphorus in aquatic consumers. *Ecology Letters* 9: 774–779, with permission from Blackwell Publishing.

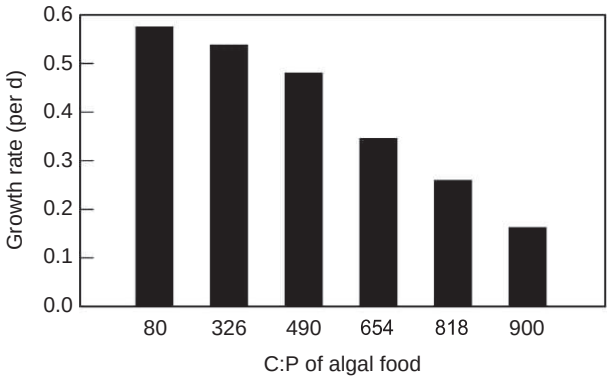

Fig. 7 The planktonic herbivore, *Daphnia magna*, has much reduced growth rate when it feeds on algae of high C:P ratio (low P content). All algal food treatments in this study were the same species of algae, *Scenedesmus acutus*, grown under different conditions to get a stoichiometric range from 80 to 900. Converting from growth rate units one can find that at low C:P, these *Daphnia* double their biomass in 1.2 days, whereas at high C:P it takes 3.8 days, or more than three times as long. Adapted from DeMott WR, Gulati RD, and Siewertsen K (1998) Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *D. magna*. *Limnology and Oceanography* 43: 1147–1161, with permission from American Society of Limnology and Oceanography.

all sites with high *Daphnia* abundance had seston C:P well below this organism's C:P TER. Seston C:P ratios were the most important variable in explaining the abundance of *Daphnia*. In general, physiological studies of TERs, laboratory growth studies, and field studies all point to a consistent conclusion, that high P herbivores like *Daphnia* are affected by stoichiometric imbalances between food and consumer.

There are some other very high imbalances between consumer and resource stoichiometry in streams and lake benthos. Certain consumers in those habitats subsist largely on nutrient-poor detritus. An example of stoichiometry affecting a stream invertebrate is given in Fig. 9. In this study, snails were given two quantities of periphyton food that had been grown under different nutrient treatments. Periphyton grown with added P (treatments + P and + N + P) had C:P of about 200 whereas C:P was 400 or more when P was not added (treatments Ambient and +N). The snails were strongly homeostatic and they showed pronounced stoichiometric effects on growth at low but not high periphyton quantity.

Although most studies of food quality have emphasized what happens when food is deficient in some element, recent studies have also shown that food may be imbalanced when it is too high in a particular element. Whether reduced food quality at high nutrient content is due to overt toxicity or because very high content of some element indicates some other chemical imbalance is not yet understood.

Nutrient recycling

Next we consider stoichiometric aspects of nutrient cycling. In particular, we consider processes that deliver nutrients to the dissolved pool. Nutrients enter the dissolved pool in inland ecosystems from the air, the surrounding land, the sediments or substrate, and also from the organisms living in the water, which release nutrients as waste products. There are stoichiometric aspects to all of the above, but here we will focus on biological resupply, or nutrient recycling by consumers. Consumers here can range from Protozoa to fish.

The stoichiometry of nutrient recycling is related to food quantity, considered above. When an organism's food is deficient enough in a particular element for it to be limited by that element, a great premium is placed on not wasting that element. In order to maintain a stoichiometric homeostasis, organisms must efficiently retain elements in short supply in their food relative to stoichiometric requirements. For the same reason, they must either not assimilate or they must release upon assimilation, elements that are in surplus to their own requirements. Stoichiometric homeostasis thus has a highly constraining effect on patterns of nutrient recycling by consumers.

Many studies on many organisms have considered the N:P ratio of release by individual aquatic organisms. In Fig. 10 we see data gathered from freshwater and marine zooplankton. Other studies with similar results have been conducted on bacteria, Protozoa, and vertebrates including fish. Fig. 10 illustrates the two principal stoichiometric effects on nutrient recycling. First, the N:P recycled is positively related to the N:P in the food ingested. Note that because of the log scale in this Figure, the N:P released is not directly proportional to the N:P eaten. Instead, as N:P in the food increases slowly, N:P released increases very quickly. This upward trajectory was predicted mathematically, and it has been shown repeatedly in different nutrient cycling studies. When feeding on food of low N:P, a homeostatic consumer must keep the N for itself but recycle excess P, so that N:P released is very low. Likewise, when feeding on food of high N:P a homeostatic consumer must release excess N but keep relatively scarce P, making N:P recycled high. The second principle stoichiometric effect on nutrient recycling comes about because of the chemical variability among

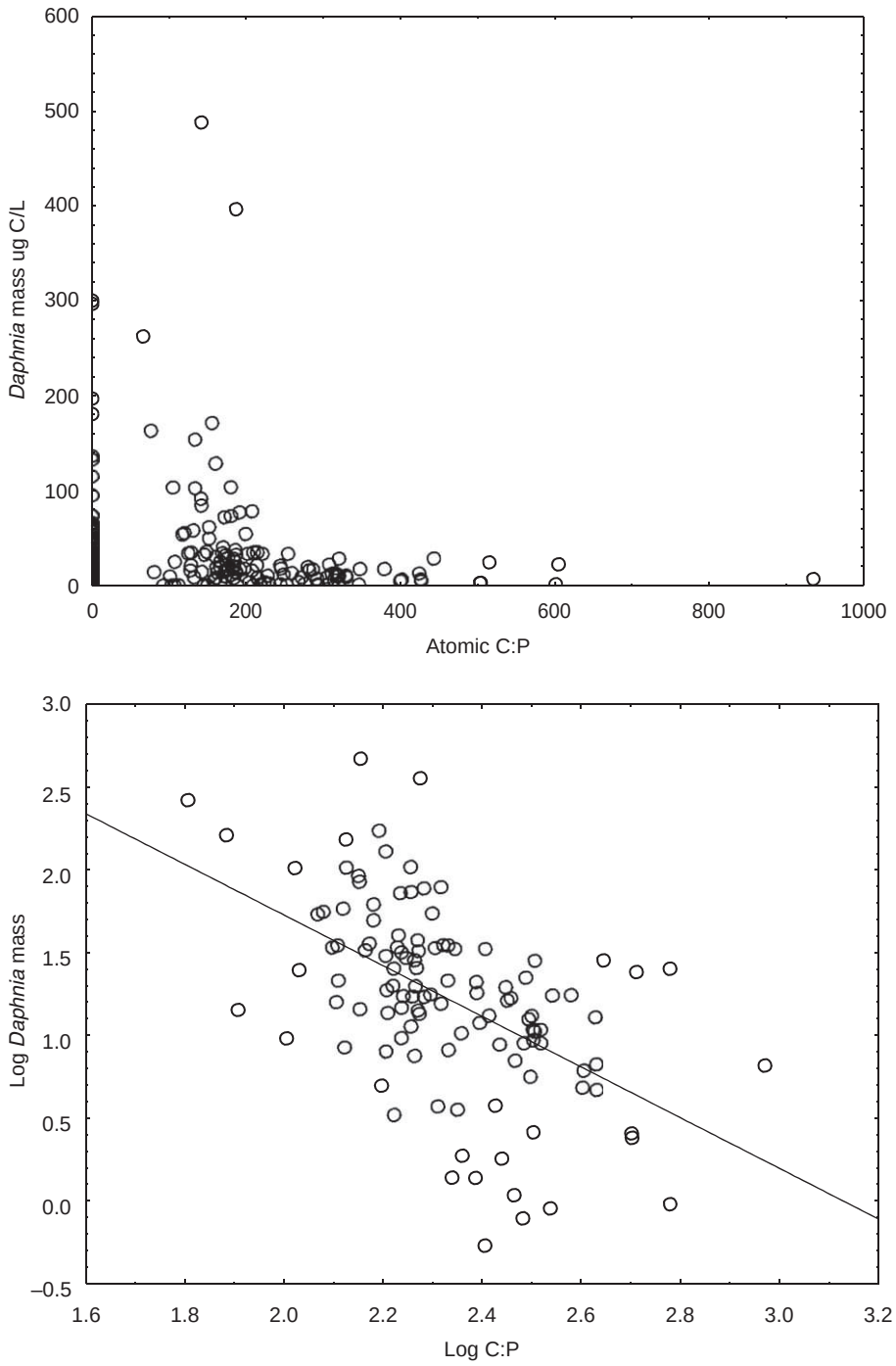

Fig. 8 Consistent with predictions of stoichiometric theory, lakes with high C:P in their seston have lower abundance of the high-P, keystone genus, *Daphnia*. Data are from a survey of 400 Norwegian lakes. The upper panel shows the data plotted on linear axes and emphasizes how large populations build up only at C:P below the *Daphnia* TER, which typically is about 300. The lower panel shows the same data plotted on logarithmic axes and shows a strong consistently negative slope. Replotted from data published in Hessen DO (2006) Determinants of seston C:P ratio in lakes. *Freshwater Biology* 51:1560–1569.

consumers. Consumers that are low in N:P will recycle at high N:P ratios and organisms that are high in N:P will recycle at low N:P. Given that many studies point to the critical importance of N:P loading as determining algal community structure, this example illustrates how ecological stoichiometry integrates species-level information with ecosystem-level processes. It is remarkable that something as potentially complicated as the rates of nutrient release by living animals relates so strongly to simple measures such as nutrient content.

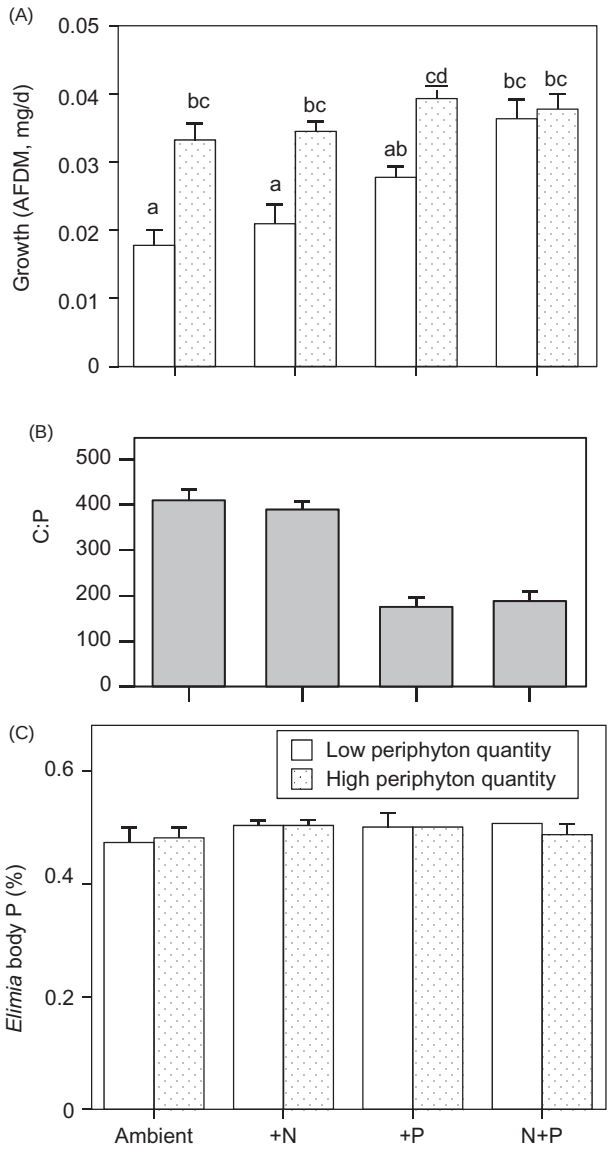

Fig. 9 Effect of nutrient addition on periphyton and snail stoichiometry. Snails (*Elimia livescens*) were reared in experimental streams (flumes) and fed periphyton on clay tiles. An approximately similar periphyton biomass (low or high) was given to snails in all treatments. The experiment lasted 34 days. (A) Snails growth varied with nutrient treatments at low periphyton quantity but not high periphyton quantity. At low periphyton quantity, additions of P stimulated snail growth. (B) The C:P of the periphyton under different nutrient treatments. (C) The %P of the snails under different nutrient treatments. Note that the periphyton have more flexible nutrient content than the snails. Adapted from Stelzer RS and Lamberti GA (2002) Ecological stoichiometry in running waters: Periphyton chemical composition and snail growth. *Ecology* 83:1039–1051, with permission from Ecological Society of America (ESA).

Community dynamics

The separate effects of stoichiometry on animal growth and nutrient cycling considered above combine to influence community dynamics. One long-term culture study found two markedly different outcomes. In one, cultures had high abundance of algae but low abundance of grazers (a 'green' world). This first outcome was seen in the cultures with high algal C:P ratio. In the other outcome, cultures had low abundance of algae but high abundance of grazers (a 'clear' world). This second outcome was seen where algal C:P ratios were low. There was a sharp threshold between the two outcomes near the threshold, small differences in growth conditions promoting different stoichiometric ratios had large effect on community dynamics. Stoichiometry played a role in separating the green and the clear world. A second interesting aspect of this study was that high grazing promoted high food quality so that zoo-plankton had a positive demographic effect on their own populations—more zooplankton meant better food and therefore higher zooplankton growth. This kind of positive feedback between population size and population growth contrasts markedly with classical ideas about population regulation.

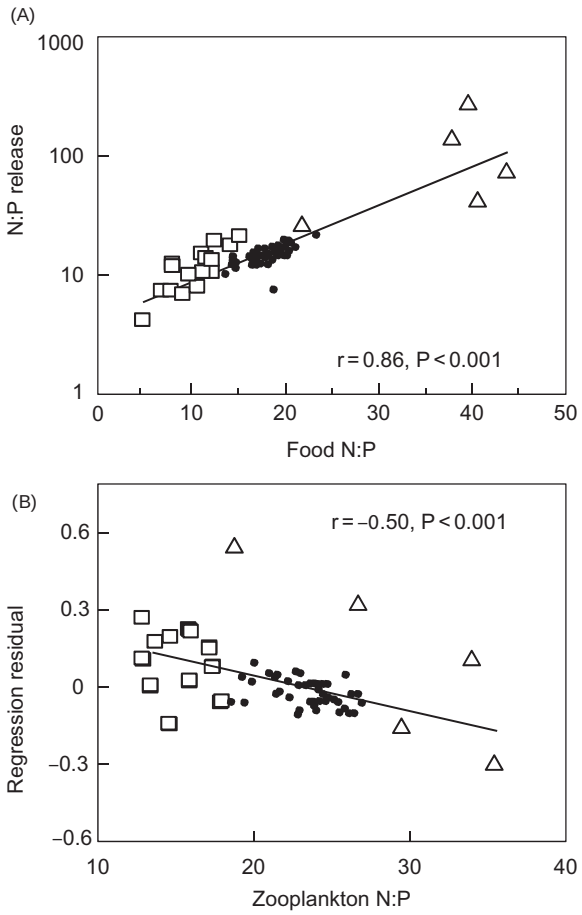

Fig. 10 Two aspects of stoichiometry altering nutrient fluxes through organisms. (A) The N:P released by zooplankton is positively related to the N:P of the food they are eating. (B) After accounting for the trend in (A), the consumers' own N:P ratio is negatively related to their N:P release (B). Reproduced from Fig. 4 in Elser JJ and Urabe J (1999) The stoichiometry of consumer-driven nutrient recycling: Theory, observations, and consequences. *Ecology* 80:735–751, with permission from Ecological Society of America (ESA).

Mathematical, theoretical analyses have uncovered other surprising aspects of community dynamics associated with stoichiometry. Stoichiometrically explicit models of grazers, algae and nutrients suggest the existence of complex dynamics, including steady population changes through time, irregular, even chaotic, nonrepeating cycling of populations, and, in some versions of models, deterministic grazer extinction.

These different community dynamics emerge quite easily and naturally from models that explicitly incorporate stoichiometry. They suggest that classical, nonstoichiometric, ideas about population regulation, dynamics, and competition may be far off base when stoichiometric effects are important.

Whole-system scale

These many stoichiometric patterns and processes that we have considered so far operate simultaneously to form aggregate stoichiometric properties of entire ecosystems. A touchstone for understanding ecosystem-level stoichiometry is the Redfield Ratio, a concept put forward by the oceanographer A.C. Redfield in the 1930s-1950s. Redfield noticed a correspondence between the C:N:P ratio in particulate matter of the surface ocean and dissolved nutrients in the deep ocean. The atomic ratio he observed was C_{106}:N_{16}:P_1, which is now called the Redfield Ratio. From this similarity he deduced that the entire global ocean had its nutrient content determined mainly by the biota. His argument was that both C and N come into stoichiometric balance with P, as set mainly by the demands of the oceanic biota. If either C or N are in short supply, the biogeochemical processes of primary production or N fixation can tap into atmospheric sources of these elements. Likewise, excesses of C or N can be vented to the atmosphere by respiration or denitrification. Phosphorus lacks an important gaseous phase, and its supply to the oceans is set by geological (or, now, human) action on the continents, which controls the rate of runoff from major river systems. The Redfield Ratio is similar to the ratios that many phytoplankton obtain when growing at either high growth rate or light limitation. The variation among species is such that if one takes an average of many different species, a C:N:P of 106:16:1 emerges. The Redfield ratio thus describes an overall mean of many species growing without strong single-element nutrient limitation.

The same kinds of measurements can be made for inland waters, but lakes, ponds, streams and rivers exhibit a greater degree of variability in their stoichiometric C:N:P ratios than do the oceans. This variability across sites can be due to many factors. Inland ecosystems are subject to widely varying inputs of elements from the atmosphere and from their watershed. They flush relatively rapidly compared with the time scales necessary for Redfield balancing mechanisms. Individual lakes, ponds, streams or rivers may be more homogeneous in terms of the many variable factors that determine biogeochemical potentials than the entire world's oceans; for example, highly unproductive lakes may lack anoxic zones that would support high levels of denitrification. They may be dominated by a small number of species during bloom conditions. There is a potentially large but variable detrital pool, poor in N or P, which may be found. Finally, they may be strongly limited by a single element, whether it be P or N or perhaps even some other nutrient. Given this large number of factors that can perturb C:N:P ratios away from Redfieldian balance, it is not surprising to see that freshwater systems are generally more stoichiometrically variable at the ecosystem level than are oceans (Fig. 11). This great

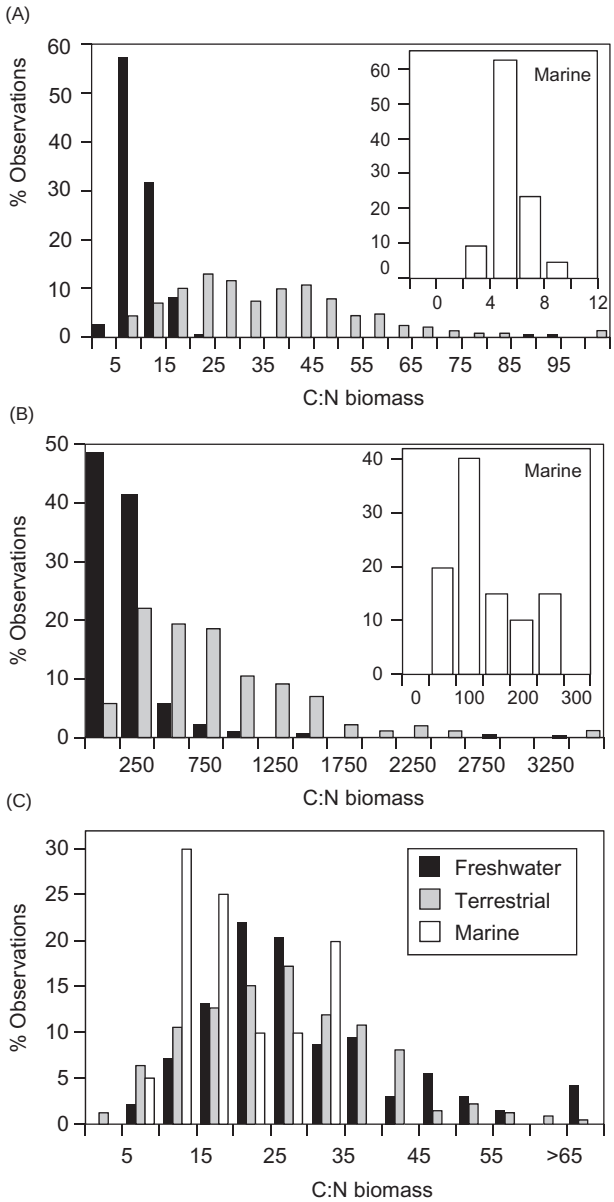

Fig. 11 Variations in C:N:P stoichiometry at the base of marine (white), freshwater (black), and (for reference) terrestrial (gray) food webs. Data for lakes and oceans represent values of seston, including all particles living and dead, whereas data for terrestrial habitats reflect values for individual leaves. Note that freshwater systems have more variable C:N, C:P, and N:P ratios than do marine systems. This means the 'raw material' for stoichiometric determination of growth rate, nutrient cycling, etc. is greater in freshwater than marine systems. Though outside the scope of this article, this Figure also shows that terrestrial systems too have great stoichiometric variability at the base of their food chains. Reproduced from Fig. 3.13 in Sterner RW and Elser JJ (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton, NJ: Princeton University Press.

stoichiometric variability is the primary force that sets into motion many of the processes already described in this article, such as food quality constraints or stoichiometric determination of nutrient recycling patterns. Let us therefore now further analyze some of this great stoichiometric variability.

One explanation for this variation is the Light: Nutrient hypothesis. Light stimulates photosynthesis and thus is related to the input of carbon into particulate matter in inland ecosystems. As we discussed earlier, rates of carbon and nutrient acquisition in autotrophs are not tightly linked. When light is plentiful but nutrients are scarce, photosynthesis can be high compared to nutrient uptake and thus there develops a high C:P or C:N ratio in autotroph biomass. Characteristics of high light environments are clear water, shallow mixing or, in the case of benthos, shallow depth. The Light:Nutrient hypothesis suggests that stoichiometric variation at the base of food chains results from the relative balance of energy (light) and nutrients (N and P) available for primary producers.

Support for the Light:Nutrient hypothesis is accumulating. C:P ratios in 65 European lakes generally declined with increasing mixing depth (and zooplankton biomass correspondingly increased, as one would predict from food quality constraints). An elegant mathematical model of how mixing depth should affect lakes by way of stoichiometric shifts corresponded to the same patterns in the data. In another study, experimentally incubating phytoplankton from three Ohio lakes at different light levels and different nutrient levels caused seston C:N:P to shift in ways predicted by the Light:Nutrient hypothesis. C:P and C:N went up at higher light and down with increased nutrients. Third, seston in 112 Norwegian lakes covering a C:P from 24 to 1842 was related to measures of nutrient availability and it showed several different effects of decreased light owing to shading by algae in more productive water columns. Seston C:P in these Norwegian lakes declined strongly with increasing phosphorus (Fig. 12). No effects of lake area, season or latitude on C:P were detected. Particulate C did not correlate with C:P. The highest C:P ratios occurred in low P, therefore unproductive, lakes. C:P increased with increased values of the ratio of Secchi depth:total P and similarly C:P increased with the POC:chlorophyll ratio (representing the relative proportion of particulate detritus; Fig. 5). As we saw earlier (Fig. 8), high P *Daphnia* in these lakes were less abundant when seston C:P was high. There is mounting evidence that inland aquatic ecosystems do respond to relative availability of light vs. nutrients and thus these abiotic factors influence ecosystem dynamics in a way that is strongly mediated by stoichiometry.

One final stoichiometric aspect at the whole ecosystem scale relates to carbon fluxes in ecosystems. The fate and cycling of carbon in ecosystems is a topic of increasing concern in today's world. The human economy is run in part on cycling of carbon and nutrients for energy production, transportation, agriculture, etc. Fossil fuel combustion combined with land use changes have resulted in excess CO_2 building up in the atmosphere. Lakes often are carbon sources (not sinks) relative to global carbon cycling due to decomposition of terrestrially derived organic matter. However, lakes, and especially reservoirs, do build up significant reservoirs of carbon in their sediments. One early study suggested that lakes and reservoirs globally accumulated organic carbon at a rate of about 200 Tg year-1, more even than the world's oceans even though the oceans cover a much greater fraction of Earth's surface. The fate of carbon cycling through ecosystems is closely related to stoichiometric ratios. It has been noted that ecosystems that are high in C:P or C:N show more carbon cycled through detrital food chain pathways, whereas those ecosystems with lower C:P or C:N ratios show more carbon channelized through herbivore/grazing pathways. We can expect that lakes and reservoirs that are higher in C:P and C:N likely bury a larger fraction of their organic carbon than do lakes at the opposite end of the stoichiometric gradient. Thus, ecological stoichiometry can be an important aspect of how inland ecosystems fit into global carbon cycles.

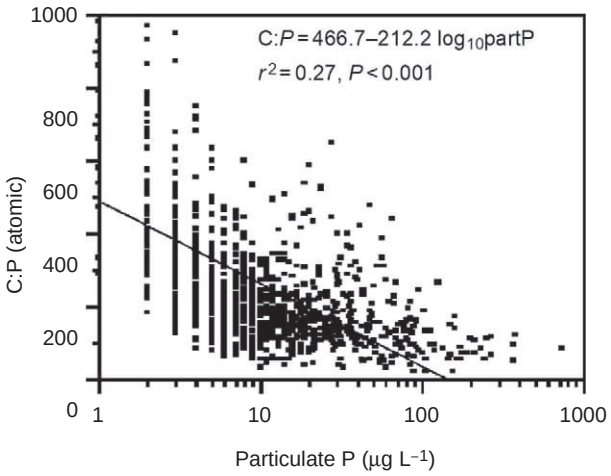

Fig. 12 Seston C:P ratios decline with increasing particulate P and therefore with overall productivity. Reproduced from Figure Hessen DO (2006) Determinants of seston C:P ratio in lakes. *Freshwater Biology* 51:1560–1569.

See Also: Fundamental concepts and theories: Trophic Dynamics and Food Webs in Aquatic Ecosystems; Structures and functions of Inland Waters - Lakes: Lacustrine Phosphorus Cycling; Phytoplankton Growth and Nutrients; Lake Food Webs; Structures and functions of Inland Waters - Rivers: Ecological stoichiometry in streams

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Relevant website

www.wikipedia.com.

The Biomass Size Spectrum

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, Lars Rudstam.

Glossary

Abundance Spectrum Logarithmic numerical abundance per unit area or volume in successive logarithmic size intervals.
Biomass Spectrum Biomass concentration (on either a linear or logarithmic axis) in successive logarithmic size intervals.
Bounded Power Law (PLB) or Truncated Pareto Distribution A mathematical function that underlies size-frequency distributions that are strongly right-tailed and are bounded by minimum and maximum sizes.
Height The coordinate value of the size spectrum at the middle of the body size axis. It is a measure of overall abundance or biomass concentration.
Individual Size Distribution (ISD) This is recommended terminology for size distributions of organisms in nature described by a PLB. All forms of size spectra are mathematical variants of the ISD.
MLE Maximum Likelihood Estimation is a statistical technique superior to OLS Regression for estimating the size spectrum exponent in many instances.
Normalized Spectra As above except biomass or abundance concentration is divided by the width of the size intervals
OLS Ordinary Least Squares Regression is a statistical fitting criterion historically used to estimate size spectrum parameters.
λ-lambda The exponent of the ISD. It is mathematically equivalent to the slope of size spectra. Negative values indicate a preponderance of small over large organisms and positive values the opposite.

Introduction

A size spectrum is the relation between the numerical or biomass concentration and the body size of organisms in a community. As typically displayed on double logarithmic axes this is a roughly linear negative trend reflecting the fact that in nature small organisms are much more abundant than large ones. In a very general way size spectra are related to the "pyramid of numbers" introduced in the 1920s by Elton (1927) (Fig. 1, based on Trebilco et al., 2013) when ecologists were interested in what factors determined the great range of organism abundance found in nature. These pyramids typically, although not exclusively, had a broad base reflecting the great abundance of small organisms and smaller upper layers for the decreasing abundance of progressively larger organisms. Elton argued that the pyramid results from the ecological interactions of larger predatory species feeding on smaller prey. Regular patterns occur because predators cannot consume prey that are too large (pack animals are an exception) nor can they acquire enough energy by hunting prey that are too small. There are limits to the heights of the pyramids because only a fraction of a prey population can be consumed by its predators until eventually there are no predators that could survive on the meagre energy supply at the top. Of course, there are exceptions to these patterns caused by the population dynamics of interacting species in temporally and spatially variable habitats, but the general concepts are robust.

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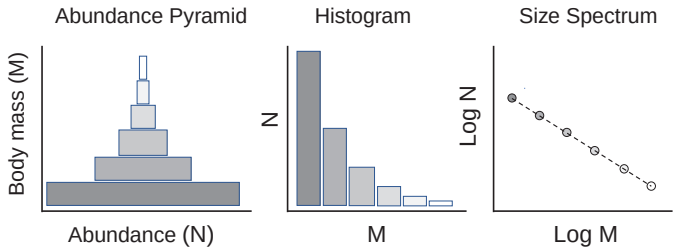

Fig. 1 The relationship among abundance pyramids, size-frequency histograms and size spectra. Redrawn from Trebilco R, Baum JK, Salomon AK and Dulvy NK (2013) Ecosystem ecology: Size-based constraints on the pyramids of life. *Trends in Ecology & Evolution* **28**: 423–431.

Shortly after Elton's ideas about organism numbers emerged, ecologists became increasingly interested in the trophic rather than size structure of communities of organisms. Expressed as "trophic" pyramids the bottom layer comprised primary producers (typically plants) with higher layers consisting of primary consumers (invertebrates, rodents, ungulates), secondary consumers (birds of prey, larger fish, big cats), etc. Studies of productivity and energy flow through food webs were based primarily on species as the study unit and their classifications by trophic position. The population dynamics of component species was an important element in field and modeling studies of this trophic "revolution."

By the early 1960s some biological oceanographers considered that progress in quantitative studies of the productivity and structure of plankton communities was limited by the common methods of characterizing organisms using taxonomic and chemical (including pigment ratios) criteria. Interest grew in the use of automated particle counters that facilitated field measurements of the size and abundance of planktonic organisms—measurements considered advantageous for developing mathematical models of energy flow through food webs. Beginning in the 1960s Ray Sheldon and his mentor Tom Parsons used a Coulter Counter to make extensive measurements of the size distribution and biomass of planktonic particles from 1 to 100 μm diameter in surface waters of the Atlantic and Pacific oceans (Sheldon and Parsons, 1967). They noted peaks of biomass reflecting variation through space and time of characteristic planktonic size groups in response to underlying physical and ecological processes in these communities. The relative ease of collecting observations on the size-based abundance of organisms, and the strong dependency of many ecological processes on body size (growth, mortality, feeding selectivity, reproduction, metabolism) facilitated a new size-structured view of communities—particularly in aquatic systems—of which the size spectrum is an integral part.

In what follows I will outline the methods used to construct size spectra, offer a brief discussion of underlying theory, and present some practical applications of size spectrum concepts in ecosystem management and modeling.

The power law

It is well known that the size-frequency distribution of organisms in nature is strongly right-tailed reflecting the rapid decline in abundance from the smallest to largest individuals (Fig. 2, based on Vidondo et al., 1997). Like many other phenomena with strongly skewed frequency distributions (e.g., sizes of moon craters, frequencies of words in a language, papers written by scientists) the one for organism size follows a Power-law distribution:

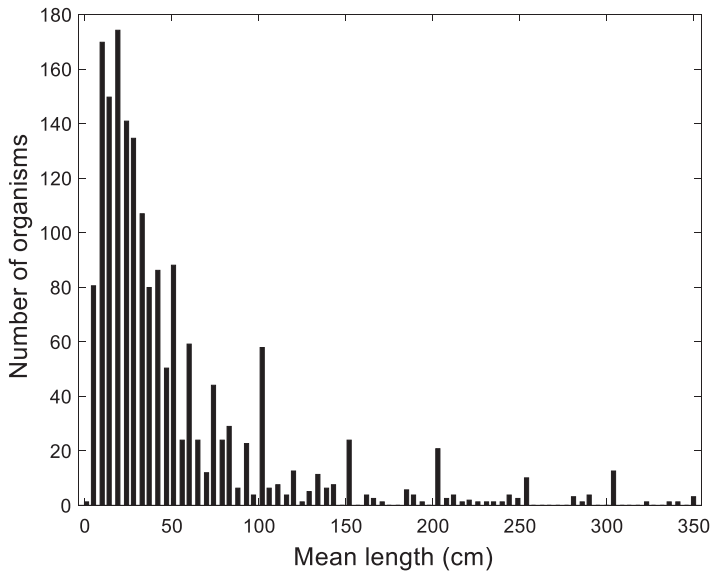

Fig. 2 Length-frequency distribution of a large mixed-species sample of Atlantic Ocean fish illustrating the long right tail typical of body size distributions in nature. Redrawn from Vidondo B, Prairie YT, Blanco JM and Duarte CM (1997) *Limnology and Oceanography* 42: 184–192.

$$f(m) = c \cdot m^{\lambda}, 0 < m_{\min} < m < m_{\max} \quad (1)$$

where m is a random variable (body mass in this case) and c and λ are constants to be estimated when fitting the function to specific data. With minimum and maximum values of mass specified, as is typical for size spectrum studies, the function is a "Bounded Power Law" (PLB) which is also known as a "Truncated Pareto Distribution." The exponent λ must be negative if abundance decreases with size. In the precise language of mathematics this is a probability density function which gives the probability that a random value of m will fall within a specified interval. To standardize terminology in size spectrum studies it is recommended that when the PLB is applied to organisms in nature it should be called the "Individual Size Distribution" (ISD). The ISD lies at the root of all abundance and biomass size spectra that vary only in how samples of organism size are measured, grouped and plotted. The ISD and its derivatives are mathematical models of abundance-size relationships in nature that can be used to make predictions such as of large organism concentration from that of more easily measured small ones, provide fitted parameters to be used as indicators of community structure, assess the structural effects of size-specific harvesting on a community, or motivate simulation models to better understand the dynamics of size-structured communities.

A primary goal of size spectrum studies is to estimate the two parameters of the ISD as will be described below. The exponent, λ is a measure of the size structure of organisms in a community. In both empirical and modeling studies of size spectra it has been found that values of λ are typically $\approx$–2 (= –1 or 0 for other presentations of size spectra, see below). Values <–2 indicate a relatively greater abundance of small than large organisms in a community (e.g., due to the harvesting of large organisms) whereas more positive values indicate the opposite (relaxed harvesting). The scaling coefficient c is typically a measure of the overall abundance or biomass of organisms at a standardized body mass.

Graphical representations of size spectra

To illustrate the variety of ways in which the ISD of organism sizes can be displayed, a simulated data set of 100,000 body masses was randomly selected from a bounded power law distribution with exponent $\lambda = -2$, minimum mass = 1, and maximum mass = 1000 using techniques described by Edwards et al. (2017). The large sample size is necessary to avoid statistical curve fitting problems because large values of the random variable (= large organisms) are extremely rare in power law distributions. For a realistic context, imagine this to represent a random sample of the abundance (#L^{-1}) of freshwater zooplankton ranging in individual body mass from 1 to 1000 μg fresh weight.

In the next sections the various forms of the ISD are illustrated. In each case estimates of the ISD are presented based on non-linear curve fitting, ordinary least squares linear regressions (OLS), or maximum likelihood estimation (MLE). MLE can be based either on the 100,000 raw masses (White et al., 2008) or when the raw data have been binned into mass intervals (MLEbin, Edwards et al., 2020). There is some debate about the statistical rigor of OLS versus MLE and this will be addressed below in Section "Slope". All calculations were done using MatLab (2020).

Histograms

An initial visualization of the pattern in such a large sample of body masses would typically involve "binning" them into a series of linear mass intervals and plotting these against the frequency of observations in each interval. This is the familiar histogram (Fig. 3A). A series of equal intervals on a *linear scale* is created and the frequency of organisms in each interval plotted against either the interval midpoint or one of the interval boundaries—typically the lower one. In linear size bins the upper boundary is the lower boundary *plus a constant*, and the width is the difference between the boundaries. The typical pattern of very abundant small organisms rapidly declining for progressively larger ones is observed and of course is well fitted by the power law from which the data came (Fig. 3A). For curve-fitting purposes this histogram has much smaller size intervals than would ever be used in practice; the power law is a continuous distribution for which accuracy of parameter estimates increases as the size interval approaches zero. A histogram with more "practical" size intervals of 20 μg is shown for comparison (Fig. 3B, Table 1).

Abundance spectrum

The researcher has an initial choice of binning their data into either linear or logarithmic mass intervals. Both have been used in the literature but as will be discussed below estimation of the parameters of the ISD and related size spectra is statistically much more precise and accurate for logarithmic intervals. The "Abundance Size Spectrum" is formed by binning the mass observations into equal logarithmic intervals and determining the frequencies per interval. Any logarithmic scale can be used, but the Coulter Counter used in early studies to measure the sizes of sampled marine "particles" grouped the data into $\log_2$-intervals and a precedent was established for this scale. Particles are grouped into classes with boundaries in a mass doubling sequence; 1–2, 2–4, 4–8, 8–16, 16–32, etc. μg which on a $\log_2$ scale would be equal intervals 0–1, 1–2, 2–3, 3–4, 4–5, etc. The $\log_2$ scale gives more mass intervals and hence greater spectrum detail than base 10 or natural logarithms, and, uniquely for this scale, the lower interval boundary is equal to interval width (e.g., interval 8–16 is 8 units wide) which will make calculations described below easier.

The 100,000 random body masses span 10 $\log_2$ intervals and the frequencies of observations in each are displayed in Table 1. These are plotted on double logarithmic axes in Fig. 3C as the Abundance Spectrum. A linear model fitted to these data using OLS

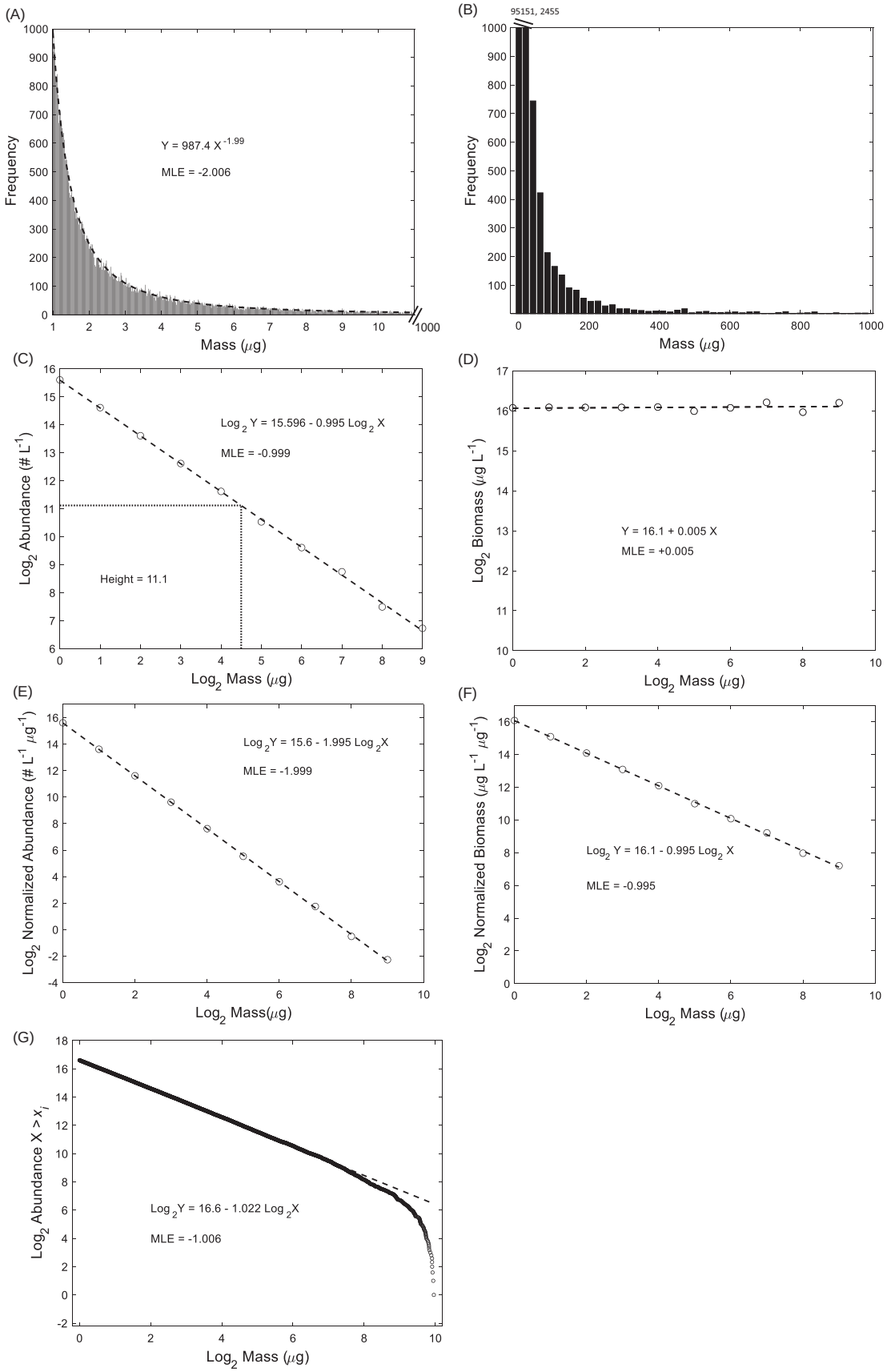

Fig. 3 (A) Length-frequency distribution of 100,000 body masses sampled from a Power Law distribution with exponent $\lambda = -2$. Fitted ordinary least squares line (OLS) and equation are shown, as is the Pareto maximum likelihood estimate of the Power Law exponent (White et al., 2008). Note the break in the X-axis extending out to the largest body mass of 1000 μg. (B) The data from Fig. 3 replotted with wider size intervals to for better visualization. Frequency values for the first two bars that extend well above the plotted area indicated. (C) The Abundance Spectrum of the random body masses in $\log_2$ mass and abundance intervals. Equation of OLS fitted line and the maximum likelihood estimate of the spectrum exponent (MLEbin method, Edwards et al., 2020) are shown. Height at the midpoint of the mass axis is shown as a standardized measure of community abundance. (D) The Biomass Spectrum with biomass plotted on a logarithmic scale. Equation of OLS fitted line and the MLEbin estimate of the spectrum exponent are shown. (E) Normalized Abundance Spectrum. Equation of OLS fitted line and MLE estimate of the spectrum exponent are shown. (F) Normalized Biomass Spectrum. Equation of OLS fitted line and MLE exponent estimate are shown. (G) Cumulative Pareto Distribution. Dashed line is an OLS fit to the linear portion of the distribution. The Maximum Likelihood estimate of λ based on all 100,000 individual mass values (–2.006) is also shown after scaling by addition of 1 for comparison with the OLS value of –1.022.

Table 1 100,000 randomly selected masses used in the construction of Fig. 3.

Mass (μg) Interval (a)[a]	*Abundance (No. L^{-1}) =# per interval (b)*	*Biomass ($\mu g\ L^{-1}$) =Σ mass per interval (c)*	*Normalized Abundance (# $L^{-1}\ \mu g^{-1}$) (b/a)*	*Normalized Biomass ($\mu g\ L^{-1}\ \mu g^{-1}$) (c/a)*
1–2	49,899	69,115	49,899	69,115
2–4	25,090	69,667	12,545	34,833
4–8	12,506	69,535	3127	17,384
8–16	6282	69,549	785	8694
16–32	3150	70,021	197	4376
32–64	1480	65,231	46	2038
64–128	783	69,091	12.2	1080
128–252	430	75,900	3.4	593
252–512	180	64,069	0.7	250
512–1024	106	75,444	0.2	147

Masses are grouped according to the form of the size spectrum, and calculations are indicated.
[a]For $\log_2$ scale interval width = lower boundary.

regression has a slope parameter b_a of −0.995 which is indistinguishable from the expected value of −1 given minor statistical error in the algorithm used to generate the sample of random masses. It can be shown mathematically that the linear parameter, b_a, of the Abundance Spectrum is one unit greater than λ, the ISD exponent, and hence can be used to estimate it ($\lambda = b_a - 1 = -2$). The MLE estimate of the ISD exponent (incremented by 1) is very close to the OLS estimate as would be expected for data simulation.

Biomass spectrum

The Biomass Size Spectrum is formed in a parallel manner except total mass rather than frequency is computed for each logarithmic mass interval (Table 1). With biomass plotted on a logarithmic scale the trend is a straight line with OLS slope $b_b = 0.005$ (within statistical error of the expected value of 0) indicating that biomass per mass interval is the same for all intervals (Fig. 3D). This is also mathematically consistent with a $\lambda = -2$ power law. The slope of the Biomass Size Spectrum is 2 units greater than λ and can be used to estimate it ($\lambda = b_b - 2$). The MLEbin estimate of λ is identical to the OLS slope. This spectrum is sometimes referred to as a "Sheldon" spectrum after Ray W. Sheldon who in 1972 wrote provocatively "that, to a first approximation, roughly equal concentrations of material occur at all particle sizes from 1 μm to about 10^6 μm, i.e., from bacteria to whales" (Sheldon et al., 1972). He expressed size as "equivalent spherical diameter"—the diameter of a sphere having the same volume as an organism—and plotted this on a $\log_2$ scale. He expressed biomass as parts per million by volume and plotted this on a linear scale. This form of the spectrum is now rarely used; however Sheldon's early observations stand as the primary motivation for all empirical and theoretical research on the Size Spectrum that followed.

Normalized abundance and biomass spectra

A problem with the Abundance and Biomass Size Spectra is that patterns depend not only on the total frequency or biomass per mass interval but also on the width of the interval which increases progressively across the logarithmic scale. This can be avoided by "normalizing" abundance or biomass values through division by the linear width of the intervals (Table 1) to give the "Normalized Abundance Spectrum" or the "Normalized Biomass Spectrum." The pattern of the Normalized Abundance Spectrum is well described by a straight line with a slope b_{na} of −1.995, close to the expected value of −2 (Fig. 3E), which follows analytically from the underlying power law. This is a direct estimate of the power law exponent ($\lambda = b_{na}$) and is close to the MLEbin estimate of −1.999. Similarly the Normalized Biomass Spectrum is a straight line with slope $b_{nb} = -0.995$ (identical to MLEbin) close to the expected value of −1 (Fig. 3F), one unit greater than λ ($\lambda = b_{nb} - 1$). This form of the spectrum is probably the one most frequently used in the literature.

Pareto distribution

Grouping measurements into intervals requires decisions about interval type and width making comparisons among studies difficult, and the choice of intervals can affect the accuracy and precision of estimates of the ISD parameter λ, a primary goal of size spectrum analysis. These problems can be avoided by analyzing the probability distribution of individual masses which requires no binning. Individual masses are ranked from smallest to largest ($i = 1 \ldots n$) and the probability of a random mass being $\geq m_i$ is estimated as $P = 1 - i/n$. The relationship between P and m is a "cumulative" distribution known as the "Pareto Distribution" which can take two forms—"Bounded" if both the minimum and maximum value of m are specified, and "Unbounded" if only the

minimum is specified. The random masses used here to illustrate forms of size spectra were generated from a Bounded distribution. P plotted against m on double logarithmic axes is a straight line for most of its range but curves down, or asymptotes, because it is bounded by the maximum mass value. A more "ecological" form of this distribution is to multiply the probabilities by the total sample size as has been done in Fig. 3G. The slope of a linear model fitted to the straight-line portion of the distribution, $b_p = -1.022$, is within fitting error of the expected value of −1. This is one unit greater than $\lambda = -2$ and can be used to estimate it ($\lambda = b_p - 1$). The MLE estimate of λ (−1.006) is very close to the OLS estimate for these data that precisely follow a Power Law.

Examples of size spectra

A selection of size spectra has been plotted in Fig. 4 to illustrate the variety of shapes and the variation in choice of units and axes. Sheldon's pioneering observation that biomass concentration is roughly equal across equal logarithmic intervals of body size is based partly on one of his early plankton spectra (Fig. 4A). Although clear peaks can be seen they are nevertheless roughly equal in maximum height (note the Y-scale is linear). The units Sheldon chose are no longer in use. The biomass spectrum for the whole food web of Lake Ontario shows peaks of biomass corresponding to the major organism groups (from left to right: phytoplankton, zooplankton, the amphipod *Diporeia*, and planktivorous fish (Fig. 4B, based on Sprules and Goyke, 1994). OLS and MLE parameter estimates are very similar. When these data are plotted as a normalized biomass spectrum (Fig. 4C, based on Sprules and Goyke, 1994) the biomass peaks are less obvious due to the logarithmic scaling and have been referred to as domes. Fitted parameters are similar for OLS and MLE. While the primary pattern for normalized spectra is linear there is generally residual variation around this "backbone" that can vary considerably in magnitude and pattern. The normalized spectrum for the Pacific Gyre (Fig. 4D, based on Rodriguez and Mullin, 1986) is very linear with residuals that appear random and are tightly clustered around the linear trend. There are no obvious domes. Lake Ontario is a much more productive system than the Pacific Gyre and the spectral patterns in these two systems accord with theory that indicates decreasing productivity of a system attenuates the domes which are caused by cascading top-down predation forces (e.g., Rossberg et al., 2019). The benthic marine biomass spectrum (Fig. 4E) also shows clear domes that span roughly two orders of magnitude in biomass. It is moot whether these are "roughly equal" but in contrast to pelagic environments the benthic habitat has a lot of physical structure that can affect the form of the size spectrum (Schwinghamer, 1981). In this case there is considerable discrepancy between OLS and MLE parameter estimates.

Size Spectrum parameter estimation

Slope

The most common method of analysis used to estimate size spectrum parameters has been to fit an ordinary least squares (OLS) regression to linear forms of the spectrum (Fig. 3) to obtain the slope (an estimate of λ after the appropriate corrections indicated above) and the intercept (an estimate of abundance or biomass). OLS regression works by choosing the parameters of a line that minimize the sum of squared deviations of Y around it. Recently White et al. (2008) and Edwards et al. (2017) have shown, using Monte Carlo simulation techniques, that the accuracy and precision of OLS parameter estimation is not uniform across forms of the size spectrum. Instead the most rigorous estimates of λ are obtained by Maximum Likelihood Estimation (MLE). MLE works by choosing a model and parameters that maximize the likelihood of obtaining the observed data. OLS analyses of spectra with *linear* size intervals results in inaccurate estimates of λ and should not be used for this purpose. OLS estimates of λ for abundance or biomass spectra (both unnormalized and normalized) with data binned into equal logarithmic intervals are generally close to MLE estimates (e.g., Fig. 4B and C) but may have wide confidence intervals. MLE estimates are both accurate and precise. This is especially true for the Pareto Function which is based on individual rather than binned observations. Edwards et al. (2020) have also shown that, if the data at hand are already in binned form giving no access to the raw observations, MLEbin estimation based on the assumption that the hidden observations *within* a bin follow a power-law distribution gives the best parameter estimates.

A possible weakness of the Monte Carlo simulations is the assumption that size spectra follow a perfect power-law distribution which gives linear normalized abundance and biomass spectra. However there is extensive evidence, both empirical and theoretical, that there is often secondary pattern in size spectra, most frequently manifest as sequential biomass "domes" reflecting the major interacting size groups in the community (Fig. 4). These effectively constitute non-random residuals around a linear spectrum model that could result in the MLE and OLS estimates of λ being different (e.g., Fig. 4E). Further research is required to resolve this matter.

Intercept

The intercept of a linear model is the value of Y where $X = 0$. In OLS analyses of size spectra the intercept has been used as a measure of overall biomass or abundance in the community at this standardized reference point. This is not recommended however because the slope and intercept are not statistically independent. One solution to this is to use 'height', the value of Y for the size interval in the middle of the X axis, as the measure of community biomass or abundance. This is independent of the slope. It works well for the Abundance Spectrum since height will be a direct estimate of the number of organisms per unit area or volume (Fig. 3C). For normalized spectra the units of height would have to be multiplied by the width of the central size interval to obtain abundance or

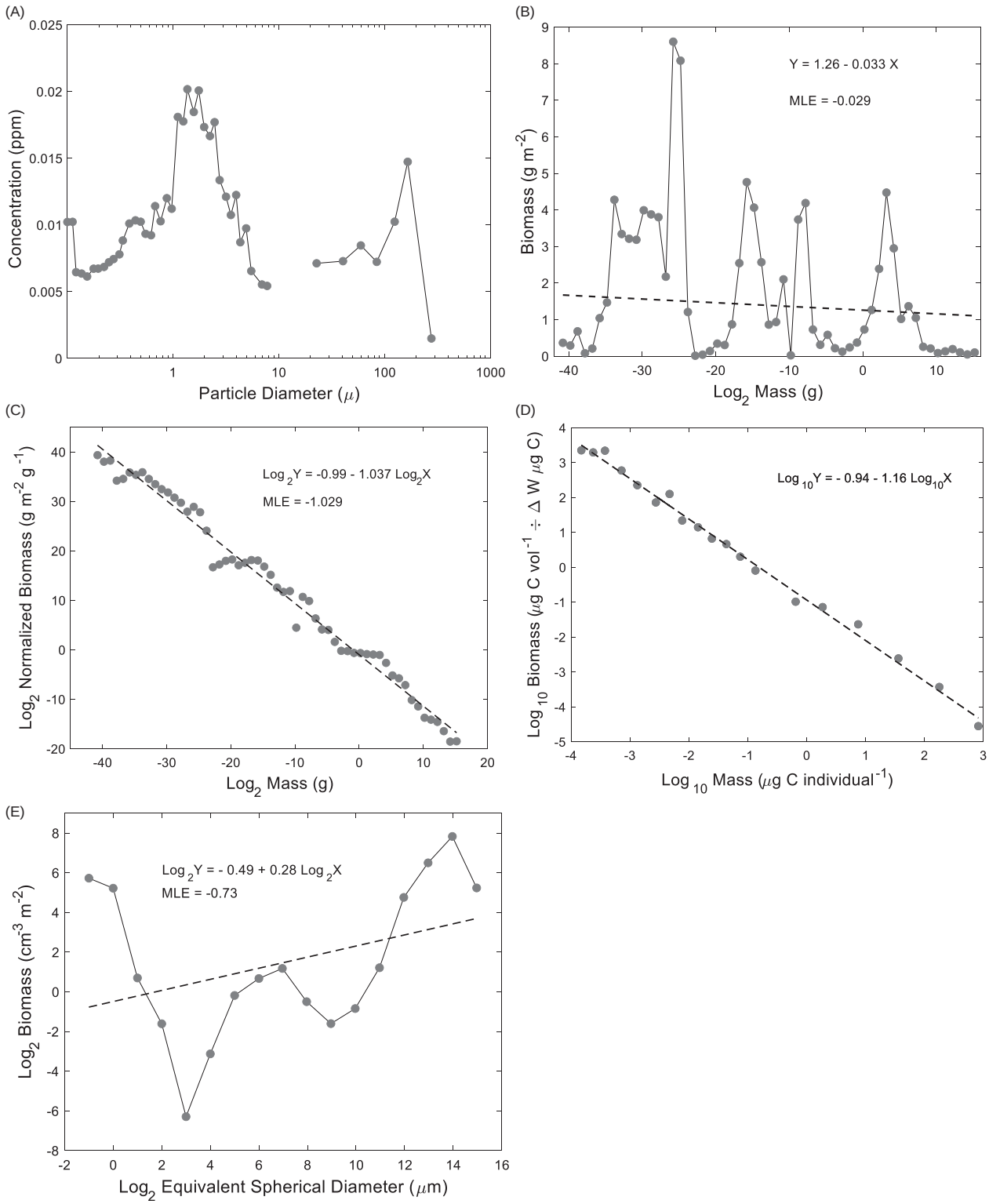

Fig. 4 (A) R. Sheldon's marine biomass spectrum comprises organisms less than 100 μm in diameter measured with a Coulter Counter and zooplankton above this range collected with tow nets. Size units presented here are no longer commonly used. (B) The biomass spectrum for Lake Ontario from bacteria to large fish averaged over seasons and spatial stations. Major biomass "domes" from left to right are phytoplankton and bacteria, zooplankton, the benthic amphipod *Diporeia*, and planktivorous fish. Equation of the OLS fitted line and the MLEbin exponent estimate are shown. (C) The Lake Ontario Normalized Biomass Spectrum from the same data as in (B). The biomass domes are attenuated in this presentation but are nevertheless visible as humps or waves. The OLS fitted line and the MLEbin exponent estimate are shown. (D) Normalized biomass spectrum for micro- and macro-plankton in the euphotic zone of the North Pacific Central Gyre with OLS fitted equation. The MLE exponent estimate cannot be computed because the unnormalized biomass data were not published. (E) Mean benthic biomass size spectrum from marine samples in the Bay of Fundy, New Brunswick and the south coast of Nova Scotia, Canada. The three domes from left to right comprise bacteria, interstitial meiofauna, and macrofauna. OLS fitted line and MLEbin exponent estimate are shown. (A) Redrawn from Sheldon RW, Prakash A and Sutcliffe WH Jr (1972) The size distribution of particles in the ocean. *Limnology and Oceanography* **17**: 327–340; (B and C) Redrawn from Sprules WG and Goyke A (1994) Size-based structure and production in the pelagia of Lakes Ontario and Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* **51**: 2603–2611; (D) Redrawn from Rodriguez J and Mullin MM (1986) Relation between biomass and body weight of plankton in a steady-state oceanic ecosystem. *Limnology and Oceanography* **31**: 361–370; (E) Redrawn from Schwinghamer P (1981) Characteristic size distributions of integral benthic communities. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 1255–1263.

biomass concentration (Figs. 3E and F). MLE techniques only estimate the exponent λ but if the primary pattern in a spectrum is linear then the spectral height could be determined by solving the linear equation passing through the intersection of the means of X and Y.

Theory

Models of interactions within communities of organisms have traditionally been based on species as the focal units and have generally been complex given the need for species-specific data on many life history and ecological processes. They have nevertheless been instrumental in advancing our insights into the dynamics of communities in nature. By contrast, in size-structured community models the unit is an individual and its primary characterization is body size. Physiological and ecological processes such as metabolism, prey selection, feeding rate, and growth efficiency are strongly size-dependent and empirical estimates of the underlying parameters of these functions are extensive.

Early size-based models were motivated by a desire to understand the size-based ecological and physiological processes underpinning Sheldon's famous observation of roughly equal biomass in logarithmic size intervals from bacteria to whales. In the simplest terms this arises because the loss of energy through a sequence of inefficient transfers from small to large organisms is balanced by progressively lower turnover times of the biomass of ever larger individuals. Sheldon et al. (1977) modeled these concepts in order to make predictions about the biomass and production of larger marine organisms of commercial interest (e.g., Peruvian anchoveta, *Engraulis ringens* Jenyns) based on more easily obtained data on the abundance of small organisms (phytoplankton and zooplankton). Kerr (1974) similarly conceived of the production of a prey population constituting the ration of a large (by a fixed size ratio) predator used to support predator metabolism and growth at size-dependent rates. When fully parameterized both modeling approaches predicted ratios of standing stocks of prey and predators to be roughly equal as empirically observed.

Sheldon and Kerr envisaged energy being transferred across size gaps from smaller to large organisms. By contrast, Platt and Denman (1977) modeled a continuous spectrum with biomass moving through time across narrow "spectral" bands of body mass. The flux of biomass through a size band was modeled by the respiration rate and turnover time of the organisms both of which are size dependent. The result was a slope of −1.22 for the normalized biomass spectrum. This model did not include predation losses so can only be taken as a preliminary effort at modeling continuous spectra as Platt and Denman noted.

Boudreau et al. (1991) postulated that, in food webs classified by organism size only, biomass production occurs at two scales. At the scale of major predator groupings (e.g., fish feeding on zooplankton) predators can capture only a fraction of the total prey biomass and can convert only a fraction of that energy to predator biomass. This is a primary "physiological" scaling that determines the overall negative slope of the (normalized) biomass spectrum. By contrast, within major predator groups larger organisms feed on smaller ones and must continuously seek prey of suitable size, concentration, and spatial distribution to meet their growing energy demands. Size dependencies of these interactions define a secondary or "ecological" scaling that manifests as biomass "domes" along the primary spectrum axis (e.g., Fig. 4). Thiebaux and Dickie (1993) analytically derived the secondary domes from a mathematical analysis of Boudreau's model.

A major advance in size spectrum models by Hartvig et al. (2011) with modification by Rossberg (2012) was a formulation comprising multiple "species" each made up of many individuals of varying body size up to the species-specific maturation size. Species are linked through feeding interactions, the strengths of which are governed by the relative body sizes of predator and prey individuals. Acquired energy is partitioned into individual growth and maintenance until maturation size is reached. Then more and more energy is allocated to reproduction until growth eventually ceases. Predation is the primary source of mortality. Organisms grow as a function of how much they eat, and they die primarily because they are eaten. These processes closely simulate interactions among individual organisms in nature. The community spectrum is derived by summing individual species spectra and steady-state solutions match the basic Sheldon expectation of roughly equal biomass across equal logarithmic size ranges. Furthermore Rossberg et al. (2019) show that dome structures commonly observed in empirical size spectra are predicted by his theory as top-down cascades that are intensified by increases in overall system productivity.

Size spectrum models are relatively simple given that component organisms are characterized by body size alone and the few ecological and physiological processes required are size dependent. Parameter values of these size-dependent processes are well documented in the literature. The models predict emergent properties of communities that are commonly observed in nature. They apply specifically to pelagic aquatic communities in which predators feed on prey smaller than themselves. It remains to be determined whether terrestrial or other aquatic communities (e.g., benthic) can be similarly modeled. Given their ability to closely simulate observed patterns of community size structure it can be said that these models capture the fundamental organizing principles of ecological systems. On the other hand size spectrum models are not suited to predicting dynamics at the species level although trait-based versions of these models do capture key life-history characteristics such as maturation size and maximum body size. There is a trade-off between increasing model complexity to represent myriad interactions among species and simpler, more easily constructed models that are limited in predictive ability. Perhaps size spectrum models represent an intermediate solution, but it cannot be denied that a variety of modeling approaches can be useful for ecosystem management.

Applications

The earliest applications of the size spectrum were to make predictions of abundance or production of one size class of organisms from spectral information on a smaller size class. For instance Sheldon et al. (1977) used a model of the relationship among standing stock, body size, and growth efficiency of predators and their prey to estimate the annual production of anchoveta in a relatively simple pelagic food web off the coast of Peru. Field observations of biomass per logarithmic interval of phytoplankton were used to predict those for copepods and thence for anchoveta based on the model above. The estimated total anchoveta standing stock in the fishing area was then multiplied by an independently measured instantaneous population growth rate to predict the annual production available to the fishery. This estimation fell within the range of actual landed catches over a 6-year period.

Slopes of two common forms of the size spectrum—the abundance and the normalized biomass size spectra—have been observed to be close to −1 across a wide range of pelagic aquatic habitats. This has been interpreted to represent the steady state condition of the size structure of natural communities not subjected to major perturbation. It suggests that deviations of the slope from this "baseline" condition could be a signal of destabilization of the community due to external perturbations such as size-selective fishing or pulses of nutrient additions. In fact size spectrum parameters have been recommended as indices for monitoring the status and trends of marine ecosystem properties by both the European Commission and the Southern Ocean Observing System. The relative simplicity and availability of body size data and the demonstrated utility of the size spectrum as an indicator of system structure make size spectrum parameters particularly useful. The slope of the size spectrum has also been interpreted as an indicator of the efficiency with which energy is transferred through the community; shallower slopes indicate high efficiency because greater numbers of larger organisms can survive. Mehner et al. (2018) showed that empirical estimates of trophic transfer efficiencies between trophic groups in lake communities of bacteria to fish were correlated with the slope of their size spectra.

Several researchers have tracked the value of spectrum slopes through time as a way of monitoring ecosystems and identifying whether, and why, community size structure has changed. For instance Blanchard et al. (2005) used various metrics, including the slope of the normalized biomass size spectrum, to track changes in the size structure of the Celtic Sea groundfish community over multiple years and locations in relation to commercial fishing pressure and sea temperature. The spectrum slope decreased (became more negative) through time indicating a loss of larger organisms due to increased fishing pressure. Mazurkiewicz et al. (2020) studied abundance and biomass spectra of undisturbed benthic macro- and meiofauna communities across six Norwegian fjords varying in species composition and bottom water temperature. They found that size spectrum shapes of these communities did not vary across localities despite variation in species composition and environmental conditions suggesting stability of size structure and hence energy transfer through the food webs. Of four fish size indicators used to detect changes in fishing mortality in a multi-species marine fisheries model Thorpe et al. (2015) showed that the slope of the abundance size spectrum was the most responsive. Barth et al. (2021) showed that an abrupt change in a time series of normalized abundance size spectrum slopes coincided with the first detection of the invasive zooplankton predator *Bythotrephes longimanus* in a small Ontario lake, but slopes returned to normal values after the invasion suggesting a return to the baseline structure of this plankton community after the initial disruption.

Beyond slopes, dynamic size spectrum simulation models have now reached the point at which they can be applied in real ecological contexts—particularly marine fish communities. Model specification of the growth and mortality of fish "species" that are characterized by their body size and distinguished from others by maturation size make them especially suitable for use in fisheries management. These models differ from previous fisheries management models in that (a) the dynamics arise from growth and predation processes internal to the model (individuals grow by feeding and die by being eaten) rather than being controlled by external growth or yield-per-recruit functions, and (b) organisms are characterized by body size rather than age. Law et al. (2015) have remarked that removing the independence of growth and mortality assumed by yield-per-recruit models leads to ".. a surprisingly different perspective .." on management of fish stocks. Furthermore the data on organism size and abundance through time required to parameterize and test size spectrum models are more easily acquired than life history information on many fish species. This is not to say one approach is better than the other but rather that a variety of model formulations will enrich the knowledge of how fish communities function and how best to manage them by balancing exploitation with conservation.

Houle et al. (2016) used a size spectrum model of the 35 most common fish species in the Celtic Sea southwest of Ireland to evaluate the relative impacts of seal predation and commercial fishing on the fish community. As is typical of size spectrum models, species are distinguished solely by the key trait of maturation body mass with other life-history traits as allometric functions of this mass. The model was calibrated to historical data on the fish community and simulations indicated that seal predation was an order of magnitude less than commercial harvests principally because there was little overlap in preferred prey of seals versus the fishery.

Blanchard et al. (2014) developed a more complex size spectrum model of 12 common species captured by the North Sea trawl fishery. Physiological, life history and foraging parameters were specified for each species as were predator-prey mass ratios and spatial overlap among species pairs—all estimated from field data. The model was calibrated to the historical fishery. Simulation results indicated that biodiversity targets (minimum biomass of all species, specified minimum proportion of large fish, the slope of the community abundance spectrum of −1.1) were 60% more likely to be reached under the sustainable yield scenario than under status quo fishing.

Finally, forces other than fishing mortality have also been explored with size spectrum models. Yool et al. (2017) used a size-structured marine benthic biomass model coupled with an ocean biogeochemistry model to explore benthos response to variations in particulate organic carbon (POC) supply under varying climate warming and ocean acidification scenarios. Results indicated that with climate warming benthic biomass decreased more than surface ocean productivity, especially at deeper sites. The model indicated this was due to acidification effects on the chemistry of the POC flux and greater remineralization over deep oceans sites due to time taken for sedimentation.

Prospectus

The tremendous advances in the theory, practice, and application of size spectra, particularly over the last 10–20 years, have cemented these concepts in the very center of aquatic ecosystem ecology. It can also be argued that this size-based approach to studying the structure and functioning of communities in nature has motivated a broader trait-based approach across all types of ecosystems. That is not to say body size is a panacea but rather that it is a complement to species-centered studies that has enriched the tools and perspectives we can bring to bear on many difficult threats to the natural world.

Standardization of the data and analyses required to construct size spectra has also advanced considerably. This is necessary for comparisons of size spectrum parameters among studies—especially the exponent λ that is an index of both the structural integrity and the energy efficiency of natural communities. Recent studies have greatly advanced the statistical procedures that give the most robust estimates of this important parameter. International organizations are encouraging investigation of size spectrum parameters as key indicators to be applied to management of natural communities—especially marine fish. Size spectrum models have become more sophisticated with increasing success as platforms for testing ideas about harvesting approaches to marine fisheries, which should also be applicable to inland water fisheries. They have also become more complex as the simple trait of body size is being extended by addition of other life history and physiological species characteristics. There will eventually be a trade-off between the two extremes.

From bacteria to whales still stands as a remarkable insight into the structure and dynamics of ecological communities and will surely continue to motivate size-based ecology for many years to come.

Recommendations

1. Use mass as the measure of body size whenever possible—either directly measured or computed from a length-weight relationship.
2. Retain all individual masses for the most rigorous MLE estimates of λ. Compare Pareto or abundance spectrum plots of the data with fitted models to ensure good fits—especially if the spectrum contains non-linear portions (domes).
3. If the data comprise masses already allocated to bins use MLE bin methods to estimate λ and plot data and fitted models. Compare with OLS fits to the abundance spectrum, especially if domes are present in the spectrum.
4. Beware of generalizing based on size spectra data for limited organism size ranges (e.g., zooplankton only or fish only). Theory and application are based on the whole food web with interacting predators and prey spanning wide size ranges.
5. As much as possible include seasonal and spatial replication in size spectrum sampling programs. A single spectrum at a place and time is but a snapshot of a dynamic community of organisms operating on different temporal scales.

See Also: Fundamental concepts and theories: Bioenergetics; Predation; Structures and functions of Inland Waters - Groundwater: Trophic Interactions in Subterranean Environments; Structures and functions of Inland Waters - Lakes: Lake Food Webs

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Further Reading

Papers That Present Reviews of Size Spectrum Concepts

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Paleolimnology: Long-Term Reconstructions of Environmental Change

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This is an update of J.P. Smol, Paleolimnology, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00207-6.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Lars Rudstam.

Introduction

The ecological and environmental conditions in lakes and rivers change on a variety of time scales. However, one of the greatest challenges faced by limnologists (as well as other environmental and ecological scientists) is the general lack of long-term monitoring data. A recent assessment of the length of typical aquatic monitoring programs concluded that about two-thirds of such studies were less than 1 year in duration, with over 80% of studies less than 3 years long (Smol, 2019). Without such temporal data, it is difficult to determine whether changes are occurring in an aquatic system and, if they are, then to identify the likely drivers of any ecosystem changes. Long-term data are especially critical in contrasting the effects of human activity versus natural environmental change on ecosystems.

Although direct instrumental data on limnological changes are often lacking, an important archive of past environmental and ecological conditions is preserved in the sediments of lakes and some river systems. The information preserved in lake sediments provides relatively comprehensive records of past limnological changes, as well as changes occurring in the surrounding terrestrial catchment and airshed.

Paleolimnology can be defined broadly as the multidisciplinary science that uses the physical, chemical and biological information preserved in aquatic sediments to track past changes in ecosystems (Cohen, 2003; Smol, 2008). Paleolimnology has enjoyed considerable progress over recent decades, with important advances in the ways paleolimnologists can retrieve and section sediment cores, new approaches to provide geochronological control for these sediment profiles, major advances in the quantity and quality of proxy information that paleolimnologists have learned to retrieve from sediments, as well as major improvements in the ways that paleolimnologists can interpret these stratigraphic changes in a statistically robust and defendable manner.

Examples using lakes will be emphasized throughout this contribution, however similar approaches are being used in wetland, river, estuarine and marine ecosystems (e.g. Weckström et al., 2017). The overall focus is on paleolimnological approaches with an emphasis on biological proxy data. Other contributions to this encyclopedia cover additional approaches.

Sediments

Lakes slowly fill up with sediments. Typically, 24 h a day, every day of the year, sediments are slowly accumulating at the bottom of lakes. The overriding principle in paleolimnology is that lake sediments accumulate in an organized fashion, with older material occurring deeper in the sediment core, and the most recent material at the surface of the core (i.e. the Law of Superposition). Not all sediment profiles are ideal for historical analyses, as some mixing processes, such as bioturbation (i.e. the mixing of the sediments by benthic organisms), may occur. Nonetheless, many of these potential problems can be assessed (e.g. using dating techniques) and it is now clear that the vast majority of lakes archive valuable records of past environmental change in a stratigraphically intact manner.

Lake sediments incorporate a tremendously rich library of information about lake processes and biological communities from both within and external to the lake. Paleolimnologists typically divide the sources of lake sediments into two broad categories: (1) allochthonous sources, which refer to material originating from outside the lake basin (e.g. soil particles, pollen grains from trees, pollution from industries); and (2) autochthonous sources, which refer to material originating from within the water body itself (e.g. dead algae or invertebrates, chemical precipitates). The amount of sediment that has accumulated can vary tremendously between lakes, and even within a single lake basin over time. A typical glaciated temperate lake may contain 4 or 5 m (or even 10 m or more) of sediment, representing the lake's history since the time of the lake's formation following the retreat of the ice sheets at the end of the last ice age (*ca* 12,000 years ago, but varies depending on location). In contrast, a lake of similar age from a polar

region may have far less sediment accumulated, as sedimentation rates are typically very low. In some regions, such as the Great Rift Valley lakes of Africa, records spanning several hundred thousand years are contained in 100s of meters of sediment.

A major advantage of paleolimnological approaches is that researchers can, to a large extent, set the time scale. For example, by taking longer sediment cores, a longer time frame can be studied. Similarly, the researcher has some control over the temporal resolution of the study. For example, by slicing the sediment core at finer intervals, more detailed records of past environmental changes can be inferred. Of course, there are also potentially serious limitations. For example, the sediment accumulation rate may be so low that even fine-resolution sampling will still not provide sufficiently fine temporal resolution to answer certain questions.

From the information preserved in sediments, paleolimnologists can reconstruct the history and development of aquatic ecosystems. There are two key steps involved in any paleolimnological investigation – (1) retrieval of the sedimentary material required for study, and (2) establishing the depth-time scale of the profile using geochronological techniques. These first two critical steps are described below.

Retrieving sediment cores

Many ingenious sediment samplers have been developed to collect sediment cores in an undisturbed manner, many of which are described in Glew et al. (2001). Each sampler has both advantages and drawbacks, and so it is first important to determine the scientific questions that researchers hope to address. For example, what time frame will be required for the paleolimnological study? Will the program include a detailed analysis of the more recent sediments, which may be used to study, for example, the influences of recent human interventions on the lake system, such as the effects of agriculture or acid rain? Or is the main focus on long-term changes, such as broad climatic shifts over millennial time scales? What temporal detail (e.g. annual, decadal, centennial) will be needed to answer these questions? The answers to these questions will determine which study lake(s) will be chosen for study, as well as what type of equipment will be required to retrieve and section the most suitable sediment samples.

The earliest corers were developed to answer questions related to long-term (centennial and millennial) scale changes in lake ontogeny. Many of the original designs were inspired by the work of M. Jull Hvorslev (1895–1989), whose seminal work on sampling soil profiles for the U.S. Army Corps of Engineers contains many of the basic principles that paleolimnologists still use today to collect sedimentary profiles (Hvorslev, 1949). Using some of these concepts, Daniel Livingstone (1927–2016) published a piston coring design (Livingstone, 1955) that is still widely used today (often with some minor modifications). The typical piston corer consists of three components: the piston and cable assembly, the core tube, and the drive head and drive rods. Many variations of the original design are available, including those that can be used on a rope. Piston corers can remove, sequentially, sediment profiles of about 1 m in length, until the required depth of sample penetration is reached (Fig. 1).

Since the mid-1980s, there has been an increased emphasis on using lake sediments to study more recent changes in lake histories, such as the effects of anthropogenic impacts on lake ecosystems. This requires the use of a corer that will carefully sample the most recent, watery sediment records, which may be disturbed or lost if collected using standard piston corers. Two major types of samplers are used: gravity corers and freeze crust corers.

A variety of gravity corers have been developed to specifically sample the most recent sediments. Many of these follow the general design of a benthic invertebrate sampler that Z. Kajak (1929–2002) developed, however significant modifications have been made to the original design, such as those developed and modified by John R. Glew (Fig. 2) or those developed by Uwitec in Austria. In its simplest form, a surface sediment gravity corer is a hollow coring tube that is carefully lowered into the recent sediments on a rope from the surface, using its own weight for penetration. However, when sampling stiffer sediments, additional weight may be

Fig. 1 Lake sediment coring on Lake Chala (Kenya), using a Livingstone-type piston corer (modified by Uwitec). Photograph courtesy of B. Cumming (Queen's University).

Fig. 2 Retrieving surface sediment cores with a Glew gravity corer from Lake Opinicon (Canada). Photograph courtesy of B. Cumming (Queen's University).

needed to achieve adequate penetration. The top of the coring tube is then closed off to create a seal, typically using a messenger that is delivered down the coring line. The gravity corer, with the tube of collected sediment, is then returned to the surface, the bottom of the core tube is plugged, and then set up for subsequent sectioning and sub-sampling.

Freeze-crust coring is another sampling method used for retrieving relatively undisturbed recent sediments. This process is also quite simple. A freeze-crust corer can take many designs, but most are either a metal box or tube that is filled with a coolant, such as frozen carbon dioxide (i.e. dry ice), as well as a fluid, such as ethanol. The filled freeze crust corer, which would now be very cold, is then slowly lowered on a rope into the sediments where in situ freezing of the sediments onto the corer will occur. During this time, the sampling rope must be anchored on a solid platform at the lake surface, such as the ice cover, to prevent it from sinking further into the sediments. After a certain period of time (the time that the sampler is left in the sediments depends on the design used, but typically from 10 to 15 min), a crust of sediment has been frozen onto the surface of the sampler. The sampler can then be retrieved, and the crust of frozen sediment can be removed and sectioned.

A large number of other coring designs are available, including those specifically developed to take long sediment cores in deep waters, such as the Kullenberg sampler. Other designs include corers designed to penetrate compact sediment profiles, such as hammer corer and vibracorers. Suffice to say that almost any lake system can now be sampled for its sediment history.

Just as there are many types of sediment samplers, there are also many ways to section the sediments. Most researchers use an extrusion system for recent sediments, whereby discrete intervals of sediment can be sliced off the core for further analyses (Fig. 3). However, for some paleolimnological analyses, researchers may want to keep the core intact until some preliminary analyses are completed, such as X-raying the sediment profile.

Fig. 3 An example of a vertical extrusion system used for sectioning recent sediment at close intervals. (A) A 1 cm slice of sediment has been extruded from the core tube. (B) The sediment section is sliced off and removed. Photographs courtesy of N. Michelutti (Queen's University).

Dating sediment cores

A critical factor in deciphering lake sediment histories is to establish an accurate depth-time profile (i.e. geochronology) of the sediment core. Without this information, it is not possible to place past environmental changes in a proper temporal perspective. Many approaches are available depending on the type of sediments, the location of the study lake, and the approximate age of the sediments themselves (Last and Smol, 2001a).

In some lakes, such as certain meromictic lakes, sediments may be annually laminated (i.e. varved; Zolitschka et al., 2015), and superficially may resemble annual tree rings. A typical biogenic varve is composed of a couplet of laminae representing 1 year of sediment accumulation. The reason why couplets form in some sediment profiles varies from lake to lake, but varves represent seasonal differences in the materials (biological, chemical, and/or mineral) reaching the sediment surface. If varved sediments can be identified, the paleolimnologist can often attain a very high degree of temporal resolution (e.g. even sub-annual changes in some cases by splitting varves into seasons). However, the annual nature of varves must first be confirmed using other dating techniques (see below), as false laminae and missing laminae may obscure the record.

In most cases, lake sediments are dated using radiometric techniques. For older sediments (e.g. on millennial scales), radiocarbon-14 (^{14}C) dating is often used. As ^{14}C has a radioactive half life of 5730 +/− 40 years, it is useful for dating sediments on millennial time scales up to approximately 45,000 years of age. In the older paleolimnological literature, many ^{14}C dates were described as "bulk dates," as the ^{14}C content of bulk sediment was often used for dating. However, over recent decades, advances in Accelerator Mass Spectrometry (AMS) technology have allowed paleolimnologists to date much smaller organic samples, such as a single seed or pine needle. As with all techniques, care must be taken to use the most appropriate material for dating, because a variety of potential error sources exists. For example, one of the most common problems with ^{14}C dating is the so-called "hard water effect," whereby "old carbon" from the local bedrock can dilute the ^{14}C content of a bulk sediment sample. Ideally, paleolimnologists try to radiocarbon date material such as terrestrial macrofossils (e.g. seeds, twigs), which are not affected by some of these problems.

As noted previously, there has been a shift in some areas of paleolimnology to focus on the more recent histories of lakes. Due to relatively long radioactive half-life of ^{14}C, it is not appropriate for dating recent sediments. Instead lead-210 (^{210}Pb), a naturally occurring isotope, is often the dating method of choice. ^{210}Pb has a half-life of about 22.3 years, and so it is ideal for dating sediments over the last century or so. In addition, other isotopes, such as cesium-137 (^{137}Cs), which is a by-product of nuclear explosions, can be used in some sedimentary sequences to further refine depth-time profiles. As stratospheric nuclear bomb testing became more common in the mid-1950s, a rise in ^{137}Cs can often be recorded in sediment profiles at this time. Bomb testing by the former Soviet Union and the USA peaked in 1963, and this is often seen as a peak in the ^{137}Cs profile, followed by a marked decline in concentrations, with the signing of the nuclear Test Ban Treaty in that year. However, in some parts of Europe and elsewhere, a second peak in ^{137}Cs can be found, marking the 1986 Chernobyl nuclear accident in the Ukraine.

Other dating methods include identifying ash layers (tephras) from known volcanic eruptions, as well as other episodic events, such as sedimentary charcoal from known forest fires. Accurate dating of sediment profiles remains a major challenge for many studies, and so, when possible, several dating methods should be used simultaneously to increase the confidence of the geochronology.

The "top-bottom" or "before and after" approach

As noted above, paleolimnologists often have the important advantage that they can set the time scales for analysis. Typically, many sediment sections in a core are analyzed for a suite of indicators. However, this is also quite time consuming, as many biological analyses are time intensive (e.g. isolation from sediments, taxonomy, microscopy, enumeration). For some research questions, though, it may be more important to study a larger number of lakes to obtain a regional assessment of environmental change. In such cases, detailed paleolimnological analyses are not practical due to time and resource restraints. Instead, paleolimnologists have developed a simple, regional assessment tool, which is often referred to as the "top-bottom approach."

The top-bottom approach is straight-forward and was originally developed to study the effects of recent human influences (e.g. acidification, Cumming et al., 1992) on lake ecosystems. In this approach, surface sediment cores spanning the last several hundred years, such as those collected with gravity corers, are taken from the lakes included in the study. However, in contrast to a standard paleolimnological assessment, where many sediment samples would be analyzed from each core, typically only two sediment samples are analyzed for indicators: the surface (or top) sediment sample, representing recent environmental conditions; and a sediment sample that predates the period of marked human impacts (or bottom sample). For example, if one was attempting to assess the differences in lakewater pH because of acidic precipitation for a region, the bottom sample should pre-date *ca* 1850 CE. By comparing ecosystem changes, as inferred from the paleolimnological indicators present in the surface sediment (i.e. recent) and deeper sediments (i.e. pre-impact), a regional assessment of environmental change can be attained. A major advantage of the top-bottom approach is that only two samples (not including samples to establish reproducibility) are analyzed for each core, as opposed to perhaps 20 or more sediment sections of a typical paleolimnological assessment of recent environmental change. The major disadvantage is that the top-bottom approach does not provide information on the timing of environmental changes – it is simply a "snapshot" approach.

Paleolimnological indicators

Lake sediments contain a wide array of physical, chemical, and biological indicators of past environmental change. Only the most commonly used indicators are discussed below, however details concerning these and other proxies are reviewed in Cohen (2003), Smol (2008), Last and Smol (2001a, b), Smol et al. (2001a, b), and Smol and Stoermer (2010).

Important information is contained in the physical structure and composition of the sediments themselves. For example, a simple visual inspection of the sedimentary sequence can provide information on color changes, texture, presence of laminae, etc. A variety of sediment logging and recording techniques are now available, especially with the advent of digital technology. In addition, radiography, X-ray, and other image analysis techniques can often reveal important bedding features that may not be visible with the naked eye (Francus, 2004). Other procedures that are commonly used include particle size analyses of the sediments, which provide important insights to help determine the process, and to some extent, the source of detrital sedimentation. Lake sediments also archive magnetic signals, which are used in a number of applications, including deciphering past erosion events.

Typically, one of the first analyses a paleolimnologist will undertake is to determine the relative proportions of water, organic matter, carbonate, and siliciclastic material (i.e. clastic sediment composed of silicon-bearing minerals such as quartz, feldspars, clay minerals) in the sediment sections. This is often done using weight loss techniques, by successively exposing the sediment to higher temperatures, and then use the differences in sample weights to estimate the percentage of the various fractions. For example, wet sediment can be dried in a drying oven set at approximately 80–100 °C, and the percentage of water can be estimated by weight loss. Combusting the same sediment in a muffle furnace at about 450 °C for a few hours will provide an estimate of the organic matter content. A further ashing to about 950 °C can be related to the carbonate content. The remaining material represents mainly siliciclastic sediments. These types of data have many applications, although they also have to be interpreted cautiously. For example, intuitively, one might expect that the percentage of organic matter in a sediment profile would be directly related to the amount of organic production occurring in the lake basin. Although to some extent this relationship holds, it is important to consider that these variables are typically expressed as percentages, and if, for example, human activities in a catchment have resulted in erosion as well as nutrient export, the siliciclastic material deposited in the lake due to the erosion may well obfuscate any signal of increased autochthonous production.

Lake sediments also archive a wide spectrum of geochemical information that can be used to interpret ecosystem changes. Typical approaches include analyses of various elements that can be used to track past biogeochemical changes in the lake and its catchment. Whilst wet chemical lab techniques are still typically used for detailed assessments, a variety of newer, non-destructive tracking techniques have become available (Rothwell and Croudace, 2015). Other geochemical data can be used to reconstruct past anthropogenic influences (Blais et al., 2015), such as mercury and lead, as well as other metals. Persistent organic pollutants, such as DDT or PCBs, also provide important records of contaminant trajectories to lake sediments. These pollution profiles can be strengthened by studying the past deposition of fly-ash particles, such as spheroidal carbonaceous particles and inorganic ash spheres, resulting from various industrial activities (Rose, 2015).

The isotopic composition of sediments provides additional paleoenvironmental information (Leng, 2006). These include isotopes of carbon that have been used in, for example, lake eutrophication work, sulfur isotopes to track the effects of anthropogenic acidification, oxygen isotopes in climatic and hydrologic change research, and nitrogen isotopes to reconstruct past changes in sources and cycling of nitrogen (and even past sockeye salmon or seabird populations). More recent approaches include determining the isotopic composition of specific indicators found in lake sediments, such as the carapaces of some invertebrates.

One of the most active areas of paleolimnological research, however, deals with biological indicators (Smol et al., 2001a, b). A central theme in ecology has always been the attempt to link the distributions of organisms to environmental conditions. A diverse array of biological indicators is preserved in lake sediments, either as morphological remains (e.g. diatom valves) or as biogeochemical fossils (e.g. pigments). It is therefore not surprising that biological paleolimnology has provided important insights into past ecosystem changes. Below, I summarize some of the dominant indicators.

Pollen grains and spores are amongst the most common morphological indicators used in paleoenvironmental studies. The study of pollen grains and spores is a large scientific discipline, called palynology, which has many applications besides paleolimnology, such as in archeology and forensic science. Plants can produce large numbers of pollen grains, which are often well preserved in sediments. Similarly, the so-called lower plants, such as mosses, produce spores that are also well represented in sediment profiles. Although most pollen grains and spores are from terrestrial vegetation, aquatic macrophytes also produce pollen. As different species of plants produce morphologically distinct pollen grains (often identifiable to the genus level, but sometimes even to the species level), it is possible to reconstruct, at least in a general way, the composition of past forests and other vegetation. This provides important information on past climate and soil development, as well as the succession of different plant species. Some pollen grains can also assist in dating sediment cores. For example, in northeastern North America, the arrival of European settlers, and their related activities of clearing forests and initiating European style agriculture, resulted in the increase in pollen grains from ragweed (*Ambrosia*).

Plants are also represented in sedimentary deposits by macroscopic remains, typically referred to as macrofossils, which include seeds, twigs, and pieces of bark. Although pollen grains can be transported long distances via wind and other vectors, plant macrofossils are less easily transported, and so they more accurately reflect local vegetation changes. In addition, as noted earlier, they are also important sources for material used in ^{14}C dating.

Algae and cyanobacteria (i.e. blue-green algae) represent major primary producers in most aquatic systems, and almost all of them leave reliable morphological and/or biogeochemical fossils. Foremost amongst these are the siliceous cell walls of diatoms

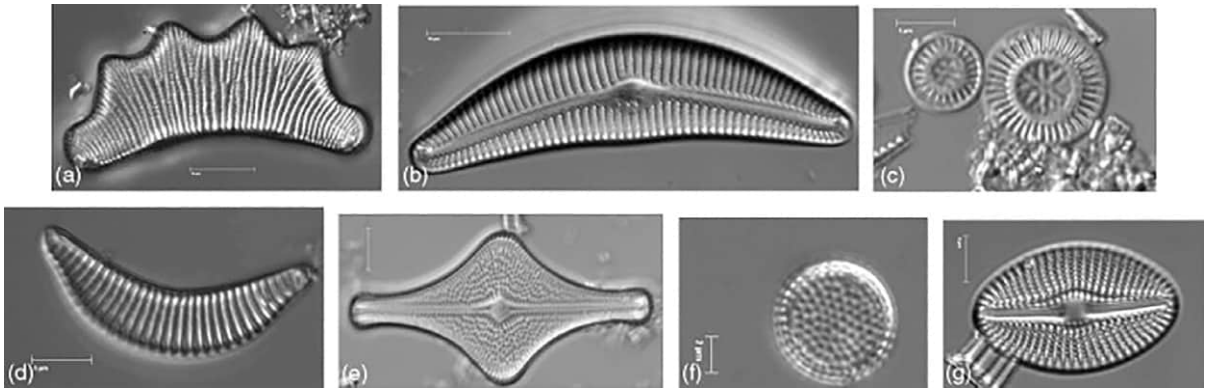

Fig. 4 Freshwater diatom valves. (A) *Eunotia*, (B) *Cymbella*, (C) *Discostella*, (D) *Semiorbis*, (E) *Brachysira*, (F) *Aulacoseira*, (G) *Diploneis*. Photographs courtesy of B. Ginn (Queen's University).

(Bacillariophyceae, Fig. 4), which are the most used indicators in paleolimnological studies, assessing a wide variety of environmental issues (Smol and Stoermer, 2010). A diatom cell wall is composed of two similar halves (or valves) joined together; two valves forming a full diatom cell are called a frustule. Diatoms, which include many thousands of species, often dominate the plankton and periphyton of most lake systems. They have many characteristics that make them ideal paleoindicators. For example, they are abundant and diverse, and their taxonomy is based on the size and sculpturing of the intricate glass cell walls that characterize individual species. As their cell walls are siliceous, they are very well preserved in most lake environments. The distributions of many diatom species are closely linked to specific limnological conditions, such as lakewater pH, salinity, nutrient levels, and so forth, and so are excellent paleoindicators.

Chrysophytes (classes Chrysophyceae and Synurophyceae) similarly can be tracked using siliceous microfossils. About 15% of chrysophyte taxa (including important genera such as *Mallomonas* and *Synura*) are characterized by an armor of overlapping siliceous scales. Similar to the diatom valves described above, these scales are species specific and can be used by paleolimnologists to track past populations of some groups. In addition to the scales, which are only produced by some taxa, all chrysophytes are characterized by the endogenous formation of siliceous resting stages, called stomatocysts (or statospores in the older literature). These cysts also appear to be species specific and are well preserved in sediments, However, unlike chrysophyte scales, the taxonomic identity of many cyst morphotypes have not yet been linked to the species that produced them, and instead cyst morphotypes are often simply referred to by temporary number designations.

Other algae also leave morphological microfossils, but are less widely used. These include vegetative or reproductive cells of certain green (Chlorophyta) algae (e.g. *Pediastrum* colonies), or the akinetes and heterocysts of some blue green algae.

All algal and cyanobacterial groups are also represented in lake sediments by a variety of biogeochemical indicators. Fossil pigments (e.g. chlorophylls, carotenoids, xanthophylls), which characterize certain groups, can be identified in sediments using high performance liquid chromatography (HPLC) or other techniques (such as visible range spectroscopy, VRS).

In addition to some of the primary producers described above, a large suite of zoological indicators is identifiable in sediments. Cladocera (Fig. 5) are represented in sediments primarily by their chitinized body parts: head-shields, shell or carapace, and post-abdominal claws. Trained taxonomists can determine the species affinities of many of these body parts. In addition, the sexual resting stages (i.e. ephippia) of Cladocera are commonly encountered.

Lakes are also the habitat for many insect larvae, with midges or chironomids (Chironomidae, Diptera) dominating many assemblages. Fossil chironomids can be identified via their chitinized head capsules (Fig. 6), which can often be classified to the generic level, or even species level. Chironomid head capsules are most often used in climate reconstructions and in tracking past

Fig. 5 Part of the chitinous exoskeleton of the cladoceran *Eubosmina longispina*. Photograph courtesy of J. Sweetman (Queen's University).

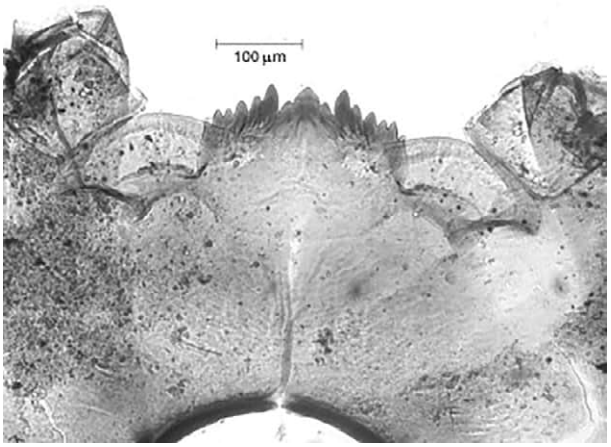

Fig. 6 A head capsule of the chironomid *Chironomus*. Photo courtesy of J. Sweetman (Queen's University).

deepwater oxygen levels. Other insect remains include the chitinized mandibles of *Chaoborus* (phantom midge) larvae. Because certain taxa cannot co-exist with fish predators, these mandibles have been used to document collapses of past fish populations (such as from lake acidification).

The Ostracoda (ostracods, also spelled ostracodes) is another widely used group of invertebrates in paleolimnological studies. Ostracods are characterized by two calcitic valves or shells that can be used to track a wide spectrum of environmental variables. Paleolimnologists not only focus on changes in species assemblages but also on the trace-element chemistry and stable isotope signatures of individual valves, as a memory of past limnological conditions is preserved in the chemistry and isotopic composition of ostracod valves.

In contrast to algal and invertebrate remains, vertebrates tend to be poorly represented in lake sediments. However, in certain environments, fish scales are common, and the inner ear bones of fish (i.e. otoliths) are increasingly being used in paleolimnological reconstructions.

New methodologies and proxies are constantly being developed. For example, there is growing interest in the application of ancient DNA analyses of lake sediments, especially for the study of taxa that do not leave distinct morphological fossils (Domaizon et al., 2017; Parducci et al., 2017). A variety of fecal markers, such as sterols and stanols, are being used to track past sewage inputs (e.g. Vane et al., 2010) as well as wildlife changes, such as seabirds and waterbirds (Hargan et al., 2018). In addition, cyanobacterial toxins, such as microcystins, are being tracked in sedimentary profiles (e.g. Zastepa et al., 2017), as are emerging stressors, such as microplastics (Yang et al., 2021). Applying "-omics" screening methods, which facilitate the visualization of small organic molecules (typically $<$1000 kDa) from sediments, is emerging as a promising way to identify new paleolimnological proxies (Bell and Blais, 2019). These approaches provide new perspectives to lake sediment studies by using high resolution mass spectrometry or nuclear magnetic resonance, along with data mining techniques, to characterize the molecular composition of organic matter in sediments in ways that can be applied to a range of environmental questions. Ongoing work appears to be promising. However, as with all proxies, issues with preservation must be considered carefully.

Determining the environmental optima of indicators

The previous section summarized some of the key indicators used in paleolimnology. However, in order to use, for example, diatom or chironomid species assemblages to infer environmental conditions, it is important to estimate the environmental optima of the indicator taxa. Some information on the ecological optima and tolerances of indicators is available in the scientific literature from previous biological surveys or similar studies. However, given the large number of taxa present, as well as the myriad of environmental variables that can influence species distributions, it can be a daunting task to link species distributions to environmental variables. The most used paleolimnological approach to provide estimates of the environmental optima of indicator taxa are to use surface sediment calibration sets (or sometimes referred to as training sets).

Surface sediment calibration sets have become common components of many paleolimnological studies. The approach is fairly straightforward. A set of calibration lakes is chosen (perhaps 80 or so in number) that reflect the gradients of limnological conditions that might be expected in the paleolimnological study being undertaken. For example, suppose the goal of the study is to reconstruct lakewater pH in a series of lakes affected by acidification. Lakes with present-day pH values ranging from 4.5 to 8.0 would represent a broad gradient in pH values. The first component of the calibration set would be a matrix of limnological and other environmental data available for the calibration lakes. The second step is to determine the distribution of indicator taxa in the 80 calibration lakes. This is done by taking surface sediment cores from each lake and identifying and enumerating the indicators in questions (e.g. diatoms) from the surface 0.5 cm or 1.0 cm of sediments (i.e. representing recently deposited biota). This represents

the second matrix of data required for developing the calibration set, namely the species matrix. The next step is to use a variety of statistical techniques to link the species distributions in the surface sediments to the measured environmental variables for the calibration lakes. Multivariate techniques, such as canonical correspondence analysis (CCA), are often used to determine which environmental variable exerts the greatest influence on species distributions (Birks et al., 2012). Transfer functions can then be constructed relating species distributions (e.g. diatom percentages) to the variables of interest (e.g. lakewater pH). The latter is typically done using statistical approaches such as weighted averaging regression and calibration. The resulting transfer functions linking species distributions to environmental variables are often quite robust.

Although quantitative approaches, such as those described above, have become commonplace in paleolimnological studies, many environmental inferences can still be accomplished using qualitative approaches. It is important not to forget basic ecology when undertaking paleolimnological reconstructions.

Paleolimnological applications

Paleolimnological approaches have now been used to assess a wide spectrum of limnological changes. Early work focused on long-term studies of lake ontogeny, however a considerable volume of more recent research has centered on determining the effects of human impacts on aquatic ecosystems. Much of this applied paleolimnology began in the 1980s with work on acidic precipitation, where paleolimnology was used to determine if lakes had acidified, and if so, when and by how much. For example, Fig. 7 shows a typical diatom stratigraphic profile for an acidified lake in Nova Scotia (Canada). The change in the dominant diatom taxa (shown as percentages) clearly shows a shift in species assemblage composition (beginning *ca* 1940, as estimated from ^{210}Pb dating) that is characteristic of more acidic waters. By using transfer functions developed from surface sediment calibration sets, the pH optima of the individual taxa can be used to provide quantitative estimates of past lakewater pH (as shown to the right of Fig. 7). These types of analyses had a critical role in demonstrating the effects of acid precipitation on lake ecosystems. Other water quality issues can be studied using similar approaches.

Another major research focus is to use paleolimnological approaches to study long-term changes in climate (Battarbee et al., 2004; Bradley, 2014), which has been receiving heightened attention with concerns about greenhouse gas induced warming.

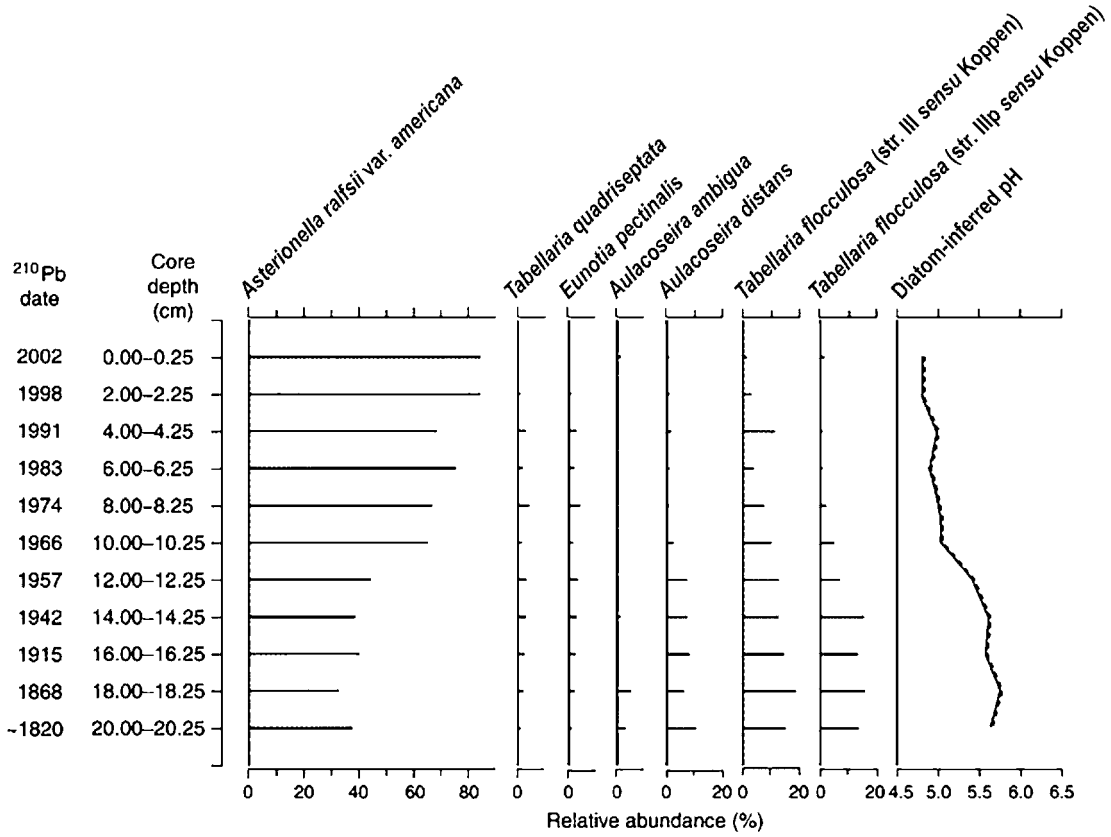

Fig. 7 A summary diagram of the dominant diatom changes (as percentages) in the recent sediments of Kejimkujik Lake (Nova Scotia, Canada). The dates of the sediment slices are estimated using ^{210}Pb dating (left of figure). To the right is the diatom-inferred pH profile, which was generated using a transfer function developed from diatoms preserved in the surface sediments of a calibration set of east coast lakes. Adapted from Fig. 3 from Ginn BK, Stewart LJ, Cumming BF, and Smol JP (2007) Surface-water acidification and reproducibility of sediment cores from Kejimkujik Lake, Nova Scotia, Canada. *Water, Air and Soil Pollution* 183: 15–24. Reproduced with the kind permission of Springer Science and Business Media.

As climatic variables influence, to some extent, all biological distributions, it is not surprising that indicators such as chironomids, diatoms, and other proxies have been shown to track climate variables, either directly (e.g. temperature reconstructions) or indirectly (e.g. via tracking past lakewater salinity changes which can be linked to past precipitation and evaporation ratios, past lake ice covers, etc.). Lake-based paleolimnological studies have been especially important in climatically sensitive polar regions (Pienitz et al., 2004), where some traditional proxies used in temperate and tropical regions are less effective in these cold extremes. Paleolimnology has played a key role in demonstrating the complexity of anthropogenic climate change when considering other environmental stressors.

Many new types of paleolimnological studies are being initiated, the majority of which are multi-disciplinary, which provide more robust environmental inferences. In addition, important synergies between different groups of scientists (e.g. the study of fossil DNA in cladoceran ephippia, working with archaeologists and conservation biologists, etc.) have heightened the interest in many paleolimnological approaches. As environmental problems continue to be identified, and as little monitoring data exist, paleolimnological studies will continue to provide critical information on environmental change in our multiple-stressor world.

See Also: Structures and functions of Inland Waters - Lakes: Macrophytes; Human pressures and management of Inland Waters: Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment

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Section introduction: Structures and Functions of Inland Waters—Lakes

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A proper introduction needs to define the objects of attention. Yet, the term "lake," while tangibzle, cannot be simply defined. If the Oxford's dictionary qualifies a lake as a large area of water that is surrounded by land, it does not specify the blurred distinction between a shallow lake and a pond using more than a relative criterion for size or depth. Similarly, the distinction between large salty lakes and seas is based upon lakes not being directly connected to any ocean or marine basins. But coastal lakes or lagoons somewhat lie in between. Some confusion therefore arises from this floating definition of lakes so that undue reliance should not be put on their given names: remember that the largest lake in the World is named after a sea (the Caspian Sea). On the other end of the size spectrum, some shallow but relatively large waterbodies named ponds end up being larger than others bearing the name of lakes. Lakes are entangled within a hydrological continuum that defies the scientific practice of categorizing objects and, ultimately, definitions for lakes remain mostly operational.

Lakes can be as small as a couple of city blocks of Chicago, Melbourne or Torino (a few hectares, as for the lakes of the historical Experimental lakes Area, a place of major scientific achievements in the field of lake science), they can be as large as a nation (Lake Baikal has the size of Taiwan). Some can be crossed by foot (the average depth of Lake Tchad is 1.5 m) while others are as deep as the height of the Burk Khalifa tower (Lake O'Higgins-San Martín in Patagonia, 836 m depth). They lie at all latitudes, from 55°S (excluding permanently ice-covered Lakes of Antarctica) and beyond 78°N (with at least 1,000 lakes even further north), and altitudes from below sea level (the Dead sea is 431 m below sea level) up to 5200 m above sea level (recently discovered Kajin Sara lake in Nepal). Some are natural, carved millions years ago (ancient lakes of the East African Rift Valley), or were formed after the last deglaciation 15–10,000 years ago (many lakes of the Fennoscandian shield), or only over the last century due to current glacial retreat (about 1200 newly created lakes for Switzerland since the little ice age) (but see Branstrator, in press). Lakes can even be created within days (such as the landslide lake of Derborence in Switzerland, created almost overnight due a massive rockfall in 1749). They can expand, shrink or disappear within decades or millennia (the Aral Sea has lost 75% in surface area since 1960). An increasing number is man-made reservoirs, which currently represent one fifth of the global lake surface (Meyer et al., 2020). Some have uninhabited catchments while some Chinese lakes, such as Taihu, lie within watersheds of several tens of million inhabitants. Some high-altitude lakes, with almost no catchment, contain pure meteoric freshwaters (Crater Lake, United States) while some lakes have waters one order of magnitude saltier than the ocean (Lake Reta/Rose in Senegal with a salinity of 380 g L^{-1}). Due to such a singularity and variability of the millions of the World's lakes, there is no typical lake, neither in terms of structure, i.e., their physical, morphological, chemical or biological components, nor in the way they function, i.e., energy, water or matter movements across components or emergent properties. Each lake is idiosyncratic, only representative for itself. To our appreciation, lake science revolves around searching for commonality and universal principles that regulate the evolution of specific lake structures and functions. And it is of course an ongoing, exhilarating and somewhat endless work. Dealing with such a variability remains a major challenge of lake science, especially since the dynamics of natural but also anthropogenic forcing factors makes it a non-stationary target.

While 75% of the planet's land surface is experiencing measurable human pressure (Venter et al., 2016), lakes, which had always been prioritized locations for human settlements, are under an increasing and diversifying constellation of anthropogenic pressures (Dudgeon et al., 2006; Jenny et al., 2020). There is therefore a crucial stake in lake management, and many relevant case studies are provided in other sections of this volume. Since many of those pressures spread to a global scale, part of the lake science is dedicated to finding common trends in how lakes respond to those global disturbances. Yet, what matters for people is actually their local lake, from which they extract values and services. Lake management applies at the scale of the watershed and requires that the singularity of the local lake is accounted for. Therefore, if global predictions at large scales tell a lot on the evolution of the Earth system, the remaining unexplained variability might impede local projections and decisions for actions. There is then a need to address as much the global trends as to reduce the variability around those trend lines, so that predictions and understanding can be tailored to the local context. For climate change for instance, both data analysis and models attest to a general warming of lakes (O'Reilly et al., 2015), changes of mixing regimes (Woolway and Merchant, 2019), and shorter ice cover (Sharma et al., 2019). Yet, if two neighboring lakes, exposed to the same climate variability, might share trends for some thermal responses to climate warming, the commonality of their responses will decrease when observing their chemical or biological components (Dokulil, 2014; Farrell et al., 2020). While variability in the lake responses can be enormous, universality should be explored through the search of causal mechanisms (Wetzel, 2001). Yet, the predictive power and accuracy of deterministic models decrease when moving from the physical to the ecological or biological aspects of lakes (Soares and Calijuri, 2021). The idiosyncrasy of lakes' responses to

climate change ultimately comes from subtle differences in their hydrological settings, geomorphology, catchment land cover and land use and history (Dokulil, 2014; Leavitt et al., 2009) posing a serious integrative challenge to adaptive management planning.

Herein, we aimed at providing an entry point for the lake science that is being developed to elucidate the fundamentals of lake processes, as the building blocks to a better understanding of lakes' singularities. Summarizing the full knowledge acquired and stabilized in lake science would take much more than 38 chapters. It implied making some choices, and ours were guided by what we considered as topics to be key knowledge for the reader to fully embrace the multiple facets of the ongoing lake science, from geomorphology and geology to physics, biogeochemistry, ecology, trophodynamics and microbiology. All chapters approach their central topic from a functional perspective, linking the structure to the emergent functions, in order to enlighten processes that might drive within and amongst lake variability. So, even if each chapter can be read independently, many of them are by

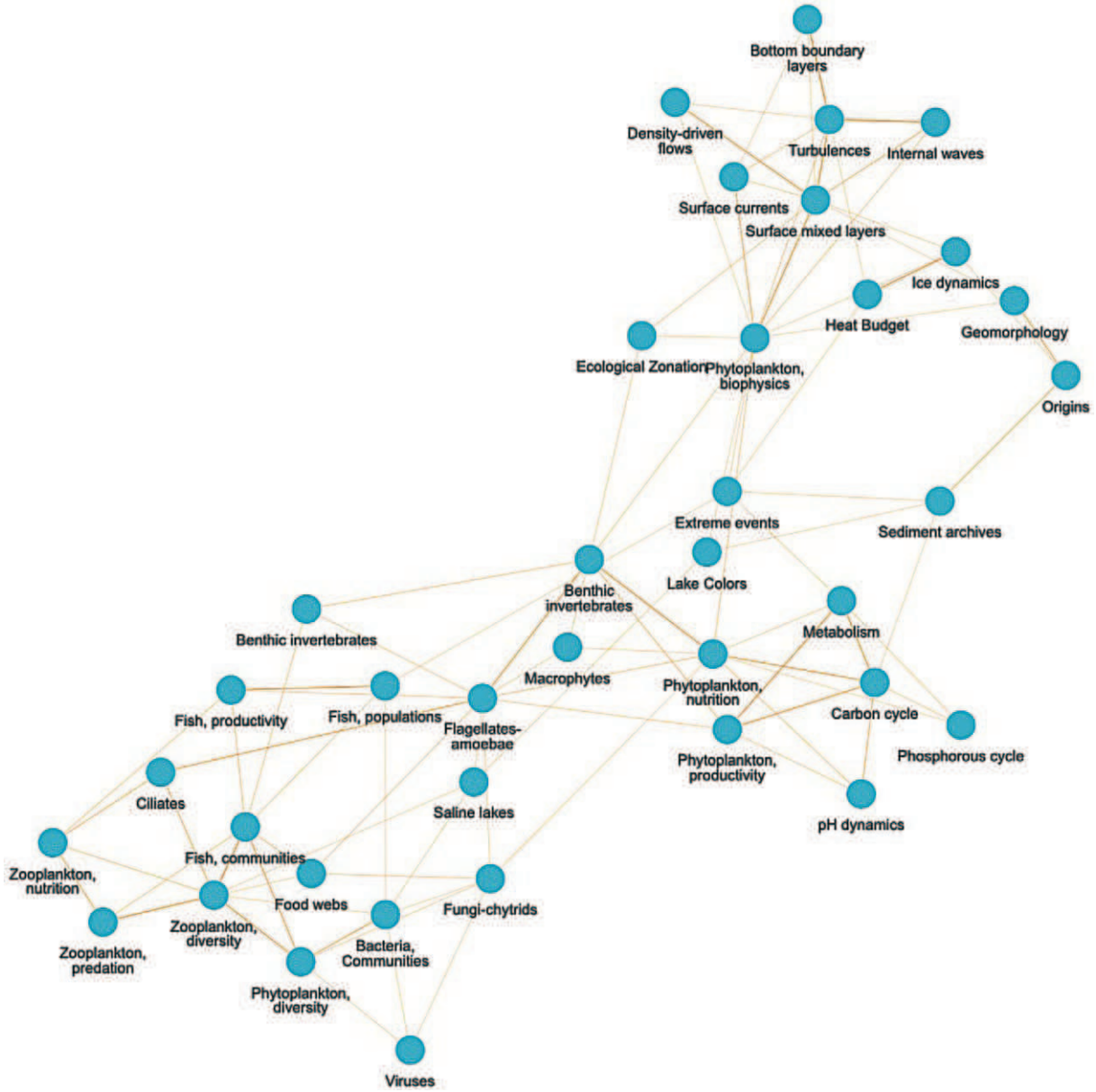

Fig. 1 Network of chapters connection based on text similarities. An interactive version available here (Supplementary Material in the online version at https://doi.org/10.1016/B978-0-12-819166-8.00205-X). Bacteria, communities (Bertilsson and Mehrshad, in press); Benthic algae (Vadeboncoeur and Katona, in press); Benthic invertebrates (Strayer, in press); Bottom boundary layers (Henderson and Nielson, in press), Carbon cycle (Prairie and Cole, in press); Ciliates (Posch et al., in press); Density-driven flows (Peeters and Kipfer, in press); Ecological zonation (Lewis, in press); Extreme events (Dokulil, in press); Fish, communities (Mehner and Brucet, in press); Fish, populations (Winfield, in press); Fish, productivity (MacLeod et al., in press); Flagellates-amoebae (Sanders, in press); Food webs (Embke and Vander Zanden, in press); Fungi-chytrids (Van Den Wyngaert and Kagami, in press); Geomorphology (Timms, in press); Heat budget (Schmid and Read, in press); Ice dynamics (Kirillin and Leppäranta, in press); Internal waves (Boegman, in press); Lake colors (Odermatt and Gege, in press); Macrophytes (Hilt et al., in press); Metabolism (Zwart and Brighenti, in press); Origins (Branstrator, in press), pH dynamics (Finlay and Bogard, in press); Phosphorus cycle (Wilkinson and Albright, in press); Phytoplankton, biophysics (Mackay et al., in press); Phytoplankton, diversity (Pomati et al., in press); Phytoplankton, nutrition (Maberly et al., in press); Phytoplankton, productivity (Dokulil, in press); Saline lakes (Schagerl, in press); Sediment archives (Arnaud and Sabatier, in press); Surface currents (Toffolon, in press); Surface mixed layers (Wells and Troy, in press); Turbulences (Fernandez-Castro et al., in press); Viruses (Schweichhart, in press); Zooplankton, diversity (Thackeray, in press); Zooplankton, nutrition (Straile and Martin-Creuzburg, in press); Zooplankton, predation (Bertolo, in press).

essence connected. In order to guide the reader within the architecture of this section, we added an interactive reading map (Fig. 1/ Supplementary Material in the online version at https://doi.org/10.1016/B978-0-12-819166-8.00205-X). This map was built using a text-mining approach on the content of the chapters. Major links were computed from the number of occurrences of the most frequent significant words from one chapter to the others. Clicking on one chapter in the interactive map will help the reader visualize which other chapters are naturally connected. This network reflects the complexity and diversity of lake science and calls for system analysis and integrative studies.

This introduction is also the opportunity to review the main research gaps in lake science as expressed by the scientists in this section. We invite readers to look at the domain specific research questions presented in the 38 articles and, here, we discuss the general trends.

16 chapters out of 38 pointed out the need for improved observations. There is in particular a lack of information regarding horizontal heterogeneities and we need to move away from the oversimplification that consists in viewing lakes as homogeneous blue dots as typically represented in geographical maps. The problem is clearly raised for the physical structure (lake thermal properties (Schmid and Read, in press) and turbulent fluxes (Fernandez-Castro et al., in press) or lake circulation (Toffolon, in press)) that would benefit for horizontally distributed observations. The littoral region is particularly undersampled and basic questions such as contribution of the benthic population to the whole lake metabolism and more generally the role of benthic algae remain largely underexplored (Hilt et al., in press; Vadeboncoeur and Katona, in press; Wilkinson and Albright, in press; Zwart and Brighenti, in press). Spatially resolved sediment cores might also bring a perspective on the long-term evolution of lakes accounting for their different habitats (Arnaud and Sabatier, in press). Many authors also pinpointed to seasonal or meteorological biases and suggested more investigation of winter limnology and ice-covered systems (Kirillin and Leppäranta, in press) as well as observations under all kinds of atmospheric forcing conditions (Dokulil, in press; Wells and Troy, in press). While global scale studies were not the central focus for most chapters, several authors also indicated geographical bias with most studies being conducted in Europe and North America (Pomati et al., in press; Schmid and Read, in press; Thackeray, in press; Zwart and Brighenti, in press). Remote sensing offers the opportunity to both improve the spatial resolution in large lakes, as well as to expand the geographical cover of monitored lakes worldwide (Odermatt and Gege, in press). Despite their large number, saline lakes are often left aside from large scale studies. Their specific ecosystem functioning remains to be understood (Schagerl, in press). Improved observations go also with technological development with as a short non-exhaustive list the generalization of eddy covariance techniques for boundary conditions (atmospheric and benthic; Henderson and Nielson, in press; Schmid and Read, in press; or e-DNA and genomic structures analysis; Mehner and Brucet, in press; Sanders, in press; Straile and Martin-Creuzburg, in press; Thackeray, in press; Winfield, in press).

Detailed observations are needed to improve our integrated approach of lakes. Linking the catchment to the lake seems to be a priority for future system-based analysis of lake functioning. Such a connection is for instance particularly relevant for explaining the evolution of the main biogeochemical cycles and in particular of the carbon cycle (Prairie and Cole, in press). It is also useful from a management view point to monitor the local anthropogenic effect for heat (Schmid and Read, in press), or any transported compounds that can alter the food web as endocrine disruptors or microplastics (Winfield, in press). Beside the catchment-to-lake perspective, a system-based integrative approach also requires connecting the main biogeochemical cycles together (Prairie and Cole, in press) as well as their response to environmental factors (Boegman, in press). Yet, all causal mechanisms are still not well established. The role of microorganisms such as parasites, fungi, bacteria or viruses and interactions on the dynamic of the benthic or pelagic lake food web (Bertilsson and Mehrshad, in press; Embke and Vander Zanden, in press; Sanders, in press; Schweichhart, in press; Vadeboncoeur and Katona, in press) or on the degradation and detoxification of pesticides, pharmaceuticals and microplastics (Van Den Wyngaert and Kagami, in press) are, for instance, still not quantitatively assessed.

Lakes are complex environmental systems and understanding and parameterizing all the interactions is a major stake to reach a better accuracy of ecological and biogeochemical models. The final identified research gap actually consists in dealing with such a complexity. Several authors called for a simplification of the complexity into something ultimately manageable to inform decision-makers with scientifically sound scenarios. The problem is for instance evident when it comes to predicting the evolution of the food web (Embke and Vander Zanden, in press). The Metabolic Theory of Ecology is seen as a potentially unifying approach to bridge fish individual to population scales (MacLeod et al., in press). Simple analytical models can also help identify the main processes driving the lake circulation (Toffolon, in press) without using complicated three-dimensional hydrodynamic models. The role of small- scale turbulence in the formation of patches of algae is also difficult to assess without reducing the degree of complexity based on theoretical arguments (Mackay et al., in press). The complexity can also be reduced by learning from past studies. Alkalinization is for instance a growing concern (Finlay and Bogard, in press) and lessons can be learnt, yet with new challenges, from past studies and actions to fight acidification. The complexity comes also from the fast changes our environment is facing. It is fundamental to evaluate the resilience of the different communities as a result of climate change (Pomati et al., in press; Posch et al., in press; Straile and Martin-Creuzburg, in press). While not mentioned by the authors, process-guided data-driven models represent an interesting opportunity to embrace the complexity (Hanson et al., 2020).

Some may find that crucial topics are missing for this table of content and we would have to agree. We first targeted a chapter on lake microclimates, as well as on the silicon cycle. We struggled to find authors for those fields, illustrating there are still many fields to explore. Some topics were also already well covered in the previous edition of the encyclopedia or in the section on fundamental principles (as for the nitrogen cycle and methane dynamics), and we will advise the curious reader to directly refer to them. Some might also regret there is no chapter dedicated to oxygen and in a sense we do too. Yet, the questions of oxygen concentrations and cycle are cross-cutting many of the chapters presented either in this section (they appeared in 33 of the 38 chapters), or in other sections of the encyclopedia. We are convinced at heart that solving the current challenges in lake science requires the interdisciplinary perspective demonstrated by the authors of the section's chapters. While highly semantical, this section calls for a stronger

interdisciplinarity (collaborative and integrative approach toward the same research goal) as opposed to a cross disciplinarity (collaborative but not integrative approach). This section should help by providing the needed common ground between the different disciplines. We have had a lot to read and review while editing this section. It was fascinating and we've learnt a lot.

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Origins of Types of Lake Basins☆

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This article is an update of D.K. Branstrator, Origins of Types of Lake Basins, in Encyclopedia of Inland Waters, Academic Press, 2009, edited by Editor: Gene E. Likens, Academic Press, https://doi.org/10.1016/B978-012370626-3.00023-5.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Caldera Name for a lake basin that forms in the chamber where magma was ejected.
Cirque Name for a lake basin resembling an amphitheater that forms in mountainous areas by glacial activity.
Fluvial Associated with a river.
Graben Name for a lake basin that forms when tectonic plates shift and produce a gap in the ground.
Karst Name for a lake basin that forms when limestone bedrock dissolves.
Kettle Name for a lake basin that forms when glacial ice is folded under soil then melts.
Moraine A glacially carried mound of soil.
Oxbow Name for a lake basin that forms in the meander of a river.
Reservoir Name for a lake basin that forms when humans dam a pre-existing river.

☆*Change History:* August 2021. DK Branstrator updated the entire article.

Introduction

Lake basins originate through a wide variety of natural and anthropogenic processes. Some of these processes are gradual and usually imperceptible (tectonic movement, fluvial erosion) while others (meteorite impact) are quick and extraordinary. To the human observer, most lakes are permanent features of the landscape. On a geologic time scale, by contrast, most lakes are fleeting and all are ultimately ephemeral. Although we have few opportunities to witness a lake's origin, the same set of lake-forming processes at work historically continue unimpeded today.

Earth's distribution of lakes is strikingly nonrandom (Fig. 1). Most lakes lie at northern latitudes and within the footprint of recent glaciation. By contrast, lakes of great depth are scattered across Earth's surface, including East Africa, revealing that the

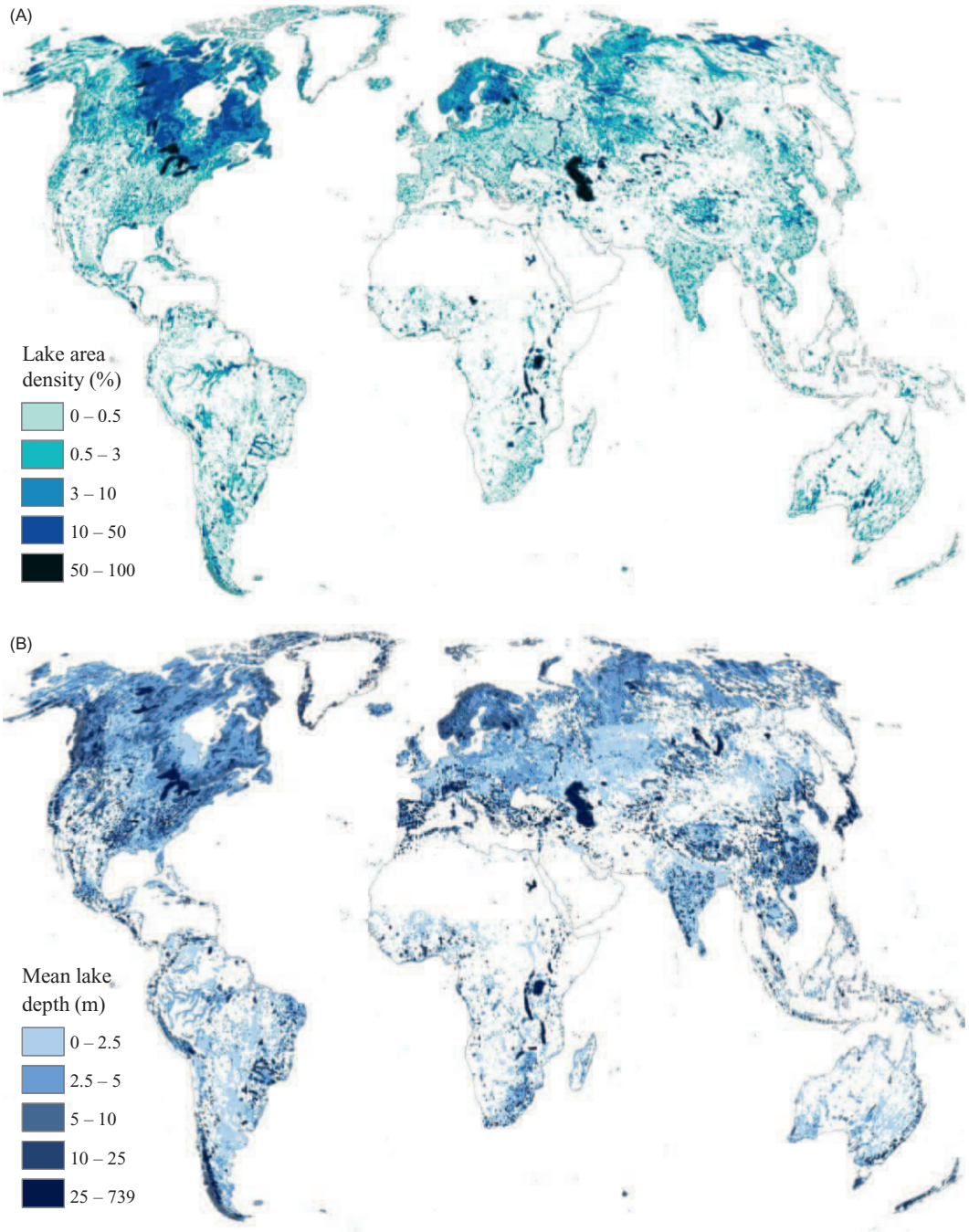


Fig. 1 Patterns of global lake distribution. (A) Lake area density given as percent area covered by lakes within a 25 km radius. (B) Average depth of all lakes within a 25 km radius, weighted by their partial area within that radius. Both maps include reservoirs from the Global Reservoir and Dam (GRanD) database. From Messager ML et al. (2016) Estimating the volume and age of water stored in global lakes using a geo-statistical approach. *Nature Communications* **7**: 13603, Reprinted by permission.

geomorphological processes producing extreme depth or volume can differ from those producing large numbers. Earth's distribution of human-made lakes is also patchy. Their origins are driven by necessity for their services (e.g., irrigation, power, and recreation) and access to water for impoundment.

Three elements are common to the origin of all lakes including (1) an environmental force, (2) a body of terrain reshaped by that force into a closed depression (basin), and (3) a water supply. The first element in the origin of a lake, an environmental force, is generally used by scientists to guide the broad classification of lake basins. G. E. Hutchinson provided one of the most extensive surveys available on the origins of lake basins in the first volume of his four-volume series, *A Treatise on Limnology* (Hutchinson, 1957). There he describes the formation of numerous distinct types of lake basins resulting from 11 principal environmental forces, including glacial, tectonic, volcanic, fluvial, organism behavior (including humans), chemical, wind, landslide, shoreline, meteorite, and organic accumulation.

The second element in the origin of a lake concerns the specific process by which an environmental force reshapes terrain into a closed depression (basin). This is the element conventionally used by scientists to name distinct types of lake basins. For example, in the case of glacial force, different names are given to basins scoured in bedrock versus those impounded by moraine. Scientists have also found it useful at times to organize lake basins quite broadly according to whether the terrain-shaping process works destructively, constructively, or obstructively. Destructive processes (glacial scouring) excavate depressions, constructive processes (moraine deposition) build rims that define depressions, while obstructive processes (landslide) build rims that barricade preexisting flows. An individual lake basin may be molded by more than one process. Because Earth's terrain is so richly varied in its composition of soil, rock structure, and topographic relief, ceaseless opportunities exist for unique outcomes in the bathymetry and shoreline structure of lake basins.

A lake district refers to a set of lakes that share a principal originating force and that reside geographically in a defined setting on the landscape. Although individual basins in a lake district are generally of similar age and origin, they can differ exceptionally in size and shape. For example, the English Lake District basins shown in Fig. 2 originated at about the same time by glacial scouring. Their different shapes and bathymetries illustrate how the interplay between an environmental force and the terrain under influence can change rapidly across short distances.

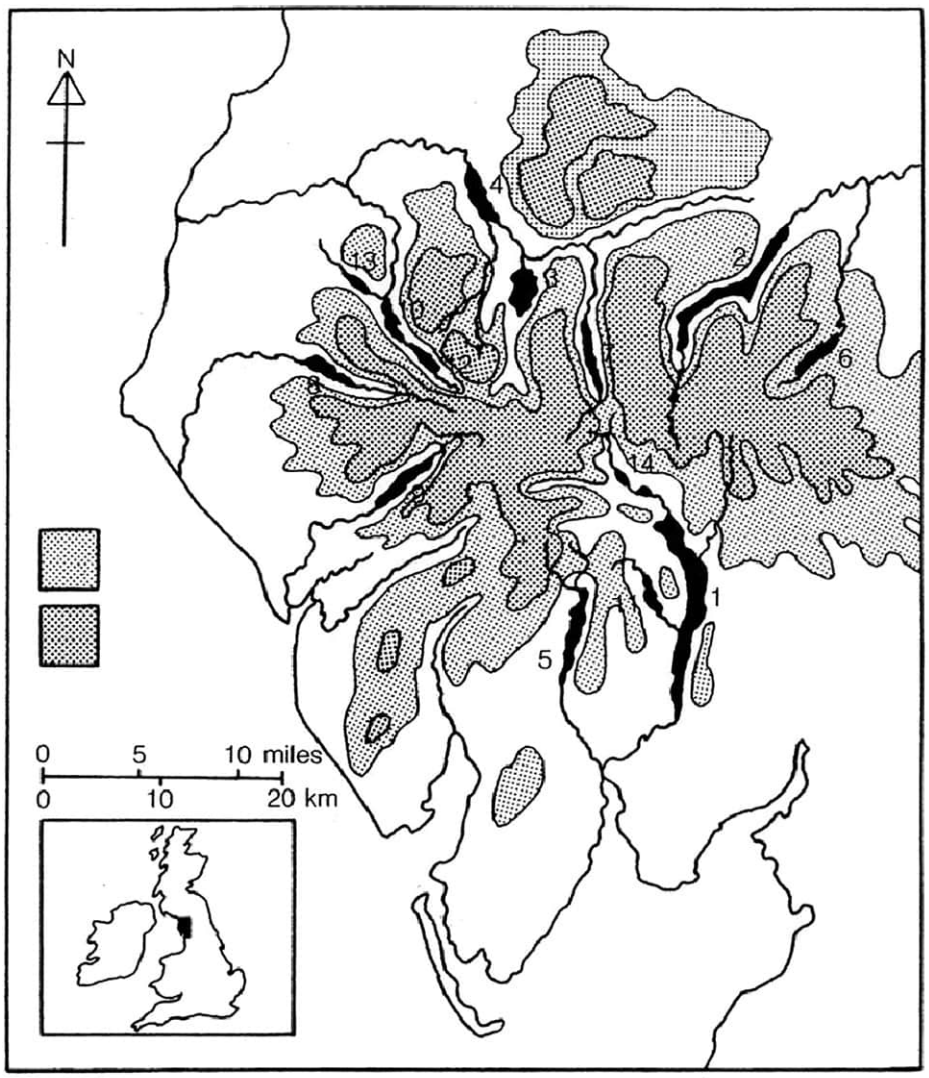
The third element in the origin of a lake is the water supply. Unlike the first two elements, water is not always present at a lake basin's inception. Water derives variously from ice, rivers, precipitation, groundwater, wetlands, and preexisting lakes. Water sources to lakes may shift through time. For instance, most glacial lakes that were filled originally by melt water are now maintained by alternative supplies (precipitation, groundwater). Scientists find it useful to differentiate between lakes connected to rivers (drainage lakes) versus those whose hydrology is reliant exclusively on precipitation and groundwater (seepage lakes). On a regional scale, water supply can be unstable, resetting the hydrologic origin of a lake long after its geologic birth. One prominent example of this phenomenon is Lake Victoria (Africa), which originated several hundred thousand years before present but was dry as recently as about 15,000 years ago (Johnson et al., 2000).

Certain types of lake-building processes can be expected to dominate over others at any moment in Earth's history. In today's inventory of natural lakes whose surface areas are ≥ 0.01 km^2 (1 ha), approximately 90% have basin origins that trace to glacial, tectonic, or fluvial forces (Table 1). Of these, glacial force far outweighs the importance of all others. This contemporary bias owes to recent and widespread glaciation during the Pleistocene when ice sheets covered nearly 25% of Earth's continents. As climate change warms Earth, glacial force is giving rise to an increasing number and size of proglacial lakes that are forming at the margins of retreating ice. In addition, as human population size burgeons, human force is giving rise to an increasing number of human-made impoundments. Both forces are notably shifting the contemporary inventory of lake types.

With global human demand for freshwater on the rise, increasing efforts are being made to inventory the distribution, size, and number of Earth's lakes. Estimates of numbers of natural lakes of various sizes down to 0.1 km^2 (10 ha) in surface area have been made by different scientists using different approaches. The total number of natural lakes ≥ 0.1 km^2 in surface area as estimated by three different studies are 1.42 million (Messager et al., 2016), 1.55 million (Lehner and Döll, 2004), and 2.30 million (Downing et al., 2006). When smaller natural lakes are included, the total number grows substantially to 304 million lakes ≥ 0.001 km^2 in surface area (Downing and Duarte, 2009). The total number of human-made impoundments (e.g., reservoirs and farm ponds) has been estimated at 77 million (Downing and Duarte, 2009), bringing the total number of all lakes (natural and human-made) to 381 million. A variety of data bases that offer global lake statistics are available to the public including HydroLAKES (https://www.hydrosheds.org/page/hydrolakes) and the Global Reservoir and Dam database (http://globald amwatch.org/grand/), also known as GRanD.

Types of Lake basins

Scientists have long appreciated that a lake's physics, chemistry, and biological potential are predictable end products of its origin. Trained scientists can infer much about a lake's current limnology by knowing its originating process. In this article, 22 specific processes that produce distinct types of lake basins (hereafter simply referred to as lakes) are enumerated and described. They are organized and presented by principal environmental force as summarized in Table 2. Organic accumulation is the only principal environmental force discussed by Hutchinson (1957) that is not considered here.



	Area (km^2)	Length (km)	Max. depth (m)	Mean depth (m)	Volume (m^3) (10^6)	Area of drainage basin (km^2)
1. Windermere	14.8	17	64	21.3	314.5	230.5
2. Ullswater	8.9	11.8	62.5	25.3	223.0	145.5
3. Derwent Water	5.3	4.6	22	5.5	29	82.7
4. Bassenthwaite Lake	5.3	6.2	19	5.3	27.9	237.9
5. Coniston Water	4.9	8.7	56	24.1	113.3	60.7
6. Haweswater	3.9	6.9	57	23.4	76.6	26.6
7. Thirlmere	3.3	6.0	46	16.1	52.5	29.3
8. Ennerdale Water	3.0	3.8	42	17.8	53.2	44.1
9. Wastwater	2.9	4.8	76	39.7	115.6	48.5
10. Crummock Water	2.5	4.0	44	26.7	66.4	43.6
11. Esthwaite Water	1.0	2.5	15.5	6.4	6.4	17.1
12. Buttermere	0.9	2	28.6	16.6	15.2	16.9
13. Loweswater	0.6	1.8	16	8.4	5.4	8.9
14. Grasmere	0.6	1.6	21.5	7.7	4.9	27.9

Fig. 2 Fourteen of the largest ice scour lakes in the English Lake District (shown blackened above) and their physical characteristics (associated table). Stippling shows surrounding relative elevation with the darker regions higher than the lighter regions. From Burgis MJ and Morris P (1987) *The Natural History of Lakes.* Cambridge: University of Cambridge, Reprinted by permission.

Table 1 Estimates of the global number and area of natural lakes ≥ 0.01 km^2 in surface area organized by principal environmental force.

Principal force	*Number of lakes*	*Percent of total lakes*	*Total lake area (km^2)*	*Percent of total lake area*
Glacial	3,875,000	74	1,247,000	50
Tectonic	249,000	5	893,000	35
Fluvial	531,000	10	218,000	9
Volcanic	1000	$<<1$	3000	$<<1$
Coastal	41,000	<1	60,000	2
Miscellaneous	567,000	10	88,000	4
Total	5,264,000	$\sim$100	2,509,000	100

A more recent study by Downing and Duarte (2009) estimates that Earth presently holds 27 million natural lakes that are ≥ 0.01 km^2 in surface area, about five times more than the total number of lakes shown here. In addition, it is estimated that Earth presently holds 277 million smaller natural lakes that are 0.001–0.01 km^2 in surface area, and 77 million human-made lakes, for a total of 381 lakes that are ≥ 0.001 km^2 in surface area.
Adapted from Kalff J (2002) *Limnology: Inland Water Ecosystems*. Upper Saddle River: Prentice Hall, Reprinted by permission.

Table 2 Common types of lakes organized by principal environmental force.

Principal force	*Lake type*	*Process of basin origination*
Glacial	Ice scour	D: Glacier excavates a depression.
	Moraine dam	C: Glacier pushes or deposits terrain to make a rim.
	Kettle	D: Stagnant glacier block displaces soil to make a depression.
	Ice dam	O: Lobe or wall of glacier prevents drainage.
	Ice basin	D,O: Depression or cavity in glacier prevents drainage.
	Thaw	O,C: Permafrost prevents drainage and soils heave to make a rim.
Tectonic	Fault block	D,C: Fracture, faulting and warping define a depression and rim.
	Reverse drainage	O: Uplift and tilting prevent drainage.
	Newland	C: Uplift of ocean floor exposes a submarine depression.
Volcanic	Volcanic crater	D: Magma chamber empties to define a depression.
	Volcanic dam	O: Volcano or cooled lava barricades a flow.
Fluvial	Plunge pool	D: Waterfall excavates a depression.
	Oxbow	D,O: Coupled erosion and deposition close a river segment.
	Fluvial dam	O: Fluvial sediments barricade a flow.
Organism behavior	Beaver pond	O: Wood and mud barricade a flow.
	Reservoir	O: Human-constructed dam barricades a flow.
	Farm pond, Mine pit	D: Human excavates a depression.
Chemical	Solution	D: Bedrock dissolves to make a depression.
Wind	Deflation	D: Wind excavates a depression.
Landslide	Landslide dam	O: Gravity moves terrain which barricades a flow.
Shoreline	Coastal	C: Sediments deposited from longshore currents close a bay.
Meteorite	Meteorite crater	D: Meteorite impact excavates a depression.

The terrain-shaping process at origination is coded as destructive (D), constructive (C), or obstructive (O).

Glacial

Glaciers transform Earth's surface through a variety of erosive and depositional processes resulting from their physical constitution, their forward motion (advance), and their recession through melting (retreat). Glaciers form through the compaction and transformation of snow and other precipitation. During the Pleistocene, glaciers reached heights of 2 km above Earth's surface, establishing enormous weight loads on the landscape. Under gravitational force imposed by their own mass, glaciers creep internally and slide along terrain, aided by relief in the landscape. Rock debris is commonly incorporated into glacial ice through abrasion and quarrying (plucking) at the basal surface. Liquid water developing on or in glaciers is heavier than ice and tends to sink and layer along the glacial sole. This lubrication further aids advance and erosive action.

As Earth's deglaciation continues at alarming rates, scientists are being presented with unprecedented opportunity to see and study glacial force as an originator of lakes. Proglacial lakes (defined below) are one type of glacial lake that is already increasing rapidly in number and size. Carrivick and Tweed (2013) review the trends which offer a glimpse of what Earth is poised to experience in the way of new and larger proglacial lakes, and the resulting environmental consequences. One spectacular example of a new proglacial lake is Lake Tasman located at the foot of the Tasman Glacier in the Southern Alps, New Zealand. Ponds that were precursors to Lake Tasman first appeared in the early 1970s. By 2008 the lake was already about 7 km length and more than 200 m deep.

Ice scour

These lakes are excavations in bedrock caused by the crushing and removal of loose debris. The depressions are generally carved during glacial advance, and deepened over cycles of retreat and readvance. In addition to the scouring effect of pure glacial ice, erosion is facilitated by protruding rock debris and melt water issuing through basal channels. Notable lakes with significant ice scouring in their origins include the Laurentian Great Lakes (Canada, United States), Great Bear Lake and Great Slave Lake (Canada), the fjord lakes in Norway, several lakes in the English Lake District (Fig. 2), Lago Maggiore (Italy), Lac Léman (France, Switzerland), Lake Te Anau (New Zealand), and innumerable small lakes carved in the pre-Cambrian shield in Canada and Europe.

Glaciers tend to preferentially exploit weaknesses in rock structure and composition. As a result, the shorelines and subsurface contours of ice scour lakes often follow preexisting fracture and transitional zones in the bedrock. An acute example of bedrock control on scouring activity is provided by a set of lakes in Minnesota (United States) where glaciers excavated the soft slate layered between resistant columns of diabase sill (Fig. 3). Quite impressive is that the long axes of these lakes lie oblique to the southerly direction of glacial advance.

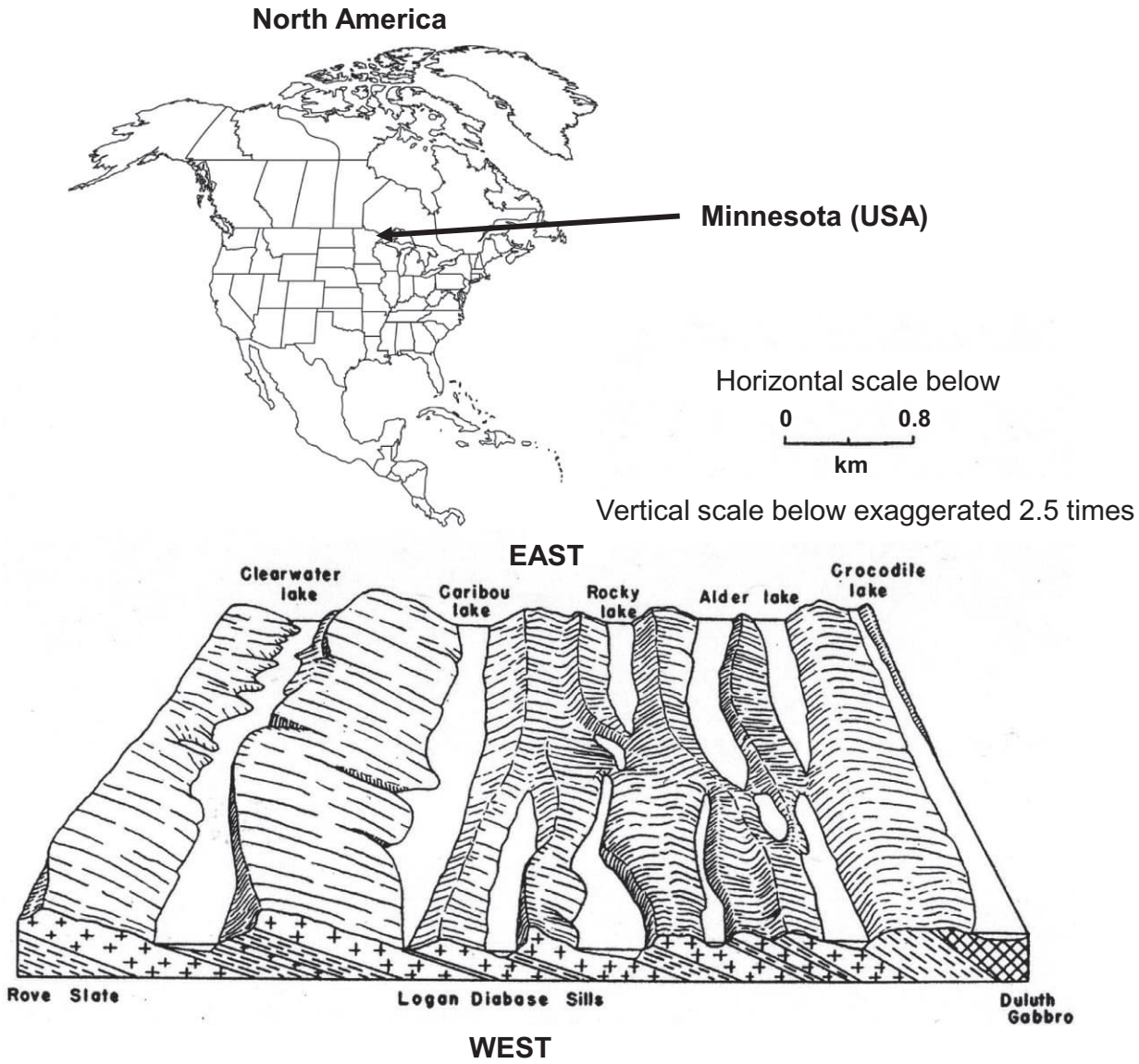


Fig. 3 Examples of some ice scour lakes in Minnesota (United States) that were carved in slate (metamorphic rock) resting between diabase sill (igneous rock). The alternating slate (–) and sill (+) are overlain by lakes (no pattern). Forested sill generally forms the terrestrial landscape separating the lakes. Adapted from Zumberge JH (1952) *The Lakes of Minnesota: Their Origin and Classification, University of Minnesota Geological Survey Bulletin 35*. Minneapolis: University of Minnesota. Continental map courtesy of Graphic Maps, Woolwine-Moen Group, Reprinted by permission.

A stunning type of ice scour lake called a cirque (tarn) originates at the snow line in mountainous relief. Cirques derive from relatively small glaciers and are characteristically bowl-shaped and bounded on the upslope shore by a steep headwall of rock. The erosive power of freezing and thawing on a seasonal basis is believed to enhance local corrosion of the lake floor and walls.

Moraine dam

Advancing glaciers push terrain at their leading edge whereas retreating glaciers deposit previously held debris as they melt. Both processes erect mounds of rock and soil on the landscape loosely referred to as moraines. Moraine dam lakes commonly reside in former river valleys with the moraine serving as a rim to complete the lake. Examples include Lake Mendota in Wisconsin and Mille Lacs Lake in Minnesota (United States), the latter lake being almost half bounded by moraine deposits (Fig. 4). Ice scour and moraine building processes regularly labor in concert to forge glacial lakes. As a result, many cirque lakes are impounded by a moraine at their downslope edge, and a vast number of lakes categorized as ice scour depend to some degree on moraine rims to maintain their current depths. The Finger Lakes in New York (United States) were joint products of ice scour and moraine building processes.

Kettle

Advancing and retreating glaciers commonly fracture and strand ice blocks. Ice blocks that become partially or fully buried in soil or in the sediment of an outwash plain can originate kettle lakes (Fig. 5). In this process, the dimensions and extent of inlay of the ice strongly dictate the lake's shape and bathymetry. Kettle lakes are characteristically deep relative to surface area and they can have complex bathymetry where two or more blocks of ice strand adjacent to one another. Kettle lakes abound in North America, Europe, and Asia. Lakes in the prairie pothole region in Canada and the lakes surveyed by pioneering limnologists E. A. Birge and C. Juday in Wisconsin (United States) are primarily kettles.

Ice dam

When glaciers themselves represent barricades that obstruct water flow they originate ice dam lakes. In regions of notable relief, an ice dam lake typically occurs where the lobe of a glacier extends down a main valley to barricade a tributary river entering from a lateral valley. The Märjelensee (Switzerland) is a well-known example. These lakes are highly transitory and can drain rapidly if the dam hemorrhages.

Lake Missoula (United States) was an ice dam lake of the Clark Fork River that grew to a depth exceeding 600 m and had a volume the combined size of present day Lake Ontario and Lake Erie (Canada, United States). The ice dam ruptured and reformed dozens of times over thousands of years. Upon rupture events, lost water produced massive floods that scoured the region of present day eastern Washington state.

Ice dam lakes also form on flatter terrain when the edge of a glacier prevents the drainage of its own melt water. Here the lake forms through ponding in front of the glacier and is more specifically termed a proglacial lake. Isostatic rebound of the recently

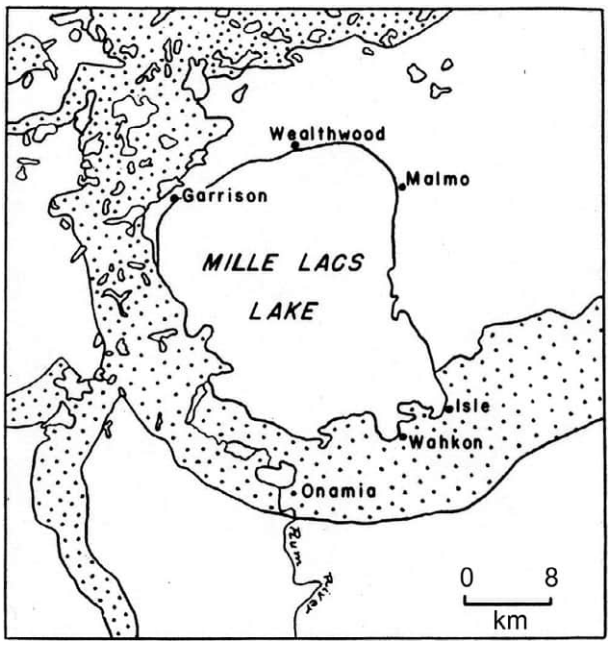


Fig. 4 An example of a moraine dam lake in Minnesota (United States). Stippling shows the moraine. Geographic reference as in Fig. 3. Adapted from Zumberge JH (1952) *The Lakes of Minnesota: Their Origin and Classification, University of Minnesota Geological Survey Bulletin 35*. Minneapolis: University of Minnesota, Reprinted by permission.

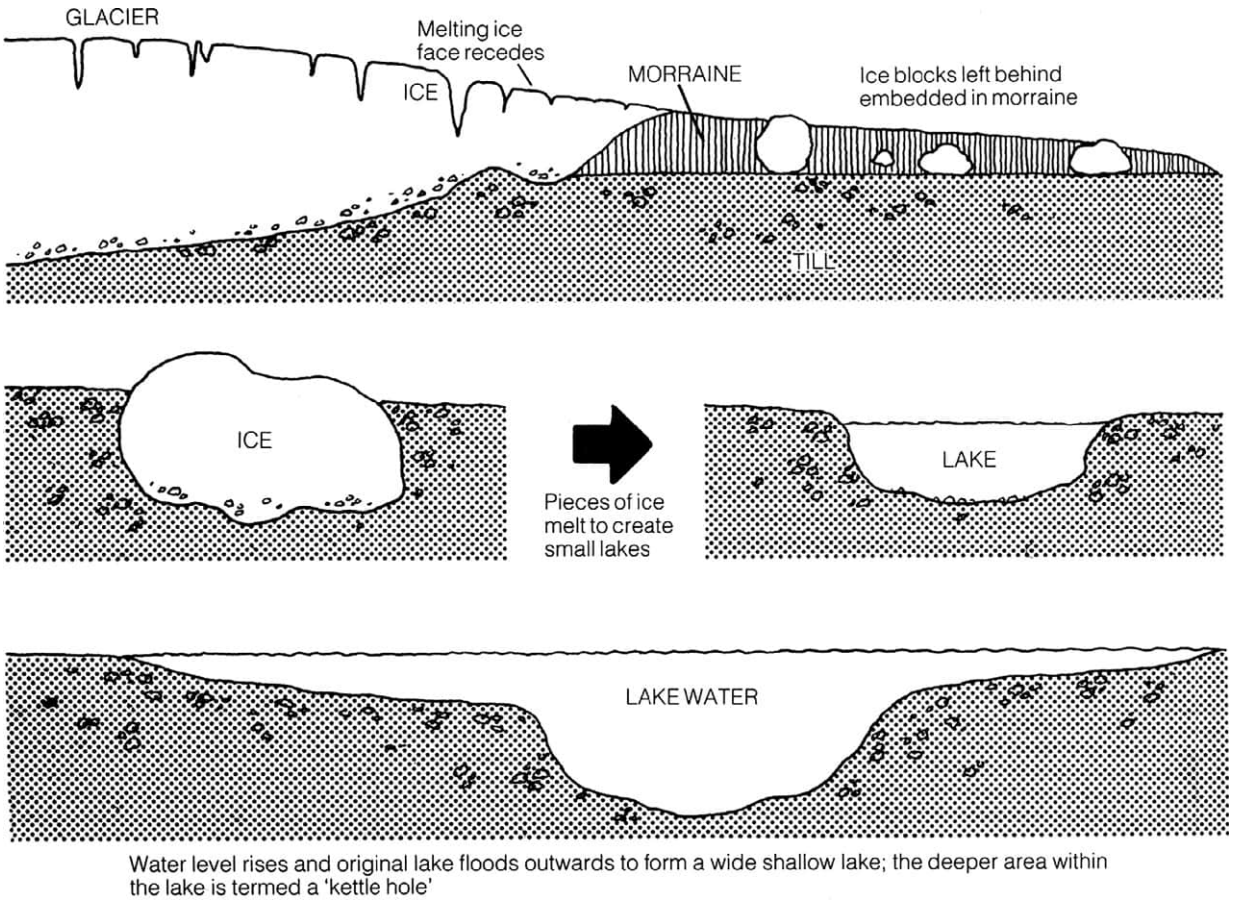


Fig. 5 A schematic of how a kettle lake forms. From Burgis MJ and Morris P (1987) *The Natural History of Lakes*. Cambridge: University of Cambridge, Reprinted by permission.

uncovered terrain may tilt it toward the glacier and enhance the ponding effect. Lake Agassiz was a large proglacial lake that covered several hundred thousand square kilometers during its life (Fig. 6). The lake changed its configuration and reach many times as the glacier retreated northward and the lake periodically drained (Teller et al., 2002). Vestiges of Lake Agassiz include Lake of the Woods (Canada, United States) and Lake Winnipeg (Canada).

Ice basin

Ice basin lakes reside either on or in a glacier. They originate when melt water, obstructed from exiting a glacier, pools either in a surface depression or internally in a glacial cavity. The depressions and cavities form as a result of glacial movement, fracture, fluvial erosion, and heat from the sun and Earth. In the case of surface depressions, the entire lake is cupped in ice. In the case of internal cavities, the lake commonly resides at the floor of the glacier and is bounded by land underneath and by ice on the walls and ceiling. Lake Vostok (Antarctica) is an example of the latter, residing some 4000 m below the Antarctic ice sheet. It is a huge lake that is several hundred meters deep at various locations with a surface area of about two thirds that of present day Lake Ontario (Canada, United States).

Thaw

Thaw (thermokarst, cryogenic) lakes have fascinated scientists for decades. These lakes cover vast coastal areas in the arctic regions of Eurasia and North America. They are best classified as periglacial because their origins depend on near-glacial conditions, but not glaciers themselves. A thaw lake originates when melt water in the surface layer of permafrost is prevented from draining downward by a deeper layer of frozen permafrost which serves as the lake floor. The surface area of a thaw lake may be quite small at first and polygon shaped. The soil rims that contain these lakes arise above fracture zones in the permafrost where annual freeze-thaw cycles lead to vertical expansion and soil upheaval. Contiguous thaw lakes will coalesce, resulting in large and small lakes in the same general area (Fig. 7).

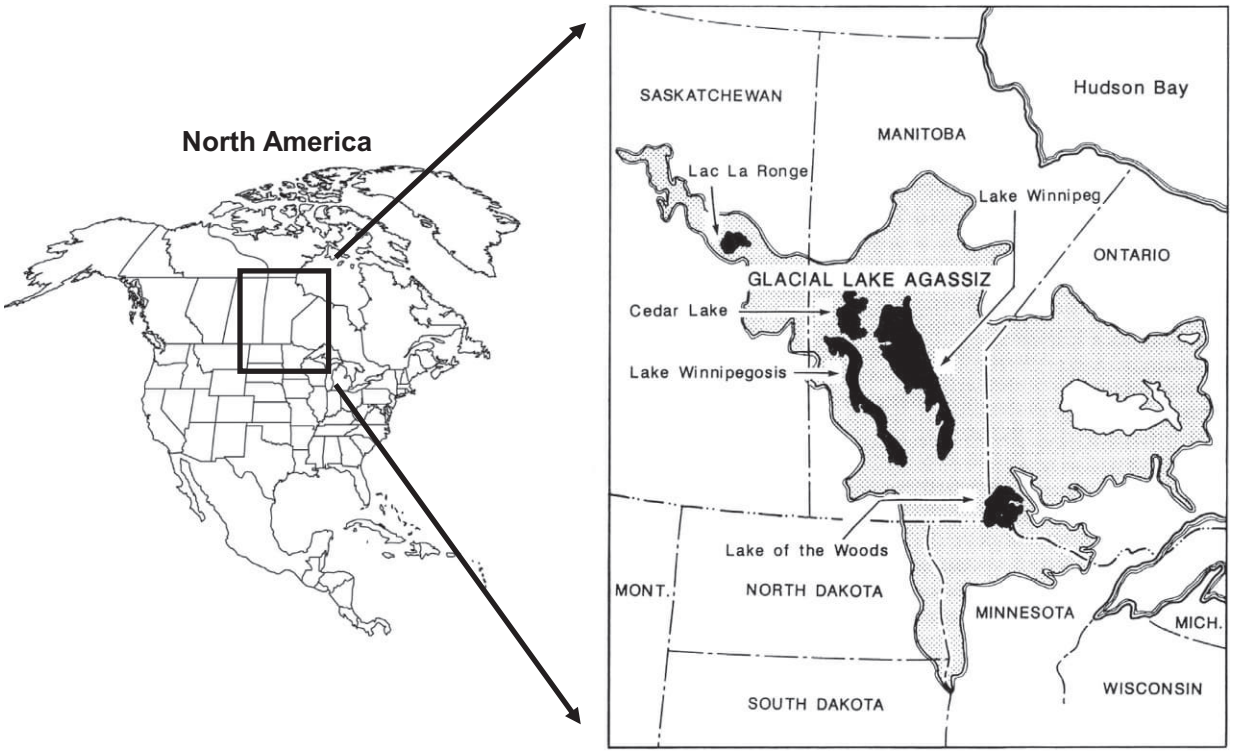


Fig. 6 The historical border of proglacial Lake Agassiz (stippling) and the current borders of five remnant extant lakes (blackened) in North America. From Timms BV (1992) *Lake Geomorphology*. Adelaide: Gleneagles. Continental map courtesy of Graphic Maps, Woolwine-Moen Group, Reprinted by permission.

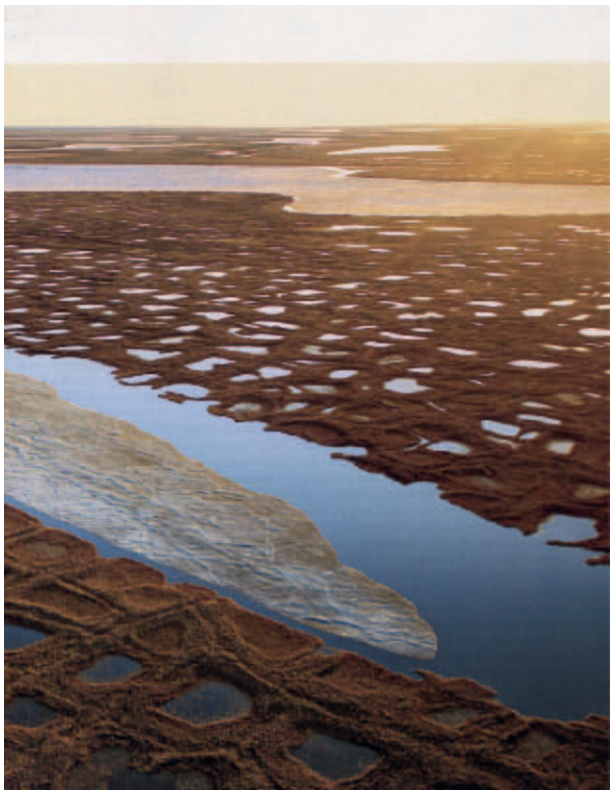


Fig. 7 Examples of thaw lakes in Alaska (United States). Joel Sartore/National Geographic Image Collection, Reprinted by permission.

Tectonic

Earth's exterior layer is comprised of a network of about a dozen relatively rigid, crustal plates that form a shell around the planet. The boundaries of these plates are zones of active slip, collision, and separation that generate what are called tectonic forces. Tectonic forces that translate upward to Earth's surface deform bedrock through fracture, rifting (separation), and warping (uplift and subsidence), resulting in the formation of mountains, oceans, and some of Earth's largest, deepest, and oldest lakes.

Fault block

Fault block lakes form where uplift and subsidence create vertical offset in adjacent blocks of fractured land. In cases where a single fault or fault complex is active, the process leads to a half-graben. This type of lake has characteristic steep-walled bathymetry on the fault side and an angled floor that slopes gradually to the opposite shore where vertical offset is minimal or nonexistent. Where multiple fault lines occur with wide parallel spacing, both sides of a land block can experience vertical offset and create a trough-shaped lake called a graben. Grabens generally contain precipitous bathymetric contours along both main shorelines (Fig. 8). Well-known examples of fault block lakes include Lake Baikal (Russia), Lake Ohrid and Lake Prespa (Europe), Lake Issyk-Kul (Kyrgyzstan), Lake Tahoe (United States), and several lakes in the Central African Rift Valley District (Fig. 9), including Lake Tanganyika, Lake Malawi, Lake Edward, Lake Albert, and Lake Rudolf. Fault block lakes are characteristically flanked by massive, steep escarpments that crest hundreds to thousands of meters above lake level (Fig. 9). Some fault block lakes that have been filled with water continuously for millions of years now house remarkably thick sediment layers such as those in Lake Baikal (~8 km thick) and Lake Tanganyika (~5 km thick). Such extraordinary sediment accumulations can only be explained if subsidence is ongoing. Evidence shows this to be the case which means that the longevity of these lakes depends in part on continual processes of origination.

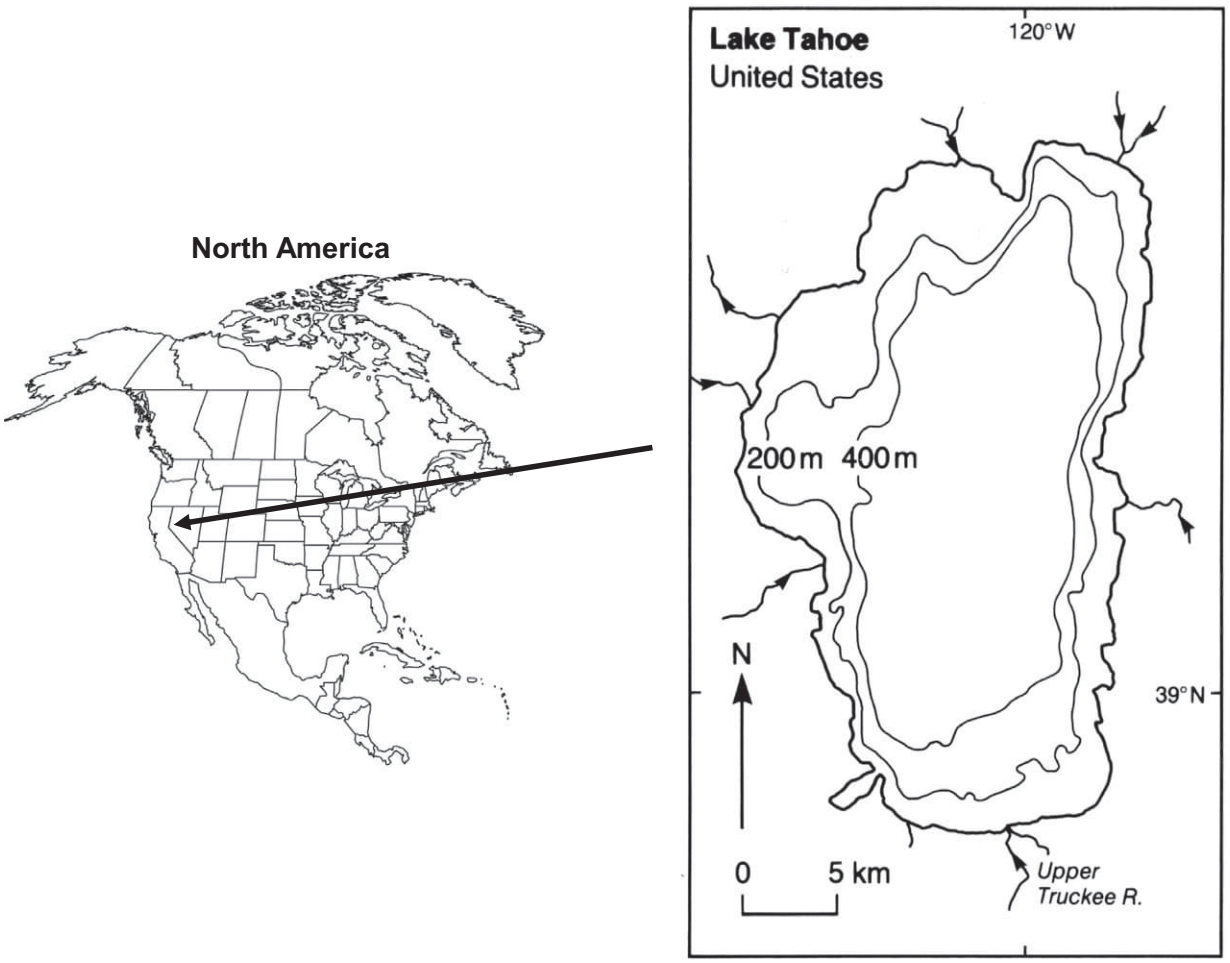


Fig. 8 The bathymetry of Lake Tahoe (United States), a graben. The lake's maximum depth is slightly over 500 m. From Burgis MJ and Morris P (1987) *The Natural History of Lakes*. Cambridge: University of Cambridge. Continental map courtesy of Graphic Maps, Woolwine-Moen Group, Reprinted by permission.

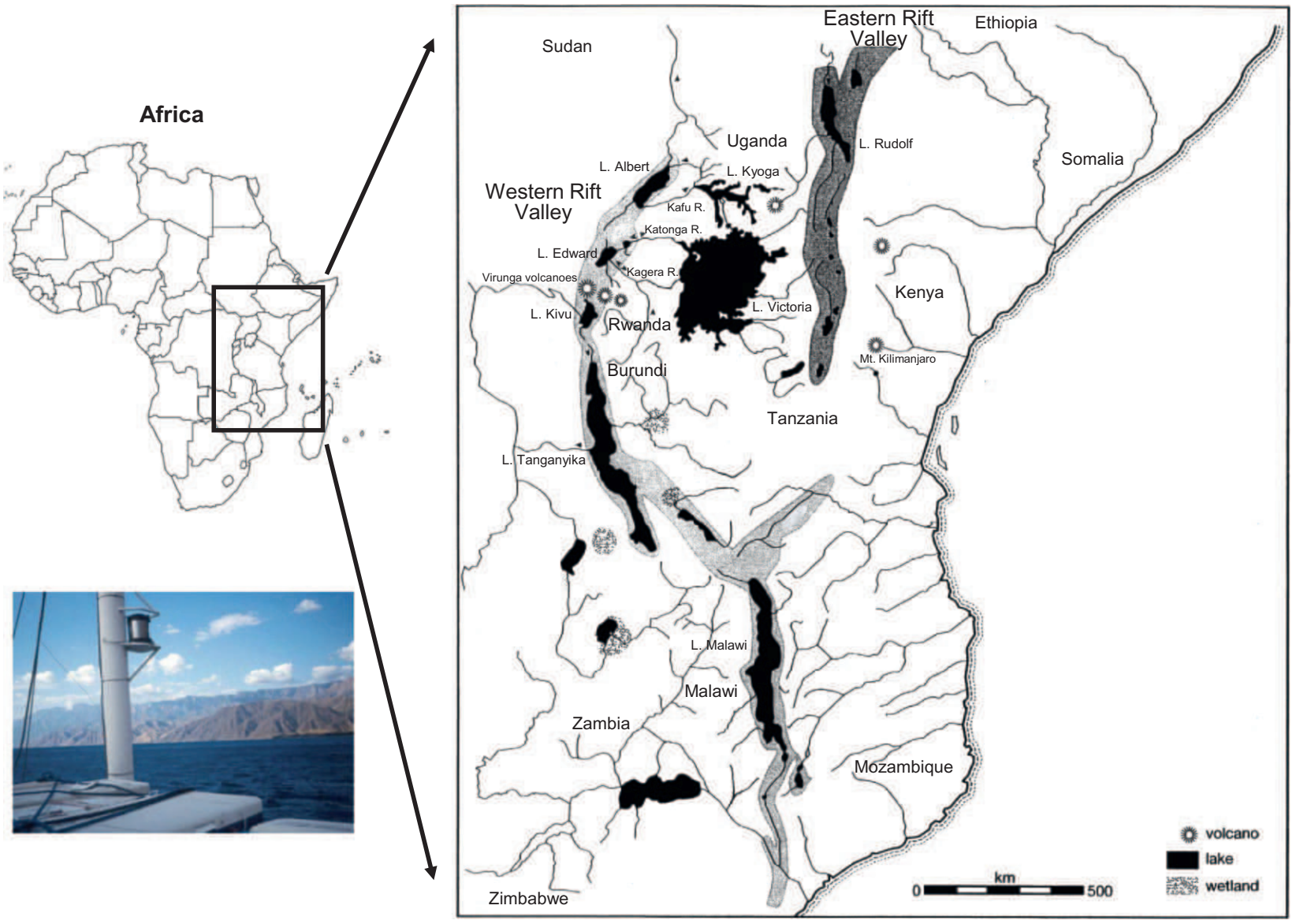


Fig. 9 Lakes in the Central African Rift Valley District (blackened). Adapted from Kalff J (2002) *Limnology: Inland Water Ecosystems.* Upper Saddle River: Prentice Hall. Continental map courtesy of Graphic Maps, Woolwine-Moen Group, Reprinted by permission. Color inset: The Livingstone Mountains of Tanzania define the eastern fault on the north side of Lake Malawi (Africa), a half-graben. By kind permission of Tom Johnson, University of Minnesota Duluth.

Reverse drainage

Reverse drainage lakes result from uplift and tilting that redirect drainage. Two well-known examples include Lake Kyoga and Lake Victoria in Africa (Fig. 9). These lakes were created when uplift around the plateau's western margin reversed flow in the Kafu, Katonga, and Kagera Rivers (Kendall, 1969). All three major rivers historically flowed east to west across the plateau but now flow west to east over much of their course, flooding what were once old river channels and riparian plains in the formation of these two lakes. The dendritic shoreline of Lake Kyoga and the angles of its bays with respect to the main arm of the lake are vestiges of an ancestral fluvial state and a history of drainage that once flowed east to west (Fig. 9).

Newland

Newland lakes originate when the sea floor is uplifted and becomes exposed. The Caspian Sea, Aral Sea, and Lake Okeechobee (Florida, United States) are examples. Not long ago, the Aral Sea was listed among the largest lakes by surface area on Earth. Diversion of its major inlets for irrigation progressively reduced its volume to a mere fraction of its historic size and the remaining water is now divided into several smaller lakes (for more information see chapter on Saline lakes).

Volcanic

Volcanism is responsible for a variety of lake types that can be divided relatively naturally into two groups. One group includes those forming directly in the volcanic chamber where magma exited. The other group includes lakes that result from obstruction imposed by the volcanic mountain itself or the expelled magma. Volcanic lakes are generally small but often deep and they comprise some of Earth's most aesthetically pleasing and noteworthy aquatic ecosystems.

Volcanic crater

Volcanic crater lakes originate in the cavities from which magma was ejected. Small volcanic crater lakes (maars) and large ones (calderas) have representatives across Earth, including many in the Eifel region (Germany), the Auvergne region (France), Indonesia, and central Africa. Because of their origin, these lakes generally have a small aspect ratio (maximum width:maximum depth), which can inhibit complete mixing (turnover) of the lake's water mass on an annual basis. Lake Nyos (Cameroon) is a maar with an aspect ratio of 9:1. In its recent history, Lake Nyos remained partially unmixed long enough to become supersaturated with carbon dioxide gas. A catastrophic episode of mass release of the gas in 1986 killed about 1700 humans and 3000 cattle (Kling et al., 1987). Crater Lake (United States) is a magnificent example of a caldera. At about 600 m depth, it is one of the top 10 deepest lakes on Earth. Lake Tazawa and Lake Okama (Japan), and Lake Taupo (New Zealand) are other examples.

Volcanic dam

Volcanic dam lakes originate as a result of drainage that is blocked by either a volcanic mountain or its expelled lava. One example is Lake Kivu which lies on the western side of the Central African Rift Valley (Fig. 9). In the origination of this lake, seven major volcanoes dammed a drainage pattern that historically flowed north into Lake Edward. Drainage in the watershed now accumulates in Lake Kivu with excess water in the lake flowing south to Lake Tanganyika. Lake Lanao (Philippines) is another example of a volcanic dam lake.

Fluvial

Running water plays a profound role in sculpting Earth's surface. Its dual ability to erode and construct, akin to glacial, tectonic, and volcanic forces, engender fluvial force with a wide range of originating processes.

Plunge pool

As the name implies, a plunge pool lake originates at the base of a waterfall where the destructive energy of falling water excavates a hollow large enough to hold water long after the river has perished. A number of lakes in eastern Washington (United States) provide examples including Dry Falls Lake.

Oxbow

An oxbow (billabong) lake originates through the coupled influence of erosion and deposition in what are often wide, gently sloping floodplains. The general process, illustrated in Fig. 10, is one whereby a meandering loop in a river is eventually abandoned as the river cuts a newer, more direct path through the bank. The old river course is sealed at both ends with sediment deposits. Oxbows are commonly serpentine or crescent shaped, which reflects their position in the old river channel. Innumerable examples of oxbows exist that can best be appreciated from aerial views (Fig. 10).

Fluvial dam

Fluvial dam lakes originate when deposited silt creates a barrier that impounds drainage. Most common among this spectrum of lakes is a lateral lake that originates when a tributary is obstructed from entering a main river by a levee at the confluence. Lateral lakes are frequent on the Danube River (Europe) and the Yangtze River (China). A second type of fluvial dam lake is called a

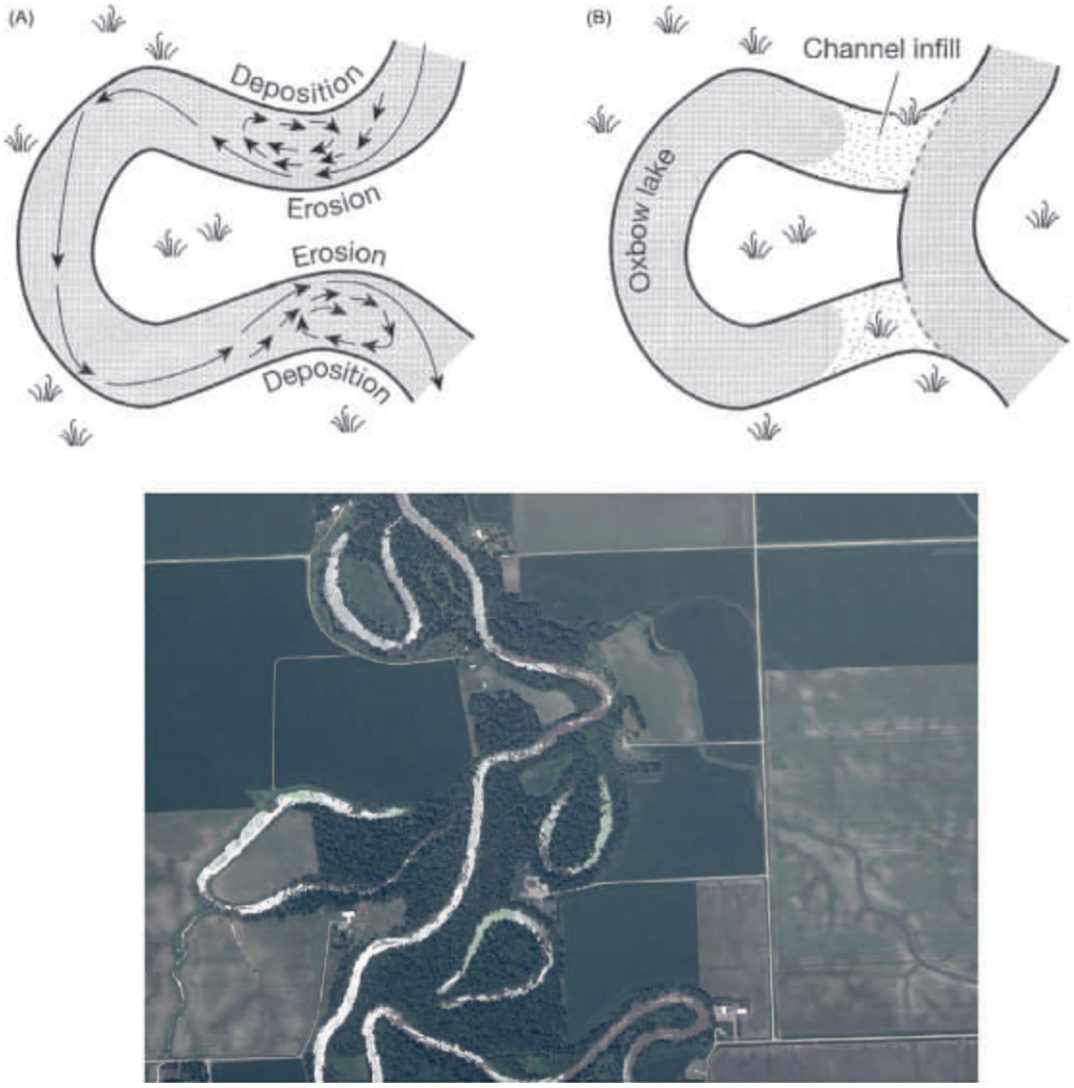


Fig. 10 Diagram of an oxbow lake during the (A) precursor phase and (B) late phase of origination. Color inset: Aerial photograph of four oxbow lakes flanking the Red River at the border of Minnesota and North Dakota (USA). *(A) Kalff J (2002) Limnology: Inland Water Ecosystems. Upper Saddle River: Prentice Hall, Reprinted by permission. (B) U.S. Department of Agriculture, Farm Service Agency, Aerial Photography Field Office, Reprinted by permission.*

floodplain lake. This type originates when a levee develops along the edge of a main river and obstructs seasonal floodwater of the main river from reentering. The volume of a floodplain lake can shift by an order of magnitude on a seasonal basis in relation to rainfall. Floodplain lakes are common throughout low-latitude, riparian regions of South America.

Organism behavior

Beaver pond

Beavers are industrious ecosystem engineers that transform land surfaces from terrestrial to aquatic. Their dams are built of wood and mud for purposes of habitat expansion and predator protection. Beaver dams may reach 4 m in height and extend for up to 0.5 km in length, giving their aquatic impoundments the dimensions of small lakes. The European beaver (*Castor fiber*) was extirpated by trappers over most of its native range by 1900 and is now being reintroduced. A dire fate of similar proportions reduced the abundance of the American beaver (*Castor canadensis*) from an estimated 60–400 million individuals only two centuries ago to 6–12 million today. The remarkable numbers of beaver at one time suggest that their ponds may have once contributed significantly to lake numbers on a global scale.

Reservoir

Reservoirs are human-made impoundments that block the natural flow of rivers and submerge formerly terrestrial surfaces. They are generally built for purposes of water supply (irrigation, drinking), power generation, flood control, or recreation. Modern, highly engineered reservoirs can store enormous volumes of water and control its passage at the outlet with great precision. The numbers and sizes of reservoirs have been growing at rapid rates since World War II. One of the largest is Bratsk Reservoir (Russia) with a volume that exceeds Lake Tahoe (United States).

Farm pond, mine pit

Humans have long been excavating Earth to retain water for agricultural purposes. These lakes, called farm ponds, are widespread globally and may be more important in their contribution to the total surface area of freshwater than once thought. Humans also excavate Earth during mining operations for rocks, metals, and gems. These depressions are called mine pits and once abandoned they can fill naturally with groundwater. Some mine pit lakes are remarkably deep. The Portsmouth Mine Pit Lake in Minnesota (United States) has a maximum depth of 150 m and a surface area of 0.5 km^2, making it the state's deepest inland lake.

Chemical

Solution

Solution (karst, doline) lakes form through a process of chemical dissolution of bedrock. The breakdown of limestone ($CaCO_3$) by natural levels of acidity in the groundwater is the most common chemical reaction involved. A solution lake generally originates as a subsurface cavern which progressively collapses under the strain of overlying soils. Solution lakes have been known to appear suddenly, and disastrously, where large underground cavities collapse all at once. Subsurface outlets and cracks in solution lakes may be sealed by residual rock, soil, or the hydrostatic pressure of the water table, including the ocean in coastal locations. They are common in the Balkan Peninsula, the European Alps, and Florida (United States).

Wind

Deflation

Deflation (playa, pan) lakes originate through erosive wind forces that remove loose terrain. The process is facilitated by an arid climate and a lack of vegetative cover, and may be aided further in some instances by intermittent fluvial erosion and animal occupation (ungulates) which can help loosen sediment and reduce its grain diameter. Deflation lakes may dry up on a seasonal basis if precipitation and runoff are unable to maintain their evaporative losses. They are common throughout arid regions in Australia, Africa, and North America. One notable example is Lake Alablab (Kenya).

Landslide

Landslide dam

A landslide is a gravitationally pushed, mass movement of debris. When one obstructs the passage of a river it originates a landslide dam lake. Because landslide debris is typically unconsolidated it erodes rapidly. These lakes are generally short-lived compared to other lake types. Two examples include Lake Janet in Glacier National Park (United States) and Lake Waikaremoana (New Zealand).

Shoreline

Coastal

Coastal lakes originate when a bay or indentation in the shoreline of a lake or ocean becomes closed to the main body of water by a bar (spit) of sediment deposited through longshore currents. It is a process similar to that which creates fluvial dam lakes. Maritime examples of coastal lakes are common in France, Australia, and New Zealand. Lake Nabugabo (Uganda) is an example of a freshwater coastal lake which was cut off from Lake Victoria. The western edge of the state of Michigan (United States) is rich with coastal lakes sealed off from Lake Michigan (Fig. 11).

Meteorite

Meteorite crater

The most bizarre of all originating processes, and one of the rarest at this moment in Earth's history, is that related to the impact of a meteorite. In this case, the catastrophic destruction and dispersal of terrain leaves a hollow called a meteorite crater lake. Examples include Pingualuit Crater Lake in Québec (Canada) and Laguna Negra (Argentina).

Fig. 11 Aerial photograph of Stoney Lake (United States), a coastal lake of Lake Michigan (background). Aerial Graphics, L.L.C., Grand Rapids, Michigan (United States), Reprinted by permission.

Knowledge gaps

- How environmental forces that originate lakes will respond to climate change including increased heating (glacial force), changing weather (fluvial force and wind force), and changing water demand (human force).
- Approaches to inventory lakes (particularly small lakes) on a global scale with accurate estimates of depth and volume.
- Approaches to track the ever changing geography of lakes (size and presence), particularly in remote areas.

Conclusion

Most lakes originate through nonliving processes but they occasionally involve the behavior of animals such as beaver, ungulates, and humans. Although a relatively limited number of recognized processes originate lakes, the path followed by any particular lake will always be unique and inherently richer and more variable than a classification scheme can convey. Understanding the origin of a lake not only serves to document the natural history of its landscape but also provides valuable context for the investigation of its past and contemporary limnology.

See Also: Structures and functions of Inland Waters - Rivers: The River Continuum Concept; Structures and functions of Inland Waters - Wetlands: The Geomorphology of River Wetlands

Further reading

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Geomorphology of Lake Basins

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This is a reprint of B. Timms, Geomorphology of Lake Basins, In Encyclopedia of Inland Waters, Edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00024-7.

Glossary

Arcuate Gilbert delta – A delta arched in plan and composed of a wide block of sediments up to the water surface.
Homopycnal inflows – Incoming water and lake water of same density, so thorough mixing of the two.
Hyperpycnal inflows – Incoming water more dense than lake water, so it flows along the bottom of the lake.
Hypopycnal inflows – Incoming water less dense than lake water, so it flows on the surface.

Introduction

Mapping is basic human activity, born in antiquity and developed today to embrace complex, multilayered geographic information systems. Maps of lakes are of more intrinsic value than terrestrial maps, because they show features below the water surface the eye cannot see. Moreover, they can be used to compute various parameters of value in understanding the structure and functioning of lakes. This chapter is devoted to explaining these parameters and to expand upon the role of lake geomorphology in limnology.

Morphometric Parameters

In the past, mapping lakes was a laborious task. Lake shorelines had to be established by such methods as transverse, stadia or plane table surveys, all time consuming, and spot depths by lead lines at fixed positions. Today, outlines of shores are easily obtained from aerial or satellite images and depth profiling done by echosounders. Exceptions include shallow ephemeral lakes, like many in Australia, which are best mapped when dry using modern terrestrial surveying equipment. Once, the basic data had to be processed by hand to produce a map, but nowadays almost all stages can be computerized. In all cases scale is important, the finer the scale, the more accurate the map. The parameters derived from these maps can be divided into those taken directly or indirectly from the map and those that are derived by computation from the primary parameters.

(a) Primary Parameters
  (i) *Lake length*. This is the length of the line connecting the two most remote points on the shoreline. It should not cross land (so in an oxbow lake the line is curved), but it may cross islands. Such measurements are of intrinsic geomorphic value only. Of more use limnologically is the *maximum effective length*, which is defined by the longest straight line over water on which wind and waves can act. While the two values are similar in large deep lakes like Africa's Lake Victoria, in island-studded lakes like Sweden's L.Vänern, the maximum effective length is 69%of the maximum length. Knowledge of this parameter is important in geomorphic studies on shorelines and in studies on seiches and stratification in physical limnology.

(ii) *Lake width* is defined by a straight line at right angles to the maximum length and connecting the two most remote shorelines. Again, of more value is the maximum effective width, which does not cross land. This, and the mean width are of use mainly in hydromechanical studies.

(iii) *Lake depth* is the maximum known depth of a lake, and is the single most important geomorphic parameter of a lake. The world's deepest lake is Lake Baikal in Siberia (1620m deep) and many large glacial, volcanic, and tectonic lakes exceed 200m in depth. By contrast, most lakes on flood plains or formed by wind are shallow, rarely exceeding 5m in depth. The limnological consequences of this are paramount and discussed later. *Mean depth* (lake volume/lake area) is also worth noting and has been used many times to explain varying productivities between lakes (e.g., the deeper the lake the less productive it is). Of the various other depth-related parameters, *relative depth*, which is the ratio of the maximum depth to the mean diameter of the lake, is useful in explaining stability of stratification in lakes. For large shallow lakes like the wind-stirred Lake Corangamite in Victoria, Australia, the value is 0.09%, while the nearby meromictic West Basin Lake in a volcanic crater, the relative depth is 3.0%.

(iv) *Direction of major axis*. It is important to know this in geomorphic and hydrodynamic studies as lakes may be aligned to dominant wind direction and hence be more subject to wind than others. For instance, in the eastern inland Australia, only those lakes with an axis near N-S grow spits under the influence of winds from the NW that close off the southeast corner (see later).

(v) *Shoreline length* is easy enough to measure by a map measurer, but is very much influenced by map scale. It is used to calculate shoreline development, a parameter used in littoral studies.

(vi) *Lake area*, once determined by planimetry, but now easily done with a computer, and hardly affected by map scale, is another of the most basic lake parameters. The world's largest lakes are of tectonic and of glacial erosion origin. At the individual country scale, lakes are often listed by area with an explanation for any pattern based on geomorphic distinctiveness of the district/mode of origin. For instance in New Zealand, geology and climate explain the dominance of large piedmont glacial lakes on the South Island, and many somewhat smaller volcanic lakes on the North Island. If the area occupied by a lake fluctuates (because it is terminal or used for water supply) then it is useful to know the area at any depth and this is visualized in a *hypsographic curve* (**Figure 1(a, c)**).

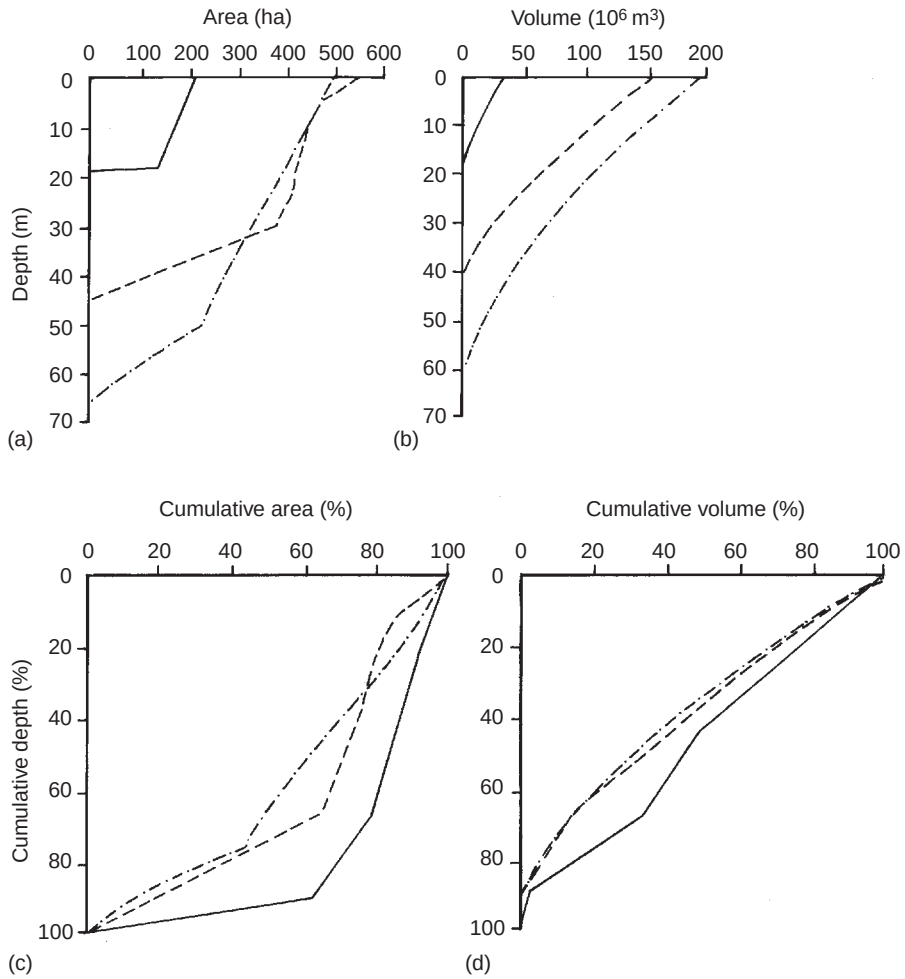

Figure 1 Absolute hypsographic (a) and volume curves (b), and relative hypsographic (c) and volume curves (d) for three maar lakes in Victoria, Australia.

(vii) *Lake volume* is calculated from summing the volumes between each contour, though for increased accuracy different formulae are used according to lake form. This is another parameter often quoted for lakes, particularly if they are large. Most impressive in this instance is Lake Baikal's massive volume of 23 000 km^3, representing one-fifth of the world's fresh water. Visualization of volume at any depth, particularly useful in lakes and reservoirs that fluctuate in depth, is achieved by a *volume/depth curve* (**Figure 1(b, d)**). In this respect, volume percentages derived from cumulative curves for reservoirs are widely quoted in the media in dry countries like Australia, where water reserves are precarious and precious.

(viii) *Insulosity* is the percentage of the lake area occupied by islands. Though some lakes have minor islands, like subsidiary cones in crater lakes, their insulosity values are of no consequence. It is mainly in glacial ice scour lakes and other lakes with highly irregular shorelines where there are many islands that this parameter exceeds ca. 10% and assumes importance. While its worth is intrinsically geomorphic, it is sometimes equated to the value of a lake for recreation, where humans require high shoreline–waterway interaction, as in Swedish lakes Vänern and Mälaren. On the other hand, sailors and waterskiers require open water for their recreation activities, so small, lakes without islands are favored. Thus, there is no relationship between insulosity and recreational use of a lake!

(ix) *Watershed to lake area/volume.* This is easy to calculate from maps and is used as an estimate of terrestrial inputs as in eutrophication studies and also as water renewal ratios for some in-lake processes.

(b) Common Derived Parameters

(i) *Shoreline development* (D_s) is a measure of the irregularity of the shoreline; its accuracy is dependent on map scale. Essentially, it is the ratio of the length of the shoreline to the length of the circumference of a circle of area equal to that of the lake. It is an index of the potential importance of littoral influences on a lake. Perfectly circular lakes have a D_s of 1.0, average lakes have values between 1.5 and 2.5, while lakes and reservoirs with much indented shorelines have values exceeding 3 (**Figure 2**). Expressed in relation to lake types, volcanic vent lakes have minimal D_ss, and lakes in dammed valleys and in ice-scoured terrain have the highest values.

(ii) *Volume development*. This index (D_v) is used to express the form of a basin, and is defined as the ratio of the volume of a lake to that of a cone of basal area equal to the area of the lake and depth equal to the maximum depth of the lake. Lakes with a D_v of 1.0 are perfectly cone-shaped and uncommon. Values <1.0 indicate a trumpted-shaped lake and are rare and values $>$ca. 2.5 indicate a beaker-shaped lake and are also uncommon (**Figure 2**). Most lakes have values somewhat greater than unity. The unusual values may be related to lake type, e.g., doline lakes usually have D_vs near 1 and claypans and maar lakes may have D_vs near 3, but sometimes D_vs may be the result of peat growth/marl deposition/shoreline slumping/erosion in the littoral, leading to values near 1. In all cases the index is a surrogate for the role of the sublittoral in a lake's limnological processes, the lower the value the greater the sublittoral influence.

(iii) *Slope* is the angle, usually expressed as a percentage of repose of the bottom sediments and can be determined directly from an echogram or from a contour map using appropriate measurements and formulae. Slopes of near 0% (profundal areas) to 20% (sublittoral slopes) are common, but occasionally values approach the maximum of 90% in a steep-shored crater, glacial erosion and lakes due to earth movements. This parameter is used mainly in sedimentological studies and to lesser extent in benthic studies in choosing suitable stations. *Mean slope* is an average for a whole lake and is derived from a contour map and application of formulae. Not surprisingly, mean values are much more subdued than slopes at designated contours and commonly range from $<1\%$ to 10%, but may exceed 25%in some lakes, e.g., Lake Barrine, a small maar in north Queensland, Australia, has a mean slope of 30%. Perhaps in interlake comparisons, visual inspections of comparative hypsographic curves (**Figure 1**) are just as instructive as are figures for mean slope, and far less troublesome to prepare.

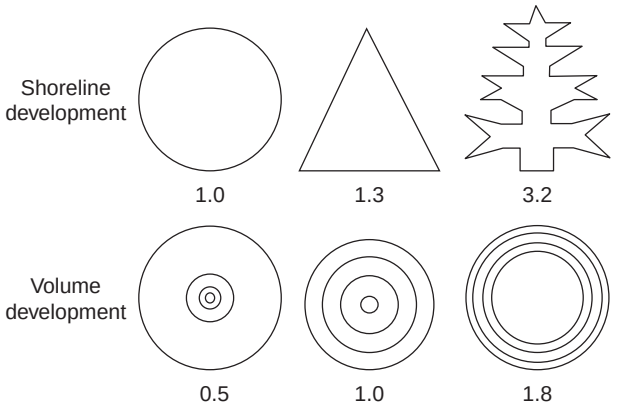

Figure 2 Graphical representation of shoreline development for three lakes of different shape, and of volume development for another three lakes of different volume distribution. In the latter, concentric lines represent depth contours.

(iv) Sometimes a derived parameter can be established for a special need. For example *Ratio of epilimnion sediment area to epilimnion volume* has been usedmore effectively than parameters based on whole lake volume in eutrophication studies because it more accurately accounts for nutrient recycling in a lake.

Lake Shapes

Many lakes have characteristic shapes determined by their mode of origin that are only partly described by their parameters. The ratio of length over width can give information on whether a lake is rectangular, circular or ellipitical and high D_ss can indicate a dendritic lake, but a simple descriptive word is usually better. *Circular* lakes (D_s near 1) are uncommon, but can be found in volcanic vents, in some deflation basins and in lakes due to meteoric impact. *Subcircular* lakes are more common and are associated with a variety of origins: volcanic craters, deflation basins, dolines, cirques, kettle-holes to name the more common ones. *Ellipitical* lakes are a special subgroup of these and are generally associated with wind deflation. *Subrectangular* elongate lakes generally are of structural origin or result for glacial erosion in valleys (piedmont lakes). Markedly *dendritic* lakes result from flooding of dissected valleys as in some coastal lagoons, some landside lakes and in many reservoirs. It is these in which D_s is high (>3). *Triangular* lakes also usually arise from flooding, usually either on floodplains or along coasts. These may be confused with circular lakes on length/width ratios, but not by their descriptor. *Lunate* (or newmoon shaped) lakes result from river meandering to form oxbows, and sometimes from asymmetrical placed subcones in volcanic craters. Highly *irregular* lakes are possible from the fusion of lake basins and in glacially scoured areas. These also may have high D_ss.

Changes with Time

Over geological time, lakes are temporary landscape features (but see later), filling with sediment and/or eroding at the outlet. Consequently lake morphometry changes with time, imperceptibly in well-watered areas, but at the other extreme, oscillating widely in terminal lakes in arid areas. The most obvious changes are lake level fluctuations and their concomittent shoreline changes. Sedimentation is less obvious, except for delta construction.

Lowered lake levels, of whatever cause, result in stranded beaches, spits and deltas. Worldwide, piedmont glacial lakes provide many examples, perhaps none better than New Zealand's Lake Wakatipu with its 10 strandlines cut into a major bench and deltaic fronts at 50m above present lake level The terminal lakes of Tibet have numerous elevated shorelines attesting to a more fluvial past, as do most of the world's large lakes in endorheic regions. Interesting as these landforms may be, and useful in aging a lake, it is the changes with decreasing depth in physicochemical processes in the lake such as thermal and chemical stratification, that are important limnologically.

In some lakes, levels have been elevated since initial formation, drowning shoreline features and river channels. Coastal marine lagoons, tied to changing sea levels, provide many examples including Lake Macquarie near Sydney, Australia, where drowned river channels and spits are clearly discernable (**Figure 3**). As in lakes with lowered levels, raised levels may change physicochemical processes, and in addition, there may be hydrodynamic changes associated with changed inflows.

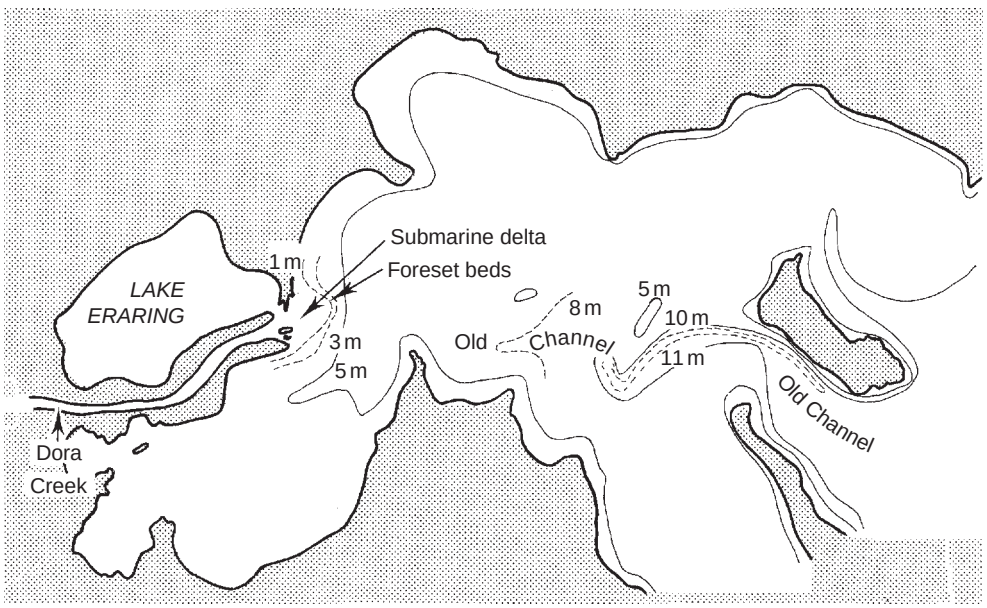

Figure 3 The western bay of Lake Macquarie, near Sydney, Australia, a drowned coastal valley, showing the former river course and a lobate delta.

All lakes accumulate sediment, either mainly from stream inflows, or biological production in the lake itself, or occasionally from overland flows and rarely by showering ash from volcanic eruptions (as in lakes around Taupo and Rotorua in New Zealand). Rates are highly variable and depend on geomorphic type, catchment size and erodability, and trophic status (and proximity to a volcano!). The most rapid accumulation is by delta building in lakes with large inflows in mountainous areas. Well-known examples include the deltaic plain at the head of Lake Geneva and the surficial sediments that divide Thuner See and Brienzer See at Interlaken, both in Switzerland. Deltaic form depends on the relative densities of lake and river water and lake currents. Arcuate Gilbert deltas due to homopycnal flows are perhaps the most common type in piedmont glacial lakes, lobate deltas associated with hypopycnal inflows in coastal marine lagoons (Figure 3), and alluvial fans in shallow desert lakes. No matter the deltaic form, lake surface area and volume are reduced, but probably with minimal influence on limnological processes in large lakes.

On the other hand, lake floor sedimentation due to submarine delta building by hyperpycnal inflows (as in Lake Pukaki in New Zealand) and by chemical or biological deposition decrease lake depth and hence may influence physicochemical processes, particularly if the sediments of productive lakes consume oxygen during stratification. Rearrangement of bottom sediments due to slumping or bioturbidation are of little geomorphic consequence, but may upset layering and hence interpretations of lake/catchment history recorded in sediment cores.

Ancient Time plus Size

While differing geomorphology, as measured by the above parameters, influences lake ecology, there are many other factors involved, one of which is geological time. Most lakes exist for hundreds to thousands of years, perhaps even a few hundred thousand years, but some persist for many millions of years, and cognisance of this, together with their size (volume, perhaps area), allows greater understanding. Scale is indeed important in limnology.

By considering a new coefficient, Touchart divides lakes into four broad groups. He estimates the scale of a lake, by taking the logarithm of the product of the age (expressed in millennia) by its volume (in cubic kilometres). Lakes with values 4–8 are almost exclusively large old structural lakes such as Baikal, Caspian, Tanganyika (values of 8), Victoria (7), Issyl-Kul, Aral, Titicaca (6), Balkhash, Tahoe (5), and Biwa, Toba, Taupo (4), among others. Most of these are largely independent of morphoclimatic hazards and have high biological endemism. For instance in Lake Baikal there are 255 species of gammarid amphipods in 35 genera, 34 of which are endemic. New Zealand's Lake Taupo is an exception, going back perhaps only a million years, but subject to many catastrophic reincarnations as recent as 1800 years ago). Biodiversity is low as a consequence of this Recent age, and also it small size (623 km^2) and being on an isolated island.

The next group usually have values 1–4 and are medium sized, largely of morphoclimatic heritage, i.e., shaped largely by the Würm glaciation. Examples include, Lakes Superior, Great Bear (4), Ontario, Winnipeg (3), Constance, Geneva (2), Te Anau, Wakatipu (both NZ)(1) among a host of others. They are often large (>10 000 km^2) and deep (200–500 m), and formed by glacial erosion. Life expectancy is in the order of only thousands/tens of thousands of years. Biodiversity is lower and morphodynmaic processes (delta-building, sedimentation) in their basin are relative important in limnological processes. These are the lakes most common in the Temperate Zone of the Northern Hemisphere where limnology developed, so they are the 'standard' lakes of text books. To a large degree both of these classes of lakes are dominated by their shear size, so that morphometric parameters other than area and depth are generally unimportant in influencing limnological processes.

A third group of lakes are small (Touchart coefficients of 1 or less) and largely influenced by current morphodynamic processes or recently inherited ones. These include fluviatile lakes, karstic lakes, aeolian lakes, and landside lakes in the first subgroup and many small glacial and volcanic lakes in the second. All are subject to changing shape and dimensions and many have a particularly precarious existence (e.g., landslide lakes). It is in these lakes where key abiotic variables (e.g., Secchi depth) are related in varying degrees to lake morphology and catchment area.

Touchart's fourth group of lakes also have coefficients of 1 or less; they are the lakes (reservoirs) of human origin. They are of variable size (in area, some challenge lakes with coefficients of 4), but are recent in origin and have a short life span. Moreover, their morphometry is forever changing and their catchments dominate their limnological processes.

Touchart largely omits consideration of short-term changing morphology, partly seen in reservoirs, but absolutely characteristic of intermittent lakes. Such lakes are uncommon where most limnologists live in Europe and North America, but prevalent in the drier parts of Asia, Africa, South America and especially Australia. Some are of very ancient lineage, e.g., Lake Chad, Lake Eyre, but lack ancient/endemic biodiversity because intermittent lakes are useless evolutionary loci. Others (e.g., seasonal lakes due to flooding; shallow lakes due to wind deflation) are temporary landscape features and if they lie in a distinct basin, are best depicted with inverse contours (i.e., bottom at 0m, highest level at x metres/centimetres to account for their fluctuations in water level (Figure 5). Most abound in geomorphic expressions of their shallowness and variability, so that a consideration of their geomorphic parameters together with their hydrologic variability can explain some ecological features.

Parameters of the Geomorphic Lake Types

Structural (Tectonic) Lakes

As shown above, many of these like Lakes Baikal and Tanganyika, are especially large, deep and old, so that they have special limnological features, that are expressed most meaningfully by their Touchart coefficients. Such lakes have D_vs a little above unity

(1.2–1.5) and moderate D_s (1.3–3.4). Many older tectonic lakes of moderate depth (e.g., Caspain Sea, Aral Sea) have D_v s <1, while the shallow intermittent ones vary according to hydrological condition. For instance in Lake Eyre D_v decreases from 1.68 when 'full'(=5.7mdeep) to 1.55 at 4mdeep to 1.43 at 1m deep, while D_s decreases from 4.7 when full (it spreads up entering creeks to give a highly indented shoreline) to much lower values when contained well within the vast salt flats. The limnology of Lake Eyre is different when full to when near empty, largely because of differing water salinities but the consequences of its differing geomorphic parameters contribute too. Lake Chad also has differing geomorphologies at different water levels, and probably so do many other shallow arid zone lakes. In addition, tectonic lakes in terminal basins have many stranded beach features useful in deducting past histories, as in many Tibetan lakes to give one set of numerous possible examples.

Meteoritic Impact Lakes

These are rare, but impressive because of their roundness ($D_s = 1$).Depths vary, but LakeUngava (=Chubb) in Quebec Province, Canada, is 251m deep and diameter about 3 km. Intermittent Lake Acraman in South Australia, although not quite round is notable because of its huge size (diameter 22km).

Volcanic Lakes

Like structural lakes, there is no one set of parameters which characterize all volcanic lakes, though some subtypes have characteristic features. One group are the maars and calderas; generally these have low D_ss (near 1), high D_vs (near 2), high littoral slopes and low profundal slopes. In an analysis of 15 Australian maars, D_s averaged 1.14 (lowest 1.01) and D_v 1.91 (highest 2.8) (**Figure 4**). Such lakes are typically dominated by their limnetic zone and have physicochemical processes not too dissimilar to the classic large lakes of limnological literature. On the other hand shallower lakes on Victorian lava fields are not that different (except for their saline waters) to shallower lakes elsewhere. These are dominated by shallow water and littoral processes due to low maximum and mean depths, low littoral slopes and often high shoreline developments. Again, the basic geomorphic differences between the various types of lakes are expressed in depth and size, and perhaps there is scope in the Touchart system to differentiate lakes with coefficients <1 within his third type.

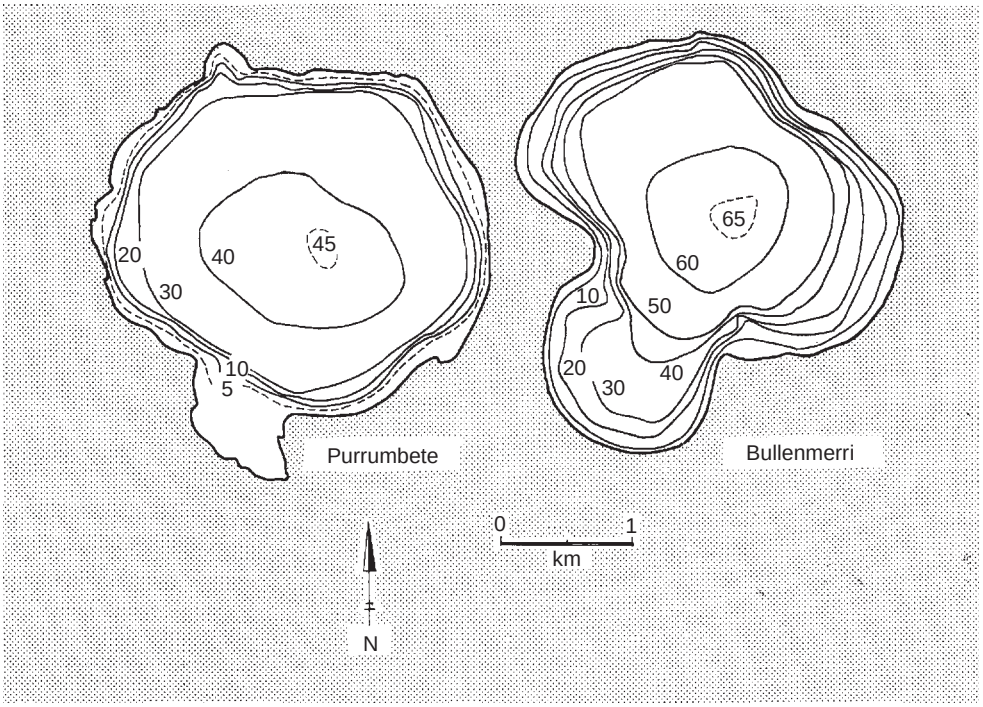

Figure 4 Bathymetric map of two maar lakes in western Victoria, Australia. Lake Purrumbete lies almost wholly within its crater, while Lake Bullenmerri lies within three adjoining craters. Both have a D_s a little >1 and a D_v near 2.

Glacial Lakes

Again there is a wide variety of limnologies better explained by the size-age coefficient of Touchart (group 2, see above) than by geomorphic parameters alone. Nevertheless for the piedmont lakes due to glacial erosion, waters are deep, and D_vs are high. For 10 such large lakes on the South Island of New Zealand, 7 are deeper than 200 m and the average D_v is 1.75. Shore and littoral features are unimportant compared with the contribution of large and deep limnetic region. Cirque lakes for another group, but their geomorphic parameters are hardly unique and influencial. The smaller kettles and the like are dominated by their small overall size and hence littoral processes.

Fluviatile Lakes

Almost all of these are small, and even if >10 km^2 are still shallow and hence belong to Touchart's group 3 and so littoral dominated. Two common types have some characteristic parameters: most oxbows are lunate-shaped with a curving maximum length and moderate D_ss (<2.5), while most blocked valley lakes are dendritic with higher D_ss (2–4). Some, e.g., the bog lakes of the Waikato, New Zealand have shorelines much smoothed by growth of littoral vegetation so that D_ss are low, as are D_vs.

Solution Lakes

As for fluviatile lakes most of these, especially dolines, are small and shallow, and though uvalas and poljes may be larger in area, they are still shallow. Perhaps the parameter of most interest is their D_v – this is often 1 or less, indicating a cone or trumpet-shaped basin. Unlike the previous fluviatile lakes, but like kettles, they may have multiple deeper subbasins.

Aeolian Lakes

Lakes formed, or largely moulded by wind action, are generally shallow (<5 m, often <1 m deep), relatively small (<100 km^2, often <1 km^2) and have sandy shores, so that shore processes are most important in their limnology. Hence spits, beaches, islands, and deltas feature in their evolution and their basin orientation is both a consequence of their development and/or a causal driver in their further evolution. Orientation to wind and effective maximum lengths for wave generation are basic controllers of their geomorphology. Many lakes in southwestern Western Australia and elsewhere are rounded or ellipitical and difference in orientation and size between areas is related to different wind directions and/or rainfall distribution. On the other side of Australia, only those lakes orientated with their major axis N-S, develop spits in the southeastern corner in an attempt at lake compartmentalization (see later) (Figure 5). These spits increase D_s, which increases the habitat for shorebirds. Under unidirectional or

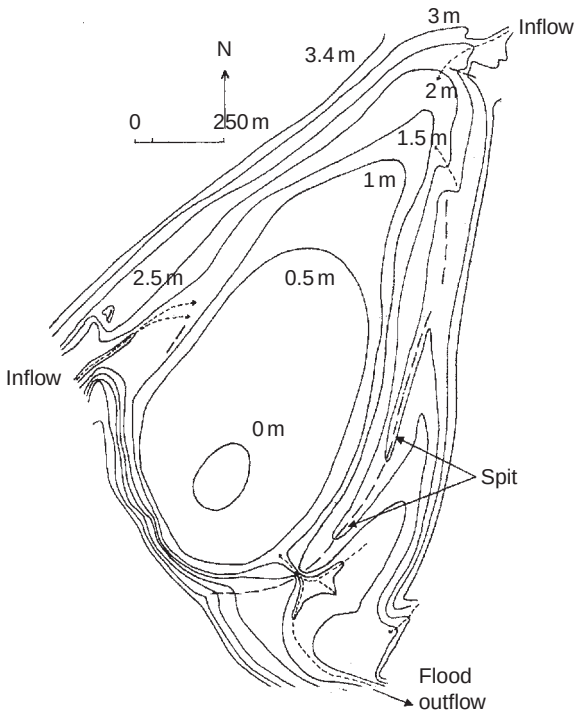

Figure 5 Bathymetric map of Lake Yumberarra, Outback Queensland, Australia. Key: beach ridges long dashes; creek channels, short dashes. Depth contours inverted from normal pattern, as this is more convenient in shallow intermittent lakes with highly variable water levels.

bidirectional winds, shallow lakes may completely segment (i.e., form separate compartments), creating smaller lakes with more shorelines and increasing the important of littoral processes.

Coastal Lakes

Although most coastal lakes are due to sea-level rise, their geomorphology is variable due to different inherited features. A few are in fjords, so may be deep and steep-sided, while most are in drowned valleys, so dendritic or triangular, and those on low coasts may be elliptical. Australia's southeast coast has numerous coastal lakes of many subtypes, as does the Landes coast of France, the Cape Cod coast of North America, the Baltic coast to name a few others. Their active depositional environment encourages delta and spit formation, and lake compartmentilization in low coasts, so that shorelines are longer than those inherited. Given most lie in windy environs, basin orientation, and effective lengths are particularly important for those lake processes dependent on wave generation.

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Lakes as Recorders of Earth Surface Dynamics From Yearly to Plurimillennial Time-Scales

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Accumulation (of sediment) When the transporting medium is not competent enough to ensure the transport of erosion products, they may accumulate in a so-called depocenter. Within their watershed, lakes are often such a final sink in which erosion products and the information they bear are trapped. Moreover, because lake bottoms are generally quiet, this accumulation of sediment is regular enough to preserve the chronological succession of information, just like pages in a book. This is why lake sediment can be considered as "natural archive."

Anthropocene The Anthropocene is a neologism forged by Paul Crutzen to designate the moment in the history of the Earth when humans emerged as a new geological force. The international commission on Stratigraphy is currently addressing the question of making the Anthropocene an official geological Era which should have started in 1950 CE with the first worldwide dispersal of artificial radionuclides due to a period of intense nuclear weapons atmospheric tests.

Erosion cycle The erosion cycle designates the succession of any processes leading to the movement of matter teared from the Earth surface and subsequently deposited. It is commonly divided in four phases: weathering, grabbing, transport and accumulation of sediment.

Grabbing Any process permitting the extraction of weathered matter (cf. weathering) from a rock or a soil, usually through a meteoric agent: rain, wind, waves.

Holocene The Holocene is the most recent geological epoch; it conventionally started 11,700 years ago with the termination of the Pleistocene Stage 4 glacial period. It is hence the most recent interglacial stage of the Pleistocene, but also the period that has witnessed the rise of organized human civilizations which eventually became one of the driving forces of the Earth dynamics. This growing influence of humans led several scientists to propose the Holocene epoch is now over and should be replaced by the Anthropocene Era.

Natural archive A natural archive is the common name given to Earth surface systems that have the capacity to record environmental conditions through time. They are the study object of paleosciences.

Paleosciences A corpus of scientific approaches aiming at reconstructing past Earth dynamics.

Transport (of sediment) Once weathered and grabbed, erosion products need a sufficiently competent flow of matter in order to be carried away from their source area; this is generally stream water, but may also be wind, avalanche, glaciers, humans etc.

Weathering Physical or chemical reworking of rocks that generate an outgoing flux of dissolved and/or particulate matter toward the Earth Critical Zone; it includes in particular all processes of soil formation from non-weathered bedrocks.

Introduction

Lakes are defined as in-land bodies of standing water. As such they represent zones of drastically reduced water velocity along stream courses and thus—almost—perfect sediment traps. Indeed, whereas, in most cases, the amount of water flowing in a lake is almost equal to the amount flowing out of it (+/– evaporation), most of the solid charge brought by stream water is trapped within the lake. This is nicely exemplified at the outlet of Lake Geneva where the alpine Rhône river gets out of the lake free of any sediment and is met by its tributary Arve river which is by contrast extremely turbid. Whereas both streams originate from a high-altitude glaciated area producing massive amounts of sediment, the difference in particles load is only explained by the presence of Lake Geneva which traps most of the sediment coming from the Upper-Rhône River catchment area (Fig. 1).

The quantity and quality of river's solid charge depend on a multitude of processes acting within a given catchment area. They hence potentially bear a lot of information about the evolution of inland areas, both submitted to natural and human-triggered forcing mechanisms. This information is subsequently stored in stratigraphic order at the bottom of lakes within sediment strata. This is why lakes are particularly interesting archives of the Earth Critical Zone dynamics (Fig. 2).

The Earth Critical Zone (ECZ) is a conceptual space defined as the thin active layer at the surface of the Earth where all the energy, matter and information exchanges that are necessary to sustain life do operate (Banwart et al., 2013). It has been defined by the US National Research Council as spanning the whole space from the top of the canopy down to the base of groundwater (Gaillardet et al., 2018). Among the recent advances in environmental sciences, the concept of ECZ theorizes the fact that social-ecological systems strongly depend on the imbrication of biotic and abiotic processes that interact at various time scales, from the second to several millennia. It is hence crucial to better know all those interacting processes, their kinetic and long-term interactions in order to understand global changes and their potential effects on planet Earth habitability (Lade et al., 2020). In this chapter, we will detail how some of the information stored in lake sediment can be extracted in order to reconstruct the evolution of the ECZ along with the complex interactions driving its dynamics.

Production and export of eroded matter within the Earth Critical Zone

Erosion processes are the main path for matter and thus information to be transferred within the Earth critical zone. They may be schematized into four phases (Fig. 3): weathering, grabbing, transport and accumulation.

Main forcing factors of weathering, grabbing and transport process may be climate- (temperature, precipitation, wind) and/or human-triggered (land-use, including agro-pastoral activities and civil engineering, such as urbanization or dam building, for instance). They are also related to natural functioning of the ECZ, such as vegetation changes or geodynamics. As a consequence, the quantity and quality of eroded material potentially bring information about all those processes.

Documenting climate-triggered changes in erosion patterns

Streams are one of the most efficient sediment conveyors on Earth and as such, they play a key role in the erosion cycle (Aksoy and Kavvas, 2005). Reconstructing changes in river-borne sediment flux and origin from lake sediment might hence reflect the history of

Fig. 1 *Left panel*: this Sediment plume entering the Cayuga Lake, New York, United States, illustrates the huge amount of sediments that are transferred from catchment areas toward Lake basins. *Right panel*: the Arve river, loaded with glacial sediment from Mont-Blanc Massif, joins the Rhône river at the output of Lake Geneva. When it enters the lake, some 80 km upstream, the Rhône river was as much loaded as the Arve river, but Lake Geneva acted as a perfect sediment trap and only let the clear water pass through.

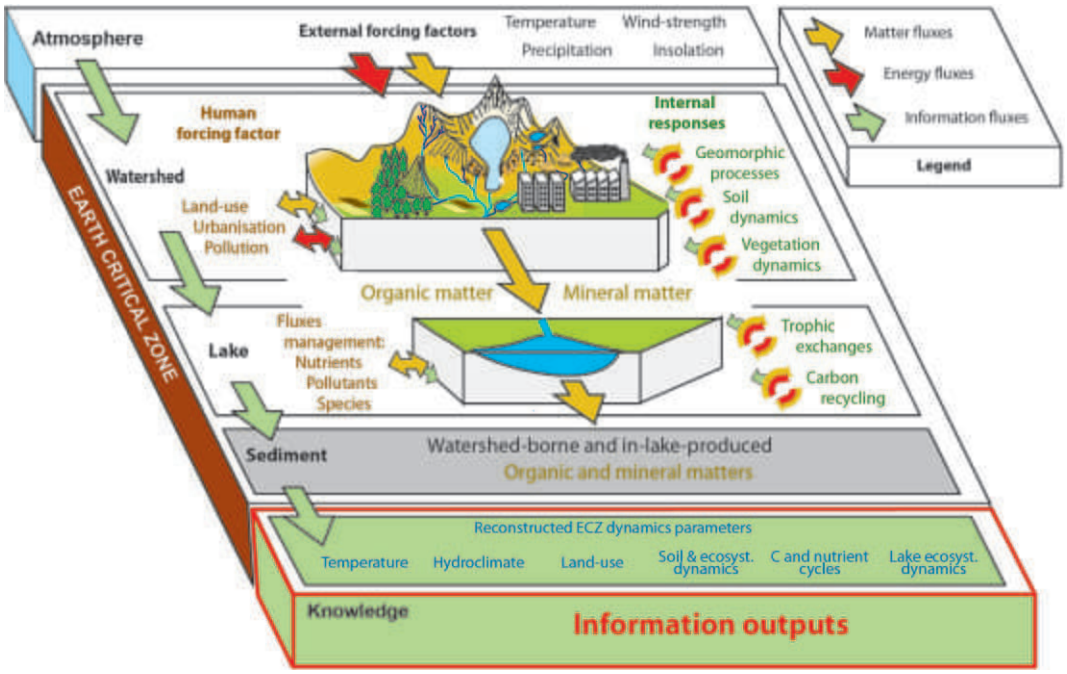
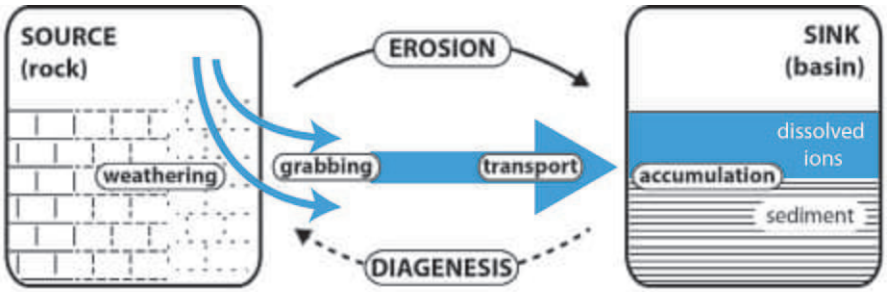


Fig. 2 Conceptual view of matter, energy and information fluxes through the Earth Critical Zone and toward a lake basin. Lake floors accumulate matter from the catchment that carries information about the ECZ dynamics. Limnogeology is the science that permits to reveal this information, hence turning mud into information.



Triggering factors		Erosion processes			
		Weathering	Grabbing	Transport	Accumulation
Climate	Temperature	Hydrolysis Frost/unfrost	**Permafrost stability** **Glacier dynamics**	Snow cover cycle	Dilution (authigenic productivity)
	Precipitation	Hydrolysis	**Glacier dynamics** **Heavy rainfall**	**Hydrological flux** **Fluvial morphology**	Terrigenous input
	Wind		Wind erosion	Air-borne transport	Aeolian deposit
Land cover		**Hydrolysis**	**Soil (de)stabilisation**	Fluvial morphology	Buffering effect (riparian forest)
Geodynamics		Rejuvenation	**Earthquake-triggered destabilisation**	Hydrosystem destabilisation	Sediment reworking

Fig. 3 Schematic view of the erosion cycle (upper panel) and its processes as well as triggering factors (lower panel). Modified after Arnaud F, Poulenard J, Giguet-Covex C, Wilhelm B, Révillon S, Jenny JP, Revel M, Enters D, Bajard M, Fouinat L, Doyen E, Simonneau A, Pignol C, Chapron E, Vannière B and Sabatier P (2016) Erosion under climate and human pressures: An alpine lake sediment perspective. *Quaternary Science Reviews* **152**: 1–18. https://doi.org/10.1016/j.quascirev.2016.09.018.

the in-land hydrology (Arnaud et al., 2012, 2016). Dust mobilization and emission by wind into the atmosphere may also be important erosive mechanisms (Shao et al., 2011). Since the dust flux can contribute >10% of the global river sediment flux, dust deposition from the atmosphere plays an important role in the biogeochemistry of the ECZ (Derry and Chadwick, 2007) and can be imprinted within lake sediment (Sabatier et al., 2020).

Most methods used to record erosion fluxes from lake sediment archives lie upon the geochemical contrast of this river-borne fraction, named "allochthonous" or "terrigenous," compared to the in-lake produced matter, named "autochthonous." In this chapter, we will focus on the use of the terrigenous fraction, as a marker of the Critical Zone dynamics. For the use of the autochthonous fraction, refer to the "Paleolimnology" chapter. However, a good knowledge of the mineral autochthonous fraction is required in order to well-distinguish it from the terrigenous one. The autochthonous fraction preserved in lake sediment can be made of bio-precipitated skeletons, typically made of carbonate or silicon and/or of organic matter. In tempered hard-water lakes, the mineral autochthonous fraction is largely dominated by bio-chimio-precipitated carbonates (see chapters on "drivers and implications of lake pH" and "the lacustrine carbon cycle"). In high altitude and/or high latitude, colder conditions preclude the precipitation of calcite and the autochthonous fraction is commonly dominated by biogenic silica (mostly diatoms remains) and organic matter.

Whatever the composition of the autochthonous fraction, measuring the evolution of a marker of one the two fractions permits assessing the erosion-borne contribution to the sediment flux. The magnetic susceptibility of sediments generally increases with higher erosion-derived material contribution and is commonly used as such a marker. Inversely, one may measure chemical proxies of organic matter, such as the total organic carbon, the abundance of chlorophyll-like pigments or the bromine content, which are often negatively correlated to the erosion-triggered sediment input.

Recording airborne erosion through dust deposit

Recent advances about very high altitudes lakes systems in granitic contexts with a low to very low watershed/lake surface ratio leading to low local erosive inputs by stream allow to reconstruct past airborne dust fluxes (Fig. 4; Jiménez-Espejo et al., 2014; Sabatier et al., 2020). These lakes present very low accumulation rates, generally 1–2 m for the entire Holocene with a strong in situ organic matter component. Hence, they can be considered as rain gauge lakes where the sediment is a mixture of autochthonous organic matter and atmospheric inputs. Tracers such as clay mineralogy allows to assess the arid dust contributions (palygorskyte) and their origins (ratio Illite/Kaolinite and Chlorite/Kaolinite) (Sabatier et al., 2020; Scheuvens et al., 2013). Other techniques such as mineral geochemistry and Sr/Nd isotopic composition allow quantitative reconstructions of past dust flux and dust origin fingerprinting.

Recording glacier fluctuations

A classic example of a direct relationship between climate and erosion is given by the reconstruction of glacier fluctuations from lake sediments. The amount of glacial sediment produced by glacier erosion is indeed related to the surface of the glacier (Dahl et al., 2003; van der Bilt et al., 2016). As a consequence, reconstructing the flux of glacier-eroded material into a lake permits to reconstruct past glacier fluctuations.

In this case, the cold lake water precludes the precipitation of carbonates. The terrigenous input is hence assessed through the relative proportions of terrigenous fraction and in-lake produced organic matter. This can be done using any of the techniques exposed above, magnetic susceptibility being among the most cost- and time-efficient and thus the most used ones (van der Bilt et al., 2016). Recent development in spectrocolorimetry also brought promising results by accurately assessing the fluctuation in organic matter content (Fouinat et al., 2017).

Such an approach has been extensively used in Scandinavia where large ice-cap glaciers have tongues flowing onto ancient glacier valley (van der Bilt et al., 2016). When those valleys get dammed, often relatively low in the catchment area, the lakes hence trap efficiently the glacier-derived terrigenous flux (Fig. 5). Moreover, their moderate altitude permits the development of primary producers whose organic matter will dilute the erosion flux whereas the surrounding forested environment provides sufficient organic macroremains for dating. On the contrary, the method is sometimes hard to apply in inner mountain ranges where glacier-fed lakes are located higher in altitude and surrounded by steep slopes. Steep slopes reduce the glacier surface and short distance between the glacier and the lake may indeed lead to a hard-to-interpret non-buffered signal. Moreover, the scarcity of datable organic macroremains in high altitude lake sediments may make them hard to date. However, applying a detailed sedimentological study may in such cases permit to construct accurate glacier fluctuations chronologies (Fouinat et al., 2017).

Erosion and paleohydrology

Large rivers may bring huge amount of sediment to lake basins (Fig. 5). In such cases, the evolution of the terrigenous input may reflect changes in regional paleohydrological conditions, assuming there is a positive feedback between more humid conditions and both accentuated erosion in the lake catchment area and more efficient transport (Arnaud et al., 2016; Wessels, 1998). Hence, high resolution continuous paleohydrological reconstructions can be established, provided one may verify that hydrology is the prime forcing factor of changes in erosion flux. This is often the case in the early times of the Holocene, because the emergence of agro-pastoralism, a human-triggered perturbation of the erosion cycle, may alter the climate-erosion relationship (Arnaud et al., 2016). As early human perturbations of the erosion rarely affected large surface areas, the choice of a large and deep lake, fed by a large catchment area will hence be more favorable for climate reconstruction than a small lake, more sensitive to human disturbances. At high altitude, landscapes are losing their interest for human activities such that highest altitude lake records are directly connected to climate changes, especially if there is a glacier in their catchment area (Arnaud et al., 2016; Fig. 6). However, in

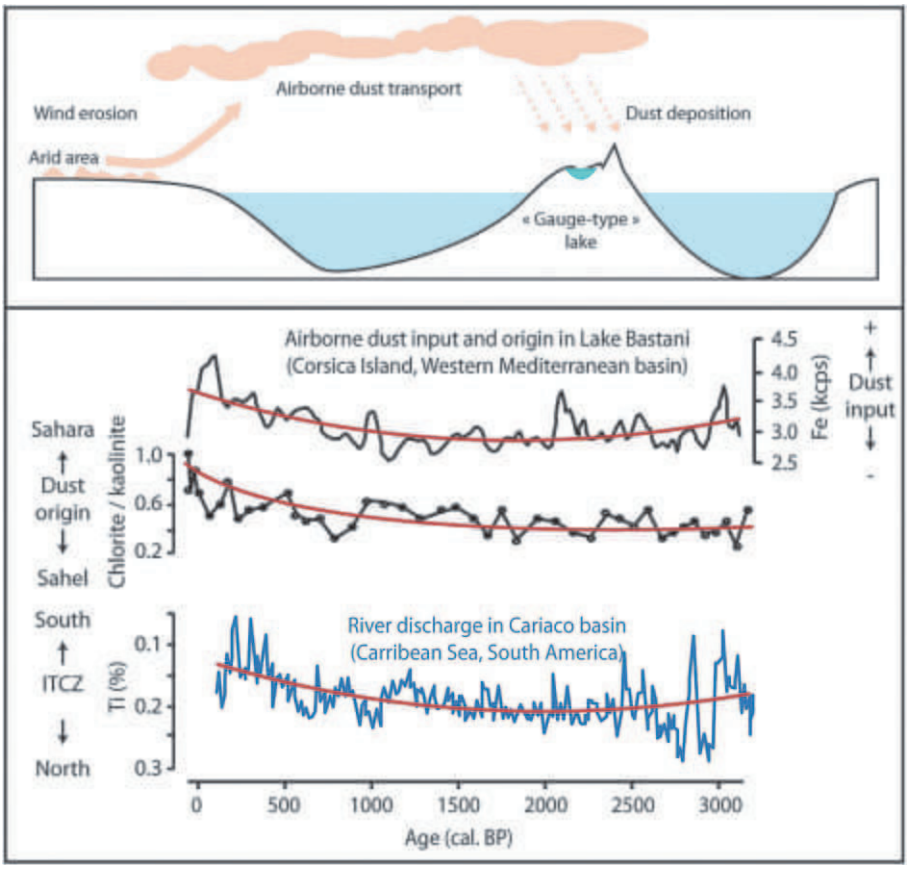


Fig. 4 (A) Schematic principle of the record of wind-driven erosion from arid area in gauge-type lake through dust deposition signal. (B) Example from Lake Bastani, Corsica (Sabatier et al., 2020), where the sediment geochemistry gave a record of dust input, while clay mineralogy gave a signal of dust origin (Sahel vs. Sahara desert). The river discharge in Cariaco Basin (Haug, 2001) illustrates how such a signal enables paleoclimatic interpretations: the increase in dust and the change in its origin reflects the independently evidenced southward migration of the Intertropical Convergence Zone (ITCZ). Modified after Sabatier P, Nicolle M, Piot C, Colin C, Debret M, Swingedouw D, Perrette Y, Bellingery M-C, Chazeau B, Develle A-L, Leblanc M, Skonieczny C, Copard Y, Reyss J-L, Malet E , Jouffroy-Bapicot I , Kelner M, Poulenard J, Didier J, Arnaud F and Vannière B (2020) Past African dust inputs in the western Mediterranean area controlled by the complex interaction between the intertropical convergence zone, the North Atlantic oscillation, and total solar irradiance. *Climate of the Past* 16: 283–298, https://doi.org/10.5194/cp-16-283-2020.

any case, it is crucial to critically assess the climatic interpretation of fluctuation in erosion fluxes. This must first be done through a deep sedimentological investigation in order to track any sign of non-climatically induced changes. In particular, any change in the composition of the terrigenous fraction must be documented and interpreted regarding the local geological setting.

One must always keep in mind that any paleo-reconstruction depends on an array of assumptions that are often impossible to be verified altogether. As a consequence, they must be interpreted very cautiously. Beyond the study of the sediment itself, it is hence crucial to confront results to independent markers, both within the same core and from independent regionally close archives. Indeed, even if precipitation may vary following more regional patterns than temperature, they are still coherent over large areas and all records based on the same assumptions should hence react together.

Geological record of flood chronicles

While they generally appear as quiet bodies of standing waters, lakes are also subject to violent sedimentation events. An abundant literature has been dedicated to the identification and documentation through time of geological deposits deriving from flood events (Gilli et al., 2013; Schillereff et al., 2014; Støren and Paasche, 2013). Potentially mobilized techniques are here very numerous, however they all lie upon the same concept of seeking for anomalous layers interbedded within the so-called "continuous sedimentation." By contrast, such layers are often called "instantaneous deposits" or "event layers" (see the chapter on "Sedimentology"). Naked eyes have been, and still are, the first tool used to identify such layers (Fig. 7). Laser grainsizers were largely used in sedimentology lab since the late 1990s'. They offered a precise description of sediment layers that was since then used to document and characterize flood layers (Arnaud et al., 2002; Wilhelm et al., 2012a). Magnetic parameters, among which

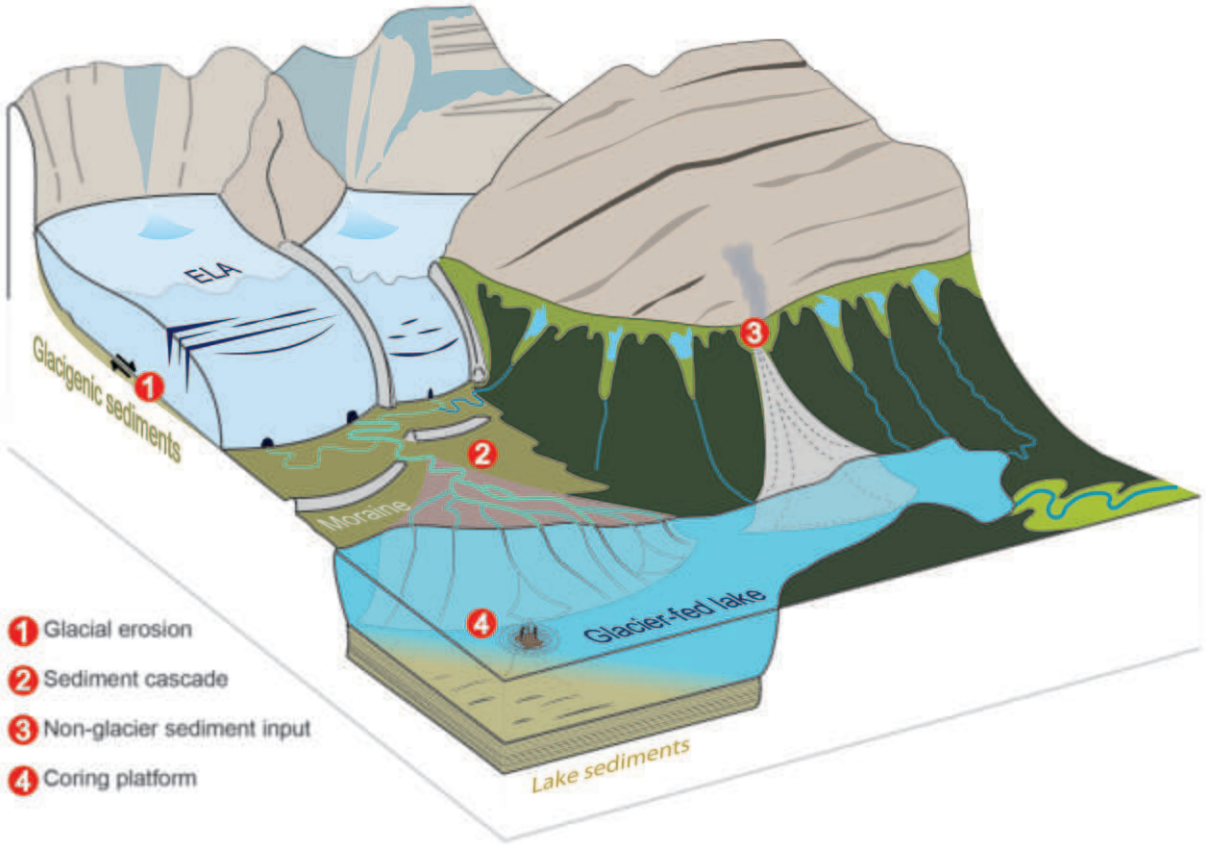


Fig. 5 Schematic view of a lake basin fed by a partially-glaciated catchment area (van der Bilt et al., 2016).

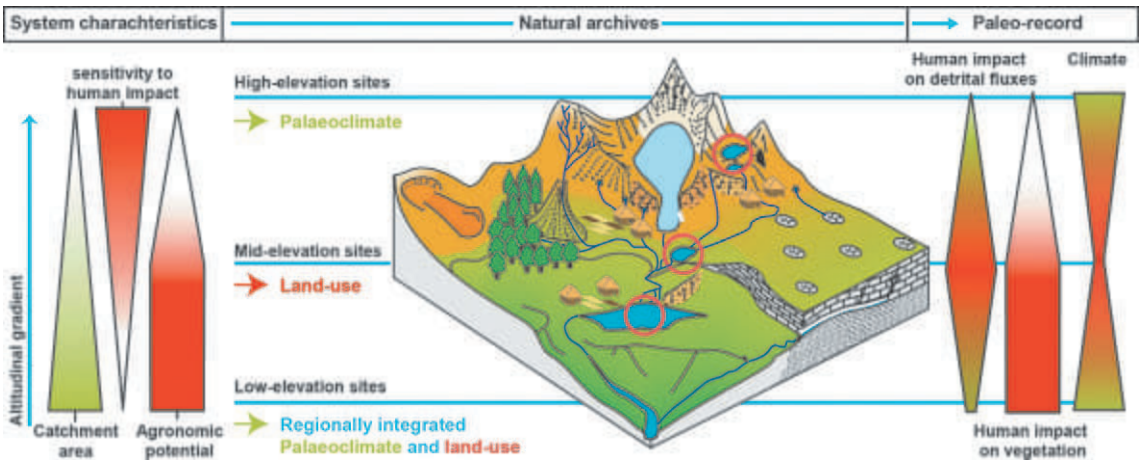


Fig. 6 Schematic representation of lake sediment sensitivity to climate and human forcing factors depending on the setting in a mountainous landscape (Arnaud et al., 2016). Arnaud F, Poulenard J, Giguet-Covex C, Wilhelm B, Révillon S, Jenny JP, Revel M, Enters D, Bajard M, Fouinat L, Doyen E, Simonneau A, Pignol C, Chapron E, Vannière B and Sabatier P (2016) Erosion under climate and human pressures: An alpine lake sediment perspective. *Quaternary Science Reviews* **152**: 1–18. https://doi.org/10.1016/j.quascirev.2016.09.018.

magnetic susceptibility is the easiest to measure, were also intensively used since the years 1980s' (Støren et al., 2016). Since years 2000s' the multiplication of XRF core scanners enabled the efficient acquisition of high resolution geochemical logs hence marking a major milestone in the development of new approaches (Wilhelm et al., 2012b). These new methods enable the detection of much thinner layers (Fig. 7) along with the measurement of their composition. It was then possible to reveal information about their source area, but also about their grainsize which reflects flood intensities (Wilhelm et al., 2012b). Even more recently, hyperspectral image of sediment cores surface was applied to the detection and characterization of unconsolidated sediment, hence opening new promising perspectives (Jacq et al., 2020).

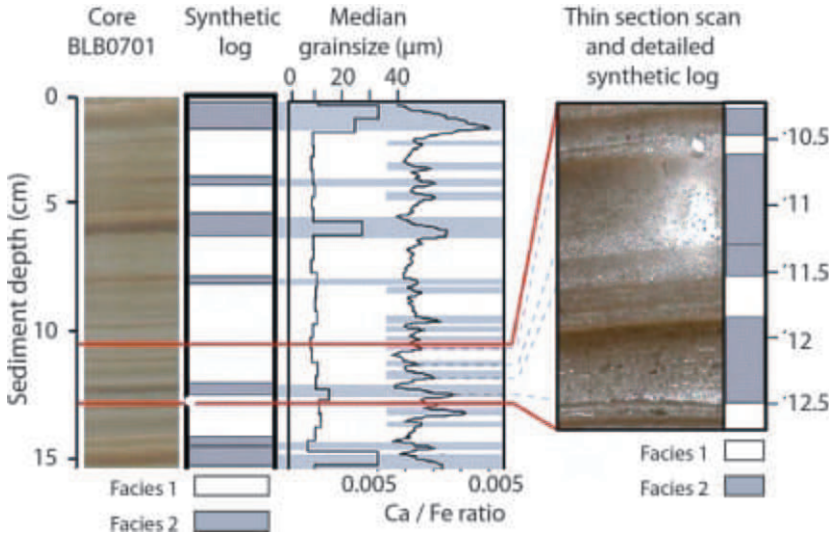


Fig. 7 Identification of flood-triggered deposits in a sediment core at various scales. From left to right: visual identification of interbedded coarser sediment layers, facies determination based on visual observation, grainsize increases (5 mm-step), XRF core scanner-based geochemical identification of coarser sediment layers that are enriched in calcium vs. iron and microscopic observation on embedded thin section showing complete flood-triggered sequences of layers: (i) basal coarsest grains, (ii) gradual upward decrease in grainsize and (iii) final "clay cap", here marked as a brown opaque layer. Modified after Wilhelm B, Arnaud F, Enters D, Allignol F, Legaz A, Magand O, Révillon S, Giguet-Covex C and Malet E (2012a) Does global warming favour the occurrence of extreme floods in European Alps? First evidences from a NW Alps proglacial lake sediment record. *Climatic Change* **113**: 563–581. https://doi.org/10.1007/s10584-011-0376-2.

Erosion processes are essential links between the occurrence of a flooding event and the transfer of this information toward the sediment accumulation. However, this link may be biased by a number of intermediate processes within the catchment area, the watershed or the lake itself. Sedimentologists thus developed a panel of techniques and concepts in order to verify the climatic relevance of hence reconstructed past floods chronicles. The two main potential misinterpretations are the false attribution of a given deposit to an actual flooding event and the false attribution of an apparent change in flood deposits recurrence rate to a change in climatic conditions.

How to relate an instantaneous deposit to a flooding event?

Attributing a given sediment layer (or sequence of layers) to a single flooding event that occurred maybe hundreds or thousands of years ago is a quite challenging task. In particular, one must remember that various processes may trigger the occurrence of instantaneous deposits. For instance, earthquakes induced deposits in lake sediment records which might be mistakenly interpreted as flood-triggered (Arnaud et al., 2002). In order to trustfully attribute an instantaneous deposit to a flooding event, it is important to study the sedimentology in detail. In particular, facies recognition is crucial as it permits to identify and characterize the different sedimentation patterns that are recurrent throughout a given sediment accumulation and thus to sort the huge amount of information stored in it. To do so, naked eyes are the primary tool, but they must be supported by quantitative information about grainsize, chemical and/or mineralogical composition and/or colorimetry. Among those parameters, the size distribution of particles is often a good indicator of the triggering mechanism.

Floods can generate turbid currents that flow on the bottom of the lake (Hsü, 1989; Lambert et al., 1984). According to the historical experiment of Hjulström (1935), in such a case, one given current velocity permits the deposition of one given particle size. This results, within a single flood-triggered deposit, in a succession of well-sorted layers of various particle sizes. Within the thickest sequences, it is possible to measure an increasing particle size from bottom to top at the base of the sequence that mirrors the increasing current velocity at the beginning of the flood event (Figs. 7 and 8). Then the deposited grainsize diminishes toward the top of the sequence as the velocity drops. In most cases, a clay cap then tops the summit of the sequence while the flood-triggered lake water turbidity settles over some days, weeks, or even months in the case of extreme floods within large and deep lakes. This whitish clayey top layer is hence often one the most convenient markers to identify a flood as a triggering mechanism. On the contrary, subaqueous slides generate matrix-supported flows which can be assimilated to subaqueous avalanches. Resulting deposits are made of a mixture of fine and coarse grains. The difference between those deposit types can be revealed by several grain-size parameters. The representation proposed by Passega in the 1960s' (Passega, 1964), i.e., a bi-plot of Q99 vs. Q50 is one them, which can be particularly useful when the event layers are thick enough to perform several grainsize measurement in them.

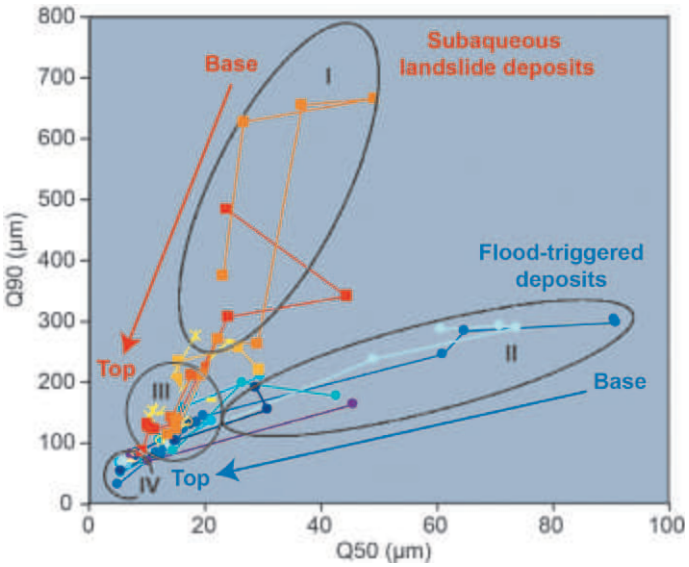


Fig. 8 Q50 vs. Q90 bi-plot, inspired from Passega (1964), from 12 subaqueous landslides deposits (in red and orange) and nine flood-triggered deposits (in blue) from Lake Anterne (Northern French Alps). Each same-color linked dots set corresponds to a single event deposit sampled every 5 mm from base to top. Note that all flood-triggered points are aligned along the same line (from sectors II, to III and IV) which is close to the 1:1 line. By comparison, samples from subaqueous landslide deposits are aligned from the high Q90 and low Q50 sector I to sector III and never reach sector IV (low Q90, low 50). See Arnaud et al. (2002) for further details.

In some cases, generally when deposits are particularly thin or, on the contrary particularly thick, sedimentological investigation are not sufficient to clearly determine the triggering mechanism of instantaneous deposits. The geometry of the deposit, at the lake basin scale, then brings essential information. Flood deposits will forcedly originate from the lake inlet and flow toward the lake bottom following the steepest slopes. On the contrary gravity reworking may originate from anywhere in the lake and will slide in mass toward the lake bottom. The geometry of a given deposit maybe determined using geophysical approaches, like reflection seismic, when it is thick enough (typically >20 cm). It may also be determined using an array of numerous cores which will have to be carefully correlated in order to determine in which of them the layer is present or not (Wilhelm et al., 2012a,b).

An increase in flood deposit frequency does not necessarily track an actual increase in flood frequency

Human land-use affected erosion processes as early as in the Neolithic period through deforestation, livestock tumbling and early cropping. Later on, deep ploughing, stream damming and soil artificialization further reinforced the human pressure on erosion fluxes. This resulted in more efficient runoff erosion, increasing both the frequency of recordable flood events and the amount of displaced sediment for a given flood intensity. In the geological record, this may result in an apparent increase in flood-layers frequency and thicknesses, independently of any climatic change. This point is still tricky for Holocene geologists which may only rely on comparison with independent markers, such as pollen, to infer the human origin of observed changes in flooding patterns. Few studies however went further by showing human-reinforced flood patterns resulted in a disruption in the grainsize-thickness relationship among flood-layers. In a human-disturbed catchment area the erodibility of soil is higher. As a consequence, a flood event of a given magnitude is able to transport more sediment, resulting in thicker deposits than it would have been without human soil disturbance (Giguet-Covex et al., 2011). However, the maximum transported grainsize is far less impacted as it depends on the river stream velocity (Hjulström, 1935) and thus on river discharge (Hsü, 1989). As a consequence, the observation of an increase in flood-layers thickness, without a marked rise in maximum grainsize is a good marker for human-triggered soil destabilization (Giguet-Covex et al., 2012).

Human disturbance of Earth Critical Zone dynamics

As stated above, human activities emerged all along the Holocene as one of the major triggering mechanisms of erosion patterns. Lake basins all around the globe witnessed this emergence which chronicle has been archived within their sediment. The effect of agro-pastoralism upon erosion was probably empirically known by the very first farmers. It was later well-known during Hellenistic period and stated for instance in Plato's dialogues *Critias* relating the dramatic loss of fertile soil due to bad land-use management. However, it has only been possible to document scientifically the history of Human-enhanced erosion in the last decades of the 20th century. Following the pioneer works by Franck Oldfield and John Dearing, notably in Papua New Guinea (Oldfield et al., 1980), lake basins appeared as particularly good candidate to record such an history. The rich information contained in lake

sediment further permits to acquire information about human land-use (pollen) as well as its effect both on land and within the lakes themselves from the same archive. Quantities of biotic and abiotic markers were then developed until recently when the development of organic geochemical markers (Dubois and Jacob, 2016) as well as lake sediment DNA (Giguet-Covex et al., 2019) was propagated, extending the range of investigation permitted by the study of lake sediment.

From erosion record to soil development history

At the difference of their geological substratum, soils are highly dynamic even at a human-life time-scale. Their current state results from a dynamic equilibrium between the weathering of underlying rocks and the erosion of the soil surface. In the absence of human forcing factors, the balance between those two processes tends to reach a steady state, hence maintaining a stable layer on which ecosystems may grow. Human activities might break this balance by soil surface destabilization. Studying past erosion fluxes permits to reconstruct the evolution of soils and downstream to identify periods of human-triggered soil disturbances. This can be done not only by recording the total amount of eroded material, but also by identifying its provenance source in the lake catchment area, as well as its weathering degree.

When the geology of the catchment area is diverse enough, the provenance source may be tracked using mineral geochemistry, or mineralogy. Isotopic indicators of rock ages are here particularly efficient. In several cases, major elements also proved to be quite good markers of provenance, however, they are also strongly affected by weathering processes and may hence not be used alone to track the sediment provenance.

Chemical weathering is the dominant process of soil formation. It results in the selective removal of the most mobile elements (e.g., potassium). More developed soils? Are hence depleted in such elements, when compared the bedrock from which they were formed. This degree of depletion can be assessed using a ratio of mobile over immobile (e.g., aluminium or titanium) elements. When applied to terrigenous lake sediment this may be used to track the degree of evolution of the soils that were eroded at a given time (Arnaud et al., 2012). This permitted to show that human soil disturbance results in apparent rejuvenation of soils evidenced by a relative enrichment in mobile elements in eroded material. Some isotopic markers, such are lithium, bore or uranium (Rothacker et al., 2018) are currently under development to track the weathering degree of eroded soils (Fig. 9).

Soils are basically made of organo-mineral complexes. Soil evolution is thus strongly linked to the evolution of organic matter. Just as for the mineral fraction, the study of the organic compounds of eroded material trapped in lake sediment brings a lot of information about soil evolution. Rather simple techniques, such the microscopic identification of organic matter types, may be completed by more sophisticated ones. Element concentration of carbon, hydrogen and oxygen in variously refractory and oxidizable organic matter fractions is extensively used in petroleum geology. It applies also perfectly to characterize the degree of maturity of organic matter in soils and downstream in lake sediment. Hence it has been shown that a human-triggered erosion event following a deforestation starts with a flux of fresh organic matter from the litter and while the erosion is eroding deeper and deeper horizons, the organic matter signal tends to be dominated by more and more refractory fractions. Inversely when human pressure weakens, or at least a new equilibrium is reached, the refractory organic matter is retained in the soil and the eroded organic matter then originates from soils of upper and fresher horizons. Using molecular organic geochemistry opens possibilities for even more detailed investigation of past soil dynamics. For instance, branched glycerol dialkyl glycerol tetraethers (brGDGTs) have recently been proved to be markers of soil pH, which is a key parameters of soil evolution, particularly in regard with organic matter dissolution and fluxes.

Tracking land-use changes

Because they are highly integrative archives, lake sediments bear information about catchment reactions but also about what caused these reactions. Pollen are of course the main and most anciently used marker of vegetation dynamics that may be acquired from lake sediment. They have long been the only way to get valuable information about human land-use, through the filter of vegetation changes. However, pollen fly in the air and are thus not strictly representative of a given catchment area. Over the last decade, a number of studies proved lake sediment DNA (sedDNA) to be a valuable complementary information source about vegetation changes (Capo et al., 2021). Sediment DNA data are not yet quantitative, but they differ from pollen information by a different taxonomic resolution and a drastically different taphonomic behavior. Indeed, taxonomic resolution of DNA results highly depends on DNA sequence libraries that are still under development. In the case of graminae and in general, non-tree species, sedDNA taxonomic resolution may be more precise than what is allowed by pollen. It has recently been understood that catchment-derived sedDNA is strongly linked to erosion processes. Indeed, most of terrestrial DNA arriving into lake sediment has been freshly eroded from soil where it was stored under the form of organo-mineral complexes, hence protected from bacterial degradation. As a consequence, terrestrial SedDNA signal tracks the dynamic of the lake catchment area only. This also implies that a certain amount of catchment erosion is necessary to properly transfer the environmental signal that is transported by SedDNA toward the lake bottom (Giguet-Covex et al., 2019).

One of the greatest advances that was made possible by SedDNA is to provide taxonom<–specific information about livestock (Giguet-Covex et al., 2014). The identification, alongside pollen, of coprophilous fungi had permitted to complete the vegetation data with an assessment of the livestock pressure upon a lake catchment area. However, this did not allow to identify which mammal species generated the feces that permitted the development of fungi (Etienne et al., 2012). With SedDNA this information is completed at a higher taxonomic level, permitting to attest the former presence of livestock as well as the relative composition of herds. Hence in a near future it will probably be possible to analyze the long-term effects of livestock farming upon the environment with a detail that had never been reached before.

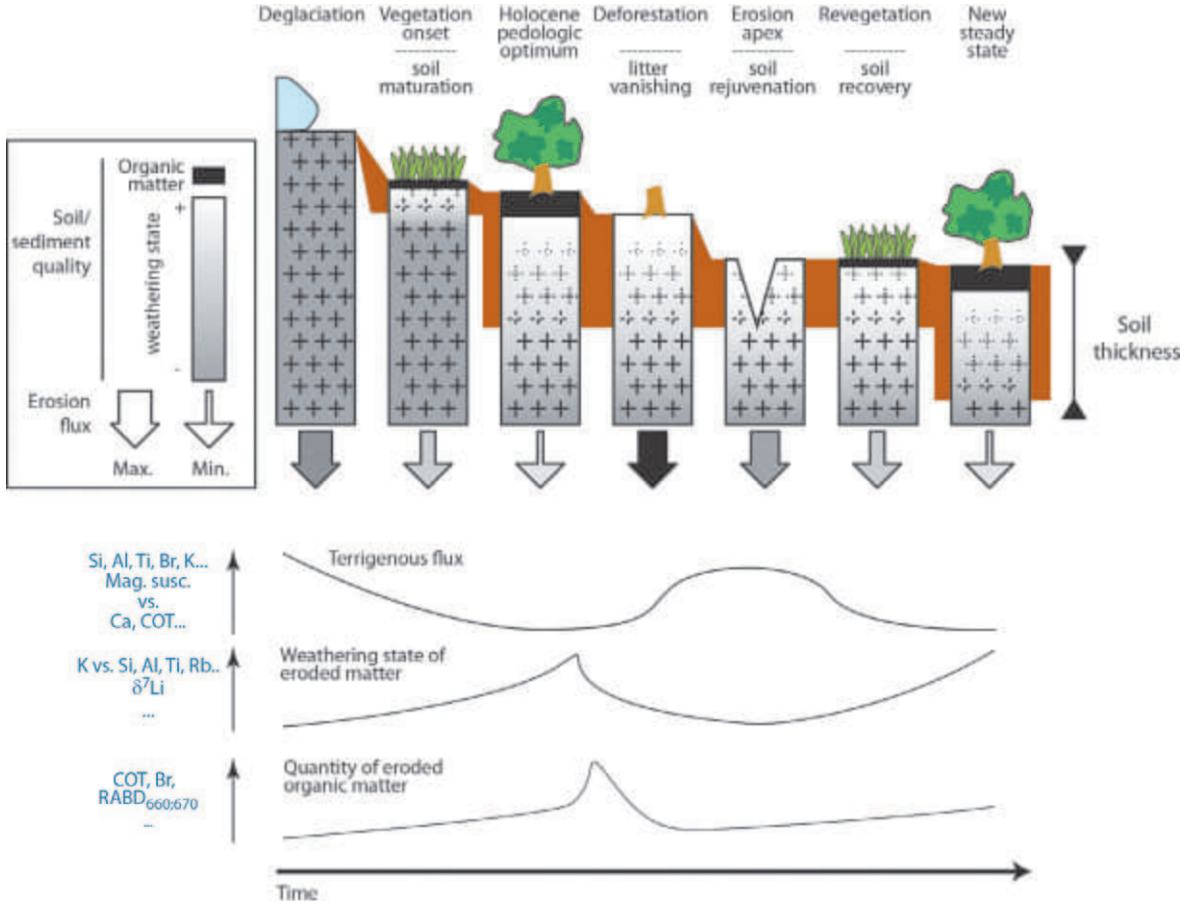


Fig. 9 Schematic representation of soil evolution following the last deglaciation (upper panel) and the corresponding theoretical record in lake sediment (curves in lower panel). Shades of grey and crosses materialize the weathering state, from bedrock (darker grey with solid crosses) to the most weathered terms (lighter grey with dotted crosses); black color represents the soil litter rich in organic matter. The soil itself is the layer overlying the non-weathered bedrock. Its thickness varies through time, as it is underlined by the brown surface. Arrows materialize the output of material due to erosion: their thickness represent the flux, whereas their color illustrates the nature of eroded material, as for soil state: shades of grey represent the degree of weathering and black represents the litter. Without human action, soil thickness tends to increase through time whereas the uppermost layer is more and more depleted in mobile elements and enriched in organic matter. Human-induced deforestation results in increasing erosion. First the litter is removed, inducing a peak organic matter transfer to the lake. If the process continues, the erosion reaches less and less depleted soil horizons, hence eliminating thousand years of soil formation within only some decades. Inspired from Bajard M, Poulenard J, Sabatier P, Develle A-L, Giguet-Covex C, Jacob J, Crouzet C, David F, Pignol C and Arnaud F (2017) Progressive and regressive soil evolution phases in the Anthropocene. *Catena* 150, 39–52. https://doi.org/10.1016/j.catena.2016.11.001.

Direct and indirect pollutions

Among human-triggered threats upon ECZ, the dispersion of extracted or man-made substances is particularly damaging for ecosystems' and downstream, humans' health. As local sediment sinks, lakes have the capacity to record the history of dispersion of those substances.

Metals were dispersed throughout the Earth environment as early as metallurgy was invented. Numerous reconstructions of metal contamination chronicles have been published over the last decades, providing a comprehensive scheme of world history of human-triggered metal dispersion. In lake sediment, the attribution of a metal peak to human activities is made difficult by the presence of the sediment matrix which can be metal-rich on its own. It is then necessary to assess the contribution of human-spread vs. naturally-present metals (see Dunnington et al., 2020 for a methodological review). The isotopic composition of some metals can be helpful to identify the origin of contamination. Lead is particularly interesting and has been extensively for such a purpose, as it is the most stable element of several radioactive decay chains. However, case studies using zinc, mercury, copper and silver, just to cite some, can be found in the literature. In case, studying both the temporal evolution of metal contamination and its potential sources permitted to better identify the causes of contamination, which is the primary stage for reducing human impact upon the environment.

Over the 20th century the chemical industry produced thousands of artificial compounds used for manufacturing processes or helping agriculture to face natural plagues. Most of them happened to be persistent in the environment, causing various threats upon ecosystems health. Those chemical species are often referred as persistent organic pollutants (POPs). They include among

others all kind of pesticides, fire delayers, solvents, fossil fuels etc. Reconstructing the concentration of those POPs in lake sediment series permits to better understand their contamination histories and pathways. It was hence possible to show that Polychlorinated biphenyl (PCBs), a fire delayer used in electric transformers until its production was progressively banned between 1978 (in the United States) and 2001 (worldwide) may move from a surface area, such as a lake or soil, toward another ECZ compartment by a succession of evaporations under warm conditions and condensations under cold conditions (Naffrechoux et al., 2015). Lake sediment-based POPs contamination history may also evidence combined effect of pollutants. It has hence been shown that the use of a powerful herbicide, the glyphosate since 1990s, was responsible in vineyards of a drastic rise in soil erosion (due to the destruction of herbs-associated rhizosphere that is an agent of soil stabilization) which downstream led to the remobilization of insecticide, such as DDT that had been applied for decades and then banned since 1973 but stored in agricultural soils (Sabatier et al., 2014). This last example shows the ECZ is a complex reactive layer in which all process may interfere together, leading to strong and potentially harmful retroactions (Fig. 10).

Even the mountains can be shaken: recording how inner-Earth dynamics affects the ECZ over human time-scale

The Earth Critical Zone is also the interface between inner and outer Earth dynamics. As such it may be affected by geodynamics, even at a human life time-scale when paroxysmal events, such as volcanic eruptions and earthquakes, occur. The strongest of those events may be particularly threatening for life beings and especially for human societies. Because they are rare at human time-scale, it is necessary to document them beyond the historical period in order to assess their returning period in a given place. In this aim, only geological records can be mobilized. Among them, lake sediment may record volcanic eruptions and earthquakes through three mechanisms: (i) atmospheric fall-out, (ii) in-lake reworking processes, (iii) indirect post-event terrigenous fluxes.

Atmospheric fall-out of volcanic products

This way of recording is quite obvious and generally simple to apply. In most cases volcanic deposits are clearly different from the continuous lake sedimentation and may be identified by visual observation or any mineralogical (including magnetics) or mineral geochemistry approaches. However, the documentation of past volcanic events can be disturbed by post-depositional reworking of the volcanic deposits. Such a reworking may occur within the lake itself, under the form of subaqueous slides, or within the catchment area where volcanic products may accumulate during the eruption and be more or less abruptly released in the following

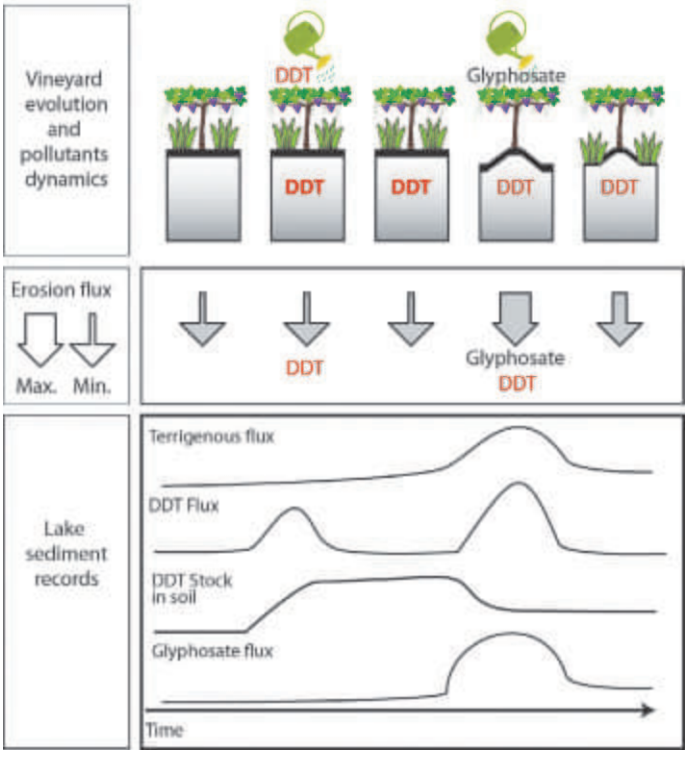


Fig. 10 Schematic representation of DDT spreading, incorporation in soil and Glyphosate-triggered released from a Vineyard (upper panel), the resultant impact in terms of erosion and pollutant fluxes (middle panel) and the corresponding theoretical record in sediment (lower panel). Inspired from Sabatier P, Poulenard J, Fanget B, Reyss JL, Develle AL, Wilhelm B, Ployon E, Pignol C, Naffrechoux E, Dorioz JM, Montuelle B and Arnaud F (2014) Long-term relationships among pesticide applications, mobility, and soil erosion in a vineyard watershed. *Proceedings of the National Academy of Sciences of the United States of America.* https://doi.org/10.1073/pnas.1411512111.

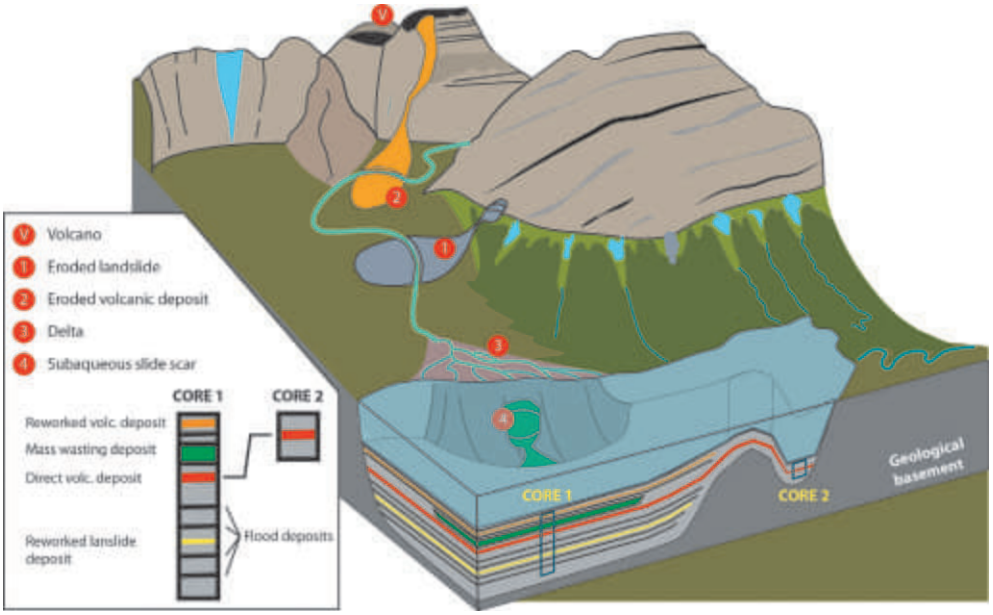


Fig. 11 Schematic representation of a lake sediment basin connected to a volcanic catchment-area submitted to regular earthquakes.

day to years through erosional processes. A detailed sedimentological study of the whole lake basin is then required in order to demonstrate that the volcanic-triggered layers came purely from the atmosphere and were thus strictly contemporaneous of an eruption (Fig. 11).

Earthquake-triggered in-lake reworking processes

Earthquake-triggered mass-wasting deposits are very common in lakes, making them natural seismographs (Strasser et al., 2013). They are favored by a high terrigenous sedimentation flux and the presence of a delta at the tributary inlet. Indeed, higher sedimentation rates result in less stable delta slopes, hence favoring the triggering of subaqueous slides (Wilhelm et al., 2016). Several triggering mechanisms may be invoked for those slides, but earthquakes are the more common ones. The main difficulty here is to distinguish those mass wasting deposits from flood triggered deposits. There is no universal recipe to do such and a detailed sedimentological study is here also required. The texture of the deposit is a meaningful information as mass wasting deposits are less well-sorted than flood deposits (Arnaud et al., 2002). The Earthquake may also trigger internal lake motions that can be large enough to resuspend sediment at the whole basin scale and ultimately lead to a typical homogenous sediment deposition layer called "homogenite" (Chapron et al., 1999). When deposits are thick enough, the geophysical imagery of the lake sediment pile brings usually precious information about the deposits shape and downstream, about their triggering mechanisms (van Rensbergen et al., 1999).

Indirect post-event terrigenous fluxes

When a powerful earthquake hit a mountainous region, it often generates massive landslides (Keefer, 2002). Those landslides result in river dams that are more or less abruptly eroded (Wang et al., 2015). When such a dam breaks, the resulting outburst may be recorded in lakes under the form of a specific layer due the sudden arrival of terrigenous sediment (Zhang et al., 2019). It may also occur that the excess in eroded material in the river course gets eroded slowly, hence increasing the sedimentation rate over several years.

One must finally notice that any combination of processes may occur (Zhang et al., 2019). For instance, an earthquake may generate a rock slide, triggering a snow avalanche, itself triggering a destabilization of a lake delta as well as a tsunami-like wave that will erode the shores of the lake, far from the delta. The sedimentologist studying lake basin must be aware of those potential mechanisms. It is necessary to propose falsifiable hypothesis in order to lead the required measurement which will finally lead to a careful interpretation of the lake basin sedimentological behavior.

Conclusion/synthesis

We aimed in this chapter at providing a non-exhaustive, but yet large overview of the strong potential of lake sediment studies when it comes to reveal the history of in-land social-ecological systems and interactions within the ECZ. Lake sediment may indeed be seen as the Swiss knife of natural archives as they are submitted to a quasi-infinite number of forcing factors, acting both outside and

within the lake itself. This diversity of forcing factors has long been seen as a weakness because of the complexity of the resulting archives. However, no other natural archive has seen more developments of new investigation techniques than lakes over the last decades. Scientists interested in the evolution of any aspect, biotic or biotic, natural and human-triggered, over recent or pluri-millenial periods, etc. of the ECZ may hence rely on a vast scientific literature and an extended methodological toolbox in order to find in lake sediments the stored information they are looking for.

Remaining challenges

- Modelling the processes from catchment area to sediment deposition.
- Developing spatial approaches based on multiple cores.
- Developing an integrated approach of main triggering mechanisms that affect the critical zone dynamics (climate, humans, geodynamics, ecological responses).

See Also: Fundamental concepts and theories: Inland Waters and Limnology; Lakes as Ecosystems; Human pressures and management of Inland Waters: Measuring Impact, Overview and Reference Conditions; Structures and functions of Inland Waters - Lakes: Currents in Well-Mixed Layers; Structures and functions of Inland Waters - Wetlands: Prehistoric Wetlands; The Landscape Role of River Wetlands

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Saline Lakes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Athallassic Not related to the sea, no connection to the sea during recent geological times.
Brine Highly concentrated saline solution.
Chemocline Interface that separates the upper water layer of standing water bodies from a deeper layer containing higher concentrations of dissolved solids.
Endorheic basin (internal drainage basin) Landlocked with no outflow.
Halocline A subtype of chemocline caused by a strong, vertical salinity gradient.
Heliothermy Heating from direct solar radiation.
Meromictic lake The water body does not fully mix during overturn.
Mixolimnion Upper water layer of meromictic lakes, which circulates during overturn.
Monimolimnion Deep water layer of meromictic lakes not involved in circulation during overturn.
Open lake (also called flow-through or exorheic lake) The lake drains into another water body; the water ultimately flows into the sea.
Polymictic lake The water body mixes frequently during the year.
Pycnocline Interface where the density gradient is greatest.
Saline lake Athallassic water body with salinity >3‰.
Salinity Amount of salt dissolved in water.
Terminal lake (also called closed or endorheic lake) Waters do not drain into the ocean and are mainly reduced by evaporation.

Introduction: What are saline lakes

Lakes are large standing water bodies occupying continental basins. Most lakes are of tectonic origin, amongst these also the largest saline lake of the world, the Caspian Sea. Based on Hammer's (1986) categorization, saline lakes have a salinity ≥3‰, reaching up to 350‰ in saturated brines (the salinity of seawater is around 35‰). Freshwater lakes show a salinity <0.5‰. The range between 0.5 and 3.0‰, referred to as subsaline, is a transitional zone in which both freshwater organisms and halophiles can co-exist (Fig. 1).

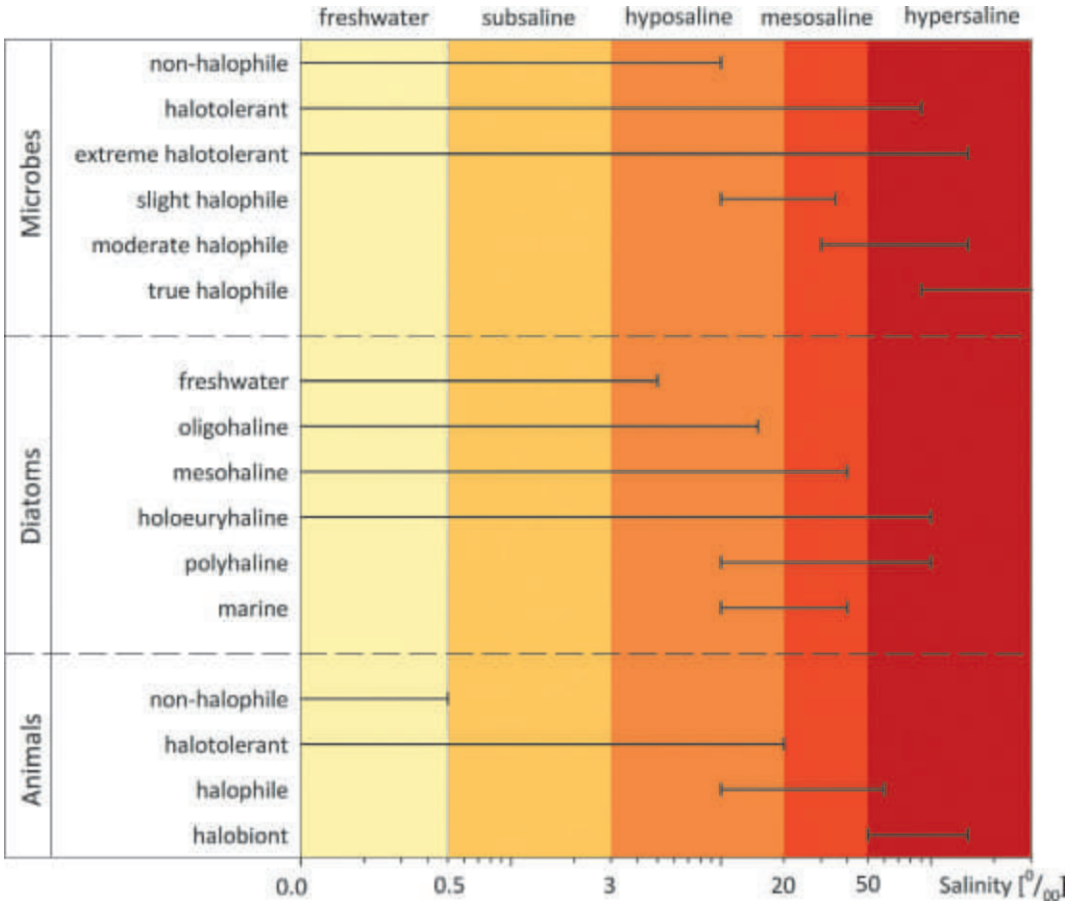

Fig. 1 Hammer's (1986) categorization of saline lakes versus classification of organisms inhabiting saline lakes. Microbes—combined data (Oren, 2006; Mesbah and Wiegel, 2011; Banciu and Sorokin, 2013); diatoms (Carpelan, 1978); Animals (Williams, 1978). Conversion factor 1 M NaCl to salinity = 58.5‰.

In contrast to thalassic water bodies such as lagoons, which are connected to the sea, athallassic lakes are located in hydrologically closed basins. Many saline lakes are permanent, but some are also ephemeral water bodies termed playa lakes or salt pans (Renaut and Gierlowski-Kordesch, 2010).

How is salt content measured?

Today, the salt content of the oceans is provided in "practical salinity units" (PSU). PSU measurements are based on conductivity, which is an unspecific measure of the total ion content of solutions. The principle behind the measurement is a drop in voltage caused by the resistance of the water (conductivity = resistance^{-1}). Because conductivity is affected by temperature, it is reported as specific conductivity at 25 °C. The conductivity unit μS cm^{-1} is mainly used in waters with low ion content, whereas salinity is a common measure for saline waters. Salinity is a unitless parameter because it was originally defined as a measure of the mass of dissolved salts in a given mass of solution. In limnology, salinity is usually reported in ‰ or parts per thousand (ppt), I therefore have retained ‰ for better readability. Early measurements until the 19th century were performed gravimetrically, but this method has several disadvantages including additional dissolved substances other than salt and the loss of volatile compounds. Today, conductivity meters are the standard instruments because they are easy to handle, robust and sensitive. Another unit in use is total dissolved solids (TDS), which is expressed as milligrams dissolved solids (particle size <2 μm) per liter water. TDS is sometimes also reported as parts per million (ppm). A rule of thumb for converting the parameters is salinity [‰] = 0.7 × conductivity [mS cm^{-1}], and TDS [ppm] = salinity [‰] × 1000.

Genesis and geochemistry

The genesis and persistence of salt lakes depend on following conditions: (1) endorheic basins lacking significant water loss by (sub)surface discharge; (2) balance of inflow (with only low precipitation) and evaporation (with only low seepage) is maintained

over longer periods; (3) an inflow sufficient to sustain the lake. Favorable regions for the formation of saline lakes are arid basins in the rain shadow of high mountains acting as a precipitation trap. As water loss is restricted to evaporation, solutes are retained in these lakes, which become increasingly saline over time. Because a significant outflow is lacking, such water bodies are also termed closed lakes or terminal lakes. In contrast, open lakes are located in open drainage basins with a balanced in- and outflow, which also results in a low concentration of solutes.

Salt lakes not only cover a wide salinity range (Fig. 2), but also show a high variability in brine composition. Generally, three main categories are recognized, namely carbonate (HCO^3/CO_3^{2-}), sulfate (SO_4^{2-}) and chloride (Cl^-) brines (Fig. 2), but in many cases a combination exists. Eugster and Hardie (1978) defined eight major brines types, which reflect both the type of bedrock and the chemical reactions of brines.

The geochemistry of a saline lake is defined by an allogenic and an autogenic step. The first step is chemical weathering of bedrock and soil. Meteoric water becomes enriched in solutes, which are defined by the lithology of the catchment area. The second step is autogenic and caused mainly by evaporation at the lake surface, followed by mineral precipitation (sediments are termed evaporites) due to oversaturation of solutes. The remaining solutes characterize the chemical conditions of the saline lake. This so-called brine evolution was first described in a flow chart by Eugster and Hardie (1978) and later revised by Deocampo and Jones (2014) (Fig. 3). The principle behind brine evolution is the different solubility of evaporites. Evaporites with low solubility such as calcite or gypsum precipitate first. This makes brines with an elevated Ca^{2+} content an exception. Other evaporites such as trona ($Na_3(HCO_3)(CO_3)\cdot 2H_2O$) or halite (NaCl) show very high solubility products. Accordingly, most saline lakes with an elevated salinity have only Na^+ as the dominant cation (Fig. 4; in few cases Mg^{2+} also plays a significant role). Regarding the anion composition, saline lakes are quite diverse.

The pH depends on the brine composition and is mostly neutral to slightly basic (mainly SO_4^{2-} and Cl^- solutes). Some lakes are however highly acidic with pH < 3 (usually a mixture of SO_4^{2-}/Cl^- with very low buffer capacity (e.g., lakes of SW-Australia) (Mernagh et al., 2016), others quite alkaline with pH > 9.5. The elevated pH is usually combined with a very high buffer capacity due to a combination of Na^+ and HCO^3/CO_3^{2-}. Such lakes are called soda (or alkaline-saline) lakes.

Physical properties

Terminal lakes are prone to water level changes (Fig. 5; Odada et al., 2006), which are often linked to large variations in lake area especially in plain basins (Fig. 6). Lake morphology, latitude, altitude, and wind exposition are key parameters for defining the mixing regime. Moreover, optical properties also influence the mixing pattern, with low transparency increasing the stability of thermal stratification. The mixing regime can also change because of climate change. Woolway and Merchant (2019) assume less frequent mixing in the future in response to global warming, but this holds true only for open lakes. In contrast, terminal lakes will respond individually depending on the local climate.

Mixing patterns

All mixing types are present, with polymixis and meromixis being frequently observed (Fig. 7).

Polymixis is quite common, because many lakes are shallow and wind-exposed. A prime example is Lake Nakuru (Kenya), where thermal stratification develops during daytime, followed by full circulation at night due to wind-induced mixing and convection

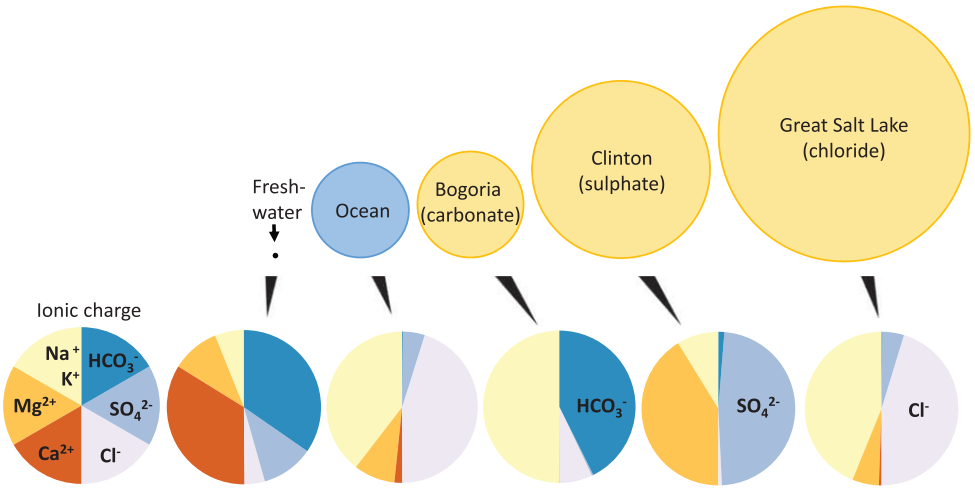

Fig. 2 Salinity ranges of freshwater, oceans and saline lakes classified according to their chemical composition. The circle areas correspond to salinity levels on a relative basis and to ion composition (meq L^{-1}).

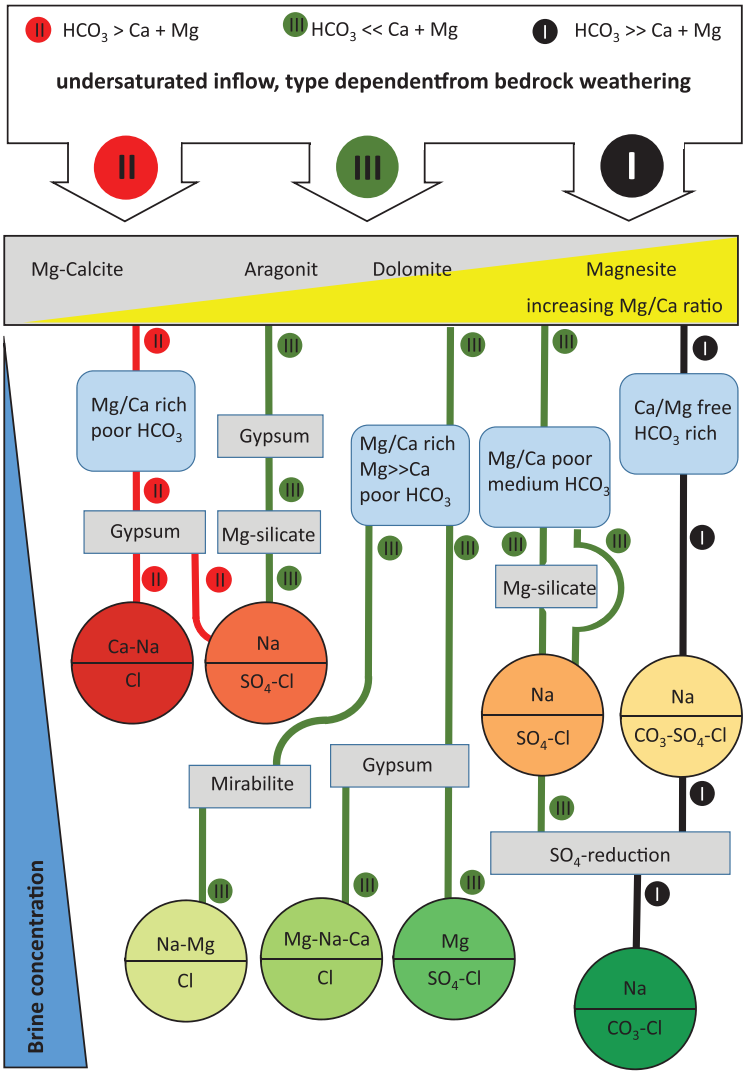

Fig. 3 Brine evolution diagram. From the lithology of the catchment area and weathering of the bedrock, three types of inflow chemistry can be distinguished, which map the general route for brine composition. Water evaporation is followed by evaporites precipitation due to oversaturation of solutes. The remaining solutes characterize the brine composition of the lake. Modified from Eugster, HP and Hardie LA (1978). Saline Lakes. In Lerman A (ed.) *Lakes: Chemistry, Geology, Physics*, pp. 237–293. New York, NY: Springer New York. 10.1007/978-1-4757-1152-3_8, and Renaut RW and Gierlowski-Kordesch EH (2010). *Lakes*. In James NP and Dalrymple RW (eds.) *Facies Models*. pp. 541–575. Geological Association of Canada.

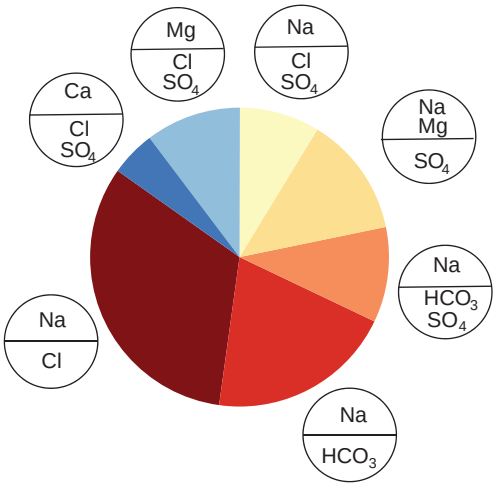

Fig. 4 Saline lakes of the world show a high variability in brine composition. Ions are considered as major ions, if they contribute more than 30% based on mmol L^{-1} (unpublished data combined with Hammer, 1986, $n = 184$).

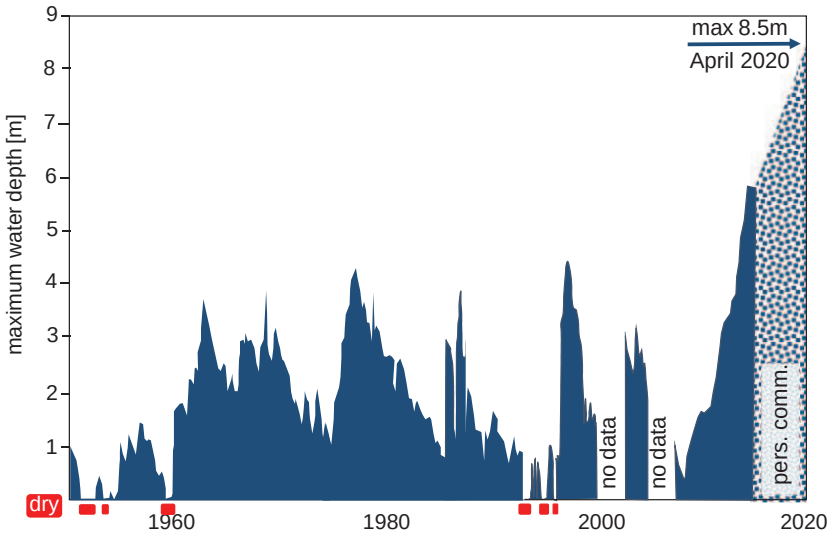

Fig. 5 Variability of water levels of Lake Nakuru (Kenya). Red bars indicate times of desiccation. Data from Odada EO, Raini J and Nedetei R (2006) *Lake Nakuru [Online]*. LakeNet—World Lake Basin Management Initiative. Available: http://www.worldlakes.org/uploads/18_Lake_Nakuru_27February2006.pdf (Accessed 30th September2015); Vareschi E (1987) *Saline Lake Ecosystems*. In Schulze E-D and Zwölfer H (eds.) *Potentials and Limitations of Ecosystem Analysis*, pp. 347–364. Berlin Heidelberg: Springer. 10.1007/978-3-642-71630-0_17, and own observations.

from surface cooling (MacIntyre and Melack, 1995). Such a diurnal pattern causes oxygen depletion in near-bottom zones, especially in hypertrophic systems with high respiration, which in turn facilitates phosphorus release from the sediments.

Meromixis is due to big differences in density of the mixolimnion and the monimolimnion (Fig. 7). The chemocline of saline systems is also referred to as a pycnocline or halocline. In many cases, the chemocline shows increased turbidity because particles are caught in this density gradient. The monimolimnion is separated over long periods from the atmosphere, making it anoxic and a sink for dissolved matter in its reduced form; it becomes further enriched with solutes and gases such as methane. Meromixis can be traced back to ectogenic (outside the system) and endogenic processes (within the system). With regard to salinity gradients, ectogenic meromixis is caused either by surface or subsurface inflow of freshwater into saline lakes or by saltwater inflow into freshwater lakes. Endogenic meromixis is induced by salt exclusion during surface ice formation. The salinity gradients between the monimolimnion and mixolimnion can be considerable. In Lake Bonney (Antarctica) for instance, the surface layer is of freshwater while near-bottom zones have a salinity >100‰ (Torii, 1975). The Vestfold Hills is an ice-free area in Antarctica with many meromictic lakes. All these lakes show increased temperatures with depth due to heliothermy (Fig. 7), but the vertical density gradient is maintained by the strong vertical salinity gradients, leading to permanent stratification lasting up to decades (Gibson, 1999). The lakes are covered with ice for 8–11 months, with ice thickness being inversely related to salinity at the surface layer. The monimolimnion of permanently ice-covered Lake Vanda (Antarctica) is the remnant of a former saline lake. The freshwater layer (with regular mixing) reaches down to around 55 m. A deep-layer chlorophyll maximum is located at the depth of the chemocline. Below the chemocline, salinity increases to >120‰, which stabilizes the water body despite an inverted temperature gradient between 0 °C at the surface and >20 °C in near-bottom zones (Fig. 7) (Schutte et al., 2020). Large saline lakes such as the Caspian Sea (Western Asia) and Lake Van (Turkey) are also meromictic; their stability of the water column is highly influenced by water level and the strength of the winter.

The mixing regime may change within short periods, e.g., due to human impact. One example is the Great Salt Lake (GSL), which was well mixed until the late 1950s, when the lake was subdivided into two basins by a railway causeway construction. Since this separation, only the southern basin is fed by freshwater inflows, which led to a steep increase in salinity from South toward North (Baxter and Zalar, 2019; Null and Wurtsbaugh, 2020). The northern arm is now fed via surface water from the southern arm (salinity about 80–170‰), whereby the solute further concentrates to saturation (270‰). The saturated brine sinks down to near-bottom zone, where it flows back to the deep layer of the southern arm, which ultimately created a meromictic water body. The Dead Sea is an example for a reverse shift from mero- to holomictic conditions. Before 1979, the lake was meromictic with a dense monimolimnion and a more diluted mixolimnion due to regular freshwater recharge. Today, because of reduced inflow (the lake level falls by about 1 m $year^{-1}$), the lake is warm monomictic with active halite precipitation of about 0.1 m $year^{-1}$ (Lensky et al., 2005).

Optical properties

Turbidity of saline waters is often increased compared to their freshwater counterparts because of particle resuspension, and due to extremely high numbers of microorganisms. Increased turbidity may also reflect the precipitation of oversaturated brines. Lake Van

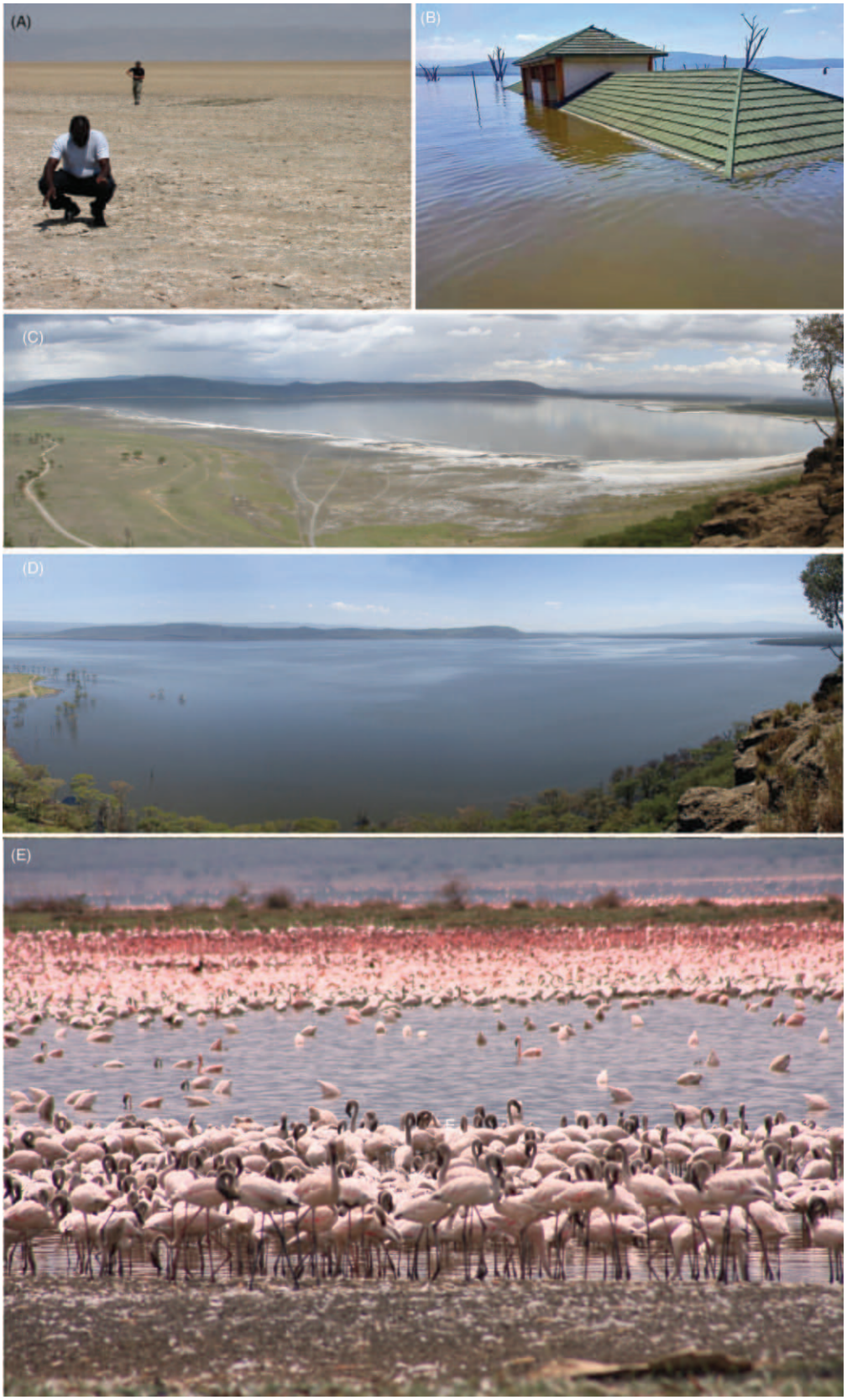

Fig. 6 Impression of alkaline saline lakes. (A) dried ephemeral Lake Eyasi (Tanzania; 2010). (B) Increased lake levels of Nakuru flooding buildings at the entrance of the Nakuru National Park in 2020 (Kenya, photo S. Oduor). (C) Amplifier Lake Nakuru in 2009 and (D) in 2013 from exactly the same viewpoint. (E) Huge flocks of flamingos at Lake Bogoria 2013 (Kenya).

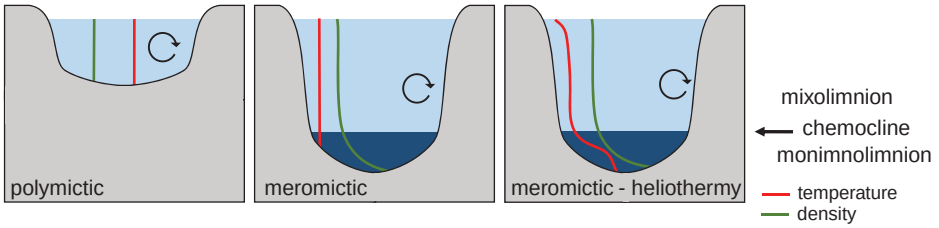

Fig. 7 Saline lakes are often polymictic due to their shallowness and wind exposure. Another common type is meromixis, because salt water has a higher density compared to freshwater. In very cold regions, an inverted temperature gradient might persist over longer periods.

is characterized by regular aragonite precipitation, a feature visible even on satellite images. This so-called "whitings" are the result of additional Ca^{2+} input from surface waters to the solute, which is already supersaturated with $CaCO_3$. Dissolved organic matter (DOM) also deserves mention. Saline lakes as terminal water bodies accumulate recalcitrant DOM, which may reach concentrations of >300 mg L^{-1}. During an extreme drought, Jirsa et al. (2013) reported DOC values up to 1 g L^{-1} in Lake Nakuru (Kenya). The DOM pool of meromictic Lake Sonachi (Kenya) is fed and modified by autochthonous microbial production, decomposition and photodegradation, with the chemocline acting as a hotspot of DOM transformations (Butturini et al., 2020).

Worldwide distribution

Lake water storage is about 0.013% of the global water, with large lakes >500 km^2 storing 92% of the water volume. The global volume of saline lakes almost approaches that of freshwater lakes, with the Caspian Sea alone contributing 93% to inland saline waters (Table 1). Saline lakes are found worldwide in semi-arid land-locked regions. About 10% of the global land area are endorheic basins (Fig. 8).

Eurasia

Eight out of the 10 largest saline lakes are located in Eurasia (Table 1). The Caspian Sea, and the dramatically shrunk Aral Sea, both located in the Aralo-Caspian Depression, are remnants of the Paratethys and dominated by Na^+ and $Cl^-/SO_4{}^{-2}$. Many small lakes, amongst them also soda lakes, are located in the Kulunda Steppe. Large saline lakes also exist in China within the endorheic Qinghai-Tibet Plateau, with Qinghai Hu being the 7th largest in the world. The Iranian Plateau hosts Lake Urmia, which was formerly listed amongst the 10 largest saline lakes in the world. Its volume, however, dropped considerably from around 35 km^3 in the mid-1990s to 2 km^3 in 2018 (Schulz et al., 2020), mainly driven by climatic conditions. The Middle East also hosts saline lakes, amongst them Lake Van and the Dead Sea.

The Dead Sea in the Syro-African Depression is the lowest place on Earth, currently 430 m below sea level. The ongoing drop in water level is associated with a change in the chemical composition of the brine and has led to a change in the mixing regime. The lake is hypersaline with around 350‰ and contrary to most other saline lakes has a very special brine with $CaCl_2$ as the dominant solute. This can be explained by the lake's history: after a lagoon was disconnected from the sea and ultimately became landlocked, the brine composition changed due to evaporation of seawater, hydrothermal springs, freshwater recharge and evaporite precipitation.

Table 1 Largest saline lakes of the world and the respective brine type. Compiled from various sources.

Lake	*Continent*	*Volume (km^3)*	*Brine type*
Caspian Sea	Asia	79,000	Na-SO_4-Cl
Issyk Kul	Asia	1730	Na-SO_4-Cl
Van	Asia	206	Na-CO_3-Cl
Turkana	Africa	204	Na- CO_3
Dead Sea	Asia	136	Na-Mg-Ca-Cl
Balkash	Asia	118	Na-SO_4-CO_3
Qinghai Hu	Asia	85	Na-SO_4-Cl
Karakul	Asia	78	Mg-$NaSO_4$-Cl
Aral Sea	Asia	27	Na-Cl-SO_4
Pyramid	North America	26	Na-CO_3-SO_4-Cl
Mar Chiquita	South America	25	Na-SO_4-Cl
Eyre	Australia	23	Na- Cl
Great Salt Lake	North America	19	Na-Mg-Cl
Salton	North America	7	Na-SO_4-Cl
Mono	North America	4	Na- CO_3-SO_4-Cl

Fig. 8 Global distribution of endorheic basins (red area).

In Europe, continental saline lakes and salt pans are common in Spain (Comin and Alonso, 1988), with some are being located in the Pannonian Basin (Boros and Kolpakova, 2018).

Africa

Soda lakes are common in the Eastern branch of the East African Rift (Schagerl, 2016). The characteristic alkaline brines reflect chemical weathering of volcanic bedrock, dominated by silicate hydrolysis (Deocampo and Jones, 2014). Lake Natron is the world's most important breeding site of Lesser Flamingos (*Phoeniconaias minor*) being a flagship species of these lakes. A special case is Lake Turkana (Kenya/Ethiopia), which had a salinity of about 2.5‰ in the 1980s (Källquist et al., 1988). Although the lake is threatened by the construction of hydropower dams accompanied by receding water levels, no current data are available. Even recent reviews (Ojwang et al., 2016) refer to the above values, which date back 30 years. Lack of lake monitoring is symptomatic for most saline lakes, especially those in developing countries.

Southern Africa also contains many saline water bodies. Most of them are ephemeral hypo- to mesosaline salt pans, and all of them are understudied. Seaman et al. (1991) provided a detailed overview of their location and chemical composition(mainly Na^+, Cl^-). Saline lakes are also located in the Sahara and in Egypt.

North America

In the rain shadow of the Pacific Coastal Mountain Range, the North Western Region and the Great Basin contain many salt lakes of different chemistry. The Great Basin contains the largest saline lake of North America, the Great Salt Lake (GSL), but also Mono Lake and the artificial Salton Sea, which are amongst the best studied saline lakes worldwide. The current lake was formed about 13,000 years ago, is the remnant of the paleolake Lake Bonneville (see "Mixing patterns" section).

The Great Plains harbors four additional endorheic basins, extending from Saskatchewan to New Mexico. The Prairie Pothole Region in the North is one of the largest inland wetland systems and a critical habitat for migratory waterfowl. The large number of lakes, many of them saline, are highly diverse biogeochemically, with Mg^{2+}/Na^+ and SO_4^{-2} being the most prominent brines. Since the mid-1990s, this region has received more precipitation, which resulted in an increased number of permanent water bodies and the dilution of saline lakes. Other endorheic basins of the Great Plains are the Mid-Continental and South Western Region, and the Chihuahuan Regions. Mexico also has some saline lakes, but they are not well studied (Alcocer and Hammer, 1998). A few lakes are also historical sites: the capital of the Aztec Empire, Tenochtitlan (today Mexico city), was built on islands of the ancient Lake Texcoco. Today, only remnants of the water body remain. The Aztecs were also known to have consumed the alkaliphilic cyanobacterium *Limnospira* (formerly *Spirulina, Arthrospira*) in pre-Hispanic times. The first outdoor cultivation facility for *Limnospira* was installed in the solar evaporator El Caracol in the late 1960, initially for Na_2CO_3 and $NaHCO_3$ extraction, but production ceased in the early 1990s.

South America

Saline lakes are mainly found in Altiplano and the Pampas. The Altiplano is a cold, high-altitude desert with some ephemeral water bodies and a few lakes. The terminal Lake Poopó is the remnant of the paleolake Lake Tauca and fed by the major outflow river of freshwater Lake Titicaca. In the past decades, Lake Poopó greatly suffered from water abstraction, mining and cropping practices. Besides Lake Poopó, Lake Tauca covered two other basins, which are nowadays mostly dry and listed amongst the largest playas worldwide: Salar de Coipasa and Salar de Uyuni, the latter considered to be the largest lithium brine resource in the world.

The Pampas harbors the 2nd-largest lake of South America after Lake Titicaca, namely Mar Chiquita (Table 1). The large water level fluctuations are correlated with wide salinity ranges between 25‰ and 360‰ (Bucher, 2019). Major eolian erosion and salt transport were observed in this lake, especially in periods of receding water level. The Salinas Grandes Basin with an area of 4700 km^2 and many ephemeral water bodies is also located in this region.

Australia

Six regions (including one in Tasmania) with mainly ephemeral lakes are distinguished. Mernagh et al. (2016) provide a review of Australian salt lakes and their mineral systems, with a special focus on mineral exploitation. Na^+ and Cl^- brines—reflecting their oceanic origin—usually dominate these lakes, but there are a few exceptions. The largest region is in the Australian desert with playa Lake Eyre. The endorheic basin of South-Western Australia contains many small saline lakes, some of them highly acidic, others saline-alkaline (Bowen and Benison, 2009).

Western Victoria also contains interesting salt lakes: Lake Corangamite is the largest permanent salt lake in Australia. The playa Lake Tyrrell is a depression of about 150 km^2, which is covered by water during winter. Due to chemical processes percolating in the aquifer in winter (mainly ferrolysis and pyrite oxidation), the water becomes acidic (Long et al., 2009). Other lakes in this region differ in chemistry due to weathering of volcanic rock, yielding high loadings of HCO_3^-/CO_3^{2-} and therefore being highly alkaline.

Antarctica

A few areas located mostly along the east and south coast remain free of snow and ice year-round. Permanent lakes are located in these so-called "oases," some of them saline (Burton, 1981). Saline water bodies are known from the Soya coast, the Vestfold Hills and the dry valleys of Southern Victoria Land (see "Mixing patterns" section). Stable isotopes analyses revealed that seawater (either via direct connection or windborne) is the origin of the brines in most of these water bodies (Matsubaya et al., 1979). A chain of three lakes is present in the Taylor Valley, with Lake Bonney and Lake Fryxell being saline. Recently, an airborne transient electromagnetic sensor survey indicated that liquid brines below the glaciers drain into these lakes (Mikucki et al., 2015), most probably originating from ancient seawater and weathering processes.

Amplifier lakes

Saline terminal lakes are especially prone to climate change because a balance between water supply and evaporation is mandatory for their existence. Amplifier lakes respond rapidly to moderate climate shifts: prolonged periods of rainfall will result in rising water levels, until a spillway is reached. If evaporation rates over longer periods exceed water supply, they will ultimately dry out. Olaka et al. (2010) demonstrated that especially alkaline-saline lakes with a high surface to volume ratio respond strongly to regional climatic shifts. Examples include Lake Abbe and Lake Nakuru in East Africa (Figs. 7 and 8) (Trauth et al., 2010). They are climate sentinels that react with short delay to environmental changes, analogous to glaciers. Lake levels of amplifier lakes are considered to record current climatic conditions, but they can also provide a basis for paleoclimatic reconstructions (De Cort et al., 2013), including those related to human evolution (Junginger and Trauth, 2013).

Organisms

Biology and physiological adaptations

Compared to other aquatic systems, saline lakes provide unique conditions that force organisms living there to develop specific adaptations. The considerations here include not only increased salinity as the fundamental stressor, but also other factors derived from an increased salt content. Depending on the brine composition, highly alkaline or acidic conditions might prevail, the density of the surrounding water might be increased and in cold regions the water temperature may sometimes be well below 0 °C. Salt lakes are classified based on salinity levels, but classification systems also have been developed based on preference of organisms for certain salt levels (Fig. 1). According to Williams (1978), halobiontic animals ("salt living") inhabit water bodies >50‰ salinity, halophilic species ("salt loving") show a preferred occurrence between 10‰ and 60‰, and halotolerant organisms prefer freshwater but tolerate salinities up to 20‰. Non-halophilic taxa are true freshwater species, which are found only below 0.5‰. Other classification systems have been developed based on other organism groups, e.g., metazoans, diatoms and microbes.

Independently of their phylogeny, organisms have developed three specific strategies to cope with extreme conditions. Avoiders escape unfavorable living conditions. Conformers adjust their metabolic processes to the respective conditions without any internal regulatory mechanisms; their internal conditions resemble those of the surrounding water. Regulators maintain the internal environment by using regulation mechanisms (homeostasis).

In saline lakes, organisms are exposed not only to increased salinity, but also to substantial shifts in salt concentration within very short periods. High salt concentrations (hypertonic conditions) of the surrounding medium cause serious problems if no protection mechanisms are developed: biological membranes are water-permeable, which would lead to continuous water loss through osmosis, resulting in plasmolysis and/or shriveling. Moreover, the increased ionic strength of the surrounding brines might cause an influx of ions into the cells. Besides morphological adjustments, Archaea and bacteria are conformers and have developed two major strategies to overcome osmolysis, namely "all-salt-in" and "low-salt-in-organic-solute-synthesis" (Oren, 2011; Sorokin et al., 2014). In the former strategy, KCl is accumulated in cells, which also requires adjustment of intracellular enzymes to overcome the problem of protein precipitation. The latter strategy includes synthesis of hydrophilic organic substances of low molecular weight such as certain amino acids (osmolytes, compatible solutes). Osmolytes—in contrast to KCl—do not interfere with metabolic activities, so no modification of enzymes is necessary. Although there are gaps in our knowledge, osmolytes are also common in eukaryotic algae (Oren, 2007) and protozoa (Gunde-Cimerman et al., 2018).

Rotifers can reach incredibly high numbers (Burian et al., 2016) and are of interest for aquaculture, but very little is known about their adaptations to salinity. *Brachionus plicatilis* is omnipresent in saline lakes between 3‰ and around 100‰ (Hammer, 1986). Lowe et al. (2005) suggested that *Brachionus* is a regulator based on Na^+/K^+ ATPase transporters. Crustaceans are quite common in saline lakes, with the branchiopod *Artemia salina*, also referred to as brine shrimp, surviving salinities between 3‰ and >250‰ (Croghan, 1958). *Artemia* is a regulator. A data compilation of worldwide copepod occurrence revealed that >25 species are found at salinities >100‰, and 12 species survive >200‰ (Anufriieva, 2015). Most copepods are probably conformers synthesizing osmolytes. *Ephydra* is another genus characteristic of saline lakes. The brine fly has Malpighian tubules for osmoregulation. The system is partly modified into a lime gland, where carbonates precipitate (Herbst and Bradley, 1989).

Vertebrates also occupy saline lakes. As opposed to invertebrates, fish are often lacking in this environment. This is because endorheic water bodies are quite isolated compared to their open counterparts, hampering movement and migration. From another perspective, however, isolation might boost endemism in such water bodies, similar to isolated mountain ranges. Hammer (1986) compiled a list of fish species naturally populating saline lakes of the world. This list reveals a clear pattern: increasing salinity results in decreased species number. Moreover, only five species tolerate >80‰. Generally, teleosts are slightly hypoosmotic to the surrounding water, which causes permanent water loss. This water loss is compensated by drinking. Gills, kidneys and the intestinal epithelium are highly involved in osmoregulation (Evans et al., 2005; Brauner et al., 2012). An additional challenge is the alkaline water of saline-alkaline lakes. The cichlid *Alcolapia grahami* (Magadi Tilapia) is adapted to such extreme conditions; its blood pH is adjusted to considerably higher levels compared to other fish. Wood et al. (2002) assumed that around 50% of the metabolic costs are traceable to acid-base regulation. *Alcolapia* drinks copiously to maintain ion balance. To escape the problem of stomach neutralization, it has developed a pyloric bypass in the gut. The bypass acts like a valve: it is closed during eating and open when drinking (empty stomach). Other physiological adaptations include obligate ureotely (Randall et al., 1989), with urea excretion across the gills. Many bird species developed salt-secreting glands in addition to kidneys to cope with salt water drinking, an essential feature for surviving in dry and salty environments.

Biodiversity and ecology

The biodiversity of photoautotrophs and heterotrophic eukaryotes in saline lakes is assumed to be low compared to the sea and to freshwater systems (Timms, 2020). It decreases continuously along a salinity gradient (Williams, 1998). This traditional view, however, needs to be scrutinized. The use of molecular taxonomic markers revealed an unexpectedly high diversity of Archaea (Menéndez-Serra et al., 2020) and other microorganisms (Alexe et al., 2017; Harding and Simpson, 2018). Additional explanations for these apparently contrasting patterns involve the application of traditional versus modern tools as well as organismic size. The number of easily recognizable taxa such as vertebrates and invertebrates is reduced with increasing salinity (Vareschi, 1987; Afonina and Tashlykova, 2020), whereas microorganisms have a "hidden" diversity (Lanzén et al., 2013). Saline lakes continue to provide unexpected new insights into microbial community composition. Just two examples are provided here. The Blood Falls is an iron-rich, blood-red, cryo-concentrated brine discharging at the glacier tongue of Taylor Glacier, which flows into Lake Bonney. This subglacial brine hosts a very stable, but previously undetected microbial community (Campen et al., 2019). Huge carbonate towers exceeding 40 m in height, built by calcifying cyanobacteria, have been discovered in Lake Van (Kempe et al., 1991).

From the classical point of view, food webs of saline lakes have a low complexity because the species inventory is limited. The evidence, however, is mounting that this statement falls short because the importance of the microbial community in both abundance and biodiversity has been largely neglected. As mentioned by Padisák and Naselli-Flores (2020), food webs of extreme environments are not necessarily simple, they are just considerably different from freshwater systems. Microbes are involved in element cycling of saline lakes (Banciu and Sorokin, 2013) and show extremely high abundances. Moreover, viruses might play a pivotal role in saline lakes (Peduzzi et al., 2014).

Saline-alkaline lakes up to mesosaline conditions rank amongst the most productive ecosystems of the world (Oduor and Schagerl, 2007). In addition to an elevated nutrient supply, high concentrations of inorganic carbon boost primary production. Key factors for community development can be categorized into allogenic environmental conditions and autogenic factors including

biological interactions (Schagerl and Burian, 2016). For saline lakes as terminal water bodies, water level with all its associated conditions is the overall allogenic key variable: changes in water levels impact the mixing regime and optical properties, the stability of the sediment-water interface, and geochemistry.

Economic concerns and threats

Commercial fishing is practiced in only a few mesosaline large lakes such as the Caspian Sea and Issyk-Kul. Another source of revenue is tourism. Beyond the environment itself, the associated organisms attract visitors. Because of their unique avifauna, some lakes have been designated as Ramsar Wetlands. Especially in lakes without fish, birds are at the top of the trophic cascade and feed on invertebrates and phototrophs. Microorganisms inhabiting the lakes are also in the focus of companies. The organisms synthesize valuable compounds and can be cultivated outdoor at extreme conditions, which precludes infections by contaminants. The chlorophyte *Dunaliella salina* is commercially exploited for ß-carotene and lutein production. *Limnospira* is cultivated in open pond systems and sold under the trade name "*Spirulina platensis*" as a food supplement. In addition, various health benefits such as anticancer and anti-inflammatory effects have been documented. Heterotrophs and their enzymes are already in use for industrial purposes; enzymes are robust against organic solvents, high temperature and salt content (Oren, 2010). Apart from these examples, other promising taxa still wait to be studied (Krienitz et al., 2016). Near the shore of saline lakes, health spas treat skin disorders, the most prominent examples being the Dead Sea and Lake Manitou (Saskatchewan). By far the largest source of income, however, is the mining and mineral industry. Besides halite, other evaporitic minerals are also mined. Trona and borax are used in the glass industry, and lithium is essential for various industrial purposes, e.g., for lithium-ion batteries.

The threats to saline lakes can be subsumed under direct anthropogenic impacts in the catchment and lake area, and climate change. Williams (2002) assumed substantial changes to the natural status of these lakes by 2025, with permanent water bodies showing a decrease in size paired with an increase in salinity, and ephemeral lakes having extended dry periods. His prediction was recently verified for several lakes (Wurtsbaugh et al., 2017; Tussupova et al., 2020). Although frequent water level changes are a typical feature of terminal lakes, human impact greatly speeds up this process. Global warming specifically affects saline lakes because they are a priori prone to climate change.

The Aral Sea is a very prominent warning example of human interference. Prior to 1960, this lake was ranked amongst the three largest saline lakes worldwide. Due to expanding irrigation, water was abstracted from the lake's main tributaries, dramatically decreasing its volume by 90% and triggering salinization (Fig. 9; Micklin, 2016). This disaster exposed former lake sediments to air, and the resulting dust deposition causes severe human health problems. Moreover, deflation substantially reduced the area of arable land due to salinization.

Lake Texcoco was once a very large lake in Mexico. The Aztecs already began to drain some areas, a practice that was later continued by the Spanish conquerors. Today, the expanding metropolis of Mexico City is located on the former lake area, and only negligible remnants of the lake remain.

The Dead Sea is being altered by human activities and is facing an ongoing reduction of its volume. In the 1970s, the southern part was separated from the northern basin and since then used as evaporation ponds for salt extraction. The water level has been receding by around 1 m per year in recent decades, mostly because of water diversion for irrigation, industrial and domestic use combined with high evaporation (Bookman, 2020). Because of its morphology, only about 20% of the initial volume was lost, and an annual halite precipitation of 0.1 m helped counteract the volume decrease.

Lake Urmia has faced a dramatic decline in water level for two decades. Within 8 years, the lake shrunk by about 60% and lost 90% of its original volume, which severely threatens the overall functionality of the system. The reasons for this decline are not fully understood, but Schulz et al. (2020) were able to prove climate change as the main trigger, additionally boosted by water abstraction of major inflows.

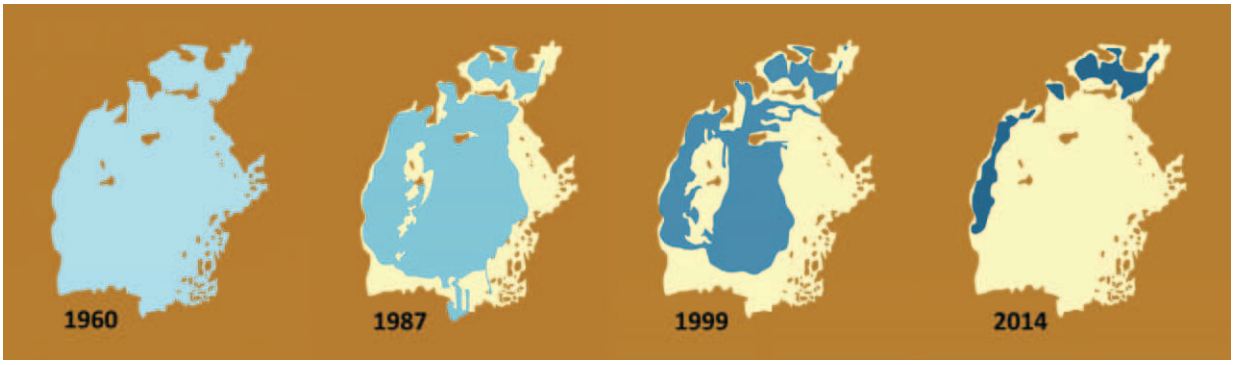

Fig. 9 The disaster of the Aral Sea. Modified from Micklin P (2016) The future Aral Sea: Hope and despair. *Environmental Earth Sciences* 75: 844. doi: 10.1007/s12665-016-5614-5.

Soda ash mining poses a threat to saline-alkaline lakes. Lake Abijata (Ethiopia) is dramatically shrinking due to water abstraction of inflows combined with soda ash production directly at the lake (Fetahi, 2016). The biology of the lake has completely changed: fish disappeared, which then triggered the loss of piscivorous birds. Other migrating birds such as flocks of flamingos no longer visit the lake because the plankton community also shifted from *Limnospira* toward other components.

The hypersaline lakes and subsurface brines of the Atacama Desert are ranked amongst the largest lithium exploitation sites worldwide. It is very likely that the biodiversity and stability of these sensible systems are highly endangered, but no environmental impact assessments and environmental protection measures have yet been performed (Gajardo and Redón, 2019). Australian salt lakes also face mineral exploitation (Timms, 2005).

In a few cases, lake restoration efforts have been successful. From the 1940s onwards, Los Angeles extracted water from tributaries of Mono Lake, resulting in a significant decrease of its volume paired with salinization. The lowered water level impaired organisms and their interactions, and also endangered the stability of tufa formations. To counteract this development, conservation efforts were undertaken, e.g., by reducing water diversion from the inflows. These efforts have already resulted in a rise of the water level.

Conclusion

Saline lakes are located in endorheic basins of all continents, including cold regions with ice-cover and high altitudes. They are often present in semi-arid to arid climates, which makes them and their tributaries an integral part of the water supply for certain land animals such as migratory birds. Contrary to the common belief outside the limnology community, they are extremely diverse in geochemistry and salinity. They represent complex and dynamic hydrological systems controlled by allogenic and autogenic factors such as tectonic activity and climatic conditions, catchment area lithology, mineral precipitation due to the different solubilities of evaporates, and biology. Organisms inhabiting these systems have adapted to brine concentrations at the limit of solubility. With increasing salinity, the biodiversity of eukaryotes drops. A few more recent studies, however, indicate that saline lakes hold a hidden diversity of prokaryotes, especially of Archaea. Due to their elevated nutrient supply combined with exceptionally high concentrations of inorganic carbon, saline-alkaline lakes rank amongst the most productive ecosystems worldwide. As terminal water bodies, saline lakes are prone to climate change and pollution, which is already illustrated by various dramatic examples. This urgently calls for comprehensive protection measures in most regions of the world.

Knowledge gaps

- Physiological adaptations to salinity and geochemistry
- Food web studies including the microbial loop and viral shunt
- Hidden biodiversity of eu- and prokaryotes
- Role of microbes in element cycling and system productivity
- Benthic-pelagic interactions
- Even regular basic measurements obtained by monitoring programs are missing

Acknowledgment

This chapter is dedicated to Aharon Oren, who is one of the leading scientists in the microbial ecology and prokaryote taxonomy of saline systems. His competence, enthusiasm, kindness and candidness have inspired many people, including the author of this chapter.

See Also: Structures and functions of Inland Waters - Wetlands: Salt Lakes

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Heat Budget of Lakes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie-Elodie Perga and Damien Bouffard.

Glossary

Albedo Fraction of incoming shortwave radiation reflected at the lake surface.
Energy flux Rate of energy exchange across an arbitrary or physically meaningful boundary (e.g., a lake surface).
Equilibrium temperature Lake surface temperature at which the net lake surface heat flux would be zero for given meteorological conditions.
Heat flux A thermal energy flux.
Incoming longwave radiation Thermal radiation at wavelengths >3000 nm directed from the atmosphere to the lake surface.
Incoming shortwave (solar) radiation Radiant energy with wavelengths between ~300 and ~3000 nm, emitted by the sun and reaching the lake surface after passing through the atmosphere.
Lake surface heat fluxes Heat fluxes between the lake surface and the atmosphere.
Latent heat flux Heat flux between the lake and the atmosphere due to evaporation or condensation.
Outgoing longwave radiation Thermal radiation at wavelengths >3000 nm emitted from the lake surface.
Sensible heat flux Heat flux between the lake and the atmosphere due to thermal conduction.
Surface mixed layer Nearly homogeneous water layer extending from the lake surface to a depth determined by recent turbulent mixing, in classical limnology also referred to as the epilimnion.

Introduction

The dynamics of heat fluxes determine lake water temperatures and stratification, which in turn impact water quality and biota. Changes in lake heat budgets are the most direct and primary effect of climate change on lakes, and the monitoring, modelling, and prediction of heat fluxes has a long history in limnology with continued growth in applications for present-day management and understanding of lakes. Due to the importance of heat fluxes to lake ecosystem functions and the need to project the response of lakes to climate change, numerous book chapters (see Wetzel and Likens, 2000) and reviews on the topic exist (Henderson-Sellers, 1986) as well as tools to support heat flux calculations (Woolway et al., 2015). Here we summarize current knowledge of lake heat fluxes and identify new future research challenges for the field of limnology.

Concepts

Components of the heat budget

Short-term temperature changes in lakes are the result of imbalance in heat losses or gains, most of which occur at the lake surface (Fig. 1). The timing and magnitude of surface energy fluxes vary in response to atmospheric conditions and the properties of the lake surface. Energy is also lost or gained to the lake below the surface, including from sub-surface inflows, sediment heat exchange, and the attenuation of penetrative radiation within the water column. The heat content of the lake (U_{tot}) is defined by the temperature and volume of the water, as well as other water properties that impact water density or specific heat. Any changes to thermal energy are driven by coincident imbalance in energy fluxes (H_X) which are positive when entering the lake:

$$U_{tot}/A = H_S + H_A + H_W + H_E + H_C + H_F + H_D$$

Where A is the surface area of the lake. Heat fluxes include downward shortwave (H_S) and longwave (H_A) radiation, outgoing longwave radiation (H_W), latent (H_E) and sensible (H_C) fluxes, advected energy (H_F), and sediment heat flux (H_D).

Accurate measurements of water temperature and volume (used to estimate U_{tot}) can be combined with detailed measurements or estimates of energy fluxes (H_X) to define seasonal patterns in lake heat budgets and temperature regimes. As an example, the seasonality of the components of the lake surface heat fluxes for a temperate and a tropical lake are displayed in Fig. 2. The values of missing or uncertain heat flux measurements can be inferred by quantifying the remaining elements of the heat budget and solving for the residuals, such as using temperature and measured energy fluxes to estimate evaporation (Lenters et al., 2005; Winter et al., 2003), or conversely, process-based lake temperature models predict temperatures by including measured or estimated heat fluxes in an energy budget model (Hipsey et al., 2019). A wide range of equations have been used in process-based models to parameterize lake surface heat fluxes. Henderson-Sellers (1986) summarized available parameterizations for all surface heat fluxes, and specific sets of equations can be found, e.g., in Livingstone and Imboden (1989), Fink et al. (2014), Woolway et al. (2015), and Hipsey et al. (2019).

Shortwave radiation

Downwelling shortwave radiation (H_S) quantifies the direct energy from the sun as the sum of all wavelengths in the range of ~300–3000 nm including near-ultraviolet, visible light, and near-infrared radiation. As such, H_S varies according to latitude, cloud cover, elevation, and any landscape features that may block the sun's rays from reaching the lake surface (e.g., tall buildings, mountains, and tree canopies). A portion of incoming radiation is reflected by the lake surface, and this loss is defined as the albedo. The shortwave albedo varies according to location (including latitude and elevation), time and day of year, and surface water conditions (e.g., presence of waves or ice cover). Empirical formulations or look-up tables are available for estimating time-varying albedo (Cogley, 1979) but it is common to assume a constant value (e.g., Lenters et al., 2005). After reflection of a fraction of incoming shortwave radiation, shortwave radiation wavelengths beyond the range of visible light are non-penetrative and are

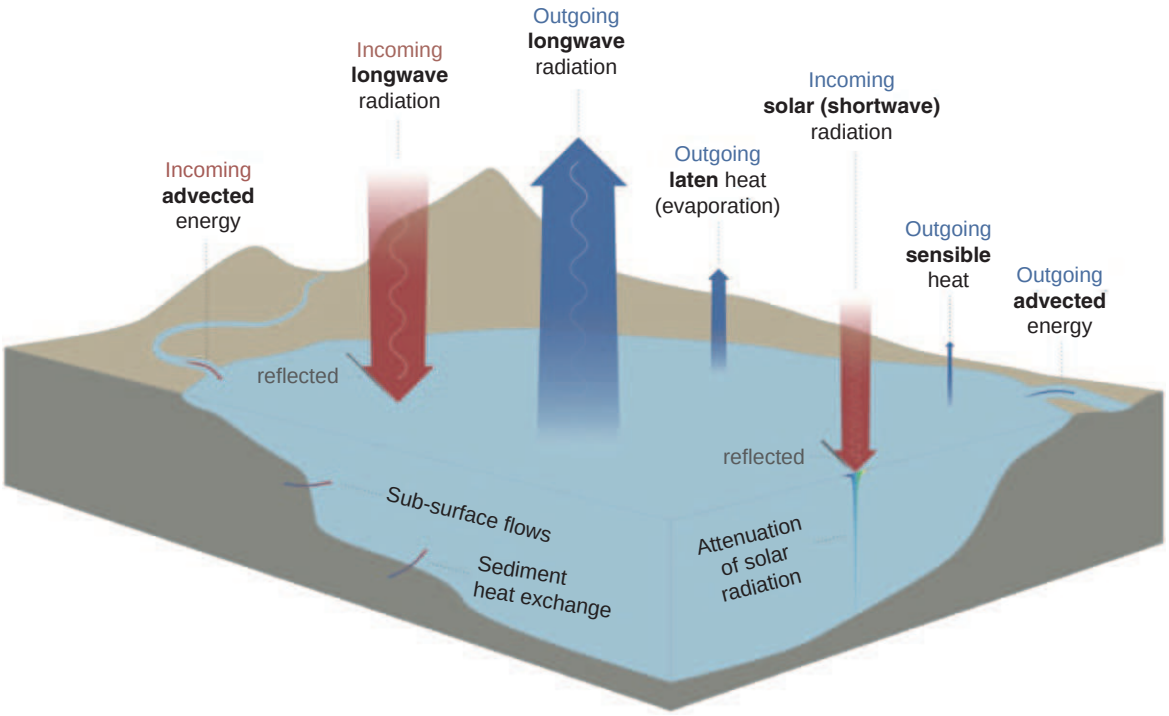

Fig. 1 Components of the heat exchange between a lake and the environment.

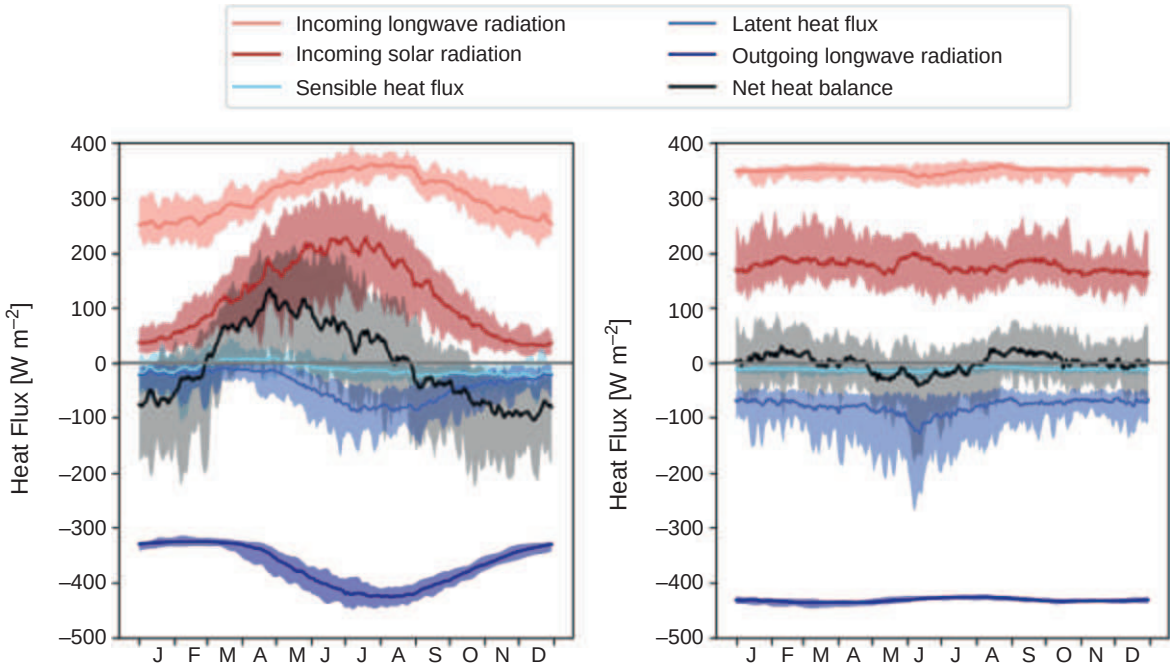

Fig. 2 Components of the surface heat fluxes for temperate Lake Zug (Switzerland) and tropical Lake Kivu (DR Congo, Rwanda). The fluxes were calculated with the lake model Simstrat (Goudsmit et al., 2002; Gaudard et al., 2018) based on meteorological data from MeteoSwiss for Lake Zug, and the MiroC5 control scenario from ISIMIP2a for Lake Kivu (F. Bärenbold, personal communication). The lines show the median values, the ranges the minima and maxima over a period of 30 years. The data were smoothed with a window of 1 week. The effects of inflows and sediment heat exchange were not included in the calculations.

treated as a surface energy flux. Radiation of shorter wavelengths penetrates below the surface to be attenuated within the water column or absorbed by the lakebed (Kirk, 1994). The percentage of non-penetrative shortwave radiative energy has been defined as ranging from 35% (Thiery et al., 2014) to 55% (Hipsey et al., 2019).

Incoming longwave radiation

Downwelling longwave radiation (H_A) is the radiative energy flux from the atmosphere, and the magnitude of this flux depends primarily on the atmospheric temperature and humidity and cloud cover. See Flerchinger et al. (2009) for various methods to estimate longwave radiation. Approximately 3% of downwelling longwave radiation is reflected at the lake's surface (the longwave albedo) and the remaining energy is absorbed by the surface of the lake.

Outgoing longwave radiation

Longwave radiation is emitted from the lake (H_W) as a function of surface water temperature (in Kelvin) to the fourth power. This outgoing energy flux is typically the largest energy loss term in a lake heat budget, more than offsetting the gains of downwelling H_A in most cases (although see Section "Overall seasonal heat budget of lakes in different climate zones"). As such, the net sum of incoming and outgoing longwave radiation is often measured near the surface of a lake with paired upward- and downward-oriented sensors, which capture H_A and the sum of H_W and the portion of H_A reflected upward, respectively. When direct measurements are not available, H_W is often estimated as $\varepsilon\sigma T_0^4$ where ε is the emissivity of water, σ is the Stefan-Boltzmann constant, and T_0 is the absolute temperature of the water surface.

Latent heat flux (evaporation/condensation)

The flux of latent heat (H_E) at the lake surface quantifies the energy lost or gained to the lake via a state change from liquid water to vapor (evaporation) or vapor to liquid water (condensation). These state changes remove or add water to the lake and are therefore also relevant to the closure of the lake's water budget. Most latent heat exchange occurs as evaporation, where the magnitude of the flux depends on the deficit of vapor in the air and the efficiency of removal, which is based on the atmospheric conditions above the lake. Common methods for estimating the latent heat flux include calculating a residual to the energy budget (Winter et al., 2003), eddy covariance (Nordbo et al., 2011), and mass transfer coefficient parameterization (Rasmussen et al., 1995; Woolway et al., 2015); alternative methods including pan evaporation, mass budget, and use of stable isotopes are also applicable to estimating evaporative water loss.

Sensible heat flux

The sensible heat flux (H_C) contrasts with latent heat exchange in that no state change occurs and energy is transferred via conduction between the lake surface and the atmosphere. As with H_E, H_C can remove or add energy to the lake depending on

the prevailing meteorological conditions and the surface temperature of the lake, although most H_C fluxes are losses from the lake. The magnitude of the H_C flux depends on the difference in temperature between air and water and the atmospheric removal. All primary methods listed above for estimating H_E either include a complementary formulation for H_C (see Woolway et al., 2015) or involve partitioning the relative contributions of H_C and H_E as part of the method (in the case of energy budget or eddy covariance methods).

Inflows

The net heat flux H_F (W m^{-2}) caused by an inflow with discharge Q_{in} and temperature T_{in} is given by Livingstone and Imboden (1989):

$$H_F = \frac{c_p \rho}{A} Q_{in}(T_{in} - T_{out})$$

where c_p and ρ are the heat capacity and density of water, respectively; and T_{out} is the outflow temperature, which is close to the lake surface temperature in most lakes. This equation assumes constant lake volume with inflow equal to outflow. For calculating the full heat budget of a lake including volume variations, all individual water fluxes and their temperatures need to be considered (Winter et al., 2003), but in that case care must be taken when comparing components of the heat budget that result from temperature changes with those resulting from volume changes.

If an inflow mixes into the surface mixed layer of a lake, the respective heat flux modifies the lake surface temperature in a similar way as a change in a surface heat flux. As a consequence, the outgoing longwave radiation and the latent and sensitive heat fluxes are modified, partially compensating the heat flux from the inflow. Conversely, if the inflow plunges into the metalimnion, as is typically the case for cold inflows in the warm season, it does not directly affect the lake surface temperature, and the net heat flux from the inflow can accumulate in the lake until the next mixing event. Cool plunging inflows can thus cause a significant cooling of a lake throughout the summer. Similarly, direct groundwater inflows can modify hypolimnion temperatures of a lake (Safaie et al., 2017).

Heat exchange with the sediment

Heat is generally transported from the water column into the sediment by conduction during the warm season and released back to the water during the cold season (Fang and Stefan, 1998), although diurnal heat exchange can also be relevant, especially in shallow lakes or littoral areas where sediments receive direct solar radiation (de la Fuente, 2014). The seasonal heat storage in sediments is relevant mainly for the heat budget of shallow lakes, where the seasonal temperature variation above the sediment is large and the heat capacity of the overlying water is comparably small. However, the amount of heat that can be stored and exchanged is limited by the thermal diffusivity of the lake sediment. Even for lakes with large seasonal temperature variation, the seasonal heat flux between the sediment and the overlying water typically does not exceed a few W m^{-2}. The effects of heat exchange between the sediment and the water are therefore most noticeable in ice-covered lakes where the heat fluxes across the lake surface are limited as well. Heat release from the sediment can be an important driver for both horizontal currents and vertical mixing in ice covered lakes (Kirillin et al., 2012).

Heat fluxes through ice cover

The presence of an ice cover completely modifies the heat fluxes at the lake surface (Leppäranta, 2015). The water temperature at the ice-water interface is fixed to 0 °C. The temperature at the surface of the ice cover reacts to meteorological conditions, resulting in a temperature gradient within the ice and a corresponding molecular heat flux. Shortwave radiation can partially penetrate the ice cover and add heat to the underlying lake water. This is particularly important in spring when the ice cover becomes thinner and incoming shortwave radiation increases. The warming of the near-surface water can then induce convective mixing below the ice cover, as water density increases with temperature at temperatures below 4 °C (Kirillin et al., 2012). The transfer of shortwave radiation through the ice cover strongly depends on the ice properties and is reduced in the presence of snow.

Anthropogenic heat fluxes

Heat can be artificially added to or removed from a lake when water is used for cooling or heating purposes. More than 4 GW of heat is introduced globally to freshwater systems from the cooling of power plants. An estimated 44% of this heat directly enters reservoirs and lakes (Raptis and Pfister, 2016) and in some cases causes considerable warming of these waterbodies. One of the best investigated case studies is Lake Stechlin, which was used for cooling a nuclear power plant from 1960 to 1996, with significant effects on its mixing and stratification regime (Kirillin et al., 2013). The remaining 56% of the heat is introduced into rivers, but can be further transported into downstream lakes (Råman Vinnå et al., 2017). More recently, freshwater systems have been increasingly used for extracting heat for heating purposes, resulting in a cooling of the waterbodies. Heat extraction from deep lakes using heat pumps provides a substantial potential for replacing fossil fuel (Gaudard et al., 2019a, b). Wastewater also typically has different seasonal temperature dynamics than natural surface waters, and its discharge into a lake can therefore modify the heat budget of a lake.

Concept of equilibrium temperature

The equilibrium lake surface temperature is a useful proxy for the responses of lakes to climate variability and climate change (Schmid et al., 2014). A lake surface equilibrium temperature can be calculated as the temperature for which the net heat flux at the

lake surface is zero given a set of meteorological conditions (Edinger et al., 1968). The lake surface temperature tends to exponentially approach this equilibrium temperature if meteorological conditions are held constant. A deviation of the lake surface temperature from the equilibrium temperature of 1 °C results in a heat flux from the lake of ~30 W m^{-2}. This heat flux would be sufficient to cool a water layer of 1 m thickness by 1 °C within 1.6 days. Consequently, for constant meteorological conditions, and assuming that the incoming solar radiation is entirely absorbed within the surface mixed layer, the lake surface temperature would exponentially approach the equilibrium temperature with a time scale of 1–2 days for a 1 m thick mixed layer or 1 month for a 20 m thick mixed layer. In shallow lakes or in stratified lakes with a shallow surface mixed layer, the lake surface temperature is therefore often close to this equilibrium temperature. For a wide range of meteorological conditions, a change in air temperature of 1 °C results in a change in lake surface equilibrium temperature of ~0.8 °C (Schmid et al., 2014). In small and shallow lakes, but also in stratified deeper lakes, a trend in air temperature is therefore expected to result in a corresponding trend in lake surface temperature of ~80% of the air temperature trend.

Overall seasonal heat budget of lakes in different climate zones

The importance and seasonality of the different heat fluxes varies with latitude and in different climate zones (e.g., Fig. 2). This results in different lake thermal regimes, and also a different sensitivity of lakes in different climate zones to climate change (Maberly et al., 2020). Climatic and lake-specific factors (such as morphometry) modulate the seasonal heat budgets in lakes and contribute to global diversity in lake thermal regimes.

In temperate and boreal climate zones, where the majority of lakes are located, the seasonality of the heat budget is mainly driven by the strong seasonality of incoming shortwave and to a lesser extent incoming longwave radiation. As a result, large seasonal amplitudes of lake surface temperatures and dimictic or monomictic mixing regimes are common in these climate zones. The lag between lake temperatures and atmospheric conditions also results in seasonality of outgoing heat fluxes (Livingstone and Imboden, 1989), including latent and sensible heat fluxes, which peak in the summer or late fall. Lakes that become cold enough for surface ice to form experience modified heat fluxes (Section "Heat fluxes through ice cover") and as day length and H_S increase in the spring, have a lagged response to warming until ice melts and surface waters return to tighter coupling with atmospheric heat exchanges.

In the tropical climate zone, incoming shortwave radiation is relatively constant throughout the year. Lake surface temperatures vary seasonally only within a few degrees Celsius, and temperature differences between the surface and bottom waters are typically small, resulting in a more dynamic behavior of the mixed layer depth than in temperate lakes (Lewis, 2000). The lowest lake surface temperatures, and consequently deep mixing events, often occur during the local dry season, when low relative humidity and seasonal winds increase evaporative heat losses and decrease incoming longwave radiation.

Indirect anthropogenic impacts on heat fluxes

Anthropogenic uses of water and land can result in significant changes to lake heat budgets, which in turn modify lake thermal regimes and ecosystem functions. Tanentzap et al. (2008) examined Clearwater Lake in Canada, where forest regrowth and deacidification (along with coincident changes in water clarity) resulted in lower wind speeds and a colder, more strongly stratified lake. Urban heating impacts on lake heat fluxes can be significant, but few studies exist that describe this phenomenon (although see Cosgrove and Berkelhammer, 2018). Using lakes as storage volumes for pumped-storage hydropower can strongly affect their heat budget and thermal properties (Kobler et al., 2018). Other examples of indirect alterations to heat fluxes via anthropogenic change include interventions that modify lake surface area, morphometry, and flowrates via impoundment, channelization, water diversion, and sedimentation. Additionally, agricultural drainage and wastewater effluents have been mostly examined for rivers, but can also affect lake heat budgets (Gaudard et al., 2018). The impact of these anthropogenic alterations on water temperatures depends on their relative magnitude in the overall energy budget of a lake.

Impacts of climate change on heat fluxes and heat budgets

All heat fluxes mentioned in Section "Components of the heat budget" can be modified by climate change. The most direct impact of climate change results from changes in air temperature. Increased air temperature leads to increased incoming longwave radiation and modifies the sensible heat flux between the lake and the atmosphere. For many individual lakes, high correlations between annual or seasonal mean air temperature and lake surface temperature have been observed. At a global scale, for a large number of lakes, the correlation between long-term trends in summer air temperature and lake surface temperature is less consistent (O'Reilly et al., 2015). This observed variability can result from different reactions of different lakes to the forcing, from surface water temperature trends in some lakes being affected by other factors (e.g., trends in clarity), or from the uncertainties in the observed trends of either air or lake surface temperature. Locally, climate change can also lead to modified incoming solar radiation, relative humidity, average wind speeds, and the timing and magnitude of hydrologic fluxes, with corresponding impacts on lake heat fluxes. For example, reduced wind speeds have been proposed to have accelerated warming of lakes in the Northern Hemisphere (Woolway et al., 2019). For boreal and temperate lakes, climate change typically results in a prolongation of the summer stratified period with a significant additional accumulation of heat throughout the summer, which then needs to be removed again in autumn before complete lake mixing can occur.

Conclusions/synthesis

The heat fluxes between lakes and the environment determine the dynamics of their thermal structure, and in consequence, are a control on biogeochemical processes in lakes. The heat budget of an individual lake depends on the local climatic conditions and is modulated by the lake's properties. While incoming shortwave and longwave and outgoing longwave radiation contribute most to the heat budget, other heat fluxes can nevertheless be relevant for driving seasonality, e.g., the latent heat flux in tropical lakes. Modification of the heat fluxes, and in consequence of the thermal structure, is the most direct impact of climate change on lakes. The heat budget of lakes can otherwise be affected by anthropogenic activities, either directly by heat discharge or extraction, or indirectly by changes in a lake's watershed.

Knowledge gaps

- The spatial heterogeneity in lake thermal properties, fluxes, and in-lake responses to forcings (e.g., evaporative cooling, locations of warm water inflows, and complex wind fields) may be relevant but has rarely been investigated.
- Direct measurements of heat fluxes (e.g., eddy covariance for sensible and latent heat) are rare.
- The representation of heat fluxes in numerical lake models is often simplistic and constrained by measurement limitations (e.g., single point weather observations).
- Data for calculating fluxes is biased to temperate regions, and few studies have taken place at high altitude or in tropical lakes.
- Studies quantifying the effects of diffuse anthropogenic heat sources (e.g., urbanization, land use change) on lake temperatures are rare.

Case studies

Lake	*Country*	*Coordinates*	*Main topic*	*Key references*
Lake Valkea-Kotinen	Finland	61°14′N/25°03′E	Measurements of heat fluxes over a boreal lake	Nordbo et al. (2011)
Lake Stechlin	Germany	53°09′N/13°01′E	Impact of thermal discharge	Kirillin et al. (2013)
Lake Constance	Germany, Switzerland	47°35′N/09°28′E	Climate change effects on heat fluxes	Fink et al. (2014)
Lower Lake Zurich	Switzerland	47°15′N/08°40′E	Contributions of forcing factors to recent warming	Schmid and Köster (2016)
Tub Lake	Wisconsin, United States	45°16′N/91°27′W	Sediment heat budget for small temperate lakes	Likens and Johnson (1969)
Mirror Lake	New Hampshire, United States	43°56′N/71°41′W	Energy budget method to estimate evaporation	Winter et al. (2003)
Lake Taihu	China	31°25′N/120°13′E	Factors driving evaporation in a subtropical lake	Xiao et al. (2020)
Nam Co	China	30°42′N/90°33′E	Heat fluxes at high altitudes	Wang et al. (2015)
Lake Kivu	DR Congo, Rwanda	02°00′S/29°00′E	Effect of rainfall on lake surface temperature	Rooney et al. (2018)
Lake Tanganyika	Burundi, DR Congo, Tanzania, Zambia	06°30′S/29°50′E	Sensible and latent heat fluxes	Verburg and Antenucci (2010)

See Also: Fundamental concepts and theories: Temperature as a Driving Factor in Aquatic Ecosystems; The Discipline of Limnology; Structures and functions of Inland Waters - Lakes: Biophysical Interactions in Phytoplankton; Ecological Consequences of Climate Extremes for Lakes; Lake Ice Formation and Melt. Under-Ice Dynamics; Small-Scale Turbulence and Mixing: Energy Fluxes in Stratified Lakes; Surface Mixed Layers in Lakes

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https://github.com/GLEON/HeatFluxAnalyzer—Lake Heat Flux Analyzer.
https://land.copernicus.eu/global/products/lswt—Copernicus Global Land Service (CGLOPS).
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Lake Colors: Interpreting Apparent Optical Properties

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This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Apparent optical properties Aquatic optical properties that depend, among others, on ambient light and observation conditions, such as attenuation and reflectance.
Inherent optical properties Aquatic optical properties that are irrespective of ambient light and observation conditions, but depend only on water and its optically active components, such as absorption and scattering.
Irradiance Radiant flux received by a surface in units Watt per square meter.
Radiance Radiant flux received by a surface in units Watt per solid angle per projected area.
Reflectance Measure of a surface's effectiveness in reflecting radiant energy, with reference to the illumination and observation geometry.
Attenuation The gradual loss of radiant flux in a given medium, in units per path length.
Remote sensing The process of observing the physical characteristics of an area by measuring its reflected or emitted radiation at a distance.
Spectroradiometry The process of measuring a radiant flux at individual wavelengths of the electromagnetic spectrum.

Introduction

Sensing color is a convenient way to obtain information about the environment. The earliest standardized measures of water color, Secchi depth and the Forel-Ule scale, use the human eye as a sensor. They were defined more than a century ago, but recently experienced a revival in citizen science. Meanwhile, the emerge of opto-electronic sensors enabled an increasing level of automation in environmental monitoring using a variety of submerged to orbiting measurement platforms. This section covers the interpretation of apparent optical properties of natural waters, which are those that depend on ambient light and observation conditions.

The transparent spectral window of pure water, human light perception and absorption by photosynthetic pigments are all ranging from 400 to 700 nm wavelength of the electromagnetic spectrum (Mobley, 1994). This may seem coincidental, or less so given that both photosynthesis and vision evolved in water-borne organisms. It was even hypothesized that eyesight sparked the evolutionary arms race referred to as *Cambrian Explosion* (Parker, 2004), emphasizing the huge practical value of eyesight. Solar illumination in the visible spectral domain is the primary energy source for human vision as well as for spectroradiometers. Observations are thus subject to different illumination conditions, namely the brightness and spectral composition of down-welling irradiance. Compensating for these conditions is key to accessing color in a reproducible manner.

 https://doi.org/10.1016/B978-0-12-819166-8.00041-4

The hues of most natural surface waters range from blue and green to brown (Giardino et al., 2019; Lehmann et al., 2018), and their brightness spans across two orders of magnitudes (IOCCG, 2018). The Forel-Ule scale is a traditional, self-contained method to classify this range according to 21 color standards (Novoa et al., 2013). In water quality remote sensing, up to 22 optical water types from statistical clustering of spectral reflectance are used to support the retrieval of color producing agents such as inorganic and organic particles, phytoplankton pigments, and dissolved organic matter from spectral reflectance (Eleveld et al., 2017; Spyrakos et al., 2018). Absorption and scattering of these agents determine also Secchi disk visibility, which is related to turbidity and the underwater light availability (Lee et al., 2015).

Earth observation satellites are used for water quality remote sensing since the launch of the ERTS-1 mission, later known as Landsat-1, in 1972 (Strong, 1974). The spectral sampling of the first multispectral scanners was coined by human light perception. Image acquisition in a red, green and blue spectral channel enabled true-color imagery that is comparable to color photographs. This scheme is still present in many Earth observation sensors. But the number of application-specific satellite missions has increased steadily over the past decades, enabling a wide range of applications related to surface water quality (IOCCG, 2018). Currently, several hyperspectral satellite sensors are emerging that sample hundreds of adjacent spectral channels and resolve an unprecedented level of color detail.

Color appearance

Sensitivity of the human eye

In the eye of people with normal vision three types of light sensitive cells (cones) allow for color vision, while another cell type (rods) enables vision during low-light conditions. Lacking cone types lead to color-blindness. Fig. 1 shows the typical distribution of cones in the central part of the retina (Zhang et al., 2019).

The different cone types allow for a bulk wavelength selection similar to a broadband multispectral sensor with overlapping bands. Their spectral response to light is given by the cone fundamentals. These are the products of spectral absorption of the cones' photo pigments multiplied by the spectral transmittances of the ocular media through which light passes to reach the retina (Judd, 1966). Each person has a slightly different color vision that varies furthermore with the viewing field and with age. Fig. 2 shows the average cone fundamentals derived from 49 persons for a field of view of 10 degrees (Stiles and Burch, 1959).

Color space

Long before cone fundamentals were known, it was demonstrated that all color perception can be evoked with three primary colors (von Helmholtz, 1852). Wright (1929) and Guild (1931) performed experiments where a target spectral radiance was matched by additive mixing of monochromatic blue (436 nm), green (546 nm) and red (700 nm) light, with the addition of a virtually negative red contribution. From these experiments three wavelength dependent functions were derived, called color matching functions (CMF), which form the basis of modern colorimetry (CIE, 2006). The CMFs relate mathematically the physical

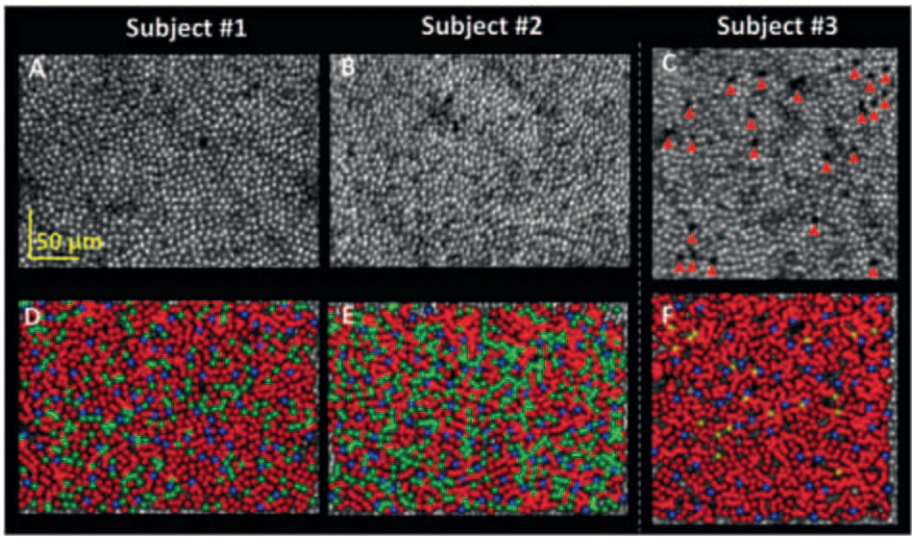

Fig. 1 Distribution of cones sensitive to shortwave (S cones, blue), midwave (M, green) and longwave (L, red) light in the central part of the retina. En face intensity images of cone mosaics (A–C) are color coded on the basis of cone classification (D–F). Subjects #1 and #2 have normal vision. Subject #3 is a deuteranope, whose missing cone outer segments, indicated by red arrows, impair green and brightness perception. Reproduced with permission from Zhang F, Kurokawa K, Lassoued A, Crowell JA and Miller DT (2019) Cone photoreceptor classification in the living human eye from photostimulation-induced phase dynamics. *Proceedings of the National Academy of Sciences* **116**: 7951–7956. doi: 10.1073/pnas.1816360116.

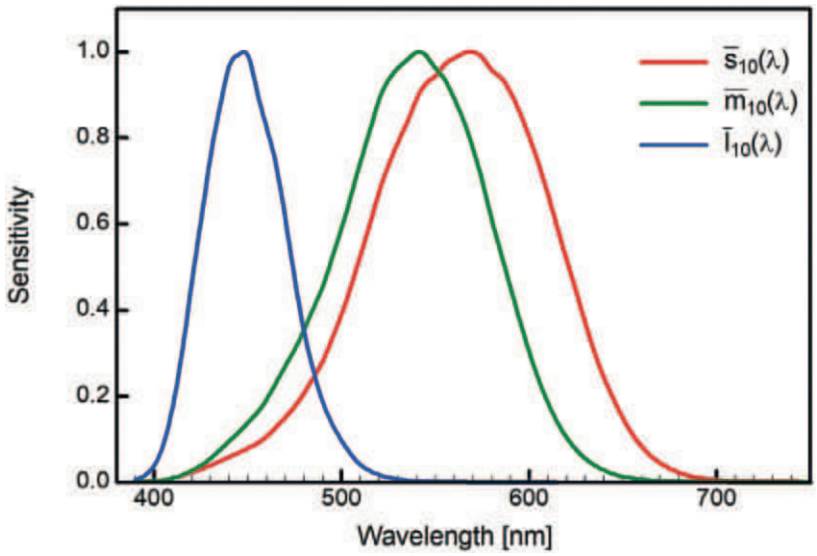

Fig. 2 Cone fundamentals for observation at 10 degrees field of view. Data from Stiles WS and Burch JM (1959) N.P.L. Colour-matching investigation: Final report (1958). *Optica Acta: International Journal of Optics* **6**: 1–26. doi: 10.1080/713826267.

quantity of radiance with the physiological perception of color. For details of this transformation refer to the "Supplementary Material" in the online version at https://doi.org/10.1016/B978-0-12-819166-8.00041-4.

Based on the CMFs, the International Commission on Illumination (CIE) published in 1931 the so-called chromaticity diagram which allows visualizing all colors in a two-dimensional plot (Fig. 3). Its curved boundary represents monochromatic light, while its straight edge from 380 to 700 nm has no physical counterpart and is called the line of purples. CIE 1931 is still the most widely used color space despite several updates and physiology-based approaches to color specification. For printing and projecting colors or displaying them on a monitor, the CIE 1931 color space has to be transformed to a technical color space like sRGB (IEC 61966-2-1, 1999).

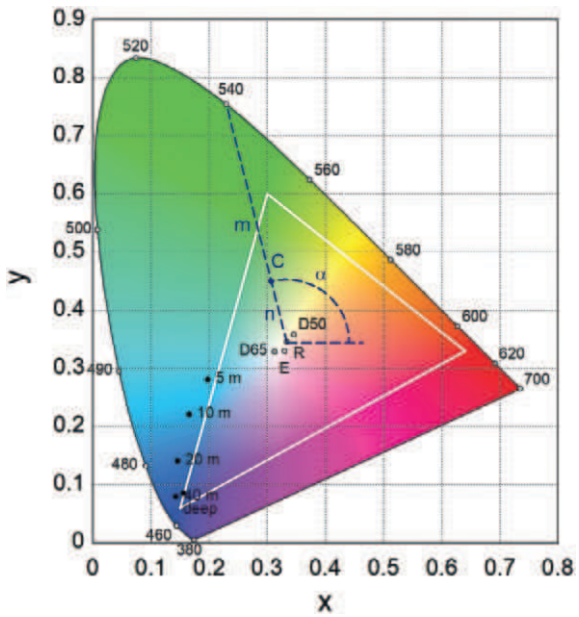

Fig. 3 The CIE 1931 chromaticity diagram. The triangle indicates the technical sRGB space for displaying colors. Equal energy point E and daylight spectra D50 and D65 are common references for white light, and R represents white for reflectance-based colorimetry. The angle α of a color C is termed hue, and the ratio n/(n + m) is called saturation; both depend on the chosen white reference. Black points: Perceived colors for a white object seen at different depths in clear, blue water.

Spectral radiance and irradiance

Spectroradiometers sample emitted, transmitted or reflected light with reference to the spectral domain. They typically comprise a monochromator that diffracts or disperses panchromatic light into distinct spectral wavelengths, and a photodetector or array of detectors that converts the monochromatic light into current. The most widely used radiometric measures are radiance and plane irradiance (Mobley, 1994). Spectral radiance L in a given direction is the fundamental radiometric quantity, from which all other radiometric quantities can be derived. It is defined with reference to position $\vec{x}$, time t, pointing direction $\hat{\xi}$ and wavelength λ as:

$$L\left(\vec{x}, t, \hat{\xi}, \lambda\right) \equiv \frac{\Delta Q\left(\vec{x}, t, \hat{\xi}, \lambda\right)}{\Delta t\, \Delta A\, \Delta\Omega\, \Delta\lambda}$$

Where ΔQ is the sampled energy, Δt is the sampling time, ΔA the detector area, $\Delta\Omega$ the solid angle of the field of view, and $\Delta\lambda$ the spectral sampling interval. The plane irradiance E is the hemispherical integral of L weighted by the cosine of each photon's incidence angle, as sensed by a plane collector. Down-welling plane irradiance represents the light incident on a flat surface, for example as down-welling irradiance E_d at top of atmosphere or ground level (Fig. 4).

In aquatic remote sensing, the parameter of interest is the water-leaving radiance L_w, a virtual quantity that corresponds to the upwelling radiance above a water surface L_u, minus the surface reflected radiance L_{surf} (Fig. 5, left). The upwelling radiance observed by spaceborne sensors at top-of-atmosphere L^{TOA} consists of L_w after atmospheric transmission t_A, and path radiance L_{path} from atmospheric scattering (Fig. 5, right). The sum of L_{surf} and L_{path} is typically one to two orders of magnitude higher than L_w, particularly in the blue, and must thus be accounted for when interpreting the color of surface waters.

Multispectral satellite sensors for land remote sensing (e.g., Landsat-8 OLI, Sentinel-2 MSI) provide high spatial resolution but a limited number of spectral bands that sample relatively large wavelength intervals, similar to the human eye (see Sections "Sensitivity of the human eye" and "Spectral reflectance"). Multispectral sensors for ocean color remote sensing (Aqua/Terra MODIS, Sentinel-3 OLCI) feature narrower spectral bands and higher radiometric accuracy at the expense of spatial resolution. Hyperspectral sensors acquire images in hundreds of contiguous, registered, spectral bands such that for each pixel a radiance spectrum can be derived (Goetz et al., 1985).

Spectral reflectance

Spectral reflectance is the ratio of upwelling to down-welling radiant fluxes for given surface, illumination and observation properties, including the sensor's spectral sampling properties. Similar to the human eye's brightness and chromatic adaptation, such normalization by a down-welling flux helps the interpretability of reflectance as opposed to the radiance reflected by a given target (Mobley, 1994). Reflectance is directionally variable and defined using conical and hemispherical incidence and exitance integrals (Schaepman-Strub et al., 2006). Aquatic reflectances in particular are defined with reference to the air-water interface. Remote sensing reflectance R_{rs} is most frequently used:

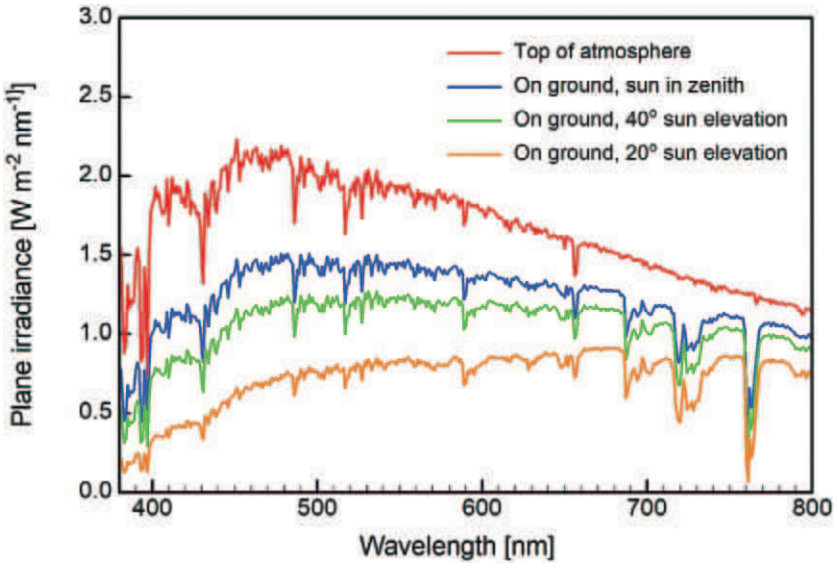

Fig. 4 Spectral plane irradiances at mean earth-sun distance. The resolution is 1 nm. The irradiances on ground were calculated for Sea level, a horizontal visibility of 15 km, an ozone concentration of 300 Dobson units and a scale height of precipitable water of 2.5 cm.

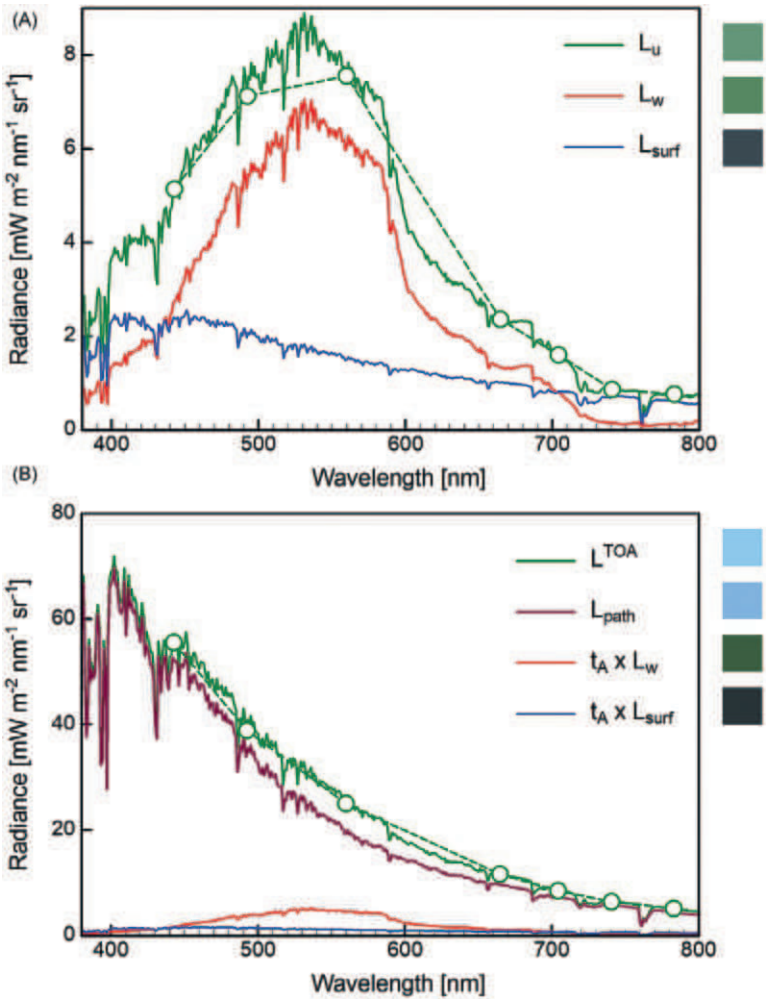

Fig. 5 MODTRAN simulated aquatic radiance spectra at bottom (A) and top of atmosphere (B). Solid lines are hyperspectral, dashed lines are resampled with Sentinel-2 band response. Plain squares indicate the human color perception for each spectral radiance.

$$R_{rs}(\lambda) = \frac{L_w(\lambda, \theta, \phi)}{E_d^{0+}(\lambda)}$$

Where L_w is water-leaving radiance in units W m^{-2} nm^{-1} sr^{-1}, i.e., the fraction of upwelling radiance passing the air-water interface in zenith direction θ and azimuth direction ϕ. E_d^{0+} is the plane down-welling irradiance just above the same interface. L_w cannot be measured but needs estimation from radiance measurements acquired just above or below the water surface.

Reflectance is a common parameter in remote sensing. It is accessible from satellite observations after compensation of atmospheric and air-water interface effects (Fig. 6), as well as from radiative transfer modeling using the constituents' absorption and scattering properties together with the light distribution of the incident light (Mobley, 1994). As reflectance is an illumination-corrected color property, it is much better suited to visualize changes of environmental parameters than radiance. For this reason, reflectance-based colorimetry has been introduced in remote sensing, which uses $R_{rs}(\lambda)$ instead of $L(\lambda)$ in the equations defining the CIE tristimulus values X, Y, Z. This corresponds to a spectrally constant illumination. Fig. 3 shows that the chromaticity coordinates of this fictive light source (x = 0.334, y = 0.346) lie between the daylight spectra D50 and D65, hence reflectance-derived colors approximate well the colors perceived by the human eye. For many multispectral satellite sensors, the hue angle (definition see Fig. 3) has been implemented as a measure of water color (Van der Woerd and Wernand, 2018). It correlates in a nonlinear way with the concentrations of colored dissolved organic matter (CDOM) and chlorophyll-a (Van der Woerd and Wernand, 2018).

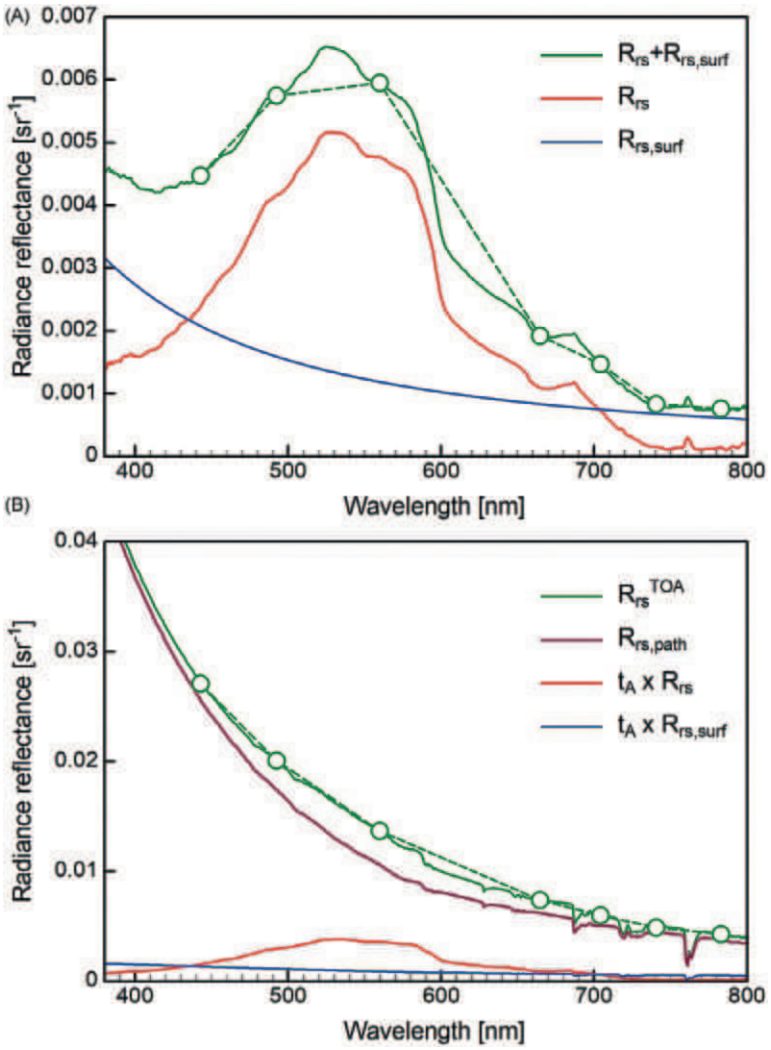

Fig. 6 Remote sensing reflectance spectra at bottom (A) and top of atmosphere (B). Solid lines are hyperspectral, dashed lines are resampled with Sentinel-2 band response.

Bio-optical modeling

Inherent and apparent optical properties

Equations relating the concentrations of water constituents to the optical properties of a water body are called bio-optical models to acknowledge the omnipresence of biological components (Morel, 2001). Two types of optical properties can be distinguished according to Preisendorfer (1961), Inherent Optical Properties (IOP) and Apparent Optical Properties (AOP).

IOP are distinct properties of water and its optically active components, such as absorption (a) and backscattering (b_b). Fig. 7 shows a and b_b for pure water and three common components: the colored fraction of dissolved organic matter (CDOM), phytoplankton and non-algal particles (NAP). The individual components' IOPs add up to the bulk IOP of natural water. All components absorb and scatter light across the entire visible spectral range, which complicates their individual estimation from optical measurements.

AOP depend additionally on the ambient light field and the viewing geometry, and they are related to the bulk processes of light transmission, reflection and extinction. Depending on illumination and viewing geometry, different definitions are used for the same process to account for the geometric conditions of the actual measurement setup. For example, nine definitions exist for the reflection at solid surfaces (Schaepman-Strub et al., 2006). When the human eye or a radiance sensor observe a horizontally extended object under natural outdoor illumination conditions, the most appropriate definition for reflection is the ratio of upwelling radiance (L_u) to plane down-welling irradiance (E_d). This ratio is known in the land community as hemispherical–conical reflectance factor (HCRF), and in the water community as remote sensing reflectance excluding reflections at the water surface. The ratio is different for measurements above the water surface (R_{rs}) and below (r_{rs}).

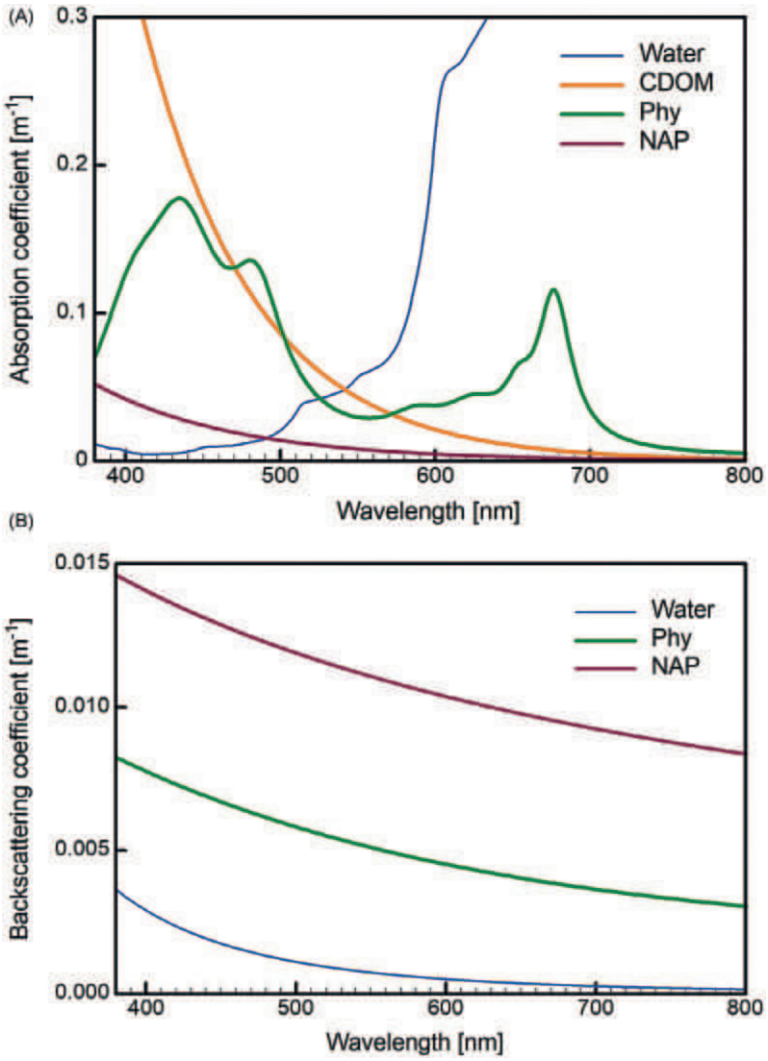

Fig. 7 Absorption (A) and backscattering coefficients (B) for oligo- to mesotrophic water, with 0.2 m^{-1} CDOM at 440 nm, 5 mg m^{-3} phytoplankton (phy) and 1 g m^{-3} non-algal particles (NAP).

Radiative transfer modeling

The radiance reflected by an object in the natural environment cannot be calculated exactly because the underlying radiative transfer equation (RTE) has no analytical solution for all practical situations. In hydrologic optics, L_u depends on the details of atmospheric conditions, the water surface geometry and the spatial distribution of a variety of molecules and particles in the water. The RTE can be solved approximately using coupled models of the atmosphere, the water surface, the water body, and in case of shallow waters, additionally of the bottom. Zhai et al. (2009) provide an overview of methods to solve the RTE and radiative transfer codes available for a coupled atmosphere-ocean system.

Several schemes are available for numerically solving the RTE in hydrologic optics, but the commercial software Hydrolight (Mobley, 1994) is most widely used. It is computationally too expensive for many applications in remote sensing, and the achievable accuracy is often limited by the variability in IOP rather than by numeric accuracy. RTE solvers are therefore often used to create a database of reference spectra for different combinations of the relevant environmental parameters. These pre-calculated spectra are then used as look-up tables and training data to derive analytical equations in the application case. Analytical equations obtained in this way are called semi-analytical models (Sokoletsky and Shen, 2014).

An example how R_{rs} of optically deep water depends on water constituents is given in Fig. 8 (Giardino et al., 2018). The plots were created using the publicly available software WASI (Gege, 2004) and its implementation of the semi-analytical R_{rs} model of Albert and Mobley (2003). The simulations are based on the IOPs of Fig. 7. Simulating r_{rs} or R_{rs} from known concentrations and IOP is called forward modeling, while obtaining IOP or concentrations from measured R_{rs} spectra is called inverse modeling. The inverse problem has often no unique mathematical solution (IOCCG, 2006) because different water compositions can produce very similar R_{rs} spectra.

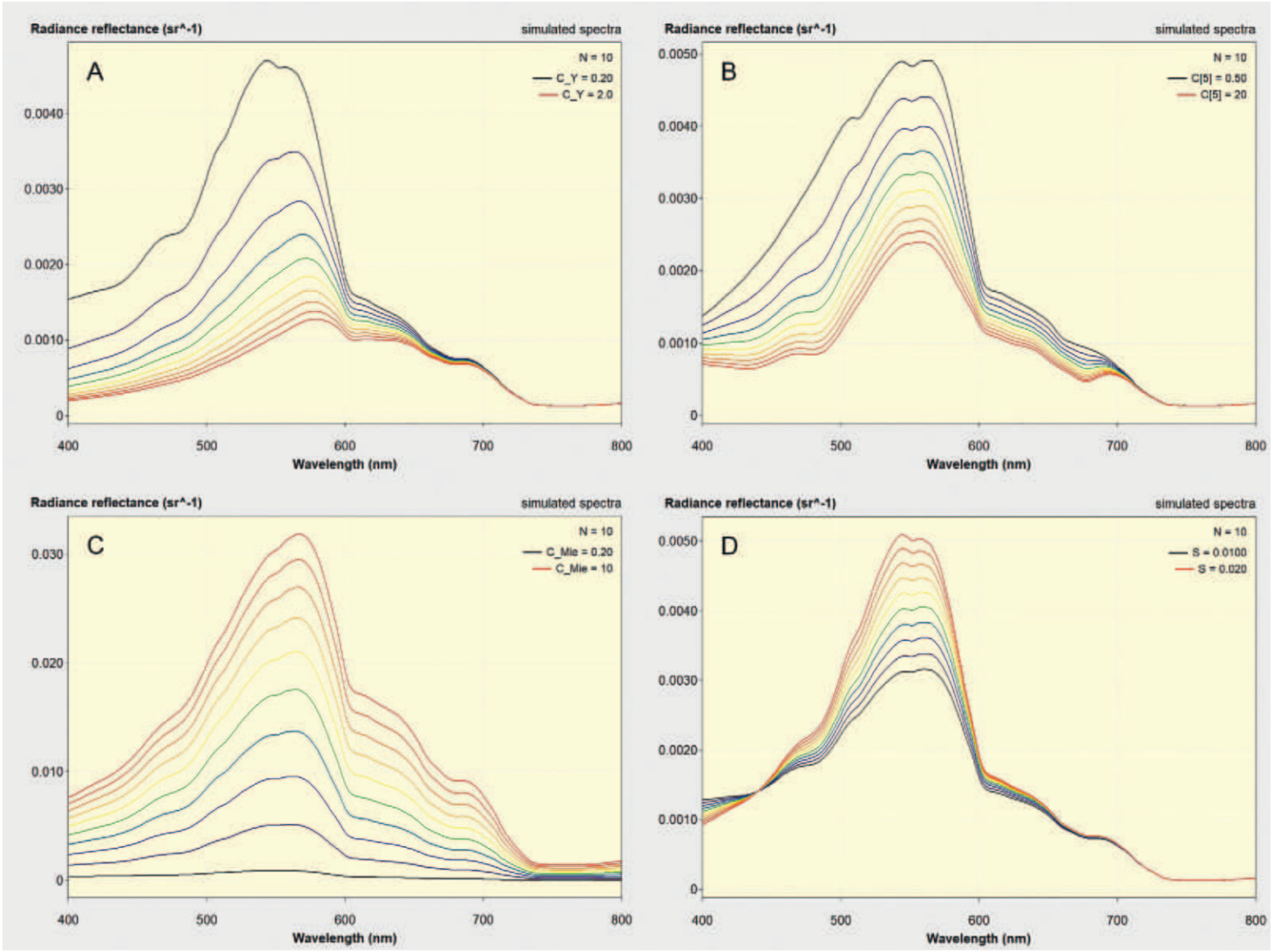

Fig. 8 Simulated remote sensing reflectance of optically deep water, using the IOP of Fig. 7 with alterations in one parameter per panel. (A) CDOM absorption at 440 nm, range 0.2–2 m^{-1}; (B) chlorophyll-a, range 0.5–20 mg m^{-3}; (C) NAP, range 0.2–10 g m^{-3}; (D) spectral slope of CDOM absorption, range 0.01–0.02 nm^{-1}. Modified from Giardino C, Brando VE, Gege P, Pinnel N, Hochberg E, Knaeps E, Reusen I, Doerffer R, Bresciani M, Braga F, Foerster S, Champollion N and Dekker A (2018) Imaging spectrometry of inland and coastal waters: state of the art, achievements and perspectives. *Surveys in Geophysics* doi: 10.1007/s10712-018-9476-0.

Bulk optical properties in aquatic research

Secchi depth

Since the 17th century, sailors and naturalists have lowered objects such as plates, tins, kitchen gear, painted thermometers or copper balls in the ocean, and recorded the depth at which they disappear (Wernand, 2010). Pietro Angelo Secchi (1864) advanced this measurement practice to a scientific standard. Secchi depth is usually measured with a white Secchi disk of 30 cm diameter in oceans, or a black and white Secchi disk of 20 cm size in lakes (Fig. 9).

Secchi disk measurements are relatively robust under different observation conditions, because the human eye adapts well to brightness variations of the ambient light. Secchi indicated that observation must be done at nadir over a water surface that is shaded by a ship or the observer. His suggestion to prevent surface reflectance by using an aquascope was however discarded in practical usage (Pitarch, 2020). The use of Secchi depth as a measure for water transparency recently experienced a revival in citizen science, for example in the scope of the Secchi disk study by the Secchi Disk Foundation, or the Secchi dip-in by the North American Lakes Management Society (see Supplementary Material in the online version at https://doi.org/10.1016/B978-0-12-819166-8.00041-4).

According to classical visibility theory, the Secchi depth was hypothesized to be inversely proportional to the sum of the encompassed water's diffuse and beam attenuation coefficients. It was shown recently that the corresponding assumptions for visibility in air are inappropriate in water, and therefore the inverse of the average diffuse attenuation coefficient of radiance reflected by the target should be used to model Secchi depth (Lee et al., 2015). Secchi depth estimates are also available from satellite remote sensing, since both diffuse attenuation and R_{rs} can be expressed in terms of bulk absorption and scattering (Lee et al., 2016).

Forel-Ule scale

When lowering objects into surface waters, they not only disappear but also change their color due to the selective transmissivity at different spectral wavelengths. In the late 19th century, F. A. Forel and W. Ule proposed mixed chemical compounds to frame a comparator scale for the color of natural waters (Fig. 10). The resulting Forel-Ule color scale comprises of eleven standards with blue to green hues (FU 1–11) and ten standards with blue-green to brown hues (FU 12–21). The scale is used to match the color of a Secchi disk at half the Secchi depth, and is similarly popular in citizen science.

The preparation protocol for the reference compounds of the Forel-Ule color scale was recently revised, and transmission measurements allow transferring the standards to the CIE chromaticity diagram (Fig. 11) by means of hue angles and dominant

Fig. 9 Secchi disk being lowered into the water of Greifensee (Switzerland).

Fig. 10 Early color reference scale owned by F.A. Forel (1841–1912), composed according to Forel (1895). Courtesy collections du Musée du Léman.

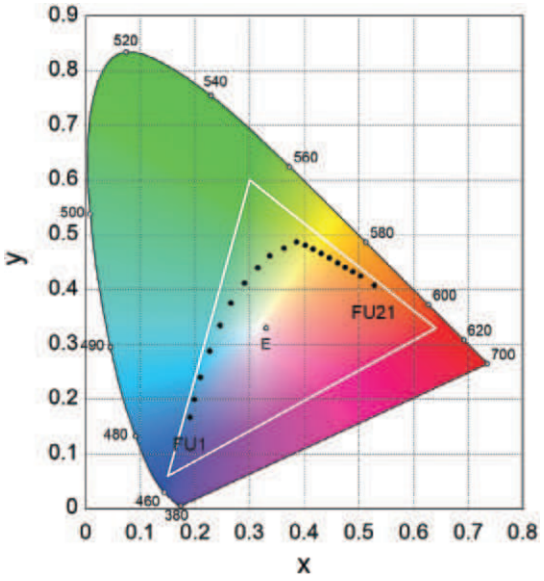

Fig. 11 Chromaticity diagram of the 21 FU standards. Based on Novoa S, Wernand MR and van der Woerd HJ (2013) The Forel-Ule scale revisited spectrally: Preparation protocol, transmission measurements and chromaticity. *Journal of the European Optical Society* **8**: 13057.

wavelengths (Novoa et al., 2013). Hue angles and dominant wavelengths can also be derived for remotely sensed R_{rs} (Van der Woerd and Wernand, 2018). By giving each hue angle a membership for its two radially adjacent Forel-Ule classes, reflectance can effectively be related to the Forel-Ule scale, which inspired the mapping of Forel-Ule classes from global Earth observation satellite data despite the scale's limited sensitivity to oligotrophic oceans (Pitarch et al., 2019).

Optical water types

Estimating water constituents from spectral reflectance is complicated by the diverse composition of natural surface waters, the diversity of their constituents, and the information content available in a limited number of spectral bands. Statistical clustering of reflectance spectra is an efficient means to improve the accuracy for an ensemble of retrieval algorithms against the background of missing universal solutions (Moore et al., 2014).

The optical water types obtained in such manner can be described in terms of their mean reflectance and typical bio-physical properties, such as the range of phytoplankton pigment concentrations or Secchi depths occurring for each of them. But the use of optical water typologies from reflectance clustering is currently limited to remote sensing signal interpretation. Most notably, the Copernicus Land Service provides trophic state estimates for more than 4000 lakes worldwide based on an ensemble approach for Optical Water Types (Neil et al., 2019; Spyrakos et al., 2018).

Remote sensing applications

Field spectrometry

Measuring reference reflectance with field spectrometers at ground level is a fundamental principle for remote sensing of all types of land cover. Such measurements, often referred to as ground truth, are used to validate satellite-observed, atmospherically corrected reflectance. Moreover, they serve as input for radiative transfer models that allow the calculation of expected upwelling radiance at the top of atmosphere, which can then be used to adjust the radiance measurements by satellites. This technique is referred to as vicarious calibration. More recently, advances in field spectrometer design promote ground measured reflectance and derived bio-physical parameters as a user-friendly water quality monitoring tool.

Vicarious calibration is essential for ocean color satellite missions, and a number of internationally coordinated programs aim to establish networks of operational ground-based facilities to acquire high-quality measurements of reference reflectance. The AERosol RObotic NETwork comprises of ground-based sun photometers for aerosol monitoring and part of the NOAA Observing System Architecture. It comprises of an Ocean Color component, AERONET-OC, whose observatories measure also water-leaving radiance in marine and lacustrine sites (Zibordi et al., 2010). RadCALNet by CEOS (https://www.radcalnet.org) and WATER-HYPERNET by ESA and BELSPO (https://waterhypernet.org/) federate similar networks of above-surface radiometers with multi- and hyperspectral resolution, respectively. The experimental Thetis profiler in Lake Geneva (Switzerland, Fig. 12) performs comparable measurements below the water surface while simultaneously acquiring IOP measurements.

Field spectrometer measurements are subject to lower uncertainty than atmospherically corrected satellite observations, and their spectral resolution is about one order of magnitude higher than most satellite sensors'. Therefore, water quality estimation from ground measured reflectance is a viable option for monitoring smaller water bodies, where the spatial resolution provided by satellites is dispensable. Various spectroradiometers can be used for this purpose, including those designed for satellite vicarious calibration measurements, as well as less precise but more user-friendly handheld devices (Hommersom et al., 2012). A main limitation of this approach, sometimes referred to as close-range remote sensing, is the compliance of methodologies and the water quality parameters they yield with monitoring requirements and sampling protocols (Bowling et al., 2017).

Satellite Earth observation

Color represented by reflectance is perhaps the most pivotal parameter in satellite remote sensing. For decades it has been input to most methods for the retrieval of water quality parameters in deep, or benthic substrates in shallow waters. The Steering Committee of the Global Climate Observing System (GCOS) is evaluating lake color in terms of spectral water-leaving reflectance as an Essential Climate Variable (ECV; WMO, 2016). In fully normalized form, water-leaving reflectance is independent of Earth-Sun distance, illumination angle and atmospheric attenuation and hence comparable (Gordon and Wang, 1994).

Satellite sensor measurements are affected by distinctive atmospheric effects, viewing angle and sun elevation dependence (see also Fig. 5). Backscattering by gas molecules and aerosols can easily exceed the signal reflected on the ground, especially over dark targets such as water bodies, and in short wavelengths. In consequence, surface waters appear brighter and their hue is usually blue when seen from space (Fig. 13, top). These effects can be rectified using image-based estimates of atmospheric optical density, which yields a water body's outer sight (Fig. 13, bottom). The water's true color is revealed when also reflection and refraction at the air-water interface are accounted for, which shifts the hue further towards long wavelengths, and yields often green to brown colors (Fig. 5, right and Fig. 13, bottom).

Colorimetry provides a framework for color calculations with reference to the light spectrum as resolved by cone fundamentals. This allows a representation of spectral reflectance vectors as scalars such as hue angle or dominant wavelength (Fig. 14, left), and ultimately as Forel-Ule classes (Fig. 14, right). Based on this approach, lake color inventories from satellite remote sensing are

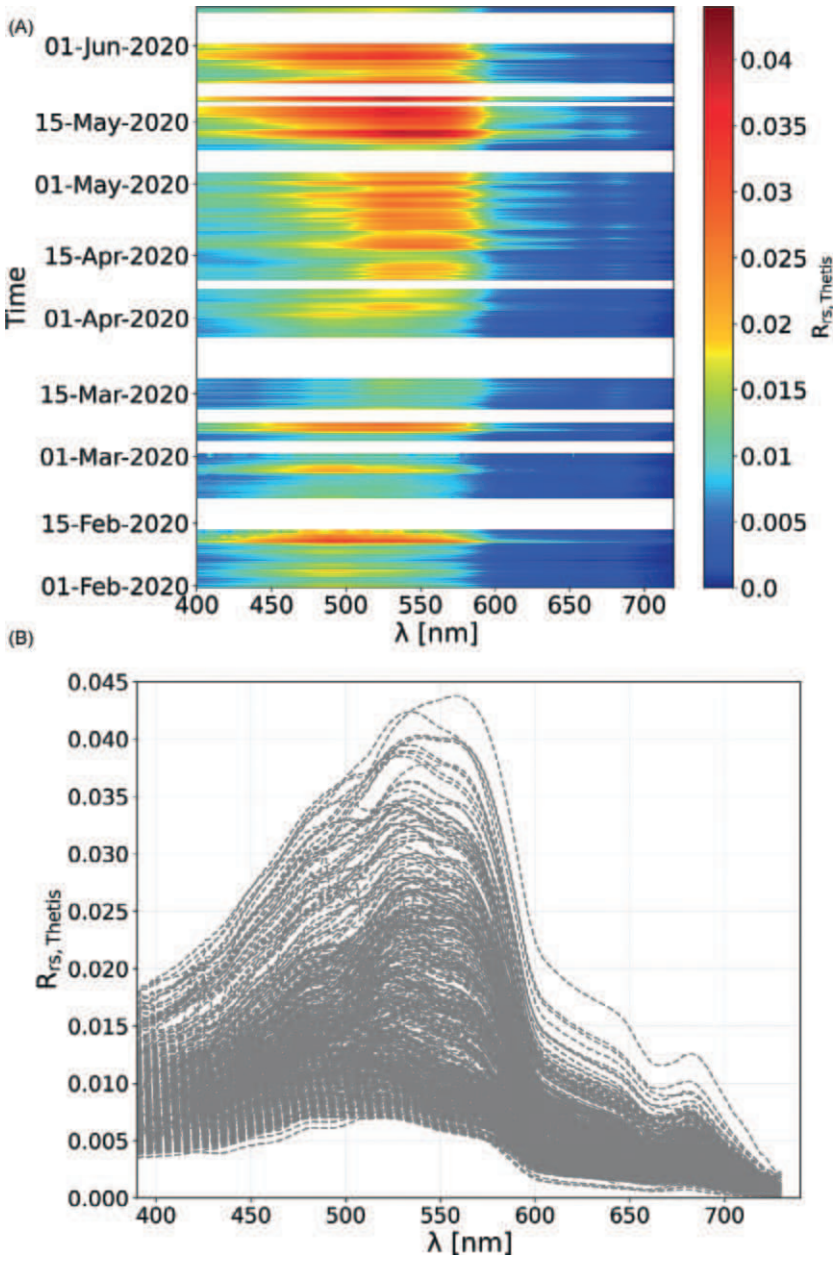

Fig. 12 Spectral remote sensing reflectance measured by the Thetis profiler in Lake Geneva (Switzerland). (A) Reflectance magnitudes increase with phytoplankton growth both seasonally and incidentally. (B) Due to higher chorophyll-a content, higher reflectances feature lower blue-to-green ratios and more prominent absorption and fluorescence emission features at 650–700 nm. Courtesy A. Irani Rahaghi and C. Minaudo.

available for lakes in New Zealand (Lehmann et al., 2018), as well as for lakes (Topp et al., 2021) and rivers (Gardner et al., 2021) in the United States. They convey visible, large-scale changes in lake water quality in the most impressive manner. It should be noted that the definition of colorimetric products is not as rigorous as for water-leaving reflectance and other spectro-radiometric parameters. They imply that the reflectance acquired by opto-electronic sensors corresponds to the radiance perceived by human eyes and cognition. Nonetheless, the emerging, indicative use of colorimetry algorithms in remote sensing might revive color assessments despite the fading use of the Forel-Ule scale in monitoring practice.

Secchi depth is a widely-used indicator for transparency monitoring, for example with regards to the Sustainable Development Goals (Shen et al., 2020). It is also used in the forcing of hydrodynamic models (Baracchini et al., 2019). Remote sensing algorithms based on the revised optical theory for Secchi depth retrieval (Lee et al., 2016) are accordingly popular, and their use was demonstrated in dozens of lake-specific studies. Latest advances in algorithm development should also enable larger scale application through a revised parameterization of attenuation anisotropy (Jiang et al., 2019).

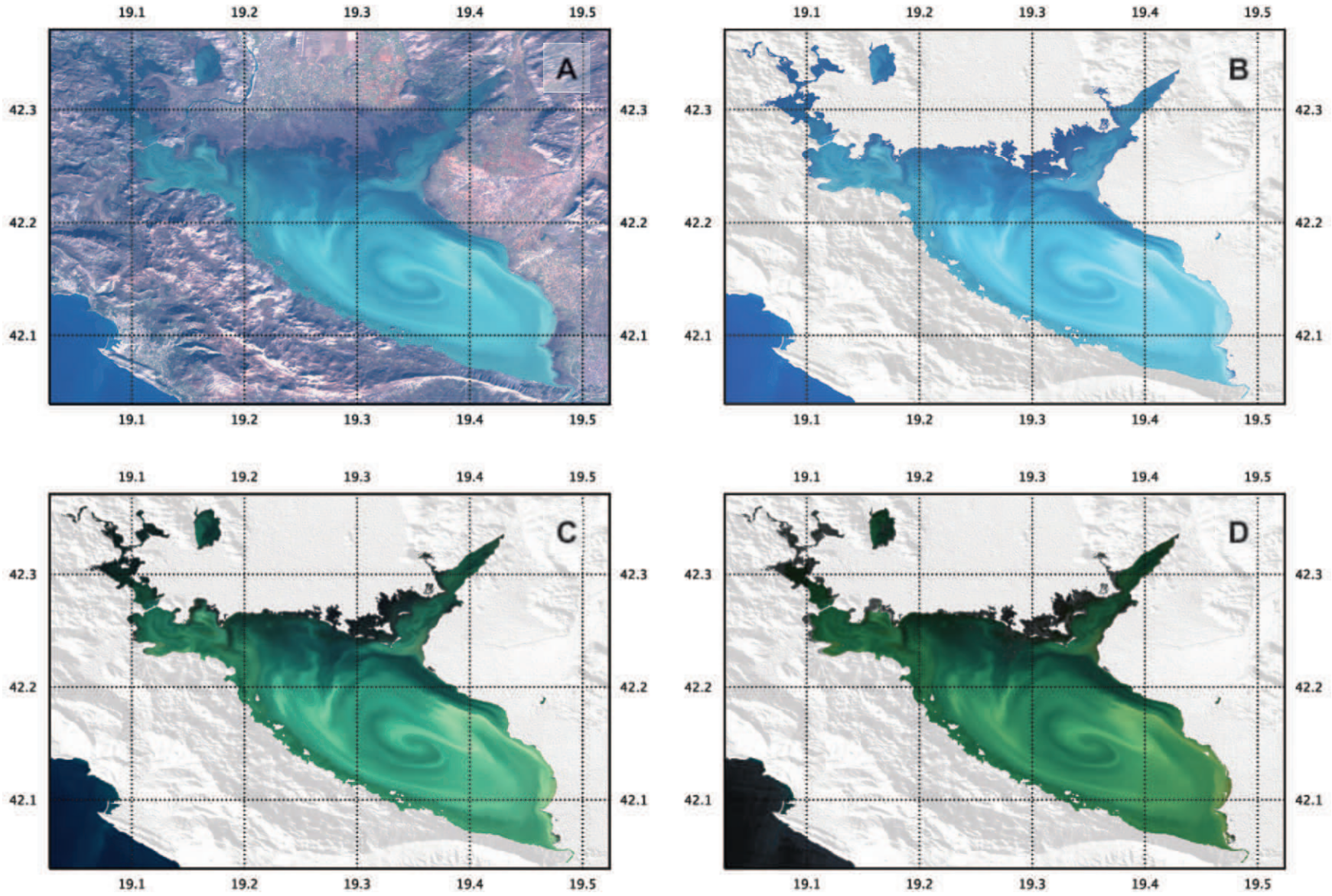

Fig. 13 Sentinel-2B 10 m RGB composites of Lake Skadar (Albania/Macedonia), 21 February 2020. Top-of-atmosphere reflectance for (A) the full view region and (B) after land-water masking, as well as (C) Sen2Cor bottom-of-atmosphere reflectance and (D) POLYMER normalized water-leaving reflectance. All images' and bands' contrasts correspond to 0–15% reflectance. Sentinel data courtesy of ESA, base map SRTM courtesy of USGS.

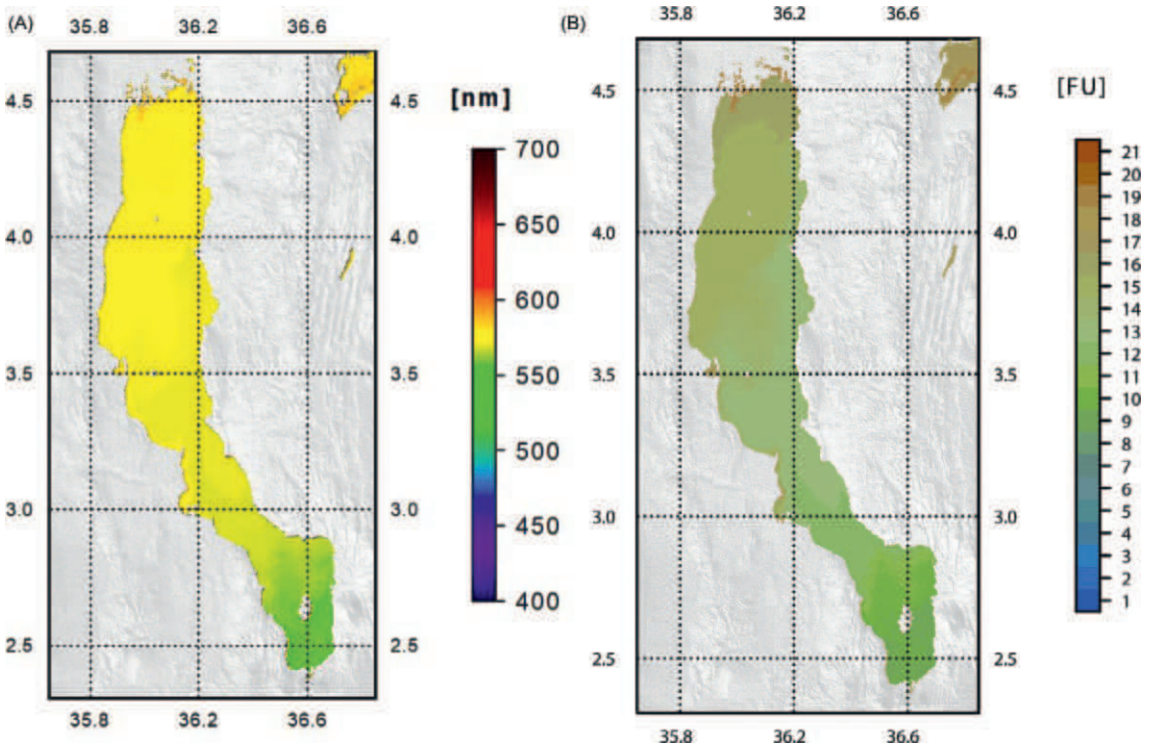

Fig. 14 Sentinel-3B 300 m colorimetry products of Lake Turkana (Ethiopia/Kenya), 15 December 2020. (A): Dominant wavelength in the range 560–580 nm. (B): Pseudo-Forel-Ule water types in the range 9–19. Sentinel data courtesy of ESA, base map SRTM courtesy of USGS.

Synthesis

Measuring and interpreting water color under natural illumination comes with challenges that can be addressed both empirically and analytically. Robust, empirical techniques based on the human perception of color, namely Secchi depth and the Forel-Ule scale, provide low-threshold water quality monitoring techniques for a large audience. Remote sensing techniques, on the other hand, comprise measurements and retrieval methods that are based on a rigorous framework of radiant definitions and radiative transfer equations, which are predominantly used by Earth observation specialists. They allow for the retrieval of bio-physical parameters such as water-leaving reflectance or chlorophyll-*a* concentration, which feed directly into recent global environmental monitoring initiatives such as GCOS or the UN Agenda for Sustainable Development. The further development of such techniques is thus the main priority. Remote sensing and measures based on human color perception are however theoretically linked by the colorimetry framework, and practically complementary in many use cases.

Knowledge gaps

- How are the Forel-Ule classes, the Optical Water Types and the bio-physical properties of ambient waters related to each other?

See Also: Structures and functions of Inland Waters - Lakes: pH of Inland Waters

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https://www.eyeonwater.org/apps/eyeonwater-colour—Forel-Ule classification using a smartphone.

Ocean optics
https://ioccg.org/resources/software/—Water Color Simulator and other software.
https://ioccg.org/what-we-do/training-and-education/ioccg-sls-2018/—Training course.

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Currents in Well-Mixed Layers

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie-Elodie Perga and Damien Bouffard.

Glossary

Anisotropy Property of being directionally dependent, as opposed to isotropy; for instance, turbulent fluxes are typically dependent on the direction (in particular, vertical vs. horizontal).
Barotropic flow A flow that it is driven by the horizontal gradient of the free-surface elevation.
Circulation Large-scale description of the currents occurring in a lake.
Coriolis acceleration/force Fictitious acceleration of particles moving in a rotating frame of reference. Earth rotation tends to deviate the flow to the right (left) in the northern (southern) hemisphere.
Eddy viscosity Space- and time-dependent coefficients that relate the average shear stress within a turbulent flow to the velocity gradient (first proposed by Boussinesq in 1877), formally analogous to the kinematic viscosity in laminar flows for Newtonian fluids.
Gyre A circular pattern of currents at the surface of or within a water body.
Momentum Product of mass and velocity of a particle, its time derivative is a force; in fluid dynamics, momentum equations formulated for the continuum mechanics are the equivalent to the Newton's second law of motion for particles.
Newtonian fluid A fluid in which the shear stresses are linearly related to the local shear rate, so that viscosity is constant and independent of the stress.
Secondary circulation A component of the flow field that develops as a result of the interaction between the dominant velocity (e.g., directly driven by the wind) and other physical processes (e.g., Coriolis acceleration).
Stratification Vertical structure of the water column with layers of different density; in a stable stratification, water density increases downwards (in the direction of gravity acceleration).
Turbulence Fluid motion characterized by instability that results in chaotic changes in pressure and flow velocity, which strongly enhance momentum exchange (a process modelled using eddy viscosity, depending on the flow field); different from the laminar flow occurring in parallel layers, where momentum is transferred only by means of dynamic viscosity (a property of the fluid).

 https://doi.org/10.1016/B978-0-12-819166-8.00012-8

Introduction

Understanding lake circulation

Water movements in lakes are generated and controlled by forces acting both on the boundaries of the water body (free surface, lake bottom) and within its volume. The wind stress on the lake surface is often the most important force producing a direct circulation, but other processes can interact with it or even predominate in specific conditions. An emblematic example is the effect of the heat exchanged with the atmosphere (or with the bottom sediments) which, by altering the water density locally, can produce convective motions (buoyancy-driven flows) leading to complete lake overturn in some cases. Another important contribution may come from inflowing waters, which introduce fluxes of mass, momentum and heat into the lake: especially during floods, the effect on the lake's movements can be substantial. Factors such as the spatial variation of the atmospheric pressure or the presence of tides are usually considered unimportant unless the lake is extremely large. In addition, water movements can be affected by the Coriolis effects due to Earth rotation.

From this introductory description, it appears that the prediction of currents in lakes is a difficult task, which depends on many physical factors and on the atmospheric forces exerted at the air-water interface. Nowadays, numerical models are routinely used to simulate the transport within lakes, but a proper exploitation of their capabilities requires both experience about the model and in-depth understanding of the physical processes. Fig. 1 shows a beautiful example of a large gyre in Lake Geneva retrieved from

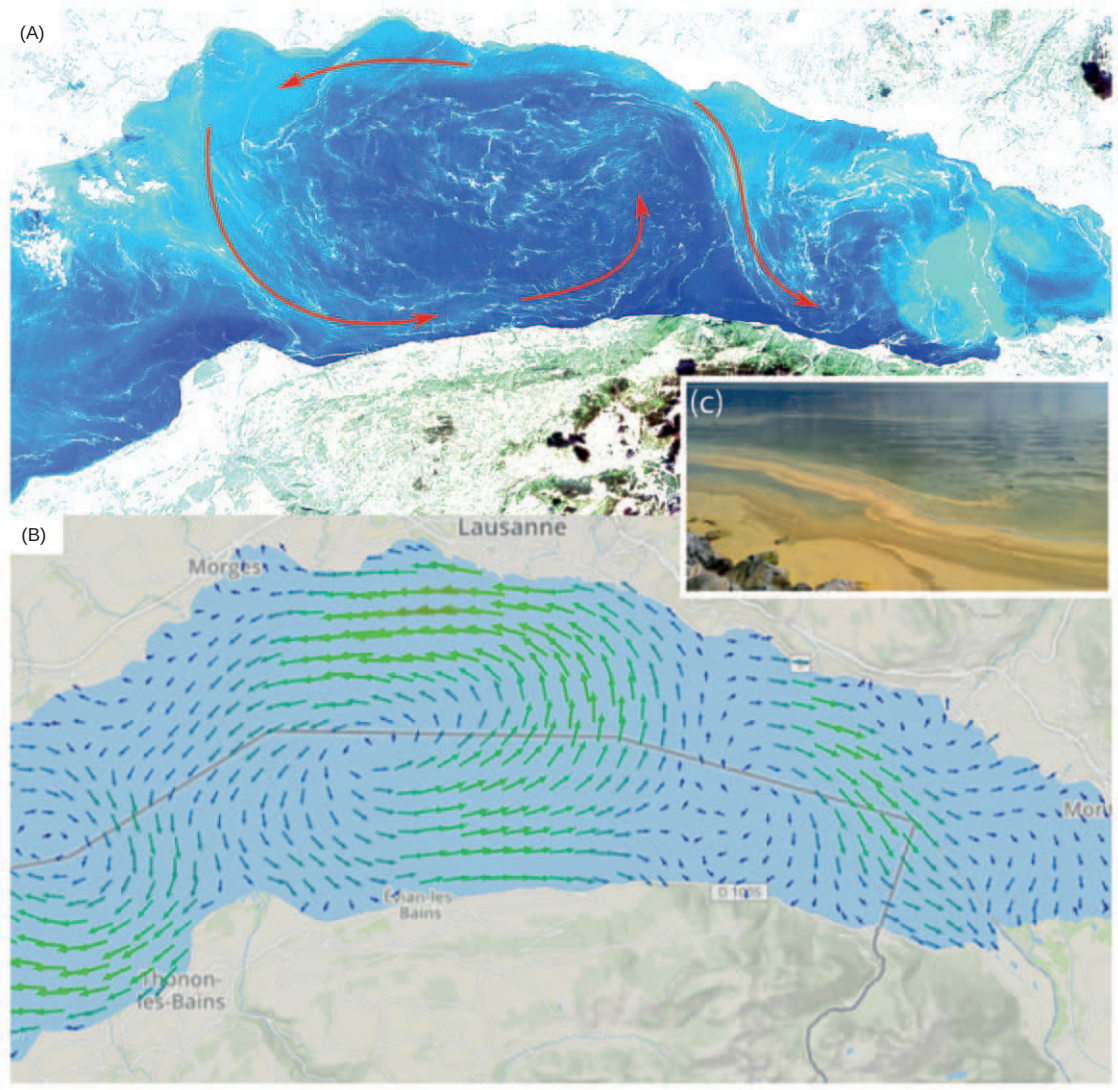

Fig. 1 An example of a large gyre in the central region of Lake Geneva (Switzerland-France) highlighted by the presence of pollen at the surface. (A) Satellite imagery from Sentinel 2, where colours have been altered to show the regions with higher concentration of pollen (lighter blue); red arrows represent a qualitative reconstruction of the main horizontal circulation. (B) Numerical simulation of the flow field obtained by Meteolakes (http://meteolakes.ch/); arrows represent the reconstructed velocity field, with colours tending to green indicating faster movements. (C) Source of pollen at the lake's northern shore (Photo: Hannah Chmiel, EPFL). Source: https://www.eawag.ch/en/news-agenda/newsportal/news-detail/pollen-reveals-huge-gyre-in-lake-geneva/, modified by altering the colours and adding the red arrows in panel A.

satellite imagery thanks to the presence of a large quantity of pollen, transported at the surface from the shores to the interior of the lake. Numerical simulations are able to reconstruct the main dynamics, even though some details cannot be captured exactly (Fig. 1B): at the current state of knowledge, a blind faith in numerical simulations is not recommended. Hence, it is essential to have a physical intuition of causes and effects, which is possible only by knowing the physics of the system and the limitations intrinsic in any model of the real world.

In this article, we aim at helping the inexpert reader to approach the physics behind water motion and the language in which it can be effectively described, i.e., the mathematics of partial differential equations (PDEs). As an introduction to such a challenging topic, we will refer to some simple cases that allow for analytical solutions. Due to lack of space, the derivation of these solutions is provided as Supplementary Material in Data 1 in the online version at https://doi.org/10.1016/B978-0-12-819166-8.00012-8.

We will focus our attention on the case of spatially constant water density ρ (homogeneous water body, also indicated as well-mixed). However, it is essential to be reminded that water movements are strongly affected by the presence of density stratification, which in natural lakes is mostly associated with water temperature gradients, although dissolved substances can also alter the density significantly. In this context, the assumption of constant density can be limited to a single well-mixed layer, where—as a first approximation—the velocity field can be described by neglecting baroclinic effects, that is, those processes where gravity interacts with density gradients.

We will proceed even further with the simplifications and consider only the water motion that is induced by the action of wind at the lake surface. For this purpose, atmospheric models are increasingly used to provide proper boundary conditions to lake models. Although considering the spatial and temporal distribution of the wind is extremely important, here we examine only cases where the wind field is simplified. The simplest case is when the wind forcing is steady or can be approximated by analytical functions. Analytical solutions derived in this case serve as conceptual tools to understand the dynamics of more complex cases.

The transmission of forces in fluids

Wind-driven flows receive an input of momentum flux at the lake surface, which diffuses into the water body entraining the water below until possibly reaching a steady state (Fig. 2). In Newtonian fluids, when the flow is laminar (i.e., for sufficiently low values of the Reynolds number) this process is due to the viscous stress between adjacent water volumes moving with different velocity. For a unidirectional flow with velocity u varying only with z (please refer to Table 1 for the notation), the shear stress can be expressed as

$$\tau = \mu \frac{\partial u}{\partial z} \tag{1}$$

where the dynamic viscosity μ, or equivalently the kinematic viscosity $\nu = \mu/\rho$, is a property of the fluid at a given temperature.

Velocities in lakes are typically low. Nevertheless, the flow tends to be turbulent in most cases, especially where density stratification does not inhibit the vertical movements. The traditional procedure of averaging high-frequency turbulent oscillations leads to the appearance of additional stresses enhancing the exchange of momentum in the averaged flow field: they have been termed Reynolds stresses. In the so-called Boussinesq model, a Fickian closure (i.e., the same as in Eq. (1) for the viscous stress in laminar flows) is adopted for Reynolds stresses, introducing the concept of eddy viscosity in analogy with the kinematic viscosity. Then, the total shear stress is computed as

$$\tau = \rho(\nu + K)\, \frac{\partial \bar{u}}{\partial z} \tag{2}$$

where $\bar{u}$ is the turbulence-averaged velocity (hereafter, we will skip the overbar and use u in the general case to simplify the notation) and ν is negligible with respect to K in well-developed turbulent flows.

Different from the laminar case, the eddy viscosity K is not a property of the fluid, but of the flow itself, making it intrinsically variable in space and time. Turbulence models of various complexity have been developed since Reynolds' pioneering contribution in 1895 (e.g., Pope, 2000; Wilcox, 2006). Among them, algebraic relations for the eddy viscosity have been proposed to describe simplified conditions. We will rely on these approximations, and eventually adopt constant and uniform values, to derive analytical solutions.

Some questions

With all these simplifications in mind, we consider some idealized geometries to detect which processes primarily affect the development of the flow field. Having said that wind-driven flows are locally forced at the air-water interface, what modulates the global response of the water body? Which are the effects of a given morphology (i.e., bathymetry) of the lake? How important is the spatial distribution of the wind field? How does it interact with the turbulent exchanges and in particular their anisotropic behaviour? Does Earth's rotation affect the flow field, and in which cases can it be neglected? These are some of the questions we want to tackle in this article.

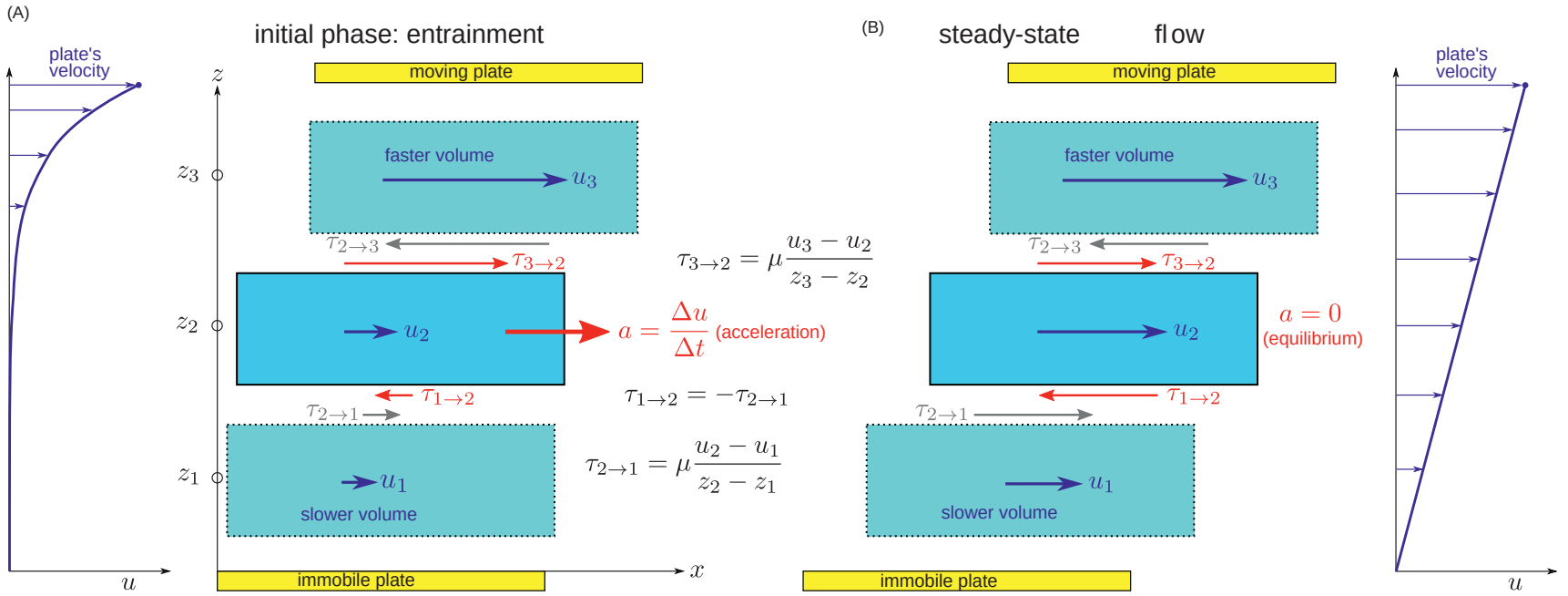

Fig. 2 Conceptual scheme illustrating the vertical transfer of momentum in a Couette laminar flow starting from still water in a Newtonian fluid. The figure considers only three layers, but the process is continuous along the vertical. (A) During the initial phase, the plate moving at the top entrains the upper volume (level z_3). The velocity difference with the central layer (level z_2) produces a shear stress that tends to accelerate it, while the slower volume at the bottom (level z_1) exerts a drag force that slows it down. The net force (for the central element having dimensions Δx and Δz, with $\Delta y = 1$) is $\rho \Delta x \Delta z\, a_2 = \tau_{3\to2}\Delta x - \tau_{2\to1}\Delta x$, which gives the acceleration $a = \rho^{-1}\, d\tau/dz$ in a continuous description. (B) A steady-state flow is reached when the central volume moves with a velocity for which the shear stresses at the top and at the bottom are balanced, and the same occurs for the lower layer, so that none of the layers is accelerated. Note that in a Newtonian fluid the shear stress depends on the difference between velocities and not on the relative displacement of the layers (different from a solid). The qualitative sketch is also valid for turbulent flows, where the momentum transfer is mostly due to eddy viscosity.

Table 1 List of symbols used in the article and their dimensional units (L: length, T: time, M: mass).

t	time	T	g	gravitational acceleration	LT^{-2}
x, y	horizontal coordinates	L	f	Coriolis parameter	T^{-1}
z	vertical coordinate (pointing upwards)	L	p	pressure	$ML^{-1}T^{-2}$
u, v	horizontal components of the velocity vector	LT^{-1}	ρ	water density	ML^{-3}
w	vertical component of the velocity (positive upwards)	LT^{-1}	ν	kinematic viscosity	L^2T^{-1}
U, V	depth-averaged velocities	LT^{-1}	A	horizontal (eddy) viscosity	L^2T^{-1}
h	depth of the layer	L	K	vertical (eddy) viscosity	L^2T^{-1}
η	free surface elevation	L	τ	shear stress	$ML^{-1}T^{-2}$
B	width (in the direction orthogonal to the main flow)	L	τ_w	wind stress at the free surface	$ML^{-1}T^{-2}$
W	wind speed	LT^{-1}	τ_b	shear stress at the bottom	$ML^{-1}T^{-2}$
ζ	depth-averaged vorticity	T^{-1}			

Governing equations

Shallow water approximation

Different approximations can be used to describe the flow field in natural water bodies such as lakes. The most general formulation for Newtonian fluids, like water, is given by the three-dimensional (3D) Navier-Stokes equations, which express the Newton's second law (i.e., acceleration is proportional to the net force, and inversely proportional to the mass) for the continuum. Unfortunately, these equations are not solvable in real cases because flow instabilities, known as turbulence (e.g., Pope, 2000), modify the internal forces. The Reynolds-Averaged Navier-Stokes (RANS) equations describe the average dynamics of turbulent flows by adopting closure relationships, as in Eq. (2), for the transfer of momentum, mass and energy due to turbulent fluctuations. The choice of the turbulence model for the eddy viscosity is a key issue for modern fluid dynamics.

In the so-called geophysical flows, the vertical scale of variation is typically much shorter than the horizontal scale (thence, the names "shallow water" or "long wave" approximations). Dimensional arguments suggest that the pressure p is hydrostatically distributed along the vertical direction. Hence, pressure is not explicitly present in the equations and can be obtained directly from the elevation η of the free surface (Fig. 3). For a homogeneous fluid (i.e., with constant density):

$$p(z) = p_0 + \rho\, g\, (\eta - z) \tag{3}$$

where the atmospheric pressure p_0 will be assumed uniform (and hence neglected) in the following considerations.

The governing equations for a homogeneous layer in direct contact with the atmosphere are reported in Table 2 (see equations of set *a*). As turbulence is typically anisotropic (the eddies' size is statistically smaller in the vertical direction, coherently with the

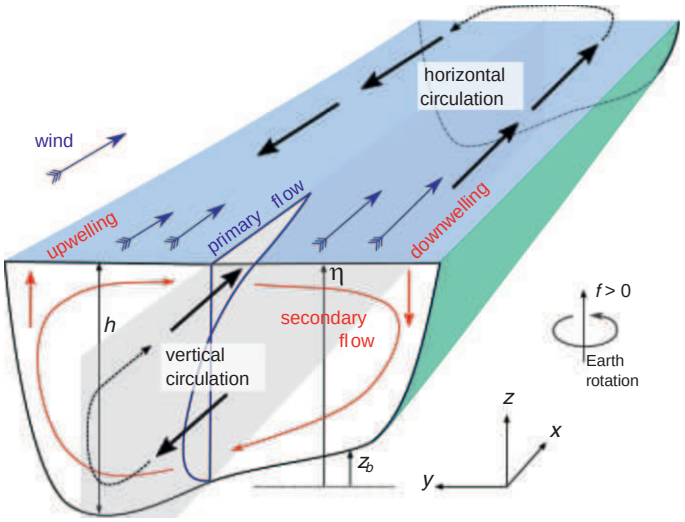

Fig. 3 Simplified geometry for the "trunk region" of an elongated lake, indicating the main notation used in the text. The primary flow can be divided into vertical (also identified as "conveyor belt" circulation, producing downwelling leeward and upwelling windward, see the grey-shaded region) and horizontal circulation (due to lateral variations of wind stress and depth). The secondary flow, due to the interaction of the primary flow with other forces (e.g., Coriolis), can produce upwelling and downwelling at the opposite shores.

Table 2 Governing equations mentioned in the text.

3D, unsteady, shallow water RANS		
(*a*.1)	*x*-momentum[a]	$\frac{\partial u}{\partial t} + u\frac{\partial u}{\partial x} + v\frac{\partial u}{\partial y} + w\frac{\partial u}{\partial z} - fv = -g\frac{\partial \eta}{\partial x} + \frac{\partial}{\partial x}\left(A\frac{\partial u}{\partial x}\right) + \frac{\partial}{\partial y}\left(A\frac{\partial u}{\partial y}\right) + \frac{\partial}{\partial z}\left(K\frac{\partial u}{\partial z}\right)$
(*a*.2)	*y*-momentum	$\frac{\partial v}{\partial t} + u\frac{\partial v}{\partial x} + v\frac{\partial v}{\partial y} + w\frac{\partial v}{\partial z} - fu = -g\frac{\partial \eta}{\partial x} + \frac{\partial}{\partial x}\left(A\frac{\partial v}{\partial x}\right) + \frac{\partial}{\partial y}\left(A\frac{\partial v}{\partial y}\right) + \frac{\partial}{\partial z}\left(K\frac{\partial v}{\partial z}\right)$
(*a*.3)	continuity	$\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0$
2D, depth-averaged, unsteady		
(*b*.1)	*x*-momentum	$\frac{\partial U}{\partial t} + U\frac{\partial U}{\partial x} + V\frac{\partial U}{\partial y} - fV = -g\frac{\partial \eta}{\partial x} + \frac{\partial}{\partial x}\left(A\frac{\partial U}{\partial x}\right) + \frac{\partial}{\partial y}\left(A\frac{\partial U}{\partial y}\right) + \frac{\tau_{wx}}{\rho h} - \frac{\tau_{bx}}{\rho h}$
(*b*.2)	*y*-momentum	$\frac{\partial V}{\partial t} + U\frac{\partial V}{\partial x} + V\frac{\partial V}{\partial y} - fU = -g\frac{\partial \eta}{\partial x} + \frac{\partial}{\partial x}\left(A\frac{\partial V}{\partial x}\right) + \frac{\partial}{\partial y}\left(A\frac{\partial V}{\partial y}\right) + \frac{\tau_{wy}}{\rho h} - \frac{\tau_{by}}{\rho h}$
(*b*.3)	continuity	$\frac{\partial h}{\partial t} + \frac{\partial}{\partial x}(Uh) + \frac{\partial}{\partial y}(Vh) = 0$
steady state, plane flow, longitudinally uniform, no Coriolis → uniform flow in the "trunk" region		
(*c*)	*x*-momentum	$0 = -g\frac{\partial \eta}{\partial x} + \frac{\partial}{\partial z}\left(K\frac{\partial u}{\partial z}\right)$
steady state, horizontally uniform, uniform eddy viscosity → Ekman spiral		
(*d*.1)	*x*-momentum	$-fv = -g\frac{\partial \eta}{\partial x} + K_0\frac{\partial^2 u}{\partial z^2}$
(*d*.2)	*y*-momentum	$-fu = -g\frac{\partial \eta}{\partial y} + K_0\frac{\partial^2 v}{\partial z^2}$
depth-averaged, steady state, longitudinally uniform, no Coriolis, → uniform flow in the "trunk" region		
(*e*)	*x*-momentum	$0 = -g\frac{\partial h}{\partial x}h + \frac{\tau_{wx}}{\rho} - \frac{\tau_{bx}}{\rho}$
unsteady, horizontally uniform, uniform eddy viscosity, no Coriolis → alternate wind		
(*f*)	*x*-momentum	$\frac{\partial u}{\partial t} = K_0\frac{\partial^2 u}{\partial z^2}$
unsteady, horizontally uniform → inertial currents		
(*g*.1)	*x*-momentum	$\frac{\partial u}{\partial t} - fv = -g\frac{\partial \eta}{\partial x}$
(*g*.2)	*y*-momentum	$\frac{\partial v}{\partial t} + fu = -g\frac{\partial \eta}{\partial y}$

[a]This approximation is not valid for flows in the equatorial region where f tends to vanish and the vertical velocity plays a role in equation (a.1).

shallow water approximation), the values of eddy viscosity along the vertical, K, and the horizontal, A, are different. In the shallow water approximation, only the x- and y-momentum equations are solved, while the z-momentum reduces to the pressure distribution (3). Then, the vertical velocity is retrieved from the continuity equation (*a*.3). The free surface η is unknown, and is usually obtained by the continuity equation integrated along the whole thickness $h = \eta - z_b$ of the homogeneous layer, with z_b the bottom elevation. This equation, labelled as (*b*.3) in the table, is expressed in terms of the depth-averaged two-dimensional (2D) velocity components $\{U, V\} = h^{-1}\int_{z_b}^{\eta}\{u, v\}\, dz$.

Steady-state approximation in a closed water body

Although the shallow water RANS equations are already a simplified version of the exact ones, they cannot be solved in general. One exceptional approximation that allows for obtaining analytical solutions is the assumption of a steady flow in a closed domain: in this idealized case, all variations in time are neglected. By dividing the domain into two parts with a surface S_γ having constant γ (but the derivation is valid for any cross-section, independent of the orientation), it directly follows from the integration of the continuity equation that the net exchange flow must be null (see Fig. 3 for the notation):

$$\int_{S_\gamma} u\, dA = \int_B U\, h\, d\gamma = 0 \tag{4}$$

Another way to interpret this condition is that the net flow must vanish as none of the two sub-domains changes its volume in time.

As a powerful conceptual tool, we will also refer to an idealized geometry used to derive analytical solutions in the past (e.g., Csanady, 1973): an elongated water body with a central prismatic "trunk region" where uniform conditions may be assumed along the main axis (x in Fig. 3) aligned with the wind. In order to help the reader understand the underlying physical processes, in the following sections we isolate the individual factors. We anticipate that all of them in general play a role in real water bodies.

Lake circulation: Unit processes

The purely vertical circulation

There is an idealized case that allows to obtain a simple analytical solution for a wind-driven flow. Let us assume a steady flow that develops exclusively in the x-z plane in an elongated lake, without any variability in the lateral direction y, neither in the geometry

nor in the forcing. Such assumption implies that we cannot consider the effect of Earth rotation, as it would couple the problem for u and v through the Coriolis acceleration. Let us further assume that, in the central trunk of this plane flow, uniform conditions are achieved, so that the continuity equation ($a.3$ in Table 2) implies that the vertical velocity is null. Hence, the x-momentum equation ($a.1$) reduces to

$$\frac{\partial}{\partial z}\left(K\frac{\partial u}{\partial z}\right) = g\frac{\partial \eta}{\partial x} \tag{5}$$

The first term describes the local imbalance between the shear stresses acting on the top and on the bottom of an infinitesimal water volume, due to velocity variations along the vertical (Fig. 2). The second term is the force resulting from the horizontal imbalance of the pressure (which is hydrostatically distributed, see Eq. 3), due to the free-surface slope. Two boundary conditions are to be specified to solve this second-order differential equation: (i) the wind stress at the free surface, τ_w; and (ii) a suitable representation of the flow resistance at the bottom, τ_b.

Fig. 4 illustrates the steady-state flow (please refer to the black lines initially; closure relations are reported in Table 3). Reconstructing the dynamics in time, we can think that the wind initially moves a thin layer of water at the surface (as in Fig. 2A). Then, the momentum is progressively transferred, by means of viscous or turbulent forces, downwards to the bottom, producing a velocity profile (Fig. 4C). The movement of the water determines a tilt of the free surface $\partial\eta/\partial x > 0$ (Fig. 4A). Integrating Eq. (5) along the vertical, we can see that three forces act on the water column:

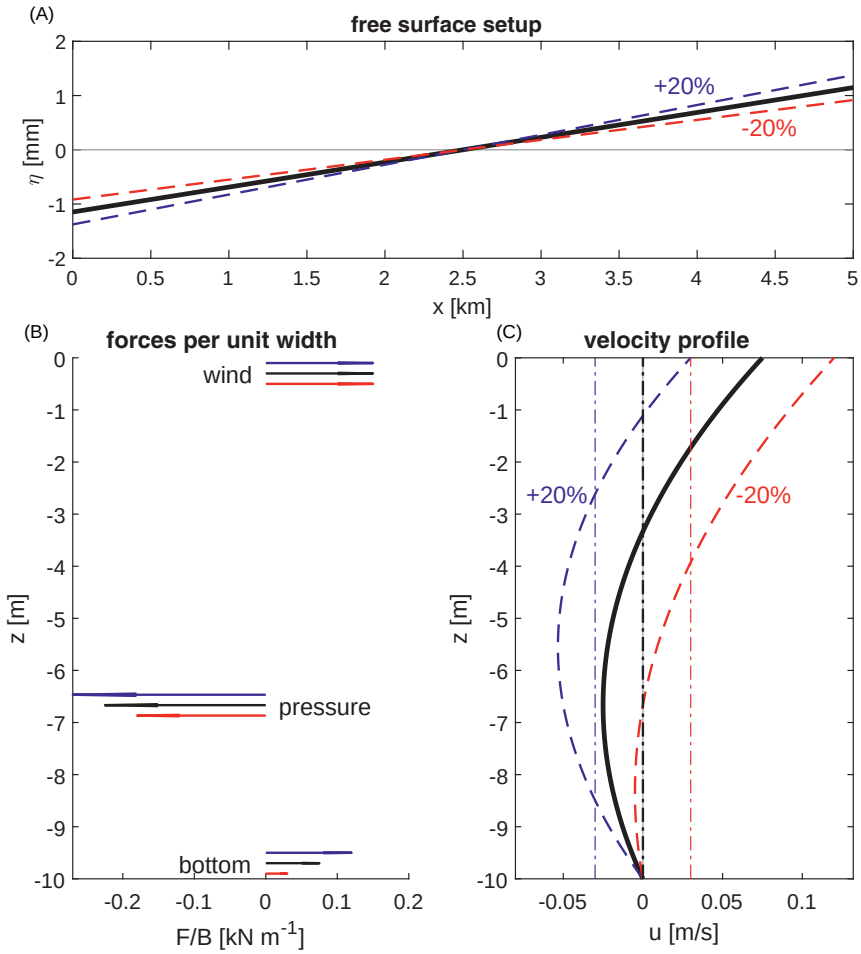

Fig. 4 Wind-driven, purely vertical, circulation for a plane flow in a closed basin, assuming steady-state conditions, uniform viscosity K_0, and no-slip ($u = 0$) at the bottom (thick black lines), compared with the results obtained altering the free surface setup by +20% (blue lines) and −20% (red lines), but for the same wind. (A) Free surface elevation along the basin respecting the steady-state condition (solid line) and modified (broken lines); note that the units are mm and km for the z- and x-axis, respectively, as the slope is very mild. (B) Force balance in the three conditions (total force F per unit width B; colours indicate the case), showing: wind force, pressure difference resulting from the free-surface slope, bottom drag (direction of the force as acting on the water). (C) Velocity profiles in steady-state balance (thick black line) and for modified setups (coloured broken lines); the corresponding depth-averaged velocity are plotted with dash-dot lines (note that only the steady-state balance respects the no-flux integral condition). [Main data: wind speed 5 m/s; depth 10 m; length 5 km; $K_0 = 10^{-3}$ m^2/s].

Table 3 Typical values and formulas for the physical parameters used in the text.

Variable	*Description/notes*	*Range of variation*
g	(approximately) constant	9.81 m/s
f	$=2\,\Omega \sin\varphi$, where:	$O(10^{-4})$ s^{-1} [a]
Ω	Earth rotation rate	7.2921×10^{-5} rad/s
φ	latitude	$-\pi/2$ to $\pi/2$
ρ	varying with temperature, pressure, dissolved substances	$\sim$1000 kg m^{-3}
A	dependent on (turbulent) flow field	$O(10^{-2}-10^{1})$ m^2/s [b]
K	dependent on (turbulent) flow field and stratification	$O(10^{-6}$–$10^{-1})$ m^2/s [b]
ν	depending on temperature	$\sim 10^{-6}$ m^2 s^{-1}
τ_w	$=\rho_a C_D W^2$, where:	$O(10^{-3}-10^{-1})$ N m^{-2} [b]
ρ_a	air density	$\sim$1.2 kg m^{-3}
C_D	drag coefficient, dependent on wind speed W	$O(10^{-3})$

[a]The symbol $O(.)$ refers to the order of magnitude of the quantity between brackets.
[b]The values are to be taken only as examples, as they depend on other variables.

$$\tau_w - \tau_b = \rho g \frac{\partial \eta}{\partial x} h \tag{6}$$

The three terms are represented in Fig. 4B as forces per unit width over the whole lake length. It is worth noting that the stress at the bottom is in the same direction of the wind stress and opposed to the horizontal component of the pressure force, as it represents the action of the boundary on the return flow in the lower part of the water column.

Assuming a null velocity at the bottom (no-slip condition) and a uniform $K \cong K_0$, Eq. (4) can be integrated twice to obtain the velocity profile

$$u(z) = \frac{z}{K_0}\left[\frac{\tau_w}{\rho} - g\frac{\partial \eta}{\partial x}\left(h - \frac{z}{2}\right)\right] \tag{7}$$

where, without loss of generality, we set $z_b = 0$ and $\eta = h$. Different profiles are possible depending on $\partial\eta/\partial x$, but only one is compatible with the requirement that $U = \int_0^h u\, dz = 0$ for a plane steady flow in a closed water body. This additional condition imposes that

$$\frac{\partial \eta}{\partial x} = \frac{3}{2}\frac{\tau_w}{\rho g h} \tag{8}$$

As a result, the downwind flow at the top is balanced by a return flow at the bottom, closing the vertical circulation exactly (the solution is reported in Table 4). The proportionality coefficient in Eq. (8) varies depending on the bottom boundary condition, being 3/2 only for the case of no-slip condition.

Fig. 4 also shows the effect of changing the free-surface setup $\eta(x)$ on the velocity profile: by increasing it (blue lines), the pressure force contrasting the flow becomes stronger and the flow is pushed back (see the negative depth-averaged velocity U in Fig. 4C). In the opposite case, flattening the free surface determines a net downwind flux, shifting a mass of water that will eventually rise the free surface downwind, thus tending to restore the equilibrium. By adding the water mass inertia to this process, periodic oscillations of the free surface can be described: they are known as *seiches* (see the last section of this article).

Despite being highly idealized, the steady-state plane flow solution helps understanding the physical driver of the return flow at the bottom and the forces acting in the system. The use of an algebraic closure for the eddy viscosity $K(z)$ does not modify the result that the shear stress varies linearly, but both the velocity profile and the setup change. The model can also be adapted to more than one layer (e.g., Heaps and Ramsbottom, 1966; Simons, 1980).

Table 4 Analytical solutions for the idealized steady-state flows in the "trunk" region.

Case	*Velocity*	*Shear stress*	*Free-surface setup*
General, with no-slip bottom boundary condition	$u = \frac{z}{K_0}\left[\frac{\tau_w}{\rho} - g\frac{\partial\eta}{\partial x}\left(h - \frac{z}{2}\right)\right]$	$\tau = \tau_w - \rho g \frac{\partial\eta}{\partial x}(\eta - z)$	$\frac{\partial\eta}{\partial x} = \frac{\tau_w - \tau_b}{\rho g h}$
Purely vertical plane flow	$u(z) = \frac{\tau_w}{\rho K_0}\frac{z}{4}\left(3\frac{z}{h} - 2\right)$	$\tau(z) = \frac{\tau_w}{2}\left(3\frac{z}{h} - 1\right)$	$\frac{\partial\eta}{\partial x} = \frac{3}{2}\frac{\tau_w}{\rho g h}$
Lateral variation of depth (with $A \cong 0$)	$u(z, y)$ as from the general solution with local $h(y)$	$\tau(z, y)$ as from the general solution with local $h(y)$	$\frac{\partial\eta}{\partial x}\int_0^B h^3(y)dy = \frac{3}{2}\frac{\tau_w}{\rho g}\int_0^B h^2(y)dy$
Lateral variation of wind stress (with $A \cong 0$)	$u(z, y)$ as from the general solution with local $\tau_w(y)$	$\tau(z, y)$ as from the general solution with local $\tau_w(y)$	$\frac{\partial\eta}{\partial x} = \frac{3}{2\rho g h B}\int_0^B \tau_w(y)dy$

Lateral vs. vertical circulation

The steady-state plane flow solution without lateral variations, derived in the previous section, can exist only in specific conditions of symmetry, which are violated in almost all real cases. In fact, four main factors may affect the velocity field: the morphology of the lake (i.e., bathymetric variations), the spatial variability of the wind forcing, the effect of Earth rotation, and the anisotropy of turbulent fluxes. All these factors induce a spatial variability of the flow field, both in the vertical direction (as in the previous case) and in the horizontal direction. While quite elaborated models have been proposed to analyse them (e.g., Simons, 1980; Winant, 2004), here we rely on the extension of the simple arguments introduced above.

Effect of variable depth

We start by showing the effect of a variable bathymetry in a real lake (Fig. 5), which has a round shape with a deeper region in the middle. The circulation that develops, represented in terms of depth-averaged velocity, is structured into two gyres, with the downwind flow at the shores and a return upwind current in the middle. How is it possible that the flow in the deeper region is against the wind? Although this case can be hardly described using a "trunk" approximation, we can exploit the idealized case to understand the underlying dynamics.

We focus on the effect of a lateral variation of the depth, neglecting Earth rotation and assuming a uniform wind over the lake. Moreover, we neglect the lateral exchange of momentum that a variable velocity would be subjected to (i.e., $A \cong 0$), which means isolating individual water columns (the effect of this assumption will be discussed later). Thus, in the trunk region, Eq. (5) continues to be valid locally, as well as the procedure to obtain the velocity profile (7). What is different is the variability of the depth $h(y)$, while the values of τ_w and $\partial\eta/\partial x$ do not vary along y (the former by assumption, the latter because a different slope would produce a lateral slope at different x). Therefore, $\partial\eta/\partial x$ can be determined as a function of τ_w by means of the integral condition (4) over the cross-section, yielding a balance similar to that in Eq. (7) but including the lateral variation of h (see Table 4). Hence, it is possible to determine the distribution of the shear stress and the flow field in the whole cross-section (Fig. 6).

Velocity with an opposite sign with respect to the wind occurs at the bottom in the deeper region (qualitatively similar to the vertical circulation in the plane flow), while the sign is aligned with the wind in the shallower region (Fig. 6B). Hence, a horizontal circulation should exist to balance the downwind flow in the shallow region (typically, close to the shore) with a return flow in the deep water (the lake's centre). This is immediately clear when looking at the depth-averaged velocity (Fig. 6D), which is negative (i.e., upwind) in the deep part.

Thus, even if the wind is spatially uniform, an overlap of horizontal and vertical circulations develops in water bodies with variable bathymetry. The horizontal circulation can be represented in a two-dimensional plane by means of the depth-averaged velocity, which is obtained by integrating Eq. (7) along the depth,

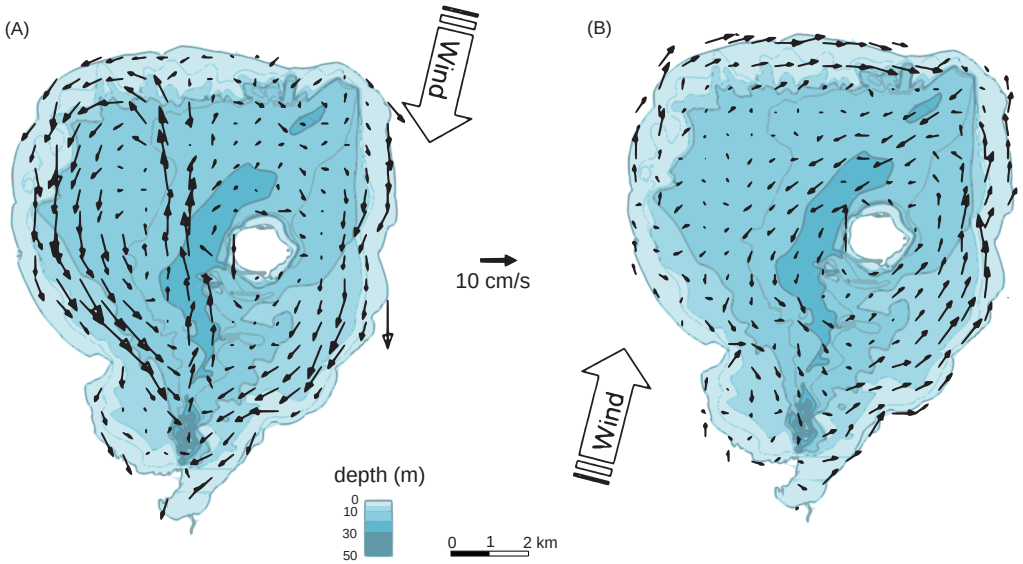

Fig. 5 An example of the two-gyre structure of wind-driven circulation depending on the variable bathymetry in Lake Rotorua, New Zealand. Arrows within the lake outline denote depth-averaged current speed and direction obtained from a 2D numerical model. The deeper region at the centre accommodates the return up-wind current, while currents are directed as the wind in the shallower coastal regions, both for northerly (A) and southerly (B) winds. Note that two different wind directions were considered, but the wind was assumed spatially uniform. The mechanism is the same as for the idealized model in Fig. 6. Modified from Gibbs M, Abell J and Hamilton D (2016) Wind forced circulation and sediment disturbance in a temperate lake. *New Zealand Journal of Marine and Freshwater Research*, 50 (2): 209–227. DOI: 10.1080/00288330.2015.1116998, combining two different figures.

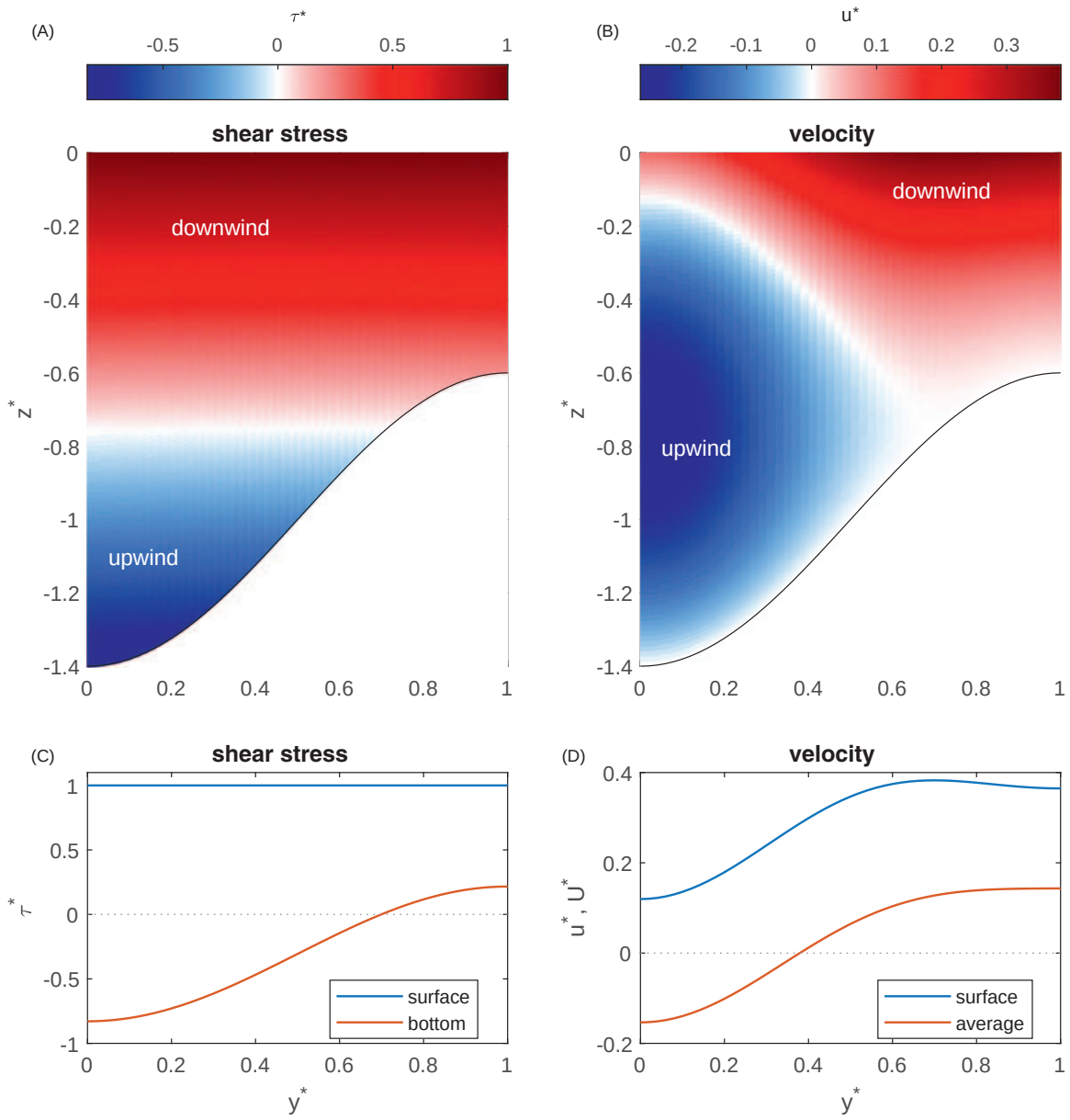

Fig. 6 Effect of depth variations. Steady-state flow field in an idealized cross-section of an elongated trunk region, for a uniform wind stress τ_{w0} but laterally variable depth $h = h_0[1 + 0.4\ cos(\pi y/B)]$, uniform eddy viscosity K_0, and no-slip conditions at the bottom. The plots refer to the dimensionless variables $z^* = (z - h)/h_0$, $y^* = y/B$, $\tau^* = \tau/\tau_{w0}$, $u^* = u\,\rho K_0/(\tau_{w0} h_0)$.

$$U = \frac{h}{K_0}\left[\frac{1}{2}\frac{\tau_w}{\rho} - \frac{1}{3} g \frac{\partial \eta}{\partial x} h\right] \tag{9}$$

and closing it with the proper value of the free-surface slope. The structure of Eq. (9) allows for recognizing that increasing h contributes to making U negative through the last term (remember that $\partial \eta/\partial x > 0$): indeed, the pressure force opposing the flow becomes stronger as the depth becomes larger.

Effect of inhomogeneous wind

A similar effect is produced by an inhomogeneous wind in a water body characterized by uniform depth. Using the same assumptions, we find the same local solution as above in each water column (which are independent from each other because the horizontal viscosity is neglected), and the integral condition (4) provides the free-surface slope $\partial \eta/\partial x = (3/2)\overline{\tau_w}/(\rho g h)$, which is the same result as in Eq. (8) but for the laterally averaged wind shear stress $\overline{\tau_w}$.

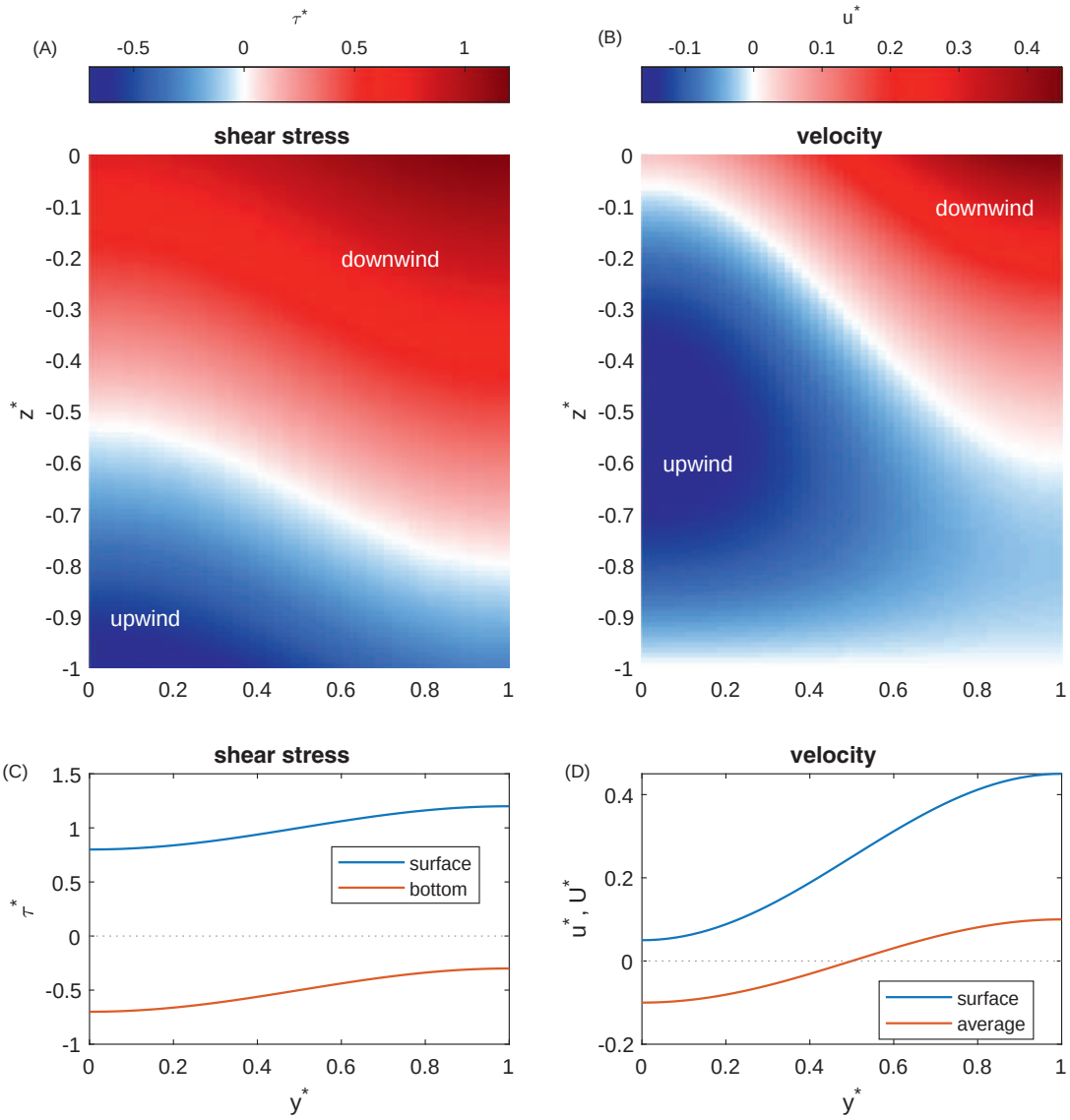

Fig. 7 Effect of wind variations. Steady-state flow field in an idealized cross-section of an elongated trunk region, for uniform depth h_0 but laterally variable wind stress $\tau_w = \tau_{w0}[1–0.2\ cos(\pi y/B)]$, uniform eddy viscosity K_0, and no-slip conditions at the bottom. Dimensionless variables are defined as in Fig. 6.

All the considerations done previously for the variable depth can be repeated in this case, which shows a depth-averaged return flow in the region where the wind is weaker (an example is shown in Fig. 7). The interpretation of the process in terms of the wind stress curl generating 2D vorticity is proposed at the end of the chapter.

The interaction of variable bathymetry and wind can alter the large-scale circulation significantly, with the return flow located in the region where the wind is sheltered (typically close to a shore) even if the depth is shallower (Podsetchine and Schernewski, 1999; Rueda et al., 2005).

Effect of Earth rotation

Considering the effect of Coriolis acceleration makes the description intrinsically more complex, since the two horizontal components of the velocity are intertwined. There is no possibility to describe the flow as occurring in parallel planes in the trunk region because the x–velocity u produces an acceleration in the y–direction, and vice versa. The simplest model considers an infinite domain, which allows for neglecting all the non-linear advective terms (similar to what happens in the uniform trunk region). Then, the two steady-state momentum equations (set *d* in Table 2) describe the balance among Coriolis acceleration, free surface slope (barotropic terms), and vertical diffusion of momentum by the eddy viscosity, for which it is assumed a constant value K_0.

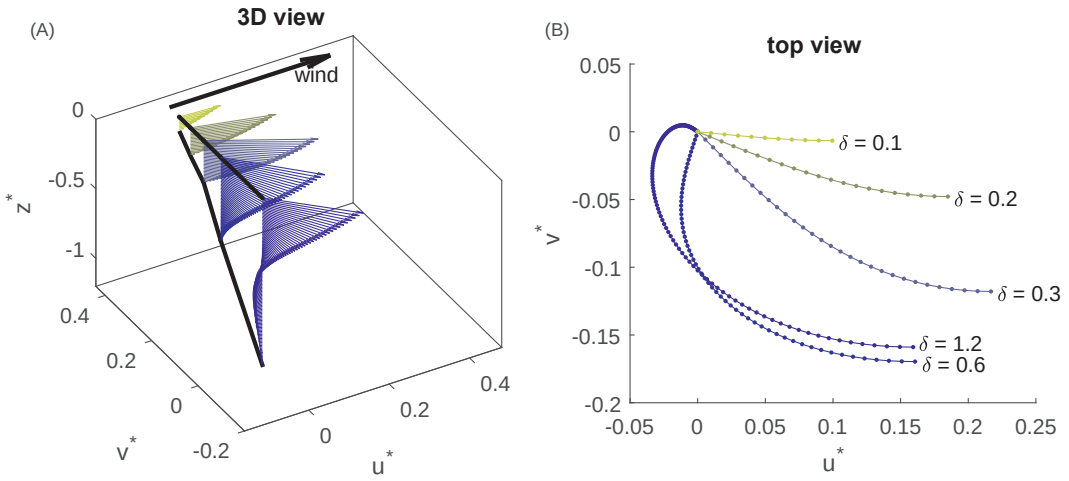

Fig. 8 Ekman spiral developing in a horizontally unbounded domain for a wind aligned with the *x*-axis (in the northern hemisphere, see the deviation of the surface velocity to the right of the wind), considering the effect of the finite depth with a no-slip condition at the bottom. (A) Five different cases depending on the local depth (note that they are independent of each other and are represented together only for drawing purposes). (B) Hodograph showing the horizontal components of the velocity at different depths. The number at the end of the curves (velocity at the surface) denotes the dimensionless depth ratio, $\delta = h/D_E$, with $D_E = \pi\sqrt{2K_0/f}$ the Ekman depth. The following dimensionless variables are used in the plot: $z^* = z/D_E$, $\{u^*, v^*\} = \{u, v\}/U_0$, with $U_0 = \tau_{w0}D_E/(\rho K_0)$; note that the length scale D_E is used instead of h to compare the results for different depths. As an example of the values in dimensional terms, we assume $\tau_{w0} = 0.03$ N/m^2 (for a wind speed of approximately 5 m/s) and $f = 10^{-4}$ s^{-1} (mid latitude): for $K_0 = 10^{-3}$–10^{-2} m^2/s, it follows that $D_E = 14$–44 m and the velocity scale is $U_0 = 0.4$–0.13 m/s (note that the actual velocity at the surface is about one order of magnitude smaller).

Ekman (1905) originally proposed a solution for these equations forced by a uniform wind in an infinite domain, neglecting the barotropic terms. For a depth much larger than the Ekman depth $D_E \sim \sqrt{K_0/f}$ (definitions proposed in literature may differ by a multiplicative factor), the flow in the surface layer does not 'feel' the effect of the bottom boundary, and the solution is represented by the well-known Ekman spiral (e.g., Hutter et al., 2011). The term "spiral" refers to the tendency of the velocity vector to rotate to the right (left) in the northern (southern) hemisphere, starting from a direction of 45 degrees with respect to the wind (Fig. 8). Where the depth is shallower, the flow tends to be aligned with the wind. It is worth noting that the definition of D_E includes the Coriolis parameter (f, depending only on the latitude) and the vertical eddy viscosity, which typically changes spatially and temporally, making the identification of a meaningful reference value K_0 difficult. Moreover, the Ekman spiral is rarely observed, as different factors can affect the flow field, among which barotropic flow (which can be dominant), the variability of the eddy viscosity, and the lack of spatial uniformity associated with the presence of boundaries (as discussed below).

There is another well-known theoretical result concerning the Ekman spiral in infinite depth: the vertically integrated transport is orthogonal to the wind (i.e., 90 degrees to the right/left in the northern/southern hemisphere). For instance, for a wind blowing along x, the y–component is quantified as $\int_{-\infty}^{0} v\, dz = \mp\, \tau_{wx}/\rho f$ (the sign depending on the hemisphere). As a result, persistent alongshore winds produce coastal downwelling or upwelling phenomena.

The assumption of infinite domain is a limitation of the traditional approach. What happens in relatively small (the meaning of "relative" is discussed later) closed water bodies? *We* have seen that lateral boundaries impose additional integral conditions to steady-state flows, as in Eq. (4), in order to respect the absence of mass exchange across any cross-section separating the water body into two regions. Referring again, for simplicity, to an elongated prismatic trunk region with the wind aligned along the main axis, two integral conditions (e.g., applied on cross-sections with fixed x and fixed y) can be used to determine the values of the free surface slope in the two directions (e.g., Kasai et al., 2000).

The process is such that, in a closed lake, a secondary circulation develops due to the effect of the Coriolis acceleration, in addition to the more intuitive "conveyor belt" circulation aligned with the wind (e.g., Ambrosetti et al., 2010; see also Fig. 3). The effects of this secondary circulation have recently been observed in Lake Garda, Italy, whose northern deep basin can be approximated using the prismatic trunk assumption (Piccolroaz et al., 2019). By artificially switching off the effect of the Coriolis force in numerical simulations (Fig. 9), it is possible to see how this process acts in elongated lakes: it affects momentum, mass and heat transport, and modifies the mechanism of deep ventilation. An interesting effect is the lateral shift of high-momentum surface flow towards the right shore (in the northern hemisphere), whereas the left shore is affected by an upward movement of low-momentum flow (Toffolon, 2013): the overall effect is an acceleration of the flow on the right shore and a reduction on the left (the opposite in the southern hemisphere).

The effect of Earth rotation on lake hydrodynamics can produce noticeable deviations of the surface velocity with respect to the wind direction (e.g., Koçyigit and Falconer, 2004) also in small lakes if they are deep enough. Actually, the intensity of the steady-state secondary circulation depends on the depth ratio, $\delta = h/D_E$, and should not be assessed using the widely used criterion

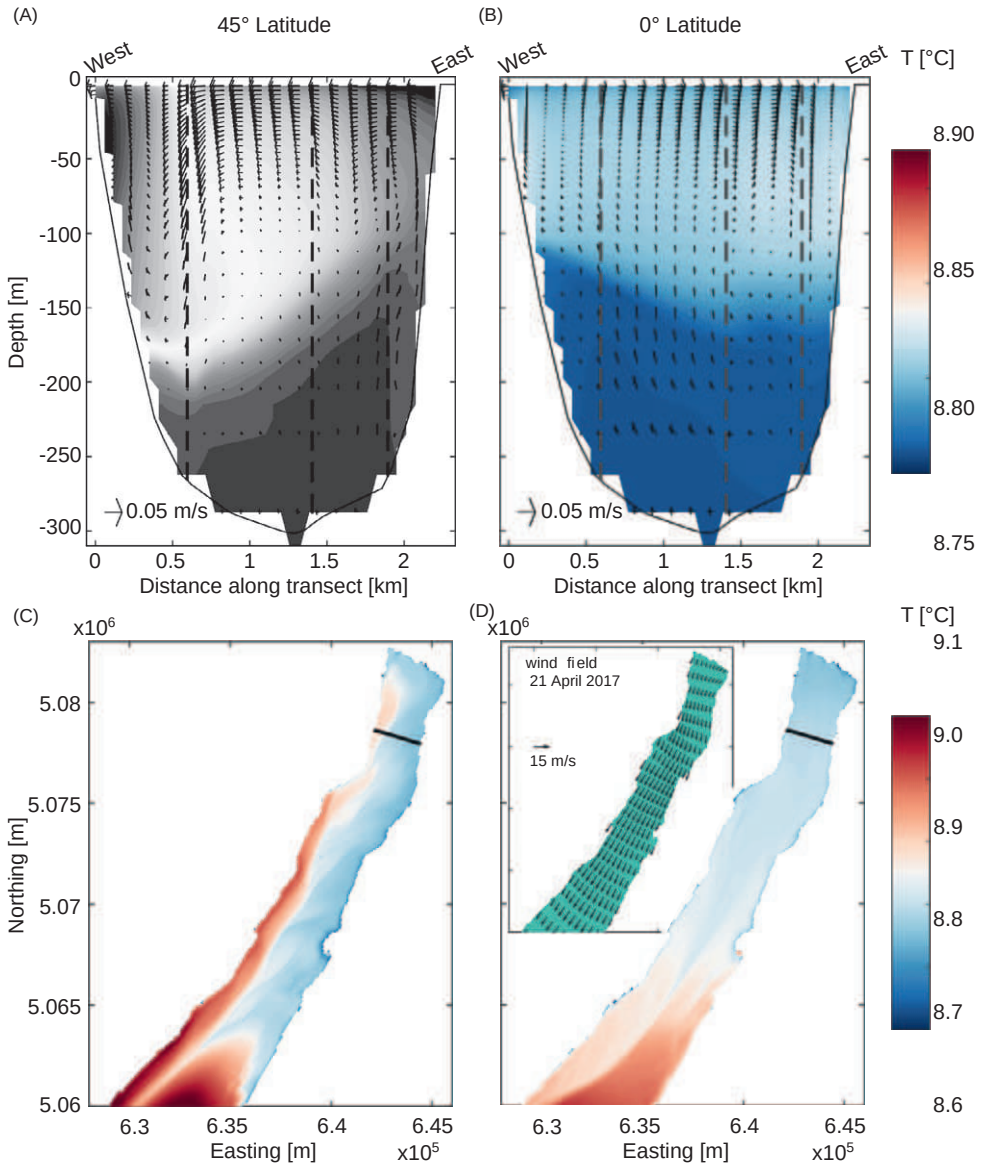

Fig. 9 The effect of Earth rotation producing a secondary flow in a wind-driven circulation, analysed by means of numerical simulations in Lake Garda, Italy, accounting for (A and C) and excluding (B and D) the Coriolis force. Upper panels: water temperature and flow field (arrows) in the transect indicated with a black line in the lower panels. Lower panels: map of surface water temperature. The inset in panel (D) shows the strong and uniform wind field blowing from north-east and aligned with the lake main axis. Modified from Piccolroaz S, Amadori M, Toffolon M and Dijkstra HA (2019) Importance of planetary rotation for ventilation processes in deep elongated lakes: Evidence from Lake Garda (Italy). *Scientific Reports*, 9: 8290. DOI: 10.1038/s41598-019-44730-1, by adding the inset in panel D.

based on the Rossby number $Ro = U_0/(fB)$ (Amadori et al., 2020). Comparing the horizontal size of a lake with the Rossby radius U_0/f is correct for waves and inertial currents, but not for this kind of secondary circulation, where the mixed layer's depth should be compared with the thickness of the Ekman layer (Hutter et al., 2014).

Effect of horizontal turbulence

When examining the previous effects, we always relied on the possibility of neglecting the horizontal viscosity. This common assumption, usually based on dimensional considerations, recognizes that in shallow flows the vertical variations are stronger than the horizontal gradient. However, this is not always true. The size of the lake, and in particular the across-wind width, enters into play for sufficiently narrow cross-sections where the extension of the boundary layers at the shore becomes comparable with the width itself, and the horizontal viscosity dampens the lateral velocity gradients.

In order to understand the dynamics, we develop a simple dimensional argument. The lateral gradient is imposed by the geometrical constraint and the only degree of freedom is the intensity of the velocity at the two sides. This means that the

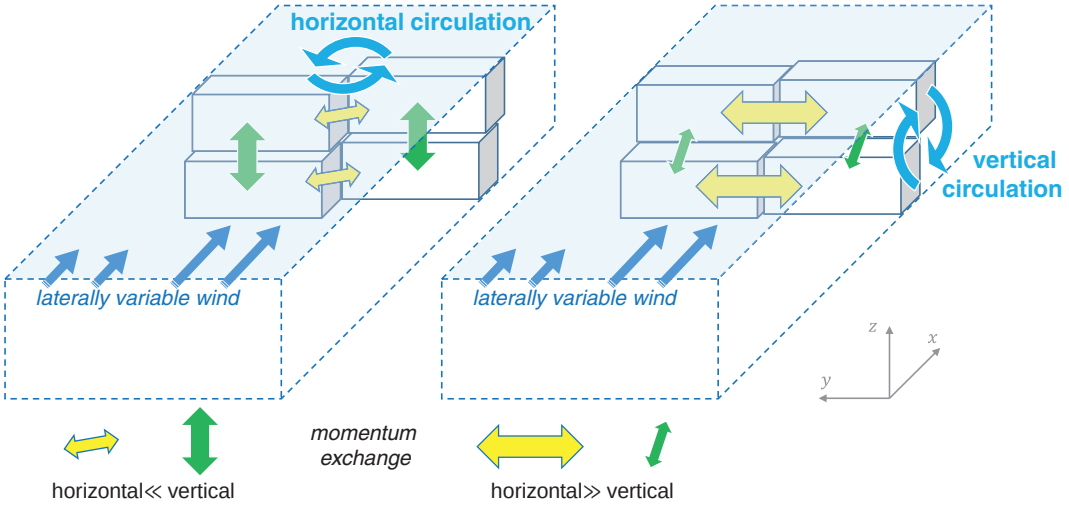

Fig. 10 Conceptual scheme of the effect of turbulence anisotropy and geometry on the development of lake circulation induced by a laterally variable wind stress with uniform depth. (Left) Horizontal circulation prevails for isotropic turbulence and shallow/wide geometry. The vertical exchange of momentum is dominant due to the large width-to-depth ratio that reduces the lateral ($\partial u/\partial y$) and enhances the vertical ($\partial u/\partial z$) velocity gradient. Hence, the lower layers tend to follow the inhomogeneous movement of the upper layers driven by the variable wind. (Right) Vertical circulation prevails for the strongly anisotropic and deep/narrow geometry. The vertical exchange of momentum is limited due to the small width-to-depth ratio and the reduced vertical eddy viscosity. Here, the whole surface layer tends to move in the same direction, as the region subjected to stronger wind effectively drags the region where wind is milder, and the lower layers are affected by the return current to compensate the mass balance (in steady-state conditions). Analogous descriptions can be done for the other factors that tend to produce a horizontal circulation (e.g., variable bathymetry, Coriolis acceleration, etc.).

acceleration resulting from the lateral flux of momentum can be quantified as $(1/\rho)\partial\tau_{xy}/\partial y = \partial(A\partial u/\partial y)/\partial y \sim A_0U_0/B^2$, with U_0 and A_0 suitable scales of the velocity and horizontal eddy viscosity, respectively. Analogously, the vertical momentum flux is $(1/\rho)\partial\tau_{xz}/\partial z = \partial(K\partial u/\partial z)/\partial z \sim K_0U_0/h^2$. The ratio between these two terms, $\alpha = (h/B)\sqrt{A_0/K_0}$, combines the aspect ratio of the cross-section and the turbulence anisotropy (Toffolon and Rizzi, 2009), whereby typically $K_0 \ll A_0$. Fig. 10 shows a conceptual scheme of the narrow/anisotropic vs. the wide/isotropic condition for the simple case of a lateral variability of the wind.

The overall effect is that, in narrow sections, the lateral gradient of the velocity is damped by the turbulent exchange of momentum. The same reasoning can be done for the vertical velocity associated with downwelling and upwelling phenomena at the two opposite shores of a narrow lake.

The world described by a depth-averaged model

Nothing more than horizontal circulation

The simultaneous presence of vertical and horizontal circulations, which can be due to different factors, all of them generally acting in real cases, poses an interesting question about the possibility to describe the flow field by means of a depth-averaged model. By averaging the RANS equations along the depth, it is possible to obtain the approximate 2D equations in primitive form (set *b* in Table 2).

The shear stress at the bottom, $\vec{\tau}_b$, needs to be closed in terms of the resolved variables, in particular the depth-averaged velocity $\vec{U}$. A common choice is to use the dimensionless Chézy coefficient, C, in the quadratic relation $\vec{\tau}_b = \rho|\vec{U}|\,\vec{U}/C^2$ (note that $C = {C_D}^{-1/2}$, with C_D a drag coefficient). Using this closure relation, the system of partial differential equations (set *b* in Table 2) can be solved in terms of U, V and η.

An obvious limitation of 2D models is the impossibility to describe the vertical circulation. We discuss this issue referring again to the simplified case of a steady-state flow in the trunk region with variable h. Neglecting horizontal viscosity, the x-momentum equation can be cast in the following form (corresponding to equation *e* in Table 2):

$$\frac{|U|U}{C^2} = -g\frac{\partial\eta}{\partial x}h + \frac{\tau_{wx}}{\rho} \tag{10}$$

This equation can be used to compute U directly, and then apply the integral condition (4) to obtain $\partial\eta/\partial x$: however, the result would be different from that obtained through Eq. (9). Moreover, for a plane flow with uniform wind and depth, the integral

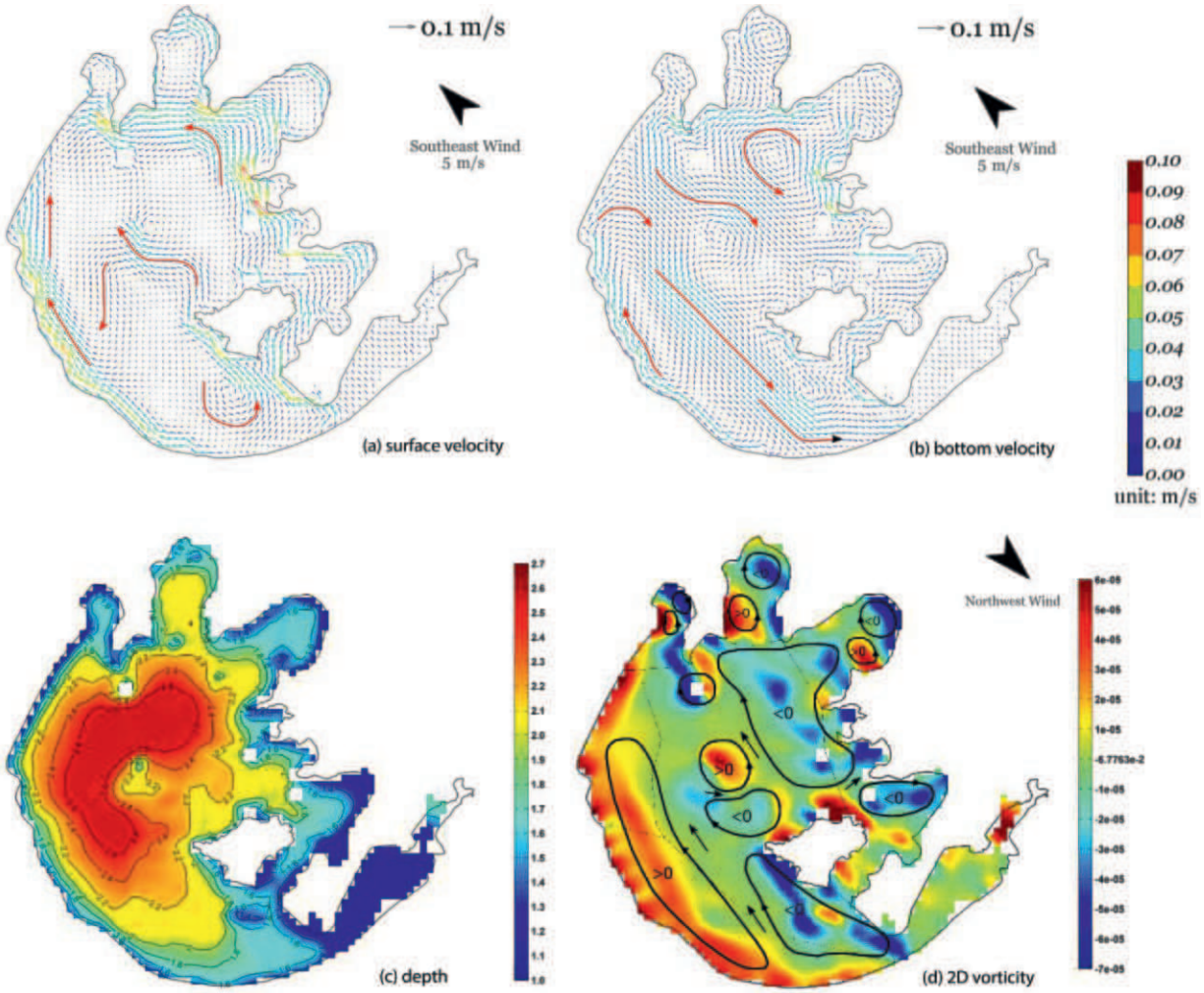

Fig. 11 A complex flow field combining horizontal and vertical circulation can develop also in shallow lakes. Taihu Lake, China, is a large (2250 km^2) but very shallow lake (mean depth 2 m; see bathymetry in panel C). Numerical simulations show that the flow field is markedly 3D, with velocity at the bottom (B) opposite to surface velocity (A) in deeper areas (for the interpretation, see the analysis of the idealize case in Fig. 6). In terms of depth-averaged circulation, the 2D vorticity field (colours in panel D) allows to recognize multiple-gyre structures (black lines approximately indicate streamlines); note that the wind direction in panel d is opposite to that in panels A and B. Modified from Liu S, Ye Q, Wu S and Stive MJF (2018) Horizontal circulation patterns in a large shallow Lake: Taihu lake, China. *Water* 10: 792. DOI: 10.3390/w10060792, combining different figures; streamlines drawn with red lines in panels a-b have been added.

condition (4) in the 2D approach imposes $U = 0$, i.e., no flow can be produced, which is of course incorrect, and only a still-water balance would be possible between the wind drag and the gravitational setup.

It is important to stress that, although very common, the assumption that the flow can be well represented by the depth-averaged velocity is often not satisfied. Even in very shallow lakes, water velocity at the bottom can be reversed with respect to that at the surface (an example is shown in Fig. 11). Only in those cases where the variability of depth or wind stress is strong enough, the development of a well-defined horizontal circulation makes the depth-averaged description reasonable (e.g., Fenocchi et al., 2016).

The 2D vorticity equation

The analyses in the previous sections were based on assumptions used to isolate the different processes. Here, we briefly examine how the 2D vorticity equation can describe the generation of horizontal circulation in more complex situations (e.g., Schwab and Beletsky, 2003). The vorticity is a measure of the rotational character of the flow. Referring to the depth-averaged velocity, the component of the vorticity vector in the z direction,

$$\zeta = \nabla \times \vec{U}_z = \frac{\partial V}{\partial x} - \frac{\partial U}{\partial y} \tag{11}$$

is a scalar quantity for a 2D x-y flow (to simplify the notation, it is implicitly assumed that only the z-component of the cross product is considered in the following equation). Hence, the vorticity equation is a single equation

$$\underset{\text{(i)}}{h^2 \frac{d}{dt}\left(\frac{\zeta + f}{h}\right)} \; \underset{\text{(ii)}}{- h\bar{A}\,\nabla^2\zeta} = \underset{\text{(iii)}}{\nabla \times \left(\frac{\vec{\tau}_w}{\rho}\right)} + \underset{\text{(iv)}}{\frac{1}{h}\frac{\vec{\tau}_w}{\rho} \times \nabla h} \; \underset{\text{(v)}}{- \nabla \times \left(\frac{\vec{\tau}_b}{\rho}\right)} \; \underset{\text{(vi)}}{- \frac{1}{h}\frac{\vec{\tau}_b}{\rho} \times \nabla h} \tag{12}$$

where the terms can be interpreted as follows. Term (i) contains the material derivative of the so-called potential vorticity; considering only this term, the vorticity increases moving to larger depths because of the need to conserve mass and angular momentum simultaneously (hence, squeezing of the water column and faster rotation). Term (ii) describes the diffusion of vorticity due to horizontal viscosity (assumed uniform for simplicity). Term (iii) is the source of vorticity due to variable wind stress (as for the idealized examples in Fig. 7). Term (iv) is the source due to variation of depth not aligned with the wind (as for the case in Fig. 6). Term (v) is a sink, as can be seen by using a simplified linear closure for the bottom shear stress, $\vec{\tau}_b \cong \rho k \vec{U}$ with $k > 0$, which allows for rewriting the term as $-\nabla \times \left(k \vec{U}\right) \cong -k\zeta$, i.e., always suppressing the existing vorticity. Term (vi) depends on the interaction of the flow field with bathymetrical variations.

Two idealized conditions can be considered to show the analogy with the cases discussed previously. The first is where depth variations are small with respect to wind stress variation, i.e., $O(\Delta h/h) \ll O(\Delta \tau_w/\tau_w)$. By neglecting the advective and diffusive terms, the vorticity equation (12) can be approximated as $h\partial\zeta/\partial t \cong \rho^{-1}\nabla \times \vec{\tau}_w - k\zeta$, which suggests that the evolution of vorticity is driven by the curl of the wind stress. Under steady forcing, vorticity tends to approach it ($\zeta \cong \nabla \times \vec{\tau}_w/\rho k$) for a sufficiently long time scale. The second is the opposite case (mostly uniform wind but strongly variable bathymetry): under the same additional assumptions, the vorticity dynamics described by Eq. (12) is dominated by the term $\vec{\tau}_w \times \nabla h$, which is responsible for the two-gyre structure in a basin with a deeper region in the middle (see the examples in Figs. 5 and 11D).

Unsteady flows

Response to variable forcing

After a detailed analysis of steady-state currents, we briefly discuss how the flow reacts to variations in the forcing due to the inertia of the water mass. Let us recall the effect of an impulse of wind stress at the surface of an infinite water body initially at rest (Fig. 2): the force transferred from the air moves the water through a downward flux of momentum along the water column. The mechanism is complex for turbulent flows because K is not constant. Assuming a reference value K_0, the length scale of the vertical region affected by the transfer of momentum grows in time as for any diffusive process, $L_D \propto \sqrt{K_0\, t}$ (e.g., Fischer et al., 1979). Hence, a well-established flow requires a time scale $T_0 \sim h^2/K_0$ to develop over a depth h. This is not a precise estimate, as different factors can affect it: the presence of a multiplicative coefficient that is larger than 1 for the actual value of L_D (e.g., see the case in Fig. 12 discussed later), or the fact that a return flow may occur at the bottom to respect mass conservation.

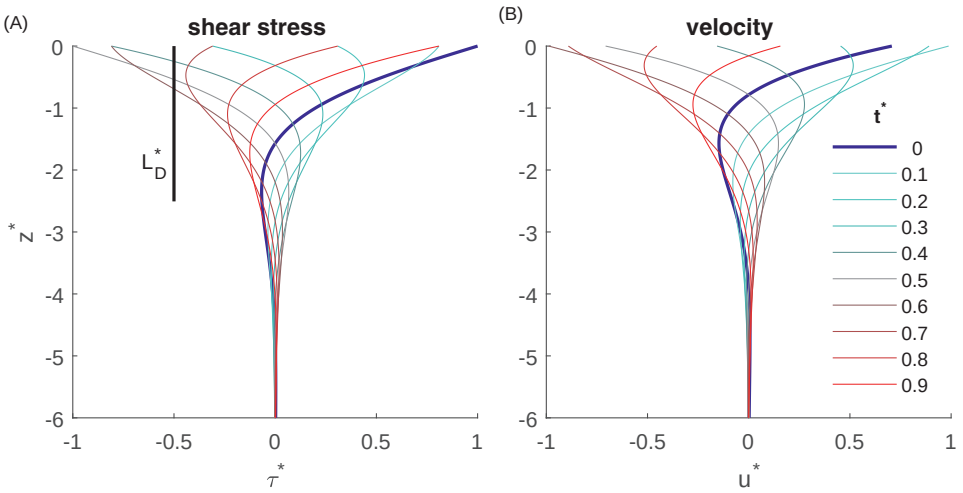

Fig. 12 The response of (A) shear stress and (B) velocity to a periodically variable wind forcing $\tau_w = \tau_{w0}\cos(\omega t)$, for a unidirectional flow in an infinite domain, neglecting Coriolis acceleration and assuming uniform and constant viscosity K_0. The length $L_D = \sqrt{2K_0T_0}\left(L_D^* = L_D/H_0 = \sqrt{2\pi}\right.$, with $H_0 = \sqrt{2K_0/\omega}$ and $T_0 = 2\pi/\omega)$ is the scale of the diffusion process and provides an indication about the depth at which momentum can penetrate. Note that it does not depend explicitly on wind speed, but in turbulent flows K_0 does, thus introducing an indirect dependence. The following dimensionless variables are used in the plot: $t^* = t/T_0$, $z^* = z/H_0$, $\tau^* = \tau_w/\tau_{w0}$, $u^* = u/U_0$ with $U_0 = \sqrt{2}\tau_{w0}/\rho\omega H_0$. As an example of the dimensional quantities, we assume $\tau_{w0} = 0.03$ N/m^2 (for a wind speed of approximately 5 m/s), $T_0 = 86{,}400$ s (daily periodicity): for $K_0 = 10^{-3}$–10^{-2} m^2/s, it follows that $U_0 = 11$–3.5 cm/s, $H_0 = 5.2$–17 m, and $L_D = 13$–42 m. It is worth noting that the larger is K_0, the smaller is U_0 because the inertia of the mass affected by the wind ($\propto L_D$) is larger.

There is a case where an analytical solution can be easily obtained and is illustrative of some general properties. For a unidirectional flow (neglecting Coriolis effects) in an infinite domain, and for constant and uniform K_0, the x-momentum equation becomes

$$\frac{\partial u}{\partial t} = K_0 \frac{\partial^2 u}{\partial z^2} \tag{13}$$

which is formally equivalent to the standard diffusion equation. If we consider a wind stress periodically alternating its direction (e.g., the daily sequence of anabatic and katabatic winds in mountain regions), the maximum depth at which momentum penetrates can be determined as a function of K_0 and of the time scale of the wind (Fig. 12).

However, the assumption that the vertical eddy viscosity is uniform and constant is incorrect. In fact, the vertical eddy viscosity is variable along the water column even in steady-state conditions. In the so-called "law of the wall" approximation (e.g., Wilcox, 2006), K grows with the distance from the bottom or the free surface, and follows an approximately parabolic profile. Moreover, the eddy viscosity is not constant in time, as turbulence is generated at the boundaries and tends to diffuse inside the water body, taking time to reach an equilibrium state. For instance, a wind pulse generates turbulent kinetic energy (TKE) at the surface, which is then advected and diffused into the water body, but it takes a relatively long time to be effective everywhere. More often, in the case of intermittent winds, TKE penetrates only down to a certain depth, even in the well-mixed surface layer. Hence, the wind-generated momentum can diffuse effectively only in a limited region of the water column close to the surface, producing velocity profiles that are quite different from the ones examined above for steady-state conditions, which only represent the asymptotic tendency of the flow.

Inertial currents and seiches

The unsteadiness of the forcing is crucial to understand the dynamics of the flow field in real conditions, but the effect is not limited to the period when the forcing is active. Two examples can illustrate how unsteady flows can persist after the original cause of the motion has stopped.

Inertial currents are ideal frictionless movements that are primarily affected by Earth rotation. They can last for some time after a strong wind event, and are the result of the balance between the inertia of the water and the Coriolis acceleration, with the possible effect of the barotropic terms (see set g in Table 2). The peculiarity of this flow is that it follows circular trajectories with constant velocity magnitude $\left|\vec{u}\right|$ and radius $R = \left|\vec{u}\right|/f$. The geostrophic flow determined by the barotropic terms, $u = g/f\,\partial\eta/\partial y$ and $v = -g/f\,\partial\eta/\partial x$, produces a shift that is orthogonal to the direction of the pressure (free-surface) gradient. A beautiful example of inertial trajectories is shown in Fig. 13.

Seiches are standing waves that occur in closed water bodies as a reaction to the instability produced by, e.g., wind setup. Knowing the celerity of propagation of gravity waves, $c = \sqrt{gh}$, and neglecting the effect of Earth rotation, the period $T_0 = 2L/(n\,c)$ of the free-surface oscillations (external seiches) can be determined given the length L of the water body and the number n of nodes of the wave. Interfacial waves, i.e., those occurring at the interface between two well-mixed layers, travel with a much slower speed, depending on the reduced gravity $g' = g\,\triangle\,\rho/\rho_0$ (with $\triangle\,\rho$ being the density difference between the two layers). Adding the Coriolis acceleration, external and internal waves earn a rotational character, leading to more complex types of motion (e.g., Kelvin and Poincaré waves).

Numerical modelling

In the last two decades, numerical models have become easily available, potentially removing the limitations that are necessary to obtain analytical solutions. However, three main issues should be considered for successful hydrodynamic simulations.

The first is the need to develop affordable and reliable turbulence models: on the one hand, the use of k-ε models is already the state of the art, but limitations are known especially in stratified conditions; on the other hand, the use of Large Eddy Simulations (LES) is becoming more common (e.g., Santo et al., 2017), but requires some specific expertise.

The second issue that strongly affects the results of hydrodynamic models is the external forcing. The one-way coupling with atmospheric models is already seen as necessary, as the only way to reconstruct a reasonable wind field on the lake surface. A further effort is needed to reconstruct reliable heat fluxes at the lake surface (a topic not discussed in this article). For instance, latent and sensible heat fluxes are affected by the atmospheric stability: testing two-way coupling options, possibly supported by comparison with field measurements, is the next step towards a physically sound description of the interface processes.

The third issue is the coupling with the ecology of the lake. Apart from the obvious effect of the currents on the transport of biological components, there is at least one process that is essential for the development of thermal stratification and, hence, for the thickness of the surface well-mixed layer: light extinction. The Secchi disk depth is routinely used as a parameter in thermo-hydrodynamic models, but its estimation in prognostic models is still challenging.

It seems that the futures challenges are tightly related with the use of increasingly complex numerical models, often developed by experts of different disciplines. Thus, why should we care about simplified analytical solutions? The answer to this question is simple: while numerical simulations can be considered analogous to (virtual) laboratory experiments, the interpretation of

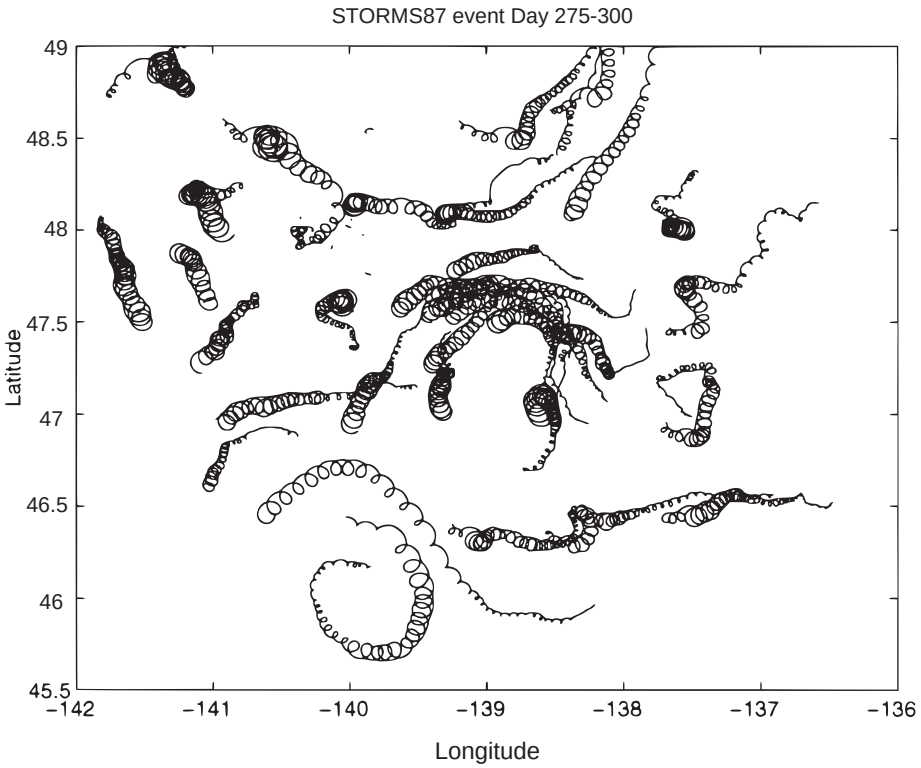

Fig. 13 Inertial currents: drifter tracks recorded during the Ocean Storms Experiment in a region off the coast of Washington. Note that a larger breadth of the trajectory corresponds to higher velocity, as $U_0 = R\,f$ with R the radius of an equivalent circle fitting the envelope. For a latitude of 47°N (whereby $f = 1.07 \times 10^{-4}$ s^{-1}), 1 degree longitude is approximately 76 km, thus the size of the large patterns in the figure is approximately 5 km, from which it is possible to estimate a maximum velocity 0.5–0.6 m/s after the storm event. Reproduced from van Meurs P (1998) Interactions between near-inertial mixed layer currents and the mesoscale: The importance of spatial variabilities in the vorticity field. *Journal of Physical Oceanography* 28 (7): 1363–1388. DOI: 10.1175/1520-0485(1998)028<1363:IBNIML>2.0.CO;2.

fundamental dynamics becomes more obscure as the complexity of the models increases (and, possibly, introduces spurious numerical artefacts). Therefore, simplified analytical models are often the best way to obtain a direct intuition of the physical processes under investigation.

Conclusions

The article presented an overview on the influence of some factors (variability of wind forcing and bathymetry, turbulence anisotropy, Earth rotation) on the basin-scale circulation in lakes. The main focus was on analytical solutions that can be derived for steady-state conditions, as a way to understand the physics governing the transport processes. Indeed, the analytical approach is effective in isolating the physical processes and in providing conceptual tools to grasp the underlying dynamics. The analytical approach is not alternative to numerical modelling; more correctly, it should be a complement of all numerical experiments. In fact, numerical models simulate the flow field and the resulting transport (e.g., of mass and heat) in realistic conditions, as they allow to include temporally and spatially varying forcing, and virtually all the processes that occur in the interior of the lake. However, the interpretation of the numerical results is not simple, and analytical solutions can provide powerful glasses to recognize and explain the observed behaviour. Moreover, the choice of the proper numerical model requires care. For instance, circulation in lakes is inherently a three-dimensional phenomenon, and two-dimensional depth-averaged models should be used only being aware of their limitations.

Knowing the trajectories of the transport in lakes is essential for all processes that involve nutrients, oxygen, temperature, and contaminants. Water quality and food webs are strongly affected by the transport patterns, and cannot be properly studied without simulating the hydrodynamics correctly. This is not an easy task and this article did not aim at being exhaustive. Here, the goal was to give a first introduction on the mathematical tools that can be useful to the scholars of all the limnological disciplines to delineate the conceptual framework for understanding how the large-scale physical processes influence the bio-geo-chemistry and the ecology of lakes.

Knowledge gaps

- Monitoring velocity in lakes is still a challenging task. In most cases, only point measurements of velocity are available, or velocity profiles along water columns collected with ADCP. The reconstruction of time-varying velocity fields, for instance at the lake surface, would be extremely important to understand the actual circulation patterns.
- Complex turbulence models are available, but the parameterization of the spatial and temporal variability of the eddy viscosity (and especially the effect of density stratification) did not improve significantly in the last decades.
- Very large uncertainties affect the estimate and the modelling of the horizontal viscosity and the understanding of its effect on the flow field.
- The interaction of the wind shear stress and the atmospheric stability with the roughness of the water surface, and hence the accurate quantification of the drag force, has not been completely clarified.
- The "golden age" of the analytical approach ended with the increasingly widespread use of numerical models. Nowadays, several studies simply present the results of numerical simulations, sometimes with a poor interpretation. Retrieving the knowledge that was developed in the second half of the 20th century might give more value to the results of the most advanced modelling efforts.

See Also: Fundamental concepts and theories: Temperature as a Driving Factor in Aquatic Ecosystems; Structures and functions of Inland Waters - Lakes: Bottom Boundary Layers; Currents in Stratified Water Bodies 1: Density-Driven Flows; Currents in Stratified Water Bodies: Internal Waves; Lacustrine Phosphorus Cycling; Small-Scale Turbulence and Mixing: Energy Fluxes in Stratified Lakes; Surface Mixed Layers in Lakes

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Examples of Online Forecasting Models for Lake Currents and Water Temperature:

http://meteolakes.ch/ (Lake Geneva)—EPFL—Meteolakes.

https://www.lubw.baden-wuerttemberg.de/wasser/bodenseeonline (Lake Constance—in German)—BodenseeOnline.

https://www.glerl.noaa.gov/res/glcfs/ (Laurentian Great Lakes)—NOAA—Great Lakes Coastal Forecasting System (GLCFS).

Currents in Stratified Water Bodies: Internal Waves☆

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This is an update of L. Boegman, Currents in Stratified Water Bodies 2: Internal Waves, Editor(s): Gene E. Likens, Encyclopedia of Inland Waters, Academic Press, 2009, Pages 539-558, ISBN 9780123706263, https://doi.org/10.1016/B978-012370626-3.00081-8.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie_Elodie Perga and Damien Bouffard.

Glossary

Baroclinic wave A wave in flow where the fluid density is a function of temperature, salinity and pressure. For example, waves on the thermocline of a lake.
Barotropic wave A wave in flow where the fluid density is a function of pressure only. For example, waves on the free surface of a lake.
Burger number Ratio of the Rossby Radius R to the lake width W; for $S = R/W < 1$ the Coriolis force will modify internal seiches into Kelvin and Poincaré waves.
Diurnal thermocline Strong vertical gradient that sets-up within the epilimnion during calm and warm conditions.
Epilimnion Warm well mixed (often turbulent) surface layer (~10 m thick) where momentum, heat, light and biogeochemical parameters are exchanged with the atmosphere.
Hypolimnion Cold, quiescent and nutrient rich bottom layer that is isolated from the atmosphere by the thermocline.
Inertial frequency The frequency $f = 2\pi/T_i$ of oscillations at the inertial period T_i.
Inertial period The time for a fluid parcel deflected by the Coriolis force to complete a full circle (inertial circle) at a particular latitude.
Internal Kelvin wave Sub-inertial (period $> T_i$) internal seiche that is modified by the Coriolis force to propagate cyclonically (clockwise/counter-clockwise in the northern/southern hemisphere) around the basin perimeter.
Internal Poincaré wave Super-inertial (period $< T_i$) internal seiche that is modified by the Coriolis force to propagate anticyclonically (counter-clockwise/clockwise in the northern/southern hemisphere) energizing strong mid-basin currents.
Metalimnion Layer between the warm epilimnion and cold hypolimnion that exhibits a strong temperature gradient, which inhibits vertical mixing of momentum, heat and biogeochemical parameters (nutrients, oxygen, etc.).
Rossby Radius $R = c_o/f$ is the length-scale (lake size) at which the Coriolis force becomes important, at a particular latitude or inertial frequency f, for fluid motion characterized by a velocity scale c_o.
Seasonal thermocline Region of the metalimnion where the vertical density gradient is strongest.
Seiche Basin-scale standing wave acting on the lake surface, thermocline or other density stratifying layers.

☆*Change History:* October 2021. L Boegman prepared the update with assistance from the section editors. Fig. 1 has been simplified, Table 2 has been added, Fig. 4 has been added, Fig. 5 has been added, text has been added on Internal Seiches under the effect of Earth Rotation.

Turbulent bottom boundary layer (TBBL) Layer of turbulent fluid above the sediments at the lake perimeter (~1 to ~10 m thick) where oscillatory seiche-induced currents drive turbulence and mixing, both in the watercolumn and across the sediment water interface, as they dissipate energy through frictional drag.

Introduction

The surface layer of a lake contains oxygen and light, which are required for growth of plankton and other aquatic life. However, the essential nutrients (e.g., phosphorus, nitrogen and carbon) are found above the sediments, where oxygen may be depleted. The watercolumn density stratification, arising from a vertical temperature gradient between the surface and lakebed, suppresses vertical mixing of nutrients and oxygen, thereby effectively isolating the oxygenated surface layer from the nutrients below.

The density stratification is an ideal environment for the generation of internal waves (i.e., interfacial waves on the thermocline). Forced by surface winds, internal waves drive oscillatory currents that energize a quasi-steady turbulent bottom boundary layer (TBBL) above the sediment bed. This turbulence provides transport through the thermocline, mixing oxygen toward the sediments and nutrients toward the surface (Imboden and Wüest, 1995; Imberger and Patterson, 1989).

Wave motions, in lakes, are initiated by the surface wind stress (Mortimer, 1974; Fischer et al., 1979). Waves occur on both the free surface (e.g., barotropic or surface seiche) and internal stratifying layers (e.g., baroclinic or internal seiche on the thermocline). The waves are categorized according to their length scale. Basin-scale waves have wavelengths that are of the same order as the lake diameter and occur as standing wave modes—or *seiches* (Fischer et al., 1979; Mortimer, 1974). Sub-basin-scale waves have wavelengths ~10–1000 m (Boegman et al., 2003). These waves are progressive and break where they shoal on sloping topography at the depth of the thermocline (Wüest and Lorke, 2003; Boegman et al., 2003, 2005b). However, wave shoaling and wave breaking is not addressed in this article.

Characteristic geometry and water-column stratification

We limit the present analysis to several characteristic types of density stratification that are commonly observed in lakes. Consider a lake basin of length L, width W and depth H. During the summer months, solar heating causes the lake to become stratified with a layered temperature structure consisting of an *epilimnion*, *metalimnion*, and *hypolimnion*; the *seasonal thermocline* being where the vertical density gradient is strongest within the metalimnion (see The Surface Mixed Layer in Lakes and Reservoirs). If the thermocline is abrupt, the lake may be approximated as a simple two-layer system of thickness h_1 and density ρ_1 over thickness h_2 and density ρ_2, where $H = h_1 + h_2$ is the total depth (Fig. 1B) (Horn et al., 2001). In lakes where a strong *diurnal thermocline* is present or the metalimnion is thick, the vertical density structure may be approximated with three contiguous fluid layers of density ρ_1, ρ_2 and ρ_3 with thicknesses h_1, h_2 and h_3 (Fig. 1C and D). The layered model for the stratification is inappropriate for polymictic lakes (e.g., shallow lakes $H < \sim 15$ m), which are often well mixed, but may also be weakly stratified (e.g., Fig. 1A); in these lakes an ephemeral diurnal thermocline may form in the epilimnion (e.g., Imberger, 1985).

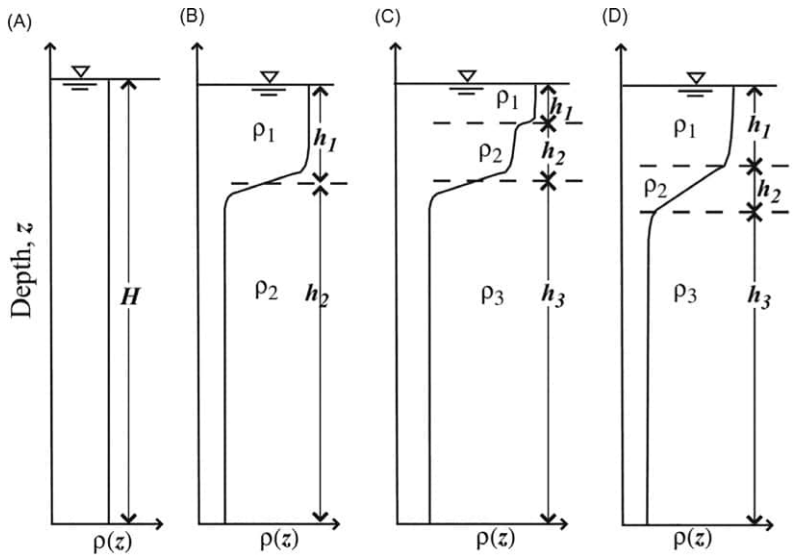

Fig. 1 Characteristic continuous water-column stratifications as found in lakes and typical layer approximations. (A) Homogeneous water-column of constant density. (B) Two-layer approximation of the continuous stratification, where the layer separation occurs at the thermocline. (C) Three-layer approximation of the continuous stratification, where the layer separation occurs at the diurnal and seasonal thermoclines. (D) Three-layer approximation of the continuous stratification, where the layer separation occurs at the upper and lower surfaces of the metalimnion.

Surface momentum transfer and wind set-up (phase 1, wind blows)

The internal waves described in this section are in lakes that are not affected by the Coriolis force due to the Earth's rotation. The wave modes that are supported depend upon the nature of the water column stratification and the wind forcing.

Wind set-up of the free surface

The action of the wind across the lake surface results in frictional momentum transfer from the wind to the water (see The Surface Mixed Layer in Lakes and Reservoirs). This transfer occurs in the form of a stress (N m^{-2}) applied at the free surface. The stress τ may be parameterized as (Fischer et al., 1979; Imboden and Wüest, 1995)

$$\tau = C_D \rho_a U_{10}^2 = \rho_o u_*^2$$

where C_D is the drag coefficient, $\rho_a = 1.2$ kg m^{-3} is the air density, $\rho_o = 1000$ kg m^{-3} is a reference (or mean) water density, $U_{10}$the wind speed measured at 10-m above the water surface and $u_* = \sqrt{\tau/\rho_o}$ is the surface shear velocity. Typically, $C_D = 1.3 \times 10^{-3}$, but this value may vary by ±40% depending upon the wind speed, water depth, and the relative temperature difference between the water surface and the atmosphere (Fischer et al., 1979; Wüest and Lorke, 2003).

The momentum transfer associated with steady winds will push the surface water to the leeward shore causing an upward displacement of the free surface, due to the presence of the solid boundary (Fig. 2A), and a simultaneous downward displacement of the thermocline. For long and shallow lakes the free surface displacement may be as large as several meters (e.g., ~2 m in Lake Erie; Hamblin, 1987).

This displacement is called wind set-up. If the wind stress is applied for sufficient time, a steady-state tilt of the free surface will occur where there is a balance between the applied wind force ($\tau \times$ surface area) and the hydrostatic pressure force due, to the desire of the free surface to return to gravitational equilibrium. Balancing these forces, at steady state, gives the interfacial (surface) displacement from the equilibrium position $\eta_s(x,t)$, where x is the longitudinal coordinate and t is time.

Wind set-up of the internal stratification

In a manner analogous to the set-up at the free surface, wind induced displacements can also occur along the thermocline. Consider a simple two-layered lake where the water piled-up at the leeward shore, by windward drift, simultaneously pushes down the thermocline while pushing up the free surface (Fig. 2B and D) (Mortimer, 1974; Monismith, 1986). The free surface remains comparatively horizontal owing to a return flow that develops in the hypolimnion, leading to vertical velocity shear through the metalimnion. A corresponding upwelling occurs at the windward shore (Fig. 2D). The steady-state slope of the thermocline surface $\eta_i(x,t)$ is given by a balance between the baroclinic gravitational pressure force from the tilted thermocline and the force due to the wind-stress acting through the epilimnion.

$$\frac{\partial \eta_i}{\partial x} = \frac{u_*^2}{g' h_1}$$

Here, $g' = g(\rho_2 - \rho_1)/\rho_o$ is the reduced gravity across the interface (thermocline), where g is the gravitational constant. The equation for the thermocline slope may be obtained through integration of η_i over the basin length (Boegman et al., 2005a).

$$\eta_i = \pm \frac{u_*^2}{g' h_1} \frac{L}{2}$$

The effect of buoyancy is evident by decreasing the density difference between the two layers, resulting in a decrease in g' and corresponding increase in η_i. A simple comparison $\eta_s/\eta_i = ((\rho_2 - \rho_1)/\rho_o)(h_1/H)$ shows that for weakly stratified deep systems, internal displacements (~1–100 m) may be more than an order of magnitude greater than their surface counterparts (~0.01–1 m); for example in Lake Baikal $\eta_s/\eta_i \sim 0.1$ m/75 m $\sim 10^{-3}$.

After the thermocline tilt has reached steady state, work done by continued winds is either dissipated internally as heat or acts to mix the water column by further deepening the surface layer (Imberger, 1985). Surface layer deepening has been characterized into four distinct regimes based on the strength of the stratification and winds (Fig. 3A) (Spigel and Imberger, 1980; MacIntyre, 2008). For strong stratification and weak winds (Regime A) the thermocline set-up is small, internal seiches persist for long times, mixing is weak, and the thermocline remains sharp. If the stratification is weaker or the winds stronger (Regimes B and C), seiche amplitudes increase and become a predominant feature, shear instabilities (e.g., Kelvin–Helmholtz billows) form leading to entrainment of the metalimnion into the epilimnion, enhanced mixing and rapid damping of the internal seiches (Saggio and Imberger, 1998, Horn et al., 2001). For weak stratification and strong winds (Regime D), shear instabilities are strong; the thermocline becomes diffuse with a steep slope and rapidly deepens toward the lakebed. This creates a sharp downwind interface and a broad upwelling at the upwind shore. The upwelled fluid forms a longitudinal temperature gradient, which completely mixes the lake horizontally. The colder upwelled water is nutrient rich and as it mixes, rapid fluctuations in temperature and biogeochemistry result.

Complete mixing will only occur near spring and fall turnover events in temperate lakes, when convection has sufficiently weakened the density stratification, or in shallow polymictic or weakly stratified arctic lakes (Boegman, 2020). In deeper lakes, seasonal stratification during summer will prevent complete mixing and upwelling of metalimnetic (partial upwelling) or hypolimnetic (full upwelling) water will occur (Imberger and Patterson, 1989).

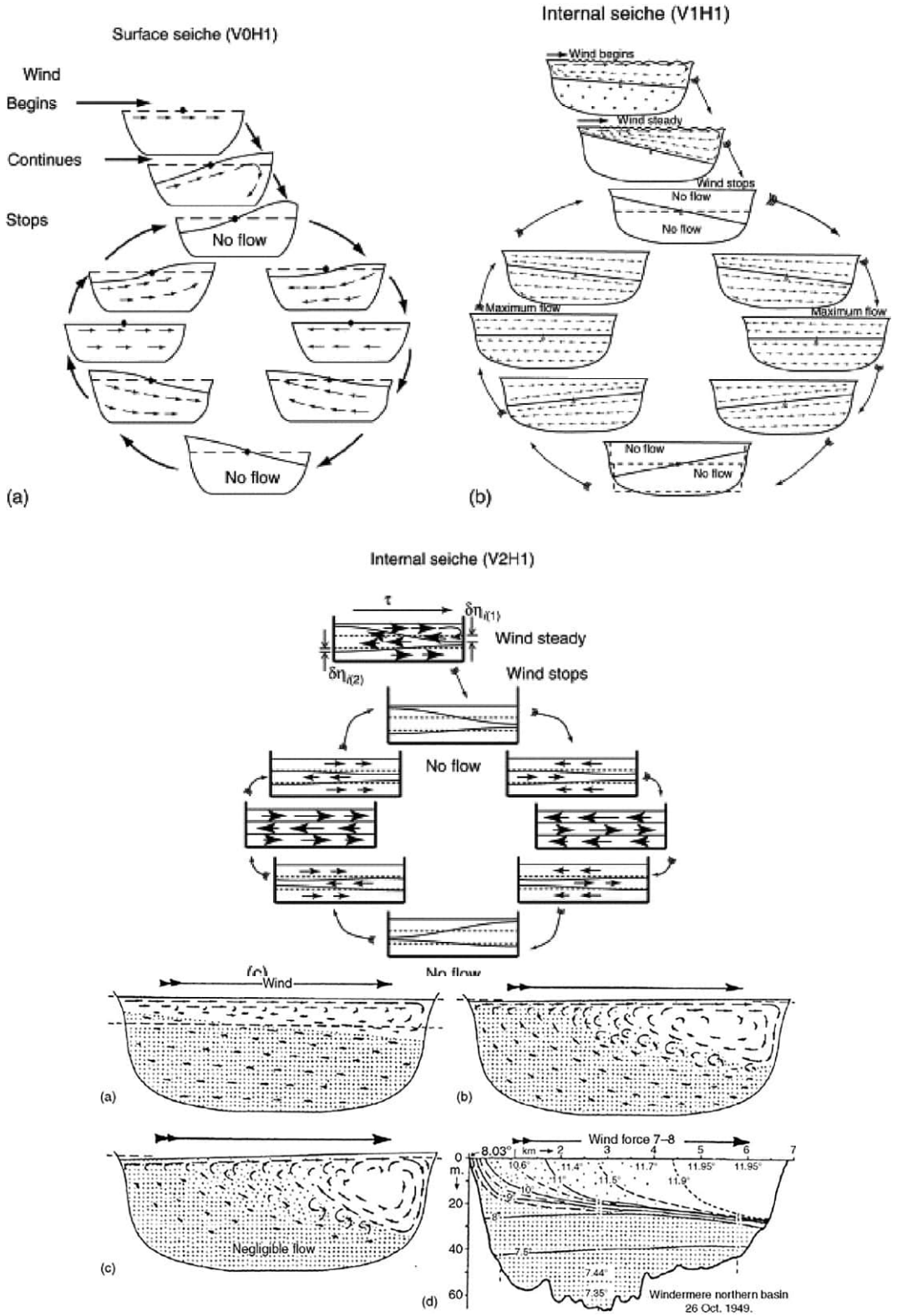

Fig. 2 Movement caused by wind stress on a hypothetical layered lake and subsequent internal seiche motion neglecting damping. (A) Horizontal mode one surface seiche in a homogeneous one-layered system. (B) Horizontal mode one vertical mode on internal seiche in a two-layered system, and (C) horizontal mode one vertical mode two internal seiche in a three-layered system. Arrows denote distribution and magnitude of water particle velocities. At $t = 0$, $(1/2)T_1$, T_1, $(3/2)T_1$, etc. the wave energy is purely in the potential form, isotherms are at their maximum tilt and there is no seiche induced flow, while at $t = (1/4)T_1$, $(3/4)T_1$, $(5/4)T_1$, etc. the energy is purely kinetic, giving rise to strong horizontal currents within the lake-basin and horizontal isotherms. (D) The response of a stratified lake to a surface wind stress. (i–iii) show the stages of development of a steady state thermocline tilt. The hypolimnion is shaded and the arrows show the relative speed and direction of the flow. (iv) Isotherm distribution and temperatures in Lake Windermere, northern basin, after a steady wind for 12 h. (E) The first three horizontal interfacial seiche modes: horizontal mode-one ($n = 1$), mode-two ($n = 2$) and mode-three ($n = 3$). Arrows denote direction of water particle velocities. Solid and dashed lines denote the interfacial displacement at one-half period intervals. Upper layer velocities for the baroclinic case are not shown and can be inferred from symmetry.

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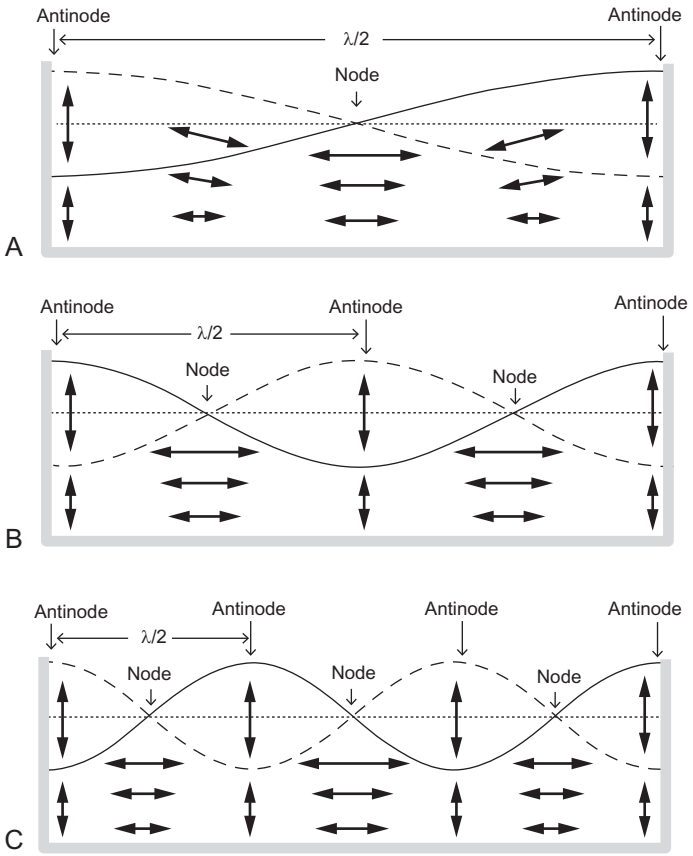

Fig.2—Cont'd (A) Reproduced with permission from Liggett JA (1994). *Fluid Mechanics*. McGraw-Hill, (B) reproduced with permission from Mortimer, C.H. (1952). Water movements in lakes during summer stratification; evidence from the distribution of temperature in Windermere. *Proceedings of the Royal Society of London. Series B*. 236: 355–404, (D) reproduced with permission from Mortimer CH (1961) Motion in thermoclines Verh. Internat. Verein. Limnol. 14: 79–83.

Basin-scale internal waves (phase 2, wind stops)

Internal seiches in a layered stratification

Horizontal modes

When steady winds drop and the surface stress condition is relaxed, the gravitational restoring force associated with the tilted interface (water surface or thermocline) becomes unbalanced. The available potential energy embodied in the tilt is released and converted to kinetic energy by gravity. The interface then oscillates in the form of a sinusoidal standing wave or seiche (Fischer et al., 1979; Boegman et al., 2005a). Antinodes are at the basin end walls and nodal points in the basin interior (Fig. 2A and E). Seiches are commonly called linear waves because the evolving wave-field is well described in space and time by the linear wave equation where c_o *is* the linear shallow water phase speed at which the crests/troughs propagate. This equation is equally applicable to interfacial waves traveling on the free-surface or thermocline using an appropriate form of $c_o = \sqrt{gH}$ or $c_o = \sqrt{g'h_1h_2/H}$, respectively. Due to the reduced effect of gravity across the thermocline, relative to the free surface ($g' \ll g$), surface waves travel at ~50 times the speed of internal waves.

The familiar standing wave patterns associated with seiches form as a result of symmetric progressive waves of equal amplitude and wavelength, but opposite sign, propagating from the upwelled and downwelled fluid volumes at the opposite ends of the basin (Fig. 2) (Boegman et al., 2005a; Fischer et al., 1979; Mortimer, 1974). These waves can by represented with cosine functions (Fig. 2E), which have nodes at the mid-basin and antinodes at the basin walls. Summing cosine equations for waves propagating in opposite directions, gives the equation for the horizontal mode one (H1) standing wave pattern (Fig. 2E(i)). For an enclosed basin, there is ½ wavelength of an H1 seiche in a lake, giving an overall wavelength $\lambda = 2L$ and a period according to the Merian formula

$$T_n = \frac{2L}{nc_o}$$

Here, $n = 1$ for an H1 seiche and is the number of nodal points or ½ wavelengths in the horizontal direction. The layer-averaged horizontal velocities associated with the H1 seiche are maximum the center of the basin (Horn et al., 2001). These velocities are zero

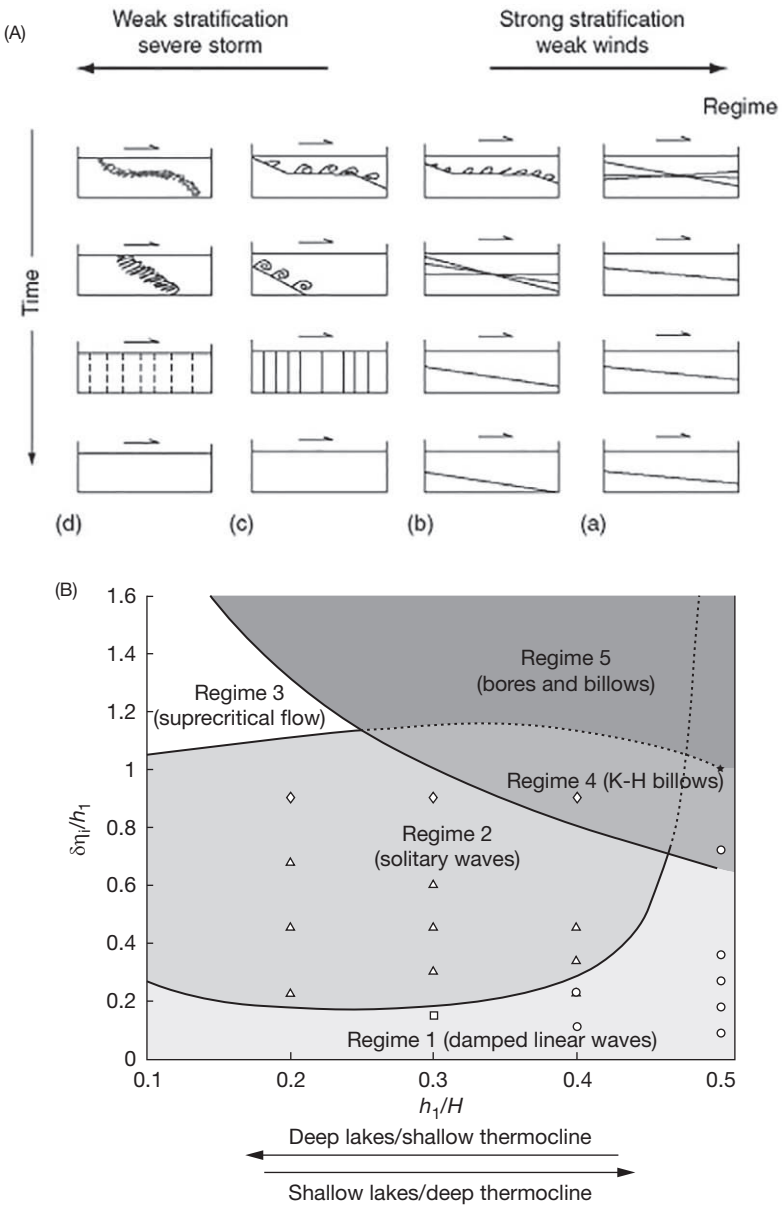

Fig. 3 (A) Schematic showing the mixed layer deepening response of a lake to wind stress. Regime A: internal waves; Regime B: internal waves and slight billowing; Regime C: strong billowing and partial upwelling; Regime D: intense billowing and full upwelling. (B) Analytical regime diagram showing the degeneration mechanisms of seiches in long rectangular lakes. The regimes are characterized in terms of the normalized initial forcing scale η_i/h_1 and the depth of the seasonal thermocline (h_1/H). Laboratory observations are also plotted (*, Kelvin–Helmholtz (K–H) billows and bore; ◊, broken undular bore; △, solitary waves; □, steepening; ○, damped linear waves). (A) Reproduced with permission from Fischer HB, List EJ, Koh RCY, Imberger J and Brooks NH (1979). Mixing in inland and coastal waters. Academic Press. Modified from Spigel RH and Imberger J (1980). The classification of mixed layer dynamics in Lakes of small to medium size. *Journal of Physical Oceanography* 10: 1104–1121, (B) reproduced with permission from Horn DA, Imberger J and Ivey GN (2001) The degeneration of large-scale interfacial gravity waves in lakes. *Journal of Fluid Mechanics* **434:** 181–207.

at the vertical boundaries, where the motion is purely vertical (Fig. 2E). The oscillatory seiche currents are low-period and quasi-steady. Observations from a variety of lakes and reservoirs show the surface and internal seiche currents to have a typical range of 0.02–0.20 m s^{-1}, with a maximum ~0.2 m s^{-1}during storms and to approach zero at the no-slip sediment boundary where the flow is impeded by friction (Valipour et al., 2015a).

Higher horizontal mode seiches ($n > 1$) have been observed in lakes. These are described by a more general solution of the linear wave equation, where the initial condition is a uniformly tilted interface, made up of the superposition of all higher horizontal modes (Spigel and Imberger, 1980; Boegman et al., 2005a; Horn et al., 2001). These solutions are composed only of odd modes

Table 1 Observed surface and internal seiche periods from a variety of lakes and the associated amplitude decay.

Lake and location	T_1 *(h)*	T_2 *(h)*	T_3 *(h)*	T_4 *(h)*	T_5 *(h)*	*Fractional decrease in amplitude with each successive period*
Surface seiches						
Tanganyika (Africa)[a]	0.075	0.038	0.028			
Loch Earn (Scotland)[a]	0.24	0.14	0.10	0.07	0.06	
Yamanaka (Japan)[a,b]	0.26	0.18	0.09			0.099
Garda (Italy)[a,b]	0.72	0.48	0.37	0.25	0.20	0.045
Geneva (Switzerland—France)[a,b]	1.2	0.59				0.030
Vättern (Sweden)[a,b]	3.0	1.6	1.3	0.97	0.80	0.113
Baikal (Russia)[a]	4.6					
Michigan (Canada—United States)[a]	9.1	5.2	3.7	3.1	2.5	
Erie (Canada—United States)[a,b]	14.3	9.0	5.9	4.2		0.322
Internal seiches						
Baldegg (Switzerland)[c]	9.3	4.6	3.1	2.1		
Lugano (Switzerland—Italy)[d]	24	12	8.0	6.2		
Windermere (England)[c]	24	13	9			
Zurich (Switzerland)[e]	45	24	17			
Loch Ness (Scotland)[c]	57	27	18	14	11	
Geneva (Switzerland—France)[c]	74	46	30	22	18	

[a]Wilson, W. (1972) Seiches. In: V.T. Chow (eds.) *Advances in Hydroscience*, vol. 8, pp. 1–94.
[b]Wüest, AJ and Farmer DM (2003). Seiches. *McGraw-Hill Encyclopedia of Science and Technology*, 9th edn.
[c]Lemmin U and Mortimer CH (1986) Tests of an extension to internal seiches of Defant's procedure for determination of surface seiche characteristics in real lakes. *Limnology and Oceanography* 31: 1207–1231.
[d]Hutter K, Salvadè G and Schwab DJ (1983) On internal wave dynamics in the northern basin of the Lake of Lugano. *Geophysical and Astrophysical Fluid Dynamics* 27: 299–336.
[e]Horn W, Mortimer CH and Schwab DJ (1986) Wind-induced internal seiches in Lake Zurich observed and modeled. *Limnology and Oceanography* 31: 1232–1254.

(i.e., $\eta_i(x,t) = 0$ when n is even). This intuitively expected because only odd modes have a nodal point at the mid-basin location, where there is zero displacement associated with a uniform tilt of the interface along the basin from the initial condition (Fig. 2A–C, and E) (Boegman et al., 2005a). By calculating the available potential energy associated with each mode, it can be shown that that more than 98% of the wave energy is contained in the H1 mode, but the energy distribution between modes may be significantly altered by resonant forcing or basin shape (Boegman and Ivey, 2012; Fricker and Nepf, 2000; Imam et al., 2020).

Examples of surface and internal seiche periods for various horizontal modes are given in Table 1. Energy will pass between potential and kinetic forms as the wave periodically oscillates with time (Fig. 2A–C, and E). At $t = 0$, $(1/2)T_1$, T_1, $(3/2)T_1$, etc. the wave energy is purely in the potential form, while at $t = (1/4)T_1$, $(3/4)T_1$, $(5/4)T_1$, etc. the energy is purely kinetic, giving rise to horizontal currents within the lake basin (Fig. 2A–C, and E). For a non-dissipative system, the modal energy distributions represent the sum of kinetic and potential energy and are independent of time. Dissipative processes will lead to a decrease in wave amplitude, but not period, with time (Table 1); unless there is sufficient mixing across the thermocline to cause a change in the stratification and hence c_o. For surface seiches the decay in amplitude with each successive period can range from 3% (Lake Geneva) to 32% (Lake Erie).

The governing equations of motion can be solved to determine modal response of a lake or reservoir to an arbitrary wind stress (Monismith, 1985), including the effects of rotation (Antenucci et al., 2000) and irregular bathymetry (Shimizu et al., 2007).

Vertical modes

Basin-scale (barotropic) wave modes that occur on the free surface have no nodes in the vertical direction and are, therefore, vertical mode zero (V0). These are the only vertical modes in a lake of constant density (e.g., Fig. 1A; V0H1 in Fig. 2A). When a single thermocline is present (Fig. 1B), V1 seiches may also occur (e.g., V1H1 in Fig. 2B). A vertical density structure approximated with three or more fluid layers (e.g., Fig. 1C and D) will support higher vertical modes (e.g., V2H1 in Fig. 2C).

Vertical mode-two seiches require a comparatively thick metalimnion (Vidal et al., 2013). They can be generated when there is an asymmetry in the tilting of the upper and lower interfaces of the stratifying layers (the diurnal and seasonal thermoclines or the upper and lower boundaries of the metalimnion (MacIntyre et al., 1999)). Laboratory and limited field data show that such asymmetries are introduced from the compression and expansion of the metalimnion along the downwind and upwind shores, respectively, under upwelling conditions (e.g., Fig. 2D(iv)). This can create strong shear across the base of the surface layer and a relatively undisturbed lower interface; whereas a V1 response occurs for comparable tilts of both interfaces and generates stronger currents in the hypolimnion (Table 2).

Higher vertical mode basin-scale internal waves have also been observed in several lakes after a sudden wind pulse has excited an initial V1H1 response, which then evolves into a V2 seiche (e.g., Wood Lake, Wiegand and Chamberlain (1987)). Resonance with

Table 2 Relevant case studies.

Lake process	*System*	*References*
Internal solitary waves	Loch Ness	Thorpe (1971)
	Seneca Lake	Hunkins and Fliegel (1973)
	Babine Lake	Farmer (1978)
	Kootenay Lake	Wiegand and Carmack (1986)
	Lake Biwa	Boegman et al. (2003)
	Laboratory	Boegman et al. (2005)
	Lake Constance	Preusse et al. (2012)
	Cayuga Lake	Dorostkar et al. (2017)
Shear instability	Lake Kinneret	Antenucci and Imberger (2001), Boegman et al. (2003), Gomez-Giraldo et al. (2008
	Lake Biwa	Boegman et al. (2003), and Saggio and Imberger (1998)
	Lake Pusiano	Botelho and Imberger (2007)
	Lake Erie	Bouffard et al. (2012)
	Lake Constance	Preusse et al. (2010)
Internal hydraulic jumps	Lake Geneva	Thorpe et al. (1996)
	Cayuga Lake	Dorostkar and Boegman (2013)
Internal seiches	Laboratory	Horn et al. (2001), Boegman and Ivey (2012), Boegman et al. (2005)
Higher vertical mode seiches	Theory	Spigel and Imberger (1980), Horn et al. (2001)
	Lake Windermere	Heaps and Ramsbottom (1966)
	Wellington Reservoir	Monismith (1985)
	Lake Zurich	Horn et al. (1986)
	Frains Lake	Lazerte (1980)
	Wood Lake	Wiegand and Chamberlain (1987)
	Lake Alpnach	Münnich et al. (1992)
	Upper Mystic Lake	Fricker and Nepf (2000)
	West Okoboji Lake	Wain et al. (2013)
Internal Kelvin and Poincaré waves	Lake Biwa	Saggio and Imberger (1998) and Shimizu et al. (2007)
	Lake Kinneret	Antenucci and Imberger (2003), Gomez-Giraldo et al. (2008), Hodges et al. (2000)
	Laboratory	Wake et al. (2005), de la Fuente et al. (2008)
	Lake Ontario	Csanady (1975), Schwab (1977)
	Lake Michigan	Mortimer (2004, *Lake Michigan in Motion*) Choi et al. (2012, *J. Geophys. Res.*), Beletsky et al. (1997)
	Lake Erie	Valipour et al. (2015b), Liu and Lamb (2011), Boegman et al. (2001)
	Lake Constance	Appt et al. (2004), de la Fuente et al. (2010)
	Lake Geneva	Lemmin et al. (2005), Bouffard and Lemmin (2013)
	Lake Simcoe	Bouffard and Boegman (2011), Flood et al. (2020)
	Lake Superior	Austin (2013)
Wind-induced setup	Theory	Thompson and Imberger (1980), Imberger and Patterson (1989), Shintani et al. (2010)
	Lake Windermere	Mortimer (1961)
	Laboratory	Stevens and Imberger (1996), Monismith (1986, *J. Fluid Mech.*)
	Lake Michigan	Mortimer (2004, *Lake Michigan in Motion*)
	Lake Ontario	Csanady (1975)
Internal wave-induced turbulence	Wellington Reservoir	Imberger and Ivey (1991)
	Lake Alpnach	Wüest et al. (2000), Lorke et al. (2002)
	Lake Constance	Lorke (2007)
	Lake Biwa	Saggio and Imberger (2001)
	Lake Erie	Bouffard et al. (2012), Lin et al. (2021), Jabbari et al. (2020)
	Lake Michigan	Cannon and Troy (2018), Troy et al. (2016)
	Ada Hayden Lake	Wain and Rehmann (2010)

the wind forcing (e.g., Lake Alpnach, Münnich et al. (1992)), sloping basin topography (Upper Mystic Lake, Fricker and Nepf (2000)) and unequal density differences between stratifying layers (Monismith, 1985) can cause this preferential excitation of higher vertical modes.

Internal seiches under the effect of Earth rotation

The effect of the Coriolis force acting on internal waves, can be quantified according to the Burger number $S = R/W$. Here, $T_E = 86{,}400$ s is the period of rotation of the Earth and $R = c_o/f$is the *Rossby radius* of deformation, which varies with latitude θ according to the *inertial frequency* $f = (4\pi/T_E) \sin \theta$ (Antenucci et al., 2000). The *inertial period*, which may be defined as $T_i = 2\pi/f$, is infinite at the equator, ~18 h in the Laurentian Great Lakes, and minimum (12 h) at the poles.

We can interpret R as the length scale over which an internal wave traveling at c_o will be influenced by rotation for a particular latitude-dependent f: for rotational effects to be significant $W > R$, or equivalently $S < 1$. For example, using a typical $c_o = 0.5$ m s^{-1} rotational effects will be significant for small lakes in the arctic ($W > \sim 3$ km), mid-sized lakes in temperate latitudes (i.e., $W > \sim 5$ km) and larger lakes near the equator (i.e., $W > \sim 100$ km). The effect of rotation is gradual and continuous; there is not a sudden transition at $S = 1$. For surface seiches, the fast phase speeds lead to $R \rightarrow$ 300 km and, correspondingly, there are few lakes that are sufficiently large for the surface seiche to be influenced by rotation (Antenucci, 2009).

Surface momentum transfer and wind set-up with Coriolis force

For lakes where $S < 1$, steady winds will generate surface currents that are deflected 45 degrees by the Coriolis force fu, acting on a fluid parcel with velocity u. The deflection is to the right/left in the northern/southern hemisphere and continues to spiral, with depth, for each contiguous fluid layer decreasing logarithmically in magnitude. The overall depth of the *Ekman layer* $D \sim 2v_T/f$, where v_T is an eddy viscosity, varies according to the strength of the wind stress and the latitude. For example, in Lake Ontario, Csanady (1982) observed a steady 7 m s^{-1} wind to generate a 10-m deep Ekman layer with an average current of 0.1 m s^{-1}.

Integrated over D, the total *Ekman drift* is oriented 90 degrees to the wind, inducing a down-welling of the thermocline along the shore to the right/left of the wind in the northern/southern hemisphere and a corresponding upwelling along the left/right shore. This situation is similar to the wind induced up- and down-welling shown in Fig. 3, but in a direction perpendicular to the wind stress. The Coriolis force is in geostrophic balance with the gravitationally induced pressure force acting on the tilted thermocline. The density gradient creates a cyclonic pressure-driven current, constrained to run shore-parallel in a counter-clockwise/clockwise direction in the northern/southern hemisphere. Conversely, an anti-cyclonic motion would be clockwise in the northern hemisphere, and counter-clockwise in the southern hemisphere.

Internal Kelvin and Poincaré waves

For the rotational case, as in the non-rotating case, when the wind stress drops the pressure gradient becomes unbalanced. The subsequent relaxation of the wind-induced thermocline tilt generates two classes of rotational basin-scale internal waves along the thermocline: (i) anticyclonic Poincaré waves (Poincaré, 1910) that extend over the width of the lake and energize currents in the interior at super-inertial frequencies (periods $< T_i$); and (ii) cyclonic Kelvin waves (Thomson, 1879) that are trapped along the boundary and propagate at sub-inertial frequencies (periods $> T_i$) around the lake perimeter (Antenucci et al., 2000, Antenucci, 2009). Various vertical and horizontal modes are possible, depending on the characteristics of the basin shape, wind stress and density stratification (Saggio and Imberger, 1998; Lemmin et al., 2005; Antenucci et al., 2000). The Kelvin and Poincaré wave solutions, to the governing equations of motion in a rotating reference frame, were developed from the analysis of wave motions in channel flows; the Kelvin wave corresponding to the wave mode propagating along the channel and the Poincaré wave corresponding to the cross-channel mode (Antenucci et al., 2000; Mortimer, 2004).

Internal Kelvin waves travel parallel to the boundary with a maximum amplitude at the shore; the wave crest is to the right/left in the northern/southern hemisphere when looking along the direction of wave propagation (Fig. 4A). The seiche pattern (Fig. 2B) is modified such that the transverse nodal line has become a central amphidromic nodal, around which the Kelvin wave propagates with an exponential decrease in amplitude in the radial cross-shore direction over an e-folding distance $\sim R$ (Fig. 4B). The phase speed c_o and wave period T_n are the same as for waves in a nonrotating reference frame. Kelvin-wave induced currents generate an along-shore coastal jet (Fig. 4B) (Csanady, 1982), which is indistinguishable from the jet that forms due to the initial wind-induced geostrophic adjustment (Csanady, 1982). The exponential slope in the cross-shore direction balances the Coriolis force and consequently there is no cross-shore flow. The Kelvin wave will interact with local topography as it propagates, generating eddies and exchange into coastal embayments (Flood et al., 2020; Wake et al., 2005).

The internal Poincaré waveform (Fig. 5A) (Antenucci, 2009, Mortimer, 2004) energizes strong mid-basin seiche currents that are deflected by Coriolis such that the orbital wave velocities form *inertial circles* with diameter $\sim R$ once per wave cycle (Fig. 5B). Two transverse progressive Poincaré waves can combine to form a cellular standing wave pattern (Fig. 5A). At very long wavelengths, Poincaré waves have a near-inertial period $\rightarrow T_i$ and the wave energy increasingly becomes kinetic (currents) as opposed to potential (amplitude), with the overall motion becoming indistinguishable from an inertial circle.

To satisfy the wave boundary conditions at the lake perimeter, it is necessary to sum the solutions from a progressive Kelvin wave and a transverse standing Poincaré wave (Fig. 5B). As the Poincaré wave impinges upon the coastline, the inertial circles become ellipses and eventually shore parallel oscillations (Troy et al., 2012; Mortimer, 2004). The degree of interaction between the Kelvin and Poincaré waves depends on S (Mortimer, 2004). For medium sized lakes ($W \sim (1 - 10)R$ or $S \sim 0.1 - 1$), both Kelvin and Poincaré waves manifest their signals throughout the basin (Fig. 5B) (Antenucci and Imberger, 2001) (e.g., Lake Simcoe, Bouffard and Boegman (2011); Lake Geneva, Lemmin et al. (2005); Lake Kinneret, Hodges et al. (2000); however, for large lakes ($W \sim 20R$ or $S \ll 1$) rotational effects predominate and the basin-scale internal wave modes become independent of one-another (e.g., Lake Erie, Valipour et al., 2015b; Lake Michigan, Choi et al., 2012); Lake Superior, Austin, 2013). Kelvin waves propagate within $\sim R$ of where the thermocline intersects the coast and Poincaré waves propagate in the basin interior (Mortimer, 2004; Antenucci et al., 2000).

Degeneration of basin-scale internal waves in lakes (phase 3)

Understanding the factors leading to wave degeneration has been a major goal of limnologists. This is because internal waves ultimately lose their energy (degenerate) to dissipation (viscous frictional heating of the fluid at mm scales) and diapycnal mixing

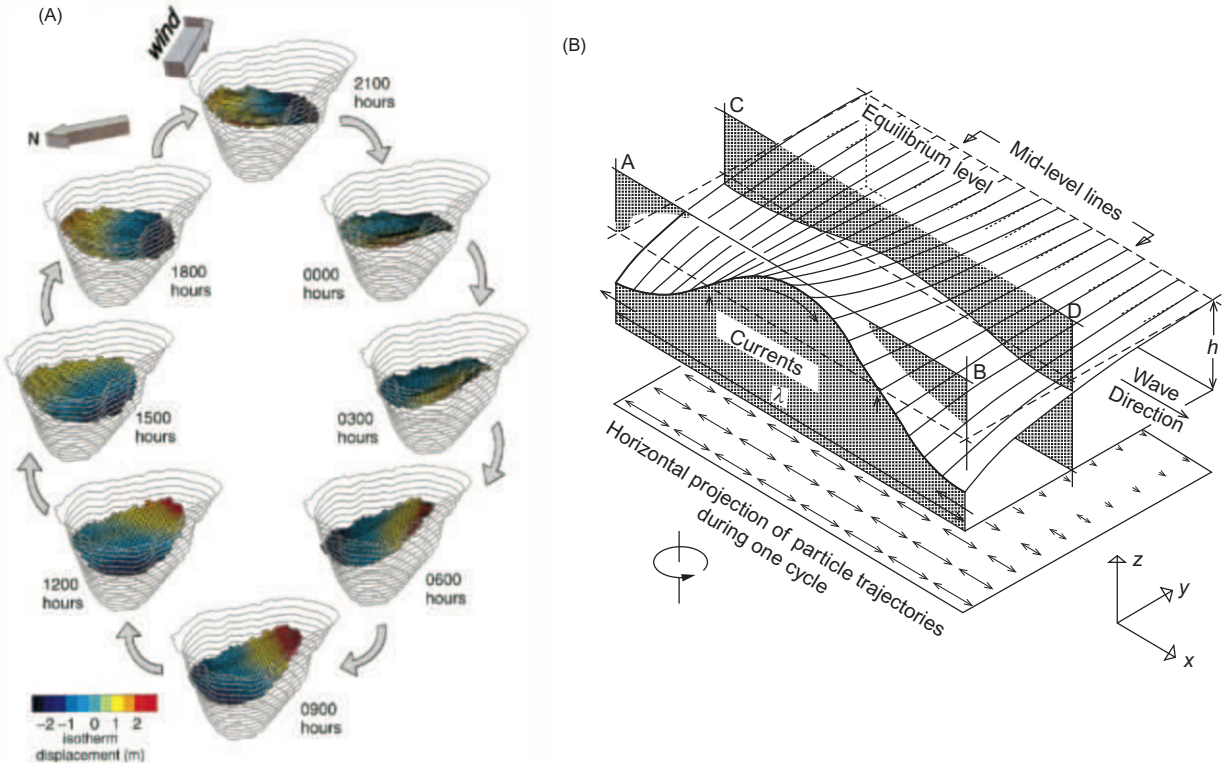

Fig. 4 (A) Computer simulated cyclonic propagation of a vertical mode-one horizontal mode-one internal Kelvin wave in Lake Kinneret starting at 21:00 h. The movement of the thermocline is indicated by the vertical displacement of the 21 °C isosurface around a central amphidromic nodal point. The Kelvin wave amplitude decreases exponentially from shore. (B) A basin-scale internal Kelvin wave progressing in the x-positive direction, with the shore located at $y = 0$. Note the shore-parallel current beneath the wave crest and exponential decay of wave amplitude (over lengthscale $\sim R$) with increasing y(see Supplementary Materials available at https://doi.org/10.1016/B978-0-12-819166-8.00067-0). (A) Computer simulated cyclonic propagation of a vertical mode-one horizontal mode-one internal Kelvin wave in Lake Kinneret starting at 21:00 h. The movement of the thermocline is indicated by the vertical displacement of the 21 °C isosurface around a central amphidromic nodal point. The Kelvin wave amplitude decreases exponentially from shore. (B) A basin-scale internal Kelvin wave progressing in the x-positive direction, with the shore located at $y = 0$. Note the shore-parallel current beneath the wave crest and exponential decay of wave amplitude (over lengthscale $\sim R$) with increasing y(see Supplementary Materials). (A) Reproduced with permission from Hodges BR, Imberger J, Saggio A and Winters KB (2000). Modeling basin-scale internal waves in a stratified lake. *Limnology & Oceanography* 45: 1603–1620. See also Mortimer CH (1974) Lake Hydrodynamics. Mitteilungen Internationale Vereinigung Limnologie **20**: 124–197, (B) reproduced with permission from Mortimer CH (1974) Lake hydrodynamics. *Mitt. Int. Ver. Theor. Angew. Limnol.* 20: 124–197. See also Antenucci J (2009) Currents in stratified water bodies 3: Effects of rotation. In *Encyclopedia of Inland Waters*. Elsevier.

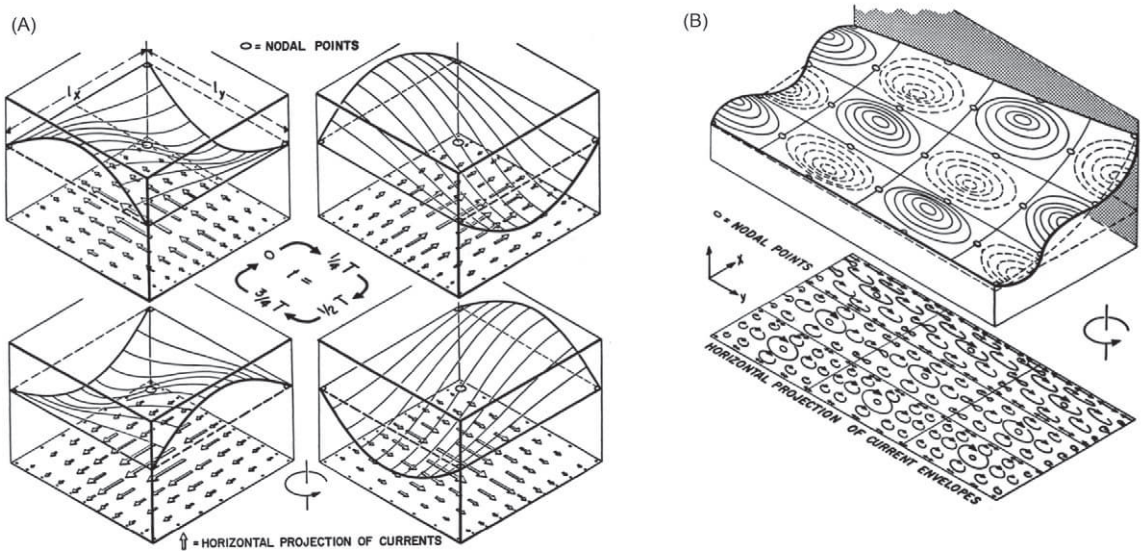

Fig. 5 (A) Anticyclonic propagation of a progressive basin-scale internal Poincaré wave cell over one wave period. Note the strong inertial currents in the cell interior. (B) Combination of a multi-cell standing internal Poincaré wave and a progressive internal Kelvin wave. The Kelvin wave propagates cyclonically around the basin perimeter; whereas, the mid-cell inertial circles, associated with the Poincaré wave, are anticyclonic or opposite to the direction of the Earth's rotation. (A and B) Reproduced with permission from Mortimer CH (1968) *Internal Waves and Associated Currents Observed in Lake Michigan During the Summer of 1963*. Center for Great Lakes Studies. University of Wisconsin-Milwaukee.

(mixing of fluid perpendicular to isopycnals or surfaces of constant density) in regions where the flow is turbulent. In turn, mixing drives biogeochemical fluxes. Turbulence is produced directly from the seiche induced currents by fluid straining in the lake interior (Bouffard et al., 2012) and TBBL (Jabbari et al., 2020; Cannon and Troy, 2018), and from processes that are uncoupled from seiche generation, such as surface wave breaking and inflows (Hamblin, 1977), which may act to disrupt the seiche motion. Seiche-induced mixing in the lake interior (Pernica et al., 2013) and TBBL (MacIntyre and Jellison, 2001) as well as internal wave shoaling and breaking (Boegman and Stastna, 2019) all impact lake biogeochemistry.

As a general rule, for deep lakes, the period of internal seiche decay is about 1 day per 40 m of water-column depth (Wüest and Farmer, 2003). For very deep lakes, e.g., Lake Baikal where $H = 1637$ m, this equates to a decay period of more than 1 month. The time scale associated with viscous damping of a basin-scale seiche T_D can be estimated from the ratio of the seiche energy to the rate of energy dissipation in the benthic boundary layer ε_{TBBL}

$T_D \sim \frac{\text{Seiche energy}}{\varepsilon_{TBBL}} \times \frac{\text{Lake volume}}{\text{TBBL volume}} \sim 1$ to 10 d for moderately sized lakes (Imberger, 1998)

The energy dissipation in the lake interior $\varepsilon_{interior}$ is neglected because observational studies show that $\varepsilon_{TBBL} > 10\varepsilon_{interior}$ (Wüest et al., 1996). As a result, degeneration of basin scale internal waves occurs primarily due to turbulence production in the TBBL rather than the interior. The degeneration can occur through four possible mechanisms that depend on the degree of wind-induced thermocline tilt (η_i/h_1) and thermocline depth (h_1/H) (Horn et al., 2001); Fig. 3B): (1) viscous damping of seiche currents in the TBBL (Imam et al., 2013; Spigel and Imberger, 1980); (2) the formation of shear instabilities in the interior (Gomez-Giraldo et al., 2008; Boegman et al., 2003); (3) the production of high-frequency nonlinear internal waves that will break on sloping topography (Boegman et al., 2005b; Preusse and Peeters, 2014); and (4) the formation of internal hydraulic jumps (Dorostkar and Boegman, 2013; Thorpe et al., 1996). By calculating the timescales over which each mechanism will occur, regimes have been delineated in which a particular mechanism will predominate (Horn et al., 2001) (Fig. 3B).

Internal wave degeneration processes are different in large lakes ($S < \sim 1$), where Coriolis impacts the thermocline setup and energy flux paths to the internal wave field (Valipour et al., 2015b; Bouffard et al., 2012; Lin et al., 2021). The internal Kelvin wave leaks energy to transverse Poincaré waves as it propagates (de la Fuente et al., 2008; Mortimer, 2004) and to high-frequency internal waves through nonlinear steepening (Boegman et al., 2005a). The internal Poincaré wave may degenerate through the formation of Kelvin-Helmholtz billows at the wave crests and troughs (Bouffard et al., 2012).

Resonant and forced internal waves

The periodicity inherent in weather patterns creates over-lake wind fields at regular frequencies. For example, the winds over Lake Erie have periodicities of 10 d and 24 h, associated with frontal weather systems and diurnal land/sea breeze phenomena, respectively (Hamblin, 1987). When the forcing frequency matches one of the natural frequencies of the basin-scale wave modes, resonant amplification will occur. Seasonal heating and deepening of the thermocline will adjust the natural frequencies relative to the forcing frequencies, thus tuning the system into and out of resonance (Antenucci and Imberger, 2003).

Laboratory experiments show that the relative frequencies of the wind forcing f_w and H1 internal seiche f_{H1}can be used to model internal wave response to periodic forcing conditions (Boegman and Ivey, 2012). When the forcing frequency of the wind stress is less than the natural frequency of the H1 internal seiche ($f_w < (2/3)f_{H1}$), the phase of the basin-scale oscillations are reset with each wind event and a forced internal seiche is generated at the same frequency as the wind forcing (Gómez-Giraldo et al., 2006). A resonant H1 seiche will occur when the frequency of the wind forcing is near the frequency of the H1 seiche ($(2/3)f_{H1} < f_w < 2f_{H1}$; Antenucci and Imberger (2003)) and when the forcing frequency is greater than the natural frequency of the H1 seiche ($f_w > 2f_{H1}$)), higher-mode horizontal seiches are generated. Resonance appears to be particularly effective in amplifying the response of the second vertical mode (e.g., Lake Alpnach (Münnich et al., 1992)) and the even horizontal modes that are not naturally energized by a wind-induced interfacial setup.

Resonance between the wind and the H1 internal mode leads to increased seiche amplitudes under relatively weak wind forcing conditions. For example, the formation of a steepened internal wave front in Loch Ness (Thorpe, 1974).

Analysis of timeseries data

The various wave, instability and turbulence processes described in this chapter are shown schematically in Fig. 7. These processes occur beneath the lake surface and so practicing limnologists do not have the luxury of being able to directly observe them in the field. Some insight regarding their spatial structure is gained from idealized laboratory and computational models but for the most part, limnologists must resort to deciphering timeseries data from thermistor chains, which are the most useful tools in their arsenal. Fig. 6 shows many of the processes from Fig. 7 as they would appear on thermistor data, which has been contoured to show isotherm displacement timeseries with depth.

During the strong wind event, shear instabilities form at the base of the surface layer (Fig. 6D). Shortly thereafter, a thermocline jet occurs within a compressed region of the metalimnion and causes a rapid expansion of the strata and localized mixing (Fig. 6E). The basin-scale internal wave energized by the wind has steepened into an internal surge supporting large amplitude nonlinear internal waves of depression and series of step like features resembling internal hydraulic jumps (Fig. 6C). The surge wave interacts with the lakebed leading to significant mixing over the bottom 20 m of the water column.

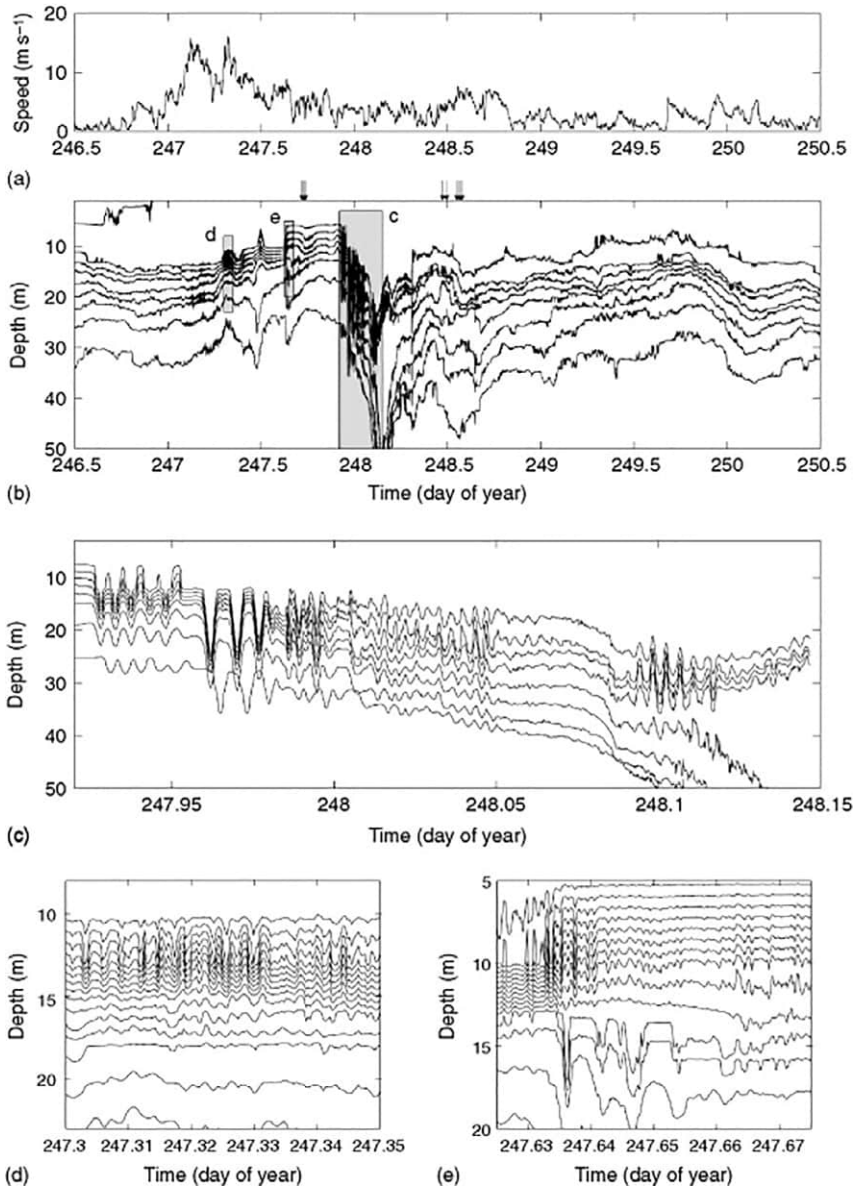

Fig. 6 Observations from Lake Biwa (Japan) in 1993 showing steepened nonlinear basin-scale internal wave front and associated nonlinear internal waves. (A) Wind speed collected at 10-min intervals showing the passage of a storm event; (B) nonlinear response of basin-scale internal wave field showing steepened wave front (2 °C isotherms); (C) magnified view of shaded region in panel b showing details of NLIWs (2 °C isotherms). (D) Magnified view of shaded region d in panel b showing shear instabilities resulting from enhanced shear at the base of the surface layer during the strong wind event (1 °C isotherms); (E) magnified view of shaded region e in panel b showing a V2 expansion of the metalimnion resulting from a thermocline jet that forms after a period of metalimnion compression (1 °C isotherms). The bottom isotherm in panels b and c is 10 °C. Reproduced with permission from Boegman L, Imberger J and Ivey GN and Antenucci JP (2003) High-frequency internal waves in large stratified lakes. *Limnology and Oceanography* 48: 895–919.

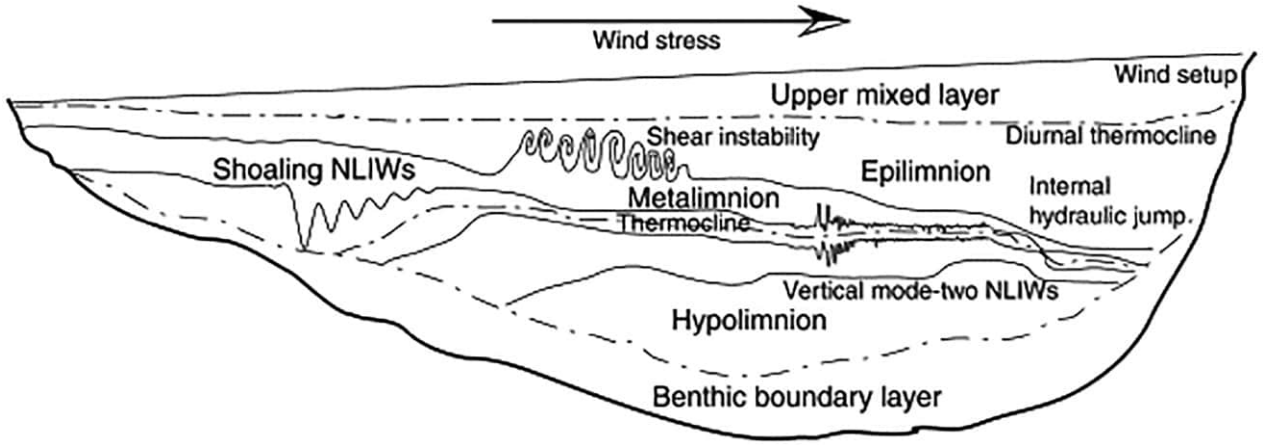

Fig. 7 Pictorial representation of the various regions of a lake and some of the wave-like physical processes that occur. See also Fig. 6.13 in Fischer HB, List EJ, Koh RCY, Imberger J and Brooks NH (1979) Mixing in inland and coastal waters. Academic Press; Fig. 15 in Imberger J (1985) Thermal characteristics of standing waters: An illustration of dynamic processes. *Hydrobiologia* 125: 7–29; and Fig. 7 in Imboden DM and Wüest A (1995) Mixing mechanisms in lakes. In A. Lerman, DM Imboden and J Gat (eds.) *Physics and Chemistry of Lakes*, pp. 83–138. Springer-Verlag.

The motions described above all result from a single intense wind event. Considering the periodic nature of surface winds, it is not surprising that periodic wave motions occur in lakes over a range of length scales and frequencies. Spectral frequency analysis is used to conveniently analyze timeseries data and determine the relative amount of energy found at each frequency.

Relevant case studies

See Table 2.

Summary

The dynamic interplay between stratification, waves, and wind is best summed up in using the conceptual model proposed by (Imberger and Patterson, 1989); Fig. 7) and supported by more recent measurements (Wüest et al., 1996, 2000; Imberger, 1998; Nakhaei et al., 2016; Lin et al., 2021). A lake behaves like an engine that is powered by the wind and does work against the potential energy embodied in the stratification. Approximately 2% of the wind energy enters the lake; of this ~80% is dissipated in the surface layer and ~20% is transferred to the basin-scale internal wave field. The basin-scale seiches energized by the wind are frictionally damped as they swash along the lakebed and by degeneration into progressive high-frequency internal waves, shear instabilities, and eventually turbulence. Approximately 90% of the seiche energy is lost energizing turbulent dissipation and mixing in the TBBL; <1/4 of which first passes through the nonlinear internal wave field prior to wave breaking and >3/4 of which is lost to frictional swashing in the TBBL. The remaining ~10% of the seiche energy results in intermittent shear instability in the basin interior. The overall mixing efficiency of the turbulence is ~15% leading to an upwards buoyancy flux that works to weaken the stratification and raise the center of gravity of the lake. The lake engine is extremely inefficient with only ~0.06% of the wind work acting to irreversibly mix the stratification; the bulk of the wind work is lost to frictional viscous dissipation, which due to the large heat capacity of water has no significant effect on the lake temperature. From this model, it is clear that while internal waves influence biogeochemical mixing and transport within a stratified waterbody, they are unable to significantly influence the stratification upon which they propagate. Wind-induced vertical mixing at basin-scales is, therefore, greatly reduced by diurnal/seasonal/meromictic stratification and only occurs in polymictic systems (Loewen et al., 2007; Boegman et al., 2008) or when convection has eroded the seasonal stratification (Bouffard and Wüest, 2019; Boegman, 2020; Ghane and Boegman, 2021).

Knowledge gaps

- How energy is transferred from basin-scale internal Kelvin and Poincaré waves to ultimate dissipation and mixing in rotational systems
- The relative importance of internal wave-induced mixing versus convection, in regulating vertical biogeochemical fluxes
- The coupling between wind-driven surface waves and internal waves in lakes
- How internal waves resuspend sediments and form nepheloid layers

See Also: Fundamental concepts and theories: Temperature as a Driving Factor in Aquatic Ecosystems; Structures and functions of Inland Waters - Lakes: Bottom Boundary Layers; Currents in Well-Mixed Layers; Currents in Stratified Water Bodies 1: Density-Driven Flows; Lacustrine Phosphorus Cycling; Small-Scale Turbulence and Mixing: Energy Fluxes in Stratified Lakes; Surface Mixed Layers in Lakes

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Currents in Stratified Water Bodies 1: Density-Driven Flows

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This is a reprint of F. Peeters, R. Kipfer, Currents in Stratified Water Bodies 1: Density-Driven Flows, In Encyclopedia of Inland Waters, Edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00080-6.

Introduction

Vertical transport of dissolved substances and heat in lakes mainly results from two different mechanisms: (a) mixing by turbulence that is usually described as a diffusive transport and (b) density-driven exchange that can be considered as an advective transport. A typical example of the latter is convection owing to surface cooling in fall, which often leads to isothermal conditions in shallow lakes of the temperate zone. Because entrainment of ambient water limits the depth of convective plumes, density-driven transport to large depth in deep lakes usually occurs along the lake boundaries and is often the result of specific and localized processes, which are discussed later.

The important role of density-driven transport for vertical exchange in lakes becomes evident if one considers that temperature stratification typical for most lakes is characterized by a decrease in water temperature with increasing water depth. Turbulent diffusion causes heat to flow from high to low temperatures and hence typically leads to a gradual continuous warming of cold deep-water regions. Thus, on a long-term average, advective processes transporting cold surface water downwards must be sufficient to compensate for the heat flux due to turbulent diffusion. The low temperatures in the deep water are usually either the remnant of isothermal conditions generated by buoyancy-driven overturn during the cold season or originate from cold density currents propagating to largest depth. Because vertical transport due to density currents plays an important role in overall deep-water renewal and heat exchange, density driven exchange processes are central to the understanding of oxygenation and nutrient transport especially in deep lakes.

In the world's largest and deepest water bodies several processes have been identified that lead to advective deep-water renewal by density currents: river inflow, e.g., in Lake Constance, Lake Geneva, and Lake Baikal; inter-basin exchange, e.g., in Lake Lucerne, Lake Baikal, or even in the Caspian Sea; differential cooling, e.g., in Lake Geneva, Lake Constance, Lake Issyk-Kul, and Lake Malawi; thermal-bar mixing, e.g., in the Lake Ontario, Lake Ladoga, Lake Michigan, and Lake Baikal; and transport due to thermobaric instabilities, e.g., in Lake Baikal and possibly in Crater Lake. All these processes have been shown to significantly contribute to deep-water renewal in lakes, although advective transport to the lake bottom was not conclusively demonstrated in all cases. More details on the different processes are given below.

In the following, we first describe the principal characteristics of density currents and the associated signals of intrusions in vertical profiles of water constituents and temperature. Then, we present several mechanisms that lead to the generation of density plumes in deep freshwater lakes and discuss which of these processes can also be responsible for deep-water renewal in tropical and saline lakes. Finally, we discuss the potential impact of changes in the catchments of lakes and in the meteorological conditions on deep-water renewal by density currents.

Characteristics of Density Currents

Density currents are driven by differences in water density, which can result from gradients in water temperature, salinity, dissolved uncharged substances, or suspended particles and are also affected by pressure. If a water mass with higher density is situated above

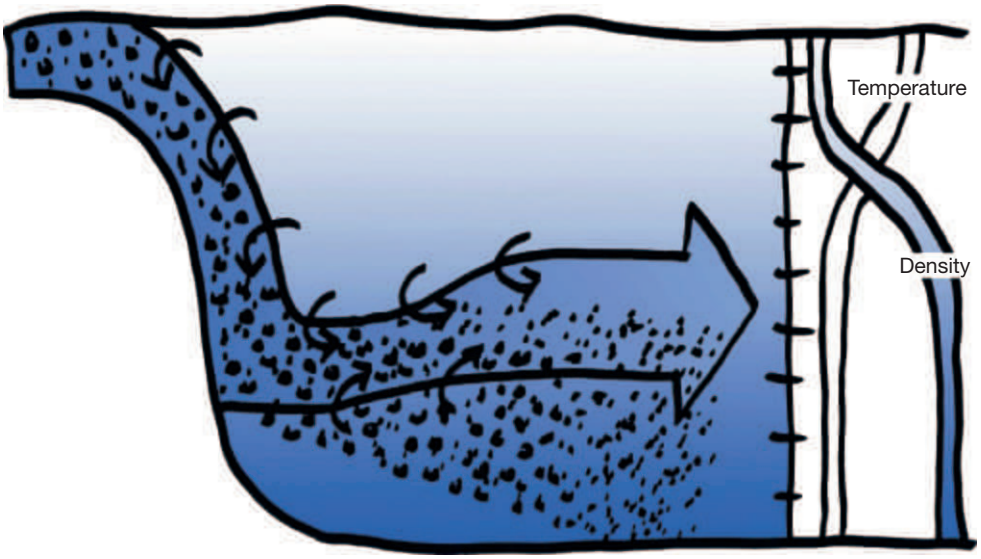

Figure 1 Schematic illustration of density currents. The shading on the left-hand side of the figure indicates an increase in density with increasing depth.

a water mass with lower density, the stratification is unstable and buoyancy causes the upper water mass to sink. In the sinking process ambient water is mixed into the sinking water mass and thus alters its density (Figure 1), thereby reducing the density difference between the density plume and the ambient water.

Furthermore, the properties of the ambient water change along the path of the sinking water mass. Hence the buoyancy of the sinking plume changes continuously as it sinks into deeper depth. Eventually, a depth is reached where the density of the density plume and the density of the surrounding water become equal. At this depth the sinking process ceases and the plume water spreads out laterally into the ambient water forming an intrusion (Figure 1). In many cases the sinking plume meets the lake boundary and then continues to sink along the lake boundary (Figure 1). In this case, entrainment of ambient water is limited to the upper side of the density plume and less ambient water is entrained per unit sinking depth. Hence the characteristic properties of the water within the density plume (e.g., temperature, salinity, suspended particles, dissolved oxygen) change more slowly and the density plumes typically can propagate to larger depths than would be possible in the open water.

The occurrence of density plumes propagating from shallow to deep water are indicated by intrusions that can be identified in CTD -profiles (conductivity as measure of salinity, temperature, and depth) and in pro files of dissolved substances and suspended particles. Figure 2 presents an ex ample from Lake Issyk-Kul (Kyrghystan), where intrusions are characterized by a higher dissolved oxygen con centration and a lower light transmission than is observe d in the ambient water.

High oxygen levels in the intrusions indicate oxygen -rich surface water that must have been transported recently because oxy gen levels have not yet been significantly reduce d by degradation processes. The low light transmission in the intrusions indicates water with a high load of suspended particles suggesting either, that the water that generated the density current was enriched in suspended particles and thus may have originated from river inflow, or, that the density plume responsible for the intrusions has propagated along the lake boundary and caused resuspension of sediments during the sinking process. Temperature is usually not a good indicator of intrusions because it is a key parameter deter mining plume density. Thus, at the depth of the intrusion, plume water and surrounding water often have about the same temperature. However, in cases where the density plume propagates down to the largest depths, as it is some times the case e.g., in Lake Baikal, temperature anomalies at the lake bottom can be used to identify density plumes.

Density Plumes Generated by External Inputs

River Inflows

The density differences required to drive density plumes originate from processes that generate horizontal or vertical gradients in water properties. An obvious example is river inflow (Figure 3).

River water usually contains an increased load of suspended particles and has a different temperature and salinity than the lake water. Hence, river inflow is commonly associated with density plumes propagating from the river mouth to larger depths. The kinetic energy associated with the inflow of the river water is usually rapidly dissipated and the horizontal density gradients resulting from the different densities of river water and lake water are the main cause of river induced transport of water masses in lakes. During summer, the density plumes induced by river inflow typically intrude at some depth within the thermocline of freshwater lakes. Because of the large temperature gradients in the thermocline, water densities change significantly within a rather narrow depth range in the lake. Hence, the probability that the density of the plume water agrees with the density in the water column of the

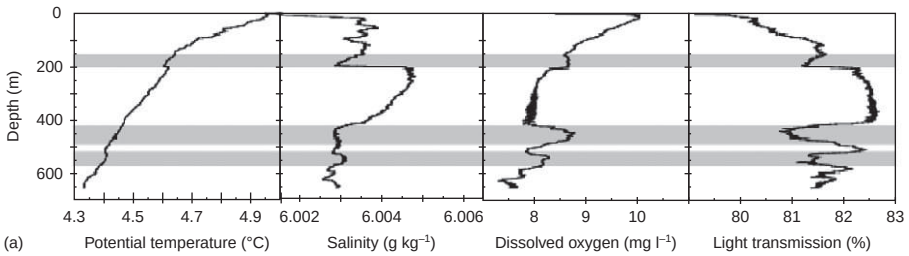

Figure 2 Intrusions as indicators of density currents. Vertical profiles of temperature, salinity, dissolved oxygen, and light transmission measured in Lake Issyk-Kul. The distinct features in these profiles suggest intrusions from density currents. Grey bars mark depth regions with high concentrations of dissolved oxygen and low light transmission, suggesting water originating from shallower depth regions. Redrawn from **Figure 2** in Peeters FD, Finger M, Hofer M, Brennwald DM, and Livingstone R Kipfer (2003). Deep-water renewal in Lake Issyk-Kul driven by differential cooling. *Limnology & Oceanography* 48(4): 1419–1431.

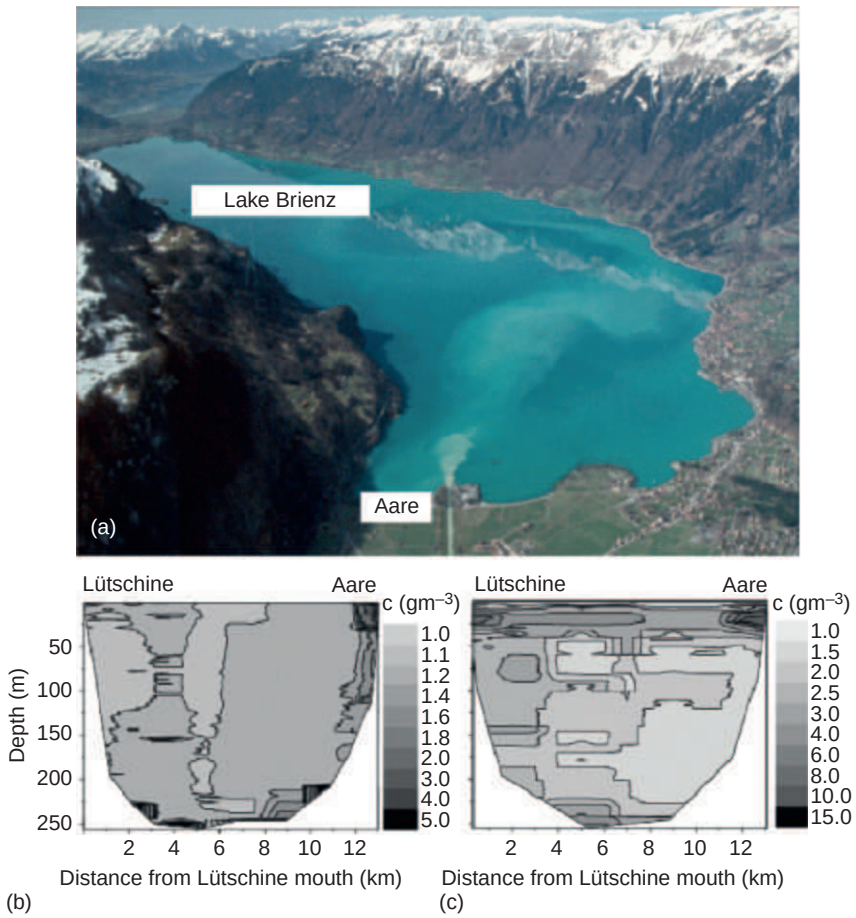

Figure 3 Density currents generated by river inflow. (a) Water of river Aare indicated by high turbidity intruding near the surface of Lake Brienz. The sharp boundaries of this surface plume indicate plunging of river water to larger depth. (b, c) Suspended particle distribution inferred from light transmission measurements in a longitudinal cross-section of Lake Brienz measured in February (b) and October (c). The particle distributions suggest that, in February water introduced by the river Aare (inflow on the right-hand side) sinks as density plume along the lake bottom towards largest depth (b). In October river Aare and river Lütchine both intrude at intermediate depth (c). (Figure 3(a) was provided by Ueli Ochsenbein; **Figure 3(b)** and **(c)** are redrawn from **Figure 7(a)** and **7(d)** in Finger D, Schmid M, and Wüest A (2006). Effects of upstream hydropower operation on riverine particle transport and turbidity in downstream lakes. *Water Resources Research* 42, W08429, doi:10.1029/2005WR004751. Reproduced/modified by permission of American Geophysical Union.

lake is especially large within the thermocline. This fact explains that river water typically intrudes in this depth range. The depth reached by the density plumes varies during the course of the year since water properties and hence the density of lake and river water changes seasonally (Figure 3). Density currents containing a high load of suspended particles are often called turbidity currents. Sedimentation of particles out of intrusions resulting from turbidity currents can reduce the density of the intruding water sufficiently that the depth of the intrusions becomes shallower over time. Density currents induced by river inflows usually

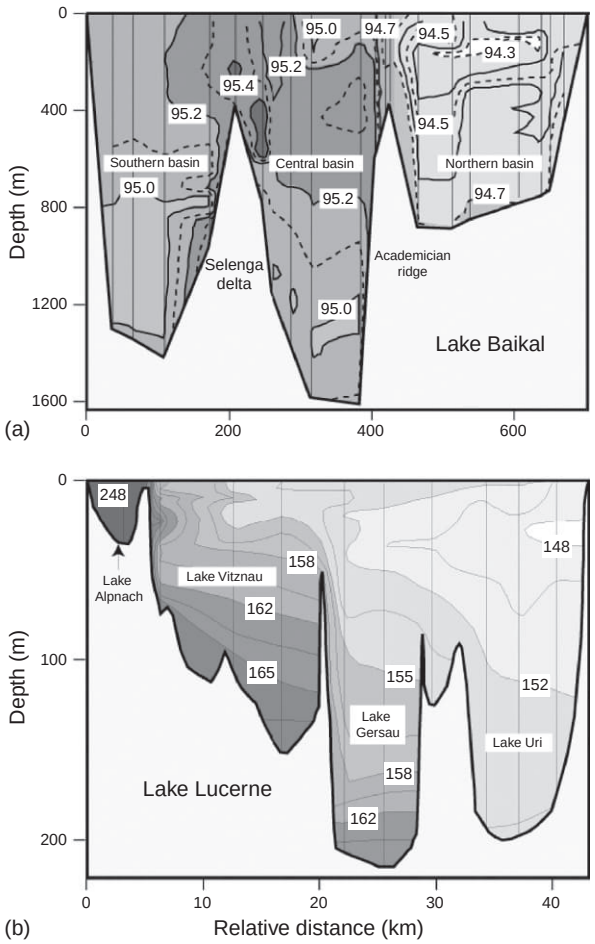

Figure 4 Density currents generated at sills between sub-basins. Vertical transects of salinity in Lake Baikal (a) and in Lake Lucerne (b). In both lakes the horizontal gradients in salinity are generated by river inflows introducing water with different ion concentration. The salinity distributions suggest that density currents are not only generated directly by river inflow as is the case in Lake Baikal at the Selenga delta (see panel a) but that density currents also occur in both lakes at the sills between sub-basins most likely driven by horizontal transport across the sill. Contours depict salinity in mg kg^{-1}. **Figure 4(a)**: redrawn from Kipfer R and Peeters F (2000). Speculation on consequences of changes in the deep water renewal in Lake Baikal, in K Minoura (ed.) *Lake Baikal a mirror in time and space for understanding global change processes*, pp. 273–280. Amsterdam, Netherlands: Elsevier. **Figure 4(b):** drawn using data from Aeschbach-Hertig W, Kipfer R, Hofer M, Imboden DM, and Baur H (1996) Density-driven exchange between the basins of Lake Lucerne (Switzerland) traced with the ^{3}H-^{3}He method. *Limnology and Oceanography* 41: 707–721.

propagate along the sloping bottom boundary before the water intrudes laterally. If the concentrations of solutes and particles are very different between the river and the lake water, the plumes can propagate down to the deepest parts of the lake. In cases where the sinking water is confined to underwater channels, e.g., density plumes propagating down the Kukui Canyon of the Selenga delta in Lake Baikal, entrainment of ambient water is reduced, and the density plume can propagate over a depth range of more than 1000m down to 1640m (see also **Figure 4(a)**).

Interbasin Exchange

River inflows not only result in localized density plumes propagating from the river mouth to larger depths but also can generate subtle large scale gradients in water properties that affect the horizontal density distribution on a basin scale. These small density gradients on a large spatial scale may contribute to the generation of density currents far from the river inflow that occur especially in the vicinity of sills separating sub-basins of the lake. This mechanism is exemplified in **Figure 4** for two lakes of different size, Lake Baikal and Lake Lucerne, that both are structured into several sub-basins separated by sills.

In both lakes large scale horizontal salinity gradients are generated by river inflows introducing water with different ion concentrations into the different sub-basins. In the case of Lake Baikal, the River Selenga introduces more saline water into the Central Basin than the Upper Angara River introduces into the Northern Basin. In case of Lake Lucerne, the River Sarner Aa introduces more saline water into the sub-basin Lake Alpnach than the River Reuss introduces into the sub-basin Lake Uri. Because

of the salinity gradients, the density of the water in the different sub-basins differs if temperature is the same. In Lake Lucerne the densest water can be found in sub-basin Lake Alpnach when winter cooling reduces surface water temperature to ~4 °C. Horizontal transport of the dense water from Lake Alpnach to the subbasin Lake Vitznau across the sill separating the two sub-basins induces a density current renewing the deep-water of sub-basin Lake Vitznau (**Figure 4(b)**). The density plume causes upwelling of cold dense water within Lake Vitznau. Horizontal transport of water across the sills between sub-basin results into a cascading of density driven transport within all sub-basins (**Figure 4(b)**). A similar process is operating in the different basins of Lake Baikal (**Figure 4(a)**). Prerequisite of these density currents generated at sills between sub-basins is (1) the structuring of the lake basin into sub-basin that prevents homogenization of water properties by horizontalmixing and (2) a heterogeneous input of water properties, as e.g., the salinity by the river inflows in **Figure 4**.

Subsurface Inflows

Besides the input from rivers, external water sources derived from groundwater inflows and from hydrothermal vents can generate density currents depending on the depths at which the inflows are located. Groundwater and hydrothermal water is usually highly enriched in ions and thus can cause salinity driven density plumes. Groundwater inflows into lakes are common in artificial lakes such as mining lakes or gravel-pit lakes or occur in karstic environments. Density currents due to hydrothermal vents have been reported for instance in Lake Baikal, where hydrothermal water is introduced in Frohliha Bay at a depth of 200–400m and propagates as a bottom following density current down to 1400m depth. In this specific case the salinity of the hydrothermal water is sufficiently large to compensate the decrease in density due to the increased water temperatures in the hydrothermal water.

Density Plumes Generated by Internal Processes

Differential Cooling

A key parameter affecting water density is temperature. However, for density currents to be induced on the basis of the temperature of water, horizontal gradients in temperature are required. Horizontal temperature gradients are generated by external surface and subsurface inflows (see earlier text) but also by internal processes. In most lakes the heat flux at the lake surface (expressed per unit area) can be considered as horizontally homogeneous because meteorological parameters and radiation do not vary significantly at the length scale of the lake basin. Nevertheless, differential cooling can generate significant temperature differences within lakes and thus generate density currents (e.g., Wellington Reservoir, Lake Geneva, Lake Constance, Lake Banyoles). Heat loss at the lake surface causes vertical convection and thus mixing of surface water with water from layers below. This process continuously mixes the cooled surface water with water from deeper layers containing heat stored during the warm season. In shallow-water regions, the reservoir of warmer deep water is exhausted earlier than in regions with large water depth. Hence, in shallow-water regions heat loss at the lake surface leads to a faster cooling of the water column than in deep-water regions. Because the cold water in the shallow-water regions has a larger density than the warmer water in the pelagic, deep-water regions, the cold water propagates downwards as a density current. Such density plumes often occur only sporadically. They are typically generated during night-time cooling in fall as has been demonstrated in e.g., Lake Constance and Lake Geneva (**Figure 5**) or during events that also induce cooling such as cold fronts or monsoons.

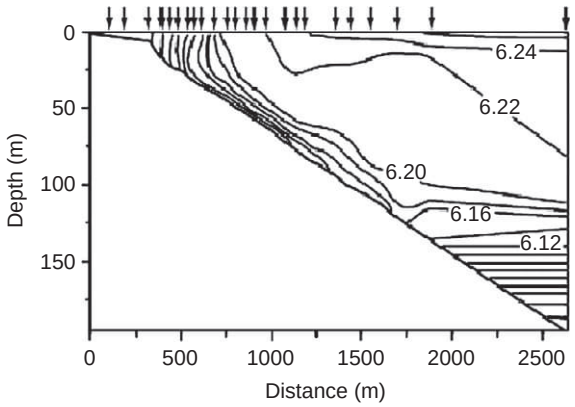

Figure 5 Density current generated by differential cooling. Contour lines represent isotherms in °C indicating a density plume generated by differential cooling in Lake Geneva. Note that the temperatures are well above 4 °C. The isotherms are constructed from CTD-data collected at the locations indicated by the arrows. Redrawn from **Figure 2(b)** in Fer I and Lemmin U. Winter cascading of cold water in Lake Geneva. *Journal of Geophysical Research* 107, NO. C6, 10.1029/2001JC000828, 2002. Reproduced/modified by permission of American Geophysical Union.

Differential cooling can result in density driven currents from any shallow region in a lake basin. Therefore it may affect a large volume of water and thus may significantly contribute to overall vertical transport. The process is particularly effective if large shelf regions are located around a deep basin. The density currents induced by differential cooling propagate along the lake bottom and can reach large depths especially if channels exist along which the density current can propagate without significant entrainment of ambient water, as is the case e.g., in Lake Issyk-Kul. Note, that in freshwater lakes differential cooling can only generate density plumes if water temperatures are above the temperature of maximum density (T_{md}) which is about 4 °C at the lake surface. Cooling below T_{md} implies a decrease in water density and thus prohibits density plume development by differential cooling. Hence, in freshwater lakes the temperature of density plumes associated with differential cooling is at least 4 °C or higher.

Thermal Bar

Temperature-driven density currents can also result from horizontal mixing of two adjacent surface water masses, one having a temperatures above and the other below T_{md}. Because of the non-linear temperature dependence of the equation of state, mixing of water masses with different temperatures always results in an increase in the mean density of the water. This process is called cabbeling. If the temperature of the mixed water is closer to the T_{md} than the water below, it sinks as a density plume. A so-called thermal bar develops which is characterized by a vertically isotherm water column with a temperature close to T_{md} separating an open water region with temperatures below T_{md} from a warmer shore region with temperatures above T_{md} (**Figure 6**).

The downward flow of dense surface water at the thermal bar can cause significant renewal and oxygenation of deep water. As time progresses the thermal bar moves further away from the shore to the open water. The dynamics of this process depends on the morphometry of the lake and on the atmospheric forcing. Mixing associated with the thermal bar has been reported for Lake Ontario, Lake Ladoga, Lake Michigan, and Lake Baikal. Because the thermal bar requires open-water temperatures below T_{md}, it occurrs mainly in lakes which become ice covered in winter.

The horizontal temperature gradients required for thermal bar development are generated by differential heating during spring warming, a process similar to differential cooling. Initially in spring, when surface-water temperatures are below T_{md}, an increase of water temperature during spring warming leads to an increase in the density of the surface waters and thus to convection. Because convection mixes the warmer surface water with colder water from below and the reservoir of the cold water from below is smaller in shallow near-shore than in deeper open-water regions the temperature in the shallow-water regions increases faster than in the deep off-shore regions. When the temperature in the shallow regions exceeds 4 °C the water column is stratified and further influx of heat is not connected to convection, but leads to an even faster increase in the water temperature. Thus, a horizontal temperature gradient typical for a thermal bar situation develops with temperatures below T_{md} at the surface of the open-water region and temperatures above T_{md} at the surface in the shallow near-shore regions. A reverse thermal bar situation with temperatures below T_{md} in the shallow-shore region and temperatures above T_{md} in the open-water region could develop in fall as a consequence of differential cooling if cooling in the shore region progresses to temperatures below T_{md}. However, in the case of the reverse thermal bar exchange processes will be dominated by horizontal density gradients below the surface (see the section on 'Differential cooling').

Thermal Baricity

Another process that can generate density plumes as a consequence of the nonlinearity of the equation of state of freshwater is the thermobaric effect. The thermobaric effect results from the fact that T_{md} decreases with increasing pressure. The generation of density currents by the thermobaric effect requires a very specific temperature stratification that occurs only in few stably stratified deep freshwater-lakes, e.g., Lake Baikal or Crater Lake. To generate density currents by the thermobaric effect, water temperatures must be below 4 °C throughout the water column. The temperature in the surface layer must increase with increasing depth, whereas the temperature in the deep-water must decrease with increasing depth. Then, the temperature profile has a maximum at intermediate depth, the so-called mesothermal maximum (**Figure 7**).

A water column with such a temperature profile is stably stratified because of the effect of pressure on fresh water density. If the water column is displaced downwards or pressure is increased, the temperature at the mesothermal maximum is higher than the local T_{md} and the water column becomes unstable. Cold water from above the mesothermal maximum can sink downwards as a density plume (**Figure 7**). Similarly, a water mass from the cold upper layer can be pushed downwards below the mesothermal maximum to a depth where its temperature is closer to T_{md} than the temperature of the ambient water. Then, it will continue to sink driven by its buoyancy until the surrounding water has the same temperature as the sinking water mass. Besides the specific temperature profile in the water column the exchange due to the thermobaric effect also requires a mechanism by which the water pressure is altered substantially and/or the water is locally pushed downwards across the depth of the mesothermal maximum. Hence density plume generation by the thermobaric effect is not very common. Several investigations have claimed that the thermobaric effect may be important for deep-water oxygenation in Lake Baikal. However, the mechanism that could cause the required downward displacement in the open water column remained unclear. Recently, wind-driven Ekman transport near the coast of the Southern Basin of Lake Baikal has been suggested to cause thermobaric instabilities.

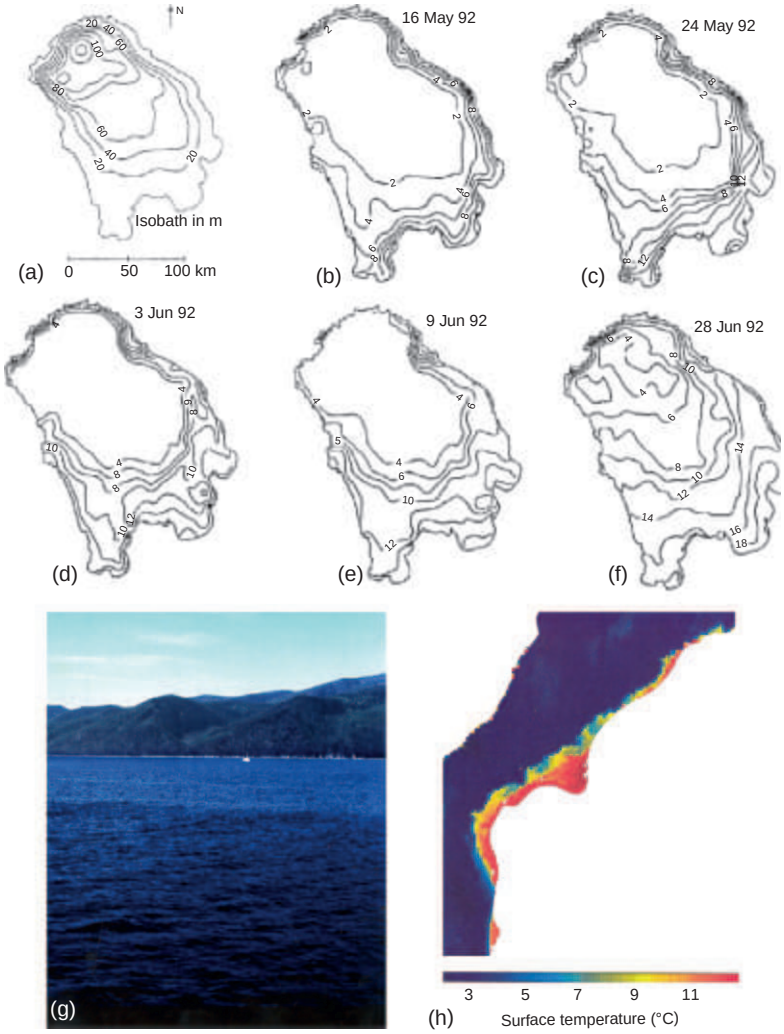

Figure 6 The thermal bar. The development of a thermal-bar in Lake Ladoga indicated by surface temperatures measured with satellites (a–f) and the observation of a thermal bar near Selenga delta in Lake Baikal (g and h). Panel (a) provides the morphometry of Lake Ladoga with depth contours given in m. Panels (b–f) depict surface temperatures with isotherms in °C. Panels (b–f) show how the thermal bar, which is located at the 4 °C isotherm, moves towards deeper water as the season progresses. The position of the thermal bar changes more rapidly in the gently sloping shallower south-eastern part of the lake than in the steep and deep northern part. In (g), the sharp boundary between near shore water and open water indicates the position of the themal bar located near the Selenga delta in Lake Baikal. The color differences result from differences in the load of suspended particles. The water trapped near shore by the thermal bar has an increased load of suspended particles owing to the nearby inflow of the Selenga River. Panel (h) shows an image of the surface temperatures near Selenga delta derived from satellite data. Density currents are generated at the sharp transition between warm shore water and cold open water characterized by a temperature close to 4 °C. White areas are land. **Figure 6(a–f)** are redrawn from **Figures 1** and **3** in Malm J, Mironov D, Terzhevikl A, and Jiinsson L (1994) Investigation of the spring thermal regime in Lake Ladoga using field and satellite data. *Limnology and Oceanography* 39(6): 1333–1348. Copyright 2000 by the American Society of Limnology and Oceanography, Inc.

Turbidity Currents Generated by Waves

Internal processes not only can generate temperature gradients but also can cause gradients in suspended particles that are sufficient to drive density currents. Shear stress at the lake bottom associated with surface waves and high-frequency internal waves can induce sediment resuspension and thus increase the load of suspended particles in the water column. If the density increase induced by the change in particle load is sufficiently large to compensate vertical density stratification, turbidity currents are generated. Because the turbidity gradient is generated by the interaction of waves with the sediment, the resulting turbidity currents usually originate either near the shore at the lake surface (surface waves) or at the depth of the thermocline (high-frequency internal waves). The turbidity currents usually propagate along the lake bottom to larger depth until they intrude into the open water.

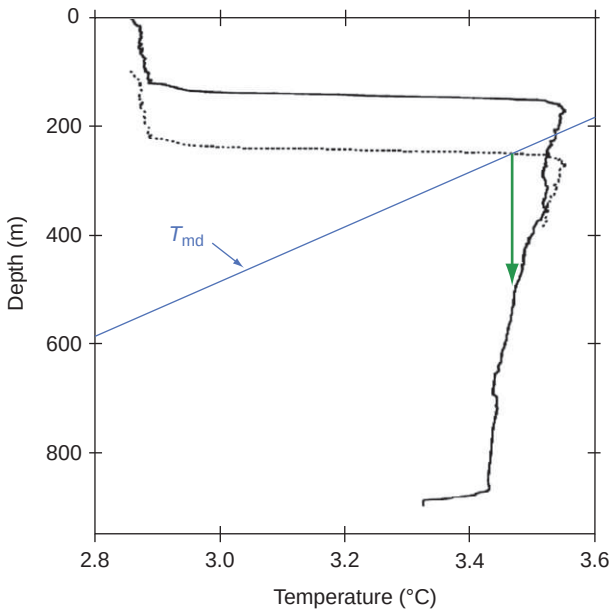

Figure 7 Schematic on the generation of density currents by the thermobaric effect. The temperature profile presented has been measured in the northern basin of Lake Baikal. The temperature of maximum density as function of depth shown for comparison is labelled with T_{md}. Vertical displacement of the temperature profile (indicated by the dashed line) leads to a density driven vertical transport that is self supporting over the depth range indicated by the arrow.

Horizontal Density Currents Generated under Ice Cover

Temperature-driven density currents can also occur under ice cover due to differential heating by solar radiation. This process is invoked if the optical properties of the ice and snow cover vary horizontally either due to a variation in the ice structure (e.g., white ice and black ice) or in the thickness of snow cover. Then, penetration of solar radiation through the ice and snow cover varies horizontally and thus induces differential heating in the surface water below the ice. This process causes convection below the ice and results in horizontal density gradients that can drive horizontal density currents. Such under-ice currents are believed to be essential for the development of algal blooms in early spring in Lake Baikal.

Density Currents in Tropical and Saline Lakes

In tropical lakes and also in saline lakes several of the processes mentioned above do not occur. Because the development of a therma bar requires a lateral transition of water temperature from above to below T_{md} at the lake surface, a thermal bar never occurs in tropical lakes where water temperatures are above 4 °C all year round and thus always exceed T_{md}. Because T_{md} decreases with increasing salinity reaching freezing temperature at about 25 g kg $^{-1}$, thermal bar development and the associated density currents also do not play an important role for the vertical exchange in saline lakes. The same arguments exclude the thermobaric effect as a significant cause of density currents in tropical and saline lakes.

In tropical lakes temperature gradients play the dominant role in the generation of density currents because at high water temperatures, slight temperature gradients imply large differences in density. Therefore, salinity gradients play a smaller role for density plume generation in tropical lakes than for lakes of temperate regions during the cold season. Convection due to night-time cooling and density currents due to differential cooling and river inflows can be expected to be the most important processes for advective deep-water renewal in tropical lakes.

In saline lakes, however, river inflows usually cannot drive density currents because rivers typically introduce freshwater that in most cases has a much lower density than the saline lake water, even if the inflow has a low temperature. For example water with a salinity of 4 g kg^{-1} and a temperature of 24 °C has a greater density than freshwater with 4 °C. Hence, river inflows can only directly drive density currents in saline lakes, if the riverine water carries a substantial load of suspended particles. Nevertheless, in saline lakes river inflows can generate large scale differences in salinity and thus may indirectly lead to density currents at sills induced by inter basin exchange as is probably the case in the Caspian Sea. Another process that is likely to cause density currents in saline lakes is differential cooling. In contrast to freshwater lakes this process can trigger density currents with temperatures well below 4 °C and even down to freezing temperature, because T_{md} can be substantially reduced or even does not exist depending on the salinity of the water.

Impact of Changes in the Environmental Conditions on Density Currents and Deep-Water Renewal

Changes in climatic conditions and human activities in catchments may affect density currents and thus vertical mixing in lakes. An increase in precipitation and in the percentage of the land made impervious by human development typically leads to a higher discharge of rivers. Enhanced river discharge is usually associated with increased erosion and a higher load of suspended particles in the river water such that density currents will propagate to larger depth. Enhanced deep-water renewal is thus anticipated in freshwater lakes. In saline lakes, however, the increase in freshwater input associated with increased precipitation reduces the density of the surface waters and thus can significantly limit the generation of density currents. Consequently, deep-water renewal may be reduced or suppressed. Deep-water exchange decreased drastically as a consequence of increased riverine discharge in the Caspian Sea and in Mono Lake, CA.

Water storage dams in the catchments of lakes have the opposite effect on density currents than soil sealing. Retention by water storage dams reduces peak discharge and the load of suspended particles in downstream rivers. This results in a decrease in the intensity of density currents and in the depth of intrusions in lakes located downstream of dams.

Climate warming can lead to a reduction of deep-water renewal in lakes because additional input of heat at the lake surface may result in an increase in density stratification of the water column and in an extension of the stratified period. Persistence of the increased stratification over many years likely depends on the lake's latitude and depth and whether warming is intensified in winter or summer or, for tropical lakes, during the monsoon period or during less windy periods.

In a warmer climate, however, mixing in freshwater lakes due to density currents associated with the thermal bar and/or the thermobaric effect may cease, if climate warming leads to an increase in surface water temperature to values above 4 °C all year round, i.e., to values above T_{md}. Because density is a nonlinear function of temperature, warming of surface water may also shift the relative importance of turbidity and salinity gradients towards temperature gradients as agent to drive density plumes.

The potential consequences of environmental change on density currents are exemplified for Lake Baikal, the deepest lake on earth. Because of the peculiar temperature profile with the mesothermal temperature maximum (see **Figure 7**), deep-water renewal in Lake Baikal is predominantly driven by salinity differences between river and lake water and between the basins of the lake. The salinity differences result in density plumes associated with riverine inflows and inter-basin exchange. Hence, changes in the catchments leading to an increase in the concentration of dissolved ions and suspended particles in river inflow will intensify deep-water mixing by density plumes. Climate warming on the other hand will not severely affect density plumes and thus deep-water renewal in Lake Baikal, as long as the lake has an annual ice cover. Higher air temperatures most likely result in a shift of ice break-up to earlier times in the year, but will not have an affect on the thermal conditions immediately after ice break-up. Hence, the conditions required to generate density plumes will not change, but may occur earlier in the season.

In summary, density currents significantly contribute to deep renewal, especially in deep and very deep lakes. The density currents can result from a variety of processes. Which of these processes are relevant in a specific lake depends on the temperature regime of the lake, its salinity and also its morphometry. The environmental conditions, e.g., precipitation in the catchments and heat flux at the lake surface affect the occurrence of density currents and the depth reached by the density plumes. Hence, changes in the environmental conditions will have consequences for deep-water renewal and oxygenation of deep lakes not only because of a change in turbulence levels, but also by their effect on the intensity of density currents.

See Also: Fundamental concepts and theories: Temperature as a Driving Factor in Aquatic Ecosystems; Structures and functions of Inland Waters - Lakes: Bottom Boundary Layers; Currents in Well-Mixed Layers; Lacustrine Phosphorus Cycling; Small-Scale Turbulence and Mixing: Energy Fluxes in Stratified Lakes; Surface Mixed Layers in Lakes

Further Reading

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Lake Ice Formation and Melt. Under-Ice Dynamics

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie_Elodie Perga and Damien Bouffard.

Glossary

Congelation ice (Also called black ice) Transparent ice with large crystals and low amount of impurities growing at the base of existing ice cover.
Snow-ice (Also called white ice) Ice with low transparency, small crystals with random orientation and significant amount of bubbles, forming typically on top of the black ice from slush.
Frazil ice Loose ice crystals formed in highly turbulent open water slightly supercooled below the freezing point.
Slush A mixture of water and snow formed by flooding of lake water on the ice surface, by liquid precipitation over snow surface, or by melt–freeze cycles.
Rotten ice Melting porous ice with water pockets between the crystals and irregular structure due to thaw-refreeze processes. At later stages, the vertical crystals of former congelation ice get disintegrated by internal melting, creating "candled ice."
Freezing-degree-days A cumulative sum of mean daily air temperatures (in degrees Celsius) for a period with temperatures lower than the freezing point. The measure is often used as an estimate of the cooling fluxes at the lake surface and of the ice growth, in particular in the Stefan's equation.
Inverse stratification Increase of water temperature with depth, typical for ice-covered freshwaters and conditioned by the increase of freshwater density with temperature in the temperature interval from 0 °C to 3.98 °C.

Introduction: Lake ice in the earth system

Freezing of lakes, physical properties of ice

The zone of freezing lakes covers most of Eurasia and North America down to around 40°N latitude at sea level (see Hutchinson and Löffler, 1956). In the Southern Hemisphere, there are only minor land areas with freezing inland water basins, in addition to Antarctica with seasonal and specific perennial frozen lakes. Most lakes contain fresh water, and their ice cover consists of congelation ice formed of the lake water and an eventual snow-ice layer on top, formed by freezing of slush on the ice (Michel and Ramseier, 1971). River ice is different from lake ice in that ice formation takes place in turbulent flow with a large fraction of

frazil ice as the result. When the salinity of the lake water is more than around 1 g kg^{-1}, the ice is significantly different from freshwater ice. The freezing point and the temperature of maximum density are depressed, and liquid brine pockets are captured between ice crystals during ice growth.

Importance of lake ice cover for climate and air-land interaction. Human use of lake ice: Transportation, food industry, recreation

The lake ice cover comprises only a small part of the cryosphere. However, it plays an important role in regional weather and climate. Ice cover is an insulating layer for heat transfer and possesses a high albedo, especially when covered with snow. Therefore, once formed, the ice cover stays stable even at significant downward heat flow in the lower atmosphere. The ice cover isolates the lake water body from the atmosphere, influencing weather conditions in lake-rich regions. Under thin ice, the warm water makes the ice surface warmer than the surrounding land with strong impact on stability and turbulent fluxes (Yang et al., 2013), and as long as there is ice in spring, the lake surface temperature is at the melting point that can be much lower than in the surrounding land (Leppäranta et al., 2019). The land–lake surface temperature difference can be more than 10 °C. Since lake ice formation and breakup are closely coupled with the local and regional climate, ice phenology is an excellent indicator of regional and local climate change.

A large fraction of freezing lakes is located in the neighborhood of major settlements, where the ice cover played an important practical role in the human life. The main issue in history has been on-ice traffic (Fig. 1B), expressed in science as the problem of the bearing capacity of ice. Later on, ice loads on man-made structures became another ice mechanics problem, but ship traffic in ice conditions has been limited to large lakes. In cold regions, people have learned to live with and utilize frozen lakes. In the past, lake ice was used to store perishable products; ice was removed during the winter and stored for use in the summer (Fig. 1A). Also, ice cover has been used for recreational purposes such as tourism and sport events.

Perennial, seasonal and "ephemeral" ice cover. Seasonal ice cover duration, its dependence on climatic conditions

The global lake ice zone can be sub-classified into three sub-zones: (1) *Perennial ice zone*, (2) Stable or *seasonal ice zone*, where ice occurs annually and ice-on and ice-off take place every year, and (3) Unstable or *ephemeral ice zone*, where ice forms but not every year (Leppäranta, 2014). The exact boundaries between the three zones are provisional because ice formation depends strongly on the continuously changing climate conditions as well as the local geography. Apart from latitude, altitude and the lake depth are the two major factors determining the ice regime of lakes. A relatively simple but insightful regionalization is offered by the mean climatic values of the near-land air temperatures in form of *negative-degree-days* (see Section "Stefan's law and simple models of the ice cover") as a proxy for the maximum ice cover thickness. The resulting picture reveals the major factors forming the global ice distribution and explains the observed seasonal ice features (Fig. 2), among them:

- perennial lake ice cover in the Northern Hemisphere is rather small, restricted to the Greenland ice cap and the northernmost parts of high Arctic (Mark 6 in Fig. 2). The factors preventing the development of a persistent ice cover are the absence of land at the high latitudes, poleward advection of warm air (in contrast to Antarctica which is isolated from warm latitudes by the westerly winds and Antarctic circumpolar current with the polar front), and the large amount of solar radiation during the polar day.
- The alpine regions of Rocky Mountains, Central Europe, Caucasus and Tibetan plateau are clearly distinguished by the southward advance of the seasonal ice zone.
- The Great Lakes (Mark 1 in Fig. 2), the Caspian Sea and the Aral Sea (Mark 4 in Fig. 2), as well as Lakes Issyk-Kul and Balkhash (Mark 3 in Fig. 2) reside at the boundary between seasonal and ephemeral ice cover, indicating the backward effect of large lakes on climatic air temperatures. The ice cover on these lakes is never purely seasonal; moreover, these large lakes directly affect the

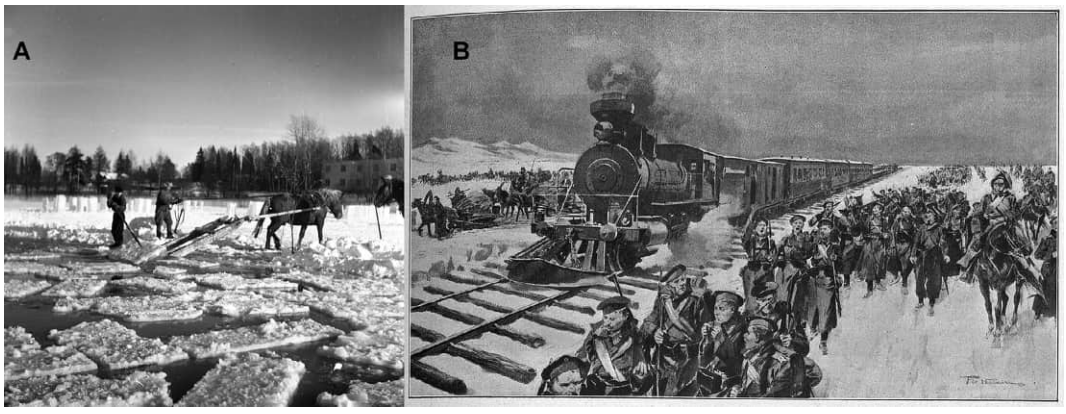

Fig. 1 (A) Ice harvesting in Lake Tuusulanjärvi in the 1960s.(B) Russian troops with a military train crossing Lake Baikal, 1904. Illustration by Frédéric de Haenen. (A) Photograph by Eino Nikkilä. Reproduced with permission from Järvenpää seura (local community cultural society). (B) Reproduced from La Ilustración Artística 1.162: 239, 4 Apr 1904. ISSN 1889-853X.

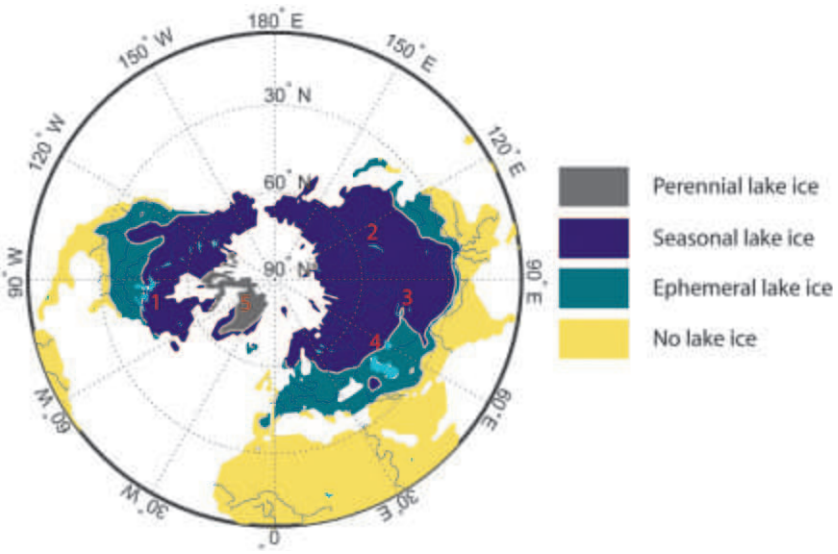

Fig. 2 Distribution of the lake ice cover over the Northern Hemisphere derived from the NCEP/NCAR global reanalysis data on near-surface air temperature for 1990–2010. The following values for the maximum seasonal ice thickness were used as lower boundaries based on observational ice data and results of lake ice modeling: 10 negative degree-days for the ephemeral ice zone; 250 negative degree-days for the seasonal ice zone; 2500 negative degree-days for the perennial ice zone.

surrounding air temperature, maintaining by this warm winters and preventing ice cover formation. A remarkable feature of the large lakes in winter is the production of heavy snow-storms due to strong cooling and evaporation from the ice-free surface (Vavrus et al., 2013). Lake Baikal (Mark 2 in Fig. 2), despite its exceptionally large water volume, has persistent seasonal ice cover, being the most remote large lake from the ocean, and located in the center of the Siberian High-Pressure Area.

The picture for the Southern Hemisphere is not provided. The amount of ice-covered lakes in the Southern Hemisphere is much lower and is basically concentrated in three areas: seasonally ice-covered alpine lakes of Andes and the Antarctic coast, and perennially ice-covered lakes of the Antarctic continent.

Physics of ice cover formation and melt. Types of lake ice

Ice cover formation

The low-flow conditions and freshness of water in most lakes of the "*seasonal ice zone*" make the process of lake ice cover formation different from that in seawater and rivers. At temperatures above the maximum density value T_{md} ($T_{md} \approx 3.98$ °C for freshwater; it decreases with increasing pressure at the rate of $\beta_P \approx 0.020$ °C per 1 bar and with increasing salinity at $\alpha_S \approx 0.22$ °C per 1 ppt), the surface cooling produces sinking of cold waters towards the lake bottom. The resulting convective mixing homogenizes the water column and removes the heat stored in deeper layers. By this, the surface temperature cannot drop below T_{md} before the whole lake body gets uniformly mixed and cooled to this temperature (exceptions are very deep or saline lakes, where T_{md} changes with depth due to thermobaric effects β_P or mineralization α_S). Once the lake temperature achieves T_{md}, any further loss of heat from the surface creates a stable vertical density gradient in the upper water column preventing heat supply from deeper waters and accelerating surface cooling. This "*inverse density stratification*" (in contrast to "direct" density stratification with temperature decrease with depth, prevailing in natural water bodies) develops in a relatively thin surface layer and is easily destroyed by external forcing. In rivers, such a mixing is produced by the persistent flow; the main mixing source in lakes is wind.

The lake ice cover is usually formed during calm conditions, typically at cold nights. Isolated by the inverse stratification from warmer deep waters, lake surface may quickly, within hours, cool down to the freezing point and by further supercooling to at most −1 °C. The primary millimeter-thin ice grows horizontally with vertical optical axes (c-axes) of crystals. The newly formed ice prevents later destruction of stratification by winds, allowing further rapid growth parallel to the temperature gradient down at the base of the ice. In some years, ice formation may start during snowfall or in the presence of surface waves resulting in frazil ice, akin permanently mixed rivers. In lakes, frazil consolidates into a solid layer after turbulence in water has damped. Crystals of frazil are fine, millimeter-scale and bear random c-axis orientation.

The uniform growth of ice at the ice base ensures regular vertical orientation of ice crystals—the reason for the high transparency and bearing capacity of young *congelation* ice, often called therefore "black ice" (see Fig. 3). If the ice formation begins with a frazil layer, congelation crystals grow below the solid ice cover but deeper their c-axes turn horizontal. In some cases, surface freeze-over can take several days to weeks, starting in shallow and wind-sheltered near-shore areas and possibly including several cycles of melt-refreeze, especially in large lakes and/or in the *ephemeral ice zone*.

Congelation ice thickness increases proportionally to the heat conducted through the ice to the atmosphere. In very dry climate—e.g. Antarctic, Andes, Tibet and Lake Baikal—the ice cover consists completely from the crystal-clear *congelation ice*.

Snow cover formation. Slush and white ice

In most lakes, snow accumulation alters the lake ice development. Due to the low heat conductivity and low transparency of snow, even a centimeter-thin snow cover effectively isolates the lake surface from the surface cooling and drastically decelerates the ice cover growth. If the snow thickness increases, flooding becomes possible when the snow weight forces the ice sheet below the level of the water surface. Therefore, the snow cover is never more than about one-third of the ice thickness. In addition, temperature at the snow-ice boundary may reach the freezing point due to the limited heat release to the atmosphere and continuous heat supply from under-ice water. As a result, a layer of *slush* (mixture of snow and liquid water) forms above the primary ice layer. *Slush* can easily freeze by release of the latent heat of its liquid part giving rise to the superimposed ice layer, also called *snow-ice* or *white ice*. Snow-ice grows from the topmost slush down, and then pockets of slush can be captured inside the ice sheet and persist for several weeks. Liquid precipitation or meltwater may also contribute to superimposed ice formation. *White ice* has incoherent structure with small size and random orientation of ice crystals, high porosity, and a lower density compared to *congelation ice* (Fig. 3). Thickness of white ice varies strongly from year to year depending on weather conditions. The relative contribution of white ice to the total ice cover generally grows towards the end of the ice-covered period. Snow-ice has low strength; a congelation ice cover is much safer for walking or driving on than an ice cover of the same thickness with a significant snow-ice fraction.

Ice melt and break-up. Surface, bottom and internal melt. Candled ice

Ice melting period begins in spring when the heat balance turns positive. Ice becomes nearly isothermal, and conduction of heat ceases. If there is a thick snow cover, the high albedo of snow delays the start-up of melting. Once the snowmelt started, the albedo

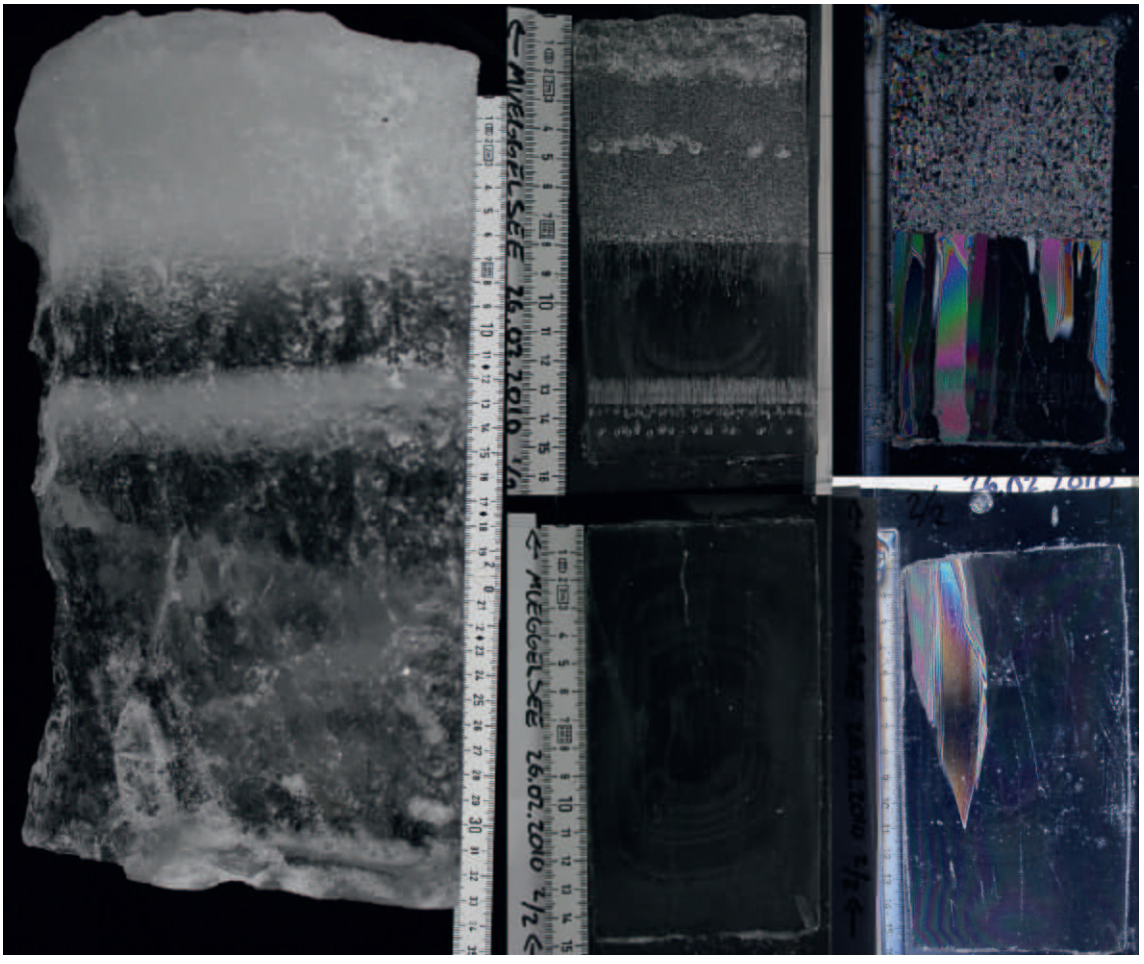

Fig. 3 Structure of the ice sample from German Lake Müggelsee in winter 2010. Clockwise from the left: the original ice sample in normal light, the thick section of the top part in normal and polarized light, and the bottom part in the polarized light and in the normal light.

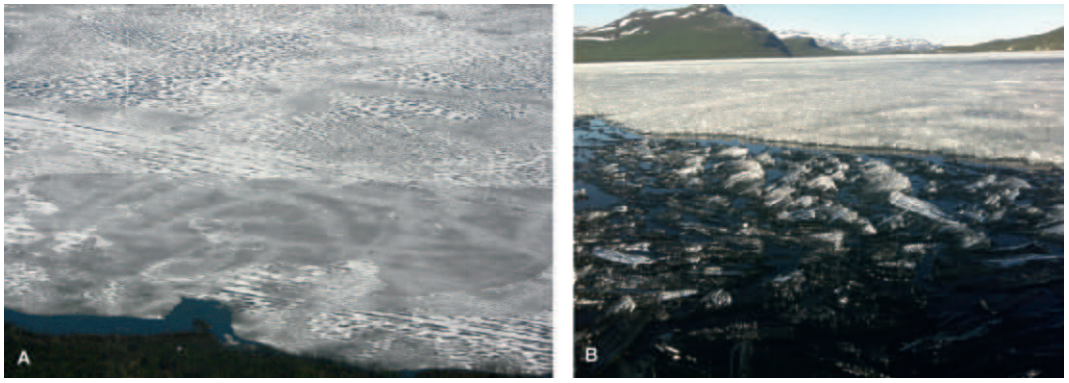

Fig. 4 (A) Photograph of the ice surface on Lake Kilpisjärvi (Finland) taken on May 29, 2013 from the nearby Saana mountain; (B) a close picture taken 2 days later, on May 31, 2013 of the ice cover edge destroyed by internal melting with floating candled ice. Photographer: Alexander F. Forrest.

decreases accelerating the melt. Due to this albedo-melting feedback, the surface of melting lake ice is patchy, with areas of snow, bare and rotten ice (Fig. 4A).

Ice melting takes place due to heat fluxes at the boundaries and by absorption of solar radiation in the ice interior. Surface melting is favored by warm air advection over the ice cover, and basal melting is forced by heat flux from the water beneath the ice. In turn, solar radiation absorption is distributed between the surface, the ice interior and the upper water column. While the boundary melting decreases ice thickness, the internal melting increases ice porosity. The relative contributions of the three melting mechanisms vary depending on the weather and under-ice flow conditions. During clear-sky calm weather, solar radiation can be the governing melting factor, and the porosity increase leads eventually to the break-up by formation of *candled ice*: loose ice crystals with meltwater between (Fig. 4B).

Heat budget of ice. Models of ice cover

Heat budget components, fluxes at the ice surface and the ice base

Ice growth/melting at the ice base results from the balance between the conductive heat flux into ice and the heat flux from the water:

$$\frac{dh}{dt} = \frac{k}{\rho_{ice} L_f} \cdot \frac{\partial T}{\partial z} - \frac{1}{\rho_{ice} L_f} Q_w, T = T_f \tag{1}$$

where h is ice thickness, k is thermal conductivity of ice, ρ_{ice} is ice density, L_f is latent heat of freezing, Q_w is heat flux from water, and T_f is the freezing point temperature (see Table 1 for numerical values).

The heat balance at the ice surface is written as

$$Q_0 = \gamma(1 - \alpha)Q_s + Q_{LW} + Q_H + Q_E + Q_P \tag{2}$$

where Q_s is the incident solar radiation, α is albedo, $\gamma \approx 0.5$ is the fraction absorbed in the near-surface layer, Q_{LW} is the net longwave radiation balance between the ice and the atmosphere, Q_H and Q_E are the turbulent sensible and latent heat fluxes, respectively, and Q_P is the heat transfer from precipitation. Heat transfer from precipitation is often neglected but can be an important short-term flux for rainfall on ice or snowfall on open water.

Radiation fluxes, the role of albedo

The first two terms in Eq. (2) sum up to the radiation balance and make the major contribution to the surface heat flux. Albedo α of bare ice is around 0.5, but over a frozen lake it varies from 0.2 to 0.9 due the strong scattering, largely depending on the liquid water and gas contents of snow and ice. Albedo of snow is above 0.5, up to 0.9 for fine-grained dry snow, 10 times higher than that of ice-free water (0.05–0.1). By this, snow drastically reduces the heating by solar radiation. The snow-albedo feedback plays a crucial role during melting phase, when snowmelt lowers the albedo and the variability of albedo becomes large due to a positive feedback mechanism in the system, which produces the typical patchy lake ice cover in spring (Fig. 4A). The longwave radiation of lake surface is close to that of black body with emissivity 0.96 – 0.98. The longwave radiation of the atmosphere is more complicated, coming from different altitudes with different emissivity. For standard weather data, a gray body analogical model is used with air temperature as the reference temperature.

Table 1 Thermal properties of freshwater lake ice and liquid water.

Property	*Ice 0 °C*	*Ice –20 °C*	*Liquid water 0 °C*
Density (kg m^{-3})	916.7	920.3	999.8
Latent heat of melting (kJ kg^{-1})	333.5	–	–
Specific heat (kJ kg^{-1} $°C^{-1}$)	2.11	1.96	4.22
Thermal conductivity (W m^{-1} $°C^{-1}$)	2.14	1.88	0.561

Thermodynamic properties of ice and snow: Heat capacity, conductivity and transparency

The thermal properties of freshwater lake ice (Table 1) depend primarily on the temperature, crystal structure and gas content. Gas bubbles with a typical size of millimeters occupy about 1% of congelation ice with small influence on the thermal properties. In snow-ice, bubbles occupy about 5%, causing notably lower density and conductivity. Other impurities have mostly minor impacts since their concentrations are small.

Snow and ice covers act as diffusive filters to the solar radiation transfer. The light attenuation coefficient is 0.1 – 5 m^{-1} for lake water, around 1 m^{-1} for congelation ice, ~5 m^{-1} for snow-ice and ~10 m^{-1} for snow (e.g., Lei et al., 2011). Gas content is the most important impurity for light transfer. Gas bubbles cause strong scattering, which is almost independent of the wavelength. Bubble-free congelation ice is normally more transparent than the liquid water of the same lake. Snow-ice possesses large amount of air from the parent snow cover and is opaque. In the melting season, the presence of liquid water has a major impact on the light transfer. Liquid water layers absorb light on long wavelengths. Dissolved substances and suspended particles are mostly rejected from the congelation ice crystal lattice growth back to lake water, but a fraction remains between crystal platelets. In snow-ice, more impurities are captured into the ice. In very humic lakes, liquid humus inclusions have been found from congelation ice resulting in stronger absorption on short wavelengths.

Stefan's law and simple models of the ice cover

The classical problem of modeling lake ice thermodynamics is the growth of congelation ice. The first ice growth model was presented by J. Stefan back in 1891. The model was based on the quasi-steady balance between the latent heat released in freezing and heat conduction through the ice (Eqs. (1)–(2)).

Later the heat flux from the ice surface to atmosphere was added:

$$\rho L_f \frac{dh}{dt} = k\frac{T_f - T_0}{h} = K_a(T_0 - T_a) \tag{3}$$

where T_0 and T_a are the ice surface and air temperatures, respectively, and K_a is air–ice heat transfer coefficient. Eliminating the surface temperature from the latter equation, the solution is

$$h(t) = \sqrt{[h(0) + b]^2 + a^2 S(t)} - b$$

$$a = \sqrt{\frac{2k}{\rho L_f}}, S = \int_0^t \left(T_f - \min\left[T_f, T_a(\tau)\right]\right)d\tau, b = \frac{k}{K_a} \tag{4}$$

where $a = 3.48$ cm $(°C \cdot d)^{-1/2}$ and $b \approx 10$ cm are the model parameters. In semi-empirical modifications, a has been replaced with a reduced coefficient $\frac{1}{2}\, a \le a^* \le a$. The case $a^* \approx 0.5\, a$ corresponds to effective snow insulation, while $a^* \approx 7\, a$ corresponds to snow-ice-only growth. The formula ignores the heat flux from water that is generally acceptable in small lakes, but does bias the simulation upward. Assuming $T_0 \approx T_a$ gives a simple rule-of-thumb formula.

$$h^2 \approx {h_0}^2 + 10\ \text{cm}^2\ (\text{d°C})^{-1}\ S \tag{5}$$

Eq. (5) is directly related to the *negative-degree-days* concept used in Section "Perennial, seasonal and "ephemeral" ice cover. Seasonal ice cover duration, its dependence on climatic conditions": when using 24-h time step of integration, the ice thickness grows as the square root of the sum of the negative-degree-days. Herewith, the formula is insightful for rough estimation of ice growth: So, e.g., at initial ice thickness $h_0 = 9$ cm, the ice grows during 1 day with the mean air temperature of –4 °C to $h = 11$ cm (note that Eq. (5) overestimates the growth rate, especially at small h_0).

Modeling the decay of lake ice is straightforward since the ice loss is due to the net gain of energy from the external fluxes (in particular, radiation) and heat conduction is less significant. The radiation balance is, however very variable because of the space–time variability of the albedo and the light attenuation coefficient. Analytic melting models are simplified energy balance models, where changes in the optical properties are parameterized. The first-order ice growth and melting models can be used to obtain the scale of ice thickness for different lakes and environmental conditions, and they are convenient tools for sensitivity analysis and evaluation of the climate change impact. The main source of uncertainties is in the treatment of the snow cover.

Advanced ice models, unresolved problems

More advanced numerical lake ice models are of two basic types: (1) Quasi-steady models, where the ice sheet is divided into layers with a quasi-steady heat flow through the system, and (2) Time-dependent models, where the vertical equation of heat conduction is directly integrated. Depending on model complexity, variation of the ice thermal properties and snow metamorphosis can be included with corresponding changes in snow thickness, density and thermal conductivity. A typical model simulates the development of four distinct layers: snow, slush, snow-ice and congelation ice. These layers interact: snow accumulation creates slush and snow-ice depending on the total thickness of ice, while the growth and decay of congelation ice depend on the snow and slush conditions. An example of simulation results is shown in Fig. 5. The modeled ice cover grew by 0.5 cm day^{-1} in December–March and ablated at 2 cm day^{-1} during April. The tuned heat flux from the water to ice was 0.5 W m^{-2}. The ice growth was highly sensitive to snow conditions and the diurnal weather cycle significantly affected the ice melt in spring.

Internal melting (Section "Ice melt and break-up. Surface, bottom and internal melt. Candled ice") is an important process in the melting season. It changes the physical properties of the ice sheet, strongly decreasing the strength of the ice, and forming liquid water pockets serving as habitats for biota (Leppäranta et al., 2019). A proper modeling of the internal melting requires inclusion of the ice porosity as a dependent model variable, which changes after the temperature reaches the freezing point, due to radiation absorption. A realistic structural profile can be obtained with locations of liquid water containing layers.

Circulation and mixing under ice

Ice-covered lakes are isolated from the wind mixing. Moreover, water temperature at the ice-water boundary is fixed at the melting point. Two factors—the ice-water interface is at the freezing point and the under-ice water is typically colder than the T_{md}—cause sinking of warmer waters to the bottom and thus determine the major characteristic of the ice-covered water bodies—*inverse thermal stratification*. The resulting circulation is close to "natural laboratory" conditions, rarely met in other natural fluids, where the drivers of under-ice circulation and mixing include (Kirillin et al., 2012):- Heat flow from sediments;

- Solar radiation penetrating the ice;
- Surface and groundwater inflows beneath the ice;
- Seiching (lakewide water body oscillations) induced by the oscillation of a floating ice sheet;

and- the Coriolis force, which does not supply any energy to water motions but rather alters the circulation pattern under the ice and affects thereby stratification and mixing.

The relative contributions of the two former energy supplying mechanisms—heat flow from sediments and solar heating—depend strongly on snow conditions, because even a thin snow cover effectively isolates the surface from solar radiation. In most regions, the ice-covered period is accompanied by snowfalls, and the snow cover disappears first during the early ice melt. It makes convenient to separate the under-ice circulation in two stages (Kirillin et al., 2012): "Winter I" (Fig. 6A) is characterized by insulation of the lake by snow cover from the solar radiation and release of summer-accumulated heat from the sediment, which serves as the main driver for circulation and mixing. "Winter II" replaces Winter I when the snow cover melts, allowing radiation to penetrate through the ice cover. The heating of the upper water column and the subsequent sinking of warmer and heavier waters produce convection, which takes place in the background of stable density stratification, such that the convectively mixed layer of

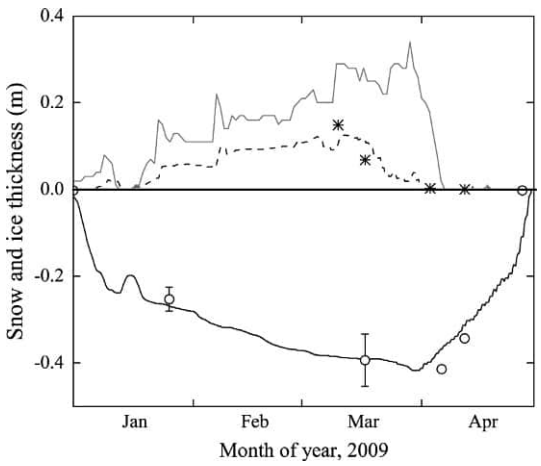

Fig. 5 Time series of observed and modeled snow and ice thickness in Lake Vanajavesi, southern Finland. The black dashed and solid lines are modeled snow and ice thickness, respectively. The dark gray line and the asterisks are the observed snow thickness on land and on the lake, respectively. The circles are the observed average ice thickness and the spatial standard deviation is indicated by the vertical bar (Yang et al., 2012).

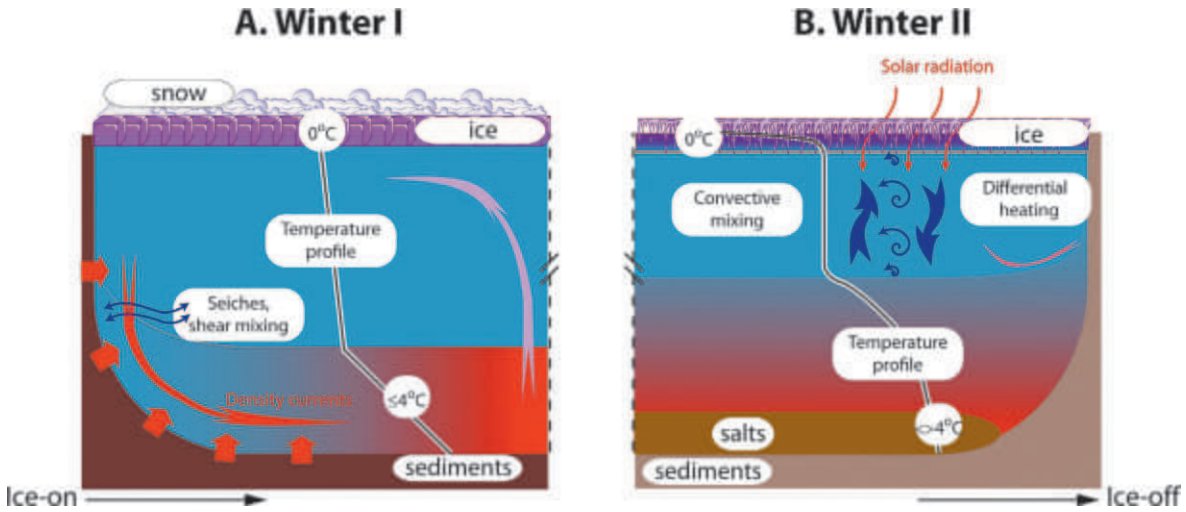

Fig. 6 A schematic of major circulation pathways in ice-covered lakes.

uniform temperature/density thickens with time and penetrates the stably stratified fluid below. Convective mixing due to solar heating dominates the circulation during the Winter II (Fig. 6B).

In dry arid climate zones (e.g. in Antarctic, East Siberia and Central Asia), mode II persists in lakes through all winter. In Antarctic Dry Valleys, it facilitates a perennial solid, thick ice layer over a liquid lake body.

Winter I: "Quiet" circulation conditions in snow-isolated lakes

Immediately after the ice-on, the release of the sediment-stored heat creates horizontal density gradients between the shallow regions and the pelagic zones and gives rise to the organized circulation pattern with the flow of the warm dense water along the bottom slopes and the upward compensating flow in the lake interior (Mortimer and Mackereth, 1958). The warm waters accumulate in the deepest parts of the lake. In shallow lakes, where sediments can accumulate significant amount of heat during summer, temperatures at the water-sediment interface are often close to T_{md}. Since the temperature effect on density decreases in the vicinity of T_{md}, even the small vertical salinity gradients due to the release of solutes from the sediment may slow down the near-bottom mixing and create a < 1 m thin layer with high concentrations of dissolved matter (Malm, 1998; Petrov et al., 2006). The rest of the water column asymptotically approaches a steady state with a quasi-linear downward density increase. Large-scale circulation patterns during Winter I are characterized by slow (≤ 1 cm s^{-1}) water motions driven by density gradients between shallow littoral and deep pelagic parts of the lake. Major mechanisms enhancing the interior mixing are the shear instabilities produced by the density currents and breaking of the internal waves.

Winter II: Convective phase of the ice-covered period

In Winter II (Fig. 6B), solar radiation penetrates through the snow-free transparent ice cover and heats up the upper water layers giving rise to the most energetic mixing process in freshwater ice-covered lakes—radiation-driven free penetrative convection. The warmer and heavier water sinks across the stratified water column and creates a horizontal mixed layer of nearly constant temperature (see the temperature profile in Fig. 6B), advancing downward at the rates of up to several meters per day (Kirillin et al., 2012). The radiatively-driven convection in ice-covered lakes is a crucial process affecting chemical and biological processes in lakes (Matthews and Heaney, 1987; Mironov et al., 2002). Besides, being a rare natural example of free convection driven by volumetric absorption of radiation in the absence of mean shear, the phenomenon has been actively investigated in a number of observational and modeling studies (Farmer, 1975; Ulloa et al., 2018; Volkov et al., 2019). Finally, the convection is a major factor controlling heat supply from the water column to the ice cover and subsequent melt at the ice base. Characteristic features of convective mixing without the mean shear include relatively slow (mm s^{-1}) vertical motions organized in coherent convective structures (cells). At later stages of ice melt, the convective pattern can be observed on the ice surface (Fig. 7A and B), attracting attention of researches by its similarity to convective cloud patterns in the atmosphere (Katsaros, 1981).

During Winter II, the shallow near-shore areas warm faster than the deep interior. The *differential heating* produces radial temperature gradients and secondary circulation (Cortés and MacIntyre, 2020) with density currents converging towards the lake center, similar to that driven by the sediment heat release in Winter I (Fig. 6). Depending on the strength of the lateral temperature gradient, the converging flow may follow the bottom of the convectively mixed layer (Ulloa et al., 2019, Fig. 6B), or plunge to the maximum lake depth (Kirillin et al., 2015, Fig. 6A). In both situations, the secondary circulation intensifies the lake-wide mixing, accelerates ice melt and ventilates the deep waters.

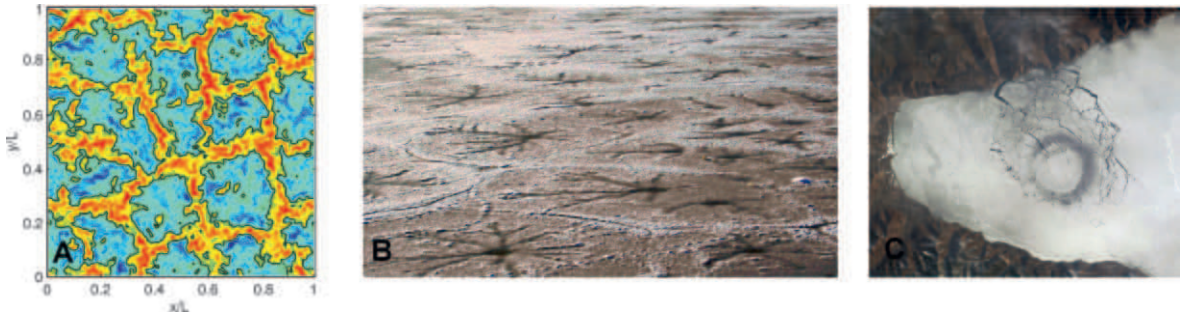

Fig. 7 Patterns on lake ice. (A) top view of vertical convective velocities under ice from large-eddy simulation modeling (Mironov et al., 2002); (B) similar patterns on the ice surface of a small pond Kleiner Kiel (Germany); (C) a circle of thin ice (dark in color, with a diameter of about 4.4 km, Lake Baikal. (A) Courtesy Dr. Dmitri Mironov. (B) Cortesy Marcus Seeger. (C) Image courtesy the Earth Science and Remote Sensing Unit, NASA Johnson Space Center. NASA photo ID ISS019-E-10556 https://eol.jsc.nasa.gov/.

The role of inflows, earth rotation, and under-ice waves

Inflows alter the under-ice circulation if their temperature and/or mineralization differ from that of the lakes. Apart from the local effects near inlets and outlets, like reduced ice thickness or altered vertical thermal stratification, inflows may drive large-scale mixing by producing *thermobaric instability* or inducing *cabbeling* (contraction by mixing). Both effects are related to the non-linearity of the water equation of state (the dependency of the water density on pressure and salt content, respectively), and are therefore the strongest at water temperatures close to T_{md}, where the temperature effects on density are minor. Herewith, inflows entering deep lakes may produce renewal of the otherwise mixing-free near-bottom waters, playing a crucial role in *deep water renewal* (Weiss et al., 1991; Schmid et al., 2008; Tsimitri et al., 2015).

Due to the low magnitudes of the under-ice current speeds, the earth rotation affects water flow even in lakes with horizontal size of $\leq$1 km: The *Coriolis force* transforms the radial density-driven water motions to rotational currents, which can occupy the whole lake (Rizk et al., 2014; Kirillin et al., 2015), or take form of localized gyres with a size from several hundred meters to tens of kilometers (Forrest et al., 2013; Kouraev et al., 2016; Granin et al., 2018). On one hand, these rotational motions effectively promote water homogenization in the horizontal plane, on the other hand, they capture the kinetic energy of density currents reducing their transformation into vertical mixing. A prominent manifestation of the Coriolis-balanced gyres is the development of ring-shaped patterns on large ice-covered lakes, first observed on Lake Baikal (Kouraev et al., 2016; Granin et al., 2018). The "Baikal rings" (Fig. 7C) with the diameter of several kilometers are formed over warm-core gyres similar to the mesoscale oceanic eddies. Ascending heat in the eddy cores accelerates ice melt and makes the gyres visible from space as areas of dark "rotten" ice turning later in open water areas (polynyas).

Ice cover prevents the formation of surface waves by the direct wind forcing. However, *standing waves* (*seiches*) contribute essentially to the under-ice circulation. The relatively thin ice cover does not cancel lake-wide oscillations of the entire water body produced by air pressure variations or wind gusts over the lake surface. These oscillations persist in the form of barotropic seiches, slowly dissipating at the solid boundaries. Seiches destroy stable thermal stratification in the thin water layer adjacent to the ice base, hence accelerating the ice melt (Kirillin et al., 2018). At the concluding stage of the ice-covered period, seiches may play a decisive role in the final mechanical destruction of the ice sheet. The second major type of waves under ice are internal or *baroclinic* basin-scale waves developing in the thermally stratified lake water bodies (Kirillin et al., 2009; Bouffard et al., 2016). Affected by rotation, these oscillations take the form of inertial gravity waves traveling around the lake—analogs of Kelvin and Poincare waves (Gill, 1982) for enclosed basins. In contrast to planar seiches, Kelvin waves reach their maximum amplitudes and current speeds near the lake shores, thereby intensifying the water-sediment mass exchange in the littoral zone (Kirillin et al., 2009).

Physical-biogeochemical interactions in ice-covered waters

Dissolved oxygen as the major indicator of biochemical processes under ice

Dissolved oxygen (DO) in ice-covered lakes is both a crucial ecological parameter and a sensitive indicator of physical transport processes. Under ice, without an oxygen supply by water aeration and reduced photosynthesis, respiration causes oxygen depletion, potentially resulting in fully anoxic conditions with negative ecological consequences, such as winter fish kill and the loss of benthic organisms. Driven by microbiological processes, oxygen consumption rates differ between lakes of various trophic levels and are the highest at the water-sediment boundary. Therefore, the risk for DO depletion under ice is greatly controlled by the ratio between lake volume and area of exposed sediment (Bengtsson and Ali-Maher, 2020). The small shallow lakes with prolonged isolation from photosynthetically active radiation by the snow cover are particularly prone to fast anoxia development (Terzhevik et al., 2009). The respiration rates of winter microbiological communities are shown to be highly temperature-sensitive, so that even a

several degrees increase of water temperatures drastically accelerates anoxia development (Golosov et al., 2007). In Central Asian lakes, photosynthesis contributes significantly to the oxygen storage under the bare ice but falls small in the presence of even a thin snow layer (Song et al., 2019).

Other dissolved gases: CO_2, HS_4, CH_4

In anoxic conditions, the hypolimnetic mineralization involves other reduced substances such as S(-II), CH_4, NH_{4+} (Matzinger et al., 2010). Among them, the under-ice production of methane (CH_4) attracts close attention of researchers because of the high greenhouse potential of CH_4. Methane is produced anaerobically by archaea via methanogenesis and is consumed by microbial methanotrophs. Accumulation of CH_4 during winter can lead to a massive CH_4 release to the atmosphere upon ice-off (Phelps et al., 1998). Unless a lake gets completely oxygen free under ice, the large part of methane is oxidized, thereby, reducing it potential contribution to the atmospheric CH_4 (Schmid et al., 2007). Apart from diffusion, the methane is transported to the surface by ebullition, which often causes accumulation of gas bubbles frozen in the ice cover. An exotic way of the methane interaction with the ice cover was reported in Lake Baikal, the only lake where methane was found in the form of solid methane hydrates forming under high pressure. Occasionally, the hydrates emerge from the depths of their formation and may reach the lake surface, being frozen into the ice cover (Granin et al., 2019).

Plankton dynamics under ice

Phytoplankton blooms are often observed under ice, as long as enough solar radiation penetrates the ice (Bižić-Ionescu et al., 2014; Song et al., 2019). Low water temperatures appear to be a secondary limiting factor for plankton growth compared with light availability, the latter largely controlled by the snow thickness. The *vertical mixing intensity*, which is directly connected to light availability by radiation-driven convection, is another crucial factor determining the phytoplankton composition and growth. At low levels of radiation and mixing, blooms of small species develop in the close vicinity of the ice base (Bižić-Ionescu et al., 2014). Also, motile species have preference because of their ability to position themselves in optimal light and nutrient environments (Hawes, 1983). Higher radiation rates produce stronger convective mixing, which can inhibit plankton growth. However, in lakes with long periods of Winter II, endemic diatom species are adapted to benefit from convective motions as a supporting mechanism and source of nutrients (Kelley, 1997; Jewson et al., 2010).

Outlook

Physics of ice-covered lakes is a relatively young but rapidly developing branch of environmental sciences. There are still many unresolved processes and interactions requiring their quantification, such as deterioration and mechanics of ice in the melting period, albedo and light transmittance of snow and ice cover, water circulation under ice-covered lakes, and biogeochemical interactions under ice. The global changes in the cryosphere are clearly pronounced in the lake ice and provide a strong impetus to intensive research on the ice season. Lake ice phenology is a good climatic indicator due to its sensitivity to the climate conditions and existence of long records (e.g. Magnuson et al., 2000; Duguay et al., 2006; Karetnikov et al., 2017). A large amount of data has been collected on lake ice phenology. Still, these phenomenological observations are insufficient for quantifying the ice season in lakes. Ice thickness is more related to the severity of the ice season but long time series for that are rare and for more complete understanding would also require information on snow accumulation.

Heat transport in the air-ice-water system has to be resolved in order to adequately describe seasonal and climatic variability in ice-covered lakes. The time scales of the physical processes under ice are slower than those typical for open water, but result in significant redistribution of heat and mass during the several months of the ice-covered period. Hence, the widespread concept of "quietness" of ice-covered lakes is not valid. Quantification of heat and mass transport in ice-covered lakes, ice melting process, and the atmospheric boundary layer over the ice is a prerequisite for solution of the key problem in global-scale lake modeling—correct prediction of the seasonal ice cover duration.

See Also: Fundamental concepts and theories: Physical Properties of Water; Temperature as a Driving Factor in Aquatic Ecosystems; Structures and functions of Inland Waters - Lakes: Measurement and Variability of Lake Metabolism; Surface Mixed Layers in Lakes; Structures and functions of Inland Waters - Rivers: High Latitude Rivers: Ecosystems Shaped by Environmental Extremes; Structures and functions of Inland Waters - Wetlands: Mountain Rivers: A Global Overview of River Channel Forms, With a Focus on Braided Rivers

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https://nsidc.org/data/G01377/versions/1—Global lake and river ice database containing ice phenology data from 865 lakes and rivers around the world.

www.lakemodel.net—Site of the lake model FLake including model of lake ice. Contains the online model FLake-Global allowing to calculate a typical ice cover duration and thickness in any lake worldwide.

https://land.copernicus.eu/global/products/lie—Lake ice satellite observations product the European Union's Earth Observation Programme Copernicus.

https://modis-snow-ice.gsfc.nasa.gov/?c=lake—Lake ice information from MODIS snow and ice product.

https://www.glerl.noaa.gov/data/ice—Great Lakes ice cover information from NOAA - Great Lakes Environmental Research Laboratory.

http://www.icerings.org/—Site dedicated to giant rings on the lake ice. Contains a collection of scientific papers, photographs from Lake Baikal and other large lakes.

http://wwwi3.ymparisto.fi/i3/tilanne/eng/IceThickness/IceThickness.htm—Near real-time observations of ice thickness on Finnish lakes performed by the Finnish Environment Institute (SYKE).

Surface Mixed Layers in Lakes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Buoyancy flux Quantifies the change of potential energy in a water body caused by a vertical density flux. Turbulent mixing in a stratified water body produces a downward buoyancy flux (or upward mass flux), which increases the potential energy of the system.

Buoyancy Upward directed force per unit mass experienced by a water parcel that has lower density than surrounding water.

Cold monomictic lake Ice-covered most of the year, mixing once a year during ice-free period in the warm season, but not warming above 4 °C.

Continuous cold polymictic lake Ice-covered part of the year, ice-free above 4 °C during the warm season, and stratified at most on a daily basis during the warm season.

Continuous warm polymictic lake No seasonal ice cover, stratifying at most for a few hours at a time.

Dimitic lake Ice-covered part of the year and stably stratified part of the year with mixing at the transitions between these two states.

Discontinuous cold polymictic lake Ice-covered part of the year, ice-free above 4 °C and stratified during the warm season for periods of several days to weeks, but with irregular interruption by mixing.

Discontinuous warm polymictic lake No seasonal ice cover, stratifying for days or weeks at a time, but mixing more than once per year.

Epilimnion Surface layer of a lake that is in contact with atmosphere and has highest levels of light. In lakes that are stratified, this layer is usually mixed and sits above the metalimnion.

Fetch The distance over which the wind can blow over a lake. The fetch depends on lake geometry and will vary with wind direction.

Hypolimnion Deep, cooler waters of a stratified lake, lying below the metalimnion. Usually this region has lower turbulence, and insufficient light for photosynthesis.

Internal seiches Basin-scale internal waves with periodic sloshing motions of the lake thermocline across the lake basin. In large lakes, the earth's rotation affects these motions.

Metalimnion Transition layer of water between the epilimnion and hypolimnion in which temperature declines with depth.

Richardson number A dimensionless ratio that compares the stabilizing effect of thermal stratification to the destabilizing effect of velocity shear. Stratified flows with high Richardson number are stable to turbulent mixing, whereas flows with low Richardson number have increased turbulence.

Stratification The vertical structure of temperature (and therefore density) in a lake. It is quantified with the Brunt-Väisälä or buoyancy frequency (N, s^{-1}), defined as $N^2 = -(g/\rho)\,(\partial\rho/\partial z)$, where ρ is the water density and z is the vertical coordinate. Waters that are stably stratified have $N^2 > 0$, whereas waters that are unstably stratified have $N^2 < 0$.

Thermocline The region in a stratified water body where the temperature drops significantly with depth, corresponding to the region of maximal stability (maximum N^2). Usually this depth is defined as the region of maximum thermal gradient (maximum dT/dz).

 https://doi.org/10.1016/B978-0-12-819166-8.00126-2

Warm monomictic lakes Lakes with no seasonal ice cover, stably stratified part of the year, and mixing once each year.
Wedderburn number A dimensionless parameter that quantifies stabilizing effect of stratification relative to destabilizing wind-induced shear. It is conceptually related to a Richardson number multiplied by the aspect ratio of the lake.

Introduction

The dynamics of the surface mixed layer of a lake are central to understanding the distribution and productivity of plankton, the dispersion of buoyant material and the exchange of gases. A key feature of freshwater lakes is that they exhibit stable thermal stratification, with lighter warmer waters at the surface and denser colder waters at depth. The presence of such thermal stratification means that mixing of the surface layer is often confined to a thin layer only several meters in depth, and is located above the thermocline (the region where temperatures drop most rapidly). Light levels in lakes usually drop exponentially with depth, so it is important to know if the surface layer is shallower or deeper than the euphotic zone in order to estimate average light levels experienced by phytoplankton (MacIntyre, 1993). The surface mixed layer is dynamic and can change depth rapidly compared to the slower changes in depth of the seasonal thermocline. Depending upon the relative strengths of wind and surface heating or cooling, the active mixed layer can extend down to a seasonal thermocline, or occasionally to the lake bed during periods of lake overturn and/or in shallow waters. In contrast, during calm periods with daily surface heating, a strong diurnal thermocline can form, limiting mixing and trapping buoyant plankton near the surface.

A starting point for the discussion of mixing in the surface layers of lakes is the classification of lakes of Lewis (1983) that is based on the seasonal thermal mixing regimes. We need to distinguish between two fundamental lake types: those lakes that are thermally stratified during a large portion of the year (mono- and dimictic) and those where winds can regularly mix waters to the lake bottom (polymictic). The surface mixed layer is constrained by depth of the thermocline in dimictic and monomictic lakes, whereas the whole water column mixes regularly in polymictic lakes and effectively the entire depth is the surface mixed layer.

In regions that experience warm summers, and very cold winters, the most common form of lakes are dimictic lakes, so called as they experience two periods of full water column mixing in spring and fall (Fig. 1). In summer there is a strong thermal stratification splitting the lake into three distinct regions, a surface epilimnion, a metalimnion where temperatures drop rapidly, and a deep cold hypolimnion in contact with the lake bed. The surface mixed layer is contained within the epilimnion during summer. In fall, the air temperatures drop, winds generally increase, and the surface layer cools and deepens until the whole water column is actively mixing. This period of fall overturn can often last for weeks or months. Cooling of the lake continues into winter, until waters drop below the temperature of maximum density, roughly 4 °C, and an inverse thermal stratification can form. The depth of the winter thermocline is in part set by mixing due to the wind fetch, so is a function of lake size (Yang et al., 2021). This period of inverse stratification can last for months in many northern lakes. In spring, there is a brief period of full water column mixing as the lake warms through 4 °C (the temperature of maximum density) after which a weak surface stratification starts to develop and confines mixing to a shallow surface layer.

In regions that experience warm summers and mild winters, the most common form of lakes are warm monomictic lakes, so called as they experience one period of full water column mixing when air temperatures are coldest during the winter. The stratification cycle in these lakes essentially looks like Summer-Fall-Spring in Fig. 1, with the key point that water temperatures never drop below 4 °C, so an inverse stratification never forms. In contrast, at very high latitudes such as the many lakes in the Canadian sub-arctic, cold monomictic lakes are common. The temperature of these lakes is below 4 °C all year, and most of the time they have an inverse stratification as in the Winter panel in Fig. 1. In the brief arctic summer, their waters warm up to near 4 °C and the lake experiences overturning.

Many shallow lakes never experience the strong thermal stratification typical of dimictic or monomictic lakes, but rather their whole water column mixes every time the wind blows or there is a significant change in air temperature. These lakes are called polymictic, and as there is no seasonal thermocline, the entire lake depth is essentially the surface mixed layer. Lewis (1983) defines four sub-types of polymictic lakes based upon latitude and whether mixing is continuous or episodic. A key feature of these lakes is that weak episodic stratification can develop, similar to the diurnal thermoclines seen in the epilimnion of dimictic and monomictic lakes. If there is a high sediment oxygen demand (typical of eutrophic lakes), hypoxia can even develop in some polymictic lakes. For instance, in a study of large eutrophic polymictic lake (Clear Lake, CA, United States), Cortés et al. (2021) observed an inverse relationship between DO saturation next to the sediments and the mean buoyancy frequency in the water column when the buoyancy frequency exceeds a threshold of $N > 0.015\ s^{-1}$. This threshold corresponded to a weak temperature gradient of less than $0.2\ °C\ m^{-1}$.

In all lake types the depth to which the surface mixed layer is actively mixing is critical for the depth distribution of buoyant plankton (Fig. 2). Often it is implicitly assumed the full epilimnion is homogenous and actively mixing (Fig. 2A), whereas usually only the upper part of a water column is actually turbulent (Fig. 2B). The difference in temperature profiles between the two cases is subtle, but as light decays exponentially with depth there is a big difference in average light levels experienced by plankton between the two cases (MacIntyre, 1993). Hence the productive layer in lakes depends upon both the depth of the surface mixed layer and the euphotic depth (Minaudo et al., 2021). In some cases, the water currents generated by wind-induced turbulence can become greater than the swimming capabilities of organisms, leading to changes in distribution of motile plankton (Pernica et al., 2013).

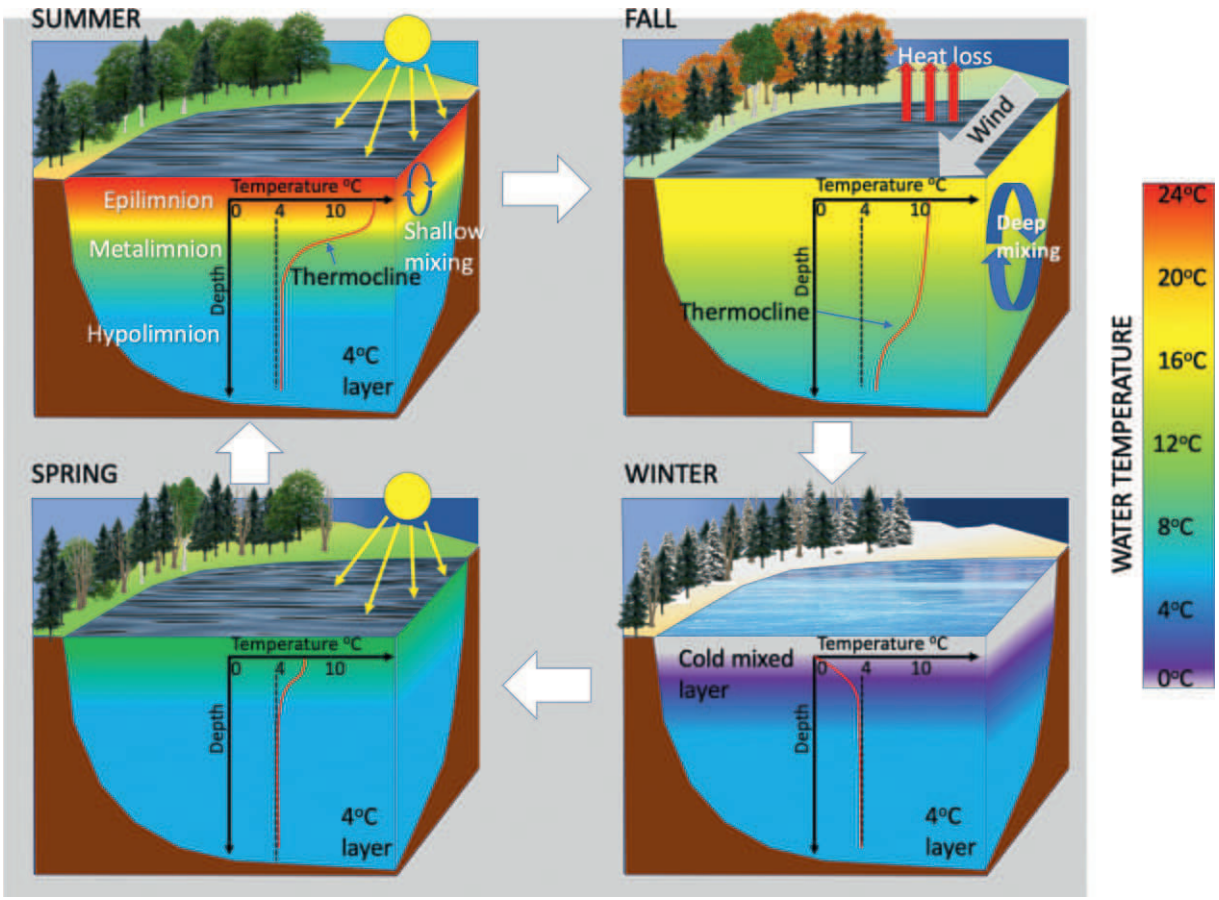

Fig. 1 A schematic of mixing and stratification in a dimictic lake, typical of temperate latitudes in Northern Eurasia or North America that experience very cold winters. The thermal stratification and mixing dynamics are sketched for Summer, Fall, Winter and Spring.

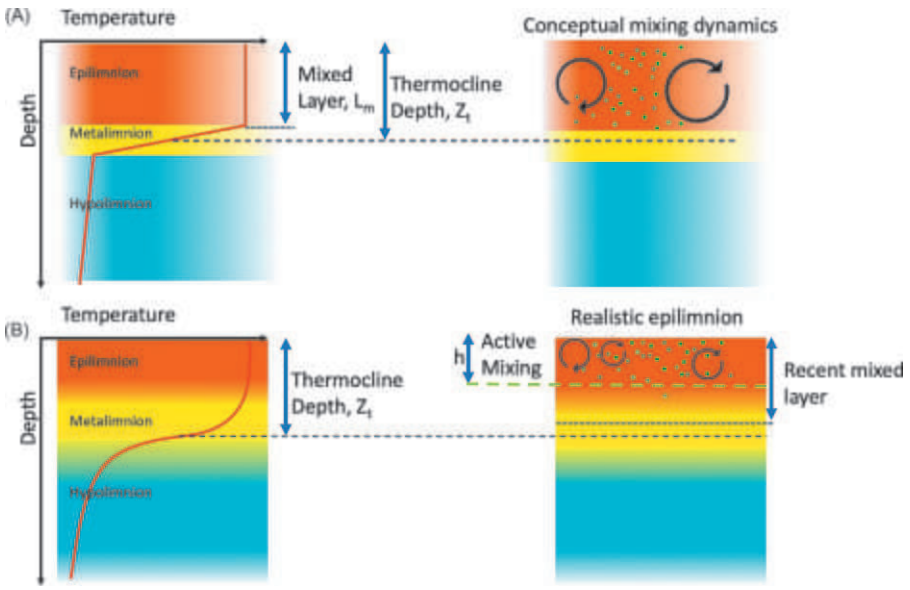

Fig. 2 (A) Often the epilimnion of lakes is assumed to have uniform properties, so that planktonic material is uniformly mixed in the epilimnion. (B) In reality, the depth of active mixing is much less than the depth of the thermocline or the depth of the recently mixed layer. The differences in mixing dynamics result in a shallower distribution of buoyant phytoplankton (illustrated as green spheres).

The depth distribution of buoyant plankton is very sensitive to diurnal variations in turbulence and stratification in the surface mixed layer. This can result in thin phytoplankton layers readily forming under low mixing conditions (Serra et al., 2007) or the formation of "scums" of harmful algal blooms (Wu et al., 2019). In a similar way, the depth distribution of buoyant microplastics is controlled by a balance between the speed at which they rise, compared to turbulent mixing rates (Kukulka et al., 2012).

Example of stratification in a dimitic lake

An example of the seasonal cycle of thermal stratification in the dimictic Harp Lake is shown in (Fig. 3; Supplemental File 1 in the online version at https://doi.org/10.1016/B978-0-12-819166-8.00126-2). This well-studied lake is located at 45.38° N, 79.13° W in Ontario, Canada. The lake has a maximum depth of 34 m but is only 500 m wide. It is sheltered by hills and forest so wind driven mixing is less important than buoyancy fluxes (Read et al., 2012). Forty high precision temperature loggers were deployed every 25 cm starting at 10 cm below a floating platform, down to 9.85 m depth, hence in Fig. 3 we only show the top 10 m where active changes take place. These PME T-Chain loggers (Precision Measurement Engineering, Vista, CA, United States) record every 10 min, and most significantly have a very high accuracy (±0.005 °C) that allows for the detection of subtle changes in thermal stratification associated with mixing. At this mid-latitude location in Canada, winters are severe with 3–5 months of ice cover. During winter, the lake has an inverse stratification (Yang et al., 2021), then after ice melts around day 109, there is a brief spring overturn, followed by a lengthy summer stratification (Yao et al., 2014). The surface waters of the lake can reach 25 °C, while the deep waters remain near 4 °C year-round (Fig. 3A). As the mixed layer is shallow, the thermocline is very strong, and the temperature drops by over 15 °C in just a few meters, so that maximum temperature gradients reach 8 °C m^{-1}, which is a very high gradient. The thermocline can be seen to deepen as summer progresses (Fig. 3B). There is a two-week period of full water overturn before ice forms on the lake on day 348.

Definition of the thermocline depth

The depth of the thermocline is most often defined as the depth where the vertical temperature gradient is greatest. In the example shown in Fig. 4, there is a very strong stratification in the metalimnion so it is unambiguous where the thermocline is located. In spring and fall in dimitic lakes, thermal profiles can be more diffuse so the classic three layers of epilimnion, metalimnion and hypolimnion are not as obvious. Similarly, warm monomictic lakes also have diffuse thermal profiles. Thus, many authors also have a minimum threshold for dT/dz in order to say a thermocline is present. For example, in Fig. 3B, the backline represents the location of maximum dT/dz, where dT/dz exceeds 1 °C m^{-1}. There are weak density gradients in fall and winter, but such a threshold is useful for defining start and end of summer stratification in dimitic lakes.

The depth of the thermocline at the end of summer in dimictic lakes has been found empirically to increase with fetch and mean wind speeds (Gorham and Boyce, 1989). For instance, Gorham and Boyce (1989) used a two-dimensional argument based on the Wedderburn number to show that the depth of the late summer thermocline was related to the magnitude of wind-driven mixing and the lake's geometry as

$$Z_T \approx \overline{u^*}\sqrt{Fetch/g'} \tag{1}$$

where u^* is the water-side wind friction velocity averaged over the summer stratified period (typically about 1/1000 of wind speed, see Read et al., 2012), the fetch is the distance the wind blows over the lake, and g′ is the reduced gravity across the thermocline, defined as $g' = g\frac{\Delta\rho}{\rho_o}$, where g is the gravitational acceleration, Δρ is the density difference across the thermocline, and ρ_o is the average density of the water column. The density of fresh water can be calculated from high resolution temperature measurements using equations in Chen and Millero (1977). Gorham and Boyce found a good agreement with their prediction when looking at end-of-summer thermocline depths Z_T in 150 lakes. A related empirical survey by Fee et al. (1996) found that Z_T during midsummer had a positive correlation with $A^{1/4}$, where A is the surface area of the lake. This observational result generally agrees with the Gorham and Boyce semi-empirical result since if the lake is circular, then $Fetch \sim A^{1/2}$. As an example of the fetch dependence, the thermocline depth in Harp Lake is less than 5 m and the fetch is less than 500 m, whereas in nearby Lake Simcoe, the later summer thermocline is 15–20 m and the fetch is closer to 50 km (Cossu et al., 2017).

The distinctions between stratified monomictic, dimictic, and polymictic lakes also depend upon whether or not the depth is shallower than that of a stable thermocline. For instance, Lewis (1983) argues that the aspect ratio of fetch to depth largely determines if lakes are polymictic, and hence have a surface mixed layer that extends to the lake bed. He quotes an empirical relationship from Ragotskie (1978) that the fetch effect can approximated according to the empirical relationship $Z_{mixed} = 4\sqrt{Fetch}$, where Z_{mixed} is the mixed layer thickness in m and $Fetch$ is in km. If the lake is shallower than this depth, it is likely to be polymictic. For instance, Lake Taihu in China is a large, shallow and almost circular lake, with area = 2250 km^2. The mean fetch is 47 km, and the predicted $Z_{mixed} = 27.5$ m. As the mean depth of Lake Taihu is 2 m, it is not surprising it is a polymictic lake with only weak ephemeral stratification (Wu et al., 2018).

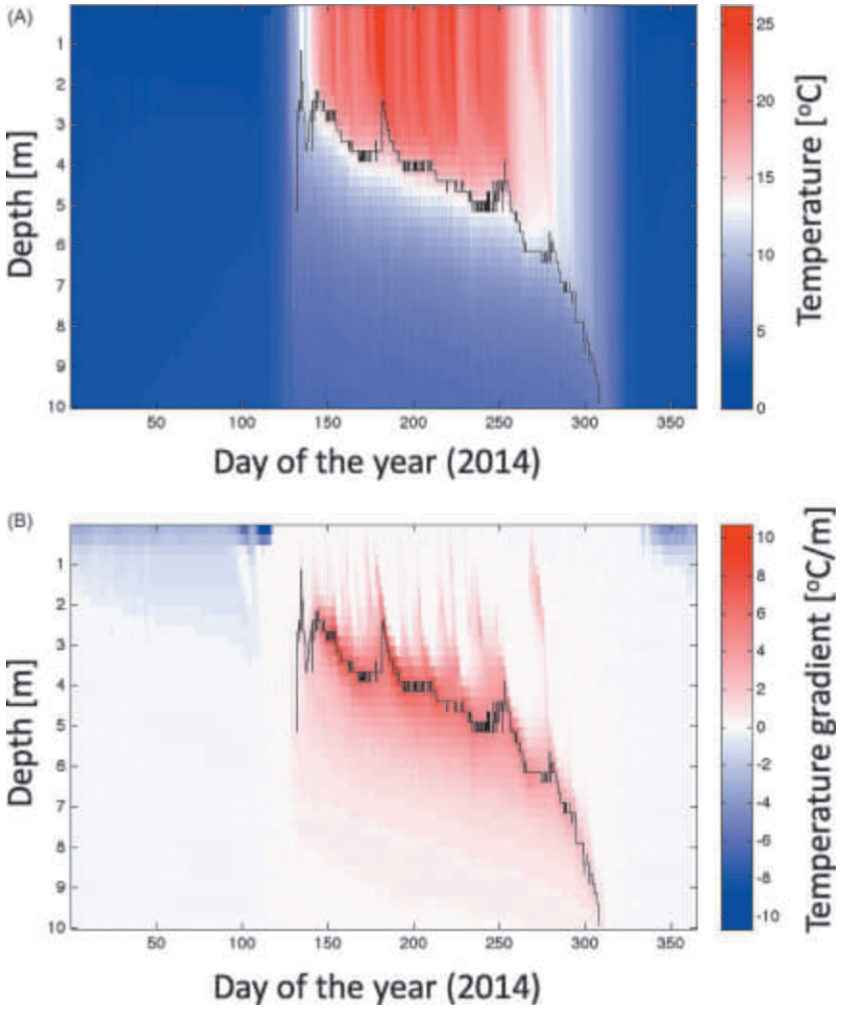

Fig. 3 A timeseries of temperature stratification in dimictic Harp Lake is shown in (A), and the very strong thermal stratification is visible during summer. The vertical temperature gradient is shown in (B). There is a very strong thermal gradient in summer and an inverse temperature gradient in winter. In early spring and fall there are periods of overturn, and hence lack of thermal gradients. The depth of maximum thermal gradient (the thermocline) is shown with a black line (Data from Dr. James Rusak, included as Supplemental File 1).

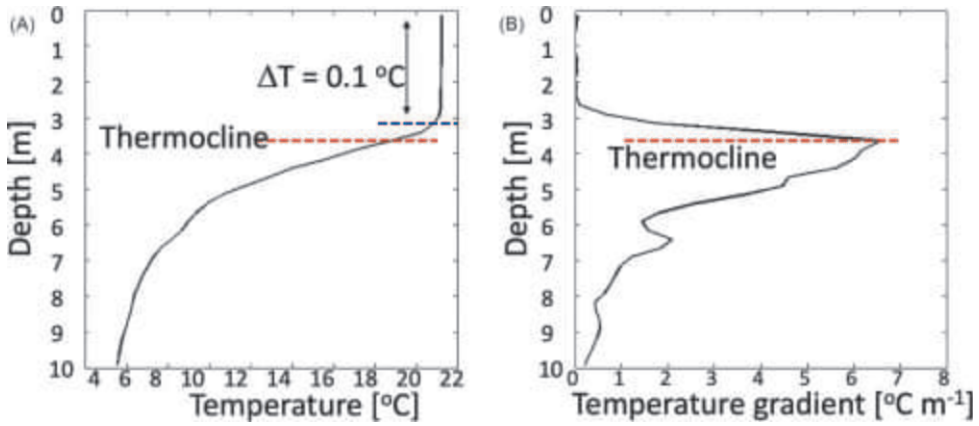

Fig. 4 (A) A thermal profile from Harp Lake on Day of Year 203.3 in 2014. The surface layer is here defined as the zone where there is less than 0.1 °C difference from the surface. (B) The vertical temperature gradient. The depth of maximum temperature gradient can be used to define the thermocline. Note, these are very strong temperature gradients, and most dimitic lakes have lower values (Data from Dr. James Rusak).

Other definitions of thermocline depth

In addition to the common definition of the thermocline being the depth of maximum temperature gradient, there are a number of other possible definitions for thermocline depth that are often used. If the temperature profile was as two layers idealized two layer, with a warm homogenous epilimnion, a very thin metalimnion and a cold homogenous hypolimnion, all the following definitions would be the same, but due to the typically diffuse thermal profiles in lakes, the following definitions can result in differences of 10–20% between definitions of thermocline depth. These differences can sometimes confound comparisons between different lakes.

One somewhat common definition of thermocline used in calculating the Wedderburn number (Robertson and Imberger, 1994; Coman and Wells, 2012) is an integral definition by calculating first moment of density as

$$Z = \int_{bottom}^{surface} \rho(z) z \, dz \Big/ \int_{bottom}^{surface} \rho(z) \, dz \tag{2}$$

This gives a weighted center of mass of density distribution, which is used to define Z, the depth of the thermocline.

In some cases, it is important to define the thermocline depth in terms of velocity gradients, instead of temperature gradients, if internal waves or "internal seiches" are the focus of ones' studies. Internal seiches are periodic sloshing motions of the thermocline across the lake basin, and seiches can induce strong currents in lakes that affect transport and mixing of pollutants, biota, and nutrients. For internal seiches, water velocities are oppositely directed above and below the thermocline, and the point of zero velocity or maximum velocity gradient are useful ways for identifying the thermocline location (see, for example, Woolway and Simpson (2017)).

There is also the concept of a biologically important thermocline, as fish habitat is often vertically portioned by thermal guilds (Plumb and Blanchfield, 2009). For instance, in many temperate dimictic lakes, cold water fish stay at temperatures below 12 °C, which often coincides with other definitions of the thermocline. Warm water fish in these stratified temperate lakes are then found only above the thermocline in summer (Brooks et al., 2022) while cold water fish sit below this thermocline (Flood et al., 2021a). In these lakes internal seiches move the thermocline up and down and hence influence fish habitat usage (Flood et al., 2021b).

Definition of the surface mixed layer depth

The surface mixed layer depth is bounded below by the depth of thermocline, but can change dynamically in response to wind and buoyancy forcing. During the summer stratification season, short periods of cool, windy weather can increase the thickness of the mixed layer temporarily without completely disrupting the deeper seasonal stratification. When warm, calm weather returns, a secondary thermocline develops in the former mixed layer, again restricting mixing to a much thinner layer (Pernica and Wells, 2012). This secondary layering may persist for a period of days or weeks, after which it is typically disrupted again by cool or windy weather. Thus, the definitions of the surface mixed layer depth often depend on small gradients of temperature or turbulence within the surface layer. Often the permanent thermocline is used as a short-hand definition as the bottom of surface mixed layer, i.e. the depth below which diurnal surface mixed layers no longer influence temperature. However, it is usually the case that the surface mixed layer is significantly shallower than this depth. Furthermore, it is crucial to distinguish between a recent "*mixed*" layer, and an actively "*mixing*" layer (Brainerd and Gregg, 1995; Pernica et al., 2014). While it is possible to use turbulent microstructure profilers to rigorously define an active surface mixed layer (Tedford et al., 2014), it is more common practice in limnology to rely on temperature profiles that often are controlled by past mixing events.

Various definitions of the surface mixed layer have been proposed, as illustrated in Fig. 5. In general, these lead to similar estimates of mixed layer depth but as they emphasize different processes, they will differ in the exact values (Wilson et al., 2020).

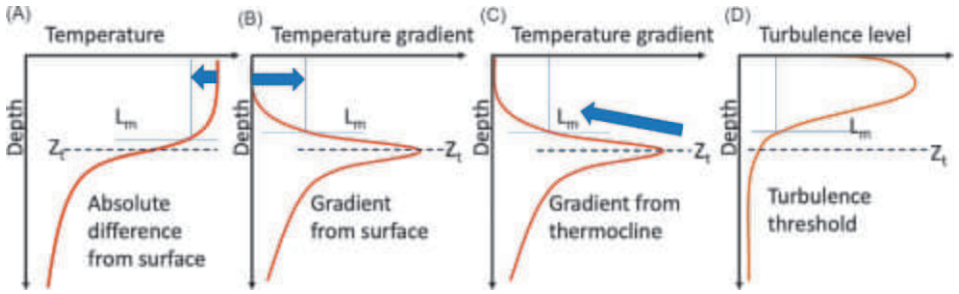

Fig. 5 There are numerous definitions commonly used for the depth of mixed layer (L_m) relative to depth of thermocline (Z_t). (A) The mixed layer can be defined in terms of a drop of temperature (or density) from the surface, (B) or a threshold gradient first encountered from above the thermocline. (C) Another definition is to fix the mixed layer depth relative to a threshold stratification that is proportional to stratification at the thermocline. (D) If turbulence can be measured or modelled then the mixed layer can be defined when turbulence drops below a threshold. (Figure modified after Wilson HL, Ayala AI, Jones ID, Rolston A, Pierson D, de Eyto E, Grossart HP, Perga ME, Woolway RI and Jennings E (2020) Variability in epilimnion depth estimations in lakes. *Hydrology and Earth System Sciences* **24**(11): 5559–5577.

In a review of different definitions, Gray et al. (2020) were most in favor of the mixed layer being defined in terms of Fig. 5A, where the depth of mixed layer is defined in terms of a drop of density of $\Delta\rho = 0.1$ kg m^{-3}, which corresponds to a change of density due to a moderate and measurable temperature change of 0.5 °C between 20.5 °C at top of mixed layer to 20 °C at the base. This is a simple pragmatic number which is easy to measure with most field equipment; however it may overestimate active mixing layer depths in some cases. Related work on mixing in the ocean surface layer has used smaller density steps of $\Delta\rho = 0.03$ kg m^{-3} (Somavilla et al., 2017) or even $\Delta\rho = 0.005$ and 0.01 kg m^{-3} (Brainerd and Gregg, 1995). These thresholds would require higher resolution temperature loggers to be determined in lakes. Detailed turbulence measurements by Pernica et al. (2014) showed that a weak thermal gradient of as little as 0.1 °C m^{-1} could suppress active turbulence, and they defined the mixed layer in terms of the depth at which a minimum buoyancy gradient threshold first occurs, as in Fig. 5B. A widely used toolbox called "LakeAnalyzer" was developed by Read et al. (2011). In their code they search up from the thermocline to find a user-specified threshold buoyancy gradient in order to define the top of metalimnion, which is assumed to be the bottom of the mixed layer (Fig. 5C). The ideal way to measure the depth of the surface mixed layer would be to directly measure the turbulence in the layer using either a microstructure profiler (Pernica et al., 2014; Lin et al., 2021; Piccolroaz et al., 2021), an underwater drone (Kaminski et al., 2021) or by using a moored acoustic doppler current profiler (Jonas et al., 2003; Tedford et al., 2014). Then with a profile of turbulence intensity, the bottom of the mixed layer could be defined in terms of a minimum turbulence threshold (Fig. 5D). In practice this is expensive, and has rarely been done for any significant timescale over which the thermocline depth changes.

Processes that control mixing in surface layer

A key parameter than determines the local stability of the surface mixed layer is the Richardson number. It is defined, at a particular point, as the ratio of the stabilizing buoyancy gradient ($N^2 = -g/\rho\ (\partial\rho/\partial z)$) to the velocity shear (dU/dz) which can cause turbulent mixing. Specifically, when $N^2 >> (dU/dz)^2$ a density stratified flow has little turbulence, whereas when $(dU/dz)^2 >> N^2$ turbulence can be strong (Ivey et al., 2008). The Richardson number is defined as

$$Ri_g(z) = -\frac{g}{\rho_o}\frac{\frac{\partial\rho(z)}{\partial z}}{\left(\frac{\partial U(z)}{\partial z}\right)^2} \tag{3}$$

where g is gravity, $U(z)$ the horizontal velocity as a function of depth z, $\rho(z)$ the density as a function of depth and ρ_o a representative mean density. It is now routine to measure velocity in the surface layer with an ADCP (acoustic doppler current profiler), and density can be calculated by using moorings chains with high resolution temperature loggers that can measure at least to 0.01 °C accuracy. Numerous studies in atmosphere, ocean and laboratory have all shown that $\mathrm{Ri_g} = ¼$ is the boundary between stable and unstable shear flows, i.e., flows with $\mathrm{Ri_g} > ¼$ are stable, whereas flows with $\mathrm{Ri_g} < ¼$ are very turbulent (Miles, 1961; Howard, 1961; Ivey et al., 2008). However, the free surface zone of the water column is problematic for ADCP measurements due to reflections, and additionally, coarse spacing of ADCP bins and thermistor locations can preclude a highly accurate estimate of the gradient Richardson number in the mixed layer, at least very close to the lake surface.

If high-precision, finely spaced measurements are not available to estimate Ri_g, a bulk version of the Richardson number can be defined in terms of bulk values across the layer depth L as

$$Ri_{bulk} = -\frac{g}{\rho_o}\frac{\Delta\rho\, L}{\Delta U^2} \tag{4}$$

where $\Delta\rho$ is the density difference, and ΔU the velocity difference across the surface mixed layer. The interpretation of Ri_{bulk} is similar to that of Ri_g, except that it is a single "bulk" stability metric for the entire mixed layer. Similar to Ri_g, when Ri_{bulk} is small, the mixed layer is expected to be turbulent, and when Ri_{bulk} is large, the mixed layer is expected to be stable. The bulk Richardson number does not have a clear-cut critical value, in contrast to the well-defined $Ri_g = \frac{1}{4}$ cutoff for Ri_g.

As an example, a density difference of $\Delta\rho = -0.1$ kg m^{-3} corresponds to a change of density due to a moderate and measurable temperature change of 0.5 °C between 20.5 °C at top of mixed layer to 20 °C at the base. If this was a 5 m deep mixed layer it would have a weak temperature gradient of $dT/dz = 0.1$ °C m^{-1}. We can re-arrange the equation of the bulk Richardson number to estimate what the maximum velocity gradient is before this temperature gradient becomes unstable, as $\Delta U = 2\sqrt{g\frac{-\Delta\rho}{\rho_o}L}$. Taking $\rho_o = 1000$ kg m^{-3} and $g = 9.81$ m s^{-2} with $L = 5$ m and $\Delta\rho = -0.1$ kg m^{-1}, then gives $\Delta U = 0.14$ m s^{-1}. Surface water currents are usually 2–3% of wind speeds, so this velocity difference across mixed layer could be generated by winds blowing at 5–7 m s^{-1}. Winds slower than this speed would not generate enough shear to mix a weakly stratified surface layer, whereas faster winds would produce enough turbulence to quickly homogenize surface layer. Thus, the bulk Richardson number can be used as a predictive tool to estimate the relative resistance of thermal gradients to various shear flows.

The depth of the surface mixed layer can also be related to the competition between the surface buoyancy flux and shear-driven turbulent mixing (Fig. 6). This idea was first advanced by Monin and Obukhov (1954) to understand the stability of the atmospheric boundary layer due to competition between wind stress and surface heat fluxes. The idea has also since been widely used to help understand mixing in oceanic and lake surface mixed layers (Farmer and Carmack, 1981; Tedford et al., 2014). The so-called Monin-Obukhov length scale is defined as $L_{MO} = -u^{*3}/kB$, where k is the von Kármán constant ($k = 0.4$), B the surface

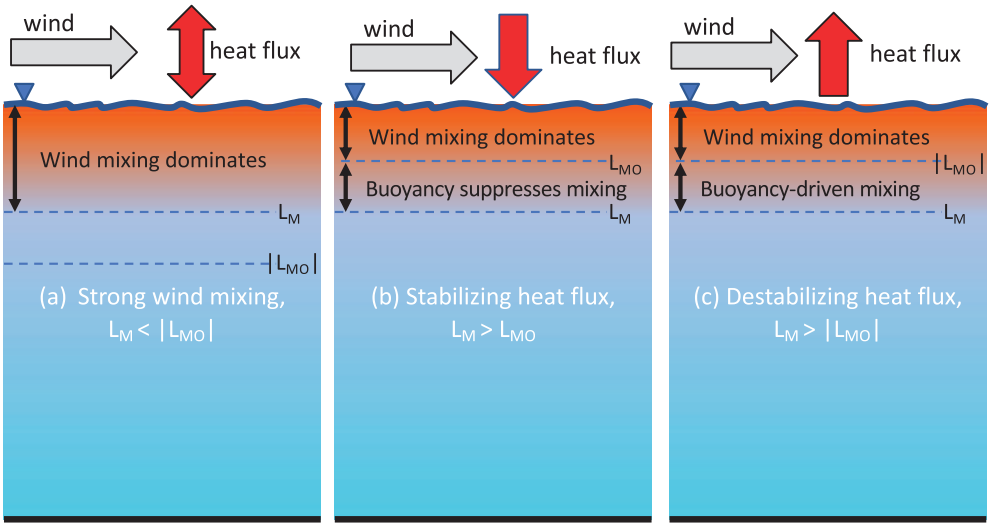

Fig. 6 A graphical interpretation of the Monin-Obukhov length scale L_{MO} compared to the surface mixed layer scale L_M. (A) When wind driven mixing is strong, the predicted Monin-Obukhov length scale L_{MO} is greater than the surface mixed layer depth, and hence stratification limits the depth over which wind driven mixing is strong. (B) When there is a stabilizing heat flux and weak winds, the wind driven mixing is only strong in the top of the surface mixed layer. (C) With a strong destabilizing heat flux, buoyancy fluxes can drive mixing to the base of the surface mixed layer.

buoyancy flux and the shear velocity is defined as $u^* = \sqrt{\tau_{wind}/\rho}$ where τ_{wind} is the surface wind-stress. The buoyancy flux can be either positive or negative depending on the relative contributions of various heat flux terms. This length scale represents the depth above which the production of turbulent kinetic energy is expected to be dominated by wind driven mixing. At depths greater than $|L_{MO}|$, turbulence would be suppressed by a stabilizing buoyancy flux and would be enhanced by an unstable buoyancy flux (convection). The length-scale L_{MO} is essentially a benchmark length scale against which to compare the depth of the mixed layer thickness to determine what process limits the boundary layer. Within this turbulent boundary layer, the levels of shear driven turbulence can be predicted by Monin-Obukhov similarity theory (Tedford et al., 2014), hence this relationship is often assumed in models of surface layer dynamics.

The surface layers of lakes are dynamic and the degree of mixing depends upon the relative importance of wind stresses and buoyancy fluxes (Fig. 7). As discussed above, the magnitude of wind stress is one key factor in determining if mixing can occur (Bouffard and Wüest, 2019). Weak mixing in a stratified epilimnion of depth L_M is shown in Fig. 7A. Here weak mixing occurs during periods when $Ri_g > 1$. The time-scale for vertical mixing is set by $T_{Mix} = L_M^2/4K_z$ and as the vertical turbulence diffusivity K_z is generally low for $Ri_g > 1$, it can take days to homogenize such a layer. For example, many studies (Pernica et al., 2013; Lin et al., 2021) find values of vertical diffusivity K_z in the range 10^{-5} m^2 s^{-1} to 10^{-3} m^2 s^{-1}, implying timescales of $T_{mix} = 8$ h to 1 month in a 10 m deep surface layer. Stronger mixing in a weakly stratified or unstratified epilimnion of depth L_M is shown in Fig. 7B. Complete mixing of the epilimnion occurs whenever stratification is weak, i.e., when there is any cooling or wind and $Ri_g \ll 1$. Other estimates for the timescale for mixing are $T_{Mix} = L_M/u^*$ or L_M/w^*. The shear velocity in water can be estimated as $u^* \sim (\varepsilon L)^{1/3}$ where ε is dissipation of turbulent kinetic energy, and the convective velocity estimated from negative buoyancy fluxes as $w^* \sim (BL)^{1/3}$

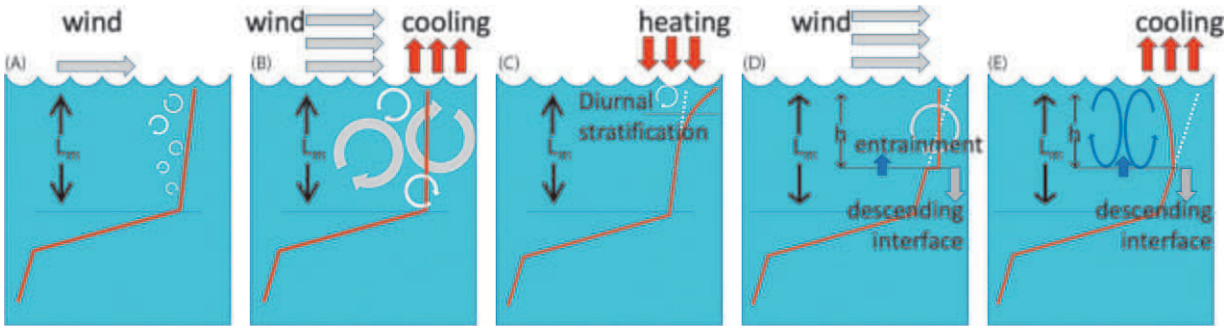

Fig. 7 A number of processes control mixing in the surface layer of lakes. The cases include (A) Weak mixing in a stratified epilimnion, (B) Mixing in an unstratified epilimnion of depth L_M, where B is the buoyancy flux (see chapter by Schmid and Read) and u^* and w^* are the shear velocity and convection velocity respectively computed as in Read et al. (2012), (C) formation of a diurnal thermocline due to surface heating (Woolway et al., 2016), (D) Wind-driven entrainment of a stratified epilimnion to a depth h (Kaminski et al. 2021), and (E) Erosion of a stratified epilimnion by entrainment to a depth h by convective cooling (Tedford et al., 2014). Figure modified from Pernica P, Wells MG and MacIntyre S (2014) Persistent weak thermal stratification inhibits mixing in the epilimnion of North-Temperate Lake Opeongo, *Canada Aquatic Sciences* 76 (2): 187–201.

(Read et al., 2012). Here the negative buoyancy flux B is related to the surface heat flux H as $B = g\alpha H/\rho C_\rho$ where α ισ the co-efficient of expansion of water, ρ the density of water and C_p the specific heat of water. Due to the non-linearity of equation of state of water, α is a strong function of temperature, and changes sign below 4 °C, such that a positive heat flux becomes a negative, destabilizing buoyancy flux.

Many lakes experience strong diurnal thermal stratification, as shown in Fig. 7C. Field observations by Woolway et al. (2016) of the magnitude of diurnal stratification in lakes have found a strong lake size dependence. During summer, they measured the near surface layer (<1 m) and found that small ponds had diurnal thermal changes of as much as 8 °C. They found that small lakes (between 10^4 and 10^6 m^2) had diurnal temperature changes of 1–4 °C, and larger lakes less than 0.5 °C diurnal changes. All of these are substantial changes, which can cause strong thermal stratification in surface layers and the inhibition of mixing (Xenopoulos and Schindler, 2001; Pernica et al., 2013).

After a period of warming, a diurnal stratification can erode quickly due to wind driven entrainment of a stratified epilimnion (Fig. 7D) or erosion of a stratified epilimnion by convective entrainment (Fig. 7E). Rapid wind driven deepening of a previously stratified epilimnion during strong winds depends upon the stability of the stratified layer, so is a function of the Richardson number. The speed at which the layer of depth h deepens, has been shown to scale as $dh/dt \approx u^*/Ri_g$ (Monismith and MacIntyre, 2009). Convective deepening of a stratified epilimnion occurs frequently, especially during cold fronts and on cold nights (Tedford et al., 2014). For this process, the speed of the descending front depends upon the buoyancy flux B, and the buoyancy frequency N as $dh/dt \approx B/hN^2$ (Turner, 1973). Recent observations in the ocean surface mixed layer have documented the overturns at the upper thermocline due to scouring motions caused by wind driven turbulence (Kaminski et al. 2021). It is thought that the large-scale wind-driven Langmuir circulations in the surface layer play an important role in advecting the turbulent motions from the air-water interface down to the top of the thermocline, where entrainment of denser waters can occur (Kaminski et al. 2021).

Example of mixed layer dynamics from Harp Lake

The use of high-resolution temperature loggers can reveal the dynamic nature of the surface mixed layer (Fig. 8). In this figure the same data is plotted as in Fig. 3, but the scales are changed to emphasize the subtle but rapid changes in stratification. Fifty days of data are shown, and the mixed layer depth is estimated by superimposing a line that depicts the depth that is 0.1 °C cooler than the surface in Fig. 8A. There is a clear diurnal signal in the depth of this contour, shallower during the day, then deeper at night. In addition, two cooling events can be seen on day of year 210 and 226, where the surface mixed layer almost reaches the depth of

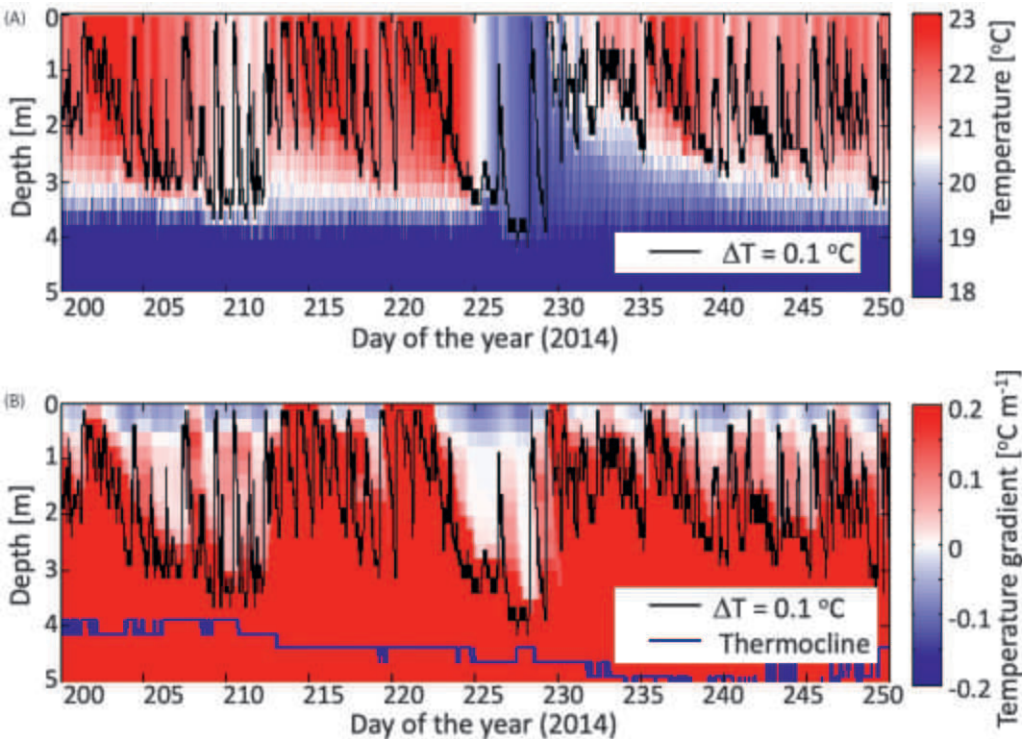

Fig. 8 Variation in depth of the mixed layer in Harp Lake during summer 2014. The temperature in the top 5 m is plotted in (A) with the black line indicating the depth where there is a 0.1 °C drop from surface water temperatures. The vertical temperature gradient is plotted in (B). Unstable negative gradients are plotted in blue, while stable gradients are plotted in red. Here the range is limited to −0.2 to +0.2 °C $m^{-1}$to emphasize the subtle changes in stratification in the upper layers.

thermocline. The subtle temperature gradients are shown in Fig. 8B, where the range has been limited to $-0.02\ ^{\circ}C\ m^{-1} < dT/dz < +0.02\ ^{\circ}C\ m^{-1}$. In contrast, data in Fig. 3B was plotted between $-10\ ^{\circ}C\ m^{-1} < dT/dz < +10\ ^{\circ}C\ m^{-1}$so that none of these subtle gradients were visible. Another key feature to note in Fig. 7B is the small negative temperature gradients in the top 50 cm of the water column. They are gravitationally unstable and so would indicate active convective mixing. All the times the surface mixed layer deepens are associated with these unstable profiles. Also compare the difference between the dynamic changes in mixed layer depth (black curve in Fig. 8B) with the very slow and steady changes in the thermocline depth (blue curve in Fig. 8B). As noted by Serra et al. (2007), such diurnal mixing can influence the vertical distribution of buoyant plankton layers.

Horizontal wind driven currents

Winds over the surface of a lake drive lateral currents in addition to vertical mixing. These surface layer currents then transport plankton, buoyant larvae, fish eggs, microplastics or oil spills downwind. A simple description of this advection is to use a wind factor (defined as the ratio $U_{surface}/V_{wind}$) to estimate the magnitude of these surface currents. The wind factor theory was originally developed for very large lakes and the ocean, for which the earth's rotation becomes important. In this case the surface currents driven by steady winds after a day can be described using the classic theory of Ekman (1905), whose famous result can be expressed using a wind factor that relates the wind velocity to the water surface velocity: $U_{surface}/V_{wind} = 0.0127/\sqrt{\sin\theta,}$ where $U_{surface}$ equals the surface water current velocity, V_{wind} is the wind velocity, and θ is the latitude (Haines and Bryson, 1961). The formula gives a constant wind factor for a specific latitude, and gives a wind factor of 2.5% at 15° N, and 1.4% at 60 ° N. More importantly, Ekman found that due to Coriolis forces the surface water current was directed at 45 degrees to right of wind in northern hemisphere, and 45 degrees to left of wind in southern hemisphere. Only at the equator does the Coriolis force vanish and currents directly follow wind direction. The classic theory of Ekman (1905) did not consider the additional influences of wave driven currents, which tend to make surface currents slightly faster and reduce influence of Coriolis deflection to less than 45 degrees, typically in range of 15–35 degrees (Krauss, 1993).

For small to medium lakes where the earth's rotation is not important, studies consistently find currents with wind factors of $U_{surface}/V_{wind} \sim 1.5$–3% (Henderson-Sellers, 1988). The steering influence of the coastlines on current direction is more pronounced in smaller lakes, as is the sheltering influence of trees (Markfort et al., 2010) so it is less common to apply Ekman theory directly. As an example, Fig. 9; Supplemental File 2 in the online version at https://doi.org/10.1016/B978-0-12-819166-8.00126-2 shows drifter data collected in June 2011 in the large shallow Lake St Clair, located on the Canada/United States border. The three drifters recorded their position via GPS every hour, from which we estimated the speeds over a three-day period. Wind speeds are taken from the Environment and Climate Change Canada meteorological station 45,147 (located at 42°25′48" N 82°40′48″ W). There is some scatter in the raw data, but the bin-averaged data is consistent with a wind factor of 2–3%. For comparison we also plot in Fig. 10 a relationship derived from 356 observations from Lake Mendota, Wisconsin, United States by Haines and Bryson (1961) where the wind factor is

$$U_{surface}/V_{wind} = 0.053/V_{wind} + 0.013 \tag{5}$$

where $U_{surface}$ and V_{wind} are in m s^{-1}.

In the pelagic regions of very large lakes, surface currents can be largely decoupled from the wind and strongly periodic during the stratified period due to the dominance of near-inertial internal Poincaré waves (Choi et al., 2012, 2015). These waves occur in large, stratified lakes for which the earth's rotation is dynamically important, and can control mixed layer transport, shear, and lateral dispersion. Internal Poincaré waves are seiches of the thermocline that are modified by the earth's rotation (Csanady, 1966; Antenucci and Imberger, 2001). For these waves, the thermocline rotates anti-cyclonically around the basin like a spinning coin, with a period approaching the local inertial period for very large lakes such as the Laurentian Great Lakes. The surface currents associated with these waves can be very large in the center of the lake, with nearly perfectly periodic currents. These currents transport material in telltale clockwise-spiraling paths (in the northern hemisphere) termed "inertial waltzes" (Mortimer, 2004; Choi et al., 2020).

Examples of near-inertial surface currents measured in Lake Michigan (United States) are shown in Fig. 10 and as an animation in a Supplemental File 3 in the online version at https://doi.org/10.1016/B978-0-12-819166-8.00126-2. The eastward and northward currents measured in the mixed layer can be seen to show strong periodicity with periods of 17.5 h. Six satellite-tracked drifters released at the center of the basin exhibit the clockwise-spiraling particle pathlines while in the lake's interior. While these currents lead to a strong absolute dispersion of drifters from their initial position, it is striking that the relative dispersion between the eight drifters is quite slow, as they move as a cluster until they reach the coastal boundary currents in Lake Michigan (see Choi et al., 2015, 2020, for additional details).

Horizontal dispersion at the lake surface

The presence of turbulence in the surface layer of lakes acts to disperse material horizontally as well as vertically. There is a rich history of measuring lateral dispersion in lakes and ocean, starting with measurements of the separation rates of disks made of sliced

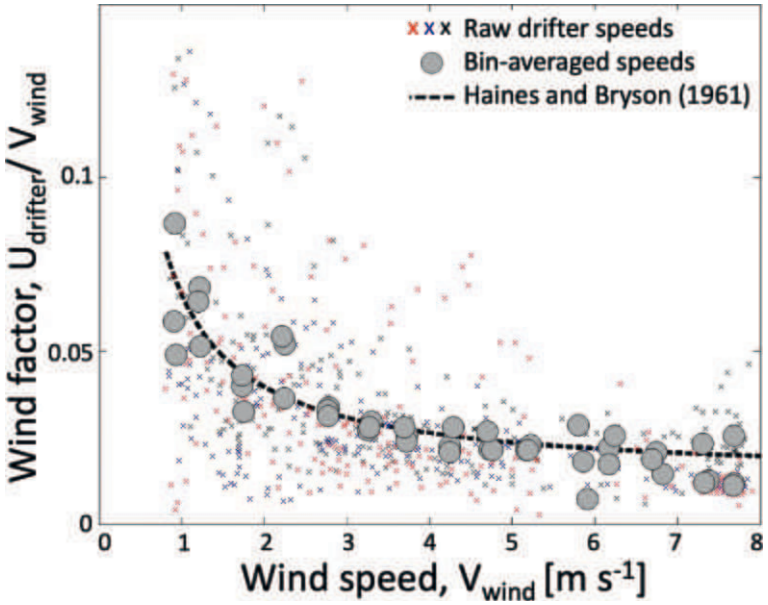

Fig. 9 Wind factor as a function of wind speed. The results from Lake St Clair show that the magnitude of the total surface current is around 3% of the wind speed at 10 m height. An animation of all drifter tracks is included in Supplemental File 2.

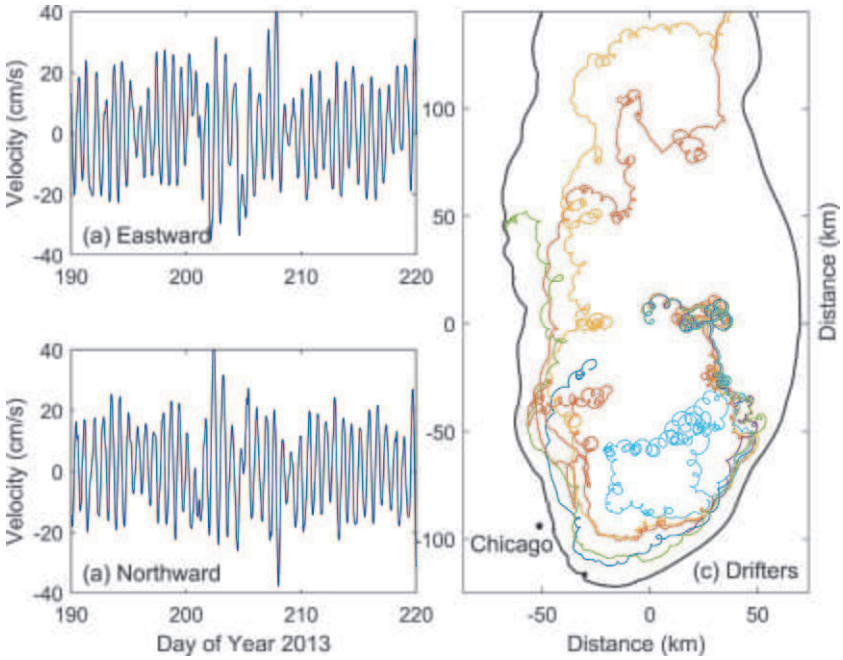

Fig. 10 Currents and drifter paths measured in Lake Michigan. Shown are the eastward and northward currents measured by an ADCP at 5 m depth over a 30 day period (A and B) and the paths of six satellite-tracked drifters followed over 115 days. Details can be found in Choi et al. (2015, 2020). The drifter track in (C) is provided as a supplementary animation.

parsnips (Richardson and Stommel, 1948), through to much more sophisticated studies using close to 1000 biodegradable GPS tracked drifters in the Gulf of Mexico (Novelli et al., 2017). The rate of lateral spreading in lakes is related to variance in horizontal velocities, and as these velocities are orders of magnitude larger than vertical velocities in mixed layer, the horizontal diffusivity is also ordering of magnitude larger. For instance, Choi et al. (2020) report horizontal dispersion coefficients of order 1 $m^2\ s^{-1}$, while the vertical diffusivity in mixed layer is much less, and of order $K_z = 10^{-5}\ m^2\ s^{-1}$ to $10^{-3}\ m^2\ s^{-1}$. The timescale for diffusion scales as $T \sim H^2/D$, where H is a length-scale and D the diffusivity. Thus, for a given time period the ratio of horizontal to vertical scales of dispersion are roughly $H_{horizontal}/H_{vertical} \approx \sqrt{D_{horizontal}/K_z}$. As the ratio $D_{horizontal}/K_z$ could be in the range 10^2 to 10^6, this implies a

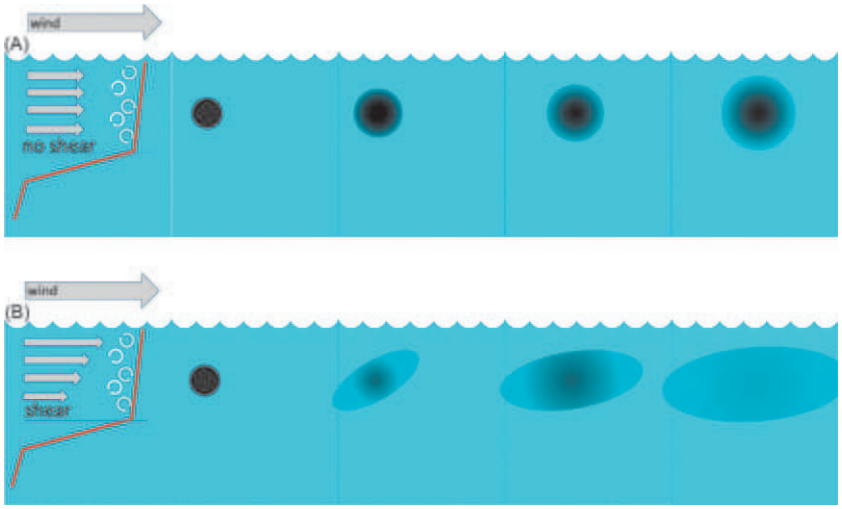

Fig. 11 Lateral dispersion in a mixed layer due to advection + turbulence (A), versus advection + vertical shear + turbulence (B). The shear is a natural result of wind driven currents. The addition of shear leads to much faster dilution rates in the second case, illustrating importance of shear driven dispersion in the surface layers of large water bodies.

ratio of dispersion scales between 10 and 1000. While this ratio is large, it is worth remembering this is also a typical aspect ratio of the width of a lake to the fetch in a lake, i.e., dispersion across a lakes' mixed layer can happen on comparable timescales to vertical mixing through the depth of a mixed layer.

An important caveat about the use of a diffusive model for dispersion is that they implicitly assume the turbulence is divergence free across the surface of a lake or ocean. This is a reasonable assumption for how dye might mix laterally in the surface layer of a lake, but the presence of converging flows in surface layers can be problematic for applying these ideas to dispersion of surface drifters. In particular, many large lakes and coastal ocean regions have converging flows in the surface layers at fronts in the waterbodies, where drifters will accumulate. A classic example in large dimictic lakes are the near-shore convergence zones during spring overturn associated with so-called "thermal bars" (Rao et al., 2004). In large scale ocean flows, fronts and other mesoscale flow features are also seen to accumulate GPS tracked drifters (Novelli et al., 2017).

The presence of shear within the surface mixed layer adds an additional mechanism that can greatly increase lateral dispersion rates (Fig. 11). Winds drive the production of both turbulence and currents, and the combination of these two processes leads to so-called "Taylor shear dispersion" whereby the effective lateral dispersion rate is much greater than the small-scale turbulence mixing rate (Taylor, 1954; Csanady, 1966). For instance, Taylor dispersion was found to be very important in a numerical study of the surface layer in Lake Michigan by Choi et al. (2015). Shear was dominated by Poincaré waves, and they found that the dominant shear structure was observed to mirror the thermal structure, with the location of maximum shear located across the thermocline. In their numerical experiments, Choi et al. (2015) found this oscillating internal wave shear greatly enhanced lateral dispersion. The estimated depth-averaged surface layer vertical turbulent diffusivity grew as shear became stronger from 10^{-5} m^2 s^{-1} to 10^{-3} m^2 s^{-1} over the stratified period, and the associated lateral dispersion coefficients are estimated as 0.1–40 m^2 s^{-1}. These predictions were largely verified in the field study of Choi et al. (2020). Significantly, Choi et al. (2020) found that the horizontal dispersion rates of the GPS tracked surface drifters were far less than for the lateral mixing rates of the dye release, emphasizing the importance of shear dispersion in mixing the dye within the surface layer. This difference in dispersion rates also implies that care must be taken in comparing dye studies to drifter studies as they measure slightly different processes of dispersion in the surface mixed layer.

Wind driven horizontal dispersion of algae within lake surface

Plankton and other floating material in lakes are not uniformly distributed in space but are patchy at multiple scales as a result of interactions between their directed motion and both large- and small-scale water currents (Pernica et al., 2013). For instance, light winds can set up circulation patterns and vertical shear that influence the distribution of phytoplankton and small zooplankton (George and Edwards, 1976) as sketched in (Fig. 12A). Stronger winds can even lead to upwelling of the hypolimnion. In a field study in Lake Opeongo, Cyr (2017) found that on windy days, phytoplankton biomass was higher along the downwind shorelines. However, she found that this was mostly due to dilution from upwellings, not just algae accumulating downwind. She noted that buoyancy and motility affect the distribution of individual taxa. Hence in this medium sized lake, with a 7 km fetch, both processes sketched in Fig. 12A and B were important. Further studies in Lake Opeongo suggested that planktivorous fish actively respond to the higher downwind concentrations of plankton (de Kerckhove et al., 2015).

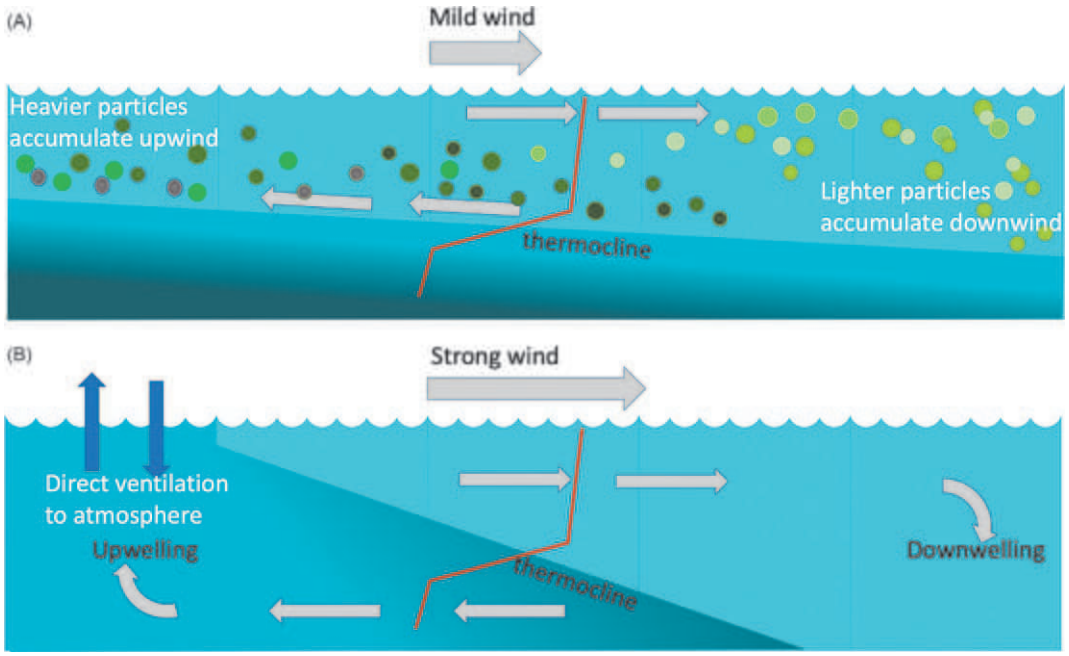

Fig. 12 (A) Under light winds a return flow can be set up in the surface layer of a stratified lake. This can form a so-called "conveyor belt" circulation in small lakes (George and Edwards, 1976) leading to basin-scale phytoplankton aggregation. (B) Strong winds can result in dramatic tilts of thermocline, so the hypolimnion can upwell at the upwind end of lake, allowing ventilation of deep waters.

Upwelling and Wedderburn number

Under strong winds, deep hypolimnetic waters can upwell to the surface of lakes (Fig. 12B). This allows deep waters to ventilate directly to atmosphere, so that briefly the surface layer is in contact with deepest regions of lakes. In eutrophic lakes with low DO at depth, this can have positive and negative impacts—positive in that deep waters can increase their oxygen levels (Reiss et al., 2020), while negative effects include fish kills due to drops in dissolved oxygen in surface waters at edges of lakes (Rao et al., 2014). Upwelling of cold water can also influence temperatures in shallow regions of large lakes (Hlevca et al., 2015; Flood et al., 2021b). Regions with persistent downwelling will generally have stable surface water temperatures.

The fundamental physics of upwelling magnitude are explained by the Wedderburn number (Stevens and Lawrence, 1997). The Wedderburn number, W, is defined as the ratio of the baroclinic restoring force to wind stress:

$$W = -\frac{g}{\rho_o}\frac{\Delta\rho\, L}{u^{*2}}\frac{L}{Fetch} \tag{6}$$

where $\Delta\rho$ is the density difference between the upper and lower layers (kg m^{-3}); L is the thickness of the upper mixed layer (thermocline depth in m); *Fetch* is the basin length-scale (m); and u* is the water-side wind friction velocity (m s^{-1}) defined as $u^* = \sqrt{(\rho_{air}/\rho_{water})C_D U_{10}^2}$ where ρ_{air} is the density of air (1.225 kg m^{-3}) and ρ_{water} that of water ($\sim$1000 kg m^{-3}); C_D is the drag coefficient between air and the water surface ($\sim 1.3 \times 10^{-3}$); and U_{10} is the wind speed measured 10 m above the water surface in m s^{-1} (Flood et al., 2021a,b).

The way Eq. (6) is written, the Wedderburn number can be seen to be related to a bulk Richardson number multiplied by the aspect ratio of the surface mixed layer.

A smaller W corresponds to a greater influence on the waterbody from wind stress, and hence a more severe thermocline tilt. When wind forcing is strong enough and long enough (greater than one-fourth of the fundamental mode period), complete upwelling can occur where the thermocline breaches the surface. The degree of upwelling due to wind driven forcing is inversely related to W as

$$\Delta L/L = 2/W \tag{7}$$

where ΔL is the degree of upwelling measured at one end of the basin (Stevens and Lawrence, 1997; Coman and Wells, 2012). An upwelling of ΔL at the upwind end results in a downwelling of ΔL at the downwind end, resulting in a cross-basin thermocline deflection of $2\Delta L$. Thus, full upwelling is expected when $W = 0.5$. However, experiments in rectangular basins show that the thermocline becomes nonlinear and curves up near the edges, leading to full upwelling at $W \approx 1$ (Shintani et al., 2010).

Wind driven upwelling events can strongly influence surface water quality and fish habitat in the surface waters of large lakes. For instance, persistent diurnal winds, mean that the upwind end of the 7 km long Hamilton Harbour basin experience frequent hypoxia as cooler hypolimnetic water are driven to the surface (Flood et al., 2021a,b). This upwelling in turn influences the depth distribution of fish located in surface mixed layer (Brooks et al., 2022). In larger lakes, upwelling is also influenced by the Coriolis force, and similar thermal and DO variability occurs in near shore regions of Lake Michigan (Troy et al., 2012), in Lake Erie (Jabbari et al., 2021) and in Lake Geneva (Reiss et al., 2020). Such upwelling is often associated with pulses of nutrients from the hypolimnion to epilimnion that can fuel algal blooms.

Conclusions/synthesis

The mixed layer of lakes is dynamic, and active mixing can often be confined to a layer much shallower than the depth of the thermocline. The vertical distribution of mixing in turn determines the vertical distribution of plankton within the surface layer, as well as other buoyant material such as microplastics. In order to capture the mixed layer dynamics, it is important that high resolution and high frequency temperature measurements be made in the surface of lakes. With modern thermistors this is now feasible. Historically the thermal profile in lakes may have only been measured weekly or even monthly, which was adequate to track evolution of seasonal thermocline, but made it hard to appreciate the rich dynamics at play in this critical region of lakes.

Knowledge gaps

- There is a need for more high-frequency and high-resolution measurements of physical properties in the mixed layer to better interpret distribution of plankton and gases. Standard measurements with 0.1 °C accuracy for temperature will miss much of the dynamics.
- The whole water column of a polymictic lake is essentially the surface layer. Mixing will also be highly episodic, with many periods where water column has weak stratification. The frequency of active mixing in such lakes needs to be better understood.
- The role of surface layer mixing in blue-green algae aggregation and potential to lead to harmful algal blooms is a key area to study.
- Due to challenges of working from boats, there is a bias towards field work in calm conditions, and there are far fewer measurements of mixed layer conditions during energetic conditions. Moored systems of autonomous underwater vehicles should be used in future studies to fill these gaps.
- The process of wind and waves driving Langmuir circulations has not been systematically studied in lakes. While there is some research in the ocean, a key difference is the smaller scale of lakes, which are likely fetch limited.
- The energy transfer between the wind and various surface mixed layer processes such as wind waves, near-surface currents, and turbulence is still not well-understood. This has important implications for the ability of models to estimate surface layer gas exchange, transport, and dispersion.

Case studies

Lake	*Country*	*Coordinates*	*Main Topic*	*Key Reference*
Lake Michigan	United States	42°42′30″N, 87°3′52″W	Lateral dispersion in surface mixed layers of a large lake	Choi et al. (2020)
Lake Opeongo	Canada	45°40′N; 78°22′W	Influence of weak stratification upon turbulence	Pernica et al. (2013)
Clear Lake	United States	39°00′N, 122°45′W	Episodic mixing in polymictic lake	Cortés et al. (2021)
Lake Pleasant, New York	United States	43°28′N; 74°23′W	Turbulence in a temperate lake during fall cooling	Tedford et al. (2014)
Lake Superior	United States	47°30′N; 89°40′W	Convection in spring warming	Austin (2019)
Lake Michigan	United States	43°04′N; 87°45′W	Seasonal variations in deep-water mixing; Convection in spring warming	Cannon et al. (2019, 2021)
Lake Opeongo	Canada	45°40′N; 78°22′W	Plankton aggregation in mixed layer	Cyr (2017)
Lake Erie and Lake Ontario	Canada/United States	42°40′N; 81°30′W 43°30′N; 78′W	Microplastics distribution in surface layer	Mason et al. (2020)

CDT acknowledges support from the US National Science Foundation, Division of Ocean Sciences, Physical Oceanography and Biological Oceanography Programs (Grant 1658156).

See Also: Fundamental concepts and theories: Temperature as a Driving Factor in Aquatic Ecosystems; Structures and functions of Inland Waters - Lakes: Bottom Boundary Layers; Currents in Stratified Water Bodies: Internal Waves; Currents in Stratified Water Bodies 1: Density-Driven Flows; Currents in Well-Mixed Layers; Lacustrine Phosphorus Cycling

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Relevant websites

https://desc.ca/data/thelma—Environmental Lake Monitoring Ark (THELMA).
https://lexplore.info/—Real time data of the surface layer in Lake Geneva.
https://www.eoas.ubc.ca/~rich/#LIM—Matlab toolbox.
https://gleon.org/research/projects/lake-analyzer—Matlab and R code package.

Bottom Boundary Layers

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Buoyancy frequency A measure of the strength of stratification, which is proportional to the vertical gradient in water density. In the simplest cases, if a parcel of fluid is displaced vertically through stable stratification and then released, it will bob up and down with the buoyancy frequency (neglecting added mass and friction). Frequencies of free internal waves never exceed the buoyancy frequency.

Diffusion Molecular diffusion is the mixing resulting from random thermal motions of molecules, leading to chemical fluxes from high concentration to low. Turbulent diffusion, by analogy, is the mixing resulting from random turbulent motions of fluid parcels, usually leading to chemical fluxes from high concentration to low. The magnitude of the turbulent flux depends in a complex manner on the properties of the turbulent flow.

Diffusive Boundary Layer (DBL) Thin (order 1-mm-thick) bed-adjacent layer, within which molecular diffusion dominates chemical fluxes (in contrast, turbulence dominates chemical fluxes above the diffusive boundary layer).

Inner turbulent boundary layer Lower region of the turbulent boundary layer, where stratification, time-dependence of flows, Coriolis, boundary-normal variations in stress, and any possible effects of the water surface can be neglected. Within this layer, dimensional analysis yields many simple and useful theories for flows and mixing.

Isotherm A contour of constant temperature. In some lakes density is determined primarily by temperature, so that isotherms also correspond to contours of constant density.

Laminar flow Non-turbulent flow. Laminar flow can often be visualized as thin layers of fluid flowing over one another in an orderly manner.

Outer boundary layer The upper region of the boundary layer, where mixing and the frictional effects of the bed remain significant, but where the simplifying assumptions applicable to the inner boundary layer do not hold. Stratification, time-dependence, Coriolis, and boundary-normal variations in stress are often important in the outer boundary layer.

Richardson number A dimensionless number useful for estimating the effect of stratification on turbulence. Very low values (nominally, magnitude <0.05) indicate minimal local effect of stratification, whereas much larger values indicate significant

effect. The gradient Richardson number, which is one of several forms of Richardson number often used, is defined as the squared ratio of the buoyancy frequency to the velocity shear (velocity shear is the vertical gradient of velocity).

Reynolds number A dimensionless number, often useful for evaluating the damping of turbulence by molecular viscosity. For sufficiently low values of Reynolds number flows are laminar, whereas for higher values flows are turbulent. The Reynolds number equals fluid velocity multiplied by a length scale and divided by the kinematic molecular viscosity. A variety of length scales are chosen for application to various flows, and the minimum Reynolds number required for turbulence varies depending on this choice.

Stratification In a stratified fluid, density varies in the vertical (strictly, after accounting for adiabatic compression). In "freshwater," density gradients often result from temperature gradients, although salinity and suspended sediments can also play a role. Stratification can be stable (dense fluid under light), in which case turbulence is inhibited, or unstable (light fluid under dense), in which case turbulence is often enhanced by free convection.

Turbulence Fluctuations in fluid flows, which appear random, taking the form of swirling eddies and gusts. Unless inhibited by viscosity or stratification, turbulent eddies often become energetic as they draw energy from more deterministic background flows (such as waves or steady currents). Above thin viscous and diffusive layers, turbulence is responsible for most boundary layer mixing.

Viscous sublayer A thin (order 1-cm-thick) bed-adjacent layer within which molecular viscosity dominates the vertical mixing of momentum (in contrast, turbulence dominates momentum fluxes in overlying layers).

Introduction

The bottom boundary layer and its sublayers

The bottom boundary layer (BBL) is a region of relative rapid mixing overlying lakebeds, riverbeds, and seabeds. A surface boundary layer, also characterized by rapid mixing, often extends downward from the water surface. Between these two boundary layers, vertical mixing is sometimes relatively inhibited in a stratified interior (Fig. 1, left). This article introduces the flows and mixing processes found in BBLs.

BBLs may extend only a small distance from the bed, and occupy only a small fraction of the total basin volume. Nevertheless, BBLs play a vital role in lakes and many other aquatic systems. For example, oxygen consumption, denitrification, and methane production are often intense within lakebed sediments, and BBL mixing is responsible for associated chemical fluxes between sediments and overlying waters. BBLs also influence the habitats of benthic organisms, and are the location of much sediment transport. BBL mixing may influence currents, even currents above the BBL. Finally, BBLs (together with surface boundary layers) are often the regions where most dissipation of mechanical energy occurs.

A variety of BBL flow regimes is found in natural lakes and rivers, depending on stratification and water velocity. We first consider conditions common in temperate lakes during summer, for which BBLs can sometimes be divided into four layers (Fig. 1, right). First is a thin "Diffusive Boundary Layer" (DBL), which extends just a millimeter or so above the bed. Within this layer chemical gradients are particularly intense, because chemical transport is limited to the very weak process of molecular diffusion. Next is a "viscous sublayer," extending about a centimeter upwards from the bed. Within this layer, turbulence is dissipated by molecular viscosity, so flow is almost laminar. Above the viscous sublayer is an inner turbulent boundary layer, extending tens of centimeters from the bed, within which swirling turbulent eddies rapidly mix chemicals, heat, and sediments. In this inner turbulent layer,

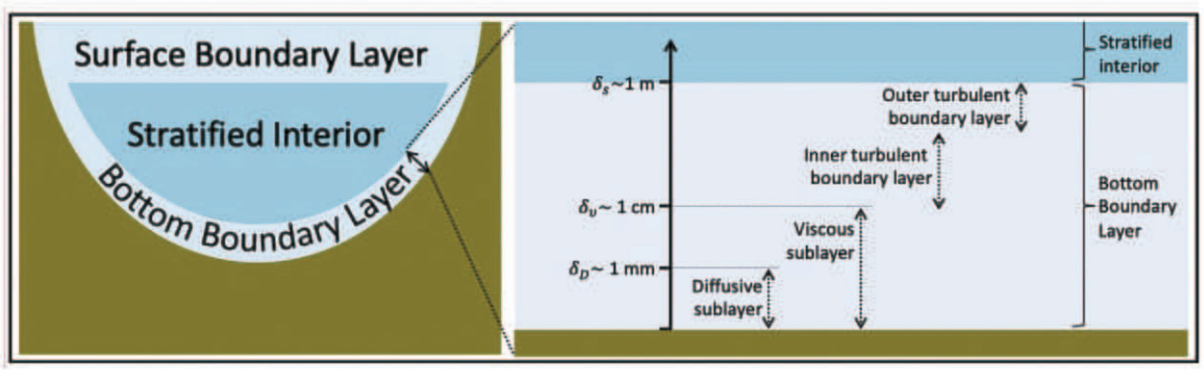

Fig. 1 Left: The bottom boundary layer is a near-bed region of rapid mixing found in many inland waters, often bounded above by a stratified interior where vertical mixing is greatly inhibited. Right: The bottom boundary layer can be divided into several layers, each characterized by different mixing processes. The layers shown, and the order-of-magnitude layer thicknesses, are observed under cm s^{-1} currents in some small stratified lakes. However, across a range of environments, the thickness of layers can vary greatly (note logarithmic vertical scale), and in some environments some layers can be absent.

stratification is too weak to directly inhibit the relatively intense turbulence. In contrast, in the overlying outer turbulent boundary layer, turbulence is progressively more inhibited by stratification with increasing elevation, until finally the stratified interior is reached a meter or more above the bed. The layers described above often lack sharp boundaries and their thickness varies greatly with flow speed, stratification, bed slope and flow direction. Additional layers can be introduced to account for factors such as Coriolis and benthic vegetation, and some layers vanish entirely in certain flow regimes.

After briefly introducing BBL mixing processes (Section "Overview of mixing processes"), we describe the inner turbulent boundary layer (Section "The inner turbulent layer"). We then consider the viscous and diffusive layers underlying the inner turbulent layer (Section "Viscous and diffusive sublayers"), before describing the overlying outer boundary layer (Section "The outer turbulent layer"). We end by examining interactions between BBLs and overlying waters, as well as a range of factors that can cause departures from the simple four-layer description (Section "Additional considerations"). Such departures are particularly common in high- and low-energy environments, and may also result from unsteady flows, Coriolis, or the presence of aquatic vegetation.

Overview of mixing processes

Within the BBL, the various layers outlined above are each defined by a dominant mixing process. Therefore, we first introduce the most important mixing processes, which include molecular diffusion and turbulent stirring.

Random thermal motions lead to molecular diffusion. For example, a chemical diffuses downward if its concentration C increases with increasing elevation above the bed z. Such downward diffusion is common for chemicals such as Oxygen and Nitrate, which are consumed in the sediments (gradients and fluxes reverse for chemicals such as methane, which are produced in the sediments). Similarly, momentum diffuses downward if the water velocity u increases with increasing elevation above the bed. Such downward diffusion of momentum is common in BBLs, because the water velocity often declines as the bed is approached, owing to bottom friction. Downward momentum diffusion can also be viewed as the frictional force exerted on underlying waters by overlying waters, and is usually expressed as horizontal force per unit horizontal area (units: Pa). The downward flux of chemical F_m and momentum τ_m resulting from molecular diffusion obey

$$F_m = D_m \frac{\partial C}{\partial z} \tag{1a}$$

$$\tau_m = \rho \nu_m \frac{\partial u}{\partial z} \tag{1b}$$

where ρ is the water density, while the effectiveness of molecular mixing is quantified by the molecular diffusivity D_m and viscosity ν_m ($m^2 s^{-1}$). Molecular mixing transports momentum much more effectively than chemicals ($\nu_m \approx 0.8 - 1.7 \times 10^{-6}$ m^2 s^{-1}, whereas for many chemicals $D_m \sim 10^{-9}$ m^2 s^{-1}, where '$\sim$' indicates order-of-magnitude). This result is summarized by the molecular Schmidt number, defined by $S_{cm} = \nu_m / D_m$, which is often $\sim 10^3$.

Random motions associated with turbulent eddies are responsible for additional mixing. Turbulence is often distinguished from more deterministic currents by a process of "Reynolds averaging"—that is, quantities such as water velocity are averaged across a series of turbulent eddies, and turbulence is defined as the departure from the averaged flow. Similarly, other quantities such as chemical concentration and water density can also be separated into a Reynolds-averaged part and a turbulent fluctuation. Reynolds-averaging is represented by an overbar, so the Reynolds-averaged concentration and velocity are $\bar{C}$ and $\bar{u}$. Turbulent mixing is more complex than molecular mixing. Nevertheless (given $\partial \bar{C}/\partial z \neq 0$ and $\partial \bar{u}/\partial z \neq 0$), it is always possible to define a turbulent diffusivity D_T and a turbulent viscosity ν_T by

$$F_T = D_T \frac{\partial \bar{C}}{\partial z}, \tag{2a}$$

$$\tau_T = \rho \nu_T \frac{\partial \bar{u}}{\partial z}, \tag{2b}$$

where F_T is the mean downward turbulent chemical flux, and τ_T (called the "Reynolds stress") is the mean downward turbulent momentum flux. Unlike D_m and υ_m, which are properties of the fluid, D_T and ν_T (also called the "eddy diffusivity" and "eddy viscosity") are properties of the turbulent flow, and vary greatly with time and location. The relative effectiveness of momentum and chemical mixing is measured by the turbulent Schmidt number $S_{cT} = \nu_T / D_T$.

The total chemical flux F is the sum of molecular and turbulent components, i.e., $F_m + F_T$. Similarly, the total momentum flux τ is $\tau_m + \tau_T$. The total downward momentum flux is transferred to successively lower layers, and ultimately transferred to the bed. The resulting bed-parallel force, expressed per unit area of bed, is called the "bed stress" and denoted τ_b.

Turbulent mixing dominates over molecular mixing (i.e., $D_T \gg D_m$ and $\upsilon_T \gg \upsilon_M$) in the inner and outer turbulent layers (Sections "The inner turbulent layer" and "The outer turbulent layer"). Conversely, molecular mixing of chemicals dominates over turbulence ($D_m \gg D_T$) in the diffusive layer, while molecular mixing of momentum dominates over turbulence ($\upsilon_M \gg \upsilon_T$) in the viscous sublayer (Section "Viscous and diffusive sublayers").

Turbulent mixing is often affected by stratification, i.e., by vertical gradients in water density. Specifically, turbulence is inhibited in the case of "stable stratification," when denser waters underly lighter waters, whereas turbulence becomes more energetic in the 'unstable' case, when lighter waters underly denser waters. The effect of stratification on turbulence is often large in the outer

boundary layer, but small in the inner layer. The turbulent Schmidt number is likely about 0.7 in unstratified flows, but substantially exceeds 1 in stably stratified flows (Smyth et al., 2005). In many lakes, density stratification is controlled by temperature. However, sediment suspension and salinity also affect density, and sometimes play a major role.

The fluxes τ and F have great practical importance. For example, the stress τ_b exerted on the bed by the overlying water flow is responsible for mobilizing sediments, and therefore is fundamental to the study of sediment transport. Furthermore, the equal and opposite force exerted by the bed on the overlying flow is a primary mechanism for dissipating currents, of importance to physical limnology. In addition, chemical fluxes F often play vital roles in biogeochemical cycles. Therefore, a recurring theme of this article will be the examination of relationships between the fluxes τ and F and more easily measured quantities such as $\bar{u}$ and $\bar{C}$. Such relationships aid the understanding of BBL dynamics, while providing useful tools for flux estimation from measurements.

The inner turbulent layer

Bed stress and the logarithmic velocity profile

Stress varies continuously with elevation, so the Reynolds stress τ_T must approach the bed stress τ_b at elevations sufficiently near the bed (but above the viscous sublayer). This section describes the turbulent "constant stress layer," which is the lower part of the turbulent BBL within which $\tau_T \approx \tau_b$ (so τ_T and τ_b can be used interchangeably throughout this section). It will be convenient to re-express stress in units of m s^{-1} by defining the "friction velocity" u_* as

$$u_* = (\tau_b/\rho)^{1/2}, \tag{3}$$

where ρ is water density.

To analyze the vertical variability of mean velocity, note that $d\bar{u}/dz$ may depend on τ, ρ and z. In the simplest cases, other variables can be neglected and the only dimensionally consistent possibility is for $d\bar{u}/dz$ to be proportional to u_*/z. This is usually written

$$\frac{d\bar{u}}{dz} = \frac{u_*}{\kappa z}, \tag{4}$$

where the empirical "von-Karman constant" $\kappa \approx 0.4$. Vertical integration yields the well-known "law-of-the-wall" logarithmic velocity profile (Fig. 2, left)

$$\bar{u} = \frac{u_*}{\kappa} \log\left(\frac{z}{z_0}\right), \tag{5}$$

where *log* denotes the natural logarithm, and the constant of integration is incorporated into the "roughness length" z_0, which is discussed in Section "Viscous and diffusive sublayers". Manipulating (3) and (5) yields

$$\tau_b = \rho u_*^2 = C_D \rho \bar{u}^2, \tag{6}$$

where the bottom drag coefficient $C_D = [\kappa/\log(z/z_0)]^2$. The bottom drag coefficient depends on flow speed or bed roughness, and on elevation above the bed, but in many practical cases with velocity measured tens of centimeters above the bed, C_D ranges between 1×10^{-3} and 4×10^{-3}.

Further dimensional analysis yields useful scalings for mixing rates. Multiplying (4) by $\rho\kappa u_* z$, and using (2b) and (3) yields

$$\nu_T = \kappa u_* z. \tag{7}$$

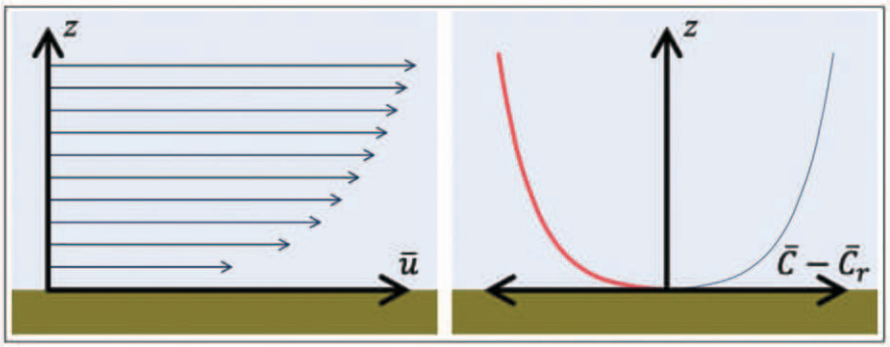

Fig. 2 Logarithmic profiles of mean velocity (left) and chemical concentration (right, with arbitrary near-bed reference concentration $\bar{C}_r$ subtracted), as predicted by inner turbulent layer theory. For chemicals that are consumed in the bed (e.g., O_2), the turbulent flux F_T is directed towards the bed, and concentration increases with elevation (thin blue curve, right panel). Conversely, for chemicals that are produced within the bed (e.g., CH_4), the turbulent flux F_T is directed away from the bed, and concentration decreases with elevation (thick red curve, right panel).

Therefore, the effectiveness of turbulent mixing, as measured by eddy viscosity, increases with flow speed (from 5 and 7) and with elevation above the bed. Furthermore, since $S_{cT} \approx 0.7$ in unstratified regions (Section "Overview of mixing processes"), similar scaling is expected for the eddy diffusivity ($D_T \approx 0.6 u_* z$, where we have used $\kappa/0.7 \approx 0.6$). Assuming a constant chemical flux F, as is expected in steady state without chemical sources or sinks, and vertically integrating (2a) then yields a logarithmic profile for chemical concentration (right panel, Fig. 2).

Additional useful scalings can be found for inner boundary layer turbulence. The turbulent kinetic energy scales with u_*^2, and velocity fluctuations with u_*. The rate of dissipation of turbulent energy is $\varepsilon = u_*^3/\kappa z$ (W kg^{-1}). This dissipation is balanced at all elevations by turbulent production, which is the energy turbulence extracts from the mean flow. We refer to the results of this section collectively as inner turbulent layer (ITL) theory.

Applications of inner turbulent layer theory

To illustrate the applications of ITL theory, consider fast and slow flows of 20 cm s^{-1} and 2 cm s^{-1}, measured at $z = 1$ m above the bed with a bottom roughness $z_0 = 0.5$ mm. In fast and slow cases, $u_* = 1$ cm s^{-1} and 1 mm s^{-1} respectively (from 5), with corresponding $\tau = 10^{-1}$ Pa and 10^{-3} Pa (from 3). Analysis based on the "Shields parameter" (which compares bed stress with the gravitational force resisting sediment motion, Fredsoe and Deigaard, 1992) suggests that the larger stress is sufficient to mobilize fine sand, whereas the smaller stress is insufficient to mobilize even fine silt (although conclusions for fine sediments may be modified by cohesive forces between grains, or by the very high porosity of some unconsolidated silty bottom layers). Further useful results can be derived concerning sediment suspension. Suspension cannot be maintained if a sediment's settling velocity w_s greatly exceeds the turbulent velocity fluctuations. Since velocity fluctuations scale with u_* (Section "Bed stress and the logarithmic velocity profile"), it follows that suspension cannot be maintained if the 'Rouse parameter' $w_s/\kappa u_*$ greatly exceeds 1. Therefore, given typical settling speeds of 6 mm s^{-1} and 0.3 mm s^{-1} for fine sand and silt respectively, only the faster flow can suspend much fine sand, whereas both flows can suspend silt for considerable time. From (7), eddy viscosities 1 m above the bed are $\upsilon_T = 5 \times 10^{-3}$ and 5×10^{-4} m^2 s^{-1}. Even the lower of these eddy viscosities exceeds molecular viscosity by a factor of hundreds, while turbulent diffusivity D_T exceeds molecular diffusivity by hundreds of thousands, highlighting the dominance of turbulent mixing over molecular diffusion.

An advantage of ITL theory is that stresses and mixing rates can be inferred from measured mean-flow profiles alone, without the need to resolve rapid turbulent fluctuations in velocity. From (5), plotting $\bar{u}/u_*$ against $log(z/z_0)$ yields a straight line (dark grey, Fig. 3A). Consequently, linear regression of measured $\bar{u}$ against $log(z)$ can be combined with (5) to yield estimates of u_* and bed stress. Numerous current meters can measure mean-velocity profiles, including Acoustic Doppler Current Profilers (ADCPs), as well as mobile impellor current meters or vertical arrays of Acoustic Doppler Velocimeters (ADVs).

In principle, just as measured and theoretical profiles of mean velocity can be compared to estimate Reynolds stress, measured and theoretical profiles of mean concentration can be compared to estimate chemical fluxes. Since only mean profiles are required, this approach would not require the high temporal resolution that is needed for alternative eddy covariance estimates (-Section "Applications, and general measurement of turbulent mixing"). Errors might result from the weakness of the chemical gradient in the turbulent layer (the most intense gradients are concentrated in the DBL, Section "Diffusive boundary layer"), although limited observations of boundary layer chemical gradients are encouraging (Deemer et al., 2015; Holtappels et al., 2011). To our knowledge this approach has not been applied to freshwater systems, but plausible fluxes have been obtained for marine (Takeshita et al., 2016) and atmospheric boundary layers.

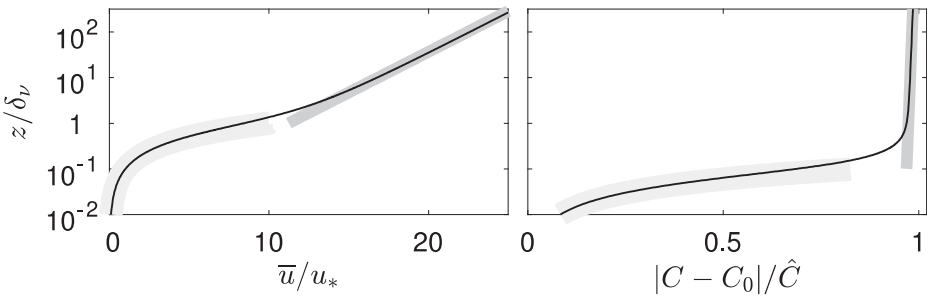

Fig. 3 Normalized vertical profiles of mean velocity (left) and chemical concentration (right). The normalized departure of chemical concentration from the value C_0 at the sediment-water interface is plotted in the right panel for a typical molecular Schmidt number $S_{cm} = 10^3$, neglecting chemical sources and sinks. Elevation normalized by viscous sublayer thickness δ_υ, velocity normalized by u_* (3), and chemical concentration normalized by typical change $\widehat{C} = 12 S_{cm}^{1/3} |F|/u_*$, appropriate for high S_{cm}, where F is the total chemical flux. Black curves are empirical profiles calculated following Deacon (1977). Thick light grey curves are viscous and diffusive models [from (8) and vertical integral of (1a)], whereas dark grey curves are logarithmic models applicable in the inner turbulent layer. Although viscous and diffusive sublayer profiles are linear, light grey lines appear curved owing to logarithmic vertical scale.

Limits to theory

Numerous factors cause departures from the attractively simple ITL theory. One complicating factor is time-dependence, which becomes particularly important for oscillating flows under surface waves with periods less than 10 s (Section "Time-dependent flows and wave bottom boundary layers"). However, ITL behavior can often be found sufficiently near the bed under long-period motions such as seiches. Stratification and Coriolis can influence outer-BBL motions (Sections "The outer turbulent layer" and "Coriolis"), but again ITL theory may apply sufficiently near the bed, especially if stratification is not too strong (although see section on Low Energy Environments). Even in unstratified flows, ITL theory applies over only a small fraction of the total water depth, partly owing to the constant-stress assumption. Finally, ITL analysis neglects molecular mixing, and consequently is inapplicable in viscous and diffusive sublayers.

Viscous and diffusive sublayers

Viscous sublayer

Turbulent mixing becomes weaker as the bed is approached (from 7). Sufficiently near the bed, turbulent mixing becomes so weak that molecular mixing dominates. Consequently, the analysis of Section "The inner turbulent layer", which neglected molecular viscosity, fails near the bed. For a smooth bed (i.e., without bottom roughness), more complete analysis shows that molecular viscosity becomes dominant at elevations much less than the viscous sublayer thickness (δ_v) with $\delta_v = 10\nu_m/u_*$. From (1b) and (3),

$$\bar{u} = \frac{10u_* z}{\delta_v} \tag{8}$$

in the viscous sublayer. Observations show a gradual transition between the linear profile (8) for $z \ll \delta_v$ and the logarithmic profile (5) for $z \gg \delta_v$ (Fig. 3A; observations also indicate $z_0 \approx 0.013\delta_v$). Natural beds are not perfectly smooth, owing to the presence of sediment grains, bedforms or benthic vegetation. However, if the height of roughness elements is substantially less than δ_v then smooth-bed results still apply. Larger roughness leads to complex, often-turbulent flows around roughness elements. Even for rough beds, ITL theory (Section "The inner turbulent layer") may apply far above the roughness elements. In such cases z_0 is proportional to the size of roughness elements, with the exact scaling depending on the element geometry.

Diffusive boundary layer

Molecular diffusivities are much smaller than molecular viscosity (i.e., molecular Schmidt numbers are very large, Section "Overview of mixing processes"). Consequently, although turbulent mixing is too weak to greatly affect momentum transport in the outer viscous sublayer (where z is only slightly less than δ_v), turbulent mixing remains significant compared with the very slow rates of molecular chemical diffusion except in the lower part of the viscous sublayer (where $z \ll \delta_v$). As a result, the most intense chemical concentration gradients are confined to a diffusive boundary layer whose thickness δ_D is much less than δ_v (Fig. 3B). Since chemical mixing is much slower in the underlying viscous and diffusive sublayers than in overlying turbulent layers, concentration gradients in overlying layers are relatively small. For smooth beds, $\delta_D \approx S_{cm}^{-\alpha}\delta_v$ where $0.25 < \alpha < 0.5$ (Deacon, 1977; Lorke et al., 2003; Lorke and Peeters, 2006).

Fig. 3B may appear to imply an increase in concentration with elevation, as expected for a downward chemical flux. However, if the flux reverses, the concentration gradient reverses (from 1a and 2a; note also the symmetry of red and blue curves in Fig. 2B). In Fig. 3B, upward- and downward-flux cases are combined in a single curve by plotting the absolute value $|C - C_0|$ on the horizontal axis.

Within the DBL the concentration profile is linear with slope determined from (1a), i.e., $C - C_0 = F_m z/D_m$, where C_0 is concentration at the sediment-water interface. Extrapolating this profile to the elevation δ_D at the top of the DBL yields the widely-used expression

$$F_m = (D_m/\delta_D)(C_u - C_0), \tag{9}$$

where C_u is concentration just above the DBL. Fast flows and energetic turbulence reduce DBL thickness (δ_D), leading to higher fluxes and higher within-layer gradients for a given $C_u - C_0$ (Lorke et al., 2003, Bryant et al., 2010, although C_0 may also vary with δ_D, e.g., Glud, 2008).

Several factors complicate analysis in some realistic cases. In addition to the diffusive flux, advection by groundwater flow can be significant in coarse sediments. Furthermore, bubbles emerging from sediments sometimes carry substantial fluxes of chemicals such as methane. Finally, filter feeders, burrowing benthic organisms and vegetation can all significantly enhance fluxes. Partly for these reasons, fluxes across the DBL often display substantial spatial variability (Glud, 2008).

Applications of viscous and diffusive boundary layer theories

To evaluate typical boundary layer thickness, consider $\nu_m = 1.1 \times 10^{-6}\text{m}^2\,\text{s}^{-1}$ and $D_m = 1.7 \times 10^{-9}\text{m}^2\,\text{s}^{-1}$, appropriate for dissolved oxygen and 15 °C. For $C_D = 2.25 \times 10^{-3}$, 2 cm s^{-1} flow gives $\delta_v = 1.3$ cm and $\delta_D = 1.5$ mm, whereas 20 cm s^{-1} flow gives $\delta_v = 1.3$ mm and $\delta_D = 0.15$ mm (using $\alpha = 0.33$).

Instruments have been developed that can resolve the thin viscous sublayer, and even the diffusive layer. For low-energy flows, specialized profiling Acoustic Doppler Velocimeters, which can resolve vertical profiles with mm vertical resolution, could provide estimates of bed stress using (8), although such measurement of velocity in the viscous sublayer is rare. Microprofilers can resolve profiles of chemical concentration with 0.1 mm vertical resolution, from which chemical fluxes can be estimated using (9). Such direct estimates of chemical fluxes are particularly valuable, although the spatial variability noted at the end of Section "Diffusive boundary layer" can be problematic.

The outer turbulent layer

Scaling stratified layer thickness

Above the inner boundary layer, stratification often inhibits turbulence. Consequently, although a logarithmic profile often fits measured mean velocity fairly well, direct measurements of Reynolds stresses and turbulent dissipation are sometimes found to be smaller than predicted by ITL theory (Holtappels and Lorke, 2011; Henderson, 2016). The influence of stratification on turbulence increases with increasing gradient Richardson number

$$Ri_g = N^2 / \left(\frac{d\bar{u}}{dz}\right)^2, \tag{10}$$

where the squared "buoyancy frequency" $N^2 = -(g/\rho)d\rho/dz$ measures the strength of stratification (N is also called the Brunt-Vaisala frequency). Where $|Ri_g| < 0.05$, stratification may have minimal effect on turbulence. In contrast, where Ri_g exceeds about 0.25–1, stratification inhibits turbulence so strongly that mixing becomes weak and intermittent.

A plausible scaling for BBL thickness δ_S (Fig. 1B) can be obtained using a "bulk Richardson number" $Ri_b = (\bar{N}\delta_S/\bar{u}_\infty)^2$, where $\bar{N}$ is vertically averaged across the BBL and $\bar{u}_\infty$ is above-BBL velocity [from (10), $Ri_b \sim Ri_g$ if $d\bar{u}/dz \sim \bar{u}_\infty/\delta_S$]. To understand the relevance of Ri_b, consider a thin BBL with $Ri_b \ll 1$, as may be created when flow suddenly accelerates. At such low Ri_b mixing is not inhibited by stratification, so the BBL will rapidly grow thicker, entraining waters from the overlying stratified interior. Initially, this thickening of the BBL rapidly increases Ri_b (because $Ri_b \propto \delta_S^2$; detailed analysis shows that mixing also often increases $\bar{N}$, further increasing Ri_b). However, the rate of BBL thickening slows dramatically when Ri_b reaches an order-one value, because stratification greatly inhibits further mixing. Therefore, in many natural cases, BBL thickness may adjust quickly towards order-one Ri_b (Trowbridge and Lentz, 1991). Requiring order-one Ri_b yields a very approximate scaling

$$\delta_S \sim \bar{u}_\infty / \bar{N}. \tag{11}$$

The ITL is limited to elevations far below δ_S. Given an upper velocity of 2 cm s^{-1} and a 10–10.5 °C temperature range, (11) suggests $\delta_S = 1$ m. Therefore, given the slow flows and significant stratification found in many small lakes, the outer BBL may reach only 1 m above the bed, and the applicability of the ITL theory is limited to elevations much less than 1 m. However, BBL thickness increases with increasing flow speed, and δ_S of several meters is common for more energetic flows, particularly in larger lakes. As expected from (11), the BBL is often relatively thick in the relatively weakly stratified hypolimnion (where $\bar{N}$ is small), and becomes thinner where the thermocline meets the sloping lakebed (Wüest and Gloor, 1998).

Modification of stratification by advection and mixing

The scaling (11) for BBL thickness is descriptive, but its predictive value is limited by the fact that $\bar{N}$ itself depends on BBL flows. For example, sheared BBL flows can modify stratification by tilting isotherms (Fig. 4). Consequently, above the sloping beds of many lakes, the oscillating flows of internal seiches alternately create and destroy BBL density stratification during downslope and upslope flows, a process called Strain-Induced Periodic Stratification (SIPS, Lorke et al., 2005). Similar oscillations are observed in chemical stratification, with implications for biogeochemical fluxes (Deemer et al., 2015). Upslope flows can even tip isotherms beyond vertical, creating overturns and free convection.

The net effect of SIPS on mixing is complex (Umlauf and Burchard, 2011). On the one hand, turbulence is enhanced by weak or unstable stratification during upslope flow, and suppressed by intensified stable stratification on downslope flow. On the other hand, mixing requires a gradient on which to act, and gradients are reduced during upslope flow, but increased during downslope flow. A further complication is that gravitational forces oppose the tilting of density contours, and these forces modify the sheared velocity profile that first tilted the contours. Other than the descriptive model (11), theoretical scalings for outer-BBL mixing and BBL thickness under SIPS are limited (although, see Brink and Lentz, 2010), and field validation is lacking.

Despite the complexity described above, some consistent patterns are observed. Specifically, mixing is relatively rapid and Ri_g is low near the bed, whereas mixing is weaker and Ri_g increases at higher elevations. Correspondingly, BBL isotherms often curve, from relatively bed-normal, indicating well-mixed conditions near the bed, towards more horizontal or bed-parallel in the outer BBL, indicating increasingly strong stratification (Fig. 4B). Intense concentration of stratification can create a step-like density jump, or "cap," at the top of the BBL (Wüest and Gloor, 1998). Despite these simple trends, detailed BBL observations in low-energy, stratified systems sometimes reveal complex behavior unrepresented by simple models (Fig. 5), highlighting a need for further research.

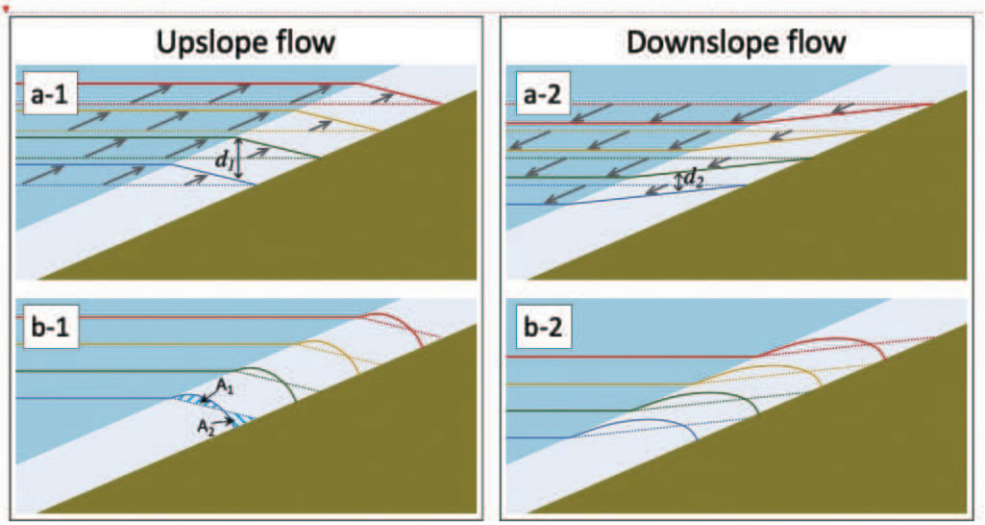

Fig. 4 Control of BBL stratification by advection and mixing above a sloping bed (in brown). For simplicity, development of stratification is illustrated as sequential stages of (A) advection and (B) mixing, although in reality these processes act simultaneously. Dotted and solid curves represent isotherms before and after each of the two stages, with warmer colored isotherms corresponding to higher temperatures. Panels a-1 and a-2: Bed-parallel flow displaces isotherms (grey arrows). Displacement, which is assumed uniform in the stratified interior (dark blue region), is reduced in the BBL (light blue region) where flows are slowed by bottom friction. This variable displacement tilts isotherms. Upslope flow reduces BBL stratification (large isotherm spacing d_1, panel a-1), whereas downslope flow increases BBL stratification (small isotherm spacing d_2, panel a-2). Panels b-1 and b-2: Mixing exchanges heat across the BBL, respectively warming and cooling the lower and upper regions of the BBL. Mixing is neglected in the stratified interior. Negligible heat transfer through the bed ensures that isotherms intersect the bed at right angles (also, since no heat is added to the BBL, areas A_1 and A_2 in panel b-1 must equal). Acting together, the combined processes of advection and mixing ensure that the final state (solid isotherms in panels b-1 and b-2) is more stratified after downslope-flow (b-2) than after upslope-flow (b-1).

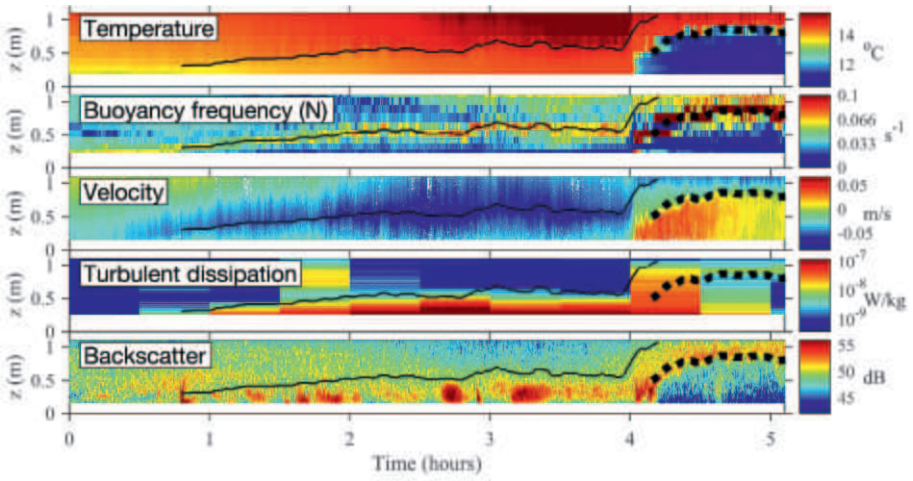

Fig. 5 Complex stratified BBL dynamics measured in small lake, where the thermocline base intersects the sloping lakebed (from Nielson and Henderson, 2021). In this lake, an internal seiche causes roughly two flow reversals each day. A 5.2-h interval around a reversal from downslope to upslope flow ($t = 4$ h) is shown. During downslope flow ($t < 4$ h), a warming bottom mixed layer (BML) develops, capped by a layer of high buoyancy frequency indicating intense stratification (solid black curve). The warming BML is a region of intense turbulence and sediment suspension (high acoustic backscatter), whereas stratification suppresses turbulence and suspension in overlying waters. At t = 4 h, the warming BML separates from the bed, owing to sudden arrival of an upslope-propagating dense cold BML (black dotted line marks the intensely stratified boundary between cold and warm layers). These observations, with BBL thickness often much less than 1 m, highlight the major stratification-induced departures from simple inner-BBL theory that can occur, even very near the bed, in low-energy stratified lakes.

Applications, and general measurement of turbulent mixing

Although ITL theories are inaccurate in the outer BBL, several instruments have been developed that can measure turbulence and associated fluxes across both inner and outer BBL regions. If turbulent fluctuations in bed-normal velocity w' and chemical concentration C' can be measured at the same location, then the turbulent chemical flux can be estimated as the mean of $C'w'$ (this approach is called "eddy covariance"). Similarly, the Reynolds stress is the mean of $\rho u'w'$, which can be measured at a point by ADVs (Holtappels and Lorke, 2011). Alternatively, some ADCPs can provide Reynolds stress profiles, particularly if "pulse coherent"

processing is used to provide low-noise velocity estimates (e.g., Henderson, 2016). However, estimating chemical fluxes is more challenging, because measuring rapid turbulent fluctuations in C' very near the velocity-measurement location, without disturbing the flow, requires streamlined fast-response probes, which are currently available for only a few chemicals (e.g., Oxygen). Nevertheless, eddy covariance has several advantages. Relative to DBL micro-profiles, eddy covariance estimates are less affected by small-scale spatial variability. Furthermore, relative to benthic flux chambers, eddy covariance is less likely to modify fluxes by disturbing mixing processes (e.g., Berg et al., 2013). Even where eddy covariance is unavailable, it may be possible to infer the flux of one chemical from the known flux of another (Holtappels et al., 2011). As turbulence becomes more intermittent in highly stratified (high Ri_g) cases, eddy covariance estimates often become noisy.

Quantification of turbulent dissipation provides useful information about mixing, and is feasible when eddy covariance estimates are unavailable. Even in strongly stratified (high Ri_g) environments, the dissipation of turbulent energy ε can be estimated from the small-scale variability in velocity or temperature (Klymak and Nash, 2010; Holtappels and Lorke, 2011; Simpson et al., 2015). When combined with models for stratified mixing, these measurements can be used to estimate turbulent diffusivity D_T (Klymak and Nash, 2010). Using estimated D_T, chemical fluxes could be estimated from relatively easily measured gradients of Reynolds-averaged chemical concentration, using (2b). In principle, this could generalize the chemical flux estimation method noted in Section "Applications of inner turbulent layer theory" to account for stratification, as may be valuable in inland waters where stratification often limits mixing, although to-date freshwater BBL applications are lacking.

Additional considerations

Time-dependent flows and wave bottom boundary layers

Time-dependence is most easily analyzed by considering an oscillating flow with velocity amplitude $\widehat{u}$ and period T, as might be observed under waves. The effects of friction on the oscillating flow are confined to a thin "wave bottom boundary layer" (WBBL), above which flow is depth-uniform. Above a smooth bed, turbulence is intensified in an unstratified WBBL if the Reynolds number $\widehat{u}^2 T/(2\pi\nu)$ exceeds about 1.6×10^5, whereas for substantially lower Reynolds numbers the WBBL is laminar. For example, oscillations with amplitudes of 0.05, 0.2 and 0.8 m s^{-1} transition to turbulence as wave period exceeds about 500, 30, and 2 s respectively. Therefore, the short-period, low-amplitude surface waves common in sheltered inland waterways often induce a laminar WBBL (boat wakes and rough beds can be important exceptions), whereas boundary layers induced by longer-period seiches and steady currents are often turbulent. The maximum WBBL bed stress is related to velocity by $\tau_{max} = \rho(f_w/2)\widehat{u}^2$, where the "friction factor" f_w plays a role similar to a drag coefficient. Friction factors depend on velocity, wave period, and bottom roughness, but often $0.02 < f_w < 0.2$ for wave periods of a few seconds, whereas lower values are common for longer periods (e.g., Fredsoe and Deigaard 1992, p. 23). In turbulent cases, unstratified WBBL thickness $\delta_T \approx \beta u_{* max} T$, where $\beta = \kappa/(2^{1/2}\pi) = 0.09$ and $u_{* max}$ is the maximum of u_* through the wave cycle. In laminar cases, WBBL thickness $\delta_T = (\upsilon_m T/\pi)^{1/2}$. Far inside turbulent wave boundary layers (when $z \ll \delta_T$, but above the viscous sublayer), time-dependence can be neglected and steady ITL theory provides a good approximation, except during brief intervals around flow reversals (although the inner BBL flow leads the outer BBL, e.g., Henderson, 2016). For long-period motions, stratification often causes large departures from the above scalings for δ_T (Section "The outer turbulent layer").

Coriolis

The earth's rotation can become significant when flows persist for more than a small fraction of a day. For steady flow over a planar bed, Coriolis leads to a limited BBL thickness δ_f, above which $d\bar{u}/dz$ and Reynolds stress approach zero. The resulting BBL is often referred to as a "bottom Ekman layer," and in the northern hemisphere flow spirals to the left as the bed is approached. Sufficiently near the bed ($z \ll \delta_f$), flow is nearly unidirectional (directed to the left of overlying velocity in the northern hemisphere) and ITL scaling applies. Above the ITL, flow is often affected by finite basin width or strain-induced stratification.

Accounting for Coriolis and strain-induced stratification over a sloping bed leads to "arrested Ekman layer" models. In such models, above-BBL currents flow parallel to bathymetric contours, so that Coriolis deflection induces sheared up- or down-slope BBL flows. These flows steadily tilt isotherms, resulting in a growing difference between the density of BBL and overlying waters. Gravity acts on this density difference, eventually bringing vertically integrated across-slope transport to a halt (Brink and Lentz, 2010). Departures from such simple planar-bed theories may result from lateral variability. Observations are lacking, although small leftward deflection of near-bed flows is often observed (e.g., Henderson, 2016).

High-energy environments

BBL thickness increases with increasing velocity and decreasing stratification (11). For sufficiently energetic cases the stratified interior can be eliminated, as the BBL overlaps with the surface boundary layer. Even in lakes with a stratified interior, the BBL can be unstratified in shallow regions, where total water depths are less than the surface mixed-layer depth.

Low-energy environments

Flows may be reduced to a few millimeters per second in small stratified lakes and ponds, and under ice. As speeds decrease, the viscous sublayer grows thicker (8), while the upper edge of the turbulent BBL approaches the bed (11). The resulting decline of δ_S/δ_v suggests a condition for the total elimination of the turbulent layers of the BBL, although field confirmation is lacking. In other physical settings, high-resolution numerical simulations show that BBL turbulence becomes very weak and intermittent in sufficiently slow stratified flows (e.g., Ruan et al., 2019). Furthermore, observations show a dramatic increase in DBL thickness, and associated near-shutdown of sediment-water chemical fluxes, when flows are very weak (Bryant et al., 2010). Such shutdown of BBL turbulence could significantly influence the biogeochemistry of low-energy regions.

In very slow flows, even weak stratification can have a major effect (11), and the stratification resulting from very low concentrations of salt or other chemicals often becomes important. Even small biogenic salinity fluxes from the sediments may shut down BBL turbulence in deep lakes (Wüest and Gloor, 1998).

Vegetated beds

In many natural waterways, aquatic vegetation greatly modifies near-bed flows. Key parameters describing vegetation geometry are n = number of stems per square meter of bed, d = mean stem diameter, and h = stem height. Given stem Reynolds number $\mathrm{Re} = \bar{u}d/\nu$ less than a few hundred, stem wakes are laminar, in which case vegetation shelters the bed and reduces mixing (although the vegetation itself can carry significant chemical fluxes). Conversely, given higher Reynolds numbers, stem wakes are turbulent and the influence of vegetation is more complex. For turbulent flows through sufficiently sparse canopies (water occupying >90% of total volume) of near-bed vegetation ($h \ll$ water depth), the reduction of steady currents within the canopy is governed by the parameter $\lambda = ndh$. Near-bed velocity is reduced only slightly when $\lambda < 0.1$, but is reduced greatly when $\lambda > 1$ (Nepf, 2012). Dependence of total near-bed turbulence on λ is therefore non-monotonic: stem wakes enhance near-bed turbulence as λ increases from zero to 0.2–0.3, but for much larger λ near-bed turbulence is reduced as the near-bed flow is reduced. Consequently, the relationship between turbulent energy and bed stress within vegetation canopies can depart from the standard ITL scaling. Sediment transport may scale with turbulent energy, rather than bed stress (e.g., Yang and Nepf, 2019). Similarly, vegetation-induced turbulence could cause departures from inner-layer relationships between stress and sediment-water chemical fluxes, although observations are lacking.

Interactions with above-BBL flows

The BBL can interact strongly with above-BBL motions. An example is provided by internal waves, which propagate throughout the stratified interior. Internal waves result from the action of gravity on tilted density contours, just as more familiar surface waves result from the action of gravity on a tilted water surface. Internal waves substantially displace isotherms while only slightly disturbing the water surface. Basin-wide internal waves ("internal seiches") are often particularly energetic, although a spectrum of higher-frequency internal waves is also often present. Internal waves may transport energy towards certain regions within lakes, causing hotspots of intensified dissipation (Thorpe, 1998). Particularly high BBL dissipation may occur where the bed slope approaches a 'critical slope' along which internal wave energy is propagated (Umlauf and Burchard, 2011). Intense mixing can also occur when internal waves break as they propagate into shallow depths (Thorpe, 1998).

Basin-wide flow patterns may further influence BBLs where dense inflowing river waters plunge down sloping lakebeds, creating bottom gravity currents. Dense bottom currents are also generated and when surface heat fluxes create particularly dense water in shallow regions, and after ice-on when sediments warm overlying bottom waters.

Through boundary-dominated mixing, BBL dynamics may modify above-BBL flows. Although the thin BBL often occupies only a small fraction of total basin volume, mixing may sometimes be so much more intense in the BBL than in the stratified interior that the BBL may be the location of most vertical mixing (Goudsmit et al., 1997). Theory suggests that remarkable, non-intuitive patterns of mean lateral advection could result, although observations are lacking (McDougall, 1989). The mechanisms for associated BBL-interior lateral exchanges are complex. Exchanges require boundary-parallel variability, because mass conservation ensures that water cannot flow out of the BBL everywhere. Several processes may generate such variability. Random small-scale mixing events, or other small-scale instability processes, may create well-mixed layers of water that slump into the interior under the influence of gravity (Thorpe, 1998). Larger-scale baroclinic instabilities can also generate BBL-interior exchanges (Wenegrat et al., 2018). More persistent exchange flows may be generated by variations in bed slope or background stratification (McDougall, 1989). Finally, the finite wavelengths of internal waves result in convergent boundary-parallel flows, which can periodically force boundary layer waters to separate from the bed (Thorpe, 1998, and Fig. 5). The relative importance of these various mechanisms is unclear.

Summary

In bottom boundary layers, chemicals and momentum are exchanged between sediments and overlying waters, with important implications for aquatic ecosystems. This exchange occurs through complex interactions between molecular diffusion, turbulent mixing, stratification, and advection. Simple theories successfully represent some of these processes, especially for energetic flows near planar beds. However, BBL dynamics are less well understood at higher elevations, in slow stratified flows, and in cases with strong lateral variability.

In the inner turbulent layer, the viscous sublayer and the DBL, simple models predict profiles of velocity and concentration, together with related fluxes. Using these models, fluxes can be estimated from measured profiles. For example, momentum fluxes are estimated by fitting logarithmic velocity profiles in the inner turbulent layer, and chemical fluxes are estimated by fitting linear concentration profiles in the DBL. Chemical fluxes could in principle be estimated by from profiles or gradients in concentration above the DBL, but to-date such applications appear to be limited to marine systems. Established techniques for non-invasive chemical flux estimation require instruments with exceptionally high resolution (sub-mm resolution for DBL studies, and sub-second resolution for eddy covariance). This restricts the set of chemicals for which fluxes that can be directly estimated.

In contrast to the lower regions of the BBL, simple models for stratified outer regions of the BBL are lacking. Important upper-BBL processes have been identified and described, but quantitative scalings have yet to be developed. Extensive research on SIPS in estuaries (e.g., Stacey and Ralston, 2005) and on the outer boundary layer in the atmosphere (Sections 4–6 of LeMone et al., 2018) may be relevant.

This article has focused on simple laterally-uniform cases, with minimal boundary-parallel variability. However, this simple description is sometimes complicated by boundary-parallel variability created by filter feeders, burrowing organisms, bottom roughness, vegetation or non-planar bathymetry.

Knowledge gaps

- Techniques such as flux chambers, diffusive boundary layer profiling, and eddy covariance have provided much useful information about chemical fluxes between sediments and overlying waters. However, for many chemicals, available techniques for flux estimation either disturb boundary layer mixing processes, or are affected by small-scale variability. Therefore, development of non-invasive flux estimation techniques for application to a broader range of chemicals may be valuable.
- In many low-energy flows, the inner boundary layer becomes very thin, while the outer boundary layer is strongly affected by stratification. Therefore, improved understanding of outer boundary layer dynamics, and development of corresponding simple models, may be valuable.
- Since mixing is so intensified in boundary layers, exchange of waters between boundary layers and the interior may influence the transport of heat and chemicals throughout stratified lakes. However, uncertainty remains concerning the relative importance of various proposed exchange mechanisms.

Important case studies

Name	*Country*	*Coordinates*	*Topic*	*References*
Lake Alpnach	Switzerland	46°57′ N 8°18′ E	Diffusive boundary layer	Lorke et al. (2003)
Lake Constance	Germany	47°83.99′ N, 9°81.89′ E	Turbulent boundary layer	Holtappels and Lorke (2011)
Lake Alpnach	Switzerland	46°57′ N 8°18′ E	Strain-induced stratification	Lorke et al. (2005)
Lacamas Lake	United States	45°37.19′ N 122°25.81′ W	Stratification and Coriolis	Henderson (2016)
Wakulla River	United States	30°12.83′ N 84°15.71′ W	Eddy covariance	Berg et al. (2013)

See Also: Fundamental concepts and theories: Temperature as a Driving Factor in Aquatic Ecosystems; Structures and functions of Inland Waters - Lakes: Currents in Well-Mixed Layers; Currents in Stratified Water Bodies: Internal Waves; Currents in Stratified Water Bodies 1: Density-Driven Flows; Lacustrine Phosphorus Cycling; Small-Scale Turbulence and Mixing: Energy Fluxes in Stratified Lakes; Surface Mixed Layers in Lakes

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Small-Scale Turbulence and Mixing: Energy Fluxes in Stratified Lakes☆

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This is an update of A Wüest, A Lorke, Small-Scale Turbulence and Mixing: Energy Fluxes in Stratified Lakes, In: *Encyclopedia of Inland Waters*, edited by GE Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00084-3.
This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Buoyancy flux, J_B Quantifies the change of potential energy in a water body caused by a vertical density flux and, by definition, it is opposed to the density flux. Therefore, a downward density flux is equivalent to an upward buoyancy flux which, in a stratified water column, makes surface waters lighter thereby reducing the potential energy. Turbulent mixing in a stratified water body produces a downward buoyancy flux (or upward mass flux), which increases the potential energy of the system.
Buoyancy Upward directed force per unit mass experienced by a water parcel having lower density than surrounding water.
Dissipation rate of temperature variance, χ_θ Rate at which small-scale fluctuations of temperature/heat created by turbulent eddies are extinguished by the smoothing effect of molecular diffusion. An equivalent concept applies to other properties and water constituents like dissolved solids (or salinity).
Dissipation rate of turbulent kinetic energy, ε The rate at which turbulent kinetic energy is dissipated to heat by internal friction caused by molecular viscosity (ν).
Gradient Richardson number, $\mathrm{Ri_g}$ Non-dimensional ratio between the stability, N^2, and the squared vertical shear of the horizontal flow velocity, $(\partial u/\partial z)^2$. It characterizes the tendency for the development of turbulence in a stably stratified water column, which is subject to vertical gradients of the horizontal currents u. A necessary condition for turbulence to occur is $\mathrm{Ri_g} < 1/4$.
Internal waves Oscillations of the internal layers of a stratified water body after a disturbance, e.g., driven by a wind event, due to the gravitational restoring force inherent to density stratification.
Mixing efficiency Non-dimensional ratio $\gamma_{mix} = J_b/\varepsilon$ expressing the rate of change of potential energy stored in the water column stratification (see buoyancy flux, J_b) relative to the rate of energy dissipation (ε).
Stratification Refers to the vertical gradient of density ρ in a water body, which confers stability by limiting vertical motions. It is quantified with the Brunt-Väisälä or buoyancy frequency (N, $\mathrm{s^{-1}}$), defined as $N^2 = -(g/\rho)\,(\partial\rho/\partial z)$, where g is the gravitational acceleration.
Thermocline The region in a stratified water body where the temperature changes significantly with depth, corresponding to the region of maximal stability (maximum N^2).
Turbulent diffusivity Proportionality factor relating the spatial gradients of a property, C, to its turbulent flux. The (vertical) turbulent diffusivity (K_z, $\mathrm{m^2\,s^{-1}}$) is defined in analogy to molecular diffusivity by using the First Fick's Law, $F_C = -K_z\,\partial C/\partial z$. Usually, turbulent diffusivity is much larger than molecular diffusivity, except in calm and extremely strongly stratified environments.
Turbulent flux Flux of a property C caused by the action of turbulent eddies within a fluid. Turbulent fluxes are directed from regions with high C values to regions with low C values, i.e., directed downgradient. This allows their expression in terms of a turbulent diffusivity, in analogy to the First Fick Law of molecular diffusion.
Vertical shear Vertical gradient of horizontal flow velocities, $\partial u/\partial z$.
Viscosity (kinematic), ν Internal friction arising between adjacent layers of fluid that are in relative motion.

☆*Change History*: August 2021. B Fernández Castro updated the abstract, text body, references, Figure 3 and added the glossary and Figures 4 and 5. Contributions from A Wüest and A Lorke.

Introduction

Nearly all lakes, reservoirs and ponds deeper than a few meters exhibit density stratification during at least part of the seasonal cycle due principally to the temperature-dependence of water density. During spring/summer—or the wet season in the tropics, when the air is warmer, particularly at nighttime—the water is heated from above and a surface layer (SL: typically a few m thick) with warmer and hence lighter water develops on top of the cooler and heavier water below (Fig. 1; Imberger, 1998). In addition, biological and hydrological processes may strengthen the density stratification by generating a vertical gradient of dissolved solids (salinity). The resulting stratification is usually depicted by a strong density gradient (also called pycnocline or metalimnion), separating the SL from the deeper part of the water column, which is more weakly stratified and referred to as hypolimnion (Fig. 1). Density stratification, as a consequence of heavier water laying below lighter water, causes a lowering of the center of mass of the water body below the center of volume by a vertical distance Δh_M. This lowering entails a reduction of the potential energy of the water body that can be approximated as $\Delta E_{pot} = H\rho g \Delta h_M$ (J m^{-2}) by considering a rectangular basin, where H is the average depth of the water body, g is the gravitational acceleration, and ρ is the density (Δh_M is negative because the center of mass is displaced downwards, and ΔE_{pot} is also negative).

Mixing of heavier water from greater depth with lighter water from the SL, implies movement of water parcels against the density gradient. A source of mechanical energy is required for this work. The amount of work needed to mix the entire water column is determined by $-\Delta E_{pot}$. Density stratification thus imposes stability on the water column and reduces—or even suppresses—vertical exchange restricting motions to occur along surfaces of equal density, i.e., mainly along the horizontal. The only exception to this constriction are small-scale turbulent eddies, which maintain a weak and continuous vertical mixing. In the absence of turbulent motions, the vertical exchange of properties would be driven exclusively by molecular diffusion operating on their mean vertical gradients, which is a very slow process. Small-scale turbulent eddies stir the water parcels, putting them in close contact with each other and enhancing the small-scale gradients, which are then eroded faster by molecular diffusivity (Fig. 2). In this way, turbulent fluxes are typically several orders of magnitude larger than expected from molecular diffusion alone.

Besides convective mixing in the SL, caused by seasonal or nocturnal surface cooling, the major source of energy for vertical mixing in lakes and reservoirs is wind, whereas river inflows usually play a minor role (Fig. 1; Imboden and Wüest, 1995). Wind-driven mixing within the stratified water body below the SL occurs indirectly through the excitation and dissipation of basin-scale currents. By blowing at the lake's surface, wind drives basin-scale surface currents that cause the stratified water body to pivot with warm water piling up at the downwind end (causing downwelling) and deep-water accumulating at the upwind end (causing upwelling). After the wind ceases, the water displacement relaxes and various types of internal motions and waves develop—including basin-scale seiches and gyres—inducing motion in the deepest layers. These large-scale currents eventually degenerate into turbulence and decay as a series of eddies that transfer the energy towards small scales, where it is dissipated as heat by viscosity. However, not all the turbulent kinetic energy is lost as heat, since turbulent eddies cause mixing of denser with lighter water, which effectively results in an upward mass flux raising the center of mass of the water body (Fig. 2).

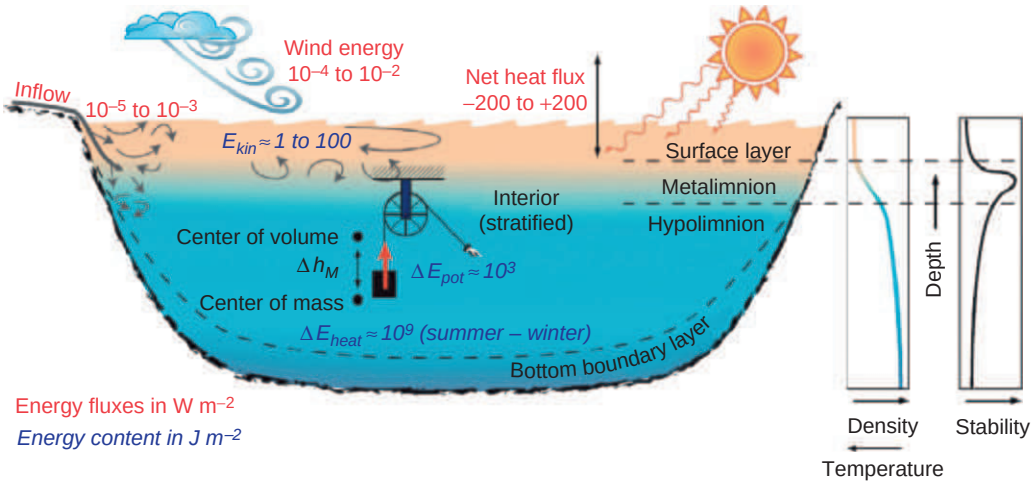

Fig. 1 Energy input (heat, wind, and river inflow; in red) to the water, expressed as fluxes (W m^{-2}) and energy content (heat, kinetic energy, potential energy; in blue) stored in the lake water body (J m^{-2}). Note that the energy fluxes and contents related to heat are many orders of magnitude larger than those of kinetic and potential energy. The effect of mixing by the river is only local and less effective than wind. The stratified part of the lake (below surface layer) has historically been divided into the metalimnion (large stability, right) and the deep hypolimnion (weak stratification) below. The lower water column can also be differentiated into the interior region (away from the boundaries), which is mostly quiescent except during storms, and the bottom boundary layer where turbulence is enhanced. Adapted from Imboden DM and Wüest A (1995) Mixing mechanisms in lakes. In Lerman A, Imboden D and Gat JR (eds.) *Physics and Chemistry of Lakes*, pp. 83–138, Springer-Verlag: Berlin.

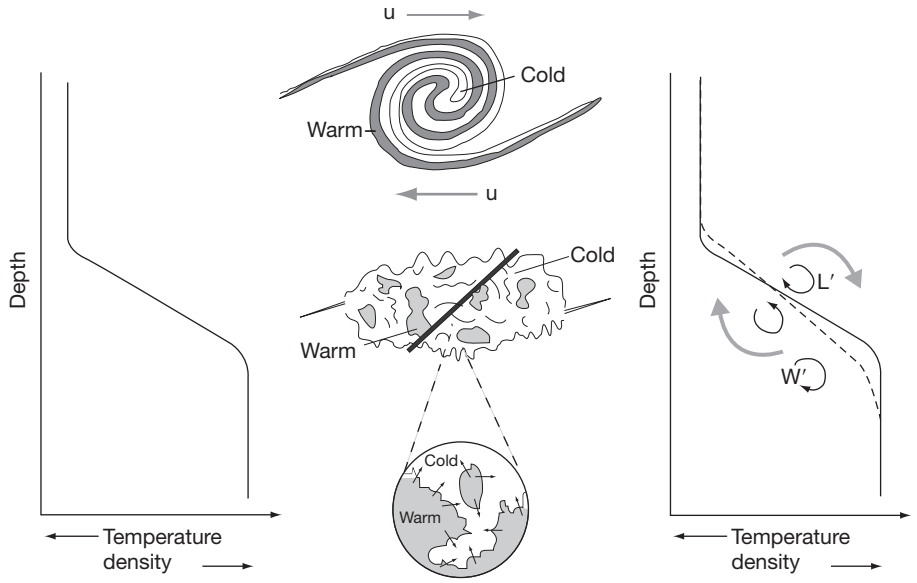

Fig. 2 The effect of turbulent mixing in a stable stratification: if the vertical gradient of horizontal currents (current shear $\partial u/\partial z$) is stronger than the stability of the water column (Eq. 2), Kelvin Helmholtz instabilities can develop (top of middle panel) bringing warmer (lighter) and cooler (heavier) water in close proximity (bottom of middle panel). Finally, heat (or any other water constituent) is mixed by molecular diffusion across the manifold small-scale interfaces, which are generated by turbulence. The turbulent exchange of small water parcels leads to a fluctuating vertical heat flux (Fig. 3) which averages to a net down-gradient (here downward) heat flux. As a result, the original temperature profile (left) is modified (right): the gradient is weakened and expanded vertically with heat transported from top to bottom, and density vice versa. This net upward mass transport results in rising the center of mass of the water body and requires energy supply. The energy needed for mixing is extracted from the kinetic energy of turbulent motions. Figure after the idea of Winters et al. (1995). Experiments were first performed by Thorpe (1973). The phenomenon of sheared stratification in lakes was reported by Mortimer (1952); and by Thorpe (1977).

In this article, we follow the energy pathways from wind stress at the air-water interface to the generation of mixing and vertical turbulent fluxes in the stratified interior of lakes. In the following sections, we address the dynamics of turbulence and mixing in terms of their energetics at the basin-scale and the key concepts describing their functioning at small scales. We focus particularly on the concept of turbulent diffusivity, which provides a quantitative measure of the intensity of turbulent fluxes, and we outline how to measure or estimate such fluxes. Next, we describe in more detail the different mixing mechanisms that operate in the surface and bottom boundaries, as well as in the interior of the water body. We end the chapter with a summary of the main points and open questions for future research.

Energetics and significance of mixing at basin-scale

Following the previous reasoning, vertical mixing in stratified lakes can be understood as a conversion of wind kinetic energy into potential energy stored in the density profile of the water body. Therefore, quantifying the pathways of energy inside lakes (i.e., performing an energy budget) is a useful, integrative approach to estimate the magnitude of turbulent fluxes in these systems. This approach has been adopted in a number of field studies (Wüest et al., 2000) and used to describe turbulent fluxes in one-dimensional lake models (Goudsmit et al., 1997). Field observations have shown that the energy pathways are rather indirect and leaky, diverting large amounts of energy towards heat by viscous dissipation at different steps. The first step of the energy transfer occurs at the air-water interface. Since water is 800 times denser than air and since momentum (and not energy) is conserved across the air-water interface, the SL receives only about 3.5% (or $1/\sqrt{800}$) of the wind energy from the atmosphere (30–300 mW m^{-2}), the remainder 96.5% being dissipated as heat in the atmospheric boundary layer. The majority of the flux transferred into the water body is either dissipated as heat in the surface boundary layer or transiently stored in surface waves, which get dissipated mostly in littoral regions, and their energy does not reach the stratified part of the water body (Wüest and Lorke, 2003). The remaining energy causes large-scale surface currents, with surface water flows with speeds of 5–30 cm s^{-1}, smaller compared to the wind velocity (2–20 m s^{-1}) (Wu, 2006), which trigger oscillatory displacements of the internal density interfaces, i.e., basin-scale internal motions. The mechanical energy reaching these deep-water currents is usually a small fraction (<1%, typically ~0.3% or <1 mW m^{-3}) of the wind energy flux from the atmosphere (Wüest et al., 2000; Fernández Castro et al., 2021). The velocities of deep-water currents are usually of a few cm s^{-1} (or ~1 J m^{-3}), one order of magnitude less energetic than those in the SL.

The internal flows decay by various processes (including friction at the lake bed, degeneration of internal waves by non-linear steepening or interaction with the slope, and shear instabilities in the interior of the water body), and their energy is dissipated by

viscous friction at rates of less than 1 mW m^{-2}. Direct turbulence measurements and indirect estimates of its effect (e.g., temporal changes in the density profiles, see "Quantification of Turbulent transport: Eddy diffusivity") show that the fraction of the turbulent kinetic energy spent in mixing against the stratification is ~10–15%, resulting in an increase of potential energy of the water body by 0.01–0.05 mW m^{-2} (Wüest et al., 2000, Fernández Castro et al., 2021). Therefore, about 0.03% of the wind energy flux is stored as potential energy. Compared to the energy required to fully overcome stratification (order of 1000 J m^{-2}; Fig. 1), it would take much longer than one season to entirely mix a moderately deep lake. This implies that wind energy input can impact the vertical density structure at times of weak stratification (beginning of the season), whereas the wind is not able to substantially change the vertical structure once the strong seasonal stratification is established. Therefore, in most regions on Earth, only very shallow waters, less than a few meters deep (such as Lake Balaton, Hungary) are found to be entirely non-stratified during the warm/wet season. The majority of lakes and reservoirs, deeper than a few meters, are thus only "partially" mixed to a limited depth, which defines the SL thickness. For those lakes that show a well-mixed SL, its maintenance is mostly supported by nighttime cooling. In this article, we focus on the "limited" mixing below the SL, which occurs in the metalimnion and hypolimnion (Fig. 1). This mixing is vital for the functioning of the ecosystem as it plays an important role in a number biogeochemical processes affecting the water quality: resuspension of sediment particles, the exchange of substances between the sediment and water, the supply of oxygen towards anoxic or suboxic regions, and the uplift of nutrients towards the photic zone, among others.

Small-scale turbulent mixing

The same concepts of stability and mixing—described in the preceding sections for the entire water body—also apply locally within the water column for small-scale vertical mixing of stratified layers. Local stability of the density stratification is quantified by the Brunt-Väisälä frequency (also buoyancy frequency) N (s^{-1}), defined (in its squared form) by:

$$N^2 = -\frac{g}{\rho}\frac{\partial \rho}{\partial z} \tag{1}$$

where g is gravity (≈9.81 m^2 s^{-1}), ρ is water density, and z is depth (positive upward). When the water body is set in motion by the wind, horizontal flow velocities (noted as u) develop within the fluid. Because of wind-forced motions, a vertical gradient of the horizontal current u (shear, $\partial u/\partial z$) is superimposed on the vertical density gradient $\partial \rho/\partial z$. Depending on the relative strength of N compared to $\partial u/\partial z$, stratified shear flows may eventually become unstable and develop into turbulence (Fig. 2). The tendency of a stratified flow towards instability (i.e., transition from a horizontal current to turbulence) is described by the gradient Richardson number,

$$Ri_g = N^2/(\partial u/\partial z)^2 \tag{2}$$

and the transition to turbulence is expected for low Ri_g values <1/4. Once established, turbulence transfers kinetic energy from basin-scale motions (~km) towards progressively smaller eddies until it is dissipated by viscous friction at the smallest possible scales (~cm). Turbulent eddies stir the water parcels, enhancing the small-scale gradients of density and other properties (Fig. 2). These small-scale gradients are smoothed by molecular diffusion. The effect of turbulence is thus to homogenize (i.e., mix) the water properties.

Although the large-scale (advective) motions are mainly horizontal, the turbulent eddies are associated with random velocity fluctuations in all three dimensions (u', v', w'). Turbulent kinetic energy (TKE; J kg^{-1}) is defined as the energy per unit mass of water that is contained in these velocity fluctuations:

$$\mathrm{TKE} = \frac{1}{2}\left\langle u'^2 + v'^2 + w'^2 \right\rangle \tag{3}$$

The intensity of turbulent motions and the energy transferred towards small-scales are described by the rate at which TKE is dissipated by viscosity and represented as ε (m^2 s^{-3} = W kg^{-1}). The intensity of turbulent mixing of scalar properties (such as temperature or density) is quantified by the rate of dissipation of small-scale gradients (or variance) by molecular diffusion, and represented by χ. This rate of variance smoothing is proportional the molecular diffusivity of the considered property (D_C, where C represents the property) and the small-scale variance of the gradients induced by turbulent stirring, $\chi \sim D_C\ (\partial C'/\partial z)^2$. It thus depends on the molecular characteristics of the property, through the value of D_C, and on the intensity of turbulence, through the generation of small-scale gradients ($\partial C'/\partial z$). Therefore, χ is usually represented with a subscript indicating this property, such as χ_θ for temperature (units: K^2 s^{-1}).

Turbulence can also be characterized in terms of size distribution of the turbulent eddies (Thorpe, 2007). The size of the largest possible turbulent eddies in stratified flows is described by the Ozmidov length scale, $L_O = (\varepsilon/N^3)^{1/2}$, since eddies larger than L_O (typically 0.1–10 m) are damped by stratification. On the other hand, the size of the smallest possible turbulent eddies (1–10 mm), able to resist the effects of molecular viscosity, is defined by the Kolmogorov length scale ($L_K = (\nu^3/\varepsilon)^{1/4}$, where ν is the kinematic water viscosity). For most properties, such as temperature and dissolved solids or gases, the molecular diffusivity is much smaller than the kinematic water viscosity ν. Subsequently, fluctuations of those quantities are observed at scales smaller than L_K. The L_K-equivalent for scalar properties is the Batchelor length ($L_B = (\nu D^2/\varepsilon)^{1/4}$), which ranges 0.4–4 mm for temperature and 0.04–0.4 mm for dissolved matter and gases.

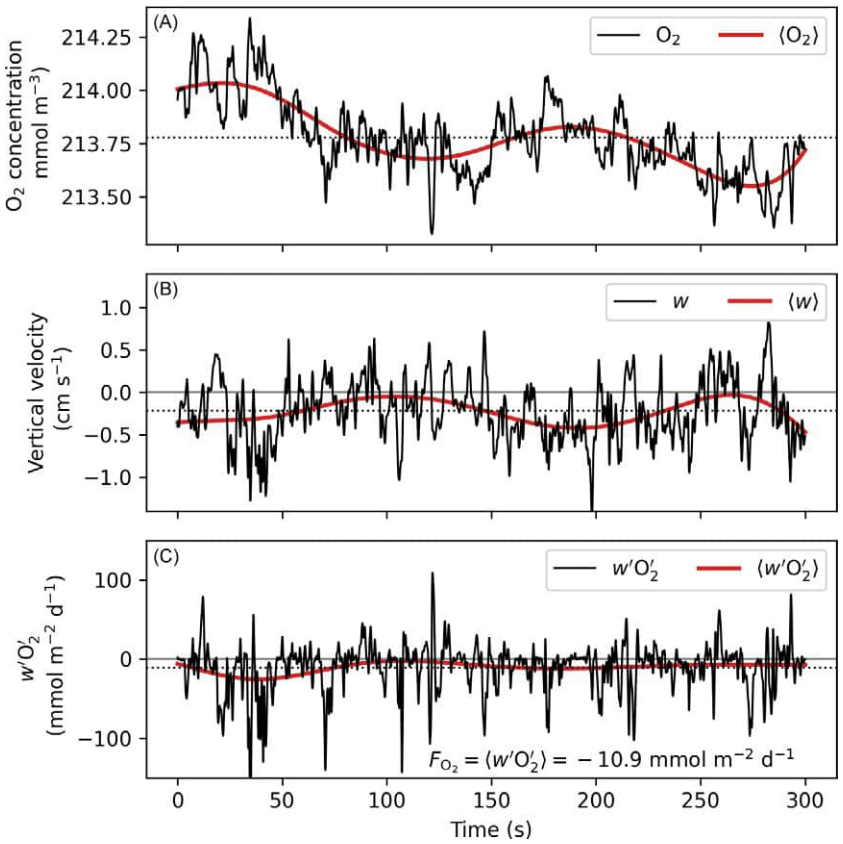

Fig. 3 Time series of O_2 concentration (black line, A) and vertical velocity w' (black line, B; positive = upward), as measured 10 cm above the sediment in the Wohlensee Reservoir (Switzerland) at a frequency of 64 Hz. Red lines indicate the temporally varying averages, determined as running means, whereas the horizontal dotted lines indicate the segment mean. Panel (C) shows the instantaneous eddy flux—covariance of w' and O_2'—and its running average. The average downward O_2 flux over the 300 s (~19,200 data pairs) is –10.9 mmol m^{-2} day^{-1} as indicated by the dotted line. Data source: Lorrai C, McGinnis DF, Berg P, Brand A and Wüest A (2010) Application of oxygen eddy correlation in aquatic systems. *Journal of Atmospheric and Oceanic Technology* **27**: 1533–1546.

Turbulent fluctuations of the vertical velocity w' transport water parcels and their constituents against the stabilizing force of density stratification (Fig. 3). The product of the vertical velocity fluctuations w' and the associated density fluctuations ρ' describes an instantaneous vertical flux of density ($w'\ \rho'$; kg m^{-2} s^{-1}). The instantaneous turbulent flux is composed of irregular fluctuations (Fig. 3). However, due to the dissipation of small-scale gradients by molecular diffusion and to the presence of a background vertical density gradient, the average flux is not zero. The non-zero component appears when averaging $w'\rho'$ over sufficiently long time as a net downgradient (i.e. upward) mass flux $<w'\ \rho'>$, which is usually expressed as a buoyancy flux J_b (W kg^{-1}).

$$J_b = -g\rho^{-1}\langle w'\rho' \rangle \tag{4}$$

Therefore, we can interpret vertical mixing as an upward flux of mass, which causes a change of the potential energy of the stratification (Figs. 1 and 2), expressed as a buoyancy flux (Eq. 4). The required energy originates from TKE, which stems from horizontal flow. Approximately 90% of the TKE, however, does not contribute to the buoyancy flux (and hence to vertical mixing) but is instead dissipated into heat by viscous friction. By defining local rates of production P (W kg^{-1}) and viscous dissipation ε (W kg^{-1}) of TKE, the simplest form of TKE balance reads as:

$$\frac{\partial}{\partial t}\mathrm{TKE} = P - \varepsilon - J_b \tag{5}$$

As mentioned above, the dissipation rate is usually much larger than the buoyancy flux, and hence the mixing efficiency γ_{mix}, which is defined as the ratio.

$$\gamma_{mix} = \frac{J_b}{\varepsilon} = \frac{-g\rho^{-1}\langle w'\rho' \rangle}{\varepsilon} \tag{6}$$

is well smaller than unity. A number of studies in stratified lakes and reservoirs revealed typical mixing efficiencies in the range of 10–15% (Ivey and Imberger, 1991; Imberger and Ivey, 1991). Nonetheless, γ_{mix} can be highly variable along the development of a turbulent event and among turbulent events, depending on the intensity of turbulence relative to stratification (Ivey et al., 2008,

Mashayek et al., 2017). Maximum γ_{mix} values of ~20%, averaged over a turbulent event, are expected when inertial forces of turbulence are comparable to buoyancy forces of stratification. However, γ_{mix} can be severely curbed by especially strong or especially weak stratification. Such situations are common in strong thermoclines and in deep bottom boundaries, respectively, where γ_{mix} can be significantly lower than 10–20%. For this reason, at least in medium-sized lakes, most of the mixing occurs within the bottom boundary layer at locations where the thermocline intersects the lake slope.

Quantification of turbulent transport: Eddy diffusivity

Turbulent eddies act on any water property or constituent as they do on density, enhancing small-scale gradients and driving turbulent fluxes. Therefore the local turbulent vertical fluxes of water constituents, such as oxygen (O_2), nutrients or organic matter are similarly described by the covariance of vertical velocity fluctuations and concentration fluctuations, $<w'\ O_2'>$ (Fig. 3; Lorrai et al., 2010). Although the instantaneous fluxes are almost of equal magnitude in the upward and downward directions, the averaging $<w'\ O_2'>$ reveals slightly larger fluxes towards the sediment, where O_2 is consumed. The turbulent fluxes are always from high to low concentrations, and replenish water constituents in locations where they are consumed by biogeochemical processes, such as O_2 in the sediments or nutrients in the photic zone.

The quantification of turbulent fluxes is therefore relevant for ecological processes and of key interest for research and management of aquatic systems. Direct measurements of turbulent fluxes can be achieved with the eddy covariance technique (Fig. 3). This technique is based on simultaneous, precise, well-resolved measurements of the turbulent fluctuations of the vertical water velocity and the property of interest (such as temperature, O_2) in a small control volume (Fig. 3). High-precision velocity measurements can be obtained with acoustic velocimeters and the method has proven useful to measure turbulent fluxes of heat and oxygen at the water-sediment interface as well as in the water column. The method has some important drawbacks as it is based on rigorous assumptions (steady-state conditions, horizontal homogeneity and negligible production or consumption of the constituent within the water column above the sediment). In addition, the method is technically challenging and costly and the observations have limited spatial representativeness. Moreover, sensors with sufficiently high resolution and sampling frequency are only available for a small number of properties.

Alternatively, turbulent fluxes in stratified waters are usually expressed using the eddy diffusivity concept. Applied to the mass flux $<w'\ \rho'>$, it implies assuming that (i) a well-defined local density gradient $\partial\rho/\partial z$ exists (due to the stratification) and (ii) the flux—in analogy to molecular diffusion—can be expressed by the eddy (or turbulent) diffusivity K_z ($m^2\ s^{-1}$) multiplied by this local gradient:

$$\langle w'\rho'\rangle = -K_z\frac{\partial\rho}{\partial z} \tag{7}$$

In this formulation, K_z describes the net vertical transport of density caused by turbulent velocity fluctuations. Therefore, in contrast to the molecular diffusion process and to the rate of variance smoothing (χ), eddy diffusivity is neither a function of the medium (water) nor of the water constituents, but rather a property of the stratified turbulent flow. In particular, K_z reflects the extent of the velocity fluctuations w' and the eddy sizes L': K_z can be interpreted as the statistical average $<w'\ L'>$ over a large number of eddies (Fig. 2 and Fig. 3).

All water properties—such as temperature or dissolved substances—are transported and mixed in the same way via the turbulent exchange by small eddies (Fig. 3). The eddy diffusivity concept can be applied to any dissolved or particulate substance and the associated vertical fluxes F can be estimated in analogy to Eq. (7) by.

$$F = -K_z\frac{\partial C}{\partial z} \tag{8}$$

where C is the considered concentration. In the last decades, two fundamentally different approaches have been used for the estimation of K_z: (i) the microstructure method and (ii) the tracer method.

The microstructure method (i) is based on the TKE balance of Eq. (5). Assuming steady-state conditions, by neglecting the left-hand side of Eq. (5), and by combining Eqs. (1), (5) and (6) yields:

$$K_z = \gamma_{\text{mix}}\frac{\varepsilon}{N^2} \tag{9}$$

This equation provides an expression to estimate K_z from field measurements of ε and N^2 and an assumed or parameterized value of the mixing efficiency. Moreover, it demonstrates the direct proportionality between K_z and the level of turbulence (ε) and the inverse proportionality on the strength of stratification (N^2), meaning that the vertical fluxes depend on an interplay between a driving force (turbulence) and a suppressing force (stratification).

An alternative microstructure method relies on the equation for temperature variance ($<\theta'^2>$) conservation, analogously to the TKE equation (Eq. 5),

$$\frac{\partial\left\langle\theta'^2\right\rangle}{\partial t} + 2\left\langle w'\theta'\right\rangle\frac{\partial\overline{\theta}}{\partial z} = \chi_\theta \tag{10}$$

where the second term on the left hand side is the variance production by turbulent motions acting on the mean vertical temperature gradient, $\frac{\partial \bar{\theta}}{\partial z}$, and χ_θ is the dissipation rate of temperature variance by molecular diffusion. By writing $\langle w'\theta' \rangle = -K_z \frac{\partial \bar{\theta}}{\partial z}$ and assuming steady state, K_z can be estimated as a function of χ_θ and the vertical temperature gradient:

$$K_z = \frac{\chi_\theta}{2\left(\frac{\partial \bar{\theta}}{\partial z}\right)^2} \tag{11}$$

This method has the advantage that it is a more direct measure of mixing and it is not contingent to any assumption regarding the efficiency of mixing γ_{mix}.

The dissipation rates of TKE and of thermal variance can be derived from observations with microstructure profilers (Kocsis et al., 1999). These instruments include high-resolution velocity and temperature sensors that allow measuring turbulent fluctuations at small scales close to the Kolmogorov and Batchelor scales (1 mm – 10 cm). The dissipation rates (ε and χ_θ) are proportional to the small-scale variance of the velocity and temperature gradients, which are normally derived by spectral analysis of the microstructure signal. This type of measurements offers a detailed vertical mapping of turbulence and mixing rates in the water column, but is often limited in temporal resolution, since it usually requires manned operation. Conversely, highly temporally resolved estimates of ε and χ_θ, and therefore K_z, in localized regions of the water column can be derived from continuous velocity and temperature measurements with high-resolution acoustic Doppler current profilers (ADCP) and temperature sensors mounted on moorings, using the so-called inertial subrange (Bluteau et al., 2017) or structure functions method (Wiles et al., 2006) (see Figs. 4 and 5 for examples).

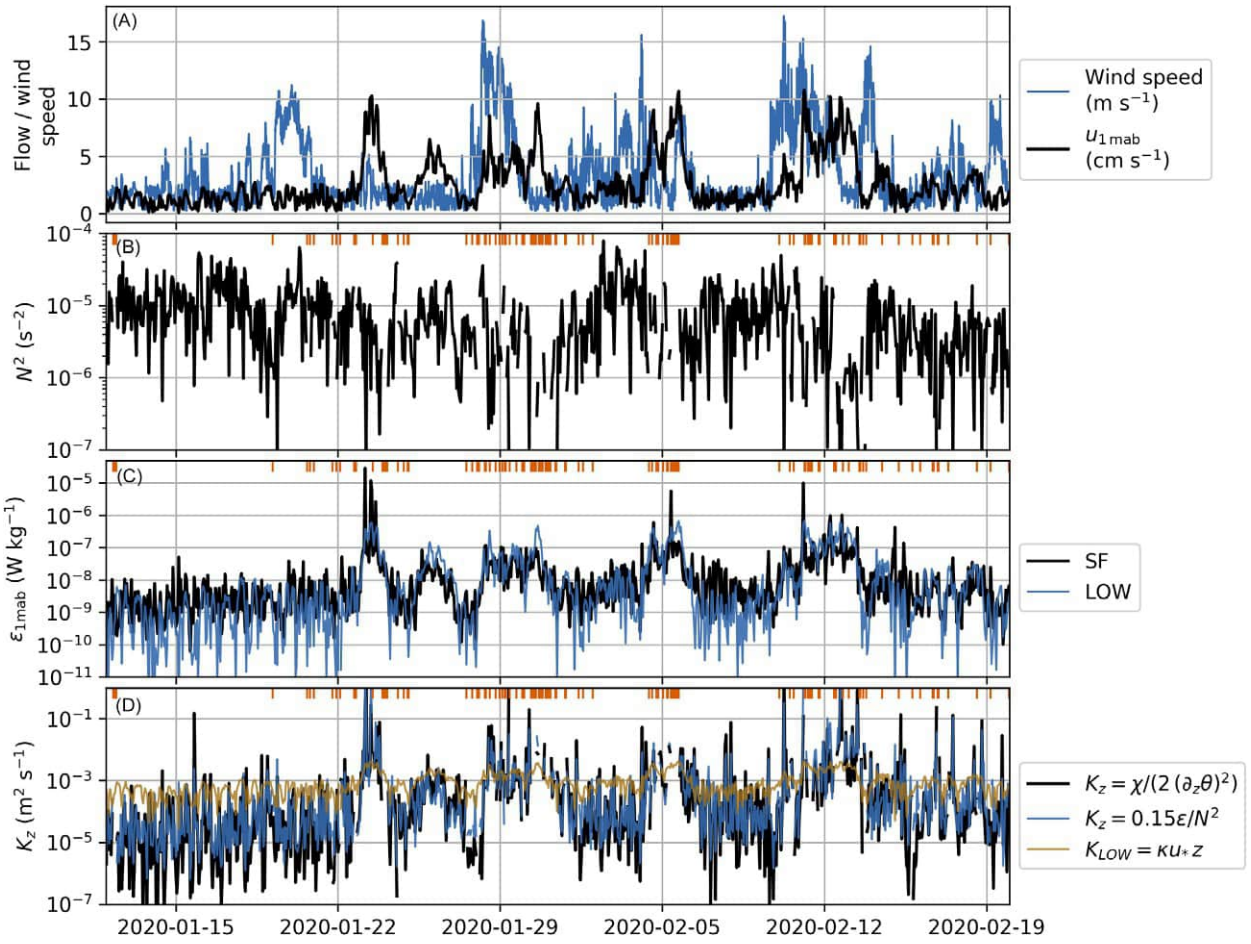

Fig. 4 Bottom boundary layer flow, stratification, dissipation and diffusivity in a slope region of Lake Geneva during a windy winter period measured with moored instruments (high resolution ADCP and thermistors). (A) Flow speed at 1 m above the lake bed ($u_{1\ mab}$, black) and wind speed at 10 m above the lake surface; (B) mean stratification (N^2) in the bottom 3 m; (C) TKE dissipation at 1 mab ($\varepsilon_{1\ mab}$) derived from high-resolution velocity measurements with the structure function method (SF) and from mean flow velocities ($u_{1\ mab}$) following the Law-of-the-Wall (LOW, Eq. 12) with an adjusted drag coefficient $C_D = 0.00368$; (D) vertical turbulent diffusivity (K_z) derived with the temperature variance method (black, Eq. 11), the dissipation method assuming $\gamma_{mix} = 0.15$ (blue, Eq. 9), and estimated from the LOW as $K_{LOW} = \kappa\, u_* z$, with $z = 1$ m and $\kappa = 0.41$ is the von Kármán constant (brown). Periods of unstable stratification ($N^2 < 0$) are indicated with orange markers on top of the axes. This figure illustrates important aspects of the BBL turbulence dynamics: (1) the indirect delayed response of the BBL currents to wind forcing (panel a), (2) the variability of TKE dissipation rates in the range 10^{-9}–10^{-6} W kg^{-1} as a response to varying near-bed velocities consistent with the Law-of-the-Wall (LOW, panel c), (3) the persistence of stratification ($N^2 \approx 10^{-5}$ s^{-2}) in sloping boundaries despite strong mixing events likely due to secondary circulations (panel b), (4) diffusivity values ranging between 10^{-5} and 10^{-4} m^2 s^{-1} during calm conditions, and 10^{-3} and 10^{-1} m^2 s^{-1} during energetic episodes (panel d), (5) the consistency between Eqs. (9) and (11) indicating an almost constant mixing efficiency of $\gamma_{mix} \approx 0.15$ (panel d), (6) the suppression of mixing by stratification, as Eqs. (9) and (11) give lower K_z values than the LOW approximation ($K_z \approx \kappa\, u_*\, z \approx 10^{-3}$ m^2 s^{-1}) during calm periods (panel d). Data source: Fernández Castro B, Bouffard D, Troy C, Ulloa HN, Piccolroaz S, Sepúlveda Steiner O, Chmiel HE, Serra Moncadas L, Lavanchy S and Wüest A (2021). Seasonality modulates wind-driven mixing pathways in a large lake. *Communications Earth & Environment*, **2**(1): 215. https://doi.org/10.1038/s43247-021-00288-3.

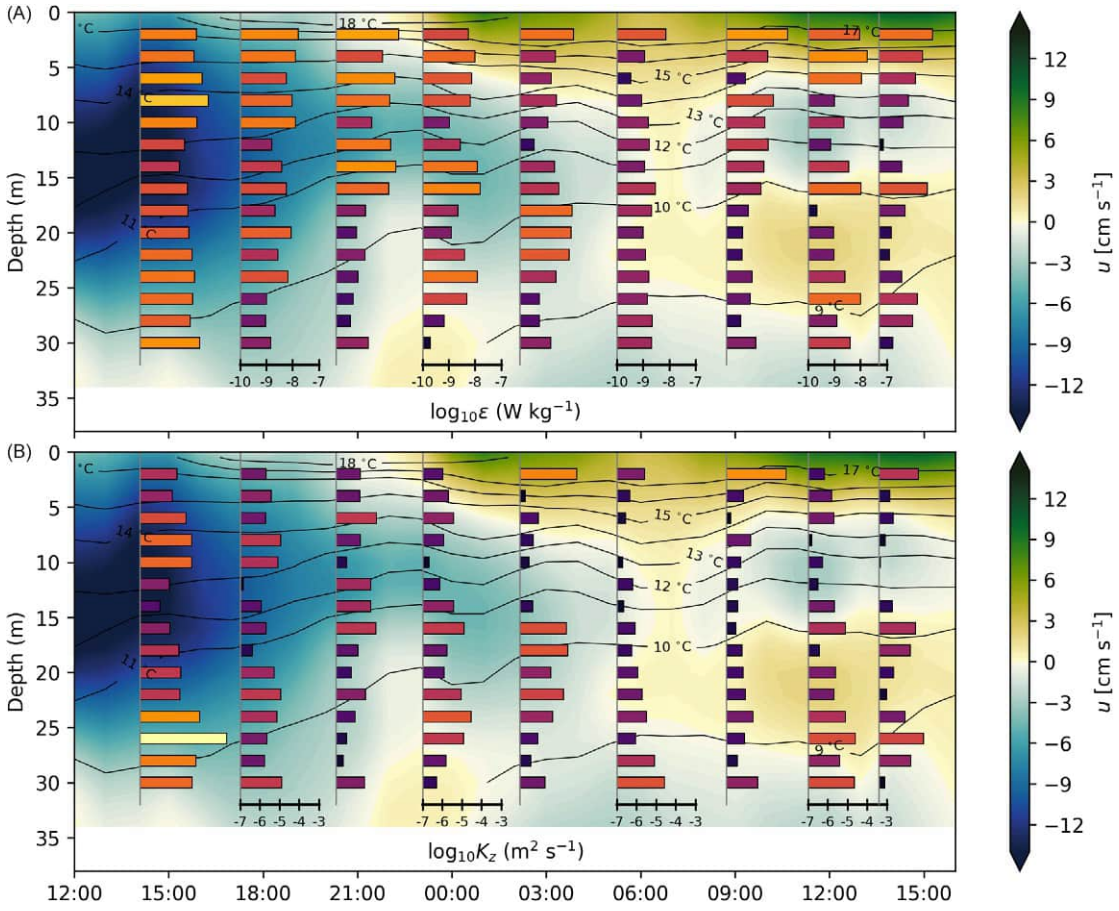

Fig. 5 Time-series of 24-h of turbulence profiles in Lake Geneva on 13–14 June 2019. Profiles of TKE dissipation (A) and diffusivity (B), collected every 3 h, are shown as bars. The magnitude of log-transformed ε and K_z are represented by the length of the bars and their color (lighter color meaning higher values). The background colored contours represent the zonal water velocity (positive eastward) measured with an ADCP. The black contours represent isotherms with a resolution of 1 °C. These observations illustrate the rapid changes in metalimnetic turbulent mixing as a response to changes in ambient stratification and shear due to the presence of basin-scale motions. The strong (~15 cm s^{-1}) westward flow centered at 15 m depth at the beginning of the period was associated with large displacements of the isotherms, causing a thermocline expansion and a reduction of stratification. Therefore, dissipation rates and vertical diffusivity were initially high at $\varepsilon \approx 10^{-8}-10^{-7}$ W kg^{-1} and $K_z \approx 10^{-5}-10^{-3}$ m^2 s^{-1}. As the currents relaxed, ε decayed to minimal values of $\sim 10^{-9}$ W kg^{-1} at 6:00 am, and the isotherms came closer together creating a highly stratified layer between 5 and 20 m depth, where K_z dropped to molecular values ($\sim 10^{-7}$ m^2 s^{-1}). Data source: Fernández Castro B, Bouffard D, Troy C, Ulloa HN, Piccolroaz S, Sepúlveda Steiner O, Chmiel HE, Serra Moncadas L, Lavanchy S and Wüest A (2021). Seasonality modulates wind-driven mixing pathways in a large lake. *Communications Earth & Environment*, **2**(1): 215. https://doi.org/10.1038/s43247-021-00288-3.

At larger spatio-temporal scales, turbulent diffusivities can be estimated from observations of the three-dimensional spreading of artificial or natural tracers. The diffusivities derived from the tracer method (ii) have the advantage of integrating all the mixing processes affecting the tracer spread over the considered period and thus are representative of mixing at the basin-scale (Fig. 6), as opposed to microstructure diffusivities, which account only for mixing events encountered by the vertical path of the profiling instruments. However, the estimation of K_z by releasing artificial tracers is time and resource consuming and thus restricted to specific studies. A more suitable alternative is offered by the heat budget method, which uses heat as a natural tracer and allows estimating K_z from a series of temperature profiles (Powell and Jassby, 1974). Below the photic zone, where the penetration of solar radiation is small, the accumulation of heat can be described as the result of the turbulent heat flux crossing a certain depth level. Because of the small magnitude of K_z, the heat budget method requires repeated temperature profiles over a sufficiently extended period (>weeks). In addition, the vertical dislocation of the isotherms by internal waves can have a first-order disturbance to heat budget, and the observations must be averaged over sufficiently long time-scales. Typical diffusivity values in stratified natural waters are listed in Table 1 and Figs. 4–7.

Turbulence and mixing in the surface boundary layer

There are fundamentally two mechanisms generating turbulence in the SL: (i) the action of wind causing wave breaking and current shear in the top few meters of the water column and (ii) cooling causing heavier water parcels to sink from the surface.

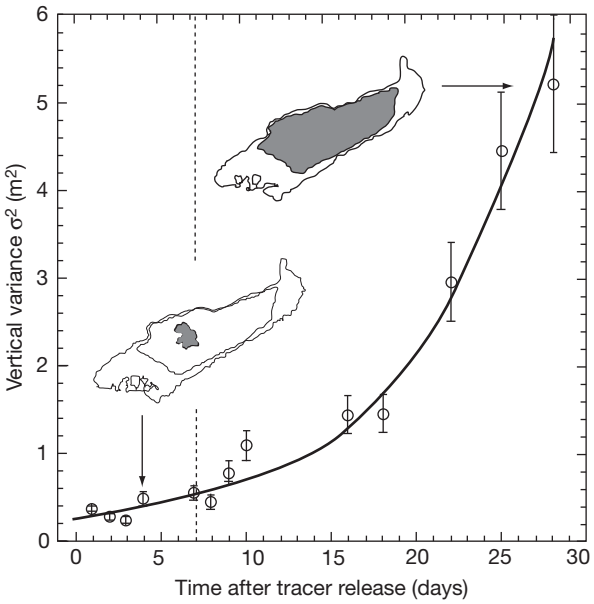

Fig. 6 Vertical spreading of the tracer Uranine after injection at 25 m depth in Lake Alpnach (Switzerland). The vertical line demarcates the initial period of 7 days, during which Uranine resided in the interior of the stratified deep water. The two insets show the lake area at the surface and at the depth of the Uranine injection, as well as the horizontal distribution of the Uranine cloud (shaded in grey) after 4 and 28 days. The slow growth of the spreading in the first 7 days illustrates the quietness in the interior. The fast growth of the vertical spreading after day 7 is due to the increasing contribution of BBL mixing after the tracer has reached the sediment at 25 m depth. Reproduced from Goudsmit GH, Peeters F, Gloor M and Wüest A (1997) Boundary versus internal diapycnal mixing in stratified natural waters. *Journal of Geophysical Research* **102**: 27903–27914, with permission from American Geophysical Union.

Table 1 Typical values of dissipation, stability and vertical diffusivity in stratified waters.

	Dissipation[a] ε *(W kg^{-1})*	*Stability* N^2 *(s^{-2})*	*Diffusivity* K_z *(m^2 s^{-1})*
Ocean thermocline	$10^{-10}-10^{-8}$	$\sim10^{-4}$	$(0.3-3)\times10^{-5}$
Surface layer	$10^{-9}-10^{-6}$	$0-10^{-5}$	$10^{-5}-10^{-2}$
Lake interior only (without BBL)	$10^{-12}-10^{-10}$	$10^{-8}-10^{-3}$	$10^{-7}-10^{-5}$
Metalimnion (basin-scale)		$\sim10^{-3}$	$(0.5-50)\times10^{-7}$
Near-shore metalimnion	$10^{-10}-10^{-6}$	$\sim10^{-3}$	$(0.3-3)\times10^{-4}$
Deep hypolimnion (basin-scale)	$10^{-12}-10^{-10}$	$10^{-8}-10^{-5}$	$(0.03-3)\times10^{-4}$

[a]During storm events values are larger by orders of magnitudes.

Cooling-driven mixing (ii) leads to homogenization of the SL and therefore to non-stratified conditions—at least for a few hours or days—before heat fluxes from/to the atmosphere or the gravitational collapse of lateral density gradients restratify the SL. Only in shallow ponds or basins with high throughflow, turbulence can have other site-specific sources.

For wind-driven mixing (i), the parameter governing the dynamics of turbulence in the SL is the surface shear stress τ (N m^{-2}), the force per unit area exerted on the water by the wind. This stress is equal to the downward eddy-transport of horizontal momentum from the atmosphere. Part of τ is consumed by the acceleration of surface waves (τ_{wave}), whereas the remaining momentum flux τ_{SL} generates currents and turbulence in the SL. By assuming a constant stress across the air-water interface, the momentum fluxes at the waterside are equal the total wind stress ($\tau = \tau_{SL} + \tau_{wave}$).

Immediately below the waves, the momentum flux, τ_{SL}, drives the vertical profiles of horizontal velocity $u(z)$. If the wind remains relatively constant for hours, steady-state conditions may develop in the SL: $u(z)$ then depicts the Law-of-the-Wall (LOW), $\partial u/\partial z = u_*(\kappa z)^{-1} = (\tau_{SL}/\rho)^{1/2}(\kappa z)^{-1}$, where $u_* = (\tau_{SL}/\rho)^{1/2}$ is the frictional velocity and κ (=0.41) is the von Kármán constant. Because the buoyancy flux in the SL (defined in Eq. 4) is not a large contribution in Eq. (5), we can assume a balance between the production and the rate of viscous dissipation (ε) of TKE. This local balance between production and dissipation of TKE determines the turbulence intensity as a function of depth throughout the SL. Under those assumptions, the dissipation,

$$\varepsilon = (\tau_{SL}/\rho)\partial u/\partial z = {u_*}^3(\kappa z)^{-1} \qquad (12)$$

is only a function of the wind-induced stress τ_{SL} (here expressed as the friction velocity u_*) and of depth z. Several experiments have demonstrated that dissipation is indeed inversely proportional to depth (Eq. 12), if averaged for long enough. However, one has to

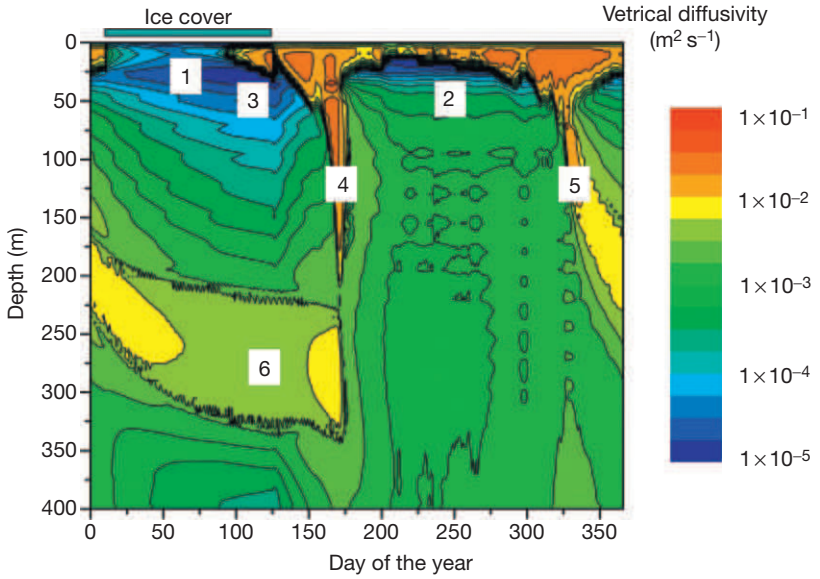

Fig. 7 Vertical diffusivities in Lake Baikal simulated with a k-epsilon model. The numbers (1–6) on the contour plot indicate the main features of the seasonal stratification and changes in diffusivity: the formation of thermal stratification with weak mixing (1) during winter under the ice and (2) during summer; (3) the formation of a radiatively-driven convectively mixed layer in spring under the ice; the deep convective mixing in (4) June and (5) November; and (6) the formation of a mixed layer near the temperature of maximum density. Here the emphasis is on the temporal and vertical structure of the turbulent diffusivity and not on the absolute accuracy, which may be difficult to achieve with turbulence modelling better than a factor of 2–3. Reproduced from Schmid M, De Batist M, Granin NG, Kapitanov VA, McGinnis DF, Mizandrontsev IB, Obzhirov AI and Wüest A (2007) Sources and sinks of methane in Lake Baikal: A synthesis of measurements and modeling. *Limnology and Oceanography* **52**: 1824–1837, with permission from American Society of Limnology and Oceanography.

be critical about the validity of Eq. (12) for two reasons: First, at the very top of the water column, breaking waves, in addition to shear stress, produce a significant part of the turbulence in the SL. This additional TKE generation at the surface can be interpreted as an injection of TKE from above. Therefore, in the uppermost layer, the turbulence exceeds the level described by Eq. (12), depending on the intensity of the wave breaking. Second, Eq. (12) relies on quasi-steady-state conditions, which may hold applicable for only limited episodes, due to the variable forcing. Third, the presence of some stratification within the SL, particularly due to solar heating during the mid-day hours, can hamper the development of the LOW logarithmic velocity layer.

Despite these restrictions, Eq. (12) gives a reasonable idea of the magnitude of energy dissipation rates and diffusivity in the stratified SL. Because ε is several orders of magnitude larger in the SL than in the interior layers and N^2 is usually small, Eq. (9) reveals that the rate of mixing is large within the SL (Table 1). Therefore, gradients of temperature, nutrients, and suspended particles are usually smallest at the surface and increase with depth. Mixing in the SL undergoes large temporal variations due to changes in wind stress and heating (day) and cooling (night) cycles. During sunny days, near-surface diurnal thermoclines are formed, where stratification ($N^2 \approx 10^{-5}$ s^{-2}) can limit the development of overturns. Under light winds ($\sim$2 m s^{-1}, $\varepsilon \approx 10^{-8}$ W kg^{-1}), turbulent eddies are constrained by the Ozmidov scale ($L_O \approx 1$ m) and mixing can be relatively weak ($K_z \approx 10^{-4}$ m^2 s^{-1}). On cloudy, windy days, the SL may mix fully and may even deepen depending upon the surface forcing. Under strong winds or intense cooling, SL stratification is eroded and the size of turbulent eddies is no longer limited by L_O but by the vertical extension of the SL. In this case, Eq. (9) is not a good estimate of K_z, because $N^2 \approx 0$. Instead, K_z can be estimated as the product of the turbulent velocity (u_*) and the SL depth (h_{SL}), $K_z = \kappa\, u_*\, h_{SL}$. For strong winds (>10 m s^{-1}) and deep SL (>10 m), $K_z \approx \kappa\, u_*\, h_{SL}$ can be as large as $\sim$0.05 m^2 s^{-1}.

Turbulence and mixing in the bottom boundary layer

Turbulence generation and mixing along the bottom boundaries of water bodies can be described in analogy to the SL. The energetics of the bottom boundary layer (BBL) are governed by the bed-shear stress due to the flow friction with the sediment, $\tau_{BBL} = \rho\ C_D\ u^2$, where C_D ($\sim 1\text{–}5 \times 10^{-3}$) is the bottom drag coefficient and u a near-bed flow velocity. Under steady-state conditions, the resulting BBL follows a vertical structure of (i) current shear (see above), (ii) rate of TKE dissipation (Eq. 12) and (iii) rate of vertical mixing similar to those described for the SL. Although the ultimate energy source for turbulence in the BBL is also wind, its action on the BBL is indirect and mediated by large-scale wind-driven currents and basin-scale internal waves, which loose energy by friction against the sediment. Moreover, along sloping boundaries in particular, the breaking of propagating internal waves and convective processes—a secondary effect of bottom friction—can produce additional TKE, leading to dissipation and mixing in excess of that predicted by Eq. (12) (Lorke et al., 2008).

As with the SL, the BBL is also often weakly stratified. Again, turbulence (Eq. 9) increases substantially when approaching the sediment and often a completely homogenized layer, a few m thick, can develop above the sediment. As a result, the contribution of the BBL to basin-scale mixing is particularly strong in sloping regions, where the BBL is adjacent to interior stratified meta- or hypolimnetic waters. This difference in stratification generates a pressure gradient driving secondary exchange flows that continuously restratify the BBL, allowing mixing to continue (Gloor et al., 2000). The BBL dynamics described here are illustrated with a time-series of flow velocities, stratification, dissipation rates and diffusivity at 1 m above the bed in a slope region of Lake Geneva during a winter period alternating strong winds and calmer conditions (Fig. 4).

Turbulence and mixing in the stratified interior

In the lake interior, away from surface and bottom boundaries (Fig. 1), the water body is largely stratified and mostly quiescent, since it is not exposed to the direct effects of the turbulent boundary layers. When sampling a property at fixed depth (such as with moored instruments), internal waves often dominate the variability over time-scales comparable to their periods (a few minutes to a few days). This is due to the transient and reversible dislocation of vertical gradients across the observation depth, whereas turbulent mixing acts as a continuous, slow process that tends to reduce those gradients. Mixing is generated by local shear instabilities related to currents and waves (Fig. 2, Eq. 2), which occur mostly where the usually weak background shear is enhanced by non-linear steepening of internal waves or wave-wave interactions. The mechanical energy needed for mixing in the interior derives mostly from basin-scale internal currents and waves. Smaller waves with higher frequencies, although generated at specific locations, can also contribute to the basin-scale energy budget (Preusse et al., 2010). At the transition between small- and large-scale waves are the near-inertial currents, which can carry—especially in large lakes—a significant portion of the mechanical energy. The response of dissipation and mixing to changes in ambient shear and stratification due to internal motions is illustrated in Fig. 5 for a summer period in Lake Geneva.

The difference in stratification between the meta- and hypolimnetic realms gives rise to distinctly different turbulence properties. High stratification ($N^2 \approx 10^{-3}$ s^{-2}) in the metalimnion can favor wave-wave interactions and dissipation rates may vary from low to moderate ($\varepsilon \approx 10^{-10} - 10^{-7}$ W kg^{-1}; Table 1, Figs. 5 and 7). However, strong stratification limits the development of turbulent eddies, with L_O ranging from <1 cm to ~10 cm. In order to drive vertical mixing, L_O must significantly exceed L_K, such that there is a well-developed range of eddies not damped by viscosity or stratification. In particular, vertical mixing gets strongly suppressed when the ratio $(L_O/L_K)^{4/3} = \varepsilon/(\nu N^2)$ falls below ~10 to 30. In the metalimnion, the onset of vertical fluxes is thus only possible at the upper range of the typically observed dissipation rates, $\varepsilon > 10^{-8}$ W kg^{-1}. The resulting vertical diffusivities range from molecular values (~10^{-7} m^2 s^{-1}, for heat) to $10^{-6} - 10^{-5}$ m^2 s^{-1}. In the hypolimnion, quiescent conditions are prevalent ($\varepsilon \approx 10^{-12} - 10^{-10}$ W kg^{-1}) but stratification is also weaker ($N^2 \approx 10^{-8} - 10^{-5}$ s^{-2}), such that large turbulent eddies ($L_O \approx 0.1 - 10$ m) can potentially develop. In deep and weakly stratified lakes, such as Lake Baikal, diffusivity can range from molecular to ~10^{-3} m^2 s^{-1} (Fig. 7; Schmid et al., 2007).

Overall, the rate of mixing in the interior away from the boundaries of lakes is usually lower than in the SL or BBL because (i) currents and shear are weak and the resulting turbulence production is reduced and (ii) stratification suppresses turbulent mixing. Direct observations of turbulence and mixing, using microstructure and tracer techniques, generally endorse this concept. In many lakes, only a few percent of the water column in the pelagic zone is found to be actively mixing (Etemad-Shahidi and Imberger, 2001). The occurrence of such turbulent patches is highly intermittent in space and time. During periods when the fluid is non-turbulent, we can expect laminar and molecular transport conditions. The observable average basin-scale diffusivity can be considered as representing the superposition of the rare turbulent events separated by molecular diffusion for most of the time. Tracer experiments and microstructure profiling conducted in small and medium-sized lakes confirmed these quiet conditions in the interior and enhanced turbulence in the boundaries. In Fig. 6, the vertical spreading of a tracer, injected into the hypolimnion, is shown for the interior (first few days) and for a basin-wide lake volume including the BBL (after a few days). From Fig. 6 it is evident that turbulent diffusivity in the interior is at least one order of magnitude lower than in the basin-wide body, including the BBL. Recent field observations have shown that this picture may be slightly different for large lakes with more intense basin-scale motions in form of Poincaré and Kelvin waves. Those seem to frequently give rise to internal instabilities and enhanced mixing at basin-scale (Bouffard et al., 2012). This was also the case in the water-column microstructure observations in Lake Geneva shown in Fig. 5. For this summer period, depth-integrated interior dissipation derived from microstructure profiles was ~0.20 mW m^{-2}. Near-bed flows were weak (<2 cm s^{-1}) and the contribution of the BBL to energy dissipation (~0.03 mW m^{-2}) was comparatively small.

In addition to these spatial differences, one has to be aware of the temporal variability. During storms, turbulent dissipation and mixing rates can be enhanced by several orders of magnitude during short episodes. The transition from quiescent to actively-mixing flows occurs rapidly once winds increase above a certain threshold relative to the stratification. The internal wave field becomes energized and turbulence can develop. However, the greatest increases occur in the BBL. It is during such storms, when most of the vertical flux takes place. This is clearly illustrated by comparing the winter (Fig. 4) and summer (Fig. 5) observations in Lake Geneva. During this winter period, the wind energy flux was five times larger than during summer (300 vs. 70 mW m^{-2}) but, in both cases, interior dissipation derived from microstructure profiles was similar ~0.2 mW m^{-2}. In contrast, BBL dissipation increased massively from ~0.03 mW m^{-2} in summer to ~0.7 mW m^{-2} in winter (see also Fernández Castro et al., 2021). In spite of these large differences, the sum of BBL and interior dissipation (~0.2 and ~0.9 mW m^{-2}, respectively) represented ~0.3% of the wind energy flux during both seasons, while the remainder 99.7% was dissipated in the atmospheric and surface boundary layers and as surface waves (Fernández Castro et al., 2021).

Synthesis and knowledge gaps

From the discussion above, we can draw the following overall scheme of the energy flux through stratified lake waters. The origin of the energy for turbulent mixing in the interior of stratified lakes is usually wind, which imposes momentum onto the water surface. Approximately 3% of the wind energy reaches the epilimnion in the form of horizontal currents and about 10% thereof (i.e., 0.3% of the wind energy) is finally transferred to the stratified water body underneath. The major part of the energy is dissipated by bottom interaction, and the minor part is dissipated in the interior by shear instabilities and breaking of internal waves. However, recent findings indicate that the partition between the bottom boundary and the interior depends on the forcing and stratification, at least in large lakes, where interior dissipation can also represent a major sink of energy. Of the dissipated energy, only ~10% contributes to a change in potential energy of stratification (mixing efficiency γ_{mix}, Eq. 6). Compared to the wind energy flux from the atmosphere, only a small fraction (~0.03%) actually causes the mixing against the stratification in the deep water, whereas the largest fraction (~99.97%) is dissipated somewhere along the flux path. Although this partitioning depends on many factors, the overall scheme likely holds within a factor of 2–3 for different lakes.

The small amount of energy available for mixing—compared to the potential energy stored in the stratification—explains why lakes deeper than a few m remain permanently stratified during the warm season. Consistent with this conclusion, the enhanced turbulence in the surface and bottom boundaries cannot erode the stable—and partly strong—stratification in the interior. Turbulent patches are intermittent and turbulent eddies are too small compared to the lake depth. As an example, the timescales to transport heat, solutes or suspended particles over a distance of 10 m would be $(10\,\mathrm{m})^2\ K_z^{-1}$; i.e., several years for $K_z = 10^{-6}\ \mathrm{m^2\ s^{-1}}$ in the metalimnion (Table 1). Therefore, two-dimensional processes, such as upwelling, contribute importantly to vertical exchanges. Despite recent progress, the spatial and temporal dynamics of mixing challenges not only experimental estimation, but also numerical simulation. Local measurements of K_z following Eq. (9) often neither resolve its spatial variability, nor its temporal dynamics and the coarse grid sizes used in numerical simulations do not capture the small scales relevant for mixing processes in the interior. Future research should target, on one side, at improving the sampling capacities through the development of autonomous turbulence-measuring devices allowing to resolve episodic and extreme mixing events, and, on the other side, at coupling of small-scale turbulence simulations with basin-scale hydrodynamic models. Fundamental knowledge on the spatio-temporal distribution of stratified turbulent fluxes in lakes is essential to anticipate the evolution of these systems in a context where climate change is profoundly altering their stratification dynamics.

See Also: Fundamental concepts and theories: Temperature as a Driving Factor in Aquatic Ecosystems; Structures and functions of Inland Waters - Lakes: Currents in Well-Mixed Layers; Currents in Stratified Water Bodies: Internal Waves; Currents in Stratified Water Bodies 1: Density-Driven Flows; Surface Mixed Layers in Lakes; Bottom Boundary Layers; Lacustrine Phosphorus Cycling

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Prokaryotic Viruses: Intriguing Players in the Aquatic Realm

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie_Elodie Perga and Damien Bouffard.

Glossary

Auxiliary metabolic genes (AMGs) Genes within phage genomes which encode enzymatic functions that optimize the metabolism of the host cell for viral reproduction during infection.
Chronic infection Stable establishment of a virus in the host cell (lysogeny). In contrast to lytic infections viral progeny is released continuously and usually *without* rupture of the host cell.
Lysis The bursting of a prokaryotic cell during the release of viral progeny.
Lysogenic/temperate infection Viral infection which leads to the stable integration of the phage genome (prophage) in the host cell. Depending on the phage, a lysogenic infection may turn out to be chronic or lead to a delayed lytic reproductive cycle.
Lytic infection Viral infection directly leading to viral reproduction and subsequent destructive release of viral progeny (lysis).
Metagenomics The isolation and sequencing of DNA from biologically complex samples; followed by the bioinformatic analysis and interpretation of the gained sequence information.
Phages Here used to refer to viruses infecting prokaryotes (i.e., bacteria and archaea). Often also used to refer to viruses of bacteria only.
Prokaryote Unicellular microorganism without cell nucleus of the domains Bacteria or Archaea.
Prophage Functional phage genome which is integrated in the host cell either within the host genome or as plasmid.
Virioplankton Viral particles dispersed in the water column of aquatic environments.

Introduction

Viruses are the most abundant and diverse biological entities in the biosphere (Dion et al., 2020). Although they are commonly known for causing disease in multicellular organisms, most viruses found in aquatic environments infect prokaryotes (Jacquet et al., 2010). This chapter therefore focuses on the activities and ecological consequences of infections caused by prokaryotic viruses, here referred to as phages. Phages in aquatic ecosystems impact their hosts not only as infectious particles killing an estimated 20% of the prokaryotic standing stock per day but also as mobile genetic elements inside host cells which can alter their hosts' metabolism and

acquire and transfer genetic information (Cordero and Polz, 2014; Zimmerman et al., 2020). Whereas phages affecting model organisms have been studied by microbiologists and molecular biologists since the early 20th century, they have been ignored in aquatic ecology till the late 1980s. Since then, phage ecology has developed into a multidisciplinary and dynamic field of research which is constantly fed by new findings from various disciplines (Ofir and Sorek, 2018). While microbiological, genetic and molecular biological studies steadily unravel new variants of phage-host interplay, the integration of these findings into coherent ecological concepts is challenging. Currently aquatic viral ecology is heavily based on data and concepts developed in marine systems. Despite genetic differences of virioplankton from marine and freshwater systems, so far, no systematic differences between the controls of the activities and the diversity of phages in marine and freshwater systems have been identified (Wilhelm and Matteson, 2008). The aim of this chapter is to give a condensed overview on the activities and ecological consequences of phage-infections in lake ecosystems based on general concepts for virus-host relationships. Specifics of lake ecosystems will be pointed out throughout the chapter and will be illustrated by two case studies in which phages exhibited (1) a remarkable impact on top-consumers in lake ecosystems and (2) played an important role in the epidemic dynamics of a (fresh)waterborne disease.

Viral taxonomy and phage morphology

Viruses are genetically unprecedentedly diverse and in contrast to cellular organisms have no single conserved gene which can be used for phylogenetic analysis and taxonomic classification. Therefore, criteria specified by the International Committee on Taxonomy of Viruses (ICTV) are mainly based on phenotypic traits like virus morphology and the type of nucleic acid constituting viral genomes, i.e., single-stranded (ss) or double-stranded (ds) deoxyribonucleic acid (DNA) or ribonucleic acid (RNA). However, the extended use of high-throughput sequencing in the past decade has led to the endorsement of the formal classification of viruses based on genetic data by the ICTV. This resulted in a major overhaul of virus taxonomy and the recent revision of the 5-rank structure to a 15-rank structure by the ICTV which, for large parts, resembles the Linnaean taxonomic scheme used for cellular organisms. Phage morphologies are important for taxonomic classification and are informative regarding the biomechanics of infection. It is yet important to note that phage morphologies are not congruent with the (much higher) genetic diversity of phages and allow little inference about potential hosts. Since most phages are significantly smaller than the wavelength of visible light, phage morphology is commonly investigated using transmission electron microscopy (TEM). Fig. 1 shows an overview of phage morphologies. In aquatic environments, tailed phages (*Caudovirales*) and icosahedral phages like *Microviridae* make up the largest fractions of morphotypes (Brum et al., 2013).

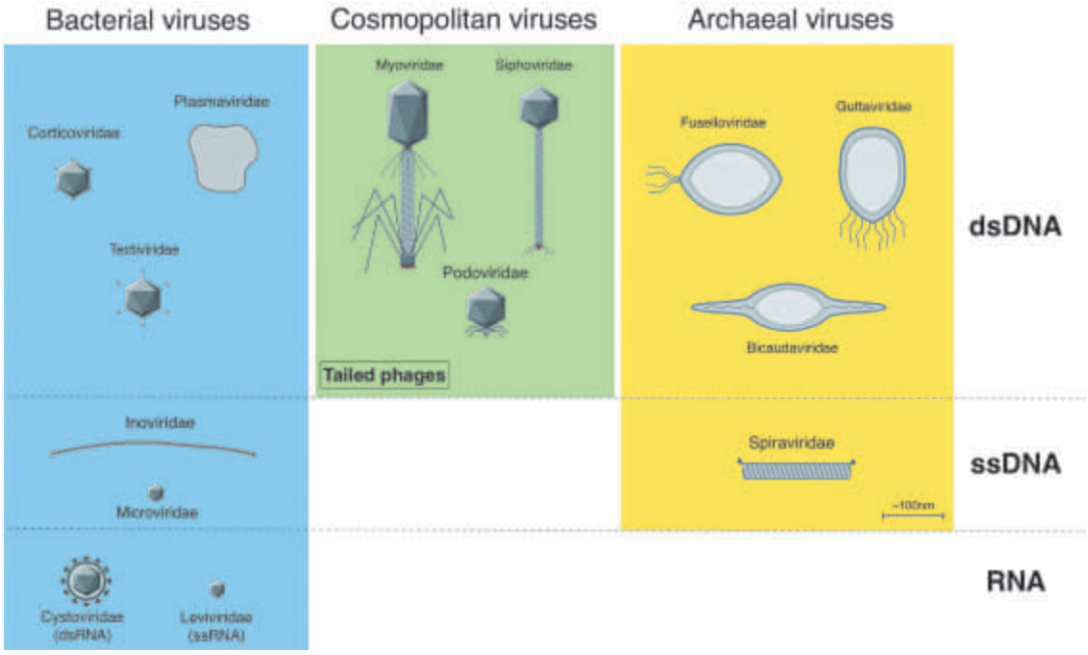

Fig. 1 Overview of phage morphologies. In most aquatic environments, phages infecting bacteria represent the largest fraction of viruses which include representatives containing each type of nucleic acid. *Myo-*, *Sipho-* and *Podoviridae* constitute the tailed phages (*Caudovirales*) members of which have dsDNA-genomes and have been found among archaeal and bacterial viruses (therefore here referred to as 'cosmopolitan'). Archaeal viruses represent only a small percentage of characterized phages. Examples found in hot springs like *Guttaviridae* and *Ampullaviridae* frequently have less regular shapes than bacterial phages. Thus far no archaeal phage containing a RNA-genome has been found.

Principles of phage-host relationships

Types of phage-infections

Phages can cause at least three different types of infections which are central to the outcome of phage-host interactions. In all cases, the phage first attaches to the surface of the host cell by specific binding to a 'phage receptor' followed by the injection of the phage genome into the host cell. What happens next differs between the types of infections. During lytic infections the phage genome serves as a template for the metabolic reprogramming of the host cell, the construction of new viral particles (i.e., virions) and the replication of the phage genome. Concomitantly, host resources become exploited and the host DNA becomes degraded. Following a latent period (in the range of hours), a variable number of phage progeny (i.e., burst size) is released during the lysis of the host cell. In lysogenic (or synonymously temperate) infections, the phage genome can either support a lytic infection or become quietly integrated into the host genome as so-called prophage. The basis on which this lysis-lysogeny decision is made is currently little understood but factors like cell size and the multiplicity of infection (i.e., ratio of phages to hosts) have been implicated. When lysogeny prevails, the prokaryotic cell is referred to as 'lysogen' or 'lysogenic cell.' In this phase most of the phage genome is inactive but potentially beneficial traits can be conferred to the host cell in a process called 'lysogenic conversion.' After a time period of variable length, prophages can spontaneously turn into a lytic cycle. Known triggers for this 'prophage induction' include DNA-damage e.g., through hydrogen peroxide, UV-C radiation and anthropogenic chemicals (Weinbauer, 2004) but also coordinated mechanisms like the recently discovered 'arbitrium' system (Erez et al., 2017). This system allows phages infecting bacteria of the genus *Bacillus* to coordinate their lysis-lysogeny decisions based on the density of the host population via virus-mediated signaling. The third infection type is referred to as chronic and is caused by members of the bacterial *Inoviridae* and the archaeal *Fuselloviridae* family. During chronic infections, the phage genome becomes integrated in the host cell as prophage (as for lysogeny) while viral progeny is produced and released without lysis of the host cell. Little is known about *Inoviridae* in natural environments but laboratory experiments using model organisms suggest a comparatively low burden for the host cell. In certain settings *Inoviridae* infections even developed mutualistic characteristics and increased the growth speed of the host (Shapiro and Turner, 2018). Most of the research about this type of infection has been carried out using phages of enterobacteria, but recent findings indicate that *Inoviridae* also play a role in a broad spectrum of aquatic bacteria (Roux et al., 2019). Fig. 2 shows an overview of the mentioned infection types.

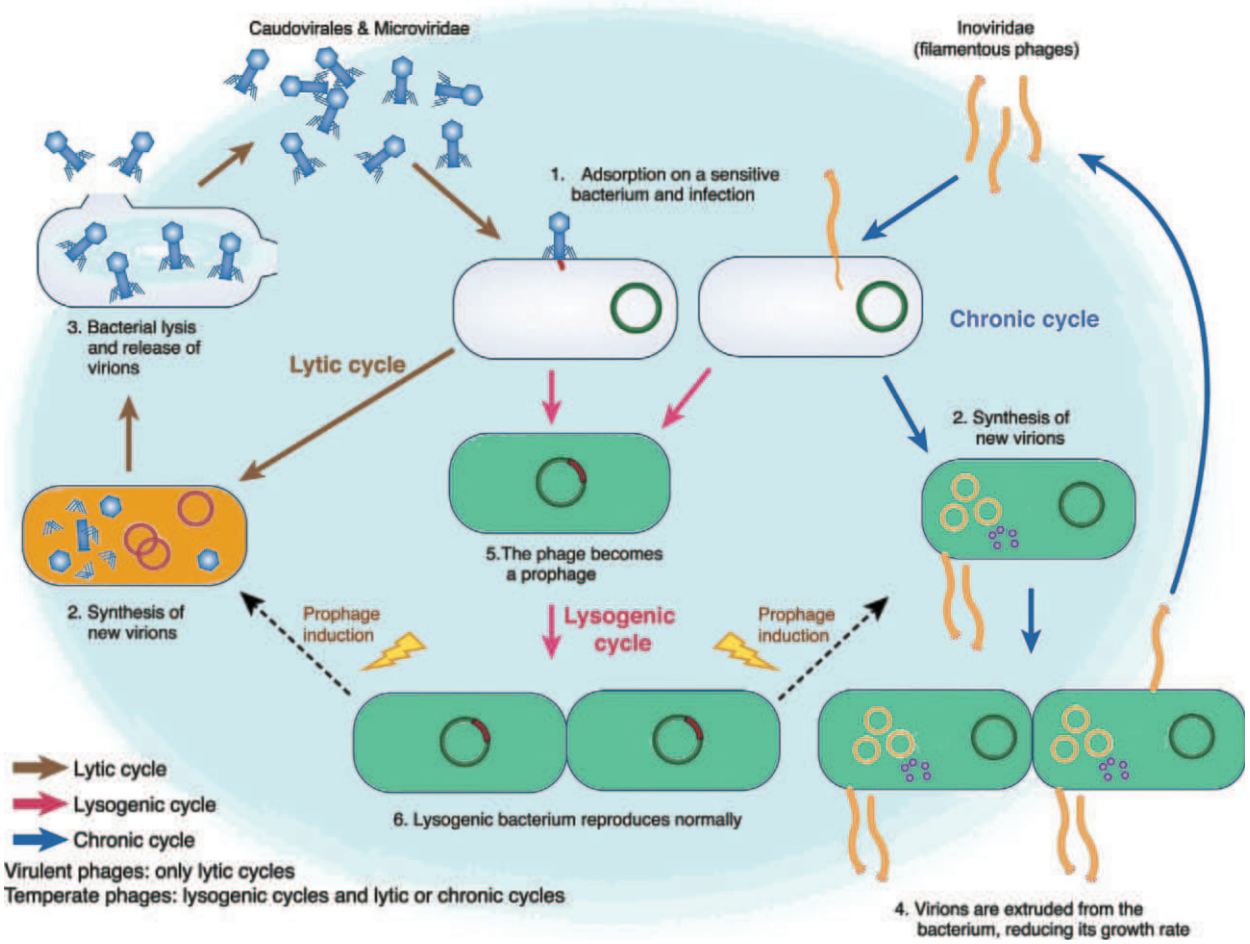

Fig. 2 Types of phage infections. Lytic infections lead to the reproduction of the phage genome, the synthesis of new virions, and the subsequent lytic release of viral progeny. Until the lysis of the host cell occurs, the metabolism of the host becomes altered by the phage (orange cell). Lysogenic infections result in the integration of the phage genome into the host cell. This can confer potentially beneficial traits to the infected cell through lysogenic conversion (green cells). *Inoviridae* cause chronic infections which combine lysogeny with the non-lytical release of virions. Modified from Sausset R et al. (2020) New insights into intestinal phages. *Mucosal Immunology* pp. 205–215. doi: 10.1038/s41385-019-0250-5.

Host-resistance and the arms race between phages and hosts

In aquatic environments a single host cell can be challenged by several distinct phages at the same time but not all phage-host encounters result in successful infection. One reason for this is the broad set of defense strategies employed by prokaryotes against phages. Phages on the other hand evolve mechanisms to bypass these defenses in a coevolutionary arms race which is a substantial driver of prokaryotic and phage-diversity (Koskella and Brockhurst, 2014). Basically, prokaryotes can either prevent, neutralize or abort infections by phages. Prevention frequently occurs through surface modifications e.g., the masking or mutating of phage receptors on the hosts surface (Hampton et al., 2020). Especially in highly streamlined genomes with comparatively fewer other resistance mechanisms, this might be the primary mode of resistance. The downside of this type of resistance is that, as phage receptors are often prominent proteins involved in nutrient uptake, altering them comes at a fitness cost for the host (van Houte et al., 2016). Phages overcome surface modifications either through the mutation of their own receptor-binding proteins, the enzymatic removal of sugars that mask docking sites on phage receptors or by using an alternative receptor for attachment. If a phage successfully overcomes this first line of defense and injects its genome into the host cell, the infection can still be neutralized by the host. Two mechanisms functioning as widespread prokaryotic 'immune system' are restriction modification- (R-M) and Clustered Regularly Spaced Short Palindromic Repeat- (CRISPR-) systems. Whereas R-M systems allow the host to assess whether DNA inside the cell is 'self' or 'non-self', CRISPR-systems respond adaptively and specifically by 'remembering and recalling' genomic bits of previously infecting phages. Phages counter R-M- and CRISPR-mediated defense e.g., by mutating parts of their genome to avoid recognition, by deactivating nucleases or even through mechanisms normally employed by the host. If a phage infection can neither be prevented nor neutralized, abortive infection (Abi) mechanisms can still limit the damage to the host population by triggering a programmed cell death in infected cells which lowers the number of released phage-progeny (Hampton et al., 2020). In addition to the systems mentioned above a series of novel defense and counter-defense mechanisms have been discovered in recent years. But not only phages and their hosts interact, also phages compete or cooperate with each other in order to overcome the host's defenses (Díaz-Muñoz et al., 2017; Dedrick et al., 2017; Landsberger et al., 2018). Competition among phages is frequently carried out through prophage-conferred 'superinfection exclusion' which either blocks the entry or replication of competing phages. This leads to a very complex interplay between phages and prokaryotes in natural systems which is difficult to disentangle.

Phage ecology in lakes

Enumeration of phages

Phages are incapable of active locomotion and are mainly transported by advection and Brownian motion (i.e., random motion of suspended particles) in the water column. Prokaryotes, if motile, sense and move along gradients of dissolved chemicals which carry no information about the location of phages. Therefore, contacts between phage and host are stochastic and mainly depend on the abundances of both partners. A series of methods for the quantification of viruses are in use today—each with their individual strengths and weaknesses. 'Plaque assays' rely on the counting of the visual signs ('plaques') phages leave when they lyse host cells growing on a culture plate. This method works well for lytic phages and when only a single type of host is investigated. However, environmental samples contain a multitude of prokaryotes of which only a tiny fraction can be cultured. It was the dominant application of such culture-based approaches that led to a significant underestimation of the number of active prokaryotes and viruses in the environment ('great plate count anomaly'). Although the necessary methodology had been developed 40 years earlier, actual abundances of dispersed viruses in aquatic environments were first attained in the late 1980s through the counting of virus-like particles (VLPs) sedimented on TEM-slides (Bergh et al., 1989). In the following years viruses have been started to be quantified using fluorescent dyes which sensitively stain nucleic acids in viral capsids in combination with epifluorescence microscopy (EFM), flow cytometry (FCM) and nanoparticle tracking analysis (NTA). If detailed genetic knowledge of the targeted phages is available, specific genotypes can also be quantified using quantitative PCR (qPCR) and the 'polony' (PCR colony) method. Notably, a recent comparative study indicated that sample preparation is delicate and that the various methods available for virus quantification might lead to significantly different results (Kaletta et al., 2020). Relative abundances of (metagenome-assembled) phage genomes can also be attained in the course of metagenomic analyses (i.e., the isolation and sequencing of viral DNA from environmental samples; Coutinho et al., 2018). An overview of methods including advantages and disadvantages is given in Table 1.

Abundances of viruses in lakes

In the water column of most lakes viral abundances fall in the range of 10^9–10^{11} VLP L^{-1}. Abundances have frequently been related to the trophic state of the waterbody (Jacquet et al., 2010). Consequently, the lowest values have been found in alpine and arctic lakes e.g., with 2×10^7 VLP L^{-1} in the Gossenköllesee (Austria) and the highest in hypereutrophic East African Soda Lakes (EASL) reaching $>10^{12}$ VLP L^{-1} (Peduzzi and Luef, 2009). Temporal (seasonal) and spatial (depth) variability within one lake may fluctuate by one order of magnitude with peak values occurring in more shallow waters or close to the surface during warmer and more productive periods (Jacquet et al., 2010). These fluctuations also occur on short temporal scales and some groups of phages like cyanophages exhibit diurnal infection patterns. Like total viral abundances, the average number of virions released per infected

Table 1 Methods for the enumeration of phages.

	Method	*Advantage*	*Disadvantage*	*Quantification*
Culture-based	Plaque assay	Simple Can also be used for phage-isolation	Requires cultivation of host	Only active and lytic phages of cultivated host
Particle-based	TEM	Information on phage morphology	Extensive manual counting	All phages
	EFM	Simple	Extensive manual counting	Low sensitivity for ssDNA and RNA viruses
	FCM	Fast	High initial cost for equipment	Low sensitivity for ssDNA and RNA viruses
	NTA	Gives also size distribution of VLPs	High initial cost for equipment	All phages
Sequence based	qPCR	Sensitive detection of specific genotype	Requires sequence information	Only specific genotype
	Polony method	Can capture diversity of gene	Requires sequence information	Group of phages sharing homologous gene
	Metagenomics	Acquisition of sequence information	Time consuming and comparatively costly	Only relative abundances of either DNA or RNA phages

TEM, transmission electron microscopy; EFM, epifluorescence microscopy; FCM, flow cytometry; NTA, nanoparticle tracking analysis; qPCR, quantitative polymerase chain reaction.

cell ('burst size') also relates to the trophic state of the water column. In oligotrophic freshwaters burst sizes of ~30 virions per infected cell and ~40 in eutrophic environments have been reported (Parada et al., 2006). Extremely low burst sizes but a high frequency of visibly infected cells (FVIC, i.e., the fraction of cells in which virion-formation is visible using TEM) have been reported from ultraoligotrophic lakes in the Arctic and Antarctic. This has been explained by 'pseudolysogeny' which might correspond to stalled infections under severe growth-limitation of the host (Anesio and Bellas, 2011). In comparison to marine environments, the total abundances of pelagic VLPs in lakes tend to be slightly higher and to vary stronger with seasons (Wilhelm and Matteson, 2008). A correlation-based study also indicated that bacterial, cyanobacterial and chlorophyll *a* concentrations might have different relative importance as drivers of viral abundance in marine and in freshwater systems. One possible explanation for these differences might be higher decay rates of viruses in lakes e.g., caused by higher concentrations of clays and particulate matter. In lake sediments VLP densities range between 10^7–10^{10} per gram dry weight in the upper layers, decreasing rapidly with depth (Jacquet et al., 2010). Sediments can also be an important reservoir for phages which can stay infectious for decades (Danovaro et al., 2008; Hargreaves et al., 2013). For an extensive review of viral abundances in a diverse set of aquatic environments readers are referred to the chapter on viruses in the previous issue of the Encyclopedia of Inland Waters (Peduzzi and Luef, 2009).

Virus-to-prokaryote ratios (VPRs) and the piggyback-the-winner (PtW) model

Even though an important first step, viral abundances alone cannot be used to directly measure their ecological impact. An attempt to define a more functional ecological parameter is the 'virus-to-prokaryote ratio' (VPR) or often synonymously named the 'virus-to-microbial cell ratio' (VMR). An extensive meta-study compiled VPRs from 210 publications and various environments (Parikka et al., 2017): In freshwater the mean VPR is 17.2 (from 0.01 to 267, $n = 229$) whereas in marine environments VPRs tend to be higher (mean 26.5, $n = 233$). The authors confirmed previous findings of a significantly positive correlation of VPR with the concentration of chlorophyll *a*, the frequency of lysogenic cells (FLC) and the frequency of visible infected cells (FVIC). A significantly negative correlation was found between VPR and temperature (hot springs tend to have very low viral abundances) and salinity (salines have both, high viral and prokaryotic abundances). However, Parikka et al. (2017) also advised 'extreme caution' when attempting to infer phage-host relationships from VPRs. A recent example for this notion is the Piggyback-the-Winner (PtW) model. PtW has been based on two findings: (1) a systematic decline of VPRs with higher microbial densities and (2) a concomitant increase in viral genes indicative of a lysogenic lifestyle (Knowles et al., 2016). PtW proposes that at higher microbial densities the frequency of lysogeny increases which in turn would suppress lytic infections (e.g., through 'superinfection exclusion'). Although this would explain the observed lowered VPRs at higher microbial densities the authors could not corroborate a positive correlation of prokaryotic densities and the frequency of chemically inducible lysogenic cells in an extensive follow-up survey (Knowles et al., 2017). Subsequently the PtW model was contended based on the current lack of 'robust empirical and theoretical support' (Weitz et al., 2017). This high-profile discourse highlights both the conceptual and technical difficulties associated with the identification of a central parameter capable of gauging viral activity in aquatic systems and the apparent need to integrate lysogenic phages into the current theoretical framework of viral ecology.

Lysogenic phages in aquatic ecosystems

One reason why the role of lysogenic phages in aquatic ecosystems is little understood is their elusive nature. They lead a double life as prophages in prokaryotic genomes which are not trivial to detect and virions which are indistinguishable from the particles of lytic phages. This makes it difficult to dissect and quantify their impact in natural systems. Previously the significance of lysogeny in prokaryotic communities has been assessed through the induction of prophages by the mutagen mitomycin C (Weinbauer, 2004; Knowles et al., 2017). Notably, not all prophages can be induced this way which can lead to significant underestimates (Köstner et al., 2019). Nonetheless, several studies in marine environments found that the frequency of lysogenic cells is high in winter and decreases rapidly during the increase of productivity in spring (McDaniel et al., 2002; Brum et al., 2016). A similar pattern has also been observed in lakes (Fig. 3; Thomas et al., 2011).

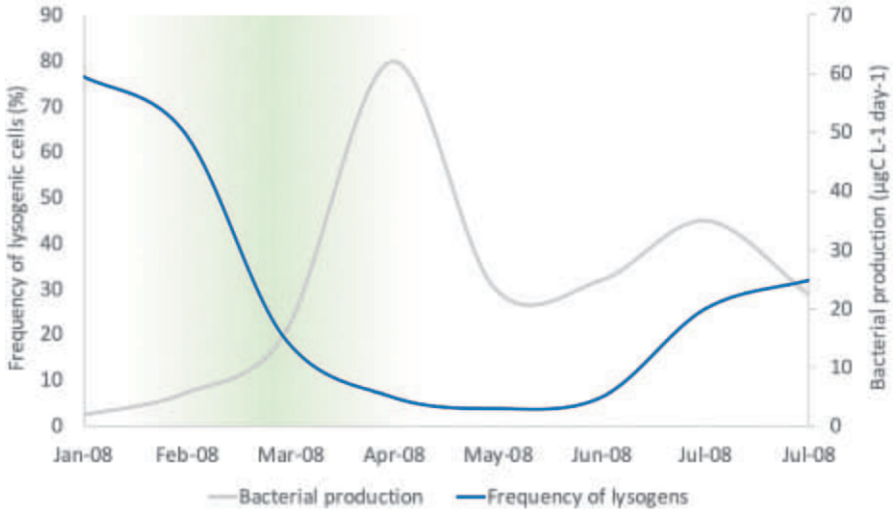

Fig. 3 Schematic representation of the seasonal trend of lysogeny in lake Bourget (France, 2008). During the winter-spring transition (green shading) the frequency of lysogenic cells, as assessed by mitomycin C induction, is inversely related to bacterial production (Thomas et al., 2011).

Experimental studies with water from Lake Pavin indicate that this switching from lysogeny to lysis might be triggered by the increase in nutrient concentrations (Pradeep Ram and Sime-Ngando, 2010). This is consistent with physiological studies showing that (1) shifts to higher nutrient concentrations can lead to quick changes in the cell size of prokaryotes and that (2) phage Lambda, the model organism for lysogenic phages, frequently opts for a lytic cycle when infecting larger cells. The recent interest in the ecological role of temperate phages has been spurred by experimental studies implicating lysogenic phages with a multitude of functionalities. Examples are the prophage-mediated defense against other phages (Dedrick et al., 2017), prophage-mediated cell-to-cell signaling (Erez et al., 2017), the scavenging and transfer of beneficial genes to host-populations, the invasion of lysogens into non-lysogenic host populations and new habitats (Brown et al., 2006) and the potentially prophage-mediated establishment of a symbiotic relationship of bacteria with aquatic metazoa (Jahn et al., 2019). Since prophages persist as genetic elements, their investigation has been significantly progressed through (meta)genomic and bioinformatic studies. Among others this led to the identification of prophages in almost half of all sequenced bacterial genomes (Touchon et al., 2016) and specifically extended our prospective knowledge about prophages of the *Inoviridae* family, suggesting that these phages are far more widespread than previously thought (Roux et al., 2019).

Metagenomic investigation of phage communities in lakes

In the past two decades, genomic and metagenomic studies of phages and their hosts revealed astonishing aspects of prokaryote-phage interplay in aquatic ecosystems. Examples are the discovery of novel phage-defense mechanisms (Hampton et al., 2020), previously overlooked prophages in prokaryotic genomes (Roux et al., 2019), the widespread occurrence of phage-encoded auxiliary metabolic genes (AMGs) in phage-genomes (Zimmerman et al., 2020), the reconstruction of genomes of non-isolated phages (e.g., Kavagutti et al., 2019), and the prediction of previously uncharacterized phage-host pairs (Coutinho et al., 2018). One major hindrance in the current metagenomic investigation of phages in lakes is their incredible genetic diversity which is not represented in existing sequencing databases and therefore has been dubbed 'the great viral unknown.' This is aggravated by biases of sequence databases towards certain well-sampled environments like the human gut and the ocean. Consequently, in metagenomic studies of viruses in freshwater environments as little as 3% and at most 30% of the sequences display reasonable sequence homology to known viral sequences (Bruder et al., 2016). The metagenomic characterization of the composition of phage communities in lakes is therefore based on conserved genomic features and sets of genes found in different groups of phages. Notably, this characterization of viral communities is not always congruent with the morphological characterization of virions in aquatic samples using TEM (Brum et al., 2013). This has also been attributed to several biases in sample preparation identified during the investigation of a large group of previously overlooked phages (Kauffman et al., 2018). Although in most investigated perennial ponds and lakes *Caudovirales* seem to dominate the viral community (e.g., Skvortsov et al., 2016), notable exceptions of lakes with a majority of ssDNA-viruses are known (e.g., Roux et al., 2012). Recent advancements in sequencing technology and bioinformatics allowed the temporal and spatial monitoring of the relative abundance of single metagenome-assembled phage genomes (i.e., phage genomes reconstructed from acquired sequencing data) in lakes. Among others this revealed that (1) in lakes individual phages have distinct dynamics of relative abundance over the course of a year, reaching from single appearances in certain months to recurrent patterns of appearance (Arkhipova et al., 2018) and that (2) the hypolimnion is constituted of different sets of phages which behave less dynamic than those in the epilimnion (Fig. 4; Kavagutti et al., 2019).

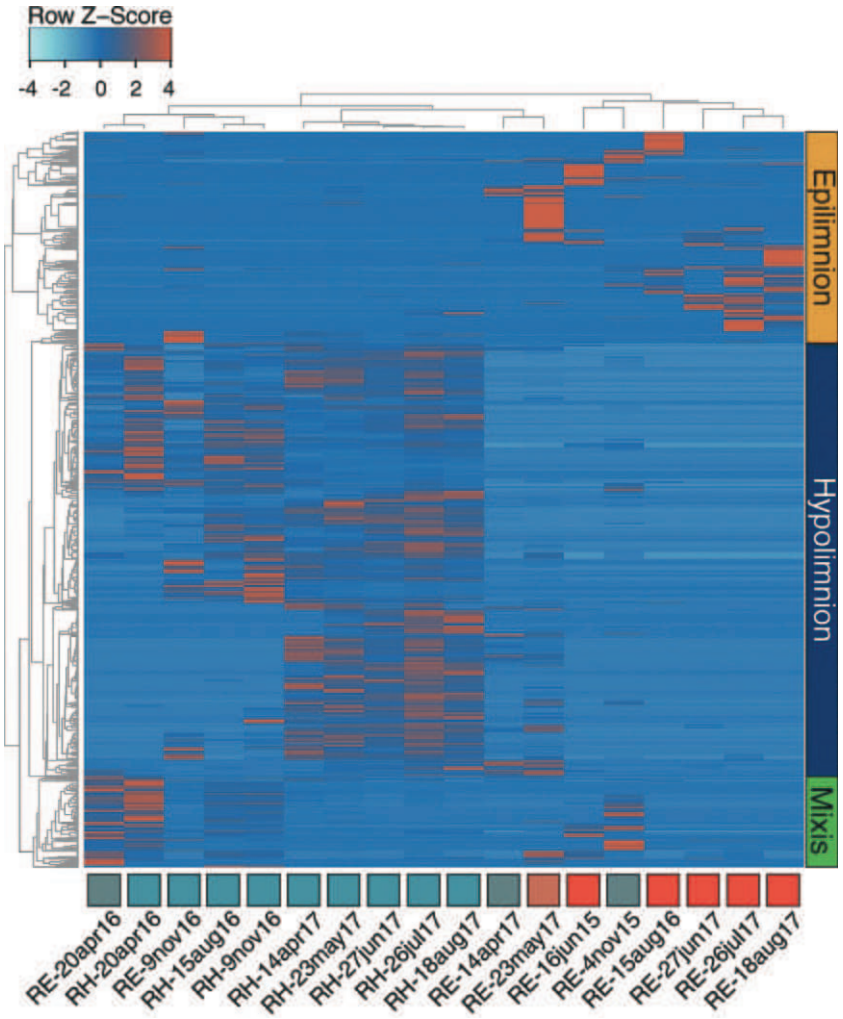

Fig. 4 Composition of the pelagic viral community of Rimov reservoir (Czech Republic, 2016–2017). Each column corresponds to a single metagenome; each line of the y-axis corresponds to the genome of one of 1398 metagenome-assembled phage genomes. Red indicates relative presence of the phage genome in the water column, light blue represents relative absence. Epilimnion (RE) and hypolimnion samples (RH) were taken at 0.5 m respectively 30 m depth during summer stratification whereas mixis samples were taken during winter/spring mixing. From Kavagutti VS et al. (2019) Phage-centric ecological interactions in aquatic ecosystems revealed through ultra-deep metagenomics. *Microbiome* **7**(1). doi: 10.1186/s40168-019-0752-0.

Ecological consequences of phage-infections in lake ecosystems

The viral shunt

One of the first ecological consequences of phage infection explored in aquatic ecosystems was the potential impact of lytic phages on carbon-cycling in the ocean. A model named 'viral shunt' assumes that lytic infections release dissolved and particulate organic matter (DOM and POM) from lysed hosts which in turn can stimulate the growth of surrounding prokaryotes and can hamper the transport of organic matter to higher trophic levels (Fig. 5). In surface waters of the ocean an estimated 6–26% of photosynthetically fixed carbon is channeled this way (Wilhelm and Suttle, 1999). For lakes such estimates are missing. However, the amount of organic carbon flowing through the viral shunt might be related to prokaryotic abundances and the current lytic activity of phages, which can vary significantly across lakes and over the year (Keshri et al., 2017; Bettarel et al., 2004; Ram et al., 2010; Meunier and Jacquet, 2015). The stimulatory effect of the viral shunt on surrounding prokaryotes on the other hand might depend on the trophic status of the water column (Wilhelm and Matteson, 2008; Jacquet et al., 2010).

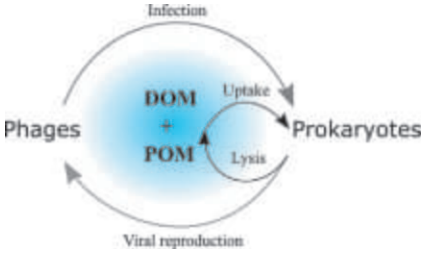

Fig. 5 The viral shunt. Virus-mediated lysis leads to the release of dissolved organic matter (DOM) and particulate organic matter (POM) which serves as an additional nutrient pool for surrounding prokaryotes.

Cyanophage-mediated inhibition of CO_2-fixation

Another ecological consequence of lytic phage-infections originates from the alteration of the host metabolism by phages during lytic infections. This has been studied in detail for cyanobacteria and cyanophages. Cyanophages often encode AMGs implicated in phosphorus acquisition and intracellular nitrogen recycling (Zimmerman et al., 2020). In addition, these phages frequently cause a significant inhibition or even complete cessation of CO_2-fixation in infected host cells during the latent phase (Puxty et al., 2016). This effect is widespread in marine *Synechococcus* and *Prochlorococcus* which are responsible for an estimated 10% of global primary production. Combined with the finding that about half of marine *Synechococcus* are infected by cyanophages at the same time, cyanophage-mediated inhibition of CO_2-fixation might affect global carbon budgets (Sieradzki et al., 2019). Originally this effect was discovered in freshwater cyanobacteria (Ginzburg et al., 1968). Although calculated estimates are missing it seems likely that this process also significantly affects primary production in lakes. Contrasting the effect of cyanophage-infections a recent metagenomic study in Lake Baikal identified AMGs that might enhance light-independent CO_2-fixation in nitrifying bacteria. Additional examples of phage-mediated metabolic tinkering in aquatic ecosystems can be found in a recent review by Zimmerman et al. (2020).

Impact of lytic phages on prokaryotic community composition

Phages have been proposed to 'maintain microbial diversity at many levels and across ecosystems' (Koskella and Brockhurst, 2014). At the level of prokaryotic communities, ambient phages have been experimentally shown to impact their composition (e.g., Weinbauer et al., 2007; Bouvier and Del Giorgio, 2007) and frequently also their species richness (Weinbauer et al., 2007; Meunier and Jacquet, 2015). Although the exact mechanisms *in situ* remain unknown this was attributed to the differential control of various members of the community by lytic phages (Fig. 6A; Schwalbach et al., 2004; Bouvier and Del Giorgio, 2007). While these experiments were carried out with marine samples, Meunier and Jacquet (2015) found that the effect of ambient phages on community richness in Lake Bourget is concentration-dependent (Fig. 6B).

However, this density-dependent relationship of VLP-concentration and species richness was not found in experiments one month earlier and one month later. Explanations for these mixed results can be derived from two concepts of classic predator-prey relationships: (1) negative-frequency dependent selection (NDS; i.e., more abundant members of the community are preferentially targeted by phages) and (2) the competitive advantage conferred to rare prokaryotic groups by the diminution of dominant ones by predators. While NDS derives from concentration-dependent phage-host contact rates in the water column, the latter might be mediated by the redistribution of nutrients from more abundant prokaryotic groups to more rare ones via the viral shunt (Meunier and Jacquet, 2015). The observed phage-mediated increase in species richness could therefore reflect an increase of previously rare community members to levels above detection, whereas in the absence of phages certain phage-controlled prokaryotic groups might become dominant (Fig. 6). The fact that not only the most abundant prokaryotic groups react in phage-treatments can be explained by the finding that the groups of prokaryotes sustaining the most phages in the water column are not necessarily the most abundant ones but can also be the most active (Bouvier and Del Giorgio, 2007). The findings that phage-treatments did not increase species richness in all experiments (Meunier and Jacquet, 2015) might be explained by the significant fluctuation of the lytic activity over the course of the year (Bettarel et al., 2004; Ram et al., 2010) and the possible insufficient resolution of the method used to discriminate different prokaryotic groups (Johnson et al., 2019). In a survey of 25 mostly shallow temperate lakes, Keshri et al. (2017) found that phage-mediated lysis could explain 33% of the variation in bacterial diversity in temperate lakes during summer (Fig. 7). However an earlier study found that bottom-up factors (nutrients and organic matter) controlled bacterial diversity more significantly than phages, ciliates and flagellates together (Berdjeb et al., 2011).

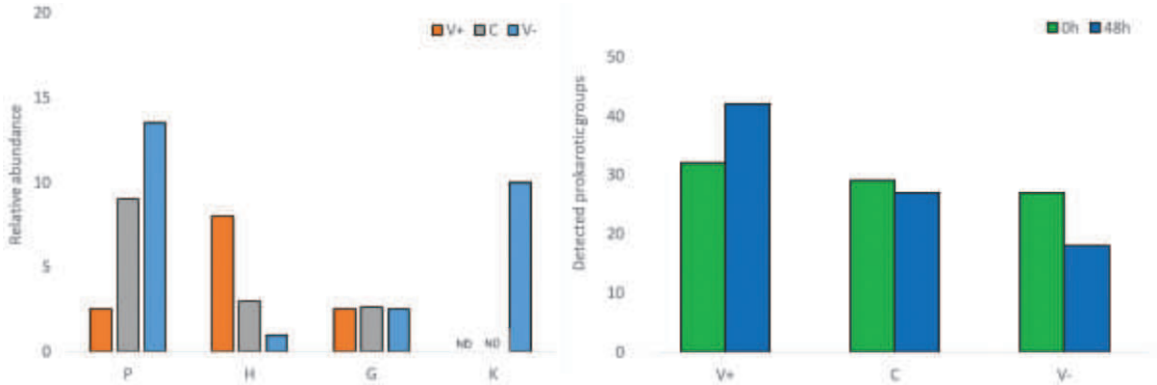

Fig. 6 (A) Schematic representation of prokaryotic groups (here arbitrary named 'P', 'H', 'G', 'K') which are differentially controlled by ambient lytic phages. P: strongly phage-controlled, abundance decreases at elevated concentrations of viruses (V+) and increases at lowered concentrations of viruses (V-); H: not phage-controlled but profits from viral predation on other groups; G: not impacted by phages; K: strongly phage-controlled, not detected (ND) in presence of ambient phages. Control (C, after Schwalbach MS, Hewson I and Fuhrman JA (2004) Viral effects on bacterial community composition in marine plankton microcosms. *Aquatic Microbial Ecology* **34**(2): 117–127. doi: https://doi.org/10.3354/ame034117; Bouvier T and Del Giorgio PA (2007) Key role of selective viral-induced mortality in determining marine bacterial community composition. *Environmental Microbiology* **9**(2): 287–297. doi: https://doi.org/10.1111/j.1462-2920.2006.01137.x). (B) Effects of the increase and decrease of the concentration of ambient viruses on the richness of prokaryotic communities after 0 h and 48 h (France, March 2013). V+: increase of the VLP-concentration to ~1.5 ×; V: control with 1 × VLP-concentration; V-: virus-reduced samples with ~0.15 × VLP-concentration. Control (C, after Meunier A and Jacquet S (2015) Do phages impact microbial dynamics, prokaryotic community structure and nutrient dynamics in Lake Bourget? *Biology Open* **4**(11): 1528–1537. doi: https://doi.org/10.1242/bio.013003).

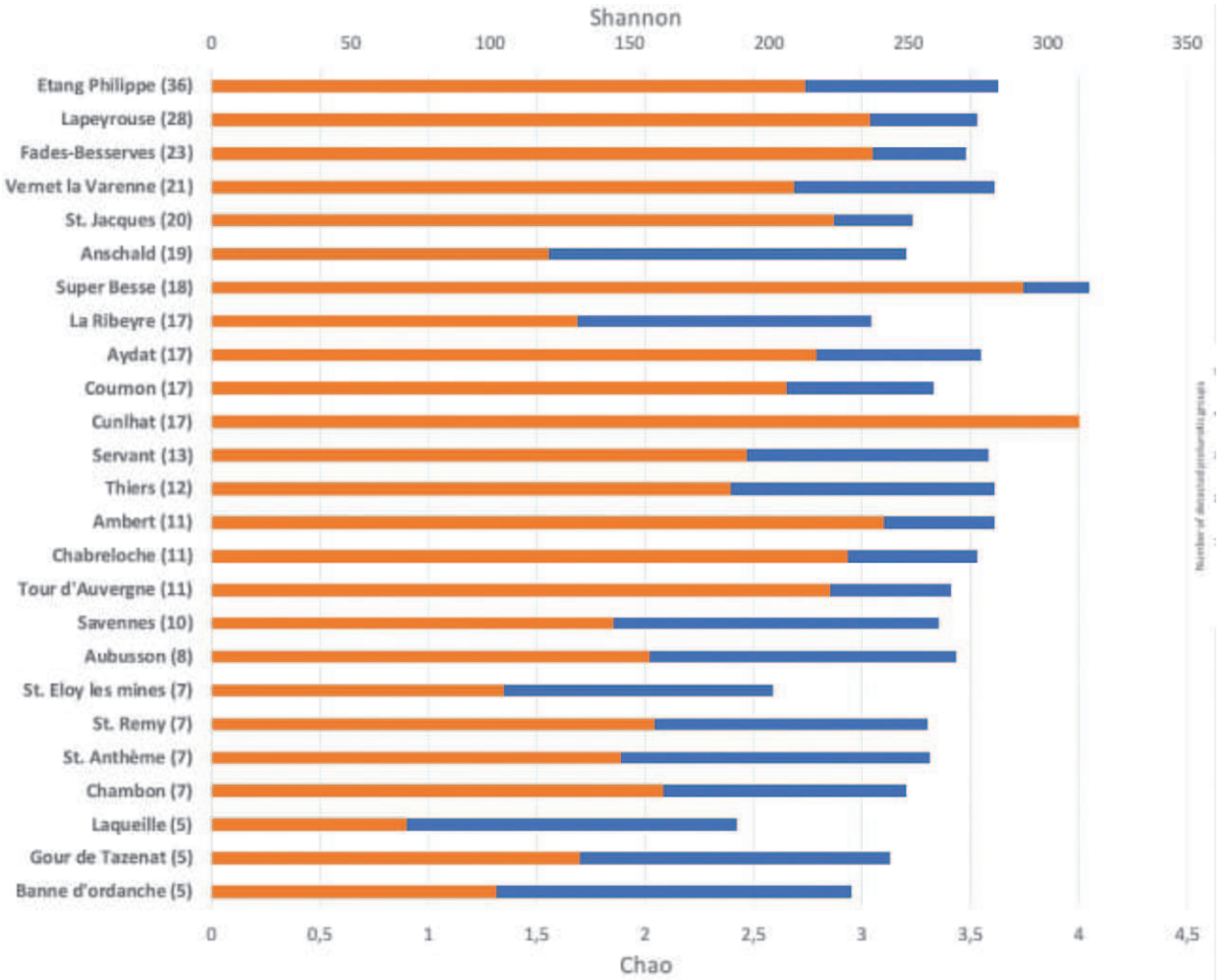

Fig. 7 Shannon- (diversity) and Chao1- (richness) values for prokaryotic communities in 25 temperate lakes as assessed by 16S rRNA (V3-V4) sequencing (July 2015). The frequency of infected cells (%) found in each lake is given in brackets next to the name of the lake. After Keshri J et al. (2017) Differential impact of lytic viruses on the taxonomical resolution of freshwater bacterioplankton community structure. *Water Research* **124**: 129–138. doi: 10.1016/j.watres.2017.07.053.

A model that integrates both phage-mediated top-down and nutrient-mediated bottom-up control is the Kill-the-Winner model (KtW; Thingstad and Lignell, 1997). KtW hypothesizes that the 'winner' in the competition for nutrients (i.e., the most abundant or most active hosts) are held in check by lytic phages through NDS. In addition, KtW emphasizes that prokaryotes have to economize between resource acquisition and investment into phage resistance which is tied to fitness trade-offs (Winter et al., 2010). These trade-offs on the other hand are thought to be a major mechanism contributing to prokaryotic diversity under changing environmental conditions. In order to assess these hypothetical explanations, a more detailed exploration of the impact of phages on prokaryotic communities in natural ecosystems is needed.

Phages as drivers of prokaryotic evolution and diversity

Prokaryotes and phages in natural ecosystems are extremely diverse. To simplify the investigation of the diversity of prokaryotic communities in the environment, operational taxonomic units (OTUs) commonly based on amplicon sequencing of a variable segment of the 16S rRNA are used. A single lake sample can host hundreds of prokaryotic OTUs (Keshri et al., 2017), each representing something in between a prokaryotic genus and a species (Johnson et al., 2019). Despite their extensive use OTUs stayed controversial in the assessment of prokaryotic diversity since extensive horizontal gene transfer (i.e., the transfer of genetic information among distinct cells) in prokaryotes (and phages) occurs even at lower taxonomic ranks (Cordero and Polz, 2014; Gregory et al., 2016). As an illustration, among >2000 strains of *E. coli* with an average genome size of 5000 genes, only around 3000 genes occur in all of them, whereas the additional genes contained in at least one *E. coli* strain cover almost 90,000 gene families (Booth et al., 2016). One prokaryotic species in any given environment disaggregates into numerous sequence-discrete populations consisting of individuals having an average nucleotide identity (ANI) of 94–100% within a single population and 80–85% between populations (Rodriguez-R and Konstantinidis, 2014). Since prokaryotes have genomes in the range of millions of base pairs, already single populations can contain a broad genetic diversity which is technically difficult to assess (Kashtan et al., 2014). Also, phages differentiate into discrete genotypic populations (Gregory et al., 2016). However, it is currently not known at which taxonomic host-rank individual phage genotypes preferentially operate in natural ecosystems. Although phages with a

broader host range have been described, most isolated phages infect hosts of the same strain or species. For these reasons the most comprehensive studies identifying phages as drivers of prokaryotic diversity are coevolutionary studies of isolated phage-host pairs in the laboratory (Koskella and Brockhurst, 2014). For example, co-cultivation of *Pseudomonas fluorescens SBW25* with the lytic phage phi2 increased the mutation rates in both partners, especially in genes relevant for phage-host interaction. This led to the rapid diversification of phage and host and constrained the acquisition of mutations beneficial for intraspecific competition (Scanlan et al., 2015). These findings reflect an arms race dynamic, i.e., the antagonistic coevolution of both partners consisting of adaptation of the host to the parasite (evolution of resistance) and counter-adaptation by the phage (restoration of infectivity). This arms race between *P. fluorescens SBW25* and phi2 decelerates after about 250 bacterial generations likely due to the increasing cumulative trade-off of resistance- respectively infectivity- mutations and gives way to sustained oscillations of individual bacterial- and phage populations which emerged from this arms race (Koskella and Brockhurst, 2014). This appears to be similar to the overall behavior of natural viral communities in the sunlit ocean (Ignacio-Espinoza et al., 2020). However, individual phage genotypes in lakes, especially those in the epilimnion, appear to be less stable than those in the open ocean which might support a different overall behavior of viral communities in lakes (Arkhipova et al., 2018; Kavagutti et al., 2019; Ignacio-Espinoza et al., 2020). While most studies and models focus on the activities of lytic bacteriophages, lysogenic (and chronically infecting) phages lack comparable experimental and theoretical frameworks. Lysogenic phages potentially have similar effects on prokaryotic communities and populations when reproducing lytically. However, the same effects might be mitigated e.g., through superinfection exclusion during the lysogenic phase (Knowles et al., 2016). How lysis-lysogeny decisions are controlled in natural ecosystems and if all lysogenic phages have a similar intrinsic tendency for the lytic respectively the lysogenic cycle remains little understood. Little is also known about the quantitative effect of phage-mediated horizontal gene transfer ('transduction') for the diversification of ambient prokaryotic populations. While numerous observations document the importance of phage-mediated horizontal gene transfer for evolutionary innovations in prokaryotes and eukaryotes (Shutt and Gray, 2006), its role in ecological processes needs further investigation.

Potential functioning of prophages in grazing-defense

Besides by lytic phages, prokaryotic mortality in lakes is often strongly controlled by protist grazers. In the case of lysogens, prophage and host share a common fate when ingested by a grazer. Under strong grazing pressure this might select for prophages conferring traits protecting their hosts against grazing. Support for this mechanism comes from two lines of evidence. First, experimental studies showing that prophage-encoded toxins kill grazers and increase the abundance of the respective lysogens (Arnold and Koudelka, 2014) and second, findings that substantiate the 'coincidental evolution hypothesis.' This hypothesis is based on the similarity of the cellular processes mediating phagocytosis in immune cells and in protist grazers and proposes that virulence factors (i.e., factors promoting the pathogenicity of bacteria) frequently evolved in bacteria in response to grazing pressure (Adiba et al., 2010). Support for this comes from the finding that various protist grazers select for virulence-related traits in waterborne pathogens like *Legionella* (Amaro et al., 2015) and from studies reporting a dual function of virulence factors in virulence as well as in grazing protection (Erken et al., 2013). Prophages are known to confer virulence factors e.g., during the pathogenesis of diphtheria, botulism and cholera and therefore can be assumed to play a role in this process. Besides prophage-encoded toxins this is supported by the widespread occurrence of prophage-encoded virulence factors in non-pathogenic environmental *Vibrio* (Castillo et al., 2018). Recently Kavagutti et al. (2019) proposed that the presence of genes implicated with the inactivation of reactive oxygen species (ROS) in 10% of phage genomes recovered from freshwater might stem from protective measures against grazers (Fig. 8). It remains to be tested how relevant the proposed role of prophages in the defense against protist grazers is in lakes and other aquatic ecosystems.

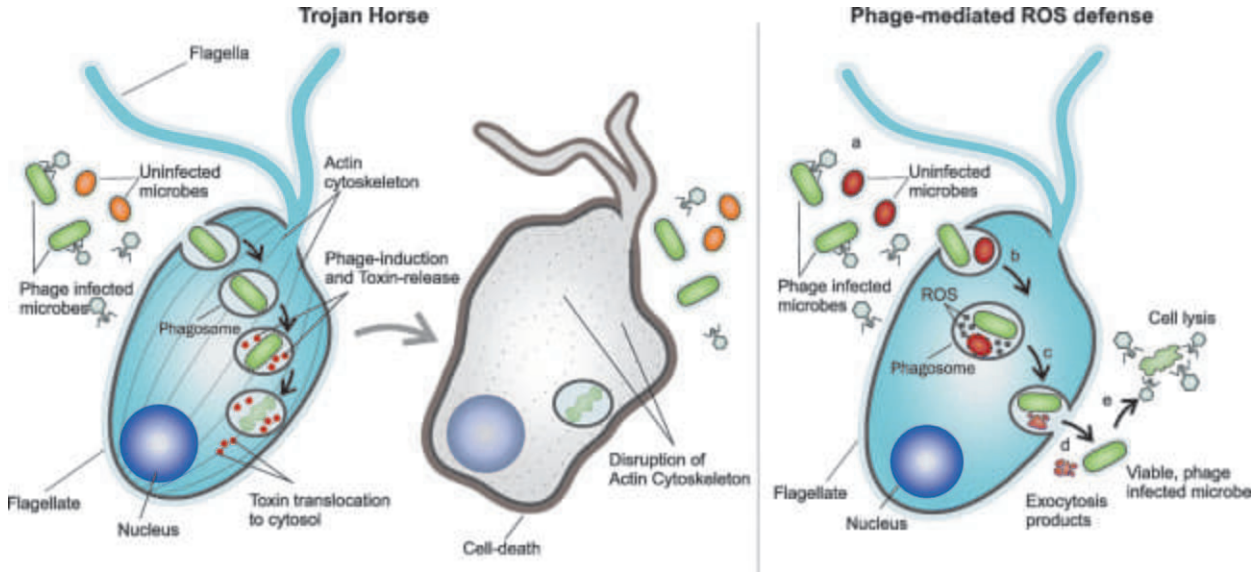

Fig. 8 Phage-mediated defense mechanisms against grazers. Left: 'Trojan horse' mechanism: A lysogen becomes ingested by a protist grazer. Digestion induces the production a phage-encoded toxin which disrupts the actin-cytoskeleton of eukaryotic cells. The toxin kills the grazer and thereby negatively selects against it. Right: A bacterium escapes the digestion by a grazer through a phage-encoded ROS-defusing mechanism. From Kavagutti VS et al. (2019) Phage-centric ecological interactions in aquatic ecosystems revealed through ultra-deep metagenomics. *Microbiome* **7**(1). doi: 10.1186/s40168-019-0752-0.

Knowledge gaps

- Roles of lysogenic phages in aquatic environments.
- Ecological factors directing lysis-lysogeny decisions.
- Archaeal phages in aquatic ecosystems.
- *Inoviridae* in aquatic ecosystems.
- Quantification of cyanophage-mediated inhibition of CO_2-fixation in lakes.

Case studies

Phage-mediated trophic cascade in east African Soda Lake

Site	*Country*	*Concept covered*	*Reference*
Lake Nakuru	Kenya	Phage-mediated trophic cascade	Peduzzi et al. (2014)

East African Soda Lakes (EASL) host large flocks of *Phoeniconaias minor* (Lesser Flamingos). These birds are considered Near Threatened by the International Union for Conservation of Nature and Natural Resources (IUCN) and conservation efforts have been hampered by a lack of understanding of their migration patterns. The preferred food source of *P. minor* is the filamentous cyanobacterium *Limnospira fusiformis* (formerly designated *Arthrospira fusiformis)* which can form extensive blooms in EASL (Schagerl, 2016). These blooms have been found to crash unpredictably due to previously unknown reasons. After ruling out other potential causes, Peduzzi et al. (2014) found that thus far uncharacterized phages caused a massive lysis of *L. fusiformis* in Lake Nakuru (Kenya). Among others, this has been assessed by the determination of the frequency of visibly infected *L. fusiformis* cells using TEM. Since phage particles become visible only during part of the infection cycle the actual number of infected cells can be assumed to be several times higher. During periods of steep declines in *L. fusiformis* biomass in lake Nakuru, up to 24% of *L. fusiformis* cells showed visible signs of infection indicating that the large majority of *L. fusiformis* cells had been infected at that time. These bloom crashes coincided with the migration of *P. minor* flocks from the affected lake and might be an important factor directing their migration behavior. Although *L. fusiformis* phages require further characterization, this study demonstrates that phages can trigger trophic cascades affecting even top consumers within lake ecosystems. It also links phage ecology to the waxing and waning of cyanobacterial blooms which impose serious risks to human health and drinking water quality in lakes worldwide.

Role of phages in cholera epidemics in Dhaka

Site	*Country*	*Concepts covered*	*References*
Dhaka	Bangladesh	Lysogenic conversion Lytic control of bacterial populations	Faruque et al. (2005a, 2005b)

Cholera still ravages in developing countries and according to WHO-numbers leads to 21,000 to 143,000 deaths per year. The transmission of the disease has been linked with the ingestion of water containing the aquatic bacterium *Vibrio cholerae* by Robert Koch as early as 1884. Today it is known that the occurrence of cholera epidemics coincides with the increased prevalence of often antibiotic resistant *V. cholerae* strains belonging to the O1 and 0139 serotypes in surface waters. A hallmark of these strains is that they have been infected by the lysogenic CTX-phage (*Inoviridae* family) which encodes the cholera toxin. Faruque et al. (2005a) revealed that during the seasonal cholera epidemic in Dhaka (Bangladesh) over a 3-year period, the incidence of *V. cholerae* O1 and 0139 in surrounding surface waters was negatively correlated with the incidence of phages lytic to these serotypes. This was further detailed in a follow-up paper (Faruque et al., 2005b) in which the abundance of one of those lytic phages (JSF4/ICP1, Seed et al., 2011) in surface waters and patient stools was found to be negatively correlated with the number of cholera patients in the 2004-epidemic. This was true for both the onset of the epidemic as well as its decline. The important role of JSF4/ICP1 and related phages was later substantiated by the genetic and molecular characterization of *V. cholerae* phages in the same region over a 10-year period (Seed et al., 2011) as well as experiments in which these phages were tested as potential therapeutic agent against cholera (Yen et al., 2017). This example illustrates that lytic phages as well as lysogenic phages play an important role in cholera epidemics and likely also for other waterborne pathogens (Feichtmayer et al., 2017). What remains to be answered is how exactly these phages interact with *V. cholerae* within aquatic environments and how this integrates with the known interplay of *V. cholerae* with other biota.

Conclusion

This chapter set out to outline general principles governing phage-host interactions. These should provide a comprehensible and well-founded basis for the understanding of potential consequences of phage infections in lake ecosystems. However, since the body of literature on phages is extensive this can only cover some aspects in phage ecology. Care was taken to choose topics which are of both ecological relevance and due to the close connection of lakes with human activities of relevance to human health.

See Also: Structures and functions of Inland Waters - Groundwater: Presence and Role of Prokaryotic Viruses in Groundwater Environments

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Relevant websites

https://talk.ictvonline.org/taxonomy/—Current taxonomic classification of viruses by the ICTV.
https://www.genome.jp/virushostdb/—Database of virus-host associations.
https://seaphages.org—Educational initiative for undergraduates 'SEA-PHAGES' (Science Education Alliance-Phage Hunters Advancing Genomics and Evolutionary Science).

Diversity and Dynamics of Bacterial Communities in Freshwater Lakes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

16S rRNA amplicon sequencing Denotes a method to describe the taxonomic composition of bacterial and archaeal communities. A diagnostic region of the 16S rRNA gene is PCR amplified from an environmental DNA sample for high throughput sequencing and subsequent annotation by comparing with previously classified 16S rRNA sequences.

Anaplerotic reaction Anaplerotic reactions are reactions that replenish intermediate compounds of a metabolic pathway in the cell.

Auxotrophy Auxotrophy is an obligate metabolic dependency typically linked to genome streamlining. Auxotrophic bacteria require exogenous source of essential biomolecules that must be provided by other members of the community who are capable of producing this biomolecule (prototroph).

Axenic cultures In microbiology, axenic culture refers to a culture that contains only a single population of microbes with no other contaminating organisms present.

Catalyzed reporter deposition-Fluorescence in situ Hybridization (CARD-FISH) CARD-FISH is an improved and more sensitive version of the Fluorescence in situ Hybridization (FISH) method that use horseradish peroxidase signal amplification. It enables detection of small, slow growing, or starving bacteria in oligotrophic environments (such as lakewater).
Copiotroph Copiotrophy is a physiological trait. Copiotrophs respond to abrupt availability of resources by rapidly assimilating them for growth.
Genomic island A genomic island is a part of genome that has evidence of horizontal transfer between different lineages. Genes present in genomic islands often provide the microbe with adaptive advantages.
Metagenomics Metagenomics refer to direct (non-selective) sequencing of DNA extracted from environmental samples. Bioinformatic analyzes of metagenomes can also enable genome reconstruction. This can provide insights about diversity and metabolism of microbial groups in the environment.
Oligotrophic microbes Oligotrophy is a physiological trait. Oligotrophs are characterized by their competitive ability in low nutrient environments and typically exhibit slow growth.
Single cell amplified genomes Genomic information obtained from single cells. Cells from complex samples are first partitioned, then lysed and subjected to whole genome amplification before sequencing and bioinformatic processing.
Streamlining theory This theory suggests that minimizing the cell size and genome complexity benefit Bacteria and Archaea specifically in low-nutrient environments. From a genomic perspective streamlining leads to smaller genome sizes with less non-coding DNA and few non-essential genes.

Introduction

Invisible to the naked eye, our freshwaters are teeming with bacterial life. Each drop of lakewater typically hosts a staggering million bacterial cells that engage in elemental cycles by assimilating, transforming, or degrading biomolecules and other bioactive elements. While their combined biomass might not be immediately impressive, their large surface area interfacing with the surrounding water, fast reproduction and functional diversity makes bacteria the true ecosystem engineers of our inland waters, analogous to the situation in most other biomes and ecosystems. As such they deserve our respect and attention. So, what have we learned about the identity and function of these invisibles since they were first seen by van Leeuwenhoek in the late 1600s?

In this chapter we first outline the history of freshwater microbiome studies and the role of methodological advances in shaping our understanding of lake bacteria. Then we review in more detail the charismatic lake bacteria and their genomic characteristics and microdiversity. We move on to the role of "metabolic landscapes" and discuss the role of bottom-up controls on the diversity and dynamics of lake bacteria. In this section we also highlight the role of lake bacteria in biogeochemical cycles. We also review the role of food web interactions in shaping communities characterized by metabolic dependencies and top-down controls and the consequences for their ecology and evolution. In the next section we discuss bacterioplankton dynamics in the context of both spatial heterogeneity, temporal change and biogeography and touch upon how different lake types affect bacterial diversity and dynamic. Finally, we present an overview and suggest an outlook on the future direction of lake bacterioplankton research.

The freshwater microbiome as we know it

There have been several technological milestones in the field of microbiology, but arguably the advances that enabled us to isolate and culture clonal populations of microorganisms on defined media was a seminal step towards a better understanding of microbial diversity and function. This capability also had a strong impact on how freshwater bacteria were perceived, with most early studies focusing on the culturable, most often copiotrophic representatives which could be brought into isolation for enumeration and characterization. This led to many groundbreaking discoveries with regards to drinking water quality and microbial physiology, but at the same time created a narrative where bacteria were marginalized and mainly seen as indicators of poor water quality with little influence on ecosystems and biogeochemical processes.

In reaching the next few technological milestones, where an array of cultivation-independent methods was being put to use for describing and studying lake microorganisms, it became clear that the scientific community had grossly underestimated both the significance and diversity of freshwater microorganisms. Direct staining and microscopic enumeration of bacterial cells gave at hand that cultivation approaches underestimate the bacterial abundances by several orders of magnitude, leading up to Staley and Konopka (1985) coining the expression "the great plate count anomaly." In the following years, the growing use of cultivation independent methods based on RNA and DNA characterization have revealed that conventional cultivation techniques typically only scratch the surface in terms of uncovering the microbial diversity of natural ecosystems and this also applies to lakes (Newton et al., 2011; Buck et al., 2021). Nevertheless, as we will describe in this chapter, significant advances have been made in this regard and cultivation-based microbiology is gradually catching up, with more and more charismatic groups of lake bacteria isolated and maintained in pure culture or stable co-culture with other organisms, changing the playfield for learning about the intricate nature of their metabolism and other traits central for their biology and functioning in the ecosystem.

A turning point for the field was no doubt the invention of PCR in the mid-1980s and subsequent use of this method to broadly amplify, clone and Sanger sequence taxonomic markers such as the 16S rRNA gene from mixed communities, an approach developed and successfully promoted by Norman Pace and colleagues. Beyond characterizing communities by sequencing such marker genes, the typically high number of rRNA molecules in individual cells also enable coupled visualization and quantification of taxonomically defined groups of organisms with fluorescence in situ hybridization (FISH). By hybridizing specific oligonucleotide probes carrying different fluorescent markers to perfectly matching rRNA targets, the spatial organization of uncultured populations could now be visualized and studied (Glöckner et al., 2000). Following these methodological milestones, a wealth of studies has described the composition of local or regional microbial communities across a broad range of ecosystems. With the accumulation of data there have also been synoptic and global community inventories for different biomes and groups of organisms, including lake bacterioplankton (Glöckner et al., 2000; Zwart et al., 2002; Newton et al., 2011). For lake studies specifically, these all point to a globally dispersed and largely shared freshwater microbiome distinct from that of adjacent terrestrial and marine ecosystems.

We are now experiencing yet another methodological revolution. The development and application of more powerful high throughput sequencing methods beyond the Sanger method have for the past 10 years flooded the scientific literature with amplicon-based microbial community data collected across both spatial and temporal scales (e.g., Peura et al., 2012; Linz et al., 2017; Ruiz-Gonzalez et al., 2017). The sequencing capacity and associated bioinformatic tools have now even developed to the point where PCR is becoming redundant and where microbial communities in larger sets of samples can be broadly described by direct shotgun metagenome sequencing at the community level (Eiler et al., 2014; Peura et al., 2015) or at the level of individual metagenome assembled genomes (He et al., 2017; Garcia et al., 2018; Mehrshad et al., 2018; Linz et al., 2018) or for individual microbial cells (Ghylin et al., 2014; Eiler et al., 2016). This paves the way for more quantitative and complete assessments of microbial communities without PCR bias and can also be combined with parallel analyzes of metatranscriptomes to assess what potential functions are being expressed under given experimental or natural conditions (Linz et al., 2020). These are exciting times to be a microbial ecologist and we can only guess what the future may bring in terms of new approaches and groundbreaking insights. One exciting prospect is to integrate microbial communities and their intricate metabolic processes in ecosystem-scale and global biogeochemical models. Some first steps have been taken in this direction (Arora-Williams et al., 2018) with exciting prospects for a new level of ecosystem understanding that look beyond the black box of microbes.

Key groups and charismatic lake bacteria

Freshwater lakes across the globe might present some differences in bacterial community composition. However, certain bacterial lineages seem to have ubiquitously occupied niches across almost all freshwater lakes. These charismatic bacterial lineages account for the majority of the freshwater bacterial census. While their quantitative contribution, prevalence and distribution patterns in lakes have been demonstrated with FISH analyses and/or 16S rRNA data as illustrated in Fig. 1, our first glimpses of their metabolic potential and genomic structure have primarily been enabled by analyzing the reconstructed genomes of cultures and more recently also single cell amplified genomes (SAGs) and/or metagenome assembled genomes (MAGs) of their representatives (Fig. 2). These metabolic insights have helped us understand their evolution, ecology and multifaceted biogeochemical roles in the ecosystem. This knowledge has also guided refined cultivation that have recently brought many of these fastidious microbes into culture, enabling more detailed studies of their physiology. In the following section we briefly summarize the state of our knowledge for representatives of some of the most abundant and charismatic freshwater bacteria. Needless to say, this inventory will not be exhaustive, but should give an overview of the functional, genomic and ecological traits in some of the abundant bacterioplankton groups retrieved in pelagic communities.

Cyanobacteria

Cyanobacteria which are quite often grouped and studied together with eukaryotic phytoplankton, are the main bacterial phototrophic primary producers in the photic layer of lakes. Important from an ecosystem perspective, freshwater Cyanobacteria that are capable of fixing nitrogen have the capacity to shape the elemental stoichiometry of the ecosystem towards the Redfield ratio (C:N:P 106:16:1) defined by the average elemental composition of living cells. Under favorable conditions (sufficient nutrient supply, stagnant/stratified waters creating niches with high light availability), many Cyanobacteria can grow excessively and produce toxic secondary metabolites leading to formation of harmful blooms. With the increasing rate of lake eutrophication due to anthropogenic pressures and climate change, cyanobacterial blooms are becoming more common particularly in lakes that are situated in populated or intensively farmed areas. Cyanobacteria with toxin producing capacity and bloom-forming potential such as *Microcystis* or filamentous *Cylindrospermopsis*, *Anabaena* and *Planktothrix* can in this way decrease the quality of water and limit the lake's services as a drinking water resource as well as its recreational value. However, not all cyanobacterial lineages have this concerning lifestyle. Many of the unicellular representatives such as the broad range of representatives from e.g., *Synechococcus* persist in the background and can still be major contributors to primary production in the lake ecosystem (Callieri, 2008). Also, within *Microcystis* and other known bloom-forming genera there seems to be high functional diversity among strains where only some strains have the capacity to form harmful secondary metabolites (e.g., microcystin) and where variable genomic traits for nutrient acquisition and dealing with oxidative stress creates phenotypic diversity (Dick et al., 2021).

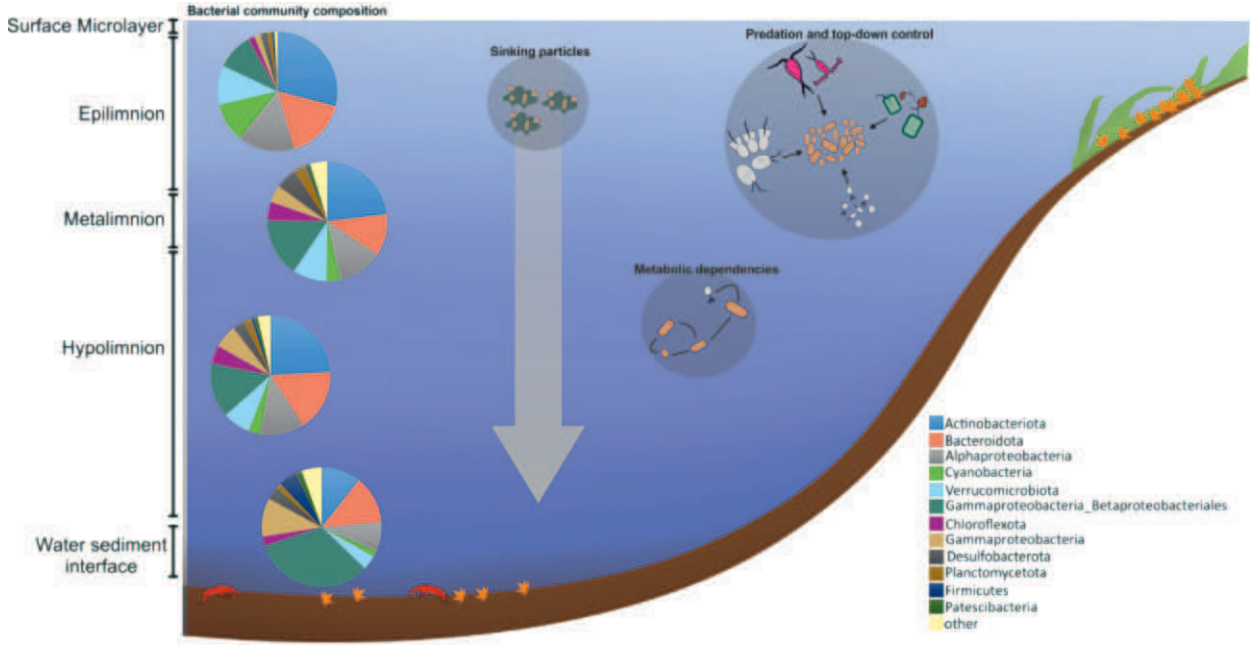

Fig. 1 Schematic illustration of a stratified lake with the composition of the bacterial community shown as pie charts in different water layers (Epilimnion, metalimnion, hypolimnion, and sediment/water interface). Bacterial community composition represented as pie charts along the depth profile is based on 16S rRNA reads extracted from metagenomic datasets of lake Erken with methods as described in (Mehrshad et al., 2018). Metagenomes are retrieved from (Buck et al., 2021).

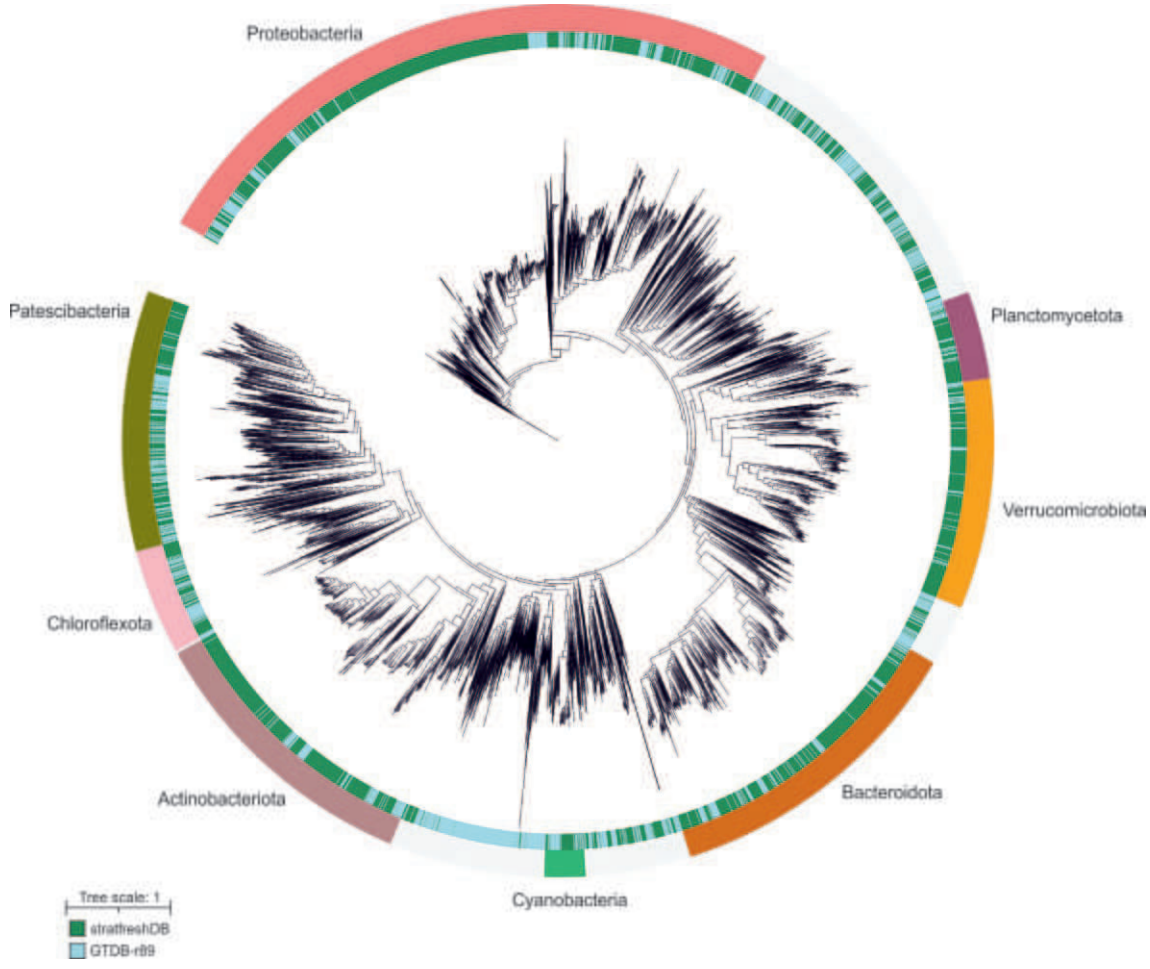

Fig. 2 Phylogenetic diversity of microbial genomes reconstructed via a comprehensive metagenomic study of freshwater lakes including 267 shotgun metagenomes from 41 stratified lakes and ponds (This dataset is called stratfreshDB). The inner circle shows the origin of genomes either from stratfreshDB or the genome taxonomy database (GTDB, https://gtdb.ecogenomic.org/) release 89. GTDB release 89 is a comprehensive database comprising of isolate genomes, metagenome-assembled genomes (MAGs), and single-amplified genomes (SAGs) (statistics of release 89 database can be found at https://gtdb.ecogenomic.org/stats/r89). GTDB offers a phylogenetically consistent and genome-based taxonomy for these genomes we have used this taxonomy throughout the text. The outer circle highlights the taxonomy of charismatic microbial phyla discussed in this chapter. Modified from Buck M, Garcia SL, Fernandez L, Martin G, Martinez-Rodriguez GA, Saarenheimo J, Zopfi J, Bertilsson S and Peura S (2021) Comprehensive dataset of shotgun metagenomes from oxygen stratified freshwater lakes and ponds. *Scientific Data* 8: 1–10. doi: 10.1038/s41597-021-00910-1.

Actinobacteriota

Actinobacteriota comprise the majority of the bacterial community in most lakes where lineage acI of Actinobacteriota are the most abundant freshwater bacteria. Members of this diverse lineage (Fig. 2) have streamlined genomes with low guanine + cytosine content in the DNA (G + C%) and small genome sizes ranging from 1.2 to 1.4 megabases (Mbp). Metabolic capabilities of the acI bacteria inferred from genomes generated from dilution to extinction cultures and single cell genomes confirm that these cells are oligotrophic chemoheterotrophs with diverse metabolic dependencies (Garcia et al., 2015; Ghylin et al., 2014). These metabolic dependencies with surrounding microbes are hindering the isolation and cultivation process of acI representatives. Looking a bit closer at this phenomenon, genome reduction or streamlining in the acI bacteria had led to auxotrophy for some amino acids and vitamins, as well as reduced sulfur compounds. Phylogenomic studies of 16 closed genomes sequenced from transiently axenic cultures further shows that they belong to nine novel species in two novel genera named "*Candidatus* Nanopelagicus" and "*Candidatus* Planktophila" (Neuenschwander et al., 2018). Comparative analyzes of these genomes suggest a high level of diversity in the genomic content, specifically in relation to carbohydrate metabolism and transport. Many genes related to these functions are encoded in genomic islands that show considerable abundances in the environmental metagenomes. This suggests high levels of microdiversity among representatives of the acI lineage. Further studies on this lineage, showed that the way to achieve sustainable cultures of acI Actinobacteriota was to add catalase to the culture media (Kim et al., 2019), with the stimulatory effect later attributed to heme supplementation (Kim et al., 2021). These cultures suggest distinct but variable preferences for reduced sulfur compounds and carbohydrates in different acI isolates. Recent progress in obtaining sustainable cultures for representatives of this lineage is now paving the way for studies that will provide a better understanding of their physiology, adaptations, and ecological role.

Apart from acI, other relatively abundant Actinobacteriota lineages in freshwater lakes include acIV and acIII. Compared to acI, the acIV lineage represents a wider biome distribution, with representatives being present in freshwaters but also in marine sediments, and soil (Newton et al., 2011; Warnecke et al., 2004). Several metagenomic-assembled genomes have been reconstructed for representative lineages within the order Acidimicrobiales that includes acIV, and 3 novel species of the genus *Ilumatobacter* from this lineage have also been isolated and taxonomically described (Ghai et al., 2014; Hugerth et al., 2015; Mehrshad et al., 2016). However, a thorough study of this specific lineage and characteristic metabolic and ecological capabilities in freshwater ecosystems is still missing. As for the acIII lineage, it belongs to order Actinomycetales and shows a notable abundance in hypersaline soda lakes and estuaries (Newton et al., 2011; Warnecke et al., 2004).

Proteobacteria

Fonsibacter

Freshwater lakes are ubiquitously dominated by subclades of SAR11 Alphaproteobacteria, a group known to be the most abundant bacterial lineage in oceanic waters. While most freshwater representatives of SAR11 belong to subclade IIIb which is more widely known as LD12, a recent study on metagenomes of Lake Baikal report a freshwater representative genome that phylogenetically forms a sister clade to subcluster I. Phylogenomic analysis suggests that LD12 bacteria have evolved from their streamlined marine counterparts and similarly have reduced genomes which are among the smallest reported for free-living bacteria (1.1–1.4 Mbp) and low G+C content (29–32%) (Eiler et al., 2016) They are adapted to freshwater oligotrophic habitats and represent an aerobic chemo-organoheterotrophic lifestyle and similar to the Actinobacteriota acI they feature auxotrophies for some amino acids and vitamins (Salcher et al., 2011). Existing genomes and a recently obtained isolate (Henson et al., 2018), suggest that they depend on reduced organosulfur compounds and ammonium as sulfur and nitrogen sources, respectively. *Fonsibacter ubiquis* LSUCC0530T is the sole cultured LD12 representative and initial physiological tests suggests that cells can double roughly every 2 days (average growth rate of 0.52 day^{-1}) with optimum growth at around 1.45 PSU salinity while they show growth up to 8 PSU.

"*Ca.* Methylopumilus"

Methylotrophs capable of using reduced one-carbon compounds such as methanol and methylamine are among the abundant freshwater bacteria. One of these prevalent freshwater methylotrophs is "*Ca*. Methylopumilus" (Salcher et al., 2019). The C1 compounds that they feed on are supposedly to a large extent produced by phytoplankton primary producers, forming the basis for strong ecological associations. Accordingly, the temporal abundance patterns of "*Ca*. Methylopumilus" are synchronous with diatom and/or cyanobacterial blooms. Representatives of this genus seem to be psychrophilic and reach their maximum abundance (ca. 4% of total prokaryotes) after such phytoplankton blooms where they thrive on released exudates (Salcher et al., 2015). Three species within "*Ca*. Methylopumilus" genus could be identified based on genome analyses of 39 isolates. Genomes from representatives of this genus seem to have small size (1.26–1.36 Mbp), low G+C content (36.7–37.4%) and streamlining attributes.

Polynucleobacter

Genus *Polynucleobacter* was first recognized and studied as a type species with obligate endosymbiotic lifestyle. This representative (*Polynucleobacter necessarius*) thrives in the cytoplasm of the ciliate species *Euplotes aediculatus*, but pelagic and free living *Polynucleobacter* representatives were also later reported to be prevalent in lake ecosystems. Pelagic *Polynucleobacter* seem to be inhabiting a wide range of niches but also feature strong seasonal dynamics in abundance and diversity patterns and also vary spatially across e.g., depth. Environmental factors such as pH, conductivity and productivity are known to impact the prevalence of different

Polynucleobacter subclusters A, B and C (Nuy et al., 2020). *Polynucleobacter* members have relatively small genome sizes (1.5–2.5 Mbp) with intermediate G+C content (40–50 mol%). Most members of this genus are organoheterotrophs whereas some contain genes for aerobic anoxygenic phototrophy and carry rhodopsins (a light-sensitive receptor protein) that may confer phototrophic potential (Hoetzinger et al., 2017).

Limnohabitans

Genus *Limnohabitans* is ubiquitous freshwater Proteobacteria and was first taxonomically classified in 2010 with *Limnohabitans curvus* as the type species. (CARD)-FISH, 16S rRNA amplicon, and metagenomic analyzes have shown ubiquitous presence of the morphologically diverse *Limnohabitans* members also known as the "R-BT cluster" in nearly all freshwater lakes worldwide, where they represent on average 12% of freshwater bacterioplankton communities (Kasalický et al., 2013; Props and Denef, 2020). Despite their fastidious nature, cultivation efforts have succeeded to bring representatives from 4 out of 5 existing *Limnohabitans* lineages (Lim A-E) into culture (more than 50 isolates). Their high cellular productivity combined with relatively larger mean cell volume compared to other prevalent epilimnetic ultramicrobacteria (i.e., microbes with cell volume $<0.1\ \mu m^3$) and susceptibility to protist predation makes *Limnohabitans* an important link in the flow of carbon to higher trophic levels in freshwater lakes. *Limnohabitans* is primarily heterotrophic bacteria that encode traits for versatile metabolic capabilities that also include the genetic elements for aerobic anoxygenic phototrophy metabolism (pufLM and bchY). They typically have large genomes (3.3–4.8 Mbp) with G+C content ranging from 56% to 60% (Kasalický et al., 2018), (though more recent genomes show a wider range for genome size and G+C content).

Chloroflexota

Chloroflexota has historically been represented by lineages capable of aerobic anoxygenic phototrophy (belonging to class Chloroflexia) in shallow freshwaters. In 2001, a 16S rRNA gene cloning-sequencing study of deeper strata (500 m) in Crater Lake (United States) reported on a novel lineage of Chloroflexota named CL500-11, that dominated the hypolimnetic bacterial community (Urbach et al., 2001). Later, studies based on 16S rRNA and (CARD)-FISH showed the ubiquitous abundance of this lineage in oxygenated hypolimnia of deep lakes, accounting for up to 26% of the total prokaryotic community. Cell volume calculations show that they are among the largest prokaryotic cells in the water column (median cell volume $0.06\ \mu m^3$). Their large population size and cell volume emphasize the large contribution of CL500-11 to the lake's bacterial biomass. The first CL500-11 MAG was reconstructed from metagenomes of the ultraoligotrophic Lake Michigan, and functional annotations suggested that CL500-11 representatives have the metabolic capability for oxidation of C1 compounds and mineralization of proteinaceous compounds and other nitrogen-rich dissolved organic matter (Denef et al., 2016). Further metagenomic analysis of the lake water column revealed a bigger phylogenetic diversity of Chloroflexota in freshwater compared to marine ecosystems (Mehrshad et al., 2018). Other freshwater Chloroflexota lineages include lineages SL56, TK10, JG30-KF-CM66, and Chloroflexia.

Planctomycetota

Planctomycetota have been recognized for their unique cell structure that is comparable yet distinct to other Gram-negative bacteria. They show variable abundances in different ecosystems ranging from <1% to 20% of the community. The known Freshwater Planctomycetota are chemoorganotrophs belonging to classes Phycisphaerae (clade CL500-3) and Planctomycetes. Inspecting the genomic potential of metagenome assembled genomes affiliated to freshwater Planctomycetota show that they contain a variety of carbohydrate-active enzymes that suggests high glycolytic potential. Additionally, some Phycisphaerae MAGs seem to encode for a cellulosome-like machinery that is hypothesized to be involved in polypeptide degradation. CARD-FISH analysis suggests that freshwater planctomycetota could be associated with sedimenting organic particles along the lake's water column (Andrei et al., 2019).

Verrucomicrobiota

While not among the most abundant bacterial phyla, Verrucomicrobiota are present in almost all freshwater lakes and contribute from 1% to 6% of the total community. For some humic lakes, higher abundances have been reported with Verrucomicrobiota contributing up to 20% of the total community. Freshwater representatives are suggested to participate in carbon cycling by degradation of glycolate and (poly)saccharides and this has also been confirmed by functional annotation of metagenome assembled genomes where functional tuning of populations to the local organic substrate pool (allochthonous vs. autochthonous) was also hypothesized (He et al., 2017). Higher nutrient availability, labile dissolved organic carbon, cyanobacterial blooms, low pH, higher temperature, and longer retention time are shown to favor the abundance of freshwater Verrucomicrobiota representatives in lakes. Estimated genome size seems to vary extensively from ca. 2 to >7 Mbp and the same applies to G+C content which range from 42% to 68% (He et al., 2017).

Patescibacteria

Ultramicrobacteria that can pass the 0.2 μm membrane filters typically used to collect bacteria from water samples, can comprise a notable proportion of the lake's microbiome. Within this operationally defined group, members of the Candidate Phyla Radiation (CPR) also referred to as Patescibacteria with representatives in the Parcubacteria (previously known as candidate division OD1) and Microgenomates (previously known as candidate division OP11), are abundantly present in hypolimnetic waters and are also found at the water-sediment interface of lakes (e.g., Peura et al., 2012). The diverse reconstructed MAGs of Patescibacteria from different freshwater ecosystems (Fig. 2) have features that imply a symbiotic lifestyle and they generally have small genome sizes and a reduced genomic repertoire that in most groups is lacking the capacity to synthesize amino acids, nucleotides, and lipids while having the capacity for fermentation. The ecological role of these microbes in lakes and their symbiotic interactions with potential hosts in freshwater ecosystems is still a hot topic that needs further study.

The enigmatic freshwater Bacteroidota

The final group that we will highlight here is certainly abundant and diverse in freshwaters (Fig. 2), but also functionally elusive, dynamic and devoid of charismatic representatives with known genomic features. While this phylum is both diverse and abundant in lakes (often >10% of 16S rRNA reads), remarkably little details are available about their ecology and biogeochemical function in the system beyond a consistent organotroph metabolism with more patchy phototrophic potential (Newton et al., 2011). The phylum seems to be overrepresented on particles and occur in high abundances associated with phytoplankton blooms where they also feature high growth and turnover (Neuenschwander et al., 2015; Newton et al., 2011). With the recent availability of a large number of Metagenome assembled genomes from freshwater Bacteroidota representatives (Buck et al., 2021), the time is now ripe for a more systematic treatise on their ecological and metabolic niches.

Microdiversity and pangenomes

Lakes are dynamic and heterogeneous ecosystems. Over time and between locations they receive variable inputs of allochthonous and autochthonous dissolved organic carbon. Most lake, at least within the temperate and boreal zone undergo seasonal stratification and complete or partial mixing across their annual cycle while as a result of this featuring dynamic niches linked to chemical and physical gradients. This spatial and temporal heterogeneity can foster microdiversification of microbial populations and lead to spatiotemporal distribution patterns for different "ecotypes" of the same or closely related species. Importantly, such microdiversification enable coexistence of closely related populations that differ in one or more eco-evolutionary traits. Such sympatric coexistence of ecotypes can confer advantages for the survival of the microbial lineage as a whole over a broader range of environmental conditions as compared to a homogeneous population and also influence their competitive ability and susceptibility to predation.

Recent studies have demonstrated that environmental factors such as temperature, oxygen concentration and redox, pH, light preference, and nutrients can cause population microdiversification and structure the distribution pattern of ecotypes (García-García et al., 2019; Hoetzinger et al., 2017; Neuenschwander et al., 2018; Props and Denef, 2020). Microdiversification has been reported for several charismatic and ubiquitous freshwater bacteria such as actinobacteriota acI, *Polynucleobacter*, and *Limnohabitans*. The growing microdiversity uncovered for these lineages is also manifested as a steady increase in the known intra-specific gene pool also defined as the pangenome. Such pangenomes represent an expanded and flexible genetic toolbox of the respective lineage.

One pertinent example is the Actinobacteriota acI which shows a high level of genomic microdiversification. Different populations encode variable genes for cross-membrane transport and carbohydrate metabolism-related genes, genomic traits which are mainly found on genomic islands prone to horizontal gene transfer. Genomic islands containing cell wall biosynthesis and modification genes as well as pili assembly genes are detected in closely related genomes of the acI lineage. These functions could be involved in defense against phage infection by modifying glycotypes in the cell surface (Neuenschwander et al., 2018). As an additional example, *Limnohabitans* genomes recovered from a lake Michigan transect showed that temperature and nutrient levels are important factors structuring microdiversity within the genus *Limnohabitans* (Props and Denef, 2020). *Polynucleobacter* genomes also contain various genes involved in nutrient assimilation and cell surface modification on the genomic islands (Hoetzinger et al., 2017). These functions are expected to bring competitive ecological advantages to the ecotypes that harbor them.

The metabolic landscape and competition for resources

Cellular stoichiometry and nutritional needs

Regardless of taxonomic affiliation, bacterial cells have certain biomolecular features in common that constrain their macromolecular composition and cellular elemental ratios. All cells have carbon as a major element and with a major contribution from amino acids and other nitrogen-rich biopolymers alongside phosphorus-rich nucleic acids and membrane lipids. It therefore comes as no surprise that these three macronutrients, either alone or in combination, often limit bacterial growth and that the success in competitively scavenging the environment for nutrients will have a strong influence on dynamics, composition and biogeochemical

function of bacterial communities in lakes (Muscarella et al., 2019; Pernthaler, 2017; Salcher et al. 2013). Accordingly, bacterial populations feature various high and low affinity transporters to import compounds that consist of such elements into the cell and/or enzymes to condition more complex nutrient-containing macromolecules in order to render them more readily assimilable or mineralize them all the way to inorganic forms that can then feed biosynthetic processes (Hamilton et al., 2017). Such traits are not evenly distributed across microbial taxa, but lineages specializing in nutrient scavenging in high-and low-substrate environments can be found, while others host efficient hydrolytic or combustive enzymes that enable them to specialize in recycling nutrients bound in detrital biomass and other types of complex organic matter.

Exploiting inorganic nutrients

There are also alternative strategies to satisfy the need for nutrients and diazotrophy (a.k.a nitrogen fixation) is one such special adaptation where cyanobacteria along with representatives from a number of other bacterial linages (and also some archaea) can reduce the abundantly available atmospheric nitrogen gas to ammonia in an energetically expensive reaction catalyzed by nitrogenases, with the potential to relieve not only the diazotroph population but by extension entire microbial food webs from nitrogen limitation (Fernandez et al., 2020). For bacterial carbon demand there are similar mechanisms where autotrophic or anaplerotic fixation of inorganic carbon can release bacterial populations or communities from being critically depending on availability of organic substrates for their nutritional demands (Peura et al., 2015). For phosphorus there is no such untapped nutrient source and beyond recycling of biomass, the processes controlling phosphorus availability in lakes relate mostly to catchment processes (including anthropogenic processes) and internal phosphorus loading from the large nutrient pools stored in sediments. Under certain circumstances (ultraoligotrophic lakes), also other elements, such as iron, may act as limiting nutrients for bacterioplankton growth, but normally most other elements for assembling bacterial cells are available in excess.

Competing for energy in organic matter

Beyond the nutritional needs to acquire essential elements, microbial growth relies on access to energy that can be used to drive molecular conversion and assembly in the cell. There is often fierce competition between microbial populations and diverse metabolic groups of organisms for such energy sources. In this context, reduced organic matter holds a pivotal role as an abundant source of chemically bound energy that can fuel fermentative and respiratory metabolic processes. The term "heterotrophic bacteria" or "organotrophs" is sometimes collectively used for the bacteria that rely on such substrates to fuel oxidative catabolic metabolism, but it is important to understand that these do not represent an ecologically or functionally coherent group (Salcher et al., 2013). Many different traits and functions have evolved that enable bacteria to exploit and use nearly every imaginable organic substrate found in nature, but for many organic substrates the occurrence of such genome-encoded traits are patchy across the bacterial domain and this forms the basis for the competitive ability of populations (Muscarella et al., 2019; Pernthaler, 2017). To complicate things further, the catabolic use of organic substrates for cellular energy mobilization is coupled to either fermentative or respiratory processes where different terminal electron acceptors are used to recover the chemically bound energy in a form that can be used to fuel cellular processes. The repertoire of such available electron acceptors has given rise to classification of organotroph populations as being either aerobes/oxytrophs, denitrifiers, sulfate reducers, iron reducers, etc. Such information carries ecological meaning, both in a sense that the metabolic mode exerts strong influence on where and when the bacterial population can grow and persist, but also with regards to how they influence the biosphere via their metabolic processes that generate products such as nitrogen gas, nitrous oxide and not least sulfide and ferrous iron with major implications for phosphorus speciation.

Alternative energy sources

Such coupled oxidation/reduction processes do not always involve reduced organic substrates as energy source. Also reduced inorganic compounds such as ammonium, reduced sulfur compounds and ferric iron can be coupled to thermodynamically feasible electron acceptors and yield energy to fuel cellular processes. Functional guilds such as nitrifiers and iron- as well as sulfur-oxidizing bacteria can be dominant community members when oxygen is in short supply and exert a strong influence on the characteristics and biogeochemical functioning of lakes (Peura et al., 2015; Arora-Williams et al., 2018). Last but not least, many organisms can also to variable extent harvest energy from solar radiation. Bacterial phototrophy, with oxygenic cyanobacteria as the primary example, played a key role in the evolution of oxygenated earth and the evolution of plants and still maintain a central role as globally significant primary producers in marine, freshwater and terrestrial environments. However, there are many more groups of phototrophic bacteria, including those that couple light harvesting systems with anoxygenic processes such as sulfide or thiosulfate oxidation (purple and green sulfur bacteria) and those that seem to use light energy more as an alternative energy subsidy that they can tap into for enhanced survival in times of starvation, including Proteorhodopsin featured in various abundant freshwater lineages as well as aerobic anoxygenic phototrophy present in groups such as Gemmatimonadota and *Limnohabitans* (Kasalický et al., 2018).

Heterogeneous resource distribution

Lakes may at a first glance be perceived as rather well-mixed and homogenous ecosystems. However, this is far from the real situation where spatial heterogeneity within lakes is manifested in many ways: (i) as a result of thermally controlled vertical stratification of the water column where solar exposed epilimnetic waters present very different conditions as compared to dark and oxygen-depleted hypolimnetic waters (ii) along steep chemical gradients at the water-sediment interface (iii) at the microscopic scale associated with living or detrital particles that present both surfaces for colonization and locally enhanced nutrient availability in the water column (iv) in response to local inputs of nutrients or pollutants from the watershed (Kraemer et al., 2020). These and other features and processes that create spatial heterogeneity in the resource landscape can have strong effects on bacterial communities and also contribute to maintaining diversity because of the multitude of niches presented (Pernthaler, 2017; Linz et al., 2017). Strongly stratified lakes do for example feature very different communities in epilimnetic and hypolimnetic water masses with typically higher diversity in the deeper water masses that are in contact with sediments and dominant populations tuned to the available substrates and light regime (Peura et al., 2012, 2015). Analogously, particle attached bacteria differ from their associated counterparts both in composition, functional attributes and seasonal dynamics (reviewed in Pernthaler, 2017). Considering that particle-association may confer predation resistance while also offering opportunities to exploit nutrients bound in the particle, this should come as no surprise.

Linking bacterioplankton to biogeochemical processes

Considering the complex and diverse composition of microbial communities and the patchy distribution of all these different genetically encoded modes of nutrient and energy acquisition, it may seem like a daunting task to ever link features seen in bacterial communities with manifested processes and characteristics at the ecosystem scale. There is however some structure to the madness and basic thermodynamic principles can usually inform about conducive metabolic modes in different lake habitats: With a steadily growing database of functional metabolic traits of the dominant bacterial groups, we are now in the process of building a foundation for a more in-depth and mechanistic understanding of the causes for the dynamic behavior of lake bacterioplankton (see further section "Key groups and charismatic lake bacteria"; Salcher et al., 2013; Muscarella et al., 2019). Additionally, there has been a recent increase in broad metagenomic and metatranscriptomic sequencing approaches to characterize the functional potential and activated metabolic processes of large collections of spatially and temporally separated samples while concomitantly mapping biogeochemical process rates and chemical change (Linz et al., 2018; Peura et al., 2015; Buck et al., 2021). This greatly increases our prospects of succeeding to link bacterioplankton to ecosystem features and in the long run improves ecosystem-level understanding and biogeochemical models using genomic data. Some first steps to move beyond the "bacterioplankton black box" and account for the dynamic nature and metabolic features of these complex communities have already been taken, mainly for marine ecosystems, but more recently also for some intensively studied lakes (Arora-Williams et al., 2018; Linz et al., 2020).

Food-web interactions

Metabolic dependencies

Many freshwater bacteria profit from (or depend) on metabolites produced by other macro- or microorganisms (Hamilton et al., 2017; Garcia et al., 2015) and consequently participate in functional consortia or metabolic networks. Some of these interactions are loosely defined and constitute non-essential interactions based on leveraging leaky metabolites produced by other community members or benefitting from "leaky processes" such as hydrolysis products generated from extracellular hydrolytic enzymes, trace-element scavenging siderophores or enzymes that degrade toxins or quench reactive oxygen species (Kim et al., 2019). However, many of the most abundant groups of freshwater bacteria have more obligate metabolic dependencies that are typically linked to genome reduction and where auxotrophic populations require exogenous source of essential biomolecules. This requirement leads to an obligate interaction between the auxotroph and at least one member of the community that can produce the required organic molecule (prototroph). The most numerically dominant freshwater lineages such as Actinobacteriota acI and *Fonsibacter* have streamlined genomes and represent auxotrophies for several amino acids, vitamins, and reduced sulfur sources (Eiler et al., 2016; Henson et al., 2018; Neuenschwander et al., 2018). This has inspired network analysis of the freshwater community leading to the conclusion that these microbes thrive in functional cohorts where their metabolic needs are supplied via their interactions (Mondav et al., 2020). While most experimental analyses explore auxotrophies for amino acids and B vitamins and some recent studies on heme auxotrophy (Kim et al., 2021), there potentially could be many other forms of auxotrophies that are still unrecognized. These unknown interactions can hinder cultivation efforts to bring environmentally relevant microbes to culture.

Predation and top down control

Lake bacterioplankton are typically under strong top-down control, largely through trophic interactions with microeukaryote predators and viruses, but also from zooplankton, predatory bacteria, and other parasites. Such mortality will broadly select for traits that confer resistance and accordingly influence bacterioplankton community composition, diversity and activity (Pernthaler,

2017). Examples of such traits to develop resistance against bacterivory can be the ability to form filaments or colonies through oversizing (e.g., Bacteroidota representatives), miniaturization (the case of highly abundant streamlined Actinobacteriota acI and *Fonsibacter*), biofilm formation, allelopathy or other inducible defense mechanisms (Pernthaler and Posch, 2009), while resistance to viral infection may be attributed to surface masking or various intracellular defense mechanisms such as CRISPR/cas systems or carrying genomic islands with genes that encode phage recognition sites (seen in "*Ca*. Nanopelagicales") (Neuenschwander et al., 2018). This defense mechanism can justify the large populations size of the streamlined Actinobacteriota despite the intense top-down control imposed by viruses.

The non-selective top-down control mainly enforced by heterotrophic nanoflagellates, protists, and zooplankton, transfers nutrients and energy directly to higher trophic level in the aquatic food web. This control has a potential stabilizing effect on bacterioplankton communities by keeping the growth of rapidly dividing population in check. Similarly, the host specific top-down controls are mainly mediated by viral infection, which finely tune the dynamics, abundance and microdiversity of their host in the lake ecosystem (Pernthaler and Posch, 2009). Phages influence the bacterial community composition either directly by infecting them or indirectly via influencing the flow of carbon in the food web. At the same time, phages can influence the entire food web either by producing dissolved organic carbon (DOC) that could be remineralized by other prokaryotes (viral shunt) or by producing sticky lysates that aggregate DOC and promote sinking, effectively shuttling organic carbon from the surface to sediments (viral shuttle). Phage-mediated microbial lysis potentially influences the community interactions by making public goods accessible to the host's neighboring cells. While the diversity and dynamics of viral genomes have been explored via metagenomic approaches (Arkhipova et al., 2017), their impact on the microbial community is less explored specifically in freshwater ecosystems.

Bacterioplankton dynamics

Selection vs. dispersal

What are the processes that create biogeographical patterns in lake bacterioplankton? Principally we can differentiate between on the one hand dispersal processes that bring in bacteria from outside the environment under scrutiny and on the other hand the perpetual process of selection which act on communities and populations and by means of population growth and mortality can shift the composition and diversity of resident microbiome (Pernthaler, 2017). To some extent, both of these mechanisms are always active, but their relative importance will vary across both ecosystems and different populations in the community. The consensus seem to be that selection (a.k.a. "species sorting") is for most lakes the dominant process shaping bacterioplankton communities (Lindström and Langenheder, 2012), but there are of course exceptions to this: lakes with short hydrological turnover that receive large inputs of water from other water bodies in the catchment, and mass effects (import of cells) associated with specific episodic events such as spring floods and heavy precipitation with intense surface runoff, biological invasions and storms causing sediment resuspension. To understand and correctly interpret changes in bacterioplankton one needs to know the conditions for the specific lake being studied and the mechanisms at play, not only at the time of sampling, but in the weeks to months preceding the observations made.

Differences between lakes

First and foremost, while many of the most abundant freshwater bacterial lineages are widely present in most freshwaters, there are marked differences in bacterioplankton communities between lakes. This has been known for decades (Zwart et al., 2002; Glöckner et al., 2000; Newton et al. 2011) and while these early syntheses were based on rather limited and scattered information, this view has recently been validated in a flood of studies that have used next generation sequencing or shotgun metagenomics for a more complete inventory of the identity and representation of bacterial taxa in these communities. The more obvious differences relate both to shifts in the relative abundances of shared classes or entire phyla (Eiler et al., 2012; Kraemer et al., 2020) as well as the distribution of more highly resolved lineages or ecotypes that may even be altogether absent in some systems (Ruiz-Gonzalez et al., 2017; Linz et al., 2017; Props and Denef, 2020). The specific factors underscoring such differences are hard to elucidate, but ecosystem productivity (Eiler et al., 2012), watershed land use (Kraemer et al., 2020) and variable geochemical conditions that define and constrain fundamental niches (Ruiz-Gonzalez et al., 2017) have been implicated as strong influencing factors. Most likely these ecosystem or landscape features will influence bacterioplankton communities via a combination of all the bottom-up and top-down structuring factors discussed in previous sections, with variable weight of the different factors in the different lakes and for the different bacterial groups.

Vertical stratification of bacterial populations

Thermal stratification is a fundamental concept in limnology with far reaching consequences for both biotic and abiotic processes. By solar heating at the lake surface combined with mixing of the uppermost water layers by wind action, distinct water masses emerge, resulting in a density-driven physical partitioning of the water column that hinders vertical transport of dissolved chemicals and planktonic organisms. This has major implications for resource availability and conducive metabolisms (see Section "Food-web interactions") and will accordingly also lead to vertical differences in bacterioplankton community composition (Fig. 1) and their realized or potential biogeochemical functions (Arora-Williams et al., 2018; Linz et al., 2018).

Such vertical structuring of bacterial populations is perhaps most notable in lakes that never or very seldom mix, or productive lakes with extended periods of stratification where the deeper layers will become oxygen-depleted. In such episodic or permanent anoxia, the hypolimnetic waters will present novel metabolic niches along chemical gradients, contrasting redox zones and in moving from low light to complete darkness. Among the more abundant groups in such deep anoxic waters we tend to find representatives from the quite widely distributed Patescibacteria (CPR) and Bacteroidota (Peura et al., 2012), but there are also local hotspots for lineages that are rare or absent in the surface waters, such as Chlorobia, Chloroflexota and members of the ε-proteobacteria (Peura et al., 2015; Mehrshad et al., 2018). Additionally, oxygen depleted hypolimnetic waters seem to host a higher bacterioplankton diversity as compared to surface waters, with an array of more rare groups that are not usually considered to be "typical lake bacteria" contributing significantly to the community (Peura et al. 2012; Linz et al., 2017).

Vertical shifts in population structure are also seen for some of the more abundant lineages that are shared between water masses. Here certain populations of *Polynucleobacter* clearly prefer the dark and oxygen scarce hypolimnion to the solar exposed and oxygen saturated surface waters while other appear to have the opposite preference (Linz et al., 2017) and the same can be seen in for example closely related populations of "*Ca*. Methylopumilus" (Salcher et al., 2015). In contrast, some of the ubiquitous lake bacterioplankton lineages such as *Fonsibacter* (LD12) and abundant members of the Actinobacteriota (acI) are overall clearly more abundant in surface waters and more highly resolved lineages seem to have only weak preference for either of the two different water masses while other factors such as lake type and season seem to matter more (Neuenschwander et al., 2018).

Changes over days, seasons and years

Resources and top down pressures that shape bacterial communities do not only vary spatially, but also change over time. This is not unique for lakes as few if any environments stay constant, but in many ways the temporal change seen in lakes can be more dramatic and harder to predict as compared to other aquatic biomes (oceanic waters, groundwaters). Such drivers act over both shorter and longer timescales with variable impacts on bacterial communities while concomitant hydrological influences may also change local communities via mass effects and homogenization.

Studies of temporal change in lake bacterioplankton has mainly focused on seasonal change and for good reasons: in many of the more lake-intensive parts of the world, the different seasons feature very different environmental conditions and host distinct and differentially composed bacterial communities (Eiler et al., 2012; Linz et al. 2017; Mondav et al., 2020). While e.g., phytoplankton seasonal dynamics have been recognized for quite some time, it has only recently been recognized that bacterioplankton also feature similar strong seasonal dynamics where populations "bloom" and collapse. Interestingly such seasonality patterns in community composition do not seem to be annually reoccurring (Linz et al., 2017), implying more complex and cryptic regulation of bacterioplankton as compared to oxygenic phototrophs. The same inter-annual variation can be seen for individual dominant lake bacterial groups such as *Fonsibacter* (Salcher et al., 2011), and "*Ca*. Methylopumilus" (Salcher et al., 2015).

As one example of such seasonality, the bacterioplankton in dimictic lake Erken (Sweden) experience dramatic change as the seasonal ice cover breaks up in April with subsequent holomixis until the water column stratifies in mid-May (Fig. 3). In this period, the abundant *Fonsibacter* (Pelagibacteraceae) and Bacteroidota populations decline dramatically and are replaced by a transient abundant Verrucomicrobiota population concomitant to a predictable spring diatom bloom which likely feed these bacteria via organic exudates. At the same time, some groups (e.g., Actinobacteriota) seem to be remarkably persistent throughout the year, at least at the broader taxonomic level. However, this may just be because of methods based on 16S rRNA sequencing with insufficient resolution. Metagenome enabled population tracking did for example uncover cryptic ecotypes with seasonal preferences hidden behind such apparent constancy for abundant lake bacterial groups such as *Limnohabitans* (Props and Denef., 2020), Actinobacteriota acI and *Fonsibacter* (Garcia et al., 2018; Neuenschwander et al., 2018). Another elusive aspect of temporal bacterioplankton community change is biotic interactions and dependencies which cause entire functionally interactive cohorts of bacteria to change in synchrony with one another (Eiler et al., 2012; Mondav et al., 2020).

Multiple lines of evidence suggest that bacterioplankton communities may also change in composition over shorter than seasonal timescales. This can for example be seen in the dynamic spring period of lake Erken (Fig. 3) and also happen during rainstorms or other extreme weather events that mix water columns or bring in large amounts of bacteria or easily exploitable substrates to the system. But what about the dramatic changes that happen over diurnal timescales? There is limited information and likely not enough time for bottom-up structuring mechanisms to cause measurable community change. Nevertheless, a recent study of bacterioplankton community change that take place over diurnal timescales clearly show that while composition do not change, there are quite prominent diel cycles in community function sensu expressed genes and also temporal partitioning of active populations (Linz et al., 2020). This type of studies will be further facilitated by the growing database of freshwater bacterial genomes with promises of further mapping of how individual bacterial populations and consortia respond functionally to various environmental drivers.

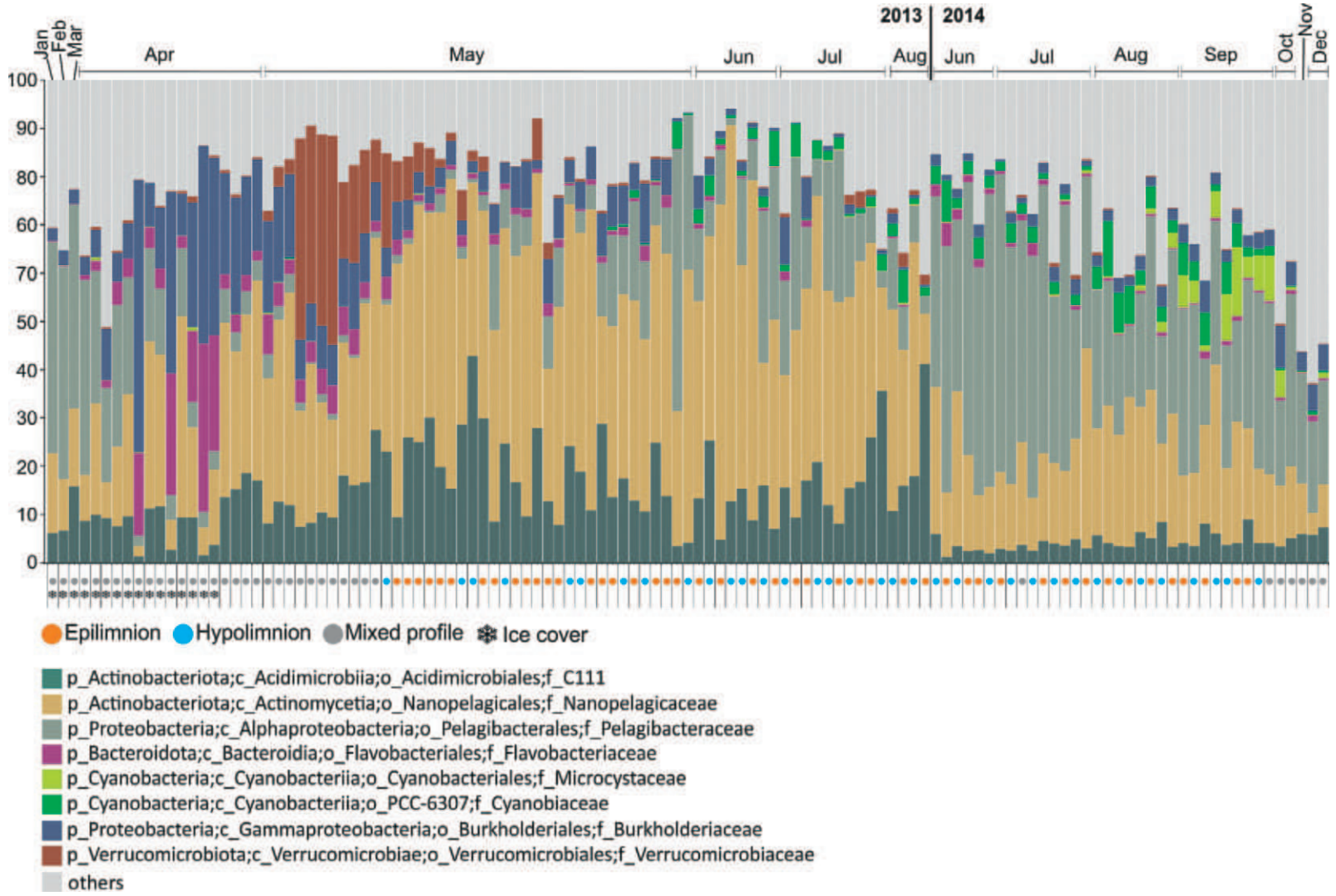

Fig. 3 Seasonal dynamics of the charismatic lake bacteria based on 16S rRNA amplicon analyzes of the Lake Erken time-series collected during 2013 and 2014. Samples are ordered based on date and the sampling month in shown on top. Based on data from (Mondav et al., 2020).

Summary and outlook

Freshwater bacterial communities are diverse and phylogenetically distinct from their counterparts in other biomes. At the core of such communities are a set of globally dispersed and abundant bacterial lineages whose biology we are now starting to uncover with genome sequencing and refined cultivation methods. While you can find these charismatic bacterial groups in nearly all freshwater lakes, their activity, abundances, population structure and microdiversity vary a lot both between and within lakes and over weekly to seasonal timescales. Why is that? While it is hard to generalize for all lakes (after all they are quite diverse in their functioning and features) we feel confident in concluding that lake bacterial communities are dynamically structured and constrained by a combination of bottom-up (resource availability) and top down (predation and mortality) mechanisms that create opportunities and challenges for the resident microbiota. Recent studies also suggest that there are surprisingly widespread and strong metabolic dependencies between different groups of lake bacteria, and this also shed new light on their dynamics and biogeography. A research challenge for the forthcoming years would be to more directly couple functional traits of these bacterial groups (and their ecotypes) to apparent distribution patterns in ecosystems and unravel the implications of their trophic interactions with the ultimate goal of using such combined information to enable the development of mechanistic, informative and robust models of "ecosystem metabolism".

Important knowledge gaps

- Physiological characteristics of the charismatic and as of yet uncultured freshwater bacteria
- Comprehensive mapping of functional traits in freshwater bacteria
- Implications of metabolic dependencies and trophic interactions in the food web for the dynamics and functioning of freshwater bacteria
- Finding the causal drivers behind biogeographical patterns and expressed functions in bacterioplankton (metatranscriptome surveys could be one idea)
- Genome-informed models for improved understanding of biogeochemical processes and cycles.

Further reading

For further reading we refer the reader to the quite extensive reference list which nevertheless is not complete. Over the years there have been a few broader reviews of the diversity and ecology of lake bacterioplankton, illustrating the increasing amount of data and development of the field. We especially recommend the early synoptic studies by Glöckner et al. (2000) and Zwart et al. (2002) which were some first attempt to describe the global freshwater microbiome. With an increasing number of studies, this was followed by an in-depth review by Newton et al. (2011) which provided a guide to the "natural history of lake bacteria." Another recent and very comprehensive review by Pernthaler (2017) followed up on this with a focus that was more on the ecology and metabolic functioning. We are still lacking an in depth "genome guide" of freshwater bacteria, but predict that this will come in the near future when such data from metagenome assembled genomes, single cell genomes and new isolates is becoming increasingly available.

- Protists: Flagellates and Amoebae
- A diversity of primary producers in lakes
- Protists:ciliates
- Lake Food Webs
- Virus: drivers of diversity

Acknowledgments

Funding that gave us time to engage in the book project was kindly provided by the Swedish University of Agricultural Sciences and the Swedish Research Council. Bioinformatics analyzes were carried out utilizing the Uppsala Multidisciplinary Center for Advanced Computational Science (UPPMAX) at Uppsala Universitet (projects SNIC 2020/5-19 and SNIC 2021/5-53).

We thank Rhiannon Mondav for saving us time by sharing the OTU tables for the Lake Erken 16S rRNA dataset and the section editors and publisher for being patient with our delays.

See Also: Fundamental concepts and theories: Methane; Nitrogen Fixation; Nitrogen; Structures and functions of Inland Waters - Lakes: A Diversity of Primary Producers in Lakes; Benthic Algae in Lake Littoral Habitats; Emerging methods and topics: Fatty Acid—Markers as Foodweb Tracers in Inland Waters

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Relevant websites

The Genome Taxonomy Database—https://gtdb.ecogenomic.org.
The SILVA database—https://www.arb-silva.de.
The RDP database—https://rdp.cme.msu.edu.
The International Society for Microbial Ecology—https://www.isme-microbes.org.

Fungi and Chytrids

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie_Elodie Perga and Damien Bouffard.

Glossary

Benthic shortcut A trophic pathway where aquatic fungi channel terrestrial-derived organic matter to higher trophic levels in the aquatic food web.
Chytridiomycosis Originally used for describing the emerging fungal disease in amphibians caused by the chytrid *Batrachochytrium dendrobatidis*. The term has been extended to the more general context of chytrid parasitism.
Cryptic species Species that are difficult to distinguish by morphology but have pronounced genetic divergence.
Hyphae Long, branching filamentous structures. In most fungi, hyphae are the main mode of vegetative growth, and are collectively called a mycelium.
Morphospecies A group of organisms regarded as a taxonomic species solely based on the sharing of distinctive morphological traits.
Mycoflux A pathway of organic matter transformation in the pelagic which involves fungal interactions leading to aggregation or disintegration of organic matter.
Mycoloop A trophic pathway where the biomass of inedible phytoplankton or pollen is transferred to higher trophic levels via edible fungal zoospores.
Osmotrophy Nutritional mode based on absorption of dissolved organic compounds from the surrounding environment. Organisms that use osmotrophy include bacteria, many species of protists and most fungi. Fungi break down enzymatically organic compounds in the external environment, before absorbing the smaller molecules resulting from external digestion.
PEG-model A model, formulated by the Plankton Ecology Group that describes the seasonal succession of plankton in lakes, an annually repeated process of community assembly during which most major external factors and internal interactions shaping communities are considered. The first model was published in 1986 and has since been under continuous development.
Pseudofungi Organisms that resemble fungi in their morphology and mode of nutrition but are phylogenetically more related to plants. Characteristics that make pseudofungi distinct from other true fungi are their cell wall composition which is mainly composed of cellulose, non-septate hyphae and multi-flagellated zoospores.
Rhizoid Small branching hyphae that anchor the chytrid fungus to the substrate, and release digestive enzymes to absorb organic material.
True fungi Organisms that belong to the kingdom Fungi. They are either single celled or have septate hyphae with cell walls primarily consisting of chitin.
Zoospore Asexual spore that lacks a cell wall and uses one or more flagella for locomotion.
Zoosporic fungi Chytrids and other early diverging fungi that have a zoosporic stage during their life cycle.

 https://doi.org/10.1016/B978-0-12-819166-8.00005-0

Introduction

Among aquatic micro-organisms such as algae, protozoans or bacteria, fungi have received so far only little attention in aquatic ecology research and are mentioned at most very briefly in biology courses, generally falling between the fields of botany and microbiology. Although fungi have been more intensively studied in terrestrial ecosystems, evidence is accumulating that they are as ubiquitous and highly diverse in aquatic ecosystems and play an important role in aquatic biogeochemical cycling. This article provides an overview on the diversity and functions of fungi in freshwater habitats, with particular emphasis on zoosporic fungi (e.g., chytrids), which are an abundant and diverse group of fungi in the pelagic zone of lakes. We will highlight recent progress regarding the high diversity of early diverging fungi, including Chytridiomycota, discovered by environmental sequencing approaches, their role in lake plankton succession, aquatic food webs and nutrient cycling, i.e., Mycoloop. Finally, we also discuss the impact of anthropogenic stressors on emerging fungal disease in freshwaters caused by parasitic chytrids.

What are aquatic fungi?—Functional and taxonomic classification

One of the first records of aquatic "true fungi" dates back to the mid-19th century when Braun discovered parasitic fungi on green algae (Braun 1856). He named these fungi "chytridien" (e.g., chytrids) which later became the phylum Chytridiomycota (Hibbett et al., 2007). Collectively, aquatic fungi were called Phycomycetes (algal-fungi) (Sparrow, 1960) (Table 1). As many Phycomycetes

Table 1 Functional and taxonomic classification of aquatic fungi.

	Previous classification	*Morpho-functional classification*	*DNA based classification Phyla containing aquatic lineages*	*Representative genera*	*Trophic interactions*
True Fungi	Ascomycota	• Aquatic Hyphomycetes/ Filamentous fungi	Ascomycota	*Tetracladium*	Saprophytic on decaying
				Clavariopsis	leaves and submerged wood
		• Aero-aquatic Hyphomycetes/ Filamentous fungi		*Crucella*	Parasitic on other fungi
				Debaryomyces (Y)	Saprophytic and symbiotic?
				Metschnikowia (Y)	Parasitic on zooplankton
	Basidiomycota	• Yeast (Y)	Basidiomycota	*Rhodotorula (Y)*	Saprotrophic
				Cryptococcus (Y)	gut endosymbionts?
					Mutualistic interaction with algae/opportunistic human pathogen
	Zygomycota	Trichomycetes/Filamentous fungi	Kickxellomycota	*Harpella*	Endosymbionts freshwater arthropods
			Zoopagomycota	*Acaulopage*	Predators of amoeba
				Zoophagus	Predators of rotifers
		Filamentous fungi	Basidiobolomycota	*Basidiobolus*	Saprotrophic and parasitic on amphibians
	Phycomycetes	Zoosporic fungi	Olpidiomycota	*Olpidium*	Parasitic on plants, animals, protists, and fungi
			Chytridiomycota	*Zygophlyctis*	Parasitic on diatoms
				Rhizophydium	Parasitic on algae Saprotrophic on pollen/
				Rhizoclosmatium	Saprotrophic on chitinous substrates
				Batrachochytrium	Parasitic on invertebrates
			Monoblepharomycota	*Monoblepharis*	Saprotrophic on water-logged twigs
			Neocallimastigomycota	*Piromyces*	Anaerobic symbiont
			Blastocladiomycota	*Blastocladiella*	Saprotrophic on plant debris
				Paraphysoderma	Parasitic on algae
			Aphelidiomycota	*Amoeboaphelidium*	Parasitic on algae
			Rozellomycota	*Rozella*	Parasitic on chytrids and oomycetes
Pseudo-Fungi			Oomycota	*Phytium*	Saprotrophic on pollen
				Olpidiopsis	Parasitic on diatoms
				Saprolegnia	Parasitic on fish/fish eggs
			Hyphochytriomycota	*Hyphochytrium*	Saprotrophic on pollen
					Parasitic on algae and resting spores of oomycetes
			Labyrinthulomycota	*Labyrinthula*	Saprophytic and opportunistic pathogens of algae

DNA based classification based on Tedersoo et al., 2018 and Wijayawardene et al., 2018.

share the morphological trait of flagellated zoospores which are the primary agents of dispersal and infection/colonization of substrates in water, they have also been classified under the term "zoosporic fungi." Since Braun's first observations of parasitic chytrids on algae, many more species have been discovered which interact with a large variety of living organisms and organic substrates (Sparrow, 1960). Chytrids have been found to display a continuum of consumer strategies ranging from obligate parasites to saprophytes (Frenken et al., 2017; Sparrow, 1960). There are even zoosporic fungi (e.g., Rozellomycota) that parasitize other parasitic chytrids of phytoplankton (Canter, 1969). With the advent of DNA-based taxonomy, it is now well established that zoosporic fungi are a polyphyletic group including true zoosporic fungal lineages (Kingdom Fungi) and pseudofungal lineages (Kingdom Chromista). This indicates that shared functional characteristics such as osmotrophy and certain growth habits arose through convergent evolution. Chytrids, which currently encompass phyla Chytridiomycota, Blastocladiomycota and Neocallimastigomycota, represent the largest group of true zoosporic fungi in freshwater lakes.

A second important ecological group of aquatic fungi was discovered by Ingold in the mid-20th century, who observed characteristic fungal spores associated with decaying leaves in streams, and which he defined as aquatic hyphomycetes (Ingold, 1942). These are filamentous fungi that reproduce mainly asexually and in addition to leaves in streams, are found on decaying macrophytes or driftwood in running river systems, wetlands or littoral of lakes. The majority of them belong to Ascomycota and few to Basidiomycota.

The Ascomycota and Basidiomycota also contain unicellular yeasts which are often found in the pelagic zone of lakes as free-floating cells, attached to substrates, or within animal hosts (Buzzini et al., 2017). Trichomycetes are another diverse ecological group of aquatic fungi that are obligate endosymbionts in the gut of many aquatic insects. They used to be a member of the phylum Zygomycota; however, molecular identification methods have shown that some Trichomycete species are more related to Protozoa than to true fungi.

There is not always a clear distinction between aquatic and terrestrial fungi. Whereas some aquatic fungi have an obligate aquatic lifestyle and complete their whole life cycle in water (residents), others have both an aquatic and terrestrial life cycle and are so called aero-aquatic fungi (Chauvet et al., 2016). Finally, terrestrial fungi may occur in water, merely by being washed or blown in, without showing any activity in water (transients). It remains a challenge to precisely characterize where species fall along this gradient of adaptation to aquatic habitats (Shearer et al., 2007).

Fungal adaptations to an aquatic lifestyle

Aquatic fungi have evolved increasing size, complexity, and metabolic functioning from small intracellular fungal parasites up to larger mycelian networks of filamentous fungi capable of decomposing large refractory organic material. Fig. 1 displays a variety of dispersal and vegetative structures of aquatic fungi with their respective size ranges. Macroscopic fungal structures, i.e., large fruit bodies, are nearly completely absent in aquatic habitats (but see *Psathyrella aquatica*, the first fungi discovered fruiting underwater, (Frank et al., 2010)).

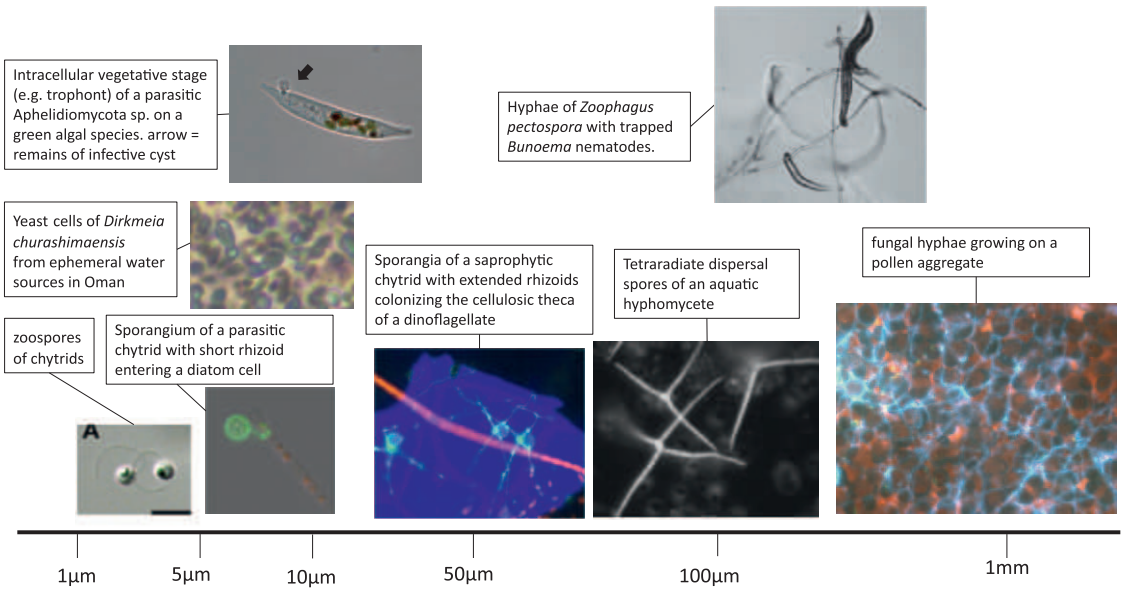

Fig. 1 Relative sizes of various dispersal and vegetative structures of aquatic fungi. Images for chytrid zoospores and Aphelidiomycota courtesy of K. Seto, University of Michigan, US. Image of yeast cells of *Dirkmeia churashimaensis* courtesy of B. Hassett, The Arctic university of Norway, Norway. Image of *Zoophagus pectospora* courtesy of W. Davies, United States Department of Agriculture, US. Image of dispersal spore of aquatic hyphomycete courtesy of C. Wurzbacher, Technical University of Munich, Germany.

Zoosporic true fungi which are ancient in term of evolution, since they diverged from the other fungal lineages ca. 750 million years ago (Medina and Buchler, 2020), have most likely an aquatic origin. Their dispersal stages show primary adaptations to an aquatic lifestyle in the form of flagellated motile zoospores. Contrary to heterotrophic nanoflagellates, fungal zoospores have unique characteristics, such as a single posterior whiplash flagellum and a large refractive lipid globule that serves as an energy reserve for fueling active zoospore movement.

The recently discovered Aphelidiomycota, endoparasites of unicellular algae, have both amoeboid and flagellated dispersal stages (Karpov et al., 2014a). In contrast to other fungi that absorb dissolved nutrients from the environment (osmotrophy), endoparasitic lineages Aphelidiomycota and Rozellomycota engulf the content of their host, like amoebae, and digest it in special vacuoles (phagocytosis). The vegetative structures of chytrids are called rhizoids, which are tiny root-like hyphae. Rhizoids anchor the chytrid to the substrate (or host) and excrete enzymes to break it down (Powell, 2017). Chytrids can modify their rhizoidal structure in response to nutrient availability in a similar way as filamentous fungi (Laundon et al., 2020).

Aquatic hyphomycetes most probably evolved from terrestrial fungi and secondary morphological adaptations to colonize aquatic environments have evolved independently in multiple lineages (Baschien et al., 2013). The asexual dispersal stages of aquatic hyphomycetes are typically tetraradiate or sigmoidal shaped and have sticky sheaths that facilitate their attachment under turbulent conditions to submerged substrates.

The size difference between the rhizoidal structures of chytrids and hyphal structures of aquatic hyphomycetes implies ecological niche differences between both fungal groups. Wurzbacher et al. (2016) formulated this as the "morphotype hypothesis," i.e., zoosporic fungi become increasingly more important on fine particulate organic matter (FPOM) such as pollen grains or algae, whereas aquatic hyphomycetes tend to colonize proportionally more the larger coarse particulate organic matter (CPOM).

Some members of Ascomycota, Basidiomycota and Zygomycota have developed trapping structures, such as adhesive spores, hyphae or rings to capture water-inhabiting micro invertebrates, like nematodes, rotifers or amoeba (Corsaro et al., 2018; Davis et al., 2019; Karling, 1936). After they have captured their prey, hyphae penetrate and digest the prey tissues. Most single celled yeasts represent fungal lineages where the ancestral hyphal growth form was abandoned. However, some yeast species still produce pseudo-hyphae or are dimorphic, i.e., they grow as single celled yeast or form true hyphae depending on environmental conditions (Harris, 2011). The diverse ecological role of yeast in aquatic ecosystems is still poorly understood (Wurzbacher et al., 2010). Yeast have been identified as members of the gut microbiota and parasites in aquatic invertebrates and animals. As saprophytes, consuming dissolved organic matter (DOM), they potentially share ecological niches with heterotrophic bacteria and compete for nutrients. Mutualistic relationships have been documented between the alga *Euglena mutabilis* and yeast of the genus *Cryptococcus*, which allow both species to colonize together extreme acidic and heavy metal polluted habitats (Nakatsu and Hutchinson, 1988). Yeast display a wide variety of extracellular enzymatic activities that can promote algae and plant growth by increasing nutrient availability and absorption (Gomes et al., 2015).

Freshwater fungal diversity in the next generation sequencing era

Although fungal diversity in terrestrial ecosystems is considered to be higher than in aquatic ecosystems, the extent of fungal biodiversity in general may need to be revisited in the light of recent molecular high-throughput sequencing approaches, which have greatly increased the discovery of uncultured taxa, or so-called "dark matter fungi" (Grossart et al. 2016). The number of fungal species is estimated to be between 2.2 and 3.8 millions, of which only around 120,000 are currently accepted and named (Hawksworth and Lücking, 2017).

Where are all the missing fungi? Aquatic habitats have certainly been overlooked and undersampled in the context of diversity (Grossart et al., 2019). The majority of fungal sequences retrieved from freshwaters are represented by Ascomycota, Basidiomycota and early diverging fungal lineages, i.e., Chytridiomycota and Rozellomycota (Lepère et al., 2019; Panzer et al., 2015; Wurzbacher et al., 2016). The active fraction of the community, identified by RNA analysis, shows the same dominant groups (Lepère et al., 2019). These proportions are also more or less in agreement with diversity estimates based on described species isolated from freshwater (Shearer et al., 2007).

In a time when biodiversity screening by high-throughput sequencing methods is becoming routine, knowledge gaps in terms of both taxonomy and marker coverage in the reference sequence databases are posing severe limitations for the ecological interpretation of environmental DNA surveys. Especially the early diverging zoosporic fungal lineages are highly underrepresented in sequence databases (Table 2). The coupling of cultivation and single-cell isolation methods with long-read sequencing technologies

Table 2 Different marker and taxonomic coverage of fungal lineages in the GenBank-NCBI sequence database.

Marker	*Fungi*	*Ascomycota*	*Basidiomycota*	*Chytridiomycota*	*Rozellomycota*	*Aphelidiomycota*
SSU	563,096 (258153)	237,592 (18751)	92,939 (21932)	2087 (1113)	130 (117)	13 (0)
ITS	844,401 (216006)	438,236 (21410)	194,133 (32618)	4273 (2810)	40 (32)	37 (31)
LSU	494,647 (107783)	276,115 (16657)	117,999 (26628)	1935 (657)	46 (31)	36 (31)

Early diverging zoosporic fungal lineages (Chytridiomycota > Rozellomycota > Aphelidiomycota) only represent < 0.5% of total fungal sequences and have a high percentage of sequences related to uncultured species (>50%) compared to Dikarya. GenBank search 01/04/2020: search example: Basidiomycota AND 18S OR SSU/(Basidiomycota AND 18S OR SSU) AND "uncultured" filter—sequence length range 300–10,000; () = number of sequences from uncultured species from the total number of sequences.

(e.g., PacBio and Nanopore sequencing) generating high-quality de novo reference data for the full ribosomal operon, is a promising approach to fill the gaps in reference sequence databases (Wurzbacher et al., 2019). This approach will facilitate access to more than a century of taxonomic and ecological knowledge on aquatic fungi.

Hidden chytrid diversity

A neglected but significant source of unrecognized fungal diversity is the restudy of known taxa, applying species recognition techniques to molecular data (Rad-Menéndez et al., 2018; Seto et al., 2020; Van den Wyngaert et al., 2017). In the beginning of this article we highlighted that chytrids have been studied for more than a century using microscopy. However, from the >400 chytrid morphospecies known to be associated as parasites or saprophytes on phytoplankton, only a few species have ribosomal DNA sequences deposited in sequence databases (see summary table in Frenken et al., 2017). Recent efforts using targeted isolation approaches in lakes have highlighted that many "dark matter fungi" and novel lineages within the early diverging fungi represent parasitic zoosporic fungi of phytoplankton (Karpov et al., 2014b; Seto et al., 2020; Van den Wyngaert et al., 2018). Some of these fungi are indeed rediscoveries of known morphospecies (Van den Wyngaert et al. 2018), whereas others represent genuinely new species (Seto and Degawa, 2018; Van den Wyngaert et al., 2017).

Until now most of our knowledge on phytoplankton-chytrid interactions is derived from in situ morphology-based identification of phytoplankton-chytrid species pairs (Sparrow, 1960). Morphological features of chytrids are, however, scarce and host identity is often used as the main guide for identification of parasitic fungi. Consequently, morphology-based identification may mask cryptic host-fungal associations (Van den Wyngaert et al., 2018). Moreover, a high degree of morphological plasticity is frequently reported among chytrids (Barr, 1973), which poses another challenge for morphological distinction among species. Whereas the presence of (semi)cryptic species causes underestimation of diversity, phenotypic plasticity overestimates this diversity (Fig. 2). An extra layer of complexity is added to phytoplankton-chytrid species interactions as phytoplankton host species are themselves prone to cryptic diversity (Van den Wyngaert et al., 2015, 2018). The use of molecular markers for species identification can overcome certain limitations of traditional morphology-based approaches to infer species diversity and host/substrate interactions of chytrids. Resolving cryptic host-fungi associations is important for interpreting biodiversity, biogeographical patterns, seasonal dynamics and population dynamics of phytoplankton-fungi interactions.

Ongoing development of molecular tools have enabled ecologists to discover novel aquatic fungi and interactions in situ. Direct isolation and sequencing of single phytoplankton-chytrid pairs from the environment have been applied to assess diversity and uncover the relationship between various fungal lineages and their specific host species. This approach has revealed that fungi attached to large diatoms include not only members of Chytridiomycota, but also Aphelidiomycota, Rozellomycota and even Ascomycete yeast (Ishida et al., 2015). Another promising approach to reveal and quantify fungal interactions in the field is catalyzed reporter deposition fluorescence in situ hybridization (CARD-FISH). Using this method, Chambouvet et al. (2019) recently discovered a novel chytrid-like-clade-1 (NCLC1) of intracellular fungal parasites of diatoms.

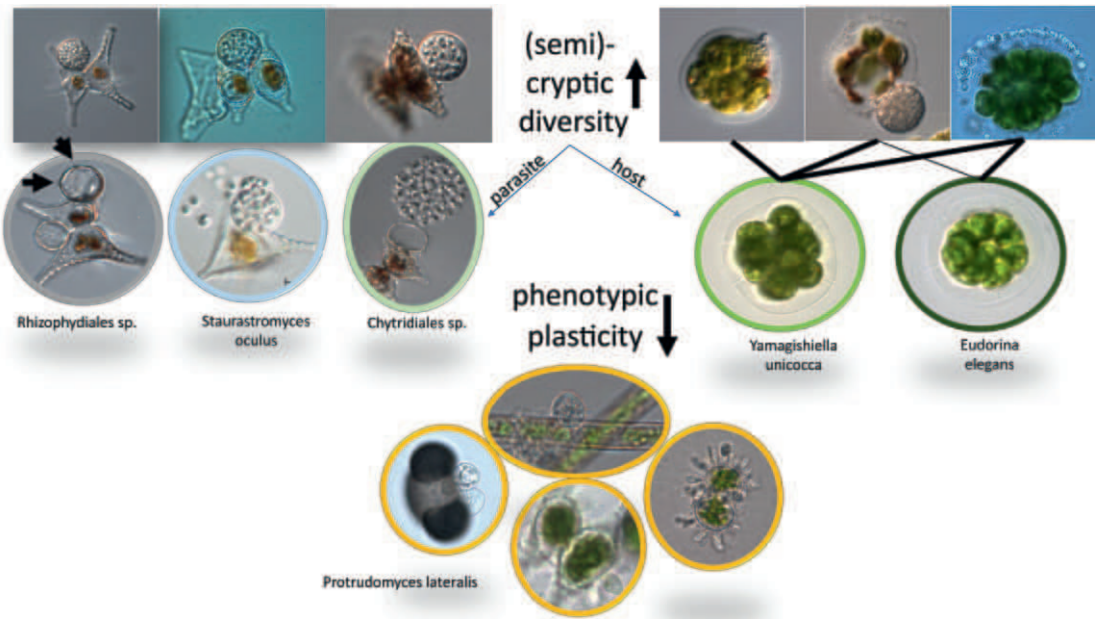

Fig. 2 Examples of cryptic diversity and phenotypic plasticity in phytoplankton-chytrid pairs. The top left shows the morphologically similar sporangia of three chytrids isolated from different lakes and infecting the same host species *Staurastrum* sp. After cultivation, subtle morphological differences in zoospore discharge can be observed and molecular analysis identifies three distantly related chytrid species. The top right shows an example of cryptic diversity in the phytoplankton host and their different susceptibility to three chytrid species. Below is shown the same chytrid species with a high degree of sporangium morphological plasticity on different phytoplankton host species and pollen substrate.

Lake fungal communities in space and time

A recent meta-analysis found that freshwater biomes have the highest fungal diversity at the phylum level (Panzer et al., 2015). This is likely attributed to the large amount of habitat/substrate diversity and temporal dynamics of environmental parameters in freshwater systems, allowing for a multitude of available niches and fungal lifestyles. The composition and relative abundance of fungi differs significantly between the type of freshwater ecosystem (e.g., streams, wetlands, lakes) and between habitats within the ecosystem (Wurzbacher et al., 2010, 2016). As is the case with most microbes, environmental selection seems to play a more important role than dispersal limitation for fungal distribution (Tian et al., 2018).

Lake morphology (i.e., size and depth) and physical and chemical properties of water (i.e., trophic status, concentrations and composition of organic matters) influence fungal colonization and thus community structure. In large, deep lakes, where organic matter is mainly supplied internally by photosynthesis of algae, zoosporic fungi, especially chytrids, dominate by parasitizing/utilizing phyto- and zooplankton (Wurzbacher et al., 2010). In contrast, in small ponds or shallow lakes where the relative importance of allochthonous organic matter from terrestrial riparian vegetation is usually higher and where submerged and emergent macrophytes are abundant, filamentous fungi such as Ascomycota dominate. The fungal community pattern throughout a longitudinal transect across southern Scandinavia was partly explained by the concentrations/composition of total organic carbon (TOC) and total phosphorus (TP) (Khomich et al., 2017). Yet, it is not clear how fungal communities change along a latitudinal gradient and how strong temperature may affect this pattern.

Within lakes, spatial variation of fungal community structure is explained by habitat and type of organic matter (CPOM or FPOM) (Wurzbacher et al., 2016). In general, fungi dominate the eukaryotic community in the benthic area of lakes and their abundance decreases in the pelagic zone. Following the "morphotype hypothesis," aquatic hyphomycetes dominate benthic and reed habitats where CPOM is the dominant organic energy source, whereas chytrids become the dominant fungi in open water where FPOM is the main type of organic matter (Fig. 4). Lake sediments mainly serve as fungal spore banks. Besides resting spores of chytrids and other resident fungi, dispersal spores of terrestrial species that are blown in by wind or washed in by rain, are frequently found in sediments (Voronin, 2014; Wurzbacher et al., 2016). Whether aquatic sediments are a dead end for these terrestrial fungi or if they represent an alternative viable habitat remains poorly studied. More complex habitats, containing a mix of CPOM and FPOM, such as periphyton biofilms are characterized by high fungal species richness and a mixed community of both filamentous and zoosporic fungi (Wurzbacher et al., 2016). Overall, these observations confirm a positive relation between habitat heterogeneity and fungal species diversity at different spatial scales.

Besides the type of organic matter, oxygen is an important environmental factor which strongly influences the presence and activity of aquatic fungi. Aquatic hyphomycetes in general need well oxygenated environments and become negatively affected by sub- or anoxic conditions. Other fungi, especially Neocallimastigomycota, are adapted to anoxic conditions (Hackstein et al., 1999). Yeast become relatively more abundant in eutrophic systems. Their increase in the pelagic zone of lakes has been reported to coincide with the crash of the annual phytoplankton spring bloom, as possible response to an autochthonous nutrient pulse (Quinn, 1984).

Temporal succession of fungi in lakes—Chytrid fungi in the PEG model

Canter and Lund (1951) were the first to show that parasitic chytrids may cause a delay in the timing of the diatom peak or may decrease the height of the peak, depending on the environmental conditions affecting growth. Moreover, as many chytrids are host specific, chytrid parasitism of one species can favor the development of others, thereby affecting seasonal succession of phytoplankton species (Canter and Lund, 1951; Van Donk and Ringelberg, 1983), as well as intraspecific diversity (Gsell et al., 2013c). Parasitic chytrids of phytoplankton have only recently been considered in the updated PEG model as an important "novel" interaction driving seasonal succession of plankton in lakes, in addition to the role of physical factors, grazing and nutrient limitation (Fig. 3, (Rasconi et al., 2012; Sommer et al., 2012)). However, as studies on chytrids in plankton assemblages are often limited to the investigation of the phytoplankton spring bloom, or focus on a single or few host-chytrid interactions, the seasonal dynamics of chytrids at the community level remains understudied in most water bodies. The few existing seasonal studies, performed in temperate lakes undergoing thermal stratification, have shown that temporal dynamics of planktonic chytrid species are closely coupled to the seasonal population dynamics of their phytoplankton hosts (Holfeld, 1998; Rasconi et al., 2012). In winter, phytoplankton activity is in general low and consequently the abundance of parasitic chytrids is likewise at a low level. Increasing nutrient availability by vernal holomixis, together with increasing light availability and rising temperatures, initiate the development of the diatom spring bloom. Chytrid infections increase due to increased host-chytrid contact rate and high prevalence of infection may be established on the dominant diatom species. The principle of "killing the winner" causes succession of species during the bloom. Lakes in forested areas experience massive pollen rains, often after the spring bloom decline in May/June, thus coinciding with the clear water phase. During this period, the abundance of parasitic chytrids sharply declines, whereas pollen grains are rapidly colonized by saprophytic chytrids. Summer and autumn months are characterized by a diverse phytoplankton assemblage leading to the association of different parasitic chytrid species of chlorophytes, diatoms and cyanobacteria, but in general with lower prevalence of infection. Favorable environmental conditions occasionally allow for short peaks of diatom species to occur in this period which may result in subsequent short but severe chytrid epidemics (Canter and Lund, 1951; Holfeld, 1998).

Whereas parasitic chytrids are mostly associated with large inedible phytoplankton species, they can also occur on smaller-sized chlorophytes and diatoms (Sparrow, 1960); however, prevalence of infection has been reported to be generally low compared to larger hosts (Canter-Lund and Lund, 1995; Rasconi et al., 2012). Nevertheless, when a small-sized (<10 μm) *Cyclotella* species made up the dominant biomass during a diatom spring bloom in the oligo-*meso*trophic Lake Stechlin (Germany), a chytrid species was

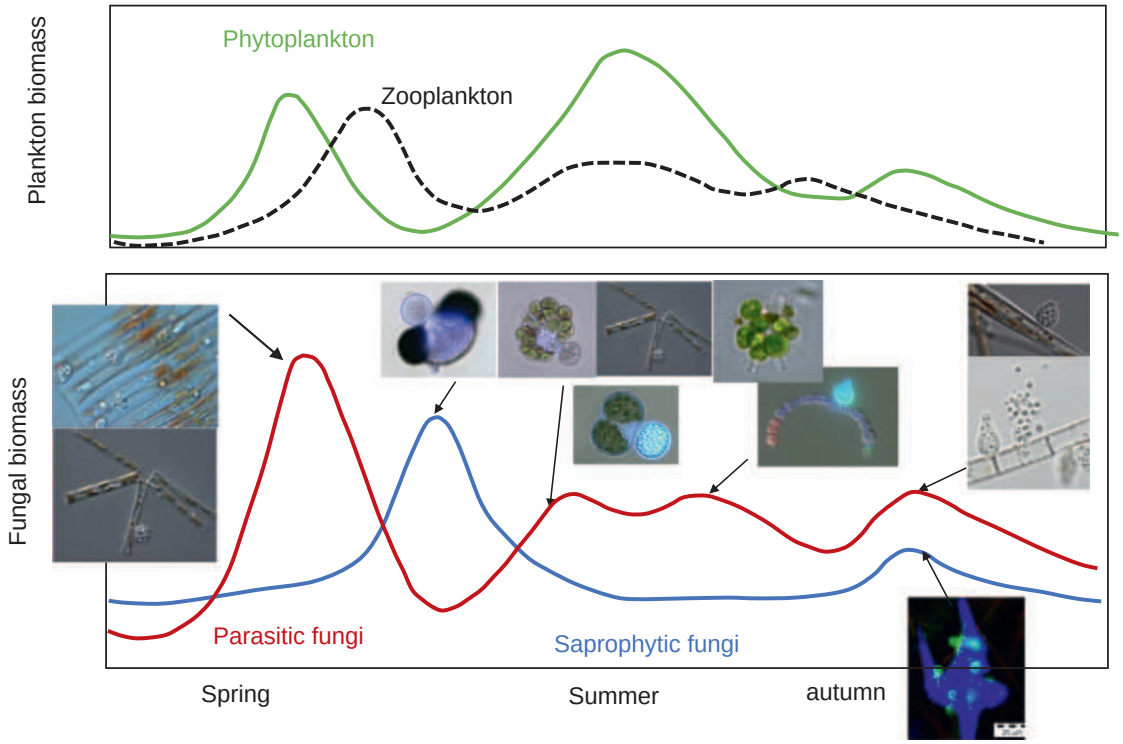

Fig. 3 PEG model of the seasonal biomass patterns of plankton and hypothetical seasonal succession of parasitic and saprophytic fungi. (Top) Seasonal biomass patterns of plankton in meso-eutrophic water bodies based on PEG model. (Bottom) Hypothetical seasonal succession of parasitic and saprophytic fungi. Parasitic fungi of diatoms increase in spring and autumn corresponding to the diatom bloom. During clear water phase when pollen deposition is significant, saprophytic fungi dominate. In summer, diverse parasitic fungi appear corresponding to the phytoplankton community with diverse green algae and cyanobacteria. In autumn, a slight increase of parasitic chytrids infecting diatoms and saprophytic chytrids on cellulosic theca of dead dinoflagellates may occur. Image of parasitic chytrid on diatom *Aulacoseira* sp. courtesy of K. Seto, University of Michigan, US.

able to infect up to 40% of the *Cyclotella* population. Diatoms are well known as preferential hosts for chytrid epidemics. Cyanobacteria which can make up a large proportion of autotrophic biomass in meso -and eutrophic lakes are also infected by chytrids, but epidemics on cyanobacterial blooms have only rarely been reported (Holfeld, 1998; Canter and Lund, 1951). The study by Rohrlack et al. (2013) suggests that oligopeptide production in the toxic cyanobacteria *Planktothrix* is part of a defensive mechanism against chytrid parasitism. In contrast, a case study in the eutrophic Lake Aydat (France) has shown that high prevalence of chytrid infection (almost 100%) can also be reached during an autumnal bloom of the potentially toxic filamentous cyanobacteria *Dolichospermum macrosporum* (Rasconi et al., 2012). In general, strong inter-annual variations in chytrid infections occur due to the complex interplay of several factors, i.e., host density, biotic and abiotic environment and co-evolutionary processes (Gerphagnon et al., 2017; Gsell et al., 2013c; Ibelings et al., 2011). No clear seasonal succession pattern could be observed in the eutrophic shallow Lake Inba (Japan), where diverse fungi infected two dominant diatoms with low prevalence of infection (<10%) (Kagami et al., 2012). These studies highlight that seasonal dynamics of chytrids may not be generalizable to all types of water bodies. Furthermore, they show the importance of long-term monitoring of chytrid-phytoplankton dynamics to understand the implications for plankton communities and food web dynamics.

Fungi in aquatic food webs

Fungi occupy multiple trophic levels in aquatic food webs, functioning as decomposers, consumers (e.g., parasites) or prey. As major decomposers of terrestrial derived organic matter, they hold a key position in coupling aquatic and terrestrial food webs. In the following section, we will introduce different trophic pathways that involve fungi in aquatic habitats with a focus on the "Mycoloop" concept (Fig. 4). Evaluating the trophic contribution of fungi in aquatic food webs and nutrient cycling remains a key challenge, besides identifying their presence, quantifying their abundance/biomass and activity.

Chytrid fungi in pelagic food web—Mycoloop

During epidemic events, when parasitic chytrids infect and kill a large proportion of the dominant phytoplankton species, the consumption by chytrids can account up to 25% of primary production in Lake Biwa (Japan) (Kagami et al., 2006). Similar

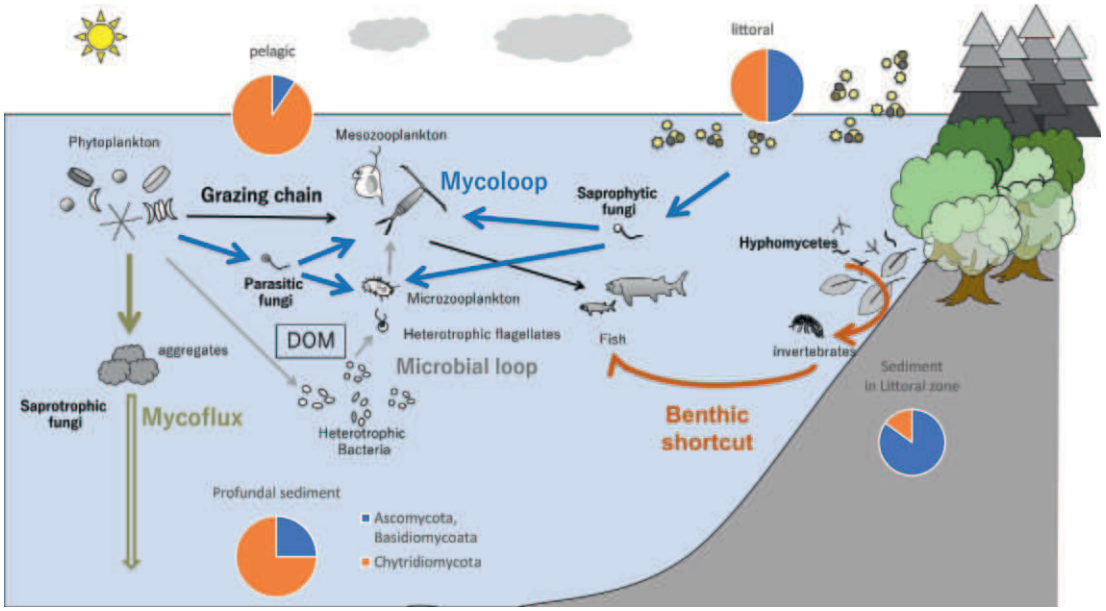

Fig. 4 Roles of fungi in aquatic food webs with community composition. Three major processes by which aquatic fungi transform and incorporate allochthonous and autochthonous organic matter into the food web are highlighted: mycoloop, mycoflux and benthic shortcut. The mycoloop refers to both parasitic and saprophytic fungi rendering inedible phytoplankton/pollens edible to zooplankton grazers either by producing zoospores or by fragmentation of the phytoplankton. The benthic shortcut/shunt refers to fungal colonization of organic litter rendering it palatable for macrozoobenthos on the sediment, which are in turn consumed by fish. The mycoflux describes fungal mediated flux through aggregation or disintegration of organic matter. The consequences are still largely unknown, but it is likely that they greatly affect aquatic carbon pump and sinking fluxes. DOM, dissolved organic matter. Pie charts indicate the general proportions of higher fungi (Ascomycota, Basidiomycota) and Chytridiomycota in each habitat.

percentages have been calculated for the oligo-mesotrophic Lake Pavin (France) (Grami et al., 2011) and eutrophic Lake Aydat (France) (Rasconi et al., 2014). Spring blooms and summer/autumn blooms dominated by large diatoms and toxic filamentous cyanobacteria respectively, are not considered as efficient links in the classical grazer chain. In contrast, chytrid zoospores, which are released after having consumed their phytoplankton host, are high-quality food for zooplankton both in terms of size (2–5 μm in diameter) and nutritional value (rich in polyunsaturated fatty acids PUFAs and cholesterols). This trophic pathway where the biomass of inedible phytoplankton is channeled to higher trophic levels via edible fungal zoospores has been conceptualized in the mycoloop (Kagami et al., 2007, 2014).

Quantifying the mycoloop in the field is challenging because of difficulties in quantifying the abundance and biomass of different chytrid life stages. Chytrids lack ergosterol, and therefore the traditional methods using this biomarker to estimate fungal biomass are not applicable (Gessner et al., 1991). The chitin stain Calcofluor white (CFW) is a fast and easily implemented staining method used to identify attached sporangia stages of chytrids (Rasconi et al., 2009). The density of parasitic chytrid sporangia during epidemics can reach 10^1–10^8 sporangia L^{-1} (Kagami et al., 2014). Limitations of CFW, however, are that it also stains cellulose by binding unspecifically to ß-1-3 and ß-1-4 polysaccharides. More specific chitin stains are based on chitinases or lectins conjugated with fluorochromes (Ota and Kawano, 2015; Wurzbacher and Grossart, 2012). Detection of chytrid infections can be improved by a CFW-WGA (wheat germ agglutinin) dual staining protocol (Klawonn et al. 2021). Recently, the use of phospholipid-derived fatty acid (PLFA) profiles have been evaluated for quantifying fungal groups in mixed communities. Although the method is promising for filamentous fungi, it currently has limitations for the detection of low chytrid biomass (Taube et al., 2019).

It is even more challenging to quantify the biomass of the free living zoosporic stage of chytrids, as the majority of chytrid zoospores lack a cell wall, making the use of chitin cell wall stains not possible. Molecular methods such as real-time qPCR (Lefevre et al., 2010; Maier and Peterson, 2016), and CARD-FISH (Hassett et al., 2019; Jobard et al., 2010) have been applied to quantify zoospores in the field and have detected zoospore abundances in lakes up to more than 600 spores mL^{-1} (Jobard et al., 2010; Kagami et al., 2014). Using CARD-FISH, Jobard et al. (2010) revealed that chytrid zoospores have often been miscounted as HNF (heterotrophic nanoflagellates), with up to 60% of HNF turning out to be chytrid zoospores.

In addition to zoospores as a food source, chytrids can fragment large filamentous cyanobacteria which may become more edible to zooplankton and strengthen the flow of the mycoloop (Frenken et al., 2020; Gerphagnon et al., 2013). Moreover, by synthesizing sterols de novo they upgrade the quality of cyanobacteria-derived organic matter for zooplankton (Gerphagnon et al., 2019). The "mycoloop" may thus substantially support zooplankton growth, especially in eutrophic systems where large inedible algae or toxic cyanobacteria dominate (Haraldsson et al., 2018; Kagami et al., 2014; Miki et al., 2011). Furthermore, in oligo-mesotrophic lakes, the mycoloop has been shown to be important. Using a linear inverse modeling approach, combining field data and parameter values derived from experimental studies, the impacts of parasitic chytrids on the pelagic food web were

quantified (Grami et al., 2011; Niquil et al., 2011; Rasconi et al., 2014). Chytrid epidemics during the diatom spring bloom channeled up to 20% of primary production via chytrid zoospores to the higher trophic levels. Zoospore consumption made up 38% of the microzooplankton diet. This resulted in a higher global trophic efficiency coupled to a higher efficiency of carbon transfer through each trophic level of the grazing chain. Chytrids reduced the sedimentation loss of large inedible algae and their contribution to the detritus pool, therefore less carbon is lost from the pelagic zone. On the other hand, chytrid infection may induce phytoplankton aggregation and enhance phytoplankton sedimentation (Kagami et al., 2005). Quantification of these processes in the field is needed in order to obtain a full understanding of the role of parasitic chytrids play in the aquatic carbon cycle.

Pollen is an important input of allochthonous organic matter to lakes located in forested areas. Unlike leaf litter, pollen grains are rich in phosphorus, and pollen deposition can contribute from 2% to 35% of a lakes total phosphorus loading (Banks and Nighswander, 2000). For the oligo-mesotrophic Lake Stechlin (Germany), situated in a highly forested area, an annual P load of 82.9 kg via pollen has been calculated, accounting for nearly half of the yearly atmospheric P input into the lake (Rösel et al., 2012). Pollen grains are hardly ingested by zooplankton nor are they well degradable by bacteria due to their extracellular wall (exine). Although chemical leaching of macro nutrients from pollen can indirectly stimulate the microbial loop (Rösel et al., 2012), chytrids are among the few microorganisms which are able to directly utilize pollen with high (30–60%) P utilization efficiency (Kagami et al., 2017). Similar to the "mycoloop" pathway described for parasitic chytrids, nutrients from inedible allochthonous pollen are incorporated into aquatic food webs by saprophytic chytrids, and transferred to higher trophic levels via zoospores (Kagami et al. 2014, 2017). When pollen rains coincide with the period of lowest phytoplankton productivity, the presence of highly nutritious fungal zoospores may continue to sustain zooplankton populations for a longer time in lakes (Fig. 3). In those cases, food limitation as a factor controlling zooplankton biomass during the clear water phase may be overestimated compared to losses by predation (Sommer et al., 1986).

The mycoloop can theoretically be further extended to encompass all pathways where saprophytic chytrids channel inedible or less degradable organic matter via zoospores to higher trophic levels. For example, planktonic aggregates or insect and crustacean exuviae, containing large amounts of refractory materials such as cellulose and chitin, can be heavily colonized by chytrids (Karling, 1945; Wurzbacher et al., 2010).

More or less unexplored is the impact of chytrids on the microbial loop. Chytrids can change the quality and quantity of organic matter, which feeds back not only to higher trophic levels but also to the microbial loop (Klawonn et al. 2021b). Chytrids enter with their rhizoids into particulate organic matter (POM) and degrade it with enzymes, which often increase the leakage of dissolved organic matter (DOM) and stimulate the growth of heterotrophic bacteria (Kagami et al., 2007, 2017). As a result, the composition of DOM is changed (Senga et al., 2018). A negative feedback on the microbial loop may also occur due to the competition between chytrids and bacteria for substrates. By quantifying cell-to-cell carbon transfer rates between phytoplankton, parasitic chytrids, and bacteria, Klawonn et al. demonstrate that a substantial part of photosynthetic C is diverted from the microbial loop to parasitic chytrids (e.g. fungal shunt). The "fungal shunt" together with the mycoloop promotes zooplankton-mediated over microbe-mediated remineralization. Fungi:bacteria ratios on pollen have also been shown to vary between lake types with fungi being most prominent in acidic dystrophic water (Wurzbacher et al., 2014).

Many knowledge gaps remain with regards to organic matter transformation pathways mediated by aquatic fungi. The term "Mycoflux" has been recently introduced and refers to currently unknown pelagic fungal interactions leading to aggregation or disintegration of organic matter (Grossart et al., 2019). Fungi actively colonize organic aggregates which may lead to the release of DOM and nutrients into the water, in turn affecting the aquatic carbon pump and sinking fluxes. Besides chytrids, yeast may play a particularly important role in nutrient recycling on plankton detritus aggregates, as peak abundances of yeast in the pelagic have been recorded to coincide with the crash of the annual phytoplankton spring bloom (Quinn, 1984).

Fungi in benthic food webs

In lakes, allochthonous leaf litter inputs can be significant; sometimes contributing up to 10% of primary production in lakes (Gasith and Hosier, 1976). Hyphomycetes are the first colonizers of leaf litter and act as primary degraders of terrigenous carbon which is further conditioned together with bacteria, then mechanically disintegrated by macroinvertebrates (Bärlocher, 1985). Fungi, particularly hyphomycetes, render leaf litter palatable and upgrade its nutritional value by lowering the carbon:nitrogen:phosphorus (C:N:P) ratio (Krauss et al., 2011). This specific pathway is termed the "benthic shortcut", which efficiently channels refractory organic matter up to higher trophic levels (Attermeyer et al., 2013). The contribution of energy from fungal mycelia to the growth of various shredders typically varies between 1% and 59% (Suberkropp, 1992). Filamentous fungi can account for more than 90% of total microbial biomass in emergent macrophytes and leaf litter (Gulis et al., 2009). Fungal biomass largely surpasses bacterial biomass especially during early stages of leaf decay (Findlay and Arsuffi, 1989), whereas at later stages of decay and on smaller organic particles, fungal biomass declines while bacterial biomass remains relatively constant (Findlay et al., 2002; Mille-Lindblom et al., 2006). However, the presence of labile algal POM greatly affects the dominance of bacteria over fungi within the degrader communities, and stimulates the overall decomposition of leaf litter (Danger et al., 2013; Fabian et al., 2017). Fungi primarily contribute to terrigenous C turnover by providing litter C for the microbial loop, whereas bacteria determine whether the supplied C substrate is assimilated into biomass and transported to higher trophic levels or is recycled back into the atmosphere. Environmental conditions such as phosphate availability may have a strong effect on these processes (Fabian et al., 2017).

Emerging fungal diseases (chytridiomycosis) in freshwater

The key drivers of aquatic ecosystem shift (i.e., eutrophication, climate warming with increasing water temperature and UV radiation, brownification, habitat alteration, invasive species and pollution) may impact fungi and their interactions with other species, and alter food web dynamics and biogeochemical cycles. Artificial aquatic ecosystems, such as sewage systems, street gutters, aquaculture and algal farms, may enhance the colonization of fungi including pathogens and parasites (Letcher et al., 2013). In general, the role of aquatic fungi in water quality management and biotechnological applications deserves more attention.

Warmer temperatures

Climate change and other anthropogenically induced stressors are expected to increase the impact of disease on host populations (Daszak et al., 2001). However, interactions between physiological stress and disease are likely to be much more complex. In the Northern Hemisphere, winters are warming at about twice the rate of summers. A consequence of warmer and shorter winters is an earlier onset of phytoplankton spring blooms in temperate lakes. Climate warming may enhance the importance of phytoplankton chytridiomycosis, as under experimental warming conditions a parasitic chytrid infecting the diatom *Synedra* accelerated the termination of the spring bloom, which was dominated by this diatom species (Frenken et al., 2016). The unique long-term study in Lake Maarsseveen (The Netherlands) has shown that cold winters with ice cover inhibit the activity of chytrids that infect the diatom *Asterionella formosa* (Ibelings et al., 2011). Temperatures below 3 °C offer a "cold" thermal refuge for the host (Bruning, 1991a; Gsell et al., 2013b). This provides a disease-free window of opportunity for *A. formosa* to grow before increasing temperatures allow the chytrid to kick in and utilize the large amount of buildup host resources. In contrast, warmer winters without ice coverage allow the chytrid to infect *Asterionella* earlier, at the start of the growing season, resulting in a lower peak of host and parasite abundance, and lower peak of infection prevalence (Ibelings et al., 2011; Van Donk and Ringelberg, 1983). Thus, although infection levels in mild winters are lower than in colder years, chytrid infections act as a species-specific loss factor, reducing the size of *Asterionella* inoculum and weakening its competitiveness (Ibelings et al., 2011). The incidence of ice-free winters is likely to increase in the future and changes in chytrid infection rates of diatoms are expected to have cascading effects on phytoplankton community structure and the entire food web. A shift from large diatoms to a mixed community in years with mild winters may benefit food webs due to the poor edibility of larger diatoms, unless the chytrid zoospores produced during epidemics significantly contribute to zooplankton nutrition (Ibelings et al., 2011; Frenken et al., 2016). Beside a "cold" thermal refuge, *Asterionella* has also a "warm" thermal refuge, with temperatures above 21 °C having a negative effect on the growth of its chytrid parasite (Gsell et al., 2013b). Global warming may therefore reduce the impact of phytoplankton chytridiomycosis during the summer, and facilitate the occurrence of high-density summer/autumn blooms of *Asterionella* due to the chytrid's lower thermal maximum (Gsell et al., 2013a). Negative effects of elevated temperature have also been found for *Batrachochytrium dendrobatidis* (Bd), the chytrid causing disease and worldwide decline in amphibians; amphibians having been reported to clear chytrid infections by seeking high temperature environments (Woodhams et al., 2003). In amphibians, the skin microbiota plays an important role in host defense and temperature dependent antifungal properties of the skin microbiota may provide an alternative mechanistic explanation for patterns of disease susceptibility related to climate change (Woodhams et al., 2014). Additional support for chytrids preferring colder temperatures comes from a long-term seasonal study in Devil's Lake (US), where highest infection levels of the chytrid *Polycaryum laeve* on *Daphnia* occurred between January and March when the lake's surface was frozen, whereas very low prevalence of infection occurred in summer (Johnson et al., 2009). However, the impact of global warming on chytridiomycosis is likely to be species-specific as the location of refugia on the temperature scale may vary from host to host. The study by Rohrlack et al. (2016) identified a large "cold" thermal refuge below 8 °C, inside which the cyanobacteria host *Planktothrix* can grow without becoming infected. In contrast to the *Asterionella*-chytrid systems, temperatures above 21 °C provided no "warm" refuge for this host. *Planktothrix* is well adapted to low light and temperatures and is capable of vertical migration, allowing it to form dense metalimnetic blooms in stratified lakes. The steep temperature gradient in the metalimnetic zone may thus provide a spatial "cold" thermal refuge, protecting a large part of the *Planktothrix* population from chytrid infection and allowing it to form blooms even under suboptimal conditions (Rohrlack, 2018). In both systems intraspecific variability in chytrid susceptibility has been demonstrated which additionally varies with temperature (e.g., host genotype × temperature interactions) (Agha et al., 2018; Gsell et al., 2013b). The effect of global warming on chytridiomycosis is thus more likely to result in species and/or genotype shifts, due to altering temperature-dependent susceptibility of the host and through enabling or disabling thermal host refugia.

Pesticides

Pesticides and other chemical contaminants are a widespread problem in freshwaters because rivers and lakes act as conduits or sinks that transport, accumulate and concentrate chemical pollutants (Relyea, 2009). Environmentally relevant concentrations of several agriculture fungicides significantly reduce chytrid infection, while not affecting the growth of cyanobacteria *Planktothrix* (Ortiz-Cañavate et al., 2019). The application of fungicides has been explored as an approach to control chytridiomycosis in amphibians. However, fungicides paradoxically increased infection and *B. dendrobatidis* induced mortality rates by suppressing the immune response of the amphibian host (Rohr et al., 2017). Pesticides that directly target host physiology, such as herbicides, have been shown to modify infection dynamics and the impact of chytridiomycosis in the *Asterionella*-chytrid system (Van den Wyngaert et al., 2013). Photosynthesis inhibiting herbicides may interfere with host-finding mechanisms of chytrids (chemotaxis) and in this

way can reduce parasite transmission under low host densities (Van den Wyngaert et al., 2014). Similar to herbicides, light limitation also causes a reduction in host photosynthesis and has likewise been shown to reduce chytrid infection on diatoms (Bruning, 1991b; Canter and Jaworski, 1981). Both findings hint towards a general mechanism of chytrid zoospores using photosynthesis-dependent chemical cues to locate their host. If this hypothesis holds true, then any environmental condition impacting host photosynthesis may lead to similar outcomes of reduced chytrid transmission potential. Considering climate change-related increases in humic matter concentration in lakes (e.g., lake brownification) causing reduced light availability, there is an urgent need to increase our knowledge on the general relationship between light and phytoplankton parasite interactions. The free-living zoospore stage of chytrids, which lacks a cell wall, is presumably the most vulnerable stage to adverse external environmental factors. When considering control strategies for chytridiomycosis, the zoosporic stage may thus be the preferred target (Frenken et al., 2019).

Conclusion

Advances in next generation sequencing technologies have given a new boost to aquatic mycology, unveiling a high diversity of molecularly uncharacterized fungal diversity in a variety of aquatic habitats. In particular, early diverging zoosporic fungal lineages, including chytrids, Aphelidiomycota and Rozellomycota, show a great potential for filling current research gaps concerning aquatic biodiversity and ecology in freshwater lakes. Chytrids are the dominant fungi in the pelagic zone of lakes, interacting with phytoplankton and other microbes as parasites or saprophytes. As they are partly being re-discovered, the integration of morphological and molecular tools has also identified novel species and interactions, refining chytrid host/substrate utilization and specificity. This is important as chytrids have, in addition to the role of physical factors, grazing and nutrient limitation, a substantial role in driving seasonal succession of plankton in lakes. Advances have been made in estimating the impact of chytrids in pelagic food webs and nutrient cycling via the Mycoloop, which still needs to be further evaluated. In general, assessing the ecological relevance of fungi in overall biogeochemical cycling still faces methodological challenges to reliably quantify biomass and activity of different fungal groups in mixed microbial communities. Species-specific variation and non-linear dynamics of host-chytrid interactions impede clear-cut predictions about the impact of anthropogenic change on chytridiomycosis.

Knowledge gaps

- Functional diversity (e.g., substrate specificity) of aquatic fungi across broader taxonomic groups
- Quantifying fungal biomass and activities within microbial communities to assess their relative contribution to biogeochemical processes
- Other organic matter transformation pathways and nutrient recycling mediated by aquatic fungi, such as Mycoflux
- Symbiotic relationships between fungi and plankton
- Life form and roles of yeasts in food web and biogeochemical cycling
- Degradation and detoxification of pesticides, pharmaceuticals and microplastics by fungi
- Anthropogenic impacts on fungal mediated interactions and its consequences
- Lack of studies on quantification of chytrid-phytoplankton dynamics in different types of freshwater ecosystems to understand relevance for plankton communities and food web dynamics.
- What are the factors driving spatial and temporal variation in phytoplankton susceptibility to chytrid infection?

Appendix: Supplementary material

Supplementary material related to this chapter can be found on the accompanying CD or online at https://doi.org/10.1016/B978-0-12-819166-8.00005-0.

See Also: Emerging methods and topics: Inland Water Fungi in the Anthropocene: Current and Future Perspectives; Structures and functions of Inland Waters - Groundwater: Presence and Role of Prokaryotic Viruses in Groundwater Environments; Structures and functions of Inland Waters - Lakes: Protists: Flagellates and Amoebae

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The Regents of the University of Californiahttps://amphibiaweb.org/chytrid/chytridiomycosis.html.

Protists: Flagellates and Amoebae[☆]

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This article is an update of R.W. Sanders, Protists, in Encyclopedia of Inland Waters, edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00131-9.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Benthic/benthos Associated with the sediment or bottom of a body of water.
Cyst A cell state within a continuous enclosure by an extracellular matrix during which the cell exhibits little activity; often used to increase survival during unfavorable environmental conditions.
Detritus Dead organic matter.
Flagellum In eukaryotes, a filamentous membrane covered structure with a skeletal component of microtubules used for movement and feeding.
Heterokont A flagellate that possesses two different types of flagella, one usually with flagellar hairs (mastigonemes); typical of many Stramenopiles.
Lorica An organic or inorganic casing or shell that incompletely surrounds a cell, sometimes called a test.
Mixotrophy The use of energy from the sun to take up nutrients and grow combined with the ability to ingest and digest prey. Some consider the symbiotic relationship between heterotrophic protists and phototrophic protists to be a form of mixotrophy.
Nanoflagellate A general description of flagellates between 3 and 20 μm in size, used mostly in ecological studies where their small size and preservation techniques preclude more precise identification.
Osmotrophic A form of nutrition in which soluble compounds are taken up by the organism.
Periphyton Photosynthetic microorganisms living attached to rocks or other surfaces; sometimes used to describe the whole community of prokaryotes and microbial eukaryotes associated with this layer.
Phagocytosis To ingest food particles by enclosing them in a membrane to internalize and form a food vacuole.
Plankton Organisms living suspended in the water column; many can swim, but are incapable of resisting currents.
Pseudopodia Transient extensions of the cell surface used for locomotion and feed in amoeba and some flagellates includes subtypes filopodia (thread-like) and lobopodia (broad), as well as the internally supported axopoda.

[☆]*Change History:* October 2021. RW Sanders prepared the update. All sections, tables and figures were revamped. Antonio Guillén provided all of the photomicrographs, but Sanders combined them into the final two figures. Original article included ciliates, but that was assigned to another author as a stand-alone chapter.

What are protists?

The protists are a diverse group of distantly related eukaryotes that includes most of what have been historically called protozoa (ciliates, amoeba, and heterotrophic flagellates) plus, in aquatic systems, phytoplankton and periphyton. The term is one of convenience used to describe an assemblage of eukaryotic organisms that falls outside of the multicellular groups of animals, land plants and fungi. Being thus defined by exclusion, the term protist is not phylogenetically useful. However, most of the high-level diversity in the eukaryotic Tree of Life (eToL) results from the organisms grouped as protists and identified, to a large degree, using molecular phylogenetics (Burki et al., 2020).

Like other eukaryotes, protist cells possess at least one membrane-bound nucleus plus endoplasmic reticulum and other organelles that can include mitochondria, chloroplasts and flagella or cilia. Some protists are colonial or related to multicellular groups, but none develop tissue. The different ecological roles filled by protists within morphologically recognized phyla led to some subgroups historically being described by both zoological and botanical nomenclature. Many monophyletic lineages (clades) include a mixture of taxa from both of the "International Codes" ("Nomenclature for algae, fungi, and plants" and "Zoological Nomenclature") (Adl, et al., 2019). For example, many dinoflagellate genera contain both phototrophic (most now recognized to be mixotrophic) and heterotrophic species; some euglenids can even switch from phototrophy to heterotrophy when photosynthetic species are induced to lose their chloroplasts and survive using dissolved organic matter for energy and carbon.

The protists do have lineages that are properly organized to represent evolutionary relationships. Some clades, which are groups of ancestral species and all their known descendants, include only protists. Alveolata (ciliates, dinoflagellates and apicomplexa), Rhizaria (amoeba and amoeba-flagellates with fine pseudopods or filopodia), and Euglenozoa (euglenids, kinetoplastids, and diplonemids) typify purely protistan clades. Other clades, however, indicate a shared ancestry between some protists and plants or animals that is closer than their evolutionary relationship to other protistan groups. For example, the choanoflagellates group with true fungi, chytrids and animals as Opisthokonts, and the green algae, including common freshwater species like *Chlamydomonas* and *Volvox*, group with the Viridiplantae. The Stramenopile clade also contains protist (e.g., diatoms) and multicellular organisms (e.g., kelps and other brown macroalgae).

As one might expect from such an evolutionarily and ecologically diverse group, making generalizations about the protists must be a cautionary exercise. Yet, for the practicing field biologist or ecologist, the small size and functional similarities of many of the protists makes grouping them together a rational practice. Subdivisions based on movement are usually easily distinguishable with light microscopy and are retained here, not because they reflect current understanding of phylogeny, but rather because they often reflect niches and form the basis of much of the study of community ecology in freshwater protists to date. The classification of these protists is represented here in Tables 1 and 2, in which some common members of freshwater flagellates and amoebae are arranged at the higher taxonomic ranking following the "nameless-rank" classification system of Adl et al. (2019). This classification scheme considers the taxonomic endings to be accidents of history without the traditional hierarchical meaning of past classification codes. Higher rankings found in both tables, indicating the taxonomic overlap of the flagellates and amoebae, include Opisthokonta, Stramenopiles, Rhizaria and Discoba.

Morphological groups

Flagellates

Flagellates have one-to-many flagella that function in motility, attachment to a substrate, and also for feeding. They are diverse (Table 1 and Fig. 1) and are the most numerous of the freshwater protists, reaching abundances in eutrophic systems that can approach 10^5 cells mL^{-1} and 10^6 cells cm^{-3} in the plankton and sediments, respectively. Purely heterotrophic free-living flagellates include choanoflagellates and bicosoecids. Choanoflagellates, with a distinctive "collar" of microvilli/pseudopodia used to trap bacteria and a single flagellum to create water currents, can have a lorica that is sometimes difficult to see with light microscopy. In fresh waters they are most often attached and/or colonial. Bicosoecids are heterokonts—possessing two different types of flagella—and often are attached by one of the flagella to a lorica or to the substrate. Cercozoans have two flagella but are amoeba-flagellates that use pseudopodia for feeding. Some species traditionally considered as amoeba also are now classified as Cercozoa (see below).

Among the several taxa of photosynthetic flagellates most groups have members that are wholly heterotrophic or that combine photosynthetic and heterotrophic nutrition (mixotrophy). Dinoflagellates, chrysomonads, euglenids, and cryptomonads have numerous phagotrophic or osmotrophic species that lack chloroplasts (Patterson, 2000). Phagotrophy of bacteria or protists by chloroplast-containing species also has been reported for dinoflagellates, chrysomonads and cryptomonads, and is discussed further below and elsewhere in this volume.

Many recent ecological field studies separate flagellates into different groups based primarily on size. This is most common in examinations of the microbial food web, where assemblages of heterotrophic nanoflagellates are enumerated collectively due to their high abundance, importance as bacterivores, and the difficulty of separating taxa in preserved samples (e.g., Šimek et al., 2018). This size-based assemblage originally described nanoplankton as $\leq$20 μm in diameter, but flagellates $\leq$5 μm often numerically dominate nanoplankton. It is difficult to separate individuals this small into different taxonomic groups by light microscopy; even division into functional groups of photosynthetic versus heterotrophic flagellates is problematic without proper

Table 1 Some common genera of heterotrophic flagellates.

Group	*Genera*	*Comments*
Opisthokonta		
Choanoflagellata		
Salpingoecidae	*Monosiga*	Phagotrophic flagellates with a single flagellum surrounded by cytoplasmic "fingers" used in feeding on bacteria; mostly sessile/attached; *Salpingoeca* with an organic theca (sheath)
	Salpingoeca	
Stramenopiles		Motile cells typically biflagellate and heterokont with tubular hairs (mastigonemes) on anterior flagella
Bigyra		
Opalozoa	*Bicosoeca*	Predominantly sedentary in a lorica, filter feed on bacteria
Ochrophyta	*Actinomonas, Ciliophrys*	Pedinellids, single flagellum, often radiating filopodia, usually stalked, feed on bacteria
	Paraphysomonas	One short and one long flagella; silica spines on cell body used to identify species requires electron microscopy
	Pedinella[a]	Apple-shaped with a posterior stalk and a single apical flagellum
	Pseudopedinella[a]	Most common in oligotrophic systems
	Spumella (Monas)	Colorless, nearly identical to *Paraphysomonas* using light microscopy
	Ochromonas[a]	Typically with chloroplast, which may be reduced in mixotrophic populations using osmotrophy or phagotrophy
	Uroglena[a]	Colonial, all photosynthetic, mixotrophic
Rhizaria		
Cercozoa	*Cercomonas*	Bacterivorous with pseudopods; glide on surfaces using long posterior flagellum
Haptista		
Haptophyta		
Prymnesiophyceae	*Chrysochromulina*[a]	Autotrophic, mixotrophic or heterotrophic. Mostly single cells; some in colonies; motile cells mostly possessing a haptonema, a filiform appendage situated between a pair of flagella
Cryptista		
Cryptophyceae	*Goniomonas, Chilomonas*	Bacterivorous; primarily photosynthetic species, some of these with low rates of phagotrophy reported (mixotrophy); *Chilomonas* species were recently reassigned, with freshwater members assigned as heterotrophic *Cryptomonas*
	Cryptomonas[a]	
Alveolata		
Dinoflagellata	*Gymnodinium*[a]	Two flagella, one horizontal around cell that gives slow spinning motion when swimming; photosynthetic, predatory and mixotrophic species
Discoba		
Euglenozoa	*Peranema, Entosiphon, Astasia*	Most euglenids have two flagella emerging from an anterior pocket, with one trailing and usually in contact with the substrate. Colorless species ingest detritus, bacteria and/ or are osmotrophic.
Euglenida		
Kinetoplastea	*Bodo, Rhynchomonas*	Only two common genera of free-living kinetoplastids; generally glide on substrates and ingest attached bacteria.

Some rankings are tentative. Most of the higher groups include photosynthetic flagellates, many of which combine phototrophic nutrition with phagocytosis (i.e., are mixotrophic).
[a]Genera with known mixotrophic species.

fixation and slide preparation methods (Sherr et al., 1993). Consequently, care must be taken to determine if literature reports combined all small protistan cells into one trophic category or functionally divided groups into autotrophic and heterotrophic forms (usually based on the presence or absence of chloroplasts). Differentiation of these forms is commonly based on epifluorescence microscopy with stains that highlight the cells' cytoplasm and filter sets that identify chloroplasts by their red autofluorescence. Flow cytometry is another useful tool that can separate autotrophs from heterotrophs based on fluorescence and size from light-scatter signals. Heterotrophic flagellates larger than 20 μm are typically much less abundant than nanoflagellates and include many, but not all, of the dinoflagellates and euglenids. These species often are more easily identified by light microscopy, either live or in preserved samples, because of their larger size; epifluorescence microscopy is also an appropriate method for enumeration.

Amoeboid protists

Amoebae are plastic cells that generally lack a fixed external morphology, although some inhabit capsules or lorica and are less plastic. They move primarily using pseudopodia with shapes that vary in different taxa from finely pointed and branching filose extensions to blunt lobopodia. Several amoeboid groups become flagellated during temporary swimming stages for dispersal, and some of these, including the stalked heliozoans ("sun animicules"), have affiliations with Stramenopiles (Table 2).

Amoebae are common on surfaces and in the sediments of freshwaters (mostly in the top cm), reaching abundances greater than 10^3 cm^{-3} in eutrophic lakes (Fig. 2). Amoebae are usually less numerous in the plankton compared to the sediment but may also be concentrated in a microlayer associated with the air-water interface. Testate amoebae have vase-shaped or spherical coverings from which the pseudopods extend, and some of these species form oil droplets or gas vacuoles that reduce their density and allow them to rise from the sediment into the plankton. Non-testate planktonic amoebae may take on stellate floating forms, a flagellated

Table 2 Some common genera of amoeboid protists with comments on habitat and food.

Group	*Genera*	*Comments*
Tubulinea		
Elardia		
Euamoebida	*Amoeba, Chaos*[a], *Hartmannella*	Food is bacteria and/or small protists (cytotrophic)
Arcellinida	*Arcella, Difflugia*[a]	Testate/shelled, benthic and planktonic stages; omnivores, algae, *Difflugia* is a diatom specialist
Discosea		
Flabellinia		
Dermamoebida	*Mayorella*[a]	Omnivorous, predators of protists, detritus
Vannellida	*Vannella, Platyamoeba*	Benthic and planktonic; food primarily bacteria
Centramoebia		
Acanthopodida	*Acanthamoeba*	Some species are facultative human pathogens, infecting eye and CNS; normally food is bacteria
Opisthokonta		
Rotosphaerida	*Nuclearia*	Food is bacteria, cyanobacteria
Stramenopiles		
Gyrista		
Actinophryidae	*Actinosphaerium*[b], *Actinophrys*[b]	Planktonic or mobile benthic; food includes other protists, rotifers
Centroplasthelida		Planktonic or mobile benthic; food is other protists/phytoplankton
Panacanthocystida		
Pterocystida	*Acanthocystis*[b], *Heterophrys*[b], *Chlamydaster*[b], *Raphidiophrys*[b]	
Rhizaria		
Cercozoa		
Granofilosea	*Clathrulina, Hedriocystis*	Benthic, sessile, often stalked, sometimes colonial; food is fine particulate matter, including bacteria
Discoba		
Heterolobosea		
Tetramitia	*Naegleria, Tetramitus, Vahlkampfia*	Food is bacteria/cyanobacteria; some *Naegleria* strains are facultative human pathogens (amoebic encephalitis)

Many amoebae have flagellated stages, and flagellated forms dominate the life stages of some groups (e.g., Stramenopiles, Cercozoa; see Table 1).
[a]Some species with zoochlorellae or photosynthetic symbionts; which can fall into the definition of mixotrophy.
[b]Heliozoans have some general similarities, which include axopodia (radiating pseudopodia stiffened by microtubule arrays), but the group is not monophyletic. With an extracellular capsule or lorica attached to substrate or free-floating cell, sometimes with a mucous sheath around cell. With biflagellate and amoeboid stages; can be colonial.

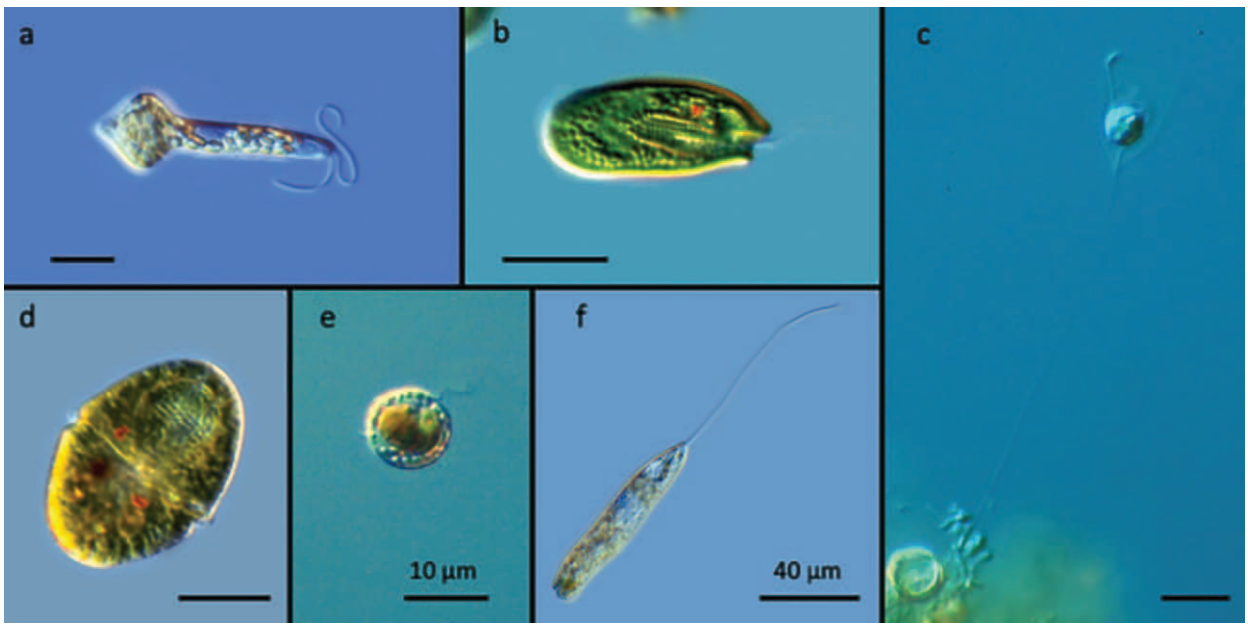

Fig. 1 Photomicrographs of representative flagellates. (A) *Astasia*, a colorless euglenid that can actively distort cell shape; biflagellate, but typically only one flagella emerges from anterior pocket; (B) *Cryptomonas*, with numerous polysaccharide storage bodies; only one of the two flagella is visible here; (C) *Bicosoeca*, immotile cell in a lorica with a long stalk and typically attached to a surface; (D) *Gymnodinium*, one flagella is in an equatorial groove, the second trailing flagella is not visible here; (E) *Ochromonas*, biflagellate with chloroplast and phagocytic capabilities, i.e., mixotrophic; (F) *Peranema*, another colorless euglenid that captures live prey via a unique mechanism using two ingestion rods near the tapering anterior pole. Scale bar 20 µm unless otherwise noted. Photo credit: Antonio Guillén.

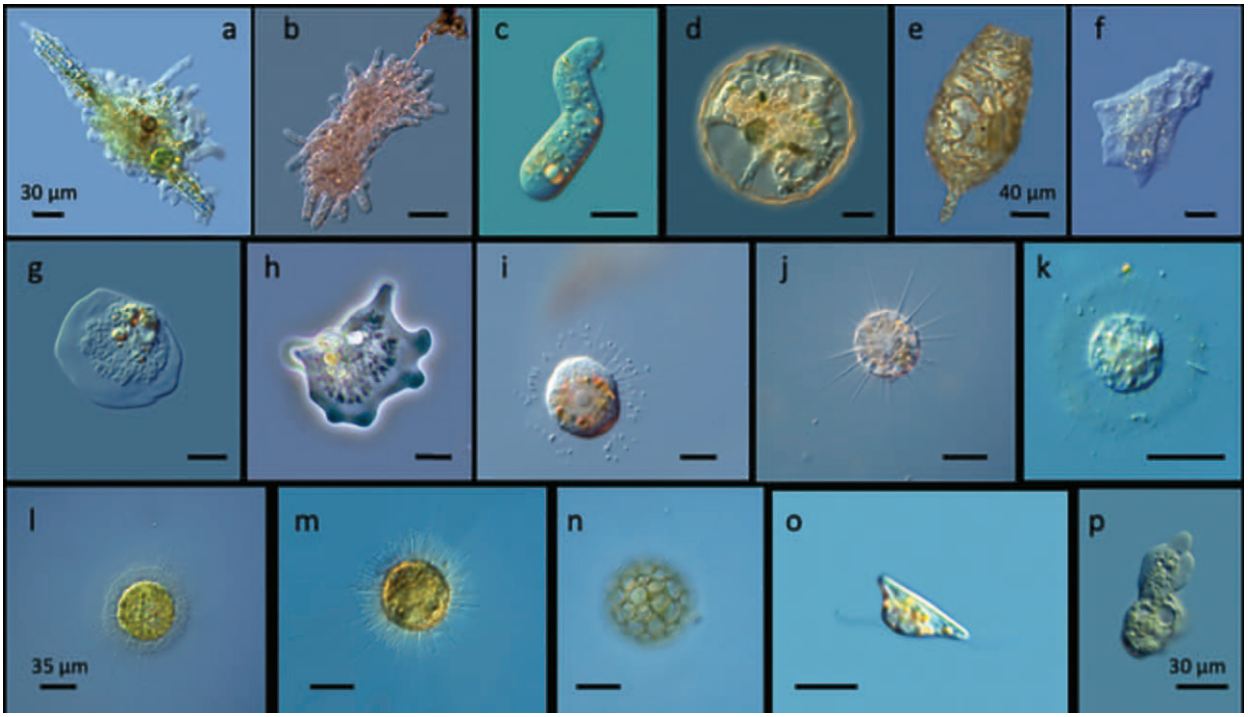

Fig. 2 Photomicrographs of representative amoebae. (A) *Amoeba*, with ingested diatom; (B) *Chaos*, similar morphology to *Amoeba* but with many nuclei; (C) *Hartmannella* moves by steady advance of the usually single pseudopod rather than the erratic, eruptive progress; (D) *Arcella*, viewed through circular test which has a hole where finger-like pseudopods emerge; (E) *Difflugia*, with tubular test; (F) *Mayorella*; (G) *Vannella*, locomotive form commonly fan-shaped, often semi-circular with broad hyaline margin; (H) *Platyamoeba;* (I) *Nuclearia*; (J) *Actinophrys*, pseudopodia extending from all parts of the body with axial filaments arising from the membrane of the single nucleus; (K) *Chlamydaster*, cell body surrounded by a mucus envelope through which axopods extend; (L) *Heterophrys*, mucous coat that often seems grainy with many radial organic spicules; (M) *Acanthocystis*, (N) *Clathrulina*, extracellular capsule attached to substrate with axopodia (not visible here) that emerge from perforations; (O) *Naegleria*, (P) *Vahlkampfia*. Scale bar 20 µm unless otherwise noted. Photo credit: Antonio Guillén.

morphology, or associate with floating detrital aggregates, none of which are taxa specific. Heliozoans are a polyphyletic group (Cavalier-Smith et al., 2015) that have some amoeboid characteristics in that they form specialized pseudopods strengthened with a microtubular array (axopods). Heliozoans are not unusual in the plankton, but they are primarily benthic predators that use the axopods to capture mobile prey such as ciliates from the water. Some species are attached to the substrate by stalks and others tumble across the sediment by changing the lengths of the axopods.

Beyond motility, most amoebae also use pseudopods to capture and/or engulf small prey including bacteria, algae and detritus. Some amoebae, including *Nuclearia delicatula* and some *Mayorella* and *Naegleria* species are specialized predators of larger particles such as filamentous cyanobacteria, and can rapidly reduce prey abundances in lakes. Photosynthetic endosymbionts are associated with several amoebae, including a heliozoan (*Acanthocystis turfacea*). This relationship is even reflected in the species names of some amoebae—both naked (*Chaos zoochlorellae, Mayorella viridis*) and testate (*Paulinella chromatophora*). Despite the widespread occurrence of some of these freshwater amoebae-algal symbioses, the degree to which the algae contribute to the nutrition of amoebae has not been well studied.

Some amoebae, including *Naegleria fowleri* and one or more *Acanthamoeba* species are facultative pathogens of humans and are the causative agents of amebic meningoencephalitis. These amoebae invade via mucus membranes of the eye or nasal passage of human swimmers, typically immunosuppressed individuals, in warm fresh waters, including unchlorinated swimming pools (Maciver et al., 2020).

Reproduction and population growth

Flagellates and amoebae reproduce asexually by binary fission, which can lead to rapid population growth. For heterotrophic protists, population growth rates are generally positively related to food concentration and temperature up to some critical level, and negatively related to species cell size. However, generation times are highly variable and maximum population growth rates of some species with relatively large size can approach those of much smaller protists. Populations of many protists can double several times per day in laboratory situations, although cell division rates of one to several days are probably more realistic for natural populations where food may limit growth. Protistan productivity in natural systems, particularly in the benthos, is not well documented and is likely higher than is generally recognized. Population growth can also be limited via predation by zooplankton,

benthic invertebrates and often other protists such as dinoflagellates and ciliates. However, the high potential growth rates enable heterotrophic protists to persist even during periods of high predation, and to respond rapidly to increases in fast-growing prey such as bacteria and photosynthetic protists.

Sexual reproduction is known for many protists but some are considered asexual, although it is difficult to determine if a protist species is entirely asexual and "absence of evidence does not constitute evidence of absence" (Maciver, 2019). When observed, sexual reproduction takes varied forms in protists, but some of the essential features are formation of gametic cells or nuclei, fusing of the nuclei and halving of the chromosome number at some point in the life cycle. Sex in protists is rarely associated with increases in population size; its occurrence interrupts asexual reproduction and the rapid population growth associated with binary fission. Sex appears to be essential for preventing senescence and extinction of clones for several protists, but is still unknown in many amoebae, in particular. Autogamy, in which the meiotic products fuse in the same cell is the normal pattern in the heliozoan *Actinophrys*. When sexual reproduction does occur, it is usually linked to environmental change, and in many cases to formation of cysts.

However, cyst formation is not always associated with sex in protists. Some protists undergo binary division in cysts, while others do not increase in number during encystment. Whether or not encystment is associated with reproduction, it is frequently a response to environmental stress. For example, *Acanthamoeba*, common in temporary bodies of water and soil, will encyst due to a variety of signals that are linked to drying out. Food shortage, increased salt concentrations, high temperature, and low oxygen all can initiate formation of desiccation-resistant cysts. For species associated with temporary aquatic habitats, this can be an important means of survival as well as dispersal.

Distribution

In the pelagic zone (water column)

Protists are able to position themselves in the water column through several mechanisms including production of gas or lipid vacuoles noted previously for the testate amoebae *Difflugia*. However, swimming with flagella is the most common way that motile algae and heterotrophic flagellates position themselves in response to a variety of gradients in a stratified water column. Light requirements compel phototrophs to maintain themselves in the euphotic zone where there is enough light to support photosynthesis at least some of the time, but many phototrophs will swim deeper to avoid bright light. Motile photosynthetic organisms with algal symbionts, such as some dinoflagellates (and ciliates), are known to migrate toward the surface in the morning and into deeper, potentially nutrient-richer layers, later in the day.

Most heterotrophic protists tend to respond to other environmental parameters such as food abundance or oxygen. The greatest numbers of bacterivorous protists are associated with areas of higher bacterial production. In contrast, algivorous protists will tend to accumulate in layers where light and nutrient levels are best for their photosynthetic prey. Some free-living heterotrophs, including the flagellates *Hexamita* and *Trepomonas*, are common in areas of sediments (see below) and the hypolimnetic layers of eutrophic waters where high organic enrichment leads to low oxygen or anoxia. The amoeba-flagellate *Mastigamoeba* lacks mitochondria and so its distribution is limited to anoxic water.

Aggregates of detritus occur in the water column (as well as the benthos) and these will often have higher abundances of bacteria. As noted above, increases in bacterial prey lead to higher abundances of heterotrophic protists on these microhabitats relative to the surrounding water—especially in oligotrophic systems (Caron, 1991). Occurrence of "benthic" protists, such as the flagellate *Bodo*, in the water column may be due to association with these aggregates. Another distinct habitat, the air-water interface, also can be enriched with protists that use the surface as a substrate. Both naked and testate amoebae, such as *Arcella*, and some flagellates (e.g., *Codonosiga*) can hang below or move atop the water's surface feeding on bacteria or phototrophs growing there.

There tends to be strong seasonal changes in the abundance and species composition of aquatic protists. Phototrophic species often decline in winter and increase again with the longer days and greater light intensity in the spring. Bacterial activity increases with autotroph activity since the photosynthetic organisms release dissolved organic matter that supplies substrate for bacteria. Heterotrophic protist populations then will increase in response to abundance of algal and bacterial prey. Temperature also tends to be positively related to protistan population growth rates, so the low photosynthesis and low growth rates of winter lead to minimum abundances of flagellates and amoebae, while their productivity tends to increase in warmer seasons.

Sediments and hard substrates

The benthic habitat in both lake and stream systems tends to accumulate organic matter and detritus, which offers both a food source and a habitat for benthic protists. Attached and motile protists can occur in high numbers on and in the sediments. Attached heterotrophic organisms typically create a current to bring suspended food from the water (e.g., *Bicosoeca*, Fig. 1), or allow material to fall or swim into specialized feeding appendages (e.g., heliozoan axopodia). Phototrophic species can form mats or biofilms, especially on hard substrates that often have high abundances of cyanobacteria with or without protistan phototrophs. Motile protists move on and through these biofilms, and also at the surface and within the sediment. In sediments with relatively high organic matter content, gradients set up with sediment depth including change in oxygen, redox potential, pH and other chemicals. As noted for the plankton above, species that prefer oxic, microaerophylic, or anoxic environments will move to appropriate depths in the sediment or will even leave the sediment and move into the water column. The sediments are a source of the anaerobic protists that appear in the water column when anoxic hypolimnia develop, typically during summer, in stratified lakes.

Ecological roles and the dynamics of protists in freshwater systems

Primary production

Although the influx of terrestrial carbon and its utilization in aquatic systems suggest that many lake and stream systems may tend toward net heterotrophy where ecosystem respiration exceeds primary production (e.g., Tranvik et al., 2009), photosynthesis still contributes significantly to the food webs of freshwater systems. Protists, including periphyton and phytoplankton, are major contributors to total aquatic primary production and respond prolifically to eutrophication in lakes and marine systems. Globally, phytoplankton account for about half of the photosynthesis on the planet. However, lakes and rivers make up only a small proportion of the surface water of the earth with a total contribution from freshwater phytoplankton of only about 1% of net global photosynthetic carbon fixation from aquatic and terrestrial ecosystems (Dokulil and Qian, 2021).

Photosynthetic species dominate the protistan biomass in the euphotic zones of lakes, but size, depth and nutrient concentration of a lake contribute to whether phytoplankton are the major primary producers. The deeper the lake and the less nearshore shallows (littoral zone), the more pronounced the phytoplankton contribution to primary production because less of the benthic area is within the euphotic zone. In addition, lakes are not uniformly distributed around the earth, so regional freshwater primary production also depends on climatic zone, latitude and altitude.

If dissolved nutrient levels are sufficient, phytoplankton also can reduce the light reaching sediments, and consequently shade the communities of periphytic algae (including photosynthetic protists) and submerged macrophytes. In shallow lakes, eutrophication may thus lead to a switch from a benthic to a pelagic dominance of primary production. In oligotrophic systems, benthic protists can contribute more to whole lake primary production; light attenuation does not so strongly limit photosynthesis in deeper water and nutrients are available from the sediment. In streams and rivers, water depth and sediment load similarly affect the relative importance of the periphyton and phytoplankton, with periphyton contributing relatively more in low to middle order streams where more light reaches the benthos.

Mixotrophy in protists

There is a range of mechanisms by which mixotrophs combine photosynthesis with heterotrophy in a single organism (Mitra et al., 2016). Consequently, we see considerable variability in the physiological abilities and relative importance of phototrophy versus phagotrophy and/or osmotrophy in mixotrophs. Light and nutrient levels affect the grazing of many mixotrophs, some seeming to increase phagotrophy when these resources are limiting (Princiotta et al., 2016; Lie et al., 2018). Mixotrophic dinoflagellates (e.g., species of *Peridinium* and *Gymnodinium*) may be the dominant bacterivores (Hitchman and Jones, 2000), though this is probably rare. However, the combined mixotrophs, primarily chrysophyte (e.g., *Dinobryon*, *Ochromonas*), prymnesiophyte (*Chrysochromulina*) and sometimes cryptophyte flagellates, can sometimes have a greater grazing impact on planktonic bacteria than all the heterotrophs (Sanders et al., 1989).

Food webs and protists

The microbial loop concept, as developed for planktonic marine systems nearly 40 years ago (Azam et al., 1983), recognized that bacterioplankton incorporate dissolved organic matter into biomass and that bacteria are subsequently ingested by heterotrophic protists. Thus, fixed organic carbon that was once considered unavailable to most pelagic organisms could be recovered and funneled into the rest of the pelagic food web via a protistan link. In freshwater systems, heterotrophic protists tend to be the major consumers of bacteria, and heterotrophic flagellates alone can sometimes remove more than 100% of the daily planktonic bacterial production. The usual dominance of bacterivory by heterotrophic flagellates reflects their high abundances, but ciliates and mixotrophic protists also can strongly reduce the abundance and alter the species composition of bacterioplankton—as can rotifers and cladocerans (Sanders et al., 1989). These multiple trophic pathways moving microbial biomass into the higher trophic levels suggest that the "microbial loop" should be considered a highly dynamic and persistent component of aquatic food webs rather than an independent entity that is distinct from the primary production-herbivore trophic pathway.

The impact of heterotrophic protists feeding on phototrophic protists in the freshwater plankton has received less attention than the trophic interactions of protists and bacteria. Many species of ciliates, amoebae and dinoflagellates ingest phytoplankton, but rotifers and crustacean zooplankton tend to cause more phytoplankton grazing mortality. Still, amoebae and ciliates can reduce populations of larger phototrophs. For example, the amoeba *Nuclearia* has been investigated as a potential biocontrol agent due to its high ingestion rates when feeding on filamentous algae and cyanobacteria (Sigee et al., 1999). In sediments, protistan herbivory accounts for $<5\%$ of periphyton production. Likewise, studies to date suggest that protists ingest only about 5% of the daily bacterial production in sediments despite having feeding rates similar to those measured in the plankton. Under long-term anaerobic conditions bacterivory by benthic protists may be relatively more important as metazoan diversity decreases, but comparative studies are lacking.

Higher trophic levels (metazoa) utilize autotrophic and heterotrophic protists in planktonic and benthic environments in freshwater and marine systems (Sanders and Wickham, 1993; Stoecker and Pierson, 2019). As noted above, autotrophic protists have long been recognized as the base of most aquatic food webs. Zooplankton and suspension feeding benthic organisms capture phytoplankton, and browsers/scrapers such as snails and various aquatic insects ingest periphyton. Heterotrophic protists, which can be as abundant as autotrophs and overlap in size, are ingested incidentally by these "herbivorous" metazoans that feed by either size- or non-selective methods.

Predation by metazoans and other protists impacts populations of heterotrophic protists. Ciliates can be important predators of flagellates in the plankton and benthos; most heliozoans (and suctorian ciliates) also feed on other protists. Predator removal (or addition) experiments in lakes demonstrated that moderate grazing by crustacean zooplankton can balance or exceed protistan population growth, and that selective feeding can alter protistan community structure. And though summer "clearwater" phases observed in many lakes generally refer to a reduction in phytoplankton, predation by zooplankton also substantially reduces heterotrophic protist populations during these phases as well. In aquatic systems, it is likely that heterotrophic protists contribute to the diet of at least some life stages of most zooplankton, many fish, mollusks, and aquatic insects that also feed on photosynthetic protists.

Nutrient cycling

The transfer of nutrients through different chemical states and ecological compartments (biotic and abiotic), biogeochemical cycling, is tightly linked to microorganisms—especially in aquatic systems where protists dominate primary production. Availability of dissolved phosphorus and/or nitrogen limits primary production, and recycling is most important where allochthonous input of N and P is low. Heterotrophic protists can be efficient nutrient remineralizers, depending on the nutrient content of their prey, and contribute to phytoplankton nutrient demand in the epilimnion of stratified lakes when measurable dissolved nutrients are low. Recycling often leads to high nutrient retention in benthic systems within the photic zone of lakes and streams. In the benthos, phototrophic and heterotrophic microorganisms, both prokaryotic and eukaryotic, tend to live in close proximity and often within boundary layers that can lead to localized nutrient limitation and a subsequent importance of recycling.

Conclusion-synthesis

Flagellates and amoebae are ubiquitous in freshwater systems. They exhibit an unequaled taxonomic diversity and a huge range of ultrastructure, physiology and ecology. These protists play important roles in aquatic food webs as primary producers, as conduits of bacterial production to higher trophic levels, as algivores and as predators of other heterotrophs; some ingest a broad range of particles, while others feed more selectively. Many of these protists are difficult to identify because of their small size or because specialized handling in preservation, staining or cultivation is needed to distinguish them. These restrictions have started to be overcome in recent decades as the use of DNA/RNA-based tools and high-throughput sequencing has increased. These molecular tools have boosted the discovery of rare and new species and allowed wide-ranging comparative studies of diversity and distribution that complement the traditional methods of observation. With the high impact of climate change on freshwater ecosystems (e.g., Williamson et al., 2019) and the central roles of microbial eukaryotes to these systems, it is important to understand not just the biodiversity, but to continue to experimentally address the ecological roles of protists in the laboratory and directly in the environments where they are found.

Knowledge gaps

- long-term community dynamics
- genetic analyzes—gene number, gene function
- cultures—most species are uncultured with little experimental data at the species level
- roles of mixotrophy at the levels of individual species to ecosystems
- effects of climate change on protist communities
- impact of parasitic protists
- interactions with aquatic fungi

See Also: Emerging methods and topics: Inland Water Fungi in the Anthropocene: Current and Future Perspectives; Fundamental concepts and theories: Trophic Dynamics and Food Webs in Aquatic Ecosystems; Structures and functions of Inland Waters - Lakes: A Diversity of Primary Producers in Lakes; Diversity and Dynamics of Bacterial Communities in Freshwater Lakes; Fungi and Chytrids; Lake Food Webs; Protists: Ciliates

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Protists: Ciliates

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie_Elodie Perga and Damien Bouffard.

Glossary

Benthic Living on/in the sediment (bottom) of running and standing waters.
Ciliates Protistan cells which are covered with cilia; the phylum Ciliophora (i.e., ciliates) belongs taxonomically to the Alveolata.
Ciliature All somatic and oral cilia of a ciliate cell.
Cytostome Part of a ciliate cell specialized for uptake of particulate food (from *cyto-*, cell and *stome-*, mouth).
Metabarcoding A method for identifying species using a short section of DNA from a specific gene (or multiple genes).
Nuclear dualism Ciliates have two kinds of nuclei (sometimes in multiple numbers), a diploid micronucleus and a polyploid macronucleus.
Planktonic Living in the free water body (pelagial) of standing and running waters, partly passively floating but many planktonic (micro)organisms are indeed motile.
Quantitative protargol staining (QPS) Albumose-silver staining of fixed planktonic ciliates on filters resulting in permanent microscopic slides for identification and quantification.
Sessile Organisms are attached to an abiotic or biotic surface.

Introduction—What are ciliates?

Book chapters about ciliates often start with the sentence: 'Ciliates (Ciliophora) are a highly developed and diversified monophyletic phylum of unicellular eukaryotes belonging to the Alveolata.' This sentence is correct, but a bit boring. The good news is that nearly all ciliate genera can already be recognized and determined by microscopy owing to their clear morphological characteristics

(Foissner et al., 1999). Thus, even beginners or non-experts in the field can enter the fascinating and esthetic world of ciliates. The bad news: they move. Here, benthic ciliates are easier to observe, as many species crawl slowly over substrates or are even attached (sessile). Already small pieces of biofilm or a few drops of sediment contain a huge variety of specimens. In contrast, planktonic ciliates and especially very tiny taxa (<30 μm) are very motile with quite complex species-specific swimming trails and some appear as real sprinters (with an incredible acceleration). Hence, a direct examination of a drop of water from a pond or lake can be very frustrating at the beginning. Already the use of a simple plankton-net or later on, of specific filtration and staining procedures (see Section "Methods to investigate the diversity of planktonic ciliates") will help to discover the world of planktonic ciliates (Foissner, 2014). This chapter aims in bringing background knowledge about ciliates in standing waters, highlighting ecological, and few taxonomic aspects, giving hints how to study them, and ending up with ideas and suggestions for fascinating aspects which may be studied in future.

Diversity of ciliates in lakes

General morphological features of a ciliate cell

There are obvious morphological characteristics (Fig. 1) which, at precise microscopic observation, often allow for an assignment to a specific group or even to a genus/species (Lynn, 2008). First, ciliates display various ciliature forms: they can (i) be completely covered with cilia in longitudinal rows, (ii) have un-ciliated (naked) cell areas, (iii) show concentrations of cilia towards the cell mouth (cytostome), or (iv) have a dense accumulation of cilia at the apical end, working as filtration apparatus and for locomotion. Only the 'adult' sessile individuals of the group Suctoria (also present in the plankton) are completely naked, whereas their free swimming swarmers still show a clear ciliature. Cell shapes of some species are very rigid and static, whereas other species are highly flexible and motile (Hausmann et al., 2003; Lynn, 2008).

Another peculiar character of ciliates is the dualism of nuclei (Fig. 1). Ciliates have a small, mostly circular micronucleus (diploid) and a large polyploid macronucleus which appears in various species-specific forms. Both types of nuclei can be found also as multiple copies within distinct taxa. Conjugation is the third striking feature, a sexual process allowing for the exchange of genetic material between individuals of the same species (or of congruent mating types within a species). Two cells partly fuse in order to exchange meiotic products previously generated from their micronuclei. Although conjugation is a strong character for this protistan group, it can be seldom observed for planktonic ciliates in situ. However, asexual reproduction by simple division of a mother in two daughter cells can often be observed in living specimens.

Some species show numerous (up to thousands) organelles below the cell surface called extrusomes (Fig. 1). Depending on the type, they act as defense system like little harpoons against predators (trichocysts), or help to catch and immobilize prey organisms (toxicysts, and haptocysts in the group Suctoria). Other types may be involved in the formation of a mucous layer around the ciliate cell (mucocysts). Contractile vacuoles (one or more per cell) are obvious cellular organelles for osmoregulation filling and emptying in regular intervals (Fig. 1). The wide variety of cell-mouth structures (cytostome) reflects the broad spectrum of feeding strategies.

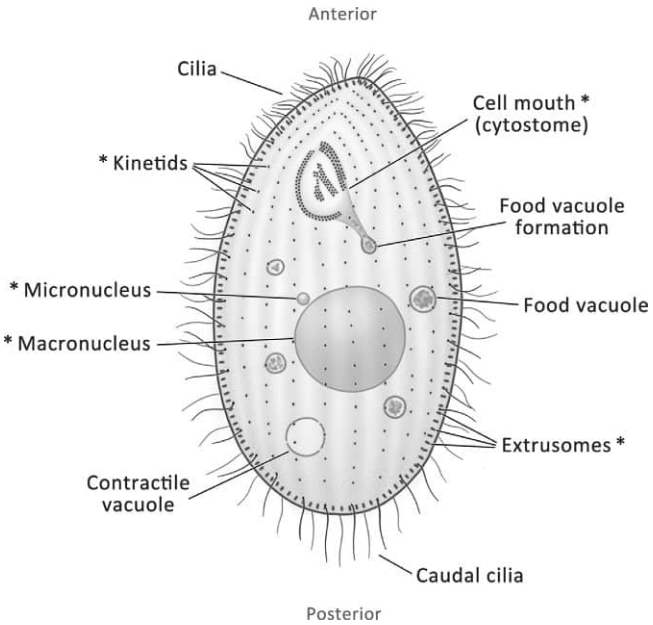

Fig. 1 Drawing of an idealized, typical ciliate cell. Most cellular characteristics are best observed on living specimens. Structures which are clearly recognizable after quantitative protargol staining (QPS), a method used for quantification of fixed planktonic ciliates, are marked with an asterisk. Drawing by Gianna Pitsch.

The formation of resting cysts would be an important trait for planktonic ciliates to overcome harsh environmental conditions; however, cysts of most representatives are unknown and only few studies were dealing with this aspect (e.g., Müller et al., 2002).

Special adaptations to planktonic life

The pelagic layer (free water body of aquatic systems) is not a stable and homogenous habitat as usually expected. In fact, it offers ciliates multiple niches for adaptation. Epilimnetic ciliate species living in the productive upper parts of lakes are confronted with continuous turbulent conditions and protists are to a certain degree trapped in this zone. Sinking into the deep, usually less productive hypolimnion has to be avoided. In this respect, planktonic ciliates developed multiple morphological adaptations (Fig. 2). First, it seems that the specific weight of many species is close to that of freshwater, reducing losses of individuals by sedimentation. Many planktonic species have a small size (<30 µm; e.g., *Balanion planctonicum*, *Cinetochilum margaritaceum*, *Urotricha* spp.), consequently they have a small mass which reduces sinking rates (Fig. 2). Larger sized species seem to be morphologically adapted to hydrodynamics by having conical (e.g., *Rimostrombidium*) or drop-like shapes (e.g., the giant genera *Pelagodileptus* and *Paradileptus*; Figs. 2 and 3).

Secondly, some genera have special bristles (e.g., *Askenasia*, *Halteria*), tentacles (e.g., *Actinobolina*), spines (e.g., *Hastatella*), and elongated cilia (e.g., *Histiobalantium*) to reduce sinking (Figs. 2 and 3). The existence of cytoplasmatic gas vesicles in planktonic ciliates to guarantee buoyancy has still to be proven. An indirect solution to avoid sinking is chosen by epiphytic and epizoic ciliates (various peritrichous genera; e.g., *Epistylis*, *Pseudohaplocaulus*, *Vorticella*), which are sessile on cyanobacterial colonies (Figs. 2 and 3), diatoms or metazooplankton. During some periods of the year, body surfaces of daphnids and especially copepods are densely covered by peritrichs and even suctorians.

However, most planktonic ciliates are free swimming in a very active way with species-specific patterns composed of forward movements, tumbles and jumps, which may be interrupted by 'resting phases' (Fig. 2). Large adoral membranelles (e.g., of *Halteria* and *Rimostrombidium*) do not only serve as filtration apparatus but are also responsible for locomotion. In the case of *Halteria*, the jumping behavior is obviously a grazing defense mechanism against predatory copepods and rotifers (Šimek et al., 2000).

All described morphological adaptations are also known for marine counterparts, but there is a major difference in the total assemblage composition between freshwaters and oceans. In contrast to marine systems, where we find a high diversity of house- (lorica) producing tintinnid ciliates (Dolan et al., 2013), in freshwater ecosystems most planktonic species are 'naked'. There are only a few species in freshwater (mostly within the genera *Codonella* (Fig. 3), *Membranicola*, *Tintinnidium* and *Tintinnopsis*) forming sticky buildings around cells in which organic and mostly inorganic particles agglutinate (Foissner et al., 1999). It might be that the

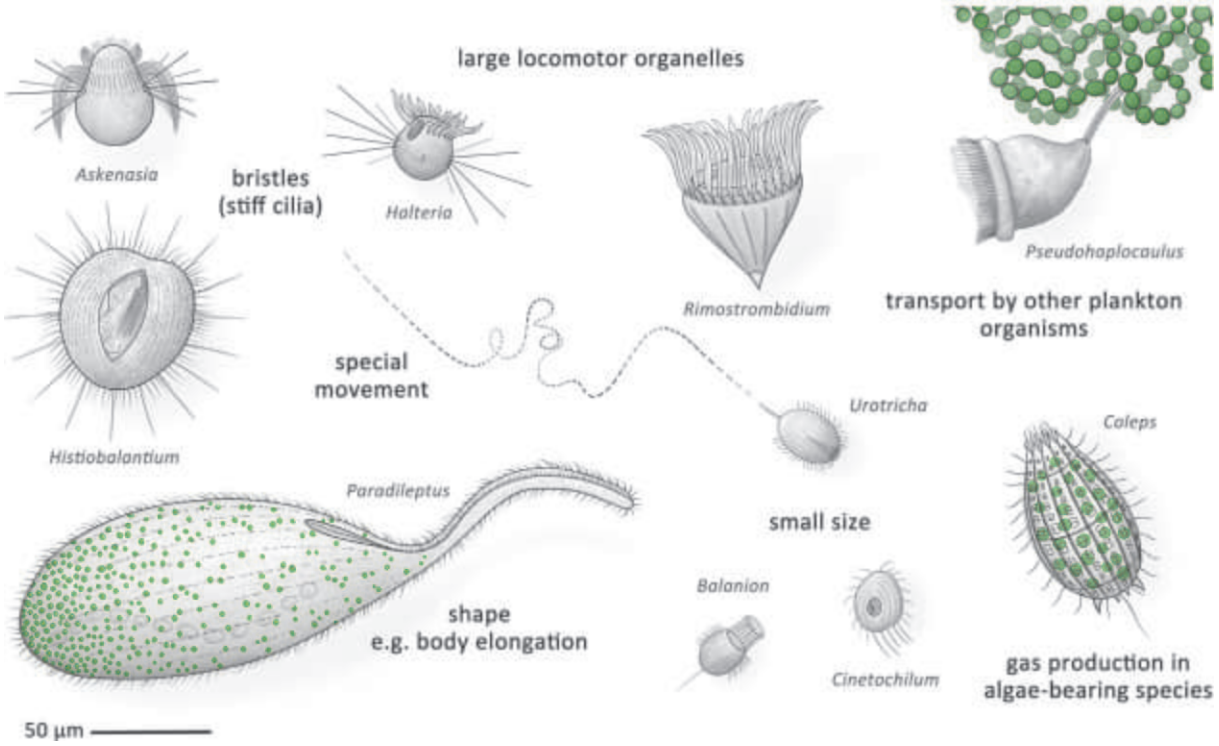

Fig. 2 A few examples of common planktonic freshwater ciliates reflecting the various special adaptations to life in the pelagic layer. Full species names: *Askenasia volvox*, *Balanion planctonicum*, *Cinetochilum margaritaceum*, *Coleps spetai*, *Halteria grandinella*, *Histiobalantium bodamicum*, *Paradileptus elephantinus*, *Pseudohaplocaulus infravacuolatus*, *Rimostrombidium lacustris*, *Urotricha furcata*. Drawing by Gianna Pitsch.

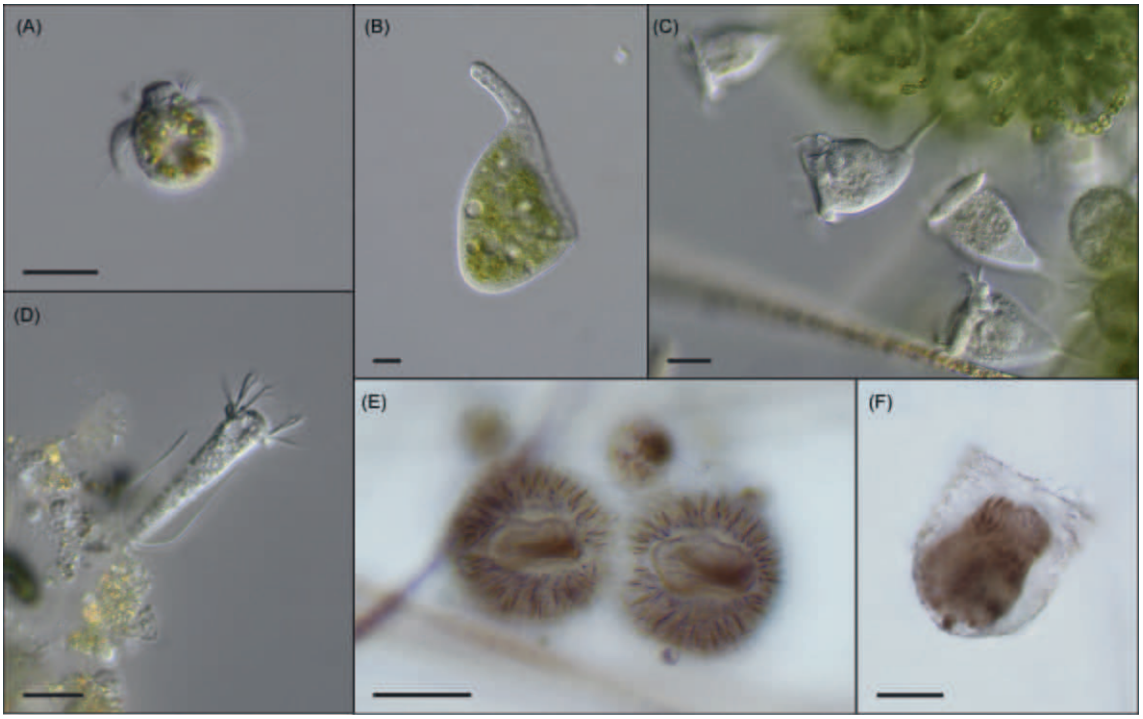

Fig. 3 Examples of common free swimming and sessile planktonic freshwater ciliates. Differential interference contrast microscopy pictures of living specimens: (A) *Askenasia* sp., (B) *Paradileptus elephantinus*, (C) four individuals of the sessile *Pseudohaplocaulus infravacuolatus* adhering to the cyanobacterium *Anabaena* sp., (D) the lorica-bearing *Cothurnia annulata* attached to a detritus floc. Bright-field microscopy pictures of fixed and Protargol stained specimens of the species: (E) *Histiobalantium bodamicum*, two cells during cell division. Apparent are the large ventral grooves (cytostome) and the numerous silver-impregnated extrusomes, (F) the lorica-forming *Codonella cratera*. Scale bar: 20 μm.

additional weight of loricae is a drawback for freshwater cells, though there may be other additional reasons for their lower frequencies in lakes and ponds.

Ecology of planktonic ciliates

Planktonic ciliates in the microbial food web

Feeding types and functional groups

From an anthropocentric point of view, many ciliate species show an incredible ratio between ingested prey volume and their own cell volume. Especially algivorous and predatory species are densely packed with food organisms—sometimes filling even the entire cell. Growth efficiencies range between 30% and 40% and are often based on volumetric data, i.e., how much prey volume had to be ingested before cell division took place. However, the feeding modes of planktonic ciliates are manifold and the selective prey uptakes too. Thus, ciliates should not be assigned to a single trophic level in the microbial food web, but represent several functional guilds acting as complex self-standing connections between various lower and higher trophic levels (Fig. 4).

Bacterivorous ciliates

Voracious bacterivores are often very tiny (e.g., *Cyclidium*-like genera) and usually dominate during the cold season or in deep cold water strata. Their feeding rates vary between 100 and 1000 bacteria ciliate^{-1} h^{-1}, depending on prey availability (i.e., functional response). Larger, especially planktonic peritrichous genera (e.g., *Pelagovorticella*, *Vorticella*), can be real 'bacterial vacuum cleaners' with uptake rates up to 15,000 bacteria ciliate^{-1} h^{-1} (Šimek et al., 2019). Consequently, besides grazing by heterotrophic nanoflagellates (HNF), also ciliates may strongly affect the fate of bacterial production and standing stock (Šimek et al., 2000). With the increasing trophic status of a pond/lake, ciliates' contribution to total grazing rates on bacteria is rising and can even be higher than rates of HNF (Šimek et al., 2019). Ciliates feeding on the size range of picoplankton (0.2–2 μm) may not only be efficient consumers of heterotrophic bacteria (Fig. 4), but also of autotrophic organisms, i.e., of coccoid cyanobacteria.

Algivorous ciliates

Strictly algivorous species exist, however only few show this unimodal feeding behavior. Indeed, the determination of in situ feeding rates of algivores is still tricky and asks for new research initiatives. Up to now, we have to come back to lab-based grazing rates for the interpretation of in situ data and even for the calculation of energy fluxes within food webs. However, most cultivated

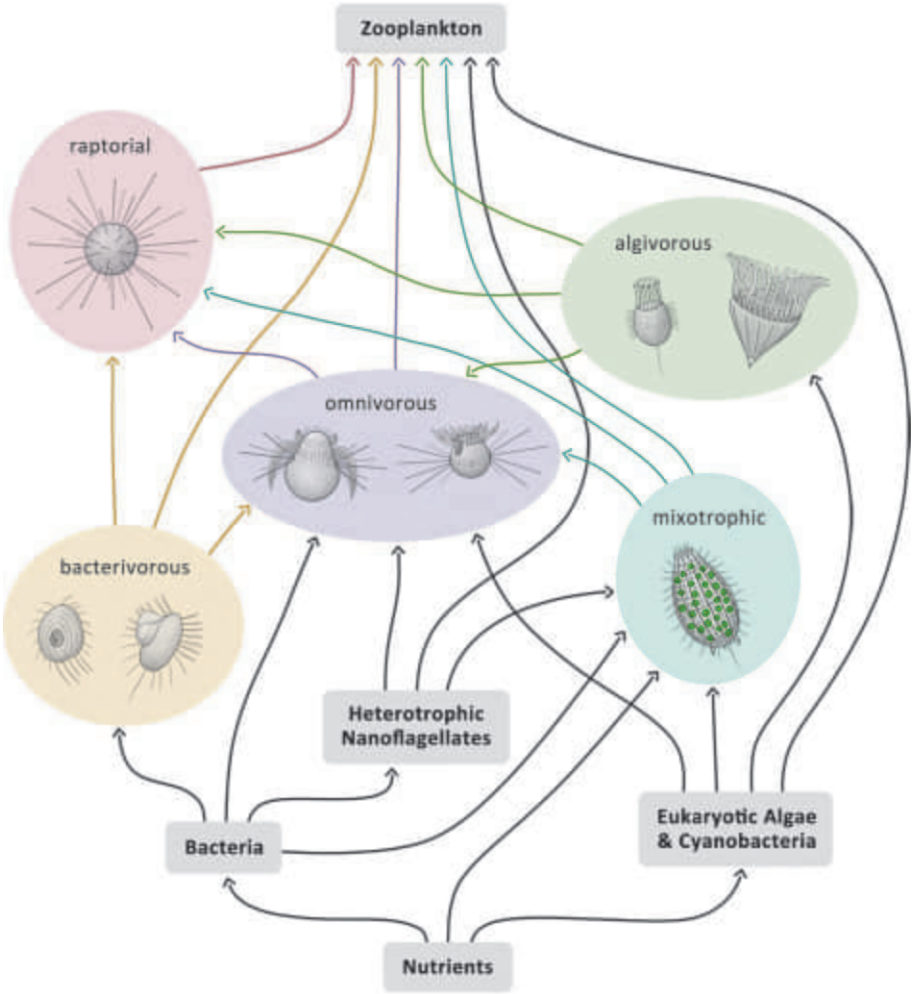

Fig. 4 Schematic representation of the complex interactions of ciliate functional guilds within the microbial food web, emphasizing the role of ciliates at different trophic levels according to their feeding modes. Drawing by Gianna Pitsch.

ciliates are kept on a single diet organism, i.e., on *Cryptomonas*. The best studied representative for algivorous ciliates is *Balanion planctonicum*. This species can radically decimate population peaks of cryptomonads, especially during their spring bloom development (Müller et al., 1991a,b).

Omnivorous ciliates

Omnivory guarantees high ecological versatility for survival throughout the year at even harsh environmental conditions. For ciliatologists, this strategy literally causes troubles to characterize the grazing impact of ciliates in a qualitative and quantitative way (Weisse, 2017).

First, it is still unknown if typical omnivorous ciliates are indeed unselective feeders, choosing prey only according to size. Actually, it seems that in addition to prey size preferences, some omnivores are more inclined to certain types of food items (i.e., rather hetero- or phototrophic organisms), still accepting both food sources in case of shortage. On the other hand, some omnivorous species, e.g., the filter feeding *Stentor roeselii*, show an immense size range and variety of ingested prey particles. Starting from hetero- and autotrophic picoplankton (0.2–2 μm), this species can phagocytize objects having nearly its own cell length. Another example concerns species of the genera *Halteria* and *Pelagohalteria*, which may have a strong impact on heterotrophic bacterial production (Šimek et al., 2000) and on picocyanobacteria, but also on algal cells with a size up to 5 μm.

These observations highlight that a quantification of in situ grazing rates is extremely challenging for omnivorous species (Šimek et al., 2019). The simultaneous use of multiple food sources (being labeled by, e.g., fluorescent dyes) definitely remains a methodological challenge (or even a nightmare). Additionally, owing to their versatile feeding modes and direct impacts on several trophic levels (Fig. 4), the categorization of omnivorous ciliates for energy fluxes within microbial food webs is still a challenge.

Mixotrophic ciliates

The real gardeners in the world of planktonic ciliates are mixotrophic representatives. During defined periods of the year (see Section "Seasonality"), they may reach high abundances profiting from their dual strategy to accept particulate food, while having at the same time algal endosymbionts and thus becoming 'phototrophic organisms'. Several species 'cultivate' indeed living algae inside their cytoplasm (e.g., *Vorticella chlorellata*, *Stokesia vernalis*), mostly belonging to the chlorophyte genera *Micractinium* and *Chlorella* (Pröschold et al., 2011). Other mixotrophic species (e.g., *Pelagostrombidium mirabile*, *Limnostrombidium viride*) are 'robber gardeners', as they keep only the plastids of ingested algae (kleptoplastids) for some time.

Other feeding types

Spectacular feeding modes are realized by predatory and histiophagous (tissue feeding) ciliates. Ciliates of the omnivorous genus *Coleps* have armored calcium carbonate plates, sometimes even with spines at both body ends. When feeding on living or dead tissue (e.g., daphnids or copepods), ciliates quickly rotate and invade their prey organisms like a 'driller' (Hausmann et al., 2003). After the first successful attack by a single ciliate, more individuals quickly join the feeding process, ending up in a crowd of 'microbial hyena' (Foissner et al., 1999). Whereas some predatory ciliates are actively moving (e.g., *Didinium*), others are rather passively waiting for prey. The unciliated life stages of the group Suctoria have multiple contractile tentacles with knobbed ends and effective extrusomes (haptocysts). When other ciliates get in contact with such haptocysts, they are rapidly immobilized and sucked out via tentacles. Beside these two examples, there is a huge behavioral variety of predatory ciliates (see Foissner et al., 1999; Hausmann et al., 2003). Nevertheless, the determination of their in situ grazing rates and impacts on energy fluxes in food webs is still understudied.

Quantitative and qualitative aspects of planktonic ciliate assemblages

Abundance and biomass

Ciliate numbers per volume water (abundance) and the assemblage composition itself are strikingly dependent on the quantity and kind of available food sources. The amount of prey organisms, in turn, depends on the trophic status of a lake/pond and on the climatic zone in which the freshwater body is located. Ciliate abundance varies from less than 1 cell mL^{-1} in surface layers of ultraoligotrophic systems and rises up to 1000 cells mL^{-1} in hypertrophic waters (Šimek et al., 2019). However, even in one ecosystem, numbers may change over the season by up to 2 orders of magnitude. Depending on the size and depth of a standing water and its mixing and stratification regime, clear vertical gradients in terms of ciliate abundances can be observed (Müller et al., 1991a; Sonntag et al., 2006). Highest abundances are expected in the epilimnion, irregular accumulations can be found also in the metalimnion and very low numbers are characteristic for deep hypolimnetic zones of large lakes. Thus, most studies focused on the productive surface layers of standing waters, resulting in schematic frameworks of typical annual successions (see Section "Seasonality"). Nevertheless, even the barren hypolimnetic environment offers a habitat for ciliates throughout the year (Müller et al., 1991a; Sonntag et al., 2006). In this habitat, ciliate assemblages are often dominated by tiny bacterivorous genera (e.g., *Cyclidium*, *Uronema*). It is still poorly understood how they survive with a rather minimalistic diet, i.e., low bacterial abundances ($\sim 10^5$ bacteria mL^{-1} in the hypolimnion versus 10^6–10^7 bacteria mL^{-1} in the epilimnion, respectively). A special community can be found at the water/sediment contact zone, i.e., especially microaerobic and anaerobic species (depending on redox conditions).

To assess the quantitative role of ciliates for energy and carbon fluxes in food webs, the determination of their total biovolume ($mm^3\ L^{-1}$) or biomass (mg fresh weight L^{-1} or μg Carbon L^{-1}) is recommended. In theory, cell dimensions should be measured from living organisms, although the task is tricky to fulfill for many agile and tiny planktonic forms. Hence, measurements are often done on fixed material, however keeping in mind fixation artifacts that seem to be species- or even growth-phase dependent (Pfister et al., 1999). A good collection of species-specific biomass values for freshwater ciliates can be found in Foissner et al. (1999). Cellvolume (μm^3) is often converted to biomass (fresh weight) assuming a specific mass of 1 ($1\ \mu m^3 = 1$ pg fresh weight). The conversion in cellular carbon is based on empirical conversion factors (Menden-Deuer and Lessard, 2000), although the published range is wide: cell volume (μm^3) is multiplied by a factor of 88 up to 323 (a value of ~200 being often used) to obtain the cellular carbon content (in fg Carbon $cell^{-1}$).

Growth rates of planktonic ciliates

Numerical response curves, i.e., the dependence of growth rates upon available food quantities, have been determined for several planktonic species. However, most studies were made in the lab on isolated strains and focused on temperature-dependent growth success of cultivated species, or even of clonal cultures (Weisse, 2017). In contrast, our knowledge on in situ growth rates is still very limited (Carrias et al., 2001). Changes in cell abundance over time can be easily converted to growth rates assuming a logarithmic rise, although resulting only in net values. For the determination of gross growth rates, information on population losses by predators and natural mortality values are needed. It is still a methodological challenge to determine these rates as, e.g., a direct evaluation of grazing rates by copepods or rotifers on ciliates is difficult to achieve. An indirect approach to judge gross growth rates is based on population dynamics in size-fractionated samples (e.g., <100 or < 150 μm fraction) to exclude metazooplankton versus unfiltered raw water. However, this technique does not work for larger ciliates which are in the same size range as small metazoan predators (nauplius larvae and juveniles of copepods, rotifers). The few reports on in situ growth rates (μ) speak for rather

fast cell divisions of <1 day ($\mu \geq 0.69$ d^{-1}) to 2 days ($\mu = 0.35$ d^{-1}) during productive periods (Carrias et al., 2001). Very high rates have been found for typical pioneer species which seem to colonize any standing water within a few days. Species belonging to the genera *Halteria* and *Pelagohalteria* represent such effective colonizers, with reported growth rates of up to 1.9 d^{-1} (Šimek et al., 2000).

Diversity aspects

According to the 'encyclopedia' of planktonic freshwater ciliates written by Foissner and co-workers, there are over 180 described real planktonic (euplanktonic) morphospecies (Foissner et al., 1999). This number is not a mantra and will definitely increase if scientists apply integrative approaches (see Section "Combining morphological and molecular approaches: Need for integrative studies"). Nevertheless, one should not expect to find the entire described diversity in a single studied lake or pond. Detailed studies based on high temporal and spatial sampling resolution report about 50 to 100 pelagic morphospecies (as a proxy) found in one ecosystem (e.g., Sonntag et al., 2006). Again, species diversity seems to be linked to the trophic status and the geographical location (climate region) of the studied system. In temperate lakes, there are a few, mostly tiny (<30 μm) genera which may numerically dominate the ciliate assemblage throughout the year (Müller et al., 1991b). However, their contribution to total ciliate biomass strikingly fluctuates over time. Typical 'omnipresent' and frequent representatives are: the genera *Balanion* (*B. planctonicum*), various species of the genera *Urotricha*, *Rimostrombidium* (*R. humile*, *R. brachykinetum/hyalinum*), *Halteria* and *Pelagohalteria*, *Mesodinium*, and diverse genera of scuticociliates (e.g., *Cyclidium*-like ciliates). A second part of diversity is formed by 'omnipresent' but less abundant taxa, e.g. species of the genus *Vorticella* or lorica-forming ciliates (tintinnids or the genus *Codonella*). The full spectrum of ciliates' diversity in the plankton is made up by rare and even ephemeral species. Nevertheless, their contribution to total ciliate biomass is often high during presence. The majority of them have fancy morphological and feeding characteristics; some can reach immense sizes with up to 1 mm length (e.g., *Pelagodileptus*). One has to inspect at least 100–300 mL of raw water (depending on the trophic status) to find these rare species (see Section "Sample collection"). Finally, many species have been reported to be ephemeral, i.e., just found at a few sampling occasions, which does not mean that they do not inhabit the ecosystem during other times. It just reflects the limits of detection of standard routines, and the problematic issue to recognize and quantify resting stages. Sequencing analyses of larger water samples showed that some of these presumably ephemeral species have indeed clear seasonal succession patterns as known for frequent representatives (Pitsch et al., 2019).

In sum, there are two golden rules when studying ciliates of standing waters. First, sampling intervals should be kept as short as possible. Population peaks of many species are reoccurring but may last for only a few days (Müller et al., 1991b). Thus, a weekly monitoring of ciliates guarantees good results. Second, be aware that average abundances of distinct species may differ by 2–3 orders of magnitude. Consequently, to study also rare and ephemeral species several methodological approaches are needed to screen also large water volumes.

Seasonality

There is a manageable number of publications on the seasonal succession of ciliate morphotype assemblages in ponds and lakes (see references in Sonntag et al., 2006; Pitsch et al., 2019). For general information on annual successions of planktonic organisms, see Sommer et al. (2012). In terms of biogeography, studies focused clearly on (i) the northern hemisphere, (ii) on ecosystems within the temperate zone, and (iii) on lakes with moderate to low trophic status (i.e., oligo-mesotrophic). A worldwide survey linking seasonal aspects in various types of lakes with typical succession patterns of ciliate assemblages is therefore still missing. Thus, the herein idealized scheme of ciliate morphospecies' seasonality is based primarily on studies originating from Central Europe with a strong focus on temperate lakes.

Depending on the trophic status of the investigated lake, one may expect two to three major peaks in total ciliates' abundance (Fig. 5). The functional guilds within the ciliate assemblage may in turn show very different seasonal developments. Any seasonality of planktonic organisms has to be seen in the context of annual changes in physico-chemical parameters (Fig. 5). Major triggers are irradiance, water temperature, thermal stratification patterns, water turbulence, and concentrations of limiting nutrients for primary producers (i.e., phosphorus, nitrogen, silica, iron). The right symphony of these parameters in spring leads to mass developments of small-sized, grazing-vulnerable algae, often dominated by cryptophytes and centric diatoms (Sommer et al., 2012; Posch et al., 2015). Increased algal production goes in parallel with a rise of extracellular products (mainly carbon compounds) which are suitable sources for heterotrophic bacteria (Šimek et al., 2014). A vernal bloom of algae and bacteria thus offers a rich food supply for ciliates (Fig. 5), but also for heterotrophic nanoflagellates (HNF). Mainly algivorous ciliates are among the first consumers of primary producers, responding much faster to the altered conditions than larger metazoan herbivores (Šimek et al., 2014; Posch et al., 2015). Thus, apparent break-downs of vernal algal blooms can be often attributed to grazing by ciliates, and partly by rotifers. The start of the growing seasons is reflected by all components of the microbial food web, with increasing numbers of algae, bacteria and HNF. This opulent menu favors omnivorous ciliates, which together with larger metazoan consumers (mainly daphnids and copepods) can lead to high clearance rates of the water column. This ends up in the clear water phase in early summer (Sommer et al., 2012), where the high water transparency reflects a period of low primary production and smaller numbers of bacteria and HNF. During the period of low food supply, mixotrophic ciliates (see Section "Mixotrophic ciliates") profit from their versatile lifestyle and can even dominate the ciliate assemblage (Fig. 5).

During summer the algal community is often dominated by larger and colonial forms (chrysophytes and diatoms), several of them also being mixotrophic (e.g., chrysophytes and dinoflagellates). Within the ciliate assemblage, representatives of all functional guilds form a highly diverse community (Müller et al., 1991b). It is also the time for many rare and ephemeral species (see Section "Diversity aspects"), and (semi-) sessile forms which use algal colonies as suitable habitat to show up. Towards autumn and

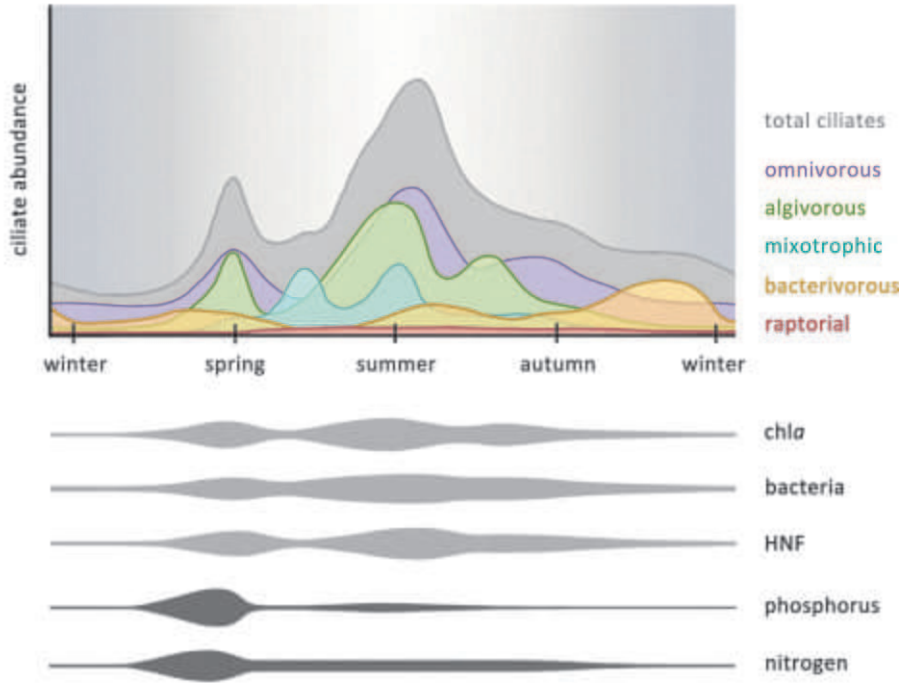

Fig. 5 Seasonal succession of total planktonic ciliates and functional guilds within the assemblage during the year. A vernal increase of nutrients (phosphorus and nitrogen) favors the growth of algae (here symbolized by chlorophyll *a* concentrations), bacteria and heterotrophic nanoflagellates (HNF). This rich 'menu of food organisms' supports the first peak in ciliate abundance. Further maxima of potential prey during summer often result in a second rise of ciliates. Note that functional guilds can show strikingly different seasonal successions. Drawing by Gianna Pitsch.

during winter, when primary production gets limited by environmental factors, omnivorous and increasingly bacterivorous taxa represent the major part of total ciliates.

The described annual succession shown in Fig. 5 is definitely an idealized scheme. In reality, the succession of ciliate assemblages is strongly affected by external drivers, such as allochthonous nutrients and pollutant loads, effects of climate warming, and any anthropogenically induced change of the ecosystem (water usage, restoration, etc.). However, it offers by its simplicity a rough framework for engaged ciliatologists and should motivate to study a lake/pond throughout the year at a high sampling frequency.

Methods to investigate the diversity of planktonic ciliates

Sample collection

One of the most common methods used for qualitative studies is plankton hauling. Nylon plankton nets with 10 μm pore size (the smaller the better) are used to simultaneously capture ciliates from large water volumes and concentrate them in a rather small volume for subsequent analyses (isolation, cultivation, characterization). In routine monitoring programs, samples are usually collected in 5 to 10 L volumes with the help of water samplers (e.g., Ruttner sampler or Niskin bottle). This strategy is preferred for quantitative analyses since the precise sampled volume is measured.

For both types of analyses, qualitative and quantitative, samples should be transported at low temperature (<15 °C) in order to minimize cell losses and shifts in the assemblage composition. Sample processing should happen without delay especially for microscopic observations of living cells. Also, the addition of fixatives (see Section "Fixation and staining techniques") and the preparation for DNA metabarcoding (see Section "DNA-based approaches: Environmental metabarcoding") should be carried out as soon as possible.

Live-cell observation, isolation and cultivation

Living ciliates can already be observed with a binocular by pouring raw water samples (preferentially from net hauls) in small Petri dishes. Be aware (and not disappointed) that only very conspicuous and large specimens can be recognized, although the bulk of ciliates diversity will elude identification by this workflow.

Accurate taxonomic identification of living ciliates usually requires phase-contrast and differential interference contrast (DIC) microscopy. To mount a microscope slide, a droplet of untreated water sample or a drop with isolated ciliates is placed on a clean glass slide. Then a coverslip with four small spots of petroleum jelly (Vaseline) in the corners is put carefully on the slide (Foissner,

2014). This method allows for gentle squeezing and slowing down specimen, thus facilitating the observation of some key morphological features. Be aware that swimming patterns are sometimes also important for species identification and should be observed on ciliates without the pressure caused by a coverslip. The use of chemicals enhancing the viscosity of water to slow down ciliates is not recommended, as these substances may alter the natural shape of observed specimens. Nevertheless, most planktonic species are tiny, usually transparent, move rapidly and have morphological characteristics which are not visible at magnifications lower than 600×. Here, samples have to be fixed and stained prior to precise taxonomic identification and quantification (see Section "Fixation and staining techniques").

The isolation of ciliates (picking) can be done with glass-micropipettes of various diameters, which are adapted to the size of the organisms of interest. Picked cells are subjected to serial washing steps using small droplets of filtrated sample or mineral water (e.g., Volvic ©), in order to reduce or even remove accompanying organisms prior to cultivation (Foissner et al., 1999). This procedure is not 'appreciated' by all species and requires some experience.

It is recommended to initialize the cultivation of planktonic ciliates by using 24-wells plates filled with pre-filtrated mineral water. Usually one to several individuals of the same species are sufficient to establish a new culture. The food source is added periodically according to the expected feeding mode. Bacterivorous filter feeders, such as *Vorticella* or *Cyclidium*, require sufficient bacterial prey provided by adding a low amount (~50 μL) of a bacterial suspension into the wells. Our in-house suspension is made by adding 5–7 wheat grains in 100 mL Volvic mineral water. After sterilization, the suspension is inoculated with a defined or mixed bacterial community. Omnivorous and algivorous ciliate species are commonly cultivated with the alga *Cryptomonas* as prey item. One can, however, not neglect that the preferred food source of many planktonic species is still unknown. After successful initiation, culture volumes should be increased. In this way, planktonic ciliates can be maintained for several weeks up to months or even years. Prerequisites for a fruitful cultivation are periodic feeding with suitable food sources, temperatures adapted to in situ conditions, light regimes with regular day-night cycles and, last but not least, a lot of patience.

Fixation and staining techniques

The fixation of water samples or cultures should preserve, in theory, the specimens' cells and their shape. Common fixatives used in microbiology such as formaldehyde, glutaraldehyde and Lugol's solution are not suited for the fixation of many species, and lead to specific artifacts (Pfister et al., 1999). Bouin's solution, which contains picric acid, formaldehyde and acetic acid, proved as best chemical for routine methods (Montagnes and Lynn, 1987).

The quantitative protargol staining (QPS) is a widely used silver-proteinate impregnation method for planktonic ciliates (Montagnes and Lynn, 1987; Pfister et al., 1999). After staining, the cell's shape and key morphological characteristics (i.e., nuclei, ciliature, cytostome structures) get visible on the resulting permanent microscopic slides. The QPS approach allows for the identification and quantification of ciliates at the same time, making it a great tool for morphology-based monitoring of planktonic assemblages.

Other techniques for more detailed investigations of ciliates using optical or scanning electron microscopy (SEM) exist. Foissner (2014) improved and reviewed a wide range of staining methods, which reveal very precise and detailed cellular features. These methods are qualitative and typically used for fine taxonomic identifications, e.g., describing a new morphospecies or the ultrastructure of specimens (Foissner, 2014; Abraham et al., 2019).

Taxonomic identification

The determination of ciliate morphospecies is still based on classical identification keys. Major references in the field are the 'blue books' published in the 1990s by Foissner and colleagues (see Foissner and Berger, 1996, and references therein; Foissner et al., 1999). These publications form a brilliant collection of taxonomic and ecological records for both, benthic and planktonic morphospecies. Despite the lack of updated versions, the data provided by identification keys proved to be in most cases accurate at species and genus levels. However, for higher taxonomic levels (beyond genera), classical phylogenies based on morphological data are often obsolete. Therefore, taxonomists rely on sequencing data and molecular-based phylogenies in order to accurately assign ciliate species to taxonomic ranks (Lynn, 2008; Gao et al., 2016) in light of the entire eukaryotic tree of life (Archibald et al., 2017). Gao et al. (2016) offer a comprehensive tree depicting the evolutionary relationships between different groups of the phylum Ciliophora.

DNA-based approaches: Environmental metabarcoding

During the last decades, the development of DNA-based tools reshaped our understanding of ciliates' diversity, taxonomy, evolutionary history, and ecology in marine and freshwater environments (e.g., Stoeck et al., 2010; Gao et al., 2016; Pitsch et al., 2019). These techniques paved the way for the analysis of large amounts of samples at high frequencies of both, spatio- and temporal scales. Furthermore, molecular analyses can surpass the sensitivity of morphological descriptions in delineating cryptic species and detecting rare ones of known and unknown lineages.

DNA metabarcoding is currently the method of choice for assessing ciliate assemblages in environmental studies. Briefly, DNA from a given sample is collected and the specific DNA, including the desired genetic barcode marker, is amplified by polymerase chain reactions (PCR). The routinely used genetic barcode markers for planktonic ciliates are the hypervariable V4 and V9 regions of

the 18S rRNA genes (Stoeck et al., 2010; Abraham et al., 2019). Using next-generation sequencing (e.g., Illumina ©), genetic material is sequenced, resulting in hundreds of thousands of amplicons. The amplicons are routinely clustered based on sequence similarity into Operational Taxonomic Units (OTUs), each OTU representing, in theory, a single taxon. Fine-tuning of laboratory and bioinformatics procedures are needed. Santoferrara (2019) provides a review on optimizing and error handling procedures for plankton metabarcoding studies. Finally, taxonomic assignments of OTUs are based on reference databases which should allow for the description and estimation of ciliates' diversity. Unfortunately, sequences of many freshwater morphospecies of ciliates are still not known, which asks for more research initiatives to expand reference databases.

Currently, one drawback of DNA metabarcoding approaches is the lack of truly and directly quantifiable data due to multiple copies (and intraspecies variations of this number) of single genes within individual cells (Gong et al., 2013). Therefore, combining molecular and morphological methods should be favored when monitoring planktonic freshwater ciliates (Pitsch et al., 2019). Abraham et al. (2019) provide an updated synthesis of classical (morphology-based), molecular (DNA-based), and statistical tools that can be used synergistically. Besides 18S rRNA genes, several other genetic barcodes are used but not further covered in this chapter (see Abraham et al., 2019; Zhao et al., 2016).

Knowledge gaps

Ecology of ciliate species: Let's open the black box

Although many species are described and known for several decades, knowledge about their ecology and ecological functions within freshwater systems is often limited. Laboratory experiments with isolated strains may help to document their species-specific feeding strategies, food preferences, and elucidate ciliates' roles within microbial food web and abundance patterns. Nevertheless, in situ techniques should be stronger emphasized on e.g., (i) using fluorescently labeled bacteria (FLBs) as food surrogates for assessing bacterivory (Šimek et al., 2019), (ii) the application of in situ hybridization techniques (FISH and CARD-FISH) for the quantification of ciliates but also the determination of their food vacuole contents, and (iii) using size-fractionation methods in combination with mesocosms to study energy fluxes within trophic levels.

Combining morphological and molecular approaches: Need for integrative studies

The development of sequencing and molecular barcoding techniques downplayed the usage of classical taxonomic identification. However, discrepancies appear frequently between morphological and molecular-based methods, and they seldom generate homogenous results. Especially, the non-quantitative character of sequencing methods for the analysis of planktonic ciliates is a central issue. However, studies combining both methods have the potential to extend our current view on ciliates' diversity and functions (Zhao et al., 2016; Pitsch et al., 2019). In this regard, classical taxonomy and the use of integrative approaches should be encouraged and promoted, especially among young researchers. Additionally, the documentation of ciliate diversity must ensure information homogeneity and accuracy of taxonomic descriptions in publications and databases (Warren et al., 2017).

Ciliates and global warming: Time to act!

Climate-induced changes within microbial food webs have striking effects on functionalities and ecosystem services of lakes and ponds. Quantitative and qualitative losses of organisms at one trophic level are cascading to lower and higher trophic levels. Therefore, in times of lake warming, monitoring of planktonic ciliates using integrative approaches is a major concern. Future research may elucidate how resilient ciliate assemblages are to sustain their ecological functions, especially as they are definitely essential key players in microbial food webs.

See Also: Structures and functions of Inland Waters - Lakes: Lake Food Webs; Protists: Flagellates and Amoebae; Zooplankton Diversity and Variation Among Lakes

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Library of Congress Cataloging-in-Publication Data
A catalog record for this book is available from the Library of Congress.

British Library Cataloguing-in-Publication Data
A catalogue record for this book is available from the British Library.

ISBN 978-0-12-819166-8

Publisher: Oliver Walter
Acquisition Editors: Priscilla Braglia
Content Project Manager: Paula Davies
Associate Content Project Manager: Greetal Carolyn
Designer: Christian Bilbow

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Klement Tockner is an internationally leading freshwater scientist, in particular in the research domains biodiversity, ecosystem science, and environmental management. He has published about 250 scientific papers including 180 ISI papers. He was editor-in-chief of the journal *Aquatic Sciences* (2005–2014) and is subject editor of the journal *Ecosystems*. He has published about 250 scientific papers including 180 ISI papers. In 2009, he edited a comprehensive book on European Rivers (Rivers of Europe, Elsevier; 2nd Edition in 2021). He is elected member of the Austrian Academy of Sciences and the German Academy of Sciences, Leopoldina.

Photo credit: David Ausserhofer

Thomas Mehner is vice director and senior researcher at the Leibniz Institute of Freshwater Ecology and Inland Fisheries in Berlin, Germany. He is limnologist and fisheries biologist by training, and has got his Diploma and Ph.D. at the University of Rostock (formerly East Germany) in 1992. In 1999, he had received his habilitation and venia legendi in limnology, which allowed him to start teaching as Privatdozent at universities. Since 1997, he has been working at IGB in several positions. He has published about 170 ISI papers, with primary focus on fish communities, lake food webs, and species interactions. However, his topical interests are broader, and he has authored and co-authored several publications on freshwater fisheries management, fish population genetics and evolutionary and behavioral ecology of aquatic organisms. He has been Handling Editor of the journals "*Aquatic Ecology*" and "*Freshwater Biology*" for several years, and he is currently member of the Editorial Boards of "Global Change Biology" and "Limnologica." Since spring 2018, he has been the president of the International Society of Limnology (SIL), the oldest and most international scientific society devoted to the study of inland waters. Thomas Mehner has taught M.Sc. courses at universities on limnology, fish ecology, fisheries management, and behavior and evolution. His one-week course on "Scientific Writing" for Ph.D. students has been run at 3 universities and in total 18 times, with >120 international students participating. He has trained many M.Sc. and Ph.D. students and supervised their theses, and he is actively mentoring undergraduates, graduates, and post-doc researchers.

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Debbie Chapman as a graduate of the University of London, Deborah Chapman started her research career as limnologist at the Freshwater Biological Association in the English Lake District. She subsequently became interested in monitoring the impacts of disposal of sewage sludge on aquatic organism and the potential for human health impacts from aquatic pollution. In 1986 she joined the United Nations Environment Programme's (UNEP) Monitoring and Assessment Research Centre (MARC) in London, participating in the international monitoring and assessment activities of UNEP and the World Health Organization (WHO), and assisting in global environment assessment programs. In 1988 she became the deputy director of MARC and took responsibility for the developing country workshops and training program, and global environment data review and compilation. After moving to Ireland in 1990, she worked as a freelance Environmental Consultant engaged mostly on international and developing country projects for WHO, UNEP, and other international organizations. She has assisted with the compilation of State of the Environment reports and has contributed to, edited, and produced more than 20 books on water resources and environmental management, including the internationally successful *Water Quality Assessments: A guide to the use of biota, sediments and water in environmental monitoring.*

In 1998 she joined UCC becoming the first lecturer in Environmental Science and then Head of Environmental Science in 2013. In recent decades her research interests have focused on water resources management, especially recreational and amenity lakes and reservoirs, developments and current practice in design and implementation of water quality monitoring programs, and human health risk assessment in relation to the use of freshwater resources and wastewater disposal. Drawing on 30 years of international experience, in 2015 she established the UNEP Global Environment Monitoring System for Water (GEMS/Water) Capacity Development Centre at UCC. This center delivers capacity development activities in water quality monitoring and

assessment worldwide for UNEP, including support for the Sustainable Development Goal indicator for good ambient water quality. She retired as director of the center in June 2021 and now acts in an advisory role and as an independent consultant.

Photo by Blythe White

Kendra Spence Cheruvelil is professor of limnology and co-director of the Data-intensive Landscape Limnology Laboratory at Michigan State University (MSU) in the Department of Fisheries and Wildlife (https://www.canr.msu.edu/fw/). She is also serving as Interim Dean of the Lyman Briggs College, which is MSU's residential college for studying the sciences and maths within their societal and global contexts (www.lbc.msu.edu). Kendra co-established the discipline of landscape limnology (https://bigdatalimno.org/research-themes/landscape-limnology/) and co-leads the LAGOS research program that is creating the research infrastructure to conduct big-data research on U.S. lakes (https://lagoslakes.org/). This large, collaborative, and interdisciplinary research program has been funded by the U.S. National Science Foundation and seeks to understand how global changes such as climate change and land use intensification affect lakes across regions and continents and through time. Dr. Cheruvelil also pushes the boundaries of how to conduct limnology research by using data-intensive science, science of team science, and open science approaches, tools, and perspectives to answer complex scientific questions. She also has an active research program to advance diversity and inclusion in the sciences (https://ee-stem.weebly.com/) and serves as an associate editor for the journals *Limnology & Oceanography Letters* and *Frontiers in Ecology & the Environment*. Prior to joining MSU, Dr. Cheruvelil was a faculty member in the Purdue University system. She has a dual Ph.D. from MSU in Fisheries & Wildlife and Ecology, Evolution, & Behavior (2004).

Photo by Shayenna Nolan

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Christian Griebler is full professor and head of the Limnology unit at the University of Vienna, Austria. He is a dedicated groundwater ecologist with core expertise in microbial ecology and biogeochemistry.

Kenneth Irvine has a broad range of multidisciplinary experience working on aquatic ecology, ecological assessment of surface waters, especially lakes and wetlands, and policy and related policies and management. After gaining a Ph. D. in 1987 at the University of East Anglia (U.K.) for a study on trophic ecology of shallow lakes, he worked for the U.K. Nature Conservancy Council, before moving to study ecosystem structure of Lake Malawi in Africa. He moved to Trinity College Dublin in 1994 Ireland. There, he continued work on the African Great Lakes, as well as building a research group working on ecological assessment in support of the EU Water Framework Directive. In 2011 he moved to IHE Delft Institute of Water Education, the Netherlands, as chair of Aquatic Ecosystems. Current work focusses on wetlands and capacity development in Sub-Sahara Africa. Recent work also includes a review of hydromorphology and links to policy. He currently sits on the Board of the Board of the *African Center for Aquatic Research and Education* (ACARE) and on the Scientific Advisory Board of the *Leibniz Institute of Freshwater Ecology and Inland Fisheries* (IGB), Berlin.

Wolfgang Junk was scientist of the Max-Planck-Institute for Limnology, Dep. Tropical Ecology, Plön during 1970–75.He was scientist of National Amazonian Research Institute, leader of the Dep. of Hydrobiology and Inland Fishery at Manaus, Brazil during 1976–79. and leader of the Working Group "Tropical Ecology" at the Max Planck Institute for Limnology in Ploen, Germany during 1980–2007.He is expertise in ecology and sustainable management of floodplains, land-water interactions, wetland classification. His main research areas arestudies on biomass, primary production, and decomposition of wetland plant communities; nutrient fluxes between land and water; adaptations of plant and animals to periodical drought and flooding; ecology of aquatic macrophytes and fish communities; biodiversity; conceptional considerations on river-floodplain systems, sustainable management of wetland resources and wetland protection with emphasis on the Amazon River floodplain and the Pantanal of Mato Grosso, Brazil. He supervised numerous M.Sc. and Ph.D. students and published more than 300 peer-reviewed publications, including several books and book chapters on Amazonian wetlands and the Pantanal of Mato Grosso. He received many honors, among them the Award of the Grande Cruz (the highest distinction of Brazil) for exceptional scientific performance, and the Cross of Merit First Class of the Federal Republic of Germany. He is corresponding member of the Academy of Sciences of Brazil.

Krantzberg is professor and lead for the engineering and public policy in the School of Engineering Practice and Technology at McMaster University offering Canada's first master's degree in engineering and public policy. Gail completed her M.Sc. and Ph.D. at the University of Toronto in environmental science and freshwaters. She worked for the Ontario Ministry of Environment from 1988 to 2001, as coordinator of Great Lakes Programs, and senior policy advisor on Great Lakes. Dr. Krantzberg was the director of the Great Lakes Regional Office of the International Joint Commission from 2001 to 2005. In 2007 she was appointed as an adjunct faculty member of the United Nations University Institute for Water and Environmental Health and participated in the twinning of the Laurentian and African Great Lakes (principally Lake Victoria). She has co-authored and edited 9 books and more than 200 scientific and policy articles on issues pertaining to ecosystem quality and sustainability and is a frequent speaker to media and the public. Her research interests include investigating Great Lakes governance capacity, analyzing interjurisdictional co-management arrangements internationally for application to the Great Lakes regime, and methods to better integrate science and engineering in policy formulation and decision-making.

Marie-Elodie Perga is associate professor of limnology at the University of Lausanne in Switzerland. Since receiving her Ph.D. from the University of Savoie-Mont Blanc (France), she has worked at the University of Victoria in Canada, and the French National Institute for Agronomy and Environment (France), before moving UNIL.

Because she is a Lindeman's groupie, her research lies at the interface of community ecology and biogeochemistry, through lake food webs and carbon processes. More recently, she added a pint of hydrodynamics with the intent to bridge physical and biogeochemical mechanisms, especially in alpine and high-altitude lakes. Her work covers centennial up to minute timescales through the combination of high-resolution paleo-records and high-frequency data from autonomous sensors.

She is also involved in promoting high-tech research on lakes, notably as a member of the steering committee of the LéXPLORE floating research platform in Lake Geneva, and in connecting science and management through a transdisciplinary network involving National Parks in France. She has published over 75 peer-reviewed papers and serves as associate editor for WIRES Water.

N. LeRoy Poff is professor of biology at Colorado State University and holds a partial appointment as distinguished professor at the University of Canberra, Australia. Since receiving his Ph.D. in 1989, his research has focused on understanding how natural and human-caused hydrologic variability regulates the interactions among species and the structure and function of riverine ecosystems. By developing techniques to quantify streamflow variability in ecologically meaningful terms and using species (functional) traits as generalized, mechanistic response variables, he has been a leader in advancing the field of hydroecology. Through his interdisciplinary and collaborative work, he has contributed fundamentally to the development of the field of "environmental flows," which aims to support sustainable management of streams and rivers at local to regional to global scales in the face of growing human water demands. His current interests are on developing better conceptual frameworks and decision support tools for science-based management of streams and rivers in our current period of rapid climate and ecological change.

Lars Rudstam is professor of fisheries and aquatic sciences in the Department of Natural Resources and the Environment, Cornell University (USA) and the director of the Cornell Biological Field Station. He has a master's degree from the Center for Limnology, University of Wisconsin-Madison and a Ph.D. from Stockholm University, Sweden. Rudstam has published over 250 papers ranging from lake physics to phytoplankton, zooplankton, mussels, mysids, fish, birds, and anglers, mostly about processes associated with food web interactions and ecosystem dynamics. He has worked in lakes in North America, Europe, and Asia as well as the Baltic Sea.

Stuart Warner works with the United Nations Environment Programme with a focus on helping countries to monitor and assess their freshwaters. He was born in England, he moved to Ireland in 2001 to work at University College Cork. Stuart has published in the areas of water quality monitoring and assessment and citizen science approaches to data collection. He has written reports on the capacity of countries to understand their freshwaters which highlight the challenges faced in different world regions. Recent efforts have focused on the development and implementation of a global water quality indicator, and the delivery of capacity development targeted at improving freshwater management. His professional interests include using both traditional and innovative approaches to understand and protect freshwater ecosystems.

Florian Wittmann is professor for physical geography and head of the Department of Wetland Ecology at the Karlsruhe Institute for Technology, Germany. He studied geography, geology, and botany at the Universities of Mannheim and Heidelberg, got his Ph.D. in physical geography at the University of Mannheim, and his lecturer qualification at the University of Bayreuth, Germany. He held post-doc positions at the Max Planck Institutes for Limnology and Chemistry, Germany, where he was working at the bilateral project between the Max Planck Society and the National Institute for Amazonian Research in Manaus, Brazil, for more than 15 years.

His research focuses on neotropical wetlands, with special interest in biogeography, plant species distribution, species diversity, forestry and sustainable management, remote sensing, biomass and primary productivity, and botany and vegetation ecology. Actually, he teaches at the Institute for Geography and Geoecology of the Karlsruhe Institute for Technology, Germany, and in the post-graduate program of Tropical Ecology—Botany at the National Institute for Amazon Research—INPA, Manaus, Brazil. He supervised numerous M.Sc. and Ph.D. students and published more than 150 peer-reviewed publications, including several books and book chapters on Amazonian wetlands.

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CONTENTS OF VOLUME 2

Structures and functions of Inland Waters - Lakes continued

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A Diversity of Primary Producers in Lakes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie_Elodie Perga and Damien Bouffard.

Glossary

Alpha diversity Local (in space and time) diversity in organisms.
Beta diversity Dissimilarity among local communities in terms of composition.
Biodiversity The diversity of life forms, including variation among species, genes and functional traits.
Community assembly The processes determining the composition and abundance of local communities starting from a pool of organisms.
DNA-barcoding Method of taxonomic identification using a short section of DNA from a specific gene or genes.
Eco-evolutionary dynamics How ecological dynamics interact with evolutionary change, with reciprocal feed-backs.
Evenness Equivalence of the abundances of individual units (e.g., taxa, genes, traits) in a community.
Flow-cytometry Technique for rapid detection, characterization and enumeration of microbial cells based on their light scatter and fluorescence properties.
Gamma diversity Regional (large scale) diversity in organisms.
Mixotrophy Refers to the ability of organisms to combine different trophic strategies, i.e., (phago-) heterotrophy and photoautotrophy, to acquire energy, carbon, nutrients or other factors for growth.
Richness Number of different units (e.g., taxa, genes, traits) represented in a community.
Trait Morphological, physiological, phenological or behavioral features of an organism—normally measured at the individual level, but sometimes measured as an average of individuals for a population, species or whole community.

Introduction

Within the variety of species we can see in lake ecosystems, we find a vast diversity of plankton species. Plankton is a collective term for all organisms inhabiting the open water space and cannot control their horizontal position in the water, thus are rather drifting than swimming. Hence plankton has no phylogenetic basis, and comprises viruses, prokaryotes and eukaryotes. Phytoplankton—literally translated from the ancient greek, "plant wanderer/drifter"—are planktonic photosynthetic autotrophs and the primary producers of the pelagic (open water) ecosystem. In fact, the collective term phytoplankton pools an incredible diversity of organisms (Fig. 1). These organisms are all microscopic, however they span four orders of magnitude in size, from roughly 1 μm to 1 mm, which corresponds to the size range of a football to the island Manhattan (Finkel et al., 2009).

Though being easily comprehensible, research in the past 20 years has rendered the above definition of phytoplankton difficult. Most of the clades comprising phytoplankton contain mixotrophic taxa which combine photosynthesis with phagotrophic uptake of prey (usually bacteria or small protists) (Flynn et al., 2012). Mixotrophy is regarded as a common life strategy in phytoplankton. The developing knowledge regarding the nutritional capabilities (and flexibility) of planktonic microorganisms challenges a

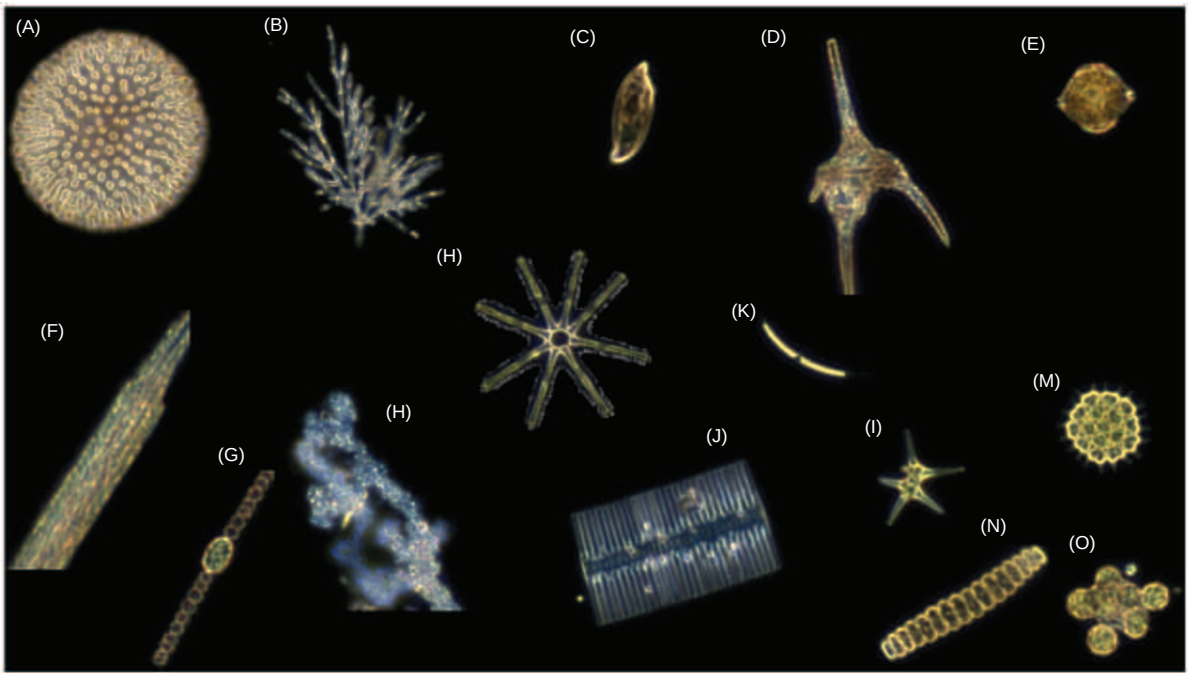

Fig. 1 A selection of phytoplankton species (objects not to scale; c-e, k and l depict individual cells, all other objectives depict colonies of the respective species). (a) *Uroglena sp.*, (b) *Dinobryon sp.*, (c) *Cryptomonas sp.*, (d) *Ceratium sp.*, (e) *Peridinium sp.*, (f) *Aphanizomenon flos-aquae*, (g) *Dolichospermum planctonicum*, (h) *Microcystis sp.*, (i) *Asterionella formosa*, (j) *Fragilaria crotonensis*, (k) *Closterium acutum* var. *variabile*, (l) *Staurastrum sp.*, (m) *Pediastrum boryanum*, (n) *Scenedesmus ellipticus*, (o) *Coelastrum reticulatum*. Taxonomic classes: (a–b): Chrysophyceae, (c) Cryptophyceae, (d–e): Dinophyceae, (f–h): Cyanophyceae, (i–j): Bacillariophyceae, (k–l): Zygnematophyceae, (m–o): Chlorophyceae. Images from underwater imaging microscopy (www.aquascope.ch).

historical dichotomy that divides them into phytoplankton (algae) and protozoa (or zooplankton), according to their respective mode of nutrition (i.e., photoautotrophs vs. heterotrophs). Our considerations in this chapter, therefore, have to be understood to include unicellular and colonial plankton irrespective of their nutritional/trophic mode, spanning a gradient of strategies between strict photoautotrophs and strict heterotrophs.

Due to their variety of species, large population numbers, and their importance as base of the food-web, phytoplankton have an essential role in aquatic ecosystems, regulating e.g., the carbon and nitrogen cycles at local water bodies, as well as at regional and global scales. It has been hypothesized that phytoplankton regulate about half of the carbon cycle at the global scale (Falkowski, 2012). They actively contribute to ecosystem services, i.e., benefits stemming from properly-functioning natural environments, such as provision of clean drinking water, decomposition of wastes and pollutants, recreation, and fisheries. As phytoplankton have short generation times (1–2 days in nature), their populations respond very sensitively to environmental changes, including human impacts at different scales (e.g., extreme weather events and pollution as well as eutrophication and climate change). To note, phytoplankton blooms (events of algal or cyanobacterial overgrowth) can occur as a consequence of anthropogenic pollution and climate warming (Huisman et al., 2018). Blooms by cyanobacteria in lakes can be dominated by species that produce toxins and injure animals, humans, food-webs and the whole ecosystem (a.k.a. harmful algal bloom). These can lead to fish die-offs, cities cutting off water to residents, or fish farms having to close down.

Here we present an essential review of the current state of knowledge with regards to the biodiversity of phytoplankton in lakes. We present the most important aspects of diversity that are pertinent to understand the importance of phytoplankton in lake ecosystems, and review the mechanisms regulating phytoplankton diversity at local and regional scales. We finally present case studies for further reading, which summarize the current state of knowledge of how environmental changes such as eutrophication and climate warming are affecting the diversity of phytoplankton in lakes, at different scales of space and time, and their consequences for lake ecosystems and the services that they provide to human society (like the case of cyanobacterial blooms).

What is biodiversity in phytoplankton

We identify biodiversity as the diversity of life forms, including variation among species, genes and functional traits (Cardinale et al., 2012). Traditionally, biodiversity has been mostly recorded at the level of taxonomic richness and evenness. For phytoplankton, microscopic identification and analysis have been the state of the art until very recently. Meanwhile, molecular methods have become critical for assessing diversity in unicellular organisms, and help overcoming obvious limitations in microscopic identification. As opposed to taxonomic information, there is an increasing interest to identify and quantify diversity in terms of ecological functions. A new focus on estimating trait diversity (both genetic and phenotypic) reflects an attempt to attain mechanistic understanding of the functional diversity of ecological communities (Litchman and Klausmeier, 2008).

Phytoplankton covers an enormous variety of shapes and sizes (Fig. 1). This enormous morphological diversity stems from an extreme phylogenetic diversity. Consider that all terrestrial plants, including mosses, ferns and trees, emerged from one major phylogenetic group, chlorophytes. Chlorophytes are but one out of many phylogenetic groups making up phytoplankton. The large phylogenetic diversity corresponds to an evolutionary diversity that encompasses multiple steps of endosymbiosis, which in turn has resulted in an enormous array of photosynthetic pigments and light harvesting systems. As a result, phytoplankton comprise manifold nutritional strategies, nutrient requirements and utilization strategies, metabolic pathways and secondary metabolites (among which are the infamous toxins produced by cyanobacteria), all acquired over nearly 1 billion years of macroevolution. Besides being the main photoautotrophic group driving the carbon cycle in pelagic ecosystems, some members of the phytoplankton, namely cyanobacteria of the family Nostocales, are the main nitrogen fixers in oligotrophic environments. Moreover, only cyanobacteria and diatoms are strictly photosynthetic, corresponding to the nutrition of typical "plants." The majority of clades making up the phytoplankton include members with diverse nutritional strategies, often combining photosynthesis with phagotrophic nutrition. Several groups like chrysophytes, dinoflagellates and cryptophytes comprise taxa that cover the full range from photoautotrophic to heterotrophic growth.

It is not easy to quantify phytoplankton diversity for a number of reasons. First, the species concept as such is problematic in organisms that may reproduce as clones. While alteration of sexual and clonal reproduction is known for many taxa, we do not know if clonal reproduction is the only way of reproduction in those where sexual reproduction has not been observed. Moreover, molecular methods reveal a high level of cryptic diversity, which again makes it difficult to assign distinct species, especially for groups that are not cultivated or cultivable. Finally, due to their short reproductive cycles (in the range of several hours to few days), phytoplankton communities exhibit enormous temporal turnover. While a single phytoplankton sample in a lake may consist of several 10 to maybe 100 morphologically distinct taxa, the annual species inventory of a lake sampled over multiple seasons may comprise hundreds of taxa.

Regional species pools at the sub-continental level usually comprise several hundred taxa (e.g., 850 taxa are found in the lakes of Fennoscandia, and 1100 species in lakes of the peri-Alpine area) (Moe et al., 2008; Pomati et al., 2019). This regional species richness is known as gamma diversity, while local richness (i.e., in each lake at each time), is called alpha diversity, and accounts for nearly a hundred species per sample. The dissimilarity, or differences, among local (i.e., lake) communities in terms of species composition is called beta diversity. Diversity in species is called taxonomic, since it's based on a classification of individual specimens based on identification keys. Individual organisms can however be classified also based on other expressed phenotypic characteristics (not necessarily taxonomic characters), for example morphological, physiological or genetic features (also known as traits).

Grouping of organisms based on morphological and/or physiological traits leads to functional classification of phytoplankton into so called functional groups. One example of morpho-functional group classification is the one proposed by Kruk et al., where taxa are assigned to classes based mostly on morphological characters (Kruk et al., 2010). In other cases, morphology and physiology can be combined with phenology and co-occurrence patterns in the environment to form sociological associations, such as Reynolds categories (Reynolds et al., 2002). Functional associations of species reflect both similar traits, and similar ecological requirements or behavior of species. Species or individual level traits (i.e., morphology of the taxon or single specimen) can be used to characterize communities in terms of overall trait diversity (the diversity of "trait values" covered by the whole community), which have the same component of taxonomic diversity: richness, evenness and dissimilarity (Fontana et al., 2016).

Similarly to the use of phenotypic (morphological and physiological) traits, also genetic traits can be used to characterize the biodiversity of phytoplankton, both within populations (i.e., individual level variation) and between species in terms of phylogenetic (evolutionary) markers and functional genes. Indeed, the classification of phytoplankton taxa has been influenced significantly by the rearrangements of groups due to phylogenetic studies that have guided periodic revisions of their taxonomy. Some expressed morphological and physiological traits are also used to guide phytoplankton classification, because they vary in correlation with phylogenetic relationships, while others do not (Narwani et al., 2015). One example of periodic re-arrangements in taxonomic classification is the clade of cyanobacteria, where morphological characters are poor descriptors of phylogenetic (evolutionary) relationships.

Trait-based approaches have been used in phytoplankton to both group organisms and to link their responses to environmental gradients, with good evidence for explanatory and predictive power. In particular, population level traits (e.g., parameters of environmental response functions) have shown high prediction of species dynamics over seasonal or long-term gradients, understanding of mechanisms leading to species coexistence and re-arrangements of phytoplankton communities due to climate change (Edwards et al., 2013; Litchman and Klausmeier, 2008; Thomas et al., 2012). Additionally, individual level variation in phytoplankton traits, which has become possible to measure only recently due to new automated technology (see further in the text—Methods to study phytoplankton diversity), has revealed high variation between individuals of the same species, fine-scale dynamics in the interaction of individual microbes, and showed high power in predicting phytoplankton community processes like productivity and resource use, compared to taxonomic diversity (Fontana et al., 2018; Krismer et al., 2017).

The application of genotyping and phenotyping tools, over the last decade, has shown how phytoplankton is characterized by a very large genetic and functional diversity. A high proportion (>80%) of unique genotypes has been reported in many phytoplankton taxa studied in marine environments, with certain populations comprising thousands of different genetic lineages (Collins et al., 2014). These high levels of genetic diversity are expected to result in variation in functional traits and fitness, and in the presence of potential cryptic species (recognizable only by genetic markers, and not by morphology), though some portion of it may also be functionally neutral. Little is known about the genetic diversity of populations of lake phytoplankton (Lebret et al., 2012). Few studies focusing on adaptation to abiotic and biotic environmental conditions across lakes have shown that, for example, populations of the diatom *Asterionella formosa* show high differentiation within lakes, even stronger than among lakes

(Van den Wyngaert et al., 2015). This may be caused in part by local selection due to host-parasite interactions. Similarly, filamentous cyanobacterial populations of *Planktothrix rubescens* have shown high genetic diversity between lakes, with strong selection for lake-specific variants that have gas vesicles (used to regulate colony buoyancy) better adapted to each lake depth and turbulence conditions (high pressure at depth can collapse gas vesicles causing sinking and death of the organism) (D'Alelio et al., 2013).

The processes shaping phytoplankton biodiversity

Community assembly

In extreme synthesis, biodiversity of natural communities is controlled by selection, speciation, dispersal and stochastic drift (Vellend, 2010). The interplay of these mechanisms over a landscape is called community assembly. Organisms from a regional pool of species, genes and traits, colonize a local environment and interact with abiotic and biotic factors to form a local community (Fig. 2). While different processes operate at diverse spatiotemporal scales (Figs. 2 and 3), spatial processes involving dispersal and relevant vectors, and historic contingencies (the past history of the regional species pool—constrained by evolution), generate large-scale biogeographic patterns in diversity. On the other hand, biotic and abiotic interactions, and priority effects (the advantage of who gets there first), occurring at small spatiotemporal scales, contribute to local co-occurrence and diversity (HilleRisLambers et al., 2012) (Fig. 2).

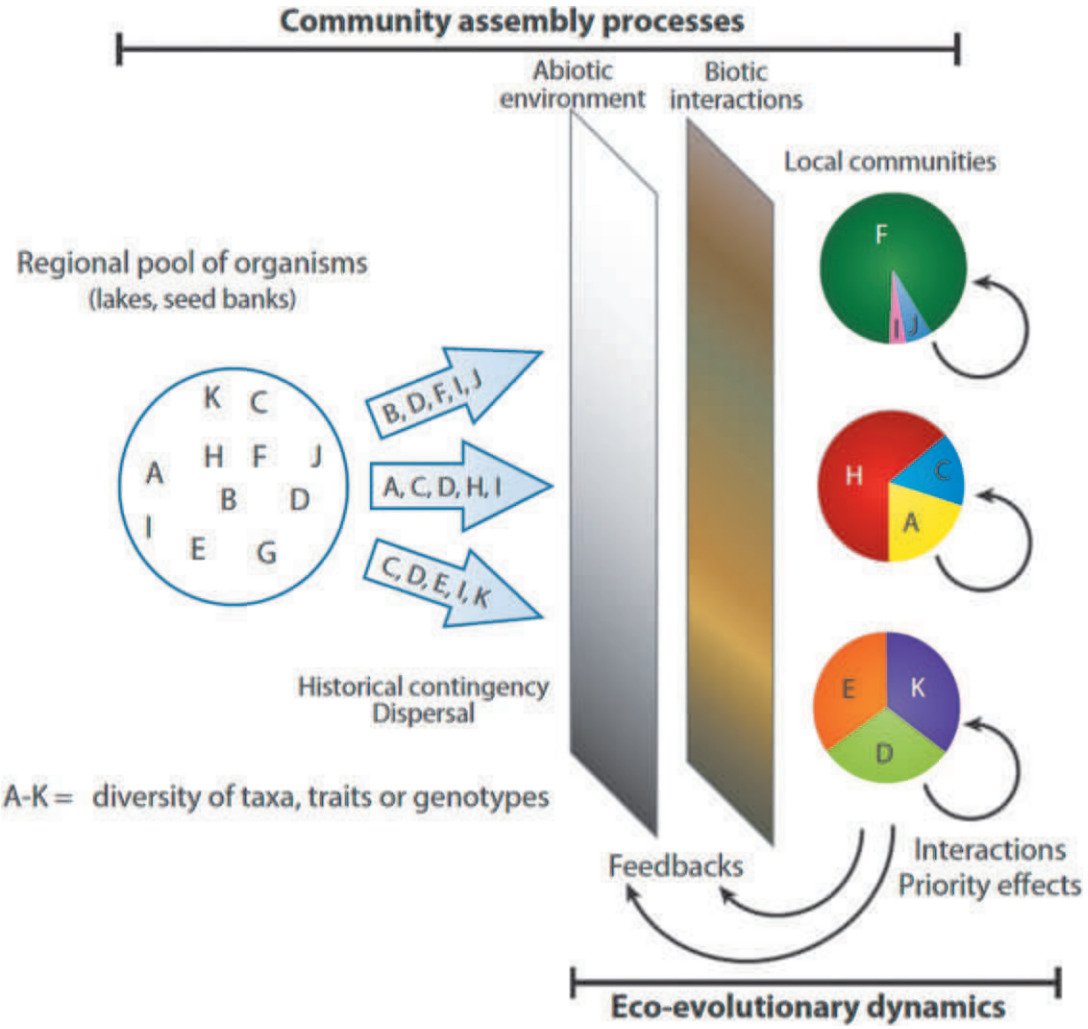

Fig. 2 The assembly of lake phytoplankton communities is influenced by ecological and evolutionary processes operating at different spatial scales. Organisms belong to a regional pool of organisms that is constrained by historical processes (including evolution). A subset of this pool (influenced by chance and dispersal limitation) is available for growth at a particular moment in time. The realized community can be seen as the result of priority effects (who gets there first has an advantage), and selection by environmental (abiotic) filters and biotic interactions (competition, facilitation, predator-prey and host-parasite dynamics). Adapted from HilleRisLambers J, Adler PB, Harpole WS, Levine JM and Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics* 43: 227–248. doi: 10.1146/annurev-ecolsys-110411-160411.

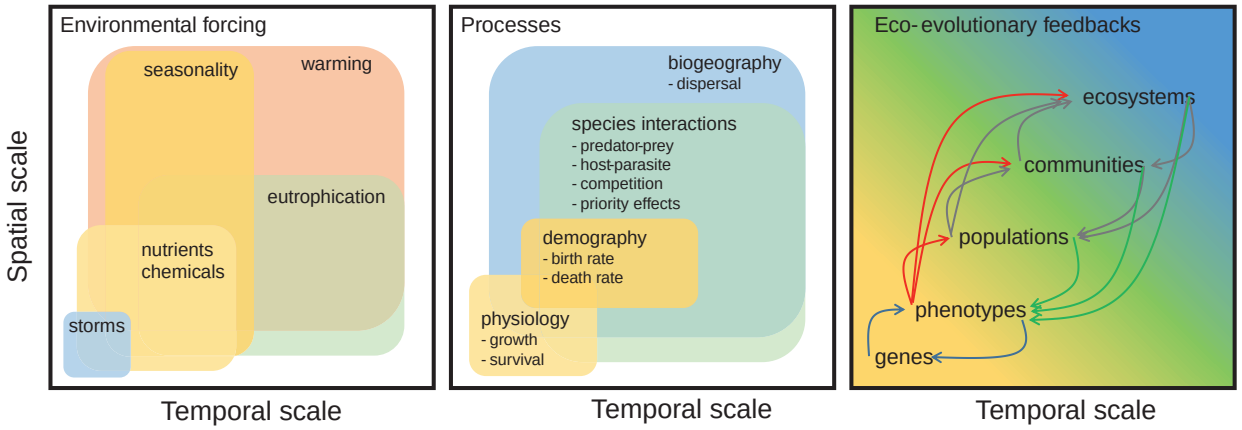

Fig. 3 The diversity of phytoplankton communities is maintained by the interaction of a spatially and temporally variable environment (both by natural and anthropogenic forcing) (A), acting on a complex set of nested processes (engaged at different spatial and temporal scales) (B), themselves influenced by eco-evolutionary feedbacks (C) (blue arrows = evolution; grey arrows = ecology; red arrows = evolution influences ecology; green arrows = ecology influences evolution; adapted from "What are eco-evolutionary dynamics?,"http://ecoevoevoeco.blogspot.com/2010/03/what-are-eco-evolutionary-dynamics.html).

Following this conceptual model, the mechanisms influencing biodiversity include both local and short-term mechanisms as well as regional processes occurring over longer timescales, and not all of the mechanisms involved are deterministic. Local communities are influenced by dispersal and also by demographic stochasticity (random death processes and disturbances). In many cases, therefore, random drift may be an important mechanism shaping the composition and relative abundances of local communities, in particular if species are very similar or equivalent in their competitive abilities (i.e., are neutral) (Rosindell et al., 2011), or have small population sizes. At the local scale, deterministic mechanisms might be more prevalent: abiotic factors like climate or nutrient levels, and biotic factors like interactions with natural enemies, can be seen as selective environmental filters, favoring organisms with only certain specific genetic, morphological or physiological traits. Local mechanisms represent the most dynamic core of the community assembly process, with responses and feed-backs between the interacting organisms and their biotic and abiotic environment (e.g., populations grow, respond to, and impact on, limiting resources or natural enemies). This local set of interactions belongs to the so-called eco-evolutionary dynamics. Interactions of co-occurring organisms with competitors, predators, mutualists, or parasites, in fact, not only depend on the abiotic environment, but can feed back to influence both abiotic factors and the interactions themselves.

Phytoplankton, in particular, is a well-known example in which eco-evolutionary dynamics occur: between consumers and resources, predators and preys, and hosts and parasites. This is due in part to their short generation time, therefore effectively coupling ecology and evolution at the same time scale, and to their potential for rapid, local and ecologically relevant adaptation given their large population sizes (Hairston et al., 2005; Thibodeau et al., 2015). Additionally, as mentioned earlier, phytoplankton are characterized by a large amount of genetic, metabolic and functional diversity, which offers many opportunities to respond to selective environmental filters.

Diversity as an emergent property of the ecosystem

The large diversity of phytoplankton species and forms that can be found at the local community scale has been puzzling aquatic ecologists for more than half a century. Hutchinson (1961) was the first scientist to highlight how phytoplankton is a particularly inspiring example of a natural community comprising a large number of different species from the same trophic level, therefore similar in terms of broad functions, which co-occur over many generations in the same (sometimes very small) water body. Hutchinson introduced the term "paradox of the plankton" to refer to this surprising diversity: "how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials?" The paradox, which is one of the most classical problems in ecology, stems from the prediction, by the principle of competitive exclusion, that in homogeneous environments species that compete for the same resources cannot coexist for long, since the best competitor should eventually prevail when a final equilibrium is reached. This paradox of high diversity is not even restricted to the species level only, since species comprise multiple genotypes that appear to fit different environmental conditions, but yet co-occur in nature.

To explain the paradox of the plankton, many solutions have been proposed by numerous scientists over the years. The principal mechanisms invoked suggest that phytoplankton communities never reach a stable equilibrium, due to both external forcing (e.g., environmental fluctuations in essential resources, disturbances), and internal species interactions generating chaotic dynamics (Fig. 3) (Roy and Chattopadhyay, 2007). Out-of-equilibrium dynamics set temporal limits for single species to become dominant, minimizing competitive exclusion. Similarly, resources (nitrogen, phosphorus, light) are not homogeneously distributed, but vary spatially and temporally. Likewise, for organisms exhibiting a high diversity in photopigments, light is not one but an array of resources (Roy and Chattopadhyay, 2007). Additionally, phytoplankton taxa can coexist if they are similar enough to be

competitively neutral (Scheffer and van Nes, 2006). All of these mechanisms are plausible and have found evidence in field or laboratory investigations. The main process allowing such a large diversity of species in lake phytoplankton communities remains however a mystery. The relative importance of the above mechanisms likely changes over space and time.

The diversity of phytoplankton, in terms of genetic, phenotypic and consequently taxonomic characters, is a property of the community that emerges from the interaction of ecological and evolutionary processes in a fluctuating environment (Fig. 3). Individuals respond to their immediate environment by regulating their gene expression, therefore adapting their phenotypes (morphology, physiology) to the environment. Such changes at the individual level influence the diversity and demography of populations, which interact with one another therefore determining the structure (richness, evenness, composition) and dynamics of communities and food-webs (Fig. 3) (Norberg, 2004). This rich and complex set of nested responses and feed-backs might explain the stunning diversity of planktonic ecosystems, and the reason why understanding such systems is still a hot research topic.

The issues above make phytoplankton communities fascinating from many different points of view: from the variety of species and forms, which highlight how explosive biodiversity can be even in small ecosystems, to the puzzling ecological and evolutionary questions of how this diversity is achieved and maintained over the long term. The processes invoked imply both deterministic (fundamentally predictable) and stochastic (fundamentally unpredictable) mechanisms, with implications for both fundamental research and applied science and management of lakes and their biodiversity. Not all the changes in an essential functional component of the biosphere like phytoplankton might in fact be predictable. This consideration is particularly relevant for lake ecosystems, which provide important resources to human societies like fisheries and drinking water, and require careful and adaptive management especially as a consequence of a general increasing prevalence of phytoplankton blooms due to climate change and eutrophication (Ho et al., 2019).

Algal blooms, i.e., mass occurrences of phytoplankton, have long been observed, and are usually associated with systems impacted by eutrophication (they may have been depicted already in the bible—"... and all the waters that were in the river were turned to blood" [Exodus 7:20]). They represent a response to anthropogenic pollution and a threat for aquatic ecosystem services (water quality, fishery, farming, recreation) worldwide, with annual societal costs in the billions of Euros (Note that the spring bloom in a lake is a seasonal, recursive natural phenomenon, not associated with eutrophication (Sommer et al., 2012).). In lakes, cyanobacteria are known to form dense blooms (Fig. 4) and produce a wide array of neurotoxins, liver toxins, cell toxins and skin irritants. Blooms can cause significant operational issues to intakes in drinking water plants, and consumption of toxins by animals or humans can result in multiple minor and major health issues (Huisman et al., 2018). Forecasting of algal blooms is a central concern in ecosystem management. The ability to anticipate blooms even just a week in advance would allow stakeholders to respond to human health or ecosystem service concerns.

Methods to study phytoplankton biodiversity

Traditional methods

The diversity of plankton communities is most commonly revealed by microscopy (Fig. 1). Only the development of optical microscopes, starting in the 17th century, enabled the first detailed characterizations of phytoplankton and their diversity by direct observation of their morphology. Early microscopic work revealed specifically the diversity of larger phytoplankton cells with distinct and rigid structures, such as diatoms (Fig. 1i–j). Further, and ongoing, advancements in optical microscopy render this method still one of the most commonly used techniques in characterizing phytoplankton biodiversity.

The maximal resolution of most light microscopes does not allow for useful magnifications above 2000x, which may not be sufficient to identify distinct morphological traits of small phytoplankton (<2 μm), but also of larger species that lack evident morphological features. The development of the electron microscope in the early 20th century enabled the investigation of cellular ultrastructures (e.g., the silica frustules of diatoms), which in turn helped to further resolve phytoplankton biodiversity. Novel developments in optical microscopy led to new techniques (e.g., confocal laser scanning microscopy or structured illumination microscopy), which allow for resolutions higher than those imposed by the diffraction limit of light microscopy. Combined with the use of specific fluorescent dyes, these techniques enable to achieve higher resolutions and directly resolve processes at the

Fig. 4 Blooms of cyanobacteria in Swiss lakes. (A) *Planktothrix rubescens*, Lake Hallwil (Eawag, Sabine Flury); (B and C) *Microcystis aeruginosa* in Greifensee (B) Eawag, Francesco Pomati; (C) Kantonales Labor ZH, Rene Schittli. From FAQ – Cyanobacteria / blue-green algae. https://www.eawag.ch/en/research/water-for-ecosystem/pollutants/faq-cyanobacteria-blue-green-algae/.

cellular level, which in turn may allow to characterize and distinguish phytoplankton beyond morphology and taxonomy, namely on the physiological functional level.

Lake water samples for microscopy are typically taken from a boat using niskin bottles (bottles that close at discrete depths) or Schroeder bottles (which intake water based on a pressure valve, for depth-integrated sampling), with a monthly frequency (as suggested by many water quality directives). The Utermöhl method is the most widely used to examine phytoplankton: the protocol presumes the use of a preservative solution (either formaldehyde or Lugol's iodine), which blocks biological activities but can damage cellular structures and shrink cell size. Samples are then sedimented, cells recovered in a counting chamber, and counted manually under an optical inverted microscope. Traditional sampling and Utermöhl-based microscopy have been applied to lake phytoplankton diversity monitoring for more than a century worldwide, and have provided historical time series (generally decades long) of species counts and biodiversity estimates that have been instrumental for understanding lake processes (Table 1).

The counting and classification of phytoplankton is however a very tedious process, and often taxonomists miss items, count some objects more than once and misclassify others (MacLeod et al., 2010). This is exacerbated by continuous taxonomic rearrangements in the classification of phytoplankton and by methodological changes over time. As a consequence of the above processes, water sampling and microscopy are very time consuming, costly, and therefore low throughput and expensive, making it challenging to measure and track phytoplankton diversity with high resolution across time and space. An additional problem of traditional monitoring data is that they often have a strong association with the person (e.g., taxonomist) collecting them. Harmonization of methods and procedures is of big concern in microscopic analysis of phytoplankton, and arguably also a source for biased data analyses in cases where data from multiple authors is merged (Moe et al., 2008). Manual microscopical identification also does not allow to consistently extract quantitative plankton morphological features, such as size, shape, or pigment information. These features are key plankton traits that determine individual, population and community responses to a changing environment, and in turn affect ecological processes (e.g., energy transfer, algal blooms), and services (e.g., fisheries, water quality). These limitations of traditional monitoring, together with the general demand for time-efficient analysis, have stimulated the development of a multitude of alternative and automated plankton monitoring tools (Johnson and Martiny, 2015; Lombard et al., 2019). New approaches can afford high-throughput and lower costs of plankton community analysis, in the laboratory and in the field, each with their own advantages and limitations. The taxonomic resolution of microscopy can be achieved and surpassed by DNA-based methods, traits can be measured by flow-cytometry and imaging, and in situ sensors can provide high-frequency real-time data on bulk community properties.

New and alternative methods

Phytoplankton contain pigments for harvesting light. Eukaryotic phytoplankton contain chlorophyll a as their core pigment, however, many accessory pigments (e.g., other types of chlorophyll, carotenoids or phycobiliproteins) are taxon-specific. Therefore many lineages have specific optical spectra; however, these accessory pigments and their abundance relative to the universal chlorophyll a are not necessarily unique to specific groups, hence precise distinctions at fine taxonomic scale are challenging (Johnson and Martiny, 2015). Nonetheless, chromatographic approaches such as high-performance liquid chromatography (HPLC) are used to obtain a broad taxonomic characterization of a given phytoplankton sample based on its pigment composition, also because they are usually economic and relatively high throughput. An advantage of pigment ratios is that they may provide information on the physiological/functional diversity of phytoplankton, because they are influenced by light (spectrum and intensity), nutrient availability and other environmental factors. Phytoplankton pigments (e.g., Chl-a, phycocyanin) can also be used to estimate abundance and diversity, in terms of broad functional groups, using remote sensing from satellites, airplanes or drones over varying areas of a water body or region. Remote sensed data can provide information about horizontal distribution of phytoplankton, or across many lakes (Ho et al., 2019), which is not possible to achieve with traditional monitoring. Remote sensed data (i.e., from satellites) are available worldwide and daily at low cost. Unfortunately remote sensing has no vertical (depth) resolution and, being based solely on main pigment type, provides little information about the taxonomic diversity of phytoplankton.

DNA amplification and sequencing, and other techniques derived by DNA-based hybridization, have become an increasingly common and cost-effective approach to estimate phylogenetic and functional diversity in phytoplankton (Johnson and Martiny, 2015). Here we will concentrate only on the most common and effective approaches. Based on highly conserved DNA regions, which are however different among taxa, such as the 18S ribosomal DNA (rDNA) for eukaryotes or 16S rDNA for prokaryotes, the so-called DNA-barcoding aims to amplify and sequence such targets. As mentioned earlier, sequencing of phylogenetic marker genes such as the 18S and 16S has helped discovering cryptic species, i.e., two or more morphologically indistinguishable species, and supported the rearrangement of taxonomic classifications. Meta-barcoding, which is referred to the amplification and sequencing of marker genes across an entire community, allows the identification and classification of organisms as Operational Taxonomic Units (OTUs), by assigning different sequences to taxa through matching of such sequences to reference databases (in which reference sequences are obtained from certified taxonomic classifications). Meta-barcoding, which can be achieved directly using environmental samples (e.g., environmental DNA or eDNA), has become common practice in biodiversity estimation in aquatic environments (Deiner et al., 2017), principally due to next generation sequencing (NGS) that is high throughput and cost-effective, and the availability of well-curated database and efficient pipelines for data analysis.

To date, meta-barcoding probably represents the state of the art to estimate the diversity of small prokaryotes and eukaryotes in phytoplankton, for which morphological characters cannot be distinguished (nevertheless, standard metabarcoding is less accurate for quantitative analysis of those taxa that are accessible to microscopic analysis). Metagenomics, i.e., the sequencing of all DNA present in an environmental sample, allows the reconstruction of genomes in uncultivated phytoplankton organisms, including their functional genes. Metatranscriptomics, which targets all RNA present in a water sample, can be used to study and quantify the diversity of expressed phytoplankton genes in the environment. In this way, metagenomics and transcriptomics provide information about the different functions of a community and these changes under different environmental conditions (Johnson and Martiny, 2015). While metatranscriptomics can provide quantitative data about expressed functions, barcoding and genomics mostly provide qualitative (presence/absence) information, and all these approaches can be severely limited by coverage in the reference databases used to annotate the sequences obtained.

Many quantitative methods have been proposed for the estimation of taxonomic and functional diversity in phytoplankton (Johnson and Martiny, 2015; Lombard et al., 2019). Here we will focus, again, on the most common and effective approaches with a particular emphasis on methods that can be automated. Flow cytometry measures fluorescence and scattering signals from single microbial cells or colonies (from viruses to eukaryotes) contained in a water sample: particles are separated using one or more stages of injection of the sample into an internal fluid system, and are oriented along their main axis through a flow-cell where they are beamed sequentially by one or multiple lasers (wavelengths are generally chosen to excite different algal pigments). The scattering (forward and side scattering) and fluorescence (from many different filters, associated with different pigment emissions) signals are parameterized and recorded for each individual particle. Depending on how many and which lasers, and fluorescence filters, flow cytometry is able to resolve several phytoplankton features including size, shape, granularity and pigment quantity and composition (Fontana et al., 2014). These measures of phytoplankton morphology and color represent important functional traits: flow-cytometry can be considered a high throughput phenotyping technique, and can provide highly valuable estimates of community diversity based on individual level phenotypic data, similar to genetic data (Johnson and Pomati, 2020). Additionally, flow-cytometry can be applied in situ under automated use, which has allowed to pioneer the study of natural phytoplankton dynamics at scales of space and time that were not possible with traditional methods (Table 1).

Imaging techniques are emerging as those that have the highest potential to yield standardized and reproducible quantification of abundance, biomass, diversity and morphology of plankton (Lombard et al., 2019). Boosted by the recent developments in the miniaturization of optics and electronics, plus continuous advances in image processing and artificial intelligence (AI) for object recognition and classification, automated imaging microscopy offers the best prospects to substitute traditional methods in the monitoring of phytoplankton biodiversity. Imaging allows us to harness the knowledge of taxonomists to train automated AI classifiers (MacLeod et al., 2010). Some of these instruments can be deployed in the field, therefore allowing high-frequency automated monitoring. Among those is worth mentioning imaging flow-cytometers, which combine the resolution of flow-cytometry laser detection and scanning with imaging of selected particles (Lombard et al., 2019). Underwater microscopes and cameras are more recent advances allowing rapid and cost-effective monitoring of phytoplankton (and zooplankton) in situ by imaging, without disrupting natural spatial aggregates, behaviors, shape, and co-localization of organisms (including symbionts and parasites). Some basic information about phytoplankton such as in situ physical morphology, natural heterospecific aggregates, or individual level interactions, have rarely been studied at the right scale due to biases introduced by sampling (Fig. 5). Underwater cameras are cheaper and more robust than previous in situ tools, and allow complete automation in functioning and data analysis (by exploiting the constantly advancing fields of image processing, whose tools are also generally open-source). New developments in underwater cameras allow to automatically image with multiple magnifications (two distinct objectives) phytoplankton and zooplankton at unprecedented spatial (10 μm to 8 mm) and temporal (seconds) resolution. Aided by automated image processing pipelines and classification by AI, this approach allows to track plankton taxa diversity (including morphological traits) at the food-web level in real-time (Figs. 1 and 5).

Case studies

Table 1 Here we provide a non-exhaustive overview of case studies analyzing phytoplankton diversity in lakes. We distinguish studies where (1) diversity itself is the dependent variable from those where (2) diversity is explaining processes, and (3) technical studies about the quantification of phytoplankton diversity. We keep the focus on inland water bodies, so references to marine studies are not reported.

Synthesis

Phytoplankton biodiversity is as fascinating today as it was a century ago, being still partially unexplored, in part due to the paucity of methods to study microbial communities with large dispersion and population sizes. Exciting times are coming ahead in terms of new technology developments, which will allow us to study the dynamic world of these mighty microbes at scales that were unimaginable only a couple of decades ago. We emphasized several aspects about the diversity of plankton, in terms of both conceptual and practical knowledge and current limitations. The need for more data, particularly at the genetic and functional level, and across scales of space and time, is motivated by questions regarding the relative importance of different mechanisms driving

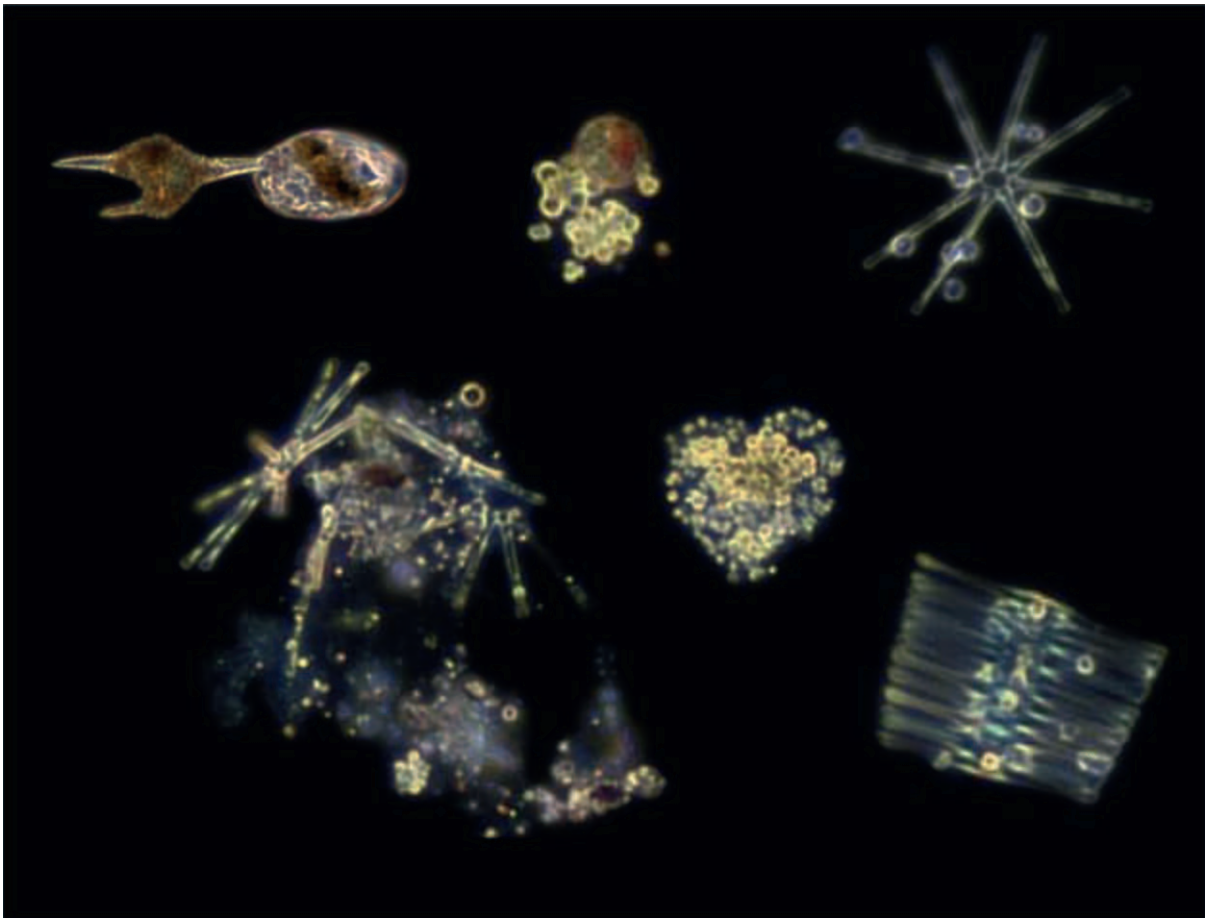

Fig. 5 Clockwise from top-left: *Ascomorpha* eating *Ceratium*, a dinoflagellate eating green algae, chytrid fungi infecting *Asterionella*, chytrid fungi infecting *Fragilaria*, a natural heterospecific aggregate of cyanobacteria and green algae in mucilaginous structure forming a heart shape, *Asterionella* and green algae forming lake snow. Images from www.aquascope.ch.

Table 1 Aims: 1—explain diversity, 2—diversity explains x, 3—technical/other.

Scale	*Site*	*Country*	*Diversity*	*Approach*	*Aim*	*Topic*	*References*
Local, long-term	Lake Zurich	Switzerland	Species	Taxonomy	1	Environmental drivers of richness and evenness	Pomati et al. (2012)
Local, long-term	Lake Zurich	Switzerland	Species	Taxonomy	1	Patterns in richness and species turnover	Matthews and Pomati (2012)
Local, long-term	Lake Zurich	Switzerland	Species	Taxonomy	1	Environmental drivers of toxic cyanobacteria	Posch et al. (2012)
Local, long-term	Experimental lake area	Canada	Species	Taxonomy	1	Case studies on temporal extinction debt as driver of changing SR	Dodson et al. (2000)
Local, short-term	Greifensee	Switzerland	Functional group	Flow-cytometry	1	Predictability of phytoplankton community dynamics	Thomas et al. (2018)
Local, short-term	Multiple lakes	Switzerland, Romania	Traits, species	Flow-cytometry, taxonomy	2	Importance of species and trait diversity for productivity and resource use	Fontana et al. (2018)
Local, short-term	Multiple lakes	Fennoscandia	Functional groups, traits, species	Taxonomy	2	Importance of species, functional groups and trait diversity for productivity and resource use	Abonyi et al. (2018)

(*Continued*)

Table 1 (Continued)

Scale	*Site*	*Country*	*Diversity*	*Approach*	*Aim*	*Topic*	*References*
Local, short-term	Ponds	Germany	Functional group, traits	Imaging, flow-cytometry	3	Seasonal succession	Dunker (2020)
Local, short-term	Lake Zurich	Switzerland	Functional group, traits	Flow-cytometry, taxonomy	1, 3	Selection on traits during spring bloom	Pomati et al. (2013)
Spatial, long-term	Multiple lakes	Switzerland	Funcional group	Metabarcoding	1	Environmental drivers in prevalence of cyanobacteria	Monchamp et al. (2018)
Spatial, long-term	Multiple lakes	Switzerland	OTUs	Metabarcoding	1	Environmental divers of community assembly	Monchamp et al. (2019)
Spatial, long-term	Multiple lakes	Switzerland	Traits	Taxonomy	1	Environmental divers of size distributions	Pomati et al. (2020)
Spatial, long-term	Multiple lakes	Finland, Norway, Sweden	Species	Taxonomy	1	Importance of diversity for stability and resource use	Ptacnik et al. (2008)
Spatial, long-term	Multiple lakes	Tropical south America	Species, ecological guilds	Taxonomy	1	Dispersal mechanisms as contributor to diatom metacommunity structure	Benito et al. (2018)
Spatial, short-term	Multiple lakes	Contiguous United States	Species	Taxonomy	1	Reporting continental scale diversity pattern, assessing local versus spatial drivers	Stomp et al. (2011)
Spatial, short-term	Multiple ponds	Netherlands	Species	Taxonomy	1	Variation partitioning on species diversity in interconnected ponds, finding predominant role of species sorting	Vanormelingen et al. (2008)
Spatial, short-term	Multiple lakes	Finland	Species	Taxonomy	1	Variation partitioning on species diversity among lakes in Finland	Soininen et al. (2011)
Spatial, long-term	Multiple lakes	Fennoscandia	Species	Taxonomy	1	Scale-dependent productivity-diversity relationship	Ptacnik et al. (2010)
Spatial, short-term	Multiple lakes	Global	Species	Taxonomy	1	Continental-scale pattern of lake diatom diversity related to spatial processes	Vyverman et al. (2007)
Spatial, short-term	Lake Biviere di Gela with surrounding ponds	Italy	Species	Taxonomy	1	Case study analyzing shared taxa among lakes as function of distance	Naselli-Flores et al. (2016)
Spatial, short-term	Lake	Greece	Species	Taxonomy	1	Experimentally testing distance effect on dispersal	Chrisostomou et al. (2009)
Spatial, short-term	Multiple reservoirs	Italy	Morpho-functional groups	Taxonomy	2, 3	Morpho-functional groups as an alternative to assess ecology of lakes	Vadrucci et al. (2017)

phytoplankton biodiversity change. Conclusive results rely on careful investigations from the field and ecological models, which need to be informed by experiments and observational data analysis. Results so far testify for very sensitive responses of phytoplankton communities to environmental change, with potential implications for the resilience of lake ecosystem processes and the conservation of freshwater habitats and the biodiversity that they harbor. These issues are particularly important in our current times, characterized by local and global human impacts, like climate change. Our ability to predict and manage lake ecosystem services strongly depends on our understanding of the mechanisms regulating diversity in an essential functional component of the biosphere like phytoplankton communities.

Knowledge gaps

1. Measuring or inferring ecologically relevant traits (e.g., physiological responses), particularly for morphologically indistinguishable species, in the smaller nano size range (i.e., <5 μm).

2. Incomplete understanding of the carbon metabolism in majority of clades (use of inorganic vs. organic C-sources).
3. Methods to study local processes at the temporal scale that matters to understand eco-evolutionary dynamics, including methods to study single cell genomes and phenotypes.
4. Understand and quantify the relevance of colonization-extinction events as opposed to "dispersal in time" (colonization from the egg-bank).
5. Extent of genetic diversity and importance of sexual reproduction versus clonal proliferation in freshwater phytoplankton, and how this contributes to functional diversity.
6. Approaches to mitigate human impact on phytoplankton diversity and conservation strategies specifically targeting phytoplankton.
7. Incomplete understanding of the effects of environmental change on phytoplankton communities, e.g., globally reduced primary production due to warming (shift toward net heterotrophy).
8. The relative importance of physiological responses, ecological interactions and evolutionary adaptation in phytoplankton community change over long-term environmental gradients and under extreme events.
9. Globally, poor coverage of monitoring programs leads to a lack of data on phytoplankton diversity (and how it changes with time) at different spatial scales.
10. Factors selecting for toxins in phytoplankton, leading to toxic algal blooms.
11. Consequences of changes in phytoplankton diversity in the food web context (other trophic levels).

See Also: Emerging methods and topics: Dust and Fog Effects on Inland Waters; Remote Sensing of Inland Water Quality; Fundamental concepts and theories: Hydrologic Setting Affects Ecosystem Processes; Structures and functions of Inland Waters - Lakes: Benthic Algae in Lake Littoral Habitats; Phytoplankton Productivity

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Relevant Websites

www.algaebase.org—Taxonomic information phytoplankton species, their distribution and up-to-date classification.
www.cyanodb.cz and www.diatoms.org/morphology—Best online databases for cyanobacterial and diatom taxonomy; also offer webinars.
FAQ – Cyanobacteria / blue-green algae—Info page about cyanobacterial blooms.

Optical microscope—Wiki information page.
Confocal microscopy—Wiki information page.
Water remote sensing—Wiki information page.
Flow cytometry—Wiki information page.
DNA barcoding—Wiki information page.
Metagenomics—Wiki information page.
AQUASCOPE—Underwater imaging of lake plankton, with real-time imaging data and information material (pictures, videos) about lake phytoplankton monitoring.

Macrophytes

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This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Alternative stable states Ecosystems may exist in several, alternative, steady states each with its self-enforcing negative feedbacks. This paradigm has been adopted from theoretical ecology and has become widely accepted and applied in shallow lake research and management.

Belt transect Band of defined width oriented at right angles to the shoreline or bank, which starts at the water line including the wash and inundation zones starting at the highest seasonal waterline and in lakes extends to the lowermost limit of the aquatic macrophyte vegetation.

Benthivory Effects of the feeding on benthic animals by benthivorous fish. This includes direct impact on macrophytes and sediment and indirect impact on other biotic and abiotic compartments.

Clonal growth Many macrophyte species groups display a clonally branching growth form, i.e., the branched plant architecture consists of repeated vegetative modules that each can survive and establish as an independent plant, and continue further clonal growth and generative reproduction. Clonal branching and subsequent fragmentation and spread may lead to the distribution of genetically identical individuals over larger distances.

Dispersal Spread over shorter or longer distances of more or less specialized vegetative plant fragments or organs, as well as generative units such as seeds and spores. The dispersed units can establish new stands of macrophytes.

Dissolved Inorganic carbon (DIC) Dissolved inorganic carbon is present in equilibrium as three species, carbonate, bicarbonate (HCO_3^-) and carbon dioxide (CO_2). The distribution over these three is governed by pH, as is steady state total concentration.

Eutrophication Increased nutrient (mainly phosphorus and/or nitrogen) availability in a water body leading to increased productivity of primary producers.

Growth form A phenotypically recognizable similarity in the functional organization of the stem, leaf, root and reproductive organs across different plant species, which is interpreted as an adaptive response of the whole plant form to its environment.

Herbivory One of many food-web interactions. The consumption of plants or plant parts by animals, loosely similar alternatives are grazing and browsing.

Maximum colonization depth Lowermost limit of the aquatic macrophytes which are adherent to or rooted in the sediment.

 https://doi.org/10.1016/B978-0-12-819166-8.00043-8

Overyielding A mixture of species performs an ecosystem function better than monocultures.
Percent volume infested/inhabited (PVI) Volume of lake inhabited by macrophytes in percent.
Periphyton Periphyton is the community of microorganisms (microalgae, micro-, meio- and mesofauna, fungi, bacteria), the surrounding matrix of co-precipitated carbonates and excreted polycarbohydrates and detritus developing on submerged surfaces. Vertical depth of periphyton communities ranges in the order of micrometers to a few centimeters.
Regime shift See alternative stable states.

Introduction

Macrophytes are "aquatic photosynthetic organisms, large enough to see with the naked eye, that actively grow permanently or periodically submerged below, floating on, or up through the water surface" (Chambers et al., 2008). They have adapted to living in aquatic environments and grow in or near water in emergent, submerged or floating forms. This definition includes vascular plants, charophytes and aquatic bryophytes. The global number of macrophyte species is not known. Aquatic vascular macrophytes (*Tracheophyta*) alone include about 3500 species (without hybrids) that occur in permanent, temporary or ephemeral inland freshwater and brackish waterbodies worldwide (Murphy et al., 2019).

Most macrophyte species have narrow global distributions. About 80% of vascular aquatic macrophytes reportedly have ranges that individually occupy <10% of the world area present within the six global ecozones which provide habitat for macrophytes. Macrophyte diversity is highest in subtropical to low tropical latitudes and at ecozone scale, macrophyte species endemism is pronounced (Murphy et al., 2019).

Based on growth forms, several major macrophyte groups can be distinguished (Den Hartog and Segal, 1964, Fig. 1A–F):

Charophytes (Fig. 1A) are a class of macroscopic green algae exhibiting a complex whorl-shaped thallus and bottom-dwelling growth forms. They mainly occur in lakes with low nutrient concentrations and can grow down to deep (40–60 m) water. In eutrophic, turbid lakes, they are restricted to shallow water.

Aquatic bryophytes (Fig. 1B) can occur at great depths (down to 140 m). Efficient, low metabolism underlies tolerance of low light levels and low year-round temperatures in the hypolimnion of deep, cold lakes, and benefit from higher nutrient and CO_2 levels. The high accumulation capacity of bryophytes for contaminants has led to their use for monitoring regional and local patterns of deposition, particularly of metals and radionuclides.

Submerged rooted macrophytes (Fig. 1C) are angiosperms and pteridophytes that can complete their life cycle fully submerged, with some species displaying amphibian plasticity. A modal depth limit is 10 m. Root uptake is the primary pathway for nitrogen, phosphorus and micronutrients of these species.

Floating-leaved macrophytes are angiosperms, rooted in submerged sediments from about 0.5 to 3 m water depth with both submerged and floating leaves. The most familiar floating-leaved plants are the water-lilies (Nymphaeaceae; Fig. 1D).

Free-floating macrophytes are aquatic plants that are found suspended on the water surface or in the water. If present, their roots are not attached to the sediment. Abundant representatives are floating species like water hyacinth (*Eichhornia crassipes*) and duckweed (*Lemna* spp., Fig. 1E). There also submerged free floating species like bladderwort (*Utricularia* spp.) and hornwort (*Ceratophyllum* spp.).

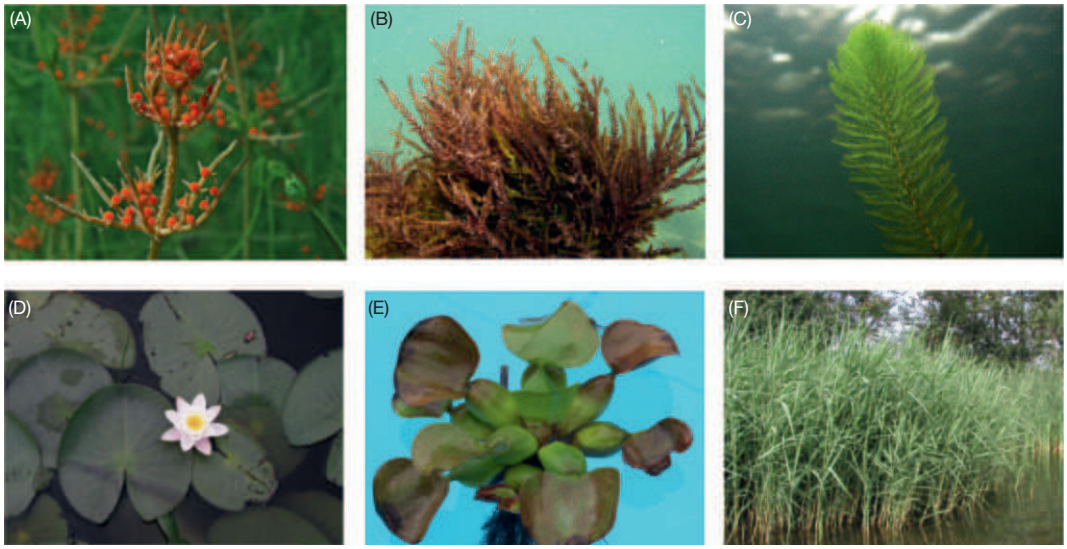

Fig. 1 Typical aquatic macrophyte species representing the different groups of growth forms in lakes (A: *Chara tomentosa*, B: *Fontinalis antipyretica*, C: *Myriophyllum heterophyllum*, D: *Nymphaea alba*, E: *Eichhornia crassipes*, F: *Phragmites australis*). Fotos: Klaus van de Weyer.

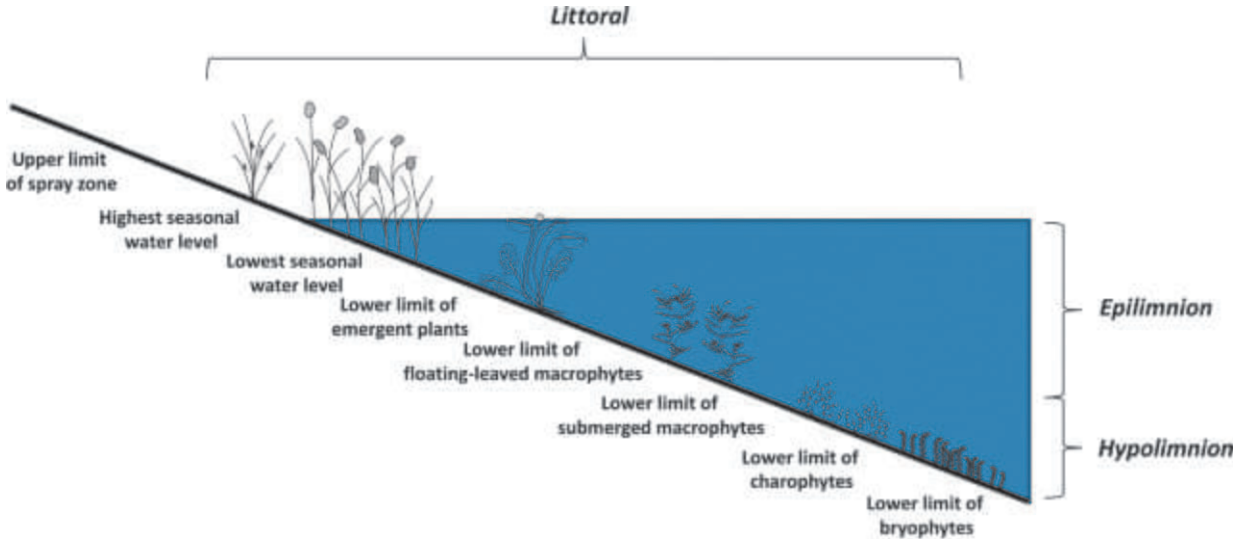

Fig. 2 Macrophyte zonation along depth gradients in the lake littoral.

Emergent macrophyte species (Fig. 1F) grow in waterlogged soils of the land-water interface, which is generally defined to be 0.5 m above the water table to about 2 m water depth. Their shoots are above the water surface and they often have rhizomes or corms. Many have developed an extensive root aeration system to cope with low oxygen levels in the sediment.

Amphiphytes can grow submerged in the water up to completely above the water, typically under fluctuating water level conditions.

Macrophytes tend to form recognizable assemblages composed of several species belonging to different growth forms. These assemblages are commonly organized along depth gradients and often form easily-distinguishable zones in relation to water depth. In general, emergent species dominate in shallow areas while the submerged ones colonize deeper sites and floating-leaved species are intermediate (Fig. 2).

A variety of macrophyte sampling and survey methodologies has been developed to measure the composition and abundance of macrophytes in lakes for specific applications including conservation, drainage impact, management, or habitat. Lake macrophyte surveys can be undertaken at different levels of intensity, but the most widely used method is based on belt transects surveyed by diving (most accurate and reproducible) or by boat. This relatively cost-effective approach allows mapping of the distribution of individual species and their abundance and provides robust data sets that can be used to generate indices and metrics (CEN, 2007). Hydroacoustics and remote sensing techniques are also increasingly used to monitor macrophyte distribution and abundance (Stocks et al., 2019).

Composition and abundance of macrophyte communities in lakes are regulated by a complex array of chemical, physical and biological factors exerting bottom-up and top-down control. In turn, macrophytes affect physical, chemical and biological conditions and processes in lakes therewith determining their state, ecosystem functions and services (Fig. 3).

Here, we review how lakes are a habitat for aquatic plants, but also how the plants affect their habitat and are habitat for other organisms. Whilst we try to cover macrophytes in lakes worldwide, we recognize that there is a bias. Only 6% of the world macrophytes species have by now been investigated in dedicated single species studies (Dalla Vecchia et al., 2020).

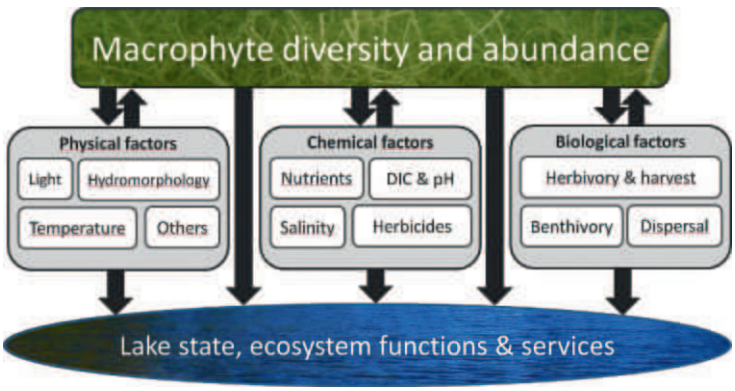

Fig. 3 Interactions between macrophyte diversity and abundance in lakes and important physical, chemical (DIC: dissolved inorganic carbon) and biological factors together affecting lake state, ecosystem functions and services.

Factors affecting macrophyte diversity and abundance in lakes

Physical factors

Light availability

Usually, light availability is the most important factor for the development of submerged macrophytes, and it determines the maximum colonization depth. Light for submerged macrophytes is attenuated by shoreline or floating vegetation, particulate suspended matter, colored dissolved organic matter, phytoplankton and periphyton, and also by self-shading in dense stands. Maximum colonization depth of charophytes is higher than that of angiosperms in clear lakes (Fig. 2). In turbid lakes, however, angiosperms can have a higher maximum colonization depth due to adaptations to poor light availability such as shoot elongation, canopy formation and rapid growth during spring. The colonization depth of macrophytes was found to decrease at latitudes above approximately N 60 degrees (Duarte and Kalff, 1987) and Middelboe and Markager (1997) estimated an average decrease in maximum depth for charophytes of 0.12 m per degree increase in latitude (ranging from N 37 degrees to 74 degrees).

Different percentages of surface light at maximum colonization depth have been reported ranging from 2% to 4% for characeans (Schwarz et al., 2000), 8–10% for *Isoëtes lacustris* (Rørslett and Johansen, 1995), 10–21% for vascular plants (Sheldon and Boylen, 1977; Chambers and Kalff, 1985). Søndergaard et al. (2013) analyzed about 750 European lakes and found maximum colonization depths relatively closely related to Secchi depths.

Light attenuation by phytoplankton and periphyton plays a key role for macrophyte abundance and species composition during changing nutrient loading to lakes (Phillips et al., 2016; Hilt et al., 2018). The dynamics of periphyton cover are only partly linked to that of phytoplankton, but a similar seasonality with spring and autumn blooms is reported (Van Dijk, 1993). Accumulation of periphyton to a densely shading cover takes time (in the order of a few weeks), and rapid expansion to the water surface is a macrophyte strategy to overcome this.

Temperature

Temperature is of high importance in determining the distribution, growth rates, timing of life history events and metabolism of macrophytes in lakes at larger spatial scales, such as latitudinal or altitudinal gradients. Macrophyte growth is affected by temperature because all enzymatic-catalyzed reactions and membrane processes in plant metabolism are temperature dependent (Brown et al., 2004). Most aquatic vascular plant species exhibit optimal rates of photosynthesis at relatively high temperatures (between 20 °C and 35 °C, Santamaría and Van Vierssen, 1997, Fig. 4). Some cold-water adapted charophytes (e.g., *Nitella hookeri*) reportedly have lower temperature ranges (Starling et al., 1974). For macrophyte species growing in both temperate and low arctic regions, the optimum temperature for growth is therefore often well above the ambient water temperature, although acclimation capacity in macrophytes is likely substantial (Pilon and Santamaría, 2002, Fig. 4) and shallow waters may warm up more rapidly than limnological data would suggest. In principle, global warming is expected to stimulate macrophyte growth in temperate (Zhang et al., 2019) and arctic lakes (Lauridsen et al., 2020). Species-specific responses to climate change among submerged macrophytes can significantly influence their species composition (Li et al., 2017). Macrophyte cover is expected to decrease under the current nutrient levels in regions where climate warming would lead to fewer frost days (Kosten et al., 2009).

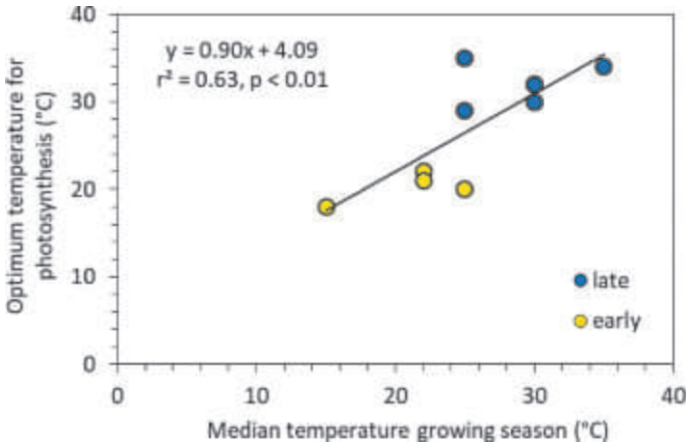

Fig. 4 Temperature effects on macrophyte growth: the optimum temperature for photosynthesis appeared correlated with the median temperature in the growing season, across a range of species, some having their growth optimum early in the season, others late, suggesting both variation among species as well as acclimation potential. Data extracted from Santamaría L and Van Vierssen W (1997) Photosynthetic temperature responses of fresh- and brackish-water macrophytes: A review. *Aquatic Botany* **58**: 135–150.

Hydromorphology

Several lake morphological characteristics interact to set the potential maximum spatial extent and depth distribution of macrophyte in lakes. First and foremost, littoral slope is critical (Duarte and Kalff, 1990). A steep slope usually only allows for narrow bands of macrophytes, whereas shallow, gradual banks can be inhabited by wide stretches of aquatic vegetation. In addition, the response strategies of macrophytes to low light conditions affect their distribution: canopy-forming species were found to prevail at sites with lower slopes because they responded to low light conditions by stem elongation and were more susceptible to drag forces. In contrast, rosette-type species tolerated shading by increased shoot chlorophyll content and thus could survive at sites with steeper slopes (He et al., 2019).

A second prime factor is wave exposure driven by fetch. A highly wave-exposed littoral will have coarse grained sediments with little fine particles and organic matter deposition—this turbulent environment sets limits to growth forms that successfully colonize it and nutrient availability is often low. Larger lakes have longer fetches and greater wave energy than smaller ones. Variation in wave action also directly influences macrophyte distribution within lakes. In wave-exposed sites rooted species with fine or dissected leaves are at an advantage over those with larger and floating leaves (Gasith and Hoyer, 1998). Wave-exposed sites generally have a lower macrophyte biomass (Madsen et al., 2001). Sediment grain size distribution covaries with sediment quality, such as organic matter and nutrient content (Chambers and Kalff, 1985). The strong variation in nutrient availability and sediment particle size also leads to variation in selection for different growth forms (Duarte and Kalff, 1990).

Shoreline development and the shading cover of trees on the banks may have a strong impact on the littoral as habitat for macrophytes. Increased shore harnessing with riffraff, boulders and concrete embankments reduces the availability of suitable habitat along relatively sheltered shorelines for littoral reed stands reaching from land into the water, and hence for a gradual transition into deeper water with changing predominance of growth forms (Radomski and Goeman, 2001). Large seasonal fluctuations in water level would compress the habitat available for submerged macrophytes (e.g., Rørslett, 1984, 1990) and, depending on the coarseness of the substrata, create a littoral zone mainly colonized by short-lived annuals or specialized emergent species that can cope with both submergence and drought. Annual winter drawdowns can decrease taxonomic richness of macrophytes (Carmignani and Roy, 2017). Amphiphytic, annual macrophyte species and helophytes reportedly can benefit from drawdown (Bornette and Puijalon, 2011). In tropical regions with strong seasonality of rainfall, submerged plant communities can be greatly reduced during periods of increasing water level and/or turbidity. Induced bank filtration can contribute to water level fluctuations and additionally negatively affect submerged macrophyte growth by interrupting seepage of CO_2 rich groundwater (Gillefalk et al., 2019).

Ice cover, also in combination with snow influences the survival of macrophytes. Some submerged macrophytes can maintain high population densities and productivity throughout the winter. For example, Boylen and Sheldon (1976) reported maximum winter photosynthetic activity to be 10–20% of summer rates. Ice scouring during spring-melt can remove large quantities of aquatic vegetation in the upper littoral (Rørslett, 1990).

Chemical factors

Nutrient availability and uptake

Nutrient availability is a key factor determining macrophyte diversity and abundance in lakes. Nutrient limitation is of particular importance for restricting biomass production in high-latitude lakes (Lauridsen et al., 2020), although accumulated biomass can still be high (Moe et al., 2013). Rule-of-thumb critical nutrient levels for maximum growth of freshwater angiosperms are suggested to be 0.13% and 1.3% dry weight for phosphorus (P) and nitrogen (N), respectively (Gerloff and Krombholz, 1966). Strong linear relationships between concentrations of N and P reflect a common biochemical basis among different aquatic plant groups (Duarte, 1992).

For most submerged macrophytes, root (or rhizoid-node complexes in charophytes) uptake is the primary pathway for the major nutrients N and P as well as micronutrients, whereas foliage uptake is the primary pathway for calcium, magnesium, sodium, potassium and sulfate (Barko and Smart, 1981). In nutrient-rich water, some species satisfy their demand for mineral nutrients by leaf nutrient uptake alone (Madsen and Cedergreen, 2002). In nutrient-poor environments, a symbiosis with arbuscular mycorrhizal fungi facilitates uptake of P and N from sediments (Søndergaard and Laegaard, 1977). This mechanism has been shown to be important for nutrient uptake by isoetids in oligotrophic lakes (Smolders et al., 2002).

Nutrient enrichment was found to increase macrophyte nutrient content and decrease the C:nutrient ratios (Velthuis et al., 2017). Up to certain thresholds (see below), nutrient enrichment to lakes may thus result in an increased macrophyte biomass with a potential for mass developments (Moe et al., 2019). Species richness of macrophytes in lakes, however, decreases with increasing nutrient loading (Jeppesen et al., 2000) or shows unimodal relationships (Vestergaard and Sand-Jensen, 2000) and eutrophication homogenized shallow lake macrophyte assemblages over space and time (Salgado et al., 2018), because isoetids are replaced by elodeids, and among elodeids small slow-growing species are replaced by large fast-growing species (Vestergaard and Sand-Jensen, 2000). Macrophyte cover also decreased above certain thresholds due to shading by periphyton and phytoplankton (see Section "Light availability"). In Danish lakes, macrophyte cover decreased at increasing total N concentrations when total P concentrations were between 0.1 and 0.4 mg P L^{-1} (Søndergaard et al., 2017). Based on an analysis of data from about 800 lake years in different climate zones in North America, South America, and Europe, Kosten et al. (2009) reported that the proportion of lakes with substantial submerged macrophyte coverage (>30% of the lake area) decreased in a sigmoidal way with increasing total P concentration, falling most steeply between 0.05 and 0.2 mg P L^{-1}.

Many temperate shallow lakes are found to show typical patterns of macrophyte loss with nutrient enrichment, developing from diverse communities via intermediate states characterized by the occurrence of only a few macrophyte species to a turbid state lacking macrophytes (Hilt et al., 2018). Paleolimnological studies of lake sediment cores and long-term data-sets revealed that lake eutrophication over the past 100–200 years has dramatically reduced macrophyte diversity and left a large proportion of species as regionally extinct and nationally red-listed (Sand-Jensen et al., 2000). Recent reductions of external nutrient input have led to macrophyte re-establishment in some lakes, but often not with the same areal cover and species richness as before eutrophication commenced (Hilt et al., 2018).

Carbon availability and uptake

CO_2 availability is a factor that can control the abundance and species composition of submerged macrophytes in lakes. All aquatic plants can use CO_2 as a carbon source, and the CO_2 concentration needed to half-saturate the photosynthesis of aquatic plants is approximately 6–13 times atmospheric levels (Demars and Tremolieres, 2009). The 10^4-fold lower diffusion coefficient of gases in water compared to air presents a major challenge to submerged macrophytes and inorganic carbon limitation of photosynthesis is a common feature (Pedersen et al., 2013). To maintain net photosynthesis, macrophytes have evolved different strategies. Some submerged species develop aerial leaves that can take up atmospheric CO_2, while others can take up CO_2 from the sediments. About 50% of the submerged macrophyte species (but not aquatic bryophytes and pteridophytes) can use HCO_3^- as a carbon source in addition to free CO_2 (Sand-Jensen and Gordon, 1986). The ratio of obligate CO_2 users to HCO_3^- users is significantly related to the HCO_3^- concentration which is generally determined by catchment properties. Increased HCO_3^- concentrations as a consequence of deforestation, cultivation of land, application of nitrate fertilizers, and reduced atmospheric acid deposition were proposed as drivers of changes in species composition in originally HCO_3^--poor lakes by allowing tall, fast growing HCO_3^- users to suppress smaller species adapted to the use of CO_2 alone (Iversen et al., 2019).

Some specialist macrophyte species display C_4 or CAM (Crassulacean Acid Metabolism) metabolism which can occur simultaneously with HCO_3^- use (Pedersen et al., 2013). Productive lakes are often depleted of free CO_2 in summer and macrophytes depending on free CO_2 availability may be restricted to areas with high organic carbon content in the sediment such as shallow protected bays or upwelling groundwater. In contrast, aquatic vegetation of lakes with low pH, low alkalinity, and thus low HCO_3^- availability, is often dominated by isoetids and bryophytes rather than HCO_3^--using elodeids (Vestergaard and Sand-Jensen, 2000). The global increase in atmospheric CO_2 may induce changes in plant productivity and species dominance. Indeed, macrophytes using CO_2 and HCO_3^- were projected to double their growth rate due to atmospheric CO_2 elevation, while the growth of macrophytes restricted to CO_2 assimilation may increase with a factor three (Schippers et al., 2004). However, because CO_2 supersaturation is widespread in lakes, increasing atmospheric CO_2 may not necessarily lead to corresponding increases in lake water free CO_2.

Salinity

Most macrophyte species are intolerant of high salinity concentrations and therefore are largely confined to freshwater lakes. Consequently, macrophyte species richness decreases with increasing salinity. Few species of submerged macrophytes (*Chara canescens*, *Lamprothamnium* spp., *Lepilaena* spp., *Ruppia* spp., *Tolypella* spp.) are restricted to brackish water and are found even in polyhaline waters (according to the Venice system, >18 psu, James et al., 2003, Schubert and Blindow, 2003). Usually, species tolerant of moderate to medium salinities (*Lemna* spp., *Myriophyllum spicatum*, *Najas* spp., *Stuckenia pectinata*, *Zannichellia* spp.), are found over the entire salinity spectrum into mesohaline waters (<10 psu) and thrive there (Hammer and Heseltine, 1988).

Herbicides

Native macrophyte communities can also be affected by herbicides that enter lakes unintentionally from e.g., agricultural run-off or antifouling paints, or intentionally as a management tool against invasions of alien macrophytes. Herbicides can be persistent in aquatic environments, with low abiotic and biotic degradation and high phytotoxicity. The effect of herbicide treatment on native macrophytes is variable and can be significant. Mikulyuk et al. (2020) reported that lake-wide herbicide treatments aimed at controlling invasive *Myriophyllum spicatum* had larger effects on native macrophytes than on the target species. A review by Vonk and Kraak (2021) concluded that an extensive catch-up must be made for macrophytes to achieve a reliable herbicide hazard and risk assessment.

Biological factors

Herbivory and harvest

In contrast to earlier views prevailing until the 1990s, top-down control by herbivores significantly affects macrophyte abundance and species composition by grazing and bioturbation (Bakker et al., 2016). Macrophyte herbivory can alter the functioning of lakes, including biogeochemical cycling, carbon stocks and primary production, transport of nutrients and propagules across ecosystem boundaries, habitat for other organisms and the level of shoreline protection by macrophyte beds (Bakker et al., 2016). Herbivores were estimated to remove a 5–10 times greater macrophyte biomass from aquatic than from terrestrial ecosystems. This may be explained by the lower C:N stoichiometry found in submerged macrophytes. Global environmental change is projected to increase herbivore impacts (Bakker et al., 2016 and references therein). The outcomes of macrophyte-herbivore interactions appear to be highly variable across aquatic ecosystems. Herbivorous taxa differ in their impact, with insects associated with smaller effects than

all other taxa (birds, mammals, crustaceans, molluscs, fish, echinoderms; Wood et al., 2017). Herbivory alone may often not be sufficient to cause macrophyte collapse, but other stressors such as shading from periphyton were found to enhance the effect of herbivores. Significant herbivore impact may thus indicate a reduced resilience of vegetation to eutrophication, making it an early warning signal for an imminent macrophyte collapse (Hidding et al., 2016).

The presence of extensive macrophyte stands can have negative effects on some forms of human use (see below) and harvesting is a common management measure applied. However, shallow lakes can have alternative stable states (see below). When a critical, in practice unknown, proportion of submerged vegetation is removed, the system can be propelled to the turbid state with a much lower macrophyte diversity and abundance due to the stabilizing effect of macrophyte cover on the clear water state (Kuiper et al., 2017).

Benthivory

The effect of benthivorous fish such as common carp (*Cyprinus carpio*) or bream (*A. brama*) on macrophytes has been documented since the 1920's Cahn (1929). Benthivorous fish can reduce the biomass and diversity of macrophytes by direct destruction. They disturb sediments while searching for food and pull rooted macrophytes out of the sediment. Breukelaar et al. (1994) showed in experimental studies, that the effects of benthivorous fish on macrophytes are related to fish biomass. Benthivory can also increase the amount of suspended sediment, enhance remobilization of nutrients from the sediment and thus contribute to reduced water transparency (Miller and Crowl, 2006; Zambrano et al., 2001). Also Vilizzi et al. (2015) found a very high impact of common carp on aquatic macrophytes.

Dispersal

Aquatic plants can be dispersed by seeds and spores as well as by vegetative fragments. The latter can be simply broken off pieces as well as specialized forms such as turions (winter buds). Dispersal takes place by water flow (hydrochory), by animals (zoochory), by wind (anemochory), or by human-mediated dispersal (hemerochory or anthropochory) (Fig. 5). Hydrochory is limited by the extent of the hydrological network that forms the habitat (Sun et al., 2019). Successful dispersal events among river networks and lake districts thus have a low probability, although the life span of clonal macrophytes may be long enough for such rare events to occur. Water birds however have the potential to transport a wide variety of aquatic plants over several hundreds of kilometers, and this is likely a common process. Both endozoochory (internal transport) and ectozoochory (external transport) are important (Figuerola and Green, 2002; Van Leeuwen et al., 2012). Water bird migratory flyway patterns are reflected in the genetic similarity among macrophyte subpopulations in the lakes that are functioning as bird stepping stones (Hidding et al., 2014). On the other hand, when new habitat becomes available, for example after lake restoration, the time window open for successful colonization may be limited (Beltman et al., 2011). Recreational boat traffic can also contribute to macrophyte dispersal, which is of particular relevance for invasive species (Johnstone et al., 1985). Alahuhta et al. (2018) investigated global patterns and found that macrophyte communities in lakes were typically not dispersal-limited within metacommunities, but spatial barriers may have hindered movements of macrophytes in some regions.

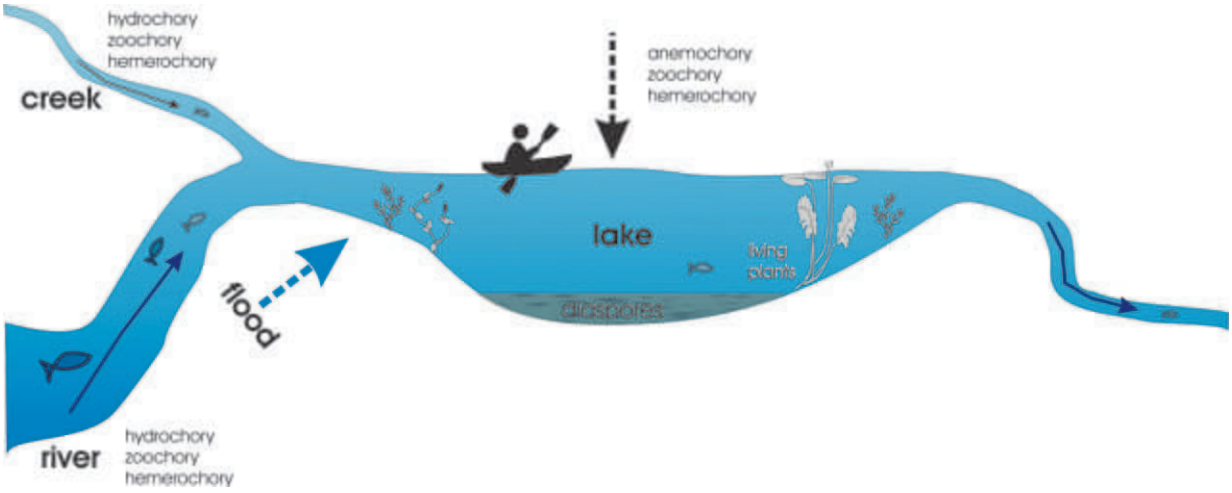

Fig. 5 Pathways of macrophyte dispersal in lakes.

Macrophyte effects on lakes

Effects on biotic components in lakes

Macrophytes in lakes can be a major food resource for invertebrates, fish, waterfowl and mammals (see above, Bakker et al., 2016). Usually, a positive relationship can be found between submerged macrophyte presence and the diversity of waterfowl, fish, benthic invertebrates, and zooplankton, while the situation was less clear for the diversity of phytoplankton, bacteria, parasites, viruses, and pathogens (Hilt et al., 2017). Enhanced recycling of P from the sediments and a positive effect of macrophytes on fish abundance, resulting in increased predation on both littoral grazers and zooplankton, are supposed to result in a high secondary productivity of lakes with abundant submerged macrophytes. However, yearly primary productivity of submerged macrophytes compared to that of phytoplankton in a lake can be minor, because macrophyte primary production depends on lake size and morphology, as well as littoral slope of the lake (Hilt et al., 2017). Submerged and emergent macrophytes also provide surface for periphyton, which plays a particularly important role in supporting fish production and in linking aquatic and terrestrial habitats through phenomena such as aquatic insect emergences, with implications for terrestrial plants, consumers, and ecosystems (Vander Zanden and Vadeboncoeur, 2020).

Macrophytes also provide refuge against planktivorous fish for zooplankton and suppress phytoplankton growth by competition for nutrients and excretion of allelochemicals that inhibit phytoplankton (Scheffer et al., 1993). Along with the effects of macrophyte on sediment resuspension, and particle sedimentation, these biotic interactions can stabilize clear-water conditions in lakes (see below). A global meta-analysis by Song et al. (2019) using 47 studies suggested that the positive effects of macrophytes on water quality were similar to or greater at lower than at higher latitudes. These findings challenged the prevailing paradigm (e.g., Meerhoff et al., 2007) of macrophytes being less effective at enhancing lake-water quality in the (sub)tropics. Macrophyte effects varied by growth forms, and Song et al. (2019) suggested that the growth forms that positively affect water quality differ between (sub)tropical and temperate areas. Submerged macrophytes were found to be more effective in reducing phytoplankton biomass than emergent and floating leaved species, particularly in the (sub)tropical area.

While an increasing species number caused overyielding and species complementarity in terrestrial plant communities, the few existing studies for aquatic plants are inconclusive, potentially due to the low species number tested (Riis et al., 2018).

Effects on abiotic parameters in lakes

Macrophytes can significantly reduce resuspension of bottom material (James et al., 2004) and increase sedimentation (Vermaat et al., 2000) inside dense stands by physically reducing water movement. Increased sedimentation also increases the removal of particulate P from the overlying water (Kufel and Kufel, 2002). Particularly dense stands may strongly affect biogeochemical processes at the sediment-water interface: in the root environment steep redox gradients are maintained by radial root oxygen loss affecting P solubility and nitrification/denitrification. Also the annual assimilation of N and P into new plant material is a net removal of nutrients from the water (Vermaat et al., 2000). In dense macrophyte stands, also the dynamics of oxygen and dissolved inorganic carbon (DIC) are strongly affected (Caraco et al., 2006). High photosynthetic activity during the daytime may raise oxygen concentrations above saturation levels and remove CO_2 and HCO_3^- (Trolle et al., 2012). Emissions of other greenhouse gases such as methane can also be affected by macrophytes in several ways (Hilt et al., 2017).

Macrophyte state shifts, decline and recovery

Submerged macrophytes were probably widespread with high cover in lakes throughout Europe and potentially many other parts of the world until cultural eutrophication from about 1950 onwards led to their decline or local eradication (Blindow, 1992). At present, an increasing number of lakes is losing submerged vegetation worldwide and loss rates are increasing (Zhang et al., 2017). Lake restoration efforts by reducing external nutrient loading or applying internal measures (Hupfer and Hilt, 2008) show variable results. In some lakes, abundance, coverage, plant volume inhabited or depth distribution of submerged macrophytes increase during reduced nutrient loading, while others show little change despite greater water clarity (Jeppesen et al., 2005).

Analyzing the long-term dynamics of submerged macrophytes in lakes with changing nutrient loading has led to the description of several patterns. In large, deep, naturally oligotrophic lake ecosystems, changes in submerged vegetation dynamics appeared to be closely related to changes in transparency coupled to phytoplankton and TP concentrations in the water (Murphy et al., 2018). In shallow lakes, submerged macrophytes can have a clearing effect on lake water due to several negative effects on phytoplankton and particle resuspension. Different feedback mechanisms prevail depending on whether charophytes or angiosperms are the dominant macrophyte group (Blindow et al., 2014). Such feedbacks have been suggested to underly the observed alternative stable states in shallow lakes—a clear, macrophyte-dominated state and a turbid, phytoplankton-dominated state (Scheffer et al., 1993). These states may appear stable for periods extending from years to decades (Scheffer and Van Nes, 2007). The occurrence of such a bistability has important implications for the possibilities of restoring eutrophied shallow lakes. Nutrient load reduction alone may not be sufficient, but an ecosystem disturbance like food web manipulation can bring the lake back to a stable clear state (Scheffer et al., 1993, Fig. 6). In deeper lakes, macrophytes may also contribute to stabilizing clearer water, but hysteresis is less likely to occur. Collapse and recovery of macrophytes in response to gradual changes in nutrient loading should thus be more predictable in deep than in shallow lakes (Sachse et al., 2014). In many north-temperate shallow lakes nutrient enrichment was associated with a

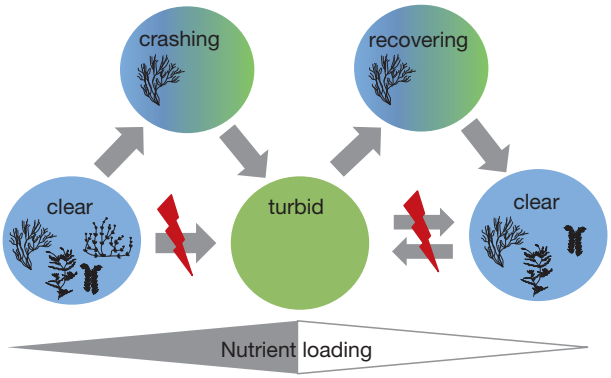

Fig. 6 Response patterns of north temperate shallow lakes to changes in external nutrient loading or strong disturbance (red flash).

reduction in the seasonal duration of macrophyte dominance and cyanobacteria blooms in summer (Hilt et al., 2018). With increased nutrient loading, lakes may thus shift from a stable clear-water state featuring a diverse plant community to a "crashing" state with fewer macrophyte species and turbid summers before the collapse to almost continuously turbid conditions lacking macrophytes (Fig. 6). Reduction of external nutrient loading can lead to an intermediate recovery state with clear-water conditions in spring and turbid water in summer and specific macrophyte communities with short growth seasons and eventually stable clear conditions with a diverse macrophyte flora if nutrient loading is reduced sufficiently or additional internal measures are applied. Lake-internal measures such as biomanipulation or sediment suction dredging can lead to unstable clear-water conditions with specific macrophyte communities that may collapse resulting in a shift back to turbid conditions unless nutrient loading is reduced. The final clear state may still differ in its macrophyte species composition from the initial state before anthropogenic nutrient loading started (Fig. 6; Hilt et al., 2018).

Macrophytes as indicators for the ecological state of lakes

Macrophyte species are long-lived compared to other aquatic organisms and likely can integrate long-term changes in environmental conditions. Their community composition can thus provide a long-term indication of overall lake condition, due to a limited response at weekly or daily time scales to changes in water clarity and chemistry. Lakes in "good ecological state" generally have a littoral zone with a high number and diversity of native aquatic macrophytes, and few or no invasive species (Poikane et al., 2018). Certain species groups are indicators for specific standing water types and are adversely affected by anthropogenic impact. Consequently, macrophytes can be used for ecological quality assessments of lakes. Mikulyuk et al. (2017) developed and tested a lake bioassessment method using aquatic macrophytes and defined an anthropogenic disturbance index for north temperate lakes. In Europe, macrophytes are one of the key metrics used to measure the ecological status of lakes under the Water Framework Directive (European Commission, 2000) and some macrophytes also serve as indicators for the European Habitats Directive (European Commission, 1992), one of the most powerful conservation policy tools in the world (Lockwood, 2006). Indeed, macrophyte communities of "good" status lakes are diverse with many charophytes and several *Potamogeton* species (Poikane et al., 2018). In New Zealand, the LakeSPI index (submerged plant indicators) was developed (Clayton and Edwards, 2006) and applied to 195 New Zealand lakes to examine how component metrics responded over gradients of anthropogenic pressures. Metrics measuring depth and diversity of native vegetation negatively correlated with independent measures of lake trophic state and were also well explained by multiple regression with lake and catchment attributes that included proxies for anthropogenic pressure (De Winton et al., 2012).

Ecosystem services of macrophyte-dominated lakes

Dense and diverse macrophyte beds can potentially contribute to several final services by their profound effects on a wide range of ecosystem functions. In their biomass, macrophytes may retain nutrients that would otherwise contribute to eutrophication reducing the lake value for the provisioning service "drinking water" and the cultural service "recreation." The same biomass may form a longer-term sink for carbon if it is sequestered in the sediment and hence contribute to greenhouse gas mitigation. Macrophyte beds form feeding and nursery grounds for fish and birds and thus contribute to the rich biodiversity that society finds sufficiently important to be legally protected, which can be considered a cultural service. Some of these fish species are important for recreational angling (a cultural service) or commercial exploitation (a provisioning service). Submerged macrophytes can be harvested as green manure, contributing to food production (a provisioning service), whilst emergent macrophytes are used for a wide variety of products (roof thatching, baskets), and are considered a potential source of biofuel (Janssen et al., 2021).

The collapse of dense macrophyte beds will have a range of cascading effects throughout the lake ecosystem and thus likely affect several final services at the same time. Due to the complexity of the functional network, changes in less apparent functions and feed-backs could lead to unexpected effects. Very dense macrophyte beds are often considered as nuisance aquatic weeds (Pieterse and Murphy, 1990) because they hamper navigation and angling, reduce the efficiency of irrigation schemes, and are considered "unaesthetic". Worldwide, mechanical, chemical and biological control programs have focused on removal of these nuisance plants without much acknowledgment of the possible benefits. It would be worth to include trade-offs between such "disbenefits" and benefits more comprehensively in the scientific and societal debate leading to informed management decisions covering all ecosystem services and all beneficiary sectors in society (Janssen et al., 2021 and references therein).

Synthesis

Lakes are an important habitat for macrophytes, particularly the littoral where sediments allow colonization and sufficient light is available. The study of the disappearance of macrophytes in many culturally eutrophicated lakes worldwide as well as their recovery has spawned an understanding of how feedbacks prevent regime shifts and maintain clear-water or turbid states. This review also shows the potential manifold of functions of macrophytes in the littoral of lakes and their great diversity. Some of these functions are of clear and direct benefit to human society whereas others are less apparent; these may include feedbacks that strengthen the macrophyte-dominated state.

See Also: Fundamental concepts and theories: Comparative Primary Production; Human pressures and management of Inland Waters: Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment; Hydromorphology—Interactions and Habitats; Structures and functions of Inland Waters - Rivers: Energetics and Food Webs in Large Rivers

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Benthic Algae in Lake Littoral Habitats[☆]

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This is an update of Y. Vadeboncoeur, Aquatic Plants and Attached Algae, in Encyclopedia of Inland Waters, edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00217-9.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Autotrophic structure The relative contribution of attached algae, phytoplankton, and macrophytes to total whole lake primary production.
Benthic Associated with the bottom of aquatic ecosystems.
Biofilm A growth form in which a mixed assemblage of microbial organisms grows on a surface. Often, bacteria and algae exude extracellular polymers that form an extracellular matrix (ECM) that holds the biofilm together.
Eutrophic A lake with high concentrations of inorganic nutrients (N, P) in the water column and high phytoplankton biomass, which often reduces light availability for benthic algae.
Fatty acids Macromolecules used in the synthesis of fat and lipids consisting of hydrocarbon chains with a terminal carboxyl group. Algae (especially diatoms) produce essential fatty acids (EFAs) that are required in the diet by metazoans for growth and development.
Filamentous algal blooms (FABs) Refers to an atypical macroscopic proliferation of filamentous benthic algae, especially green algae or cyanobacteria. FABs have been increasingly reported in lakes with high water quality and high light penetration.
Food web A group of organisms relying upon the same basal resources and linked by feeding relationships.
Grazer An animal that consumes primary producers such as algae or macrophytes.
Lake metabolism The sum of all photosynthetic and respiratory processes within the lake.
Macrophyte Literally "large plant". An aquatic vascular plant. Also, macroscopic green algae that have a growth form that resembles a vascular plant (Characeae).
Oligotrophic A lake with low concentration of water column nutrients (N, P) and consequently low phytoplankton biomass. These lakes often have very clear water which facilitates the growth of benthic algae.
Periphyton The consortium of benthic algae, bacteria, archaea, fungi, and animals that form biofilms and structured turfs on and around submerged surfaces in lakes, rivers, and wetlands.
Photic zone The part of the lake bottom or water column where there is sufficient light for photosynthetic organisms to grow. Typically, this is thought to extend to a depth of 1% light penetration. However, living benthic photosynthetic organisms have been observed at depths where $<0.1\%$ surface light is available.
Top-down control The influence of consumption on the biomass of the trophic level immediately below the consumer.

Overview

Photosynthetic organisms, including cyanobacteria, eukaryotic algae and vascular plants (macrophytes) flourish in the well-lit surface waters of lakes. Benthic, or bottom-dwelling, algae and cyanobacteria are not simply settled phytoplankton, but grow in

[☆]*Change History*: October 2021. Y Vadeboncoeur and L Katona updated the chapter.

structured biofilms and complex turfs made up of photosynthetic (autotrophic, or "self-feeding") and heterotrophic organisms. The stratified growth form of biofilms creates complex resource gradients that make it inappropriate to apply paradigms developed for phytoplankton to benthic algae. In this chapter, we describe the taxonomic diversity of benthic algae in lakes and review the abiotic and biotic factors that affect their growth and abundance. We briefly summarize monitoring techniques and speculate on the effects of climate change (temperature, lake level, and circulation patterns) on littoral algal assemblages.

Taxonomic composition of benthic algae

Illuminated lake bottoms are coated with a dynamic living slime composed of cyanobacteria, algae, heterotrophic bacteria, fungi, and small animals. This complex association of living, largely microscopic, organisms is called periphyton. This chapter focuses on the autotrophic components of periphyton, and we use the inclusive term "algae" to refer to non-vascular photosynthetic organisms, including cyanobacteria. Benthic algal assemblages are overwhelmingly dominated by three groups of algae: prokaryotic cyanobacteria, diatoms (Bacillariophyceae) and green algae (Chlorophyta) (Fig. 1).

Cyanobacteria occur on surfaces throughout the littoral zone. Many coccoid cyanobacterial taxa (e.g. *Aphanocapsa*, *Chroococcus*) commonly occur in benthic habitats, but filamentous cyanobacteria often dominate biomass. Motile filamentous cyanobacteria in the Oscillatoriales, including *Oscillatoria* and *Phormidium*, form tissue-like mats over soft (unconsolidated sediments) and hard (rock) substrate (Fig. 1A). These motile taxa readily move in response to changing light conditions, and many are adapted to low light conditions in the deep transitional habitats between the photic and aphotic zones. Some (e.g., *Leptolyngbya* sp., *Microcoleus paludosus*, *Phormidium murrayi*) form toxins that can poison or kill birds and mammals (Wood et al., 2020). Nitrogen-fixing (N-fixing) filamentous cyanobacteria with basal heterocysts (e.g., *Calothrix*, *Tolypothrix*, and *Rivularia*) are commonly attached to rocks in high light littoral habitats of oligotrophic lakes (Fig. 1B).

Diatoms are a ubiquitous component of periphyton (Fig. 1C and D), and have a characteristic silica cell wall. Unicellular taxa include motile, non-motile, and stalked single-celled forms, and some taxa are filamentous. Adnate taxa that grow closely appressed to the substrate are among the first photosynthetic taxa to establish a biofilm on clean rocks. In waved-washed rocky shores, these low-profile taxa may be the only algae that persist. In quiescent habitats, adnate species will be overgrown by taxa that produce a mucilaginous stalk (e.g., *Gomphonema*) that allows them to protrude above the understory taxa and take advantage of higher light conditions at the mat surface (Fig. 1D). Highly mobile, raphid taxa (e.g., *Navicula*) thrive at low light intensities and in sediments because they can glide up and down in pursuit of optimum light conditions (Lowe, 1996). Some taxa in the Rhopalodiacaeae have symbiotic N-fixing cyanobacteria (Lowe, 2003) and are prevalent in the well-lit upper littoral habitats of very nutrient poor lakes. Unlike in the phytoplankton, diatoms are abundant throughout the year in benthic habitats, presumably because silica is readily available at the sediment water interface.

Filamentous and single-cell green algae (Fig. 1E and F) are common in lake littoral zones, but their presence is strongly affected by grazing and disturbance. Unicellular species in the order Desmidiales (Fig. 1F) are common in undisturbed shallow sediment habitats and macrophyte beds. Unattached filamentous taxa in the order Zygnematales, including *Zygnema*, *Spirogyra* and *Mougeotia*, can form dense clouds growing up from the lake bottom in protected bays, wetlands, and other low energy habitats. In high energy wave zones, green algae that can attach firmly to rocky substrates such as *Ulothrix zonata*, *Cladophora glomerata*, and *Stigeoclonium* can form dense turfs many centimeters thick with fronds elongating into the water column. These filamentous green algae require high light and the densest growths sometimes occur at the very upper limit of wave action forming a green "bathtub ring" of algae in large lakes (Fig. 1E).

Most algae have unique morphologies and are large enough to be seen using light microscopy. However, identification of algae is time-consuming and requires expertise. DNA metabarcoding using next-generation sequencing techniques enables the rapid identification of microbes from environmental samples with unprecedented resolution. Metabarcoding uses short sequences of extracted DNA to identify taxa, making it more sensitive than microscopy at detecting rare species and distinguishing species that have similar morphologies. In general, there is good agreement between metabarcoding and morphological identification for eukaryotic algae and cyanobacteria (Groendahl et al., 2017). Using primers that target prokaryotic (16S rRNA gene) and eukaryotic (18S rRNA gene) organisms allows for the exploration of algal-bacterial interactions within periphyton.

Littoral habitats

Benthic algae form biofilms on submerged unconsolidated organic sediments (epipelon) (Fig. 1A), sand (epipsammon) (Fig. 1C), rocks (epilithon) (Fig. 1E), wood (epixylon), animals (epizoon) and plants and macroalgae (epiphyton) (Fig. 1D). The distribution of these substrata within littoral zones is non-random. Portions of lakeshores can either be exposed to wave action (high energy, erosional habitats) or protected from waves by land masses that intercept wind (depositional habitats). Organic sediments, downed trees, and macrophyte beds are more common in depositional habitats along shorelines, while erosional shorelines are dominated by boulders, cobbles, and sand. With distance from shore, the lake bottom becomes increasingly dominated by soft sediments. Whether sediments are composed of inorganic sand or organic muds depends upon the lake's landscape position (high or low in the watershed), the geologic parent material, and the topography of the landscape. High slope areas of the lake bottom may have areas of exposed rock, whereas flat areas will be dominated by organic sediments accumulated from the lake and the surrounding landscape. The structural heterogeneity of the littoral zone and the distribution of substrates relative to light are strong determinants of the structure and function of benthic algal assemblages (Lowe, 1996; Cantonati and Lowe, 2014).

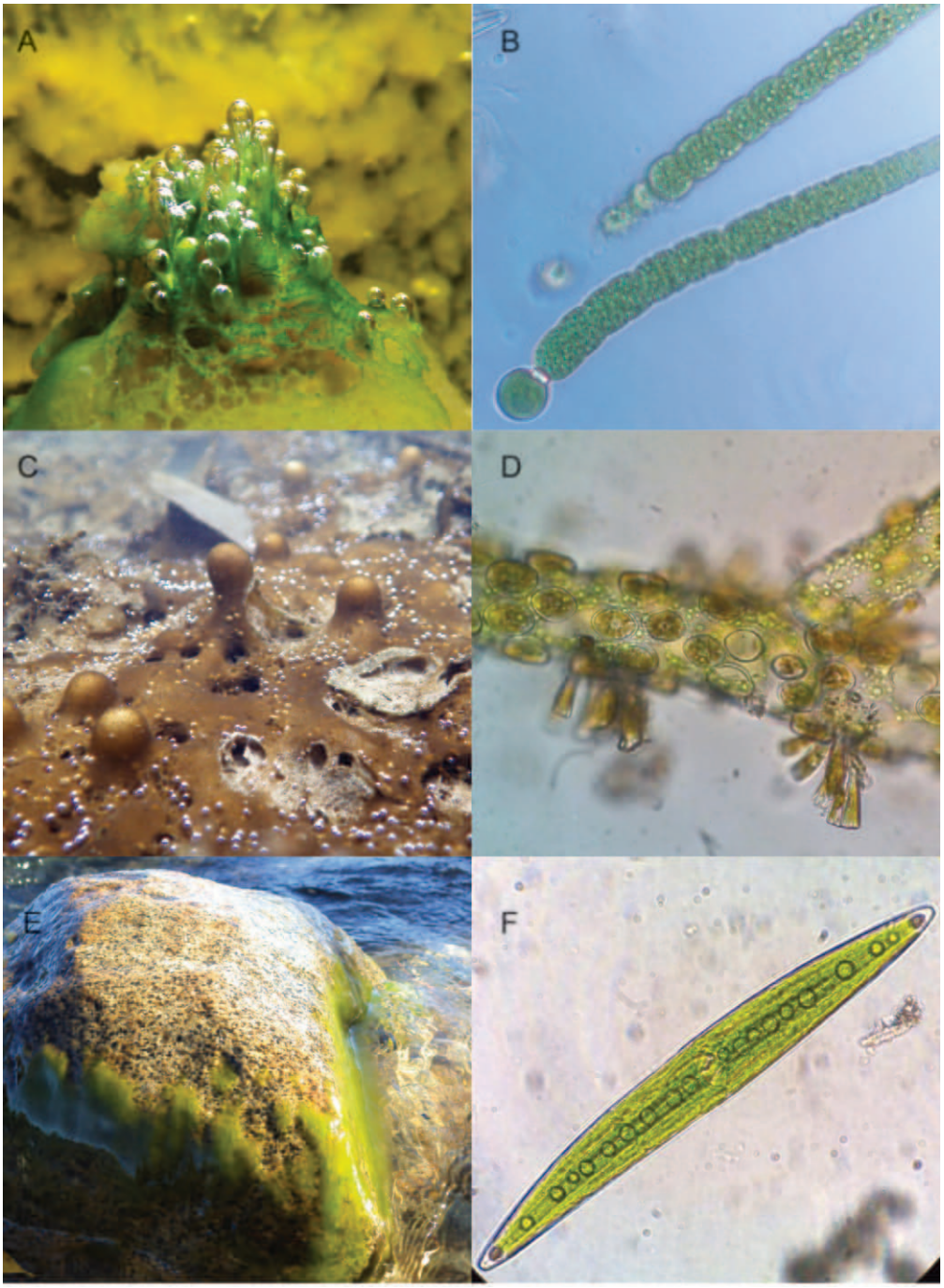

Fig. 1 Cyanobacteria (A, B), diatoms (C, D) and green algae (E, F) dominate benthic algal assemblages in lakes. High photosynthesis rates trap oxygen bubbles in the biofilms of A and C. (A) A biofilm dominated by the cyanobacterium *Oscillatoria* in an experimental aquarium. (B) The cyanobacterium *Calothrix* (Rivulareaceae) has a basal heterocyst where N-fixation occurs. (C) A biofilm dominated by diatoms gives sandy sediments a golden hue. (D) A filamentous green alga (*Cladophora*) is overgrown with epiphytic diatoms including closely appressed ovoid *Cocconeis* and stalked *Rhoicosphenia*. (E) A rock along the shoreline of Lake Tahoe (USA) is coated with a thick turf of *Spirogyra*. (F) The desmid green alga *Closterium* can be found in shallow benthic habitats in lakes, and epiphytically on submerged vegetation. Photos credits: A, C–F by Leon Katona; B by Rex Lowe.

Growth-regulating resources: Light, nutrients, and temperature

Light is necessary to fuel photosynthesis and attached algae only grow in the photic zone where the substrate intercepts enough light for photosynthetic rates to exceed basic metabolic requirements. Benthic algal composition changes markedly with depth in response to changes in light because taxa are adapted to different wavelengths and light intensities (Lowe, 1996). Filamentous

green algae require high light, and are abundant in shallow, rocky habitats of clear lakes. Attached cyanobacteria in the Rivulariaceae and diatoms in the Rhopalodiales are common in high light rocky habitats because high photosynthesis rates are necessary to support energy demanding N-fixation (Higgins et al., 2003). Many raphid diatoms efficiently use light energy and photosynthesize at very low irradiances. Cyanobacteria in the Oscillatoriales form thin mats in deep, low light environments and can use long-wavelength energy because they have auxiliary pigments. We know that the lower depth limit for benthic algae is well below the photic zone (defined by 1% surface light). Viable, healthy benthic algal assemblages have been retrieved or observed from habitats that receive less than 0.1% surface light, but comprehensive sampling of deep habitats is still necessary to determine the extent of benthic algal distribution in lakes.

The water column is just the first matrix that controls light availability to periphytic algae. As biofilms accrue vertically, rapidly growing cells on the surface shade cells at the base of the biofilm, inducing senescence. This self-shading impairs the integrity of biofilms on hard substrates and induces sloughing. Similarly, epiphytic diatoms and cyanobacteria growing on the much larger thalli of filamentous green algae will shade and compromise the health of their host (Fig. 1D; Furey et al., 2012). Rapid light attenuation on epipelic biofilms creates vertically structured laminated communities with marked changes in pigments and photosynthesis over the scale of millimeters (Hawes et al., 2014).

Algal growth is limited by the availability of nutrients, especially nitrogen (N) and phosphorus (P) (Borchardt, 1996; Elser et al., 2007; Harpole et al., 2011). Although nutrient concentrations in the water and sediments tend to increase with depth, it is not clear that this has a strong influence on algal distribution because of the overwhelming negative effect of decreasing light availability with depth. Benthic algae living on sediments, macrophytes, or animals (such as snails or mussels) rely on nutrients leaked or excreted from the substratum for growth. Unconsolidated sediments (the most abundant surface for algal growth) accumulate N and P, and epipelic algal biomass and production are often decoupled from water column nutrients (Figs. 2–5; Vadeboncoeur et al., 2003). Furthermore, boundary layers on all types of surfaces decrease the diffusion rate of inorganic nutrients into the biofilm, and as biomass accrues, microbial nutrient recycling within the biofilm becomes increasingly important to new algal growth. High nutrient concentrations in groundwater and at the sediment water interface can cause excessive benthic algal growth (Figs. 2 and 4; Higgins

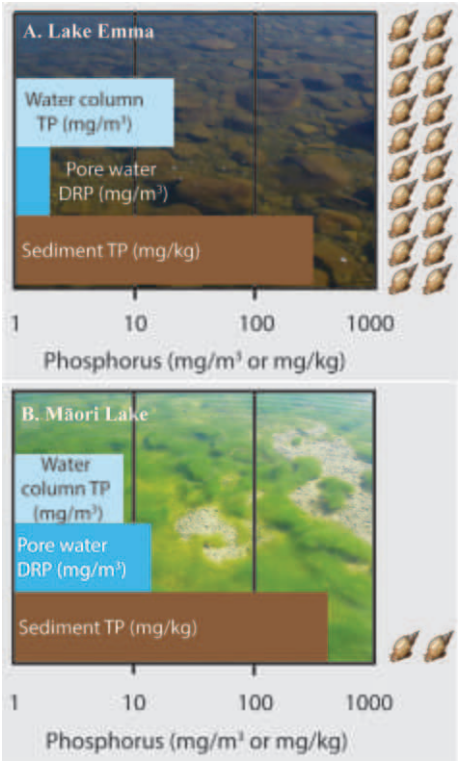

Fig. 2 The visibility of benthic algae depends upon the availability of resources that help algae grow and the abundance of animals that eat algae. In two adjacent subalpine New Zealand lakes, Lake Emma (A) has thin biofilms of diatoms and cyanobacteria, while Māori Lake (B) has dense growths of the green alga, *Spirogyra*. Water column nutrient concentrations in Lake Emma (A) are higher than in the filamentous algal bloom (FAB) afflicted Māori Lake (B). However, sediment-associated nutrients (which benthic algae can access) are higher in Maori Lake than in Lake Emma. Comparatively low densities of the New Zealand mud snail (*Potamopyrgus antipodarum*) in Māori Lake (each snail represents 1 grazer/m2) may allow *Spirogyra* to flourish. From Waters S, Verburg P, Schallenberg M, and Kelly D (2021) Sedimentary phosphorus in contrasting, shallow New Zealand lakes and its effect on water quality. *New Zealand Journal of Marine and Freshwater Research* 55: 592–611; Stewart SD, Kelly D, Laroche O, Biessy L, and Wood SA (2021) Individual diet specialization drives population trophic niche responses to environmental change in a predator fish population. *Food Webs* 27: e00193; and Vadeboncoeur Y, Moore MV, Steward SD, Chandra S. et al. (2021) Blue waters green bottoms: Benthic filamentous algal blooms (FABs) are an emerging threat to clear lakes worldwide. *BioScience* 71: 1011–1027.

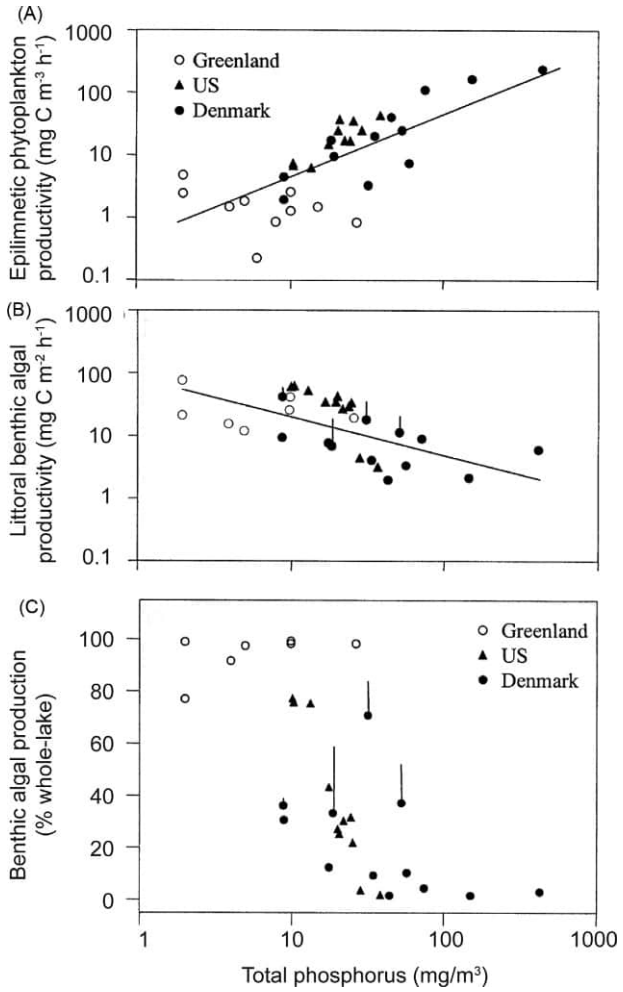

Fig. 3 Benthic and planktonic productivity in small northern lakes. Although phytoplankton productivity increases with increasing nutrient load (A), the increased phytoplankton biomass shades littoral algae, causing a decrease in benthic algal productivity (B). Therefore, as nutrient loading to surface water increases, autotrophic structure shifts from dominance by benthic algae to dominance by planktonic algae. Each point represents average productivity in a single lake. From Vadeboncoeur Y, Jeppesen E, Vander Zanden MJ, Schierup H-H, Christoffersen K, and Lodge DM (2003) From Greenland to green lakes: Cultural eutrophication and the loss of benthic energy pathways in lakes. *Limnology and Oceanography* 48:1408–1418.

et al., 2008, Timoshkin et al., 2018; Waters et al., 2021). However, high nutrient concentrations in the water column also stimulate phytoplankton that shade benthic algae, retarding their growth (Figs. 3 and 5). Thus, maximum benthic algal biomass and production usually occurs in lakes with low to moderate water column nutrient concentrations.

Algal growth rates increase with increasing temperature through much of the temperature range experienced in most lakes (0–30 °C). The temperature optima for diatom growth tend to be lower than for green algae, and cyanobacteria are the most tolerant of high temperatures (>30 °C), but there are many exceptions to these broad patterns. For example, cyanobacteria are very tolerant of temperature extremes and dominate benthic mats in both polar lakes and hot pools (Vincent and Quesada, 2012). Temperature determines maximum specific growth rates and succession in community composition throughout the year. Seasonal cycles of benthic algal biomass, with a winter minimum and spring maximum, and taxonomic turnover in oligotrophic lakes have been documented (Wetzel, 2001). However, winter sampling of littoral habitats is extremely rare, and more research is needed to ascertain how littoral algal biomass varies over time. In a turbid, eutrophic Danish lake, maximum epipelic algal production occurred in spring when light penetration to the sediments was highest (Fig. 5; Liboriussen and Jeppesen, 2003). Climate warming is likely to warm littoral zones faster than offshore waters and this may promote more profuse growth of filamentous green algae and cyanobacteria (Wood et al., 2020).

Interactions with heterotrophic microbes

Many algae and bacteria have characteristic external extracellular coatings (sheaths) that affect transport of metabolites into the cell. In aggregate, these structures produce an extensive extracellular matrix (ECM) composed of extracellular polysaccharides (EPS),

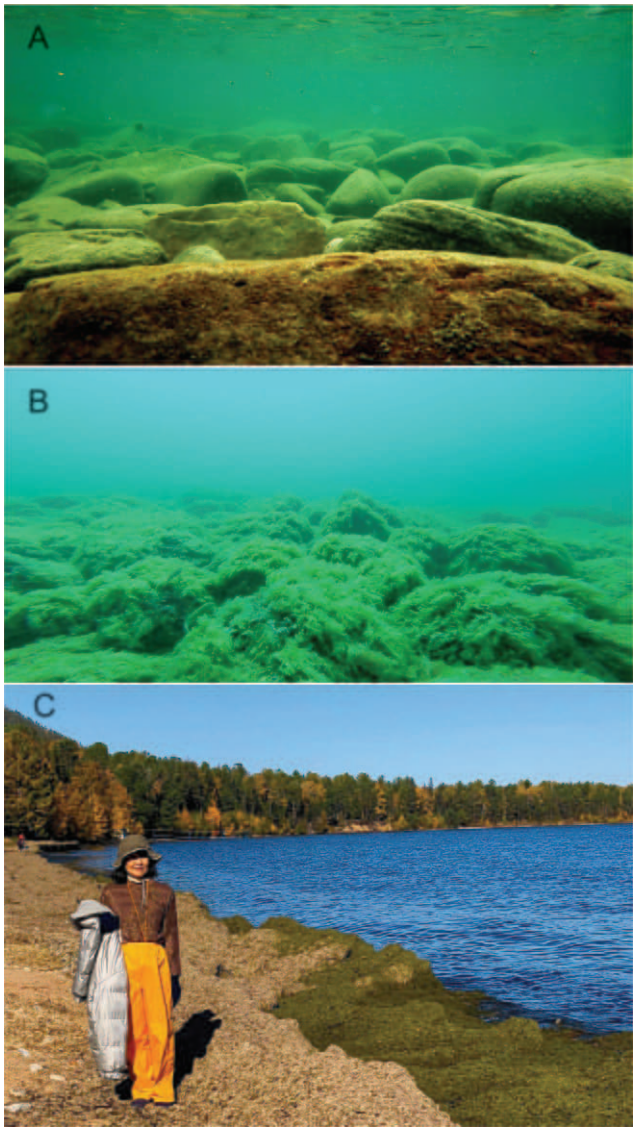

Fig. 4 Filamentous algal blooms (FABs) are an emerging threat to clear lakes. (A) The wave-washed littoral zones of large, oligotrophic lakes, like Lake Superior (USA/CA), typically support thin skins of diatoms and cyanobacteria along the rocky shore. (B) Lake Michigan (USA) is also a large, oligotrophic lake, but an invasive mussel transports nutrients to the benthos, promoting dense growths of the filamentous green alga, *Cladophora*. (C) Lake Baikal (RU) has extraordinarily low nutrient concentrations in the water, limiting phytoplankton growth. However, nutrient pollution of the ground water causes dense growths of filamentous green algae that wash up on shore. The green area of shore is wash up from the current growing season, while the brown material that researcher Masumi Yamamuro is standing upon is from the previous year (see Vadeboncoeur et al., 2021). Photo credits: (A) Leon Katona; (B) Harvey Bootsma; (C) Marianne Moore.

proteins, and DNA fragments that give the biofilm cohesion. This external scaffold slows the exchange of metabolites and nutrients with the environment beyond the biofilm, and provides a matrix within which extracellular enzymes can be used to exploit nearby organic resources. The ECM also stabilizes soft, organic sediments, reducing resuspension. New molecular techniques are providing a fascinating window on the function and composition of ECM associated with periphyton, and this is a rich, relatively unexplored, area of research (Scott et al., 2014).

Biofilms blanket unconsolidated sediments on the lake bottom, and algal constituents often dominate biomass in the euphotic zone. Epipelic algae influence carbon, nitrogen and phosphorus fluxes across sediment-water interfaces. For instance, oxygen produced during algal photosynthesis reduces the daytime exchange of phosphorus across the sediment-water interface, affecting redox gradients (Carlton and Wetzel, 1988; Wood et al., 2015). Within the biofilm itself, the steep oxygen gradients caused by diminishing photosynthesis with depth can generate a gradient in heterotrophic microbial metabolism (Hawes et al., 2014), with oxidation of labile algal exudates on the biofilm surface to fermentation of refractory detritus deeper in the sediments. These vertical oxygen gradients also cause layering of microbial taxa in biofilms. For example, the photoheterotrophs (purple sulfur bacteria) require very low oxygen environments and occur in deep layers of microbial biofilms (Martínez-Alonso et al., 2005).

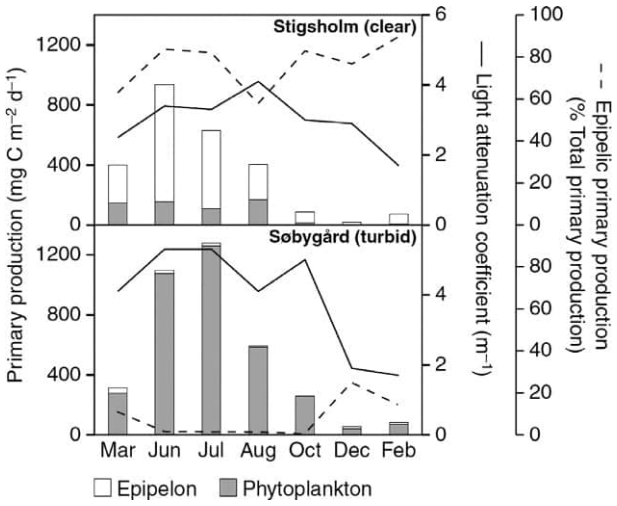

Fig. 5 Seasonal variation in productivity of benthic epipelic algae and phytoplankton in two Danish lakes. Lake Stigsholm has lower phosphorus concentrations (96 μg P L^{-1}) and is relatively clear, while lake Søbygård is eutrophic (275 μg P L-1) and turbid from high phytoplankton biomass. Epipelic productivity is much higher in the clear lake relative to the turbid lake because more light hits the lake bottom. Both epipelic and phytoplankton productivity tends to peak during the warm summer months. This is not true of epipelic productivity in the turbid lake which remains low during the summer months because epipelic algae are shaded by phytoplankton. In the clear lake, epipelon dominates autotrophic structure, while in the turbid lake, phytoplankton productivity dominates. From Liboriussen L and Jeppesen E (2003) Temporal dynamics in epipelic, pelagic and epiphytic algal production in a clear and a turbid shallow lake. *Freshwater Biology* 44:418–431.

Algae and heterotrophic bacteria both need inorganic N and P to grow, and algae benefit when bacteria mineralize nutrients from dead cells. Algae use light to produce labile organic carbon that provides an energy source for heterotrophic bacteria. When there is abundant non-algal organic carbon available (e.g., when terrestrial dissolved organic carbon creates tea-colored lakes) bacteria can outcompete algae for nutrients (Halvorson et al., 2020). However, in high light environments interactions between autotrophic and heterotrophic constituents of biofilms may be more mutualistic. Living and dead algae are a source of labile, easily exploited organic carbon for heterotrophic bacteria, which in turn, recycle the inorganic nutrients necessary for algal growth (Halvorson et al., 2020).

Top-down effects on benthic algae

Benthic algae are nutritious, easily digestible, rapidly renewing food resources for grazing animals (Vadeboncoeur and Power, 2017). An examination of periphyton under the microscope reveals an abundance of protozoans, rotifers, copepods, nematodes, and larval chironomids moving among the algal and bacterial cells ingesting diatoms, ECM, and detritus. Many larger invertebrates such as snails and some larval insects have specialized scraping mouthparts that efficiently remove algal biofilms at their base, leaving noticeable, bare grazing "scars" on hard surfaces. Others, including mayflies, chironomids, stoneflies, and caddisflies have mouthparts adapted to sweep benthic algae and detritus from soft and hard surfaces. Algivorous fish are a dominant trophic guild in tropical lakes, accounting for up to 40% of fish species in some lakes (Vadeboncoeur et al., 2011). Grazers in lakes can exert top-down control on benthic algae affecting the amount of algae that accumulates on a surface (Fig. 6), the rate of productivity, and the types of algae that dominate the assemblage.

Grazers reduce the amount of benthic algae that accumulate on surfaces in littoral zones. When grazers are prevented from consuming benthic algae in grazing exclusion experiments, algal biomass rapidly increases (Steinman et al., 1987; Steinman, 1996). A compilation of results from experiments in freshwater and marine habitats suggest that grazers, on average, reduce algal biomass by 56% (Hillebrand, 2009) and reduce spatial variability in algal biomass (Hillebrand, 2008). The effect of grazing on algal biomass depends upon how effectively grazers can remove biofilms from surfaces and upon grazer density. Efficient grazers with scraping mouthparts (e.g., the radulas of snails) can scrape to the bottom of a biofilm on rocks, but more selective grazers will consume surface epiphytic algae off larger algae and plants (Furey et al., 2012), which may affect algal composition more than algal biomass. The diversity of grazer sizes, densities, and efficiencies creates variability in their effect (Hillebrand, 2008).

Grazers often have the strongest effect on algal biomass in the early successional stages of a biofilm (Steinman, 1996). Any bare substrate, such as a newly scoured rock or an emerging macrophyte, is first colonized by bacteria and low growing diatoms. With time, the periphyton becomes more structurally complex and larger filamentous algae become established. Grazers can keep algal assemblages at early successional stages, dominated by prostrate and low-profile taxa that persist in the face of continuous nipping and scraping. Filamentous green algae can be too large and awkward for some insect grazers to handle and ingest. Larger grazers can prevent the establishment of attached filamentous green algae, but once established, these taxa form dense turfs or foliose aggregations that escape grazer control (Fig. 6; Power, 1990, Harrison and Hildrew, 2001). Many filamentous chlorophytes, such

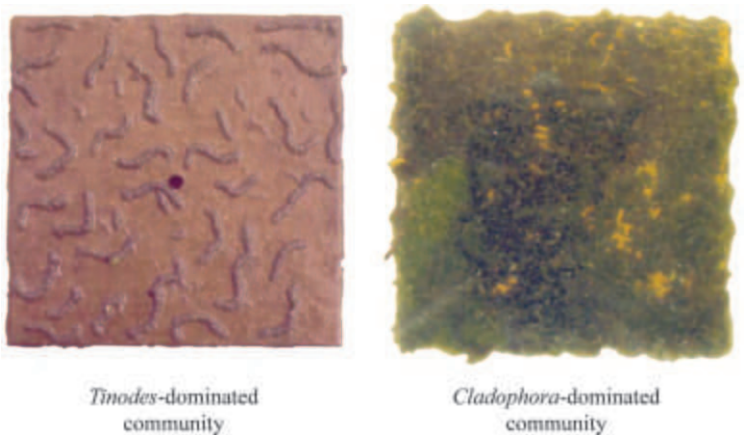

Fig. 6 The distribution of an invertebrate grazer, *Tinodes waeneri*, controls the distribution of benthic algal biomass in a eutrophic English lake. (A) The caddisfly lays its eggs in the vicinity of riparian trees, leading to patches of the nearshore littoral zone with high densities of *Tinodes* and low benthic algal biomass. (B) At similar depths, but distant from oviposition sites, *Tinodes* is rare and a luxuriant growth of the green alga, *Cladophora glomerata*, covers the lake bottom. From Harrison SSC and Hildrew AG (2001) Epilithic communities and habitat heterogeneity in a lake littoral. *Journal of Animal Ecology* 70: 692–707.

as *Cladophora*, become colonized by epiphytic diatoms and cyanobacteria. Micrograzers, such as chironomids, live in the filamentous algal assemblage, consuming epiphytes and indirectly benefiting the algal host (Furey et al., 2012).

Although it is tempting to think of grazing as inherently negative because algal cells are eaten and (perhaps) digested, grazing usually benefits algae left uneaten. Benthic algal growth is limited by light and the rate of nutrient acquisition. When animals consume cells from the surface of biofilms or from the surface of macroalgae, the cells deeper in the assemblage experience an increase in light. Additionally, grazers excrete N and P in their waste that, by meeting nutrient demand, increases algal growth rate. Thus, removal of biomass by grazers tends to increase biomass-specific productivity of benthic algae (Steinman, 1996).

The role of benthic algae in food webs

Primary producers are the energetic foundation of any food web because these autotrophic organisms transform inorganic carbon into organic carbon that is subsequently used as food by heterotrophic microbes and animals. Three sources of primary production in lake food webs are littoral macrophytes, benthic algae, and phytoplankton. Additionally, imported particulate terrestrial detritus (e.g., leaves and wood) is a food source for benthic invertebrates, while dissolved substances leached from terrestrial plants are used by bacteria (Mehner et al., 2016). These internally and externally derived basal resources are not equally nutritious. Macrophytes and terrestrial detritus are largely derived from vascular plants that are structurally complex, difficult to digest, and have high concentrations of carbon relative to nitrogen (C:N). High C:N is an index of low food quality. Algae, whether benthic or planktonic, have fewer structural compounds than vascular plants, and have a relatively low C:N. Thus, algae are a higher quality food than macrophytes and terrestrial leaves. High quality basal resources such as algae are often more efficiently entrained into food webs because they are selectively sought after by animals but also because growth efficiency (growth per gram consumed) is higher than for foods that are difficult to digest or contain low concentrations of the N necessary for protein synthesis.

Not all algae are equally nutritious and accessible. Filamentous green algae contain difficult to digest cellulose, have a low N content relative to other algae, and often pass through invertebrate guts undigested (Moore, 1977). Cyanobacteria are relatively high in protein (N), lack cellulose, and may be more digestible than filamentous green algae. Diatoms are lipid-rich and produce the essential fatty acid EPA that is required for the normal development of many animals (Guo et al., 2016). The abundance, seasonal persistence and high food quality of diatoms make them a critical component of lake food webs. Diatoms are readily digested, and can thrive under high grazing pressure. This algal super-food often dominates benthic algal biomass, and is efficiently consumed and assimilated by primary consumers. Additionally, the biofilm growth form presents consumers with algal carbon in a much more concentrated form than the planktonic algae dispersed in the water column (Vadeboncoeur and Power, 2017). Thus, the benthic caddisflies, mayflies, and snails that consume benthic algae are many orders of magnitude larger than zooplanktonic primary consumers in the water column. The large size of benthic primary consumers makes them an important resource for fish (Fig. 7).

The widespread use of natural tracers, including stable isotopes of C, N, and H, and fatty acids, has revealed that benthic algae are an integral basal resource for primary consumers and fish in lakes. Compilations of stable isotope data from lakes throughout the world demonstrate that fish species, regardless of trophic level, rely on benthic algal sources of carbon for about 50% of their growth (Vander Zanden et al., 2011). This does not mean that 50% of fish production in lakes is ultimately derived from attached algal carbon because this metric is not adjusted for the relative abundance of different types of fishes within individual lakes. However,

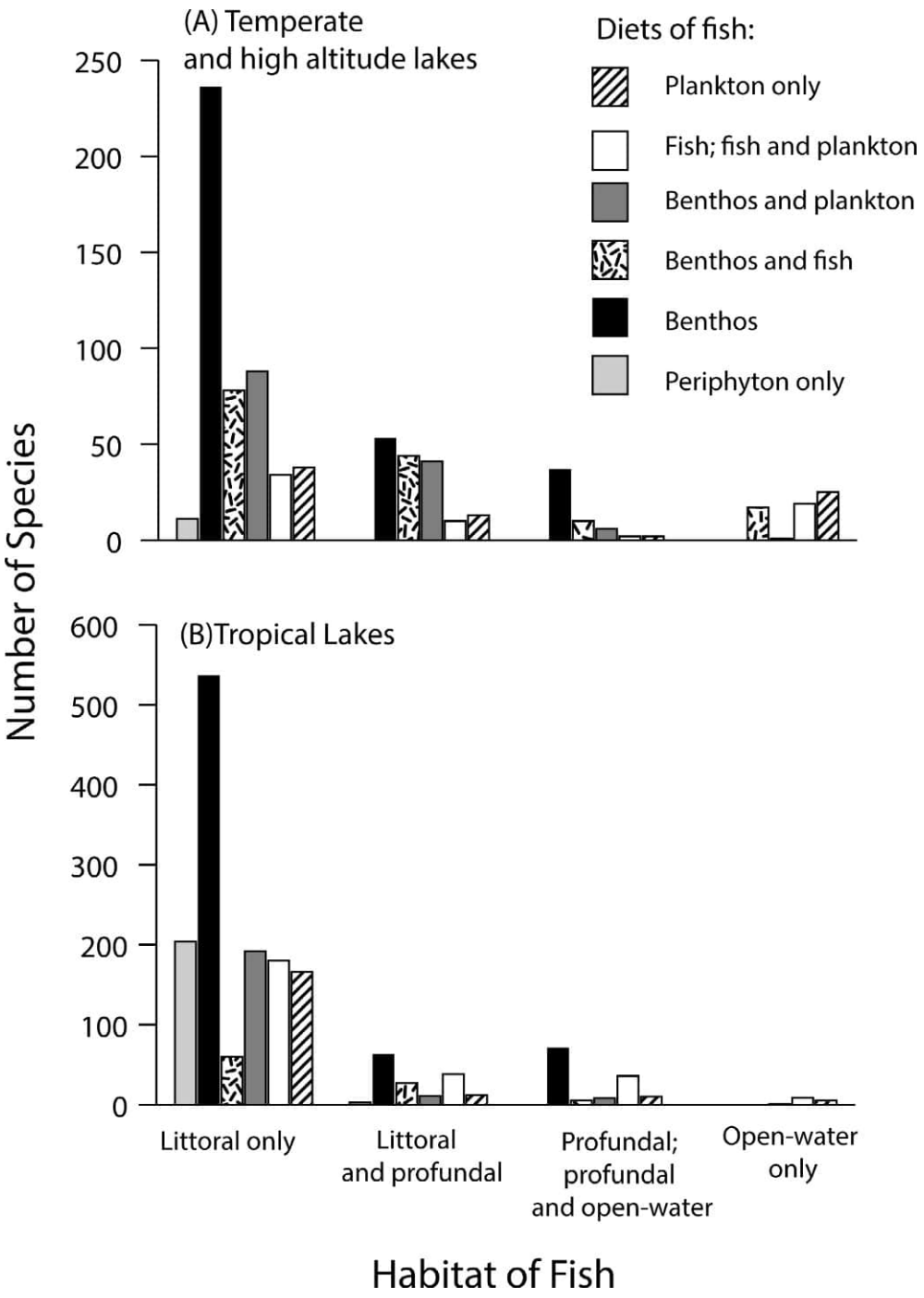

Fig. 7 Littoral zones, and the carbon fixed by benthic algae, support the majority of fish diversity in the largest lakes in the world. Few species live exclusively in the vast open water (limnetic) habitats of these lakes or in the deep profundal waters below the zone of light penetration. Rather, most fish species are concentrated in the thin rind of littoral habitat at the edge of these huge lakes. (A) In temperate latitudes, few littoral fish directly consume benthic algae, but the fish eat the zoobenthic invertebrates that consume benthic algae. (B) In tropical lakes many fish are themselves grazers, directly consuming benthic algae. From Vadeboncoeur Y, McIntyre PB, and Vander Zanden MJ (2011) Borders of biodiversity: Life at the edge of the world's large lakes. *BioScience* 61:526–537.

most fish species rely on the algal base of the littoral food web either by directly consuming benthic algae (e.g., grazing fishes in tropical lakes) or indirectly by consuming invertebrates that grazed on benthic algae (Fig. 7; Vadeboncoeur et al., 2011). Although it is widely accepted that benthic algae are an integral and dominant part of lake food webs, littoral basal resources are still understudied and under-monitored relative to planktonic elements of the food web (Vander Zanden and Vadeboncoeur, 2020).

Benthic algae and whole-lake metabolism

Littoral zones and benthic algae contribute substantially to the total amount of gross primary production (GPP) in lake metabolism (Vadeboncoeur et al., 2003; Van de Bogert et al., 2007; Ask et al., 2009). Relative contributions of benthic algae to ecosystem GPP are highest in small, shallow, clear lakes and lowest in large, clear lakes and eutrophic lakes (Fig. 3). This variability reflects the influence of surface water nutrients, which usually have a larger effect on phytoplankton than on periphyton, and the effect of lake morphometry, which influences how much of the lake bottom is exposed to light (Vadeboncoeur et al., 2008).

Light is critical for both benthic and planktonic algal production and many lakes have high concentrations of colored dissolved organic carbon (DOC) that limit algal productivity. In humic lakes, DOC reduces productivity of both benthic and planktonic algae (Vadeboncoeur et al., 2008; Ask et al., 2009; Karlsson et al., 2009) and in some lakes, algae on the fringing bog vegetation may dominate ecosystem GPP and contribute substantially to secondary production of zooplankton and zoobenthos (Vesterinen et al., 2017).

Primary production in small, shallow (average depth < mixing depth) lakes can be overwhelmingly dominated by benthic algae or dominated by phytoplankton depending upon surface water nutrient concentrations (Figs. 3 and 5). Shallow, clear lakes in high latitudes (arctic and boreal lakes) as well as clear shallow mountain lakes are usually unaffected by anthropogenic nutrient inputs and are dominated by benthic algal production (Rautio et al., 2011). Eutrophication driven by surface water N and P pollution increases shallow lake productivity and shifts the autotrophic structure toward increasing dominance by phytoplankton. As water column concentrations of total phosphorus (TP) and total nitrogen (TN) increase, phytoplankton increasingly shade benthic algae and consequently phytoplankton dominate whole-lake metabolism. In shallow lakes, internal loading of nutrients from the lake sediments exacerbates eutrophication and dominance of phytoplankton (Fig. 3C).

The contributions of benthic algae to whole ecosystem GPP declines as lake area and depth increase. Littoral zone area is a small fraction of total lake area in small steep-sided mountain lakes or large tectonic lakes like Lakes Baikal, Malawi, and Tanganyika. However, such lakes are usually oligotrophic and the littoral habitat that does exist can support complex autotrophic communities that are highly productive, leading to area-specific production of benthic algae that can be many times that of phytoplankton (O'Reilly, 2006; Malkin et al., 2010). In the largest lakes in the world, low surface area to volume ratios mean that the amount of carbon fixed by the vast open water pelagic habitat dwarfs that of benthic algae (O'Reilly, 2006). However, the littoral zones of these lakes can extend to over 60 m deep, form the most extensive continuous freshwater habitat in the world, and support the majority of biodiversity in these lakes (Fig. 7; Vadeboncoeur et al., 2011). Thus, it is a mistake to overlook the functional importance of littoral habitats in large lakes based on the small contribution to whole ecosystem GPP. Unfortunately, many clear lakes are suffering from nearshore benthic filamentous algal blooms (FABs), and limnologists are ill-equipped to respond to this threat because nearshore habitats of large lakes are overlooked in lake monitoring programs (Fig. 4; Vadeboncoeur et al., 2021).

Monitoring benthic algae

Benthic algae are not routinely monitored in lakes (DeNicola and Kelly, 2014), but they ought to be, and the methods developed for rivers and wetlands (e.g., Biggs and Kilroy, 2000; Steinman et al., 2006) are readily applied to littoral zones. Biomass is assessed as AFDM, chlorophyll, or comprehensive pigment analysis using HPLC (Steinman et al., 2006). Chlorophyll must be measured using an acidification step that corrects for degraded chlorophyll (phaeophytin) because periphyton often contains a large proportion of dead cells that will inflate biomass estimates if unaccounted for. Comparison of chlorophyll data within and among lakes needs to be interpreted with care because algal taxonomic composition changes markedly with depth and cellular chlorophyll concentrations increase with decreasing ambient light (depth). It is best to combine biomass measurements with analyses of taxonomic composition. These can include simple microscopic examinations to document dominant taxa or detailed quantifications of taxonomic composition and biovolume (Biggs and Kilroy, 2000). Fatty acid analysis is a synthetic approach that provides qualitative information on dominant algal phyla, microbial components and food quality for consumers (Guo et al., 2016). Quantifying C, N, and P content of algae can be used to further assess food quality.

The rate of carbon fixation by benthic algae can be measured in chambers in situ or in the lab with either bulk oxygen exchange or ^{14}C methods (Vadeboncoeur et al., 2003; Devlin et al., 2016), but in most cases benthic productivity is high enough to make oxygen measurements a much simpler and preferable approach. Chamber measurements from different depths and substrates are integrated with morphometry, light, and substratum distribution to model whole lake benthic algal primary production. Pulse Amplitude Modulated (PAM) fluorometry is a useful tool for assessing photosynthetic capacity of biofilms in situ and for describing variation in photosynthesis with depth (Devlin et al., 2016; Hawes et al., 2014). Diel oxygen curves monitored by oxygen sondes deployed in the littoral zone can be used to monitor littoral contributions to whole lake metabolism but deployment position, and wind and mixing patterns affect data interpretation (Van de Bogert et al., 2007; Brothers and Vadeboncoeur, 2021).

Most metrics of benthic algal biomass and production are expressed per square meter of lake bottom (soft sediments, boulder) or substratum (e.g., macrophyte or cobble). Thus, sampling designs of naturally occurring algal assemblages must incorporate approaches that isolate algae in a known area. Biofilms growing on soft sediments or very gelatinous colonies on rocks can be collected with core samples. Corers can be constructed from Perspex tubes or cut-off syringes. A 20 mL syringe (inner diameter ~1 cm) will collect sufficient material for biomass or species composition measurements. Once the core is collected the syringe is inverted and the upper 0.5–1.0 cm is retained based on visual inspection of the depth of algal colonization. Perspex corers are

excellent for collecting intact sediment cores for measuring primary productivity. Clear and dark chambers of a known area can be deployed over sediments or rocks and equipped with oxygen loggers to measure photosynthetic rates in situ.

Relatively uniform artificial substrata, such as clay tiles (Fig. 6) and glass microscope slides, are used to grow benthic algae in situ or in the laboratory with an inoculum. Deployment of nutrient diffusing substrata (NDS) is useful for determining which nutrients (e.g., N, P, Si) limit benthic algal growth and can be useful in diagnosing the driver of nuisance benthic algal proliferations in lakes. NDS samples can be used for taxonomic, biomass, or productivity assessments, allowing for exploration of the structure and function of periphyton under different nutrient conditions (Steinman et al., 2006). DeNicola and Kelly (2014) and Poikane et al. (2019) provide excellent reviews of how different monitoring designs capture (or fail to capture) patterns and processes relevant to littoral zone degradation.

Benthic algae and global change

Increases in air and water temperature alter physical dynamics in lakes in ways that both reduce and enhance benthic algal growth. Increases in water temperature stimulate benthic algal growth and may alter the types of algae that are present in lake littoral zones (Wood et al., 2020; Vadeboncoeur et al., 2021). Filamentous cyanobacteria and green algae are generally more tolerant of increases in temperature compared to diatom-dominated assemblages. Greater warming of nearshore water and substrate than of offshore waters creates thermal bars that trap water and material flowing off the landscape in the littoral zone. Increases in air temperature can stimulate wind waves that may reduce benthic algal biomass accumulation on substrata in nearshore areas. Conversely, strong wave action may increase lake turnover events, moving nutrient-rich hypolimnetic water into the littoral zone to stimulate benthic algae. Climate-driven fluctuations in lake levels can scour benthic algae, but also enhance the flow of nutrient-rich groundwater and advect nutrients from the landscape into nearshore areas for use by benthic algae. Increased atmospheric transport of nutrients is leading to a widespread loss of oligotrophic lakes in North America (Stoddard et al., 2016), and benthic algae may be early responders to the widespread change in nutrient availability.

The benthic algae that grow on illuminated surfaces in lakes (Fig. 1) are a fascinating, taxonomically diverse group of organisms that are often overlooked in lake research. Although benthic algae are less well-studied than phytoplankton, periphyton contribute substantially to aquatic food webs and to whole-lake metabolism. Anthropogenic stressors including climate change, nutrient pollution, extensive use of herbicides and pesticides, and increased human access to remote lakes are contributing to changes in littoral zone function (Stewart et al., 2021). Many of these stressors may be shifting benthic algae from a cryptic, low growing resource that ultimately provides energy for fish, to a prolific, unsightly green scum along the shoreline of clear lakes. The public, managers, and scientists can work together to document and mitigate this growing threat to pristine lakes.

Knowledge gaps

- Interactions between heterotrophic microbes and algae in the periphytic phycosphere
- Phenology, growth, and taxonomic shifts in benthic algae in response to a warming world
- Non-nutrient drivers of Filamentous Algal Blooms
- Effects of benthic toxic cyanobacteria on food webs and humans

See Also: Structures and functions of Inland Waters - Lakes: Lacustrine Phosphorus Cycling; Macrophytes; Phytoplankton Productivity; Structures and functions of Inland Waters - Rivers: High Latitude Rivers: Ecosystems Shaped by Environmental Extremes; Structures and functions of Inland Waters - Wetlands: Section introduction: Wetland Ecology

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Relevant Websites

https://www.algaebase.org/—AlgaeBase is a global algal database of taxonomic, nomenclatural and distributional information on algae.
https://diatoms.org/—Diatoms of North America is a collaborative effort to document the diversity of diatom species in North America.
http://intotherift.org/—Into the rift is an interactive journey with scientists exploring the littoral ecosystem of Lake Tanganyika.

Benthic Invertebrate Fauna, Lakes and Reservoirs

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This is a reprint of D.L. Strayer, Benthic Invertebrate Fauna, Lakes and Reservoirs, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00161-7.

Glossary

Benthos – The community of organisms living around surfaces (e.g., sediments, plants) in aquatic ecosystems.
Bioturbation – Sediment mixing caused by the activities of organisms.
Macrobenthos – Benthic animals large enough to be retained on a coarse (usually ~0.5-mm mesh) sieve.
Meiobenthos – Benthic animals too small to be retained on a coarse (usually ~0.5-mm mesh) sieve, but large enough to be retained on a fine (usually ~0.05-mm mesh) sieve.
Zoobenthos – The community of animals living around surfaces (e.g., sediments, plants) in aquatic ecosystems.

Introduction

Benthos includes all animals that live in association with surfaces in lakes and reservoirs. This includes animals that live in and on sediments of all kinds (mud, sand, stones), as well as animals that live in, on, or around aquatic plants or debris. Animals large enough to be retained on a coarse sieve (usually 0.5- mm mesh) are called macrobenthos, those that pass through a coarse sieve but are retained on a fine sieve (usually ~0.05mm) are called meiobenthos, and those that pass through even fine sieves sometimes have been called microbenthos, although this last term is rarely used. It is customary to ignore the small benthic animals, but studies have shown that animals too small to be caught on a 0.5-mm mesh may constitute >95% of the individuals, ~25% of the biomass, ~50% of the metabolic activity, and >50% of the species in a zoobenthic community.

Composition and Biological Traits of the Lacustrine Zoobenthos

The density of zoobenthos depends strongly on the mesh size of the sieve used for the study (Figure 1). Densities of macrobenthos (i.e., animals large enough to be caught on a 0.5-mm mesh) in lakes typically are 1000–10 000m^{-2}, while the total density of all benthic metazoans probably usually is ~1 000 000 m^{-2}. There is a great deal of variation in densities within and among lakes, so that densities reported for a given mesh size range over ~100-fold within and among lakes.

Estimates of zoobenthic biomass usually include only the macrobenthos and exclude large bivalves. Because small benthic animals usually constitute a small part of zoobenthic biomass, estimates of the biomass of the macrobenthos probably are nearly equivalent to the entire zoobenthos. However, it appears that the meiobenthos may be especially important in unproductive habitats (Figure 2). Macrobenthic biomass without large bivalves ranges from ~0.2 to 100 g dry mass m^{-2}, and dense populations of large bivalves can increase these values by >10 g DM m^{-2}. Zoobenthic biomass rises up to a point with increasing phytoplankton production, then asymptotes or even declines with further increase in phytoplankton production. Zoobenthic biomass also tends to be highest in shallow lakes, where rooted plants are abundant, where the lake bottom is flat or gently sloping, in warm lakes or in the epilimnion of stratified lakes, and in lakes of low color.

There are relatively few data on the production rates of entire macrobenthic assemblages and almost no estimates that include the small benthic animals. One would expect to see as much variation in rates of production as in biomass, and based on the expected ratio of annual production to biomass of ~5 for animals of macrobenthic size, production of the lacustrine macrobenthos might range from ~1 to 500 g DM m^{-2} $year^{-1}$. Production of smaller benthic animals in lakes might be about the same order of

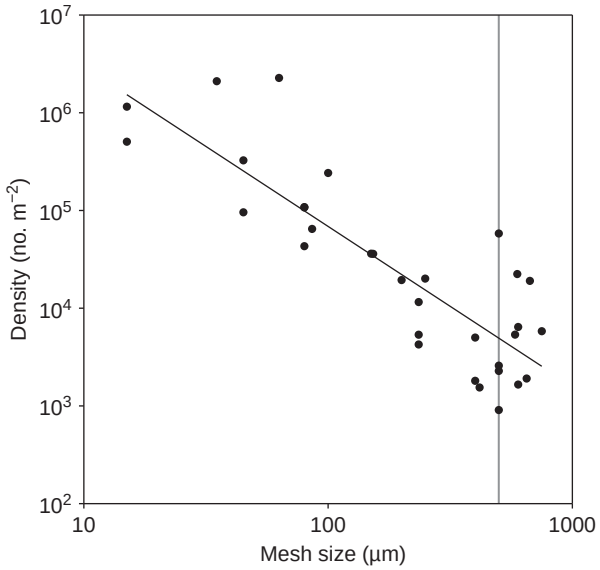

Figure 1 Reported density of zoobenthos as a function of sieve mesh size in a series of lakes from the northern temperate zone ($r^2 = 0.72$, $p < 0.000001$). The vertical gray line marks the 500-μm mesh commonly used for macrobenthos.

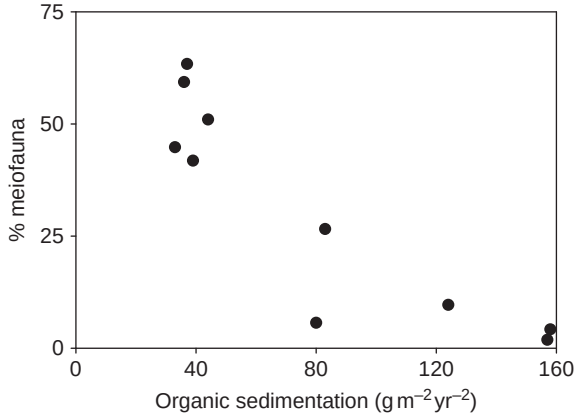

Figure 2 Percentage of zoobenthic biomass belonging to the meiofauna, as a function of organic sedimentation at various sites in the profundal zone of Lake Paijanne, Finland ($r^2 = 0.79$, $p = 0.0006$). Adapted from Hakenkamp *et al.* (2002), after data of Särkkä (1995).

magnitude, based on the sparse data now available. Production of the macrobenthos increases with increasing primary production (Figure 3), with no hint of an asymptote or downturn at very high primary production, as has been seen for macrobenthic biomass.

The lacustrine zoobenthos is enormously diverse; a typical lake contains hundreds of species from 12 to 15 animal phyla (Table 1, Figure 4). The macrobenthos often is numerically dominated by oligochaetes and chironomid and chaoborid midges, although large-bodied mollusks may dominate the biomass of the community. Aquatic insects other than dipterans (such as mayflies) may be abundant, especially in shallow lakes. Nematodes usually are by far the most numerous of the meiobenthos (and of the zoobenthos as a whole), although gastrotrichs, rotifers, and microcrustaceans often are abundant as well. Many important families are ecologically important in lakes around most parts of the world, including the Chironomidae and Chaoboridae in the Diptera; the Ephemeridae in the Ephemeroptera; the Tubificidae (including the 'Naididae') in the Oligochaeta; the Unionidae and Sphaeriidae in the Bivalvia; the Lymnaeidae and Planorbidae in the Gastropoda; the Chydoridae, Canthocamptidae, and Cyclopidae among the microcrustaceans; and the Chaetonotidae in the Gastrotricha. In contrast, several important groups are restricted to particular biogeographic regions (mysid shrimps and gammarid amphipods chiefly in the Northern Hemisphere, hyriid bivalves in the Southern Hemisphere) or habitats (ephydrid flies or brine shrimp in fishless or saline inland waters). Human introductions have vastly increased the ranges of several ecologically important species of the lacustrine zoobenthos that once had small geographic ranges, most notably *Dreissena* spp. (zebra mussels, Bivalvia), *Mysis* (opossum shrimp, Crustacea), and several crayfish species.

Because the lacustrine zoobenthos is so diverse, it is difficult to generalize about the biological traits of its members. The largest animals in the community (bivalves and decapods, $>10^1$ g dry mass) are more than 10 billion times larger than the smallest (rotifers and gastrotrichs, $\sim 10^{-9}$ g DM), so this community spans an enormous range of body sizes. Life spans of zoobenthic

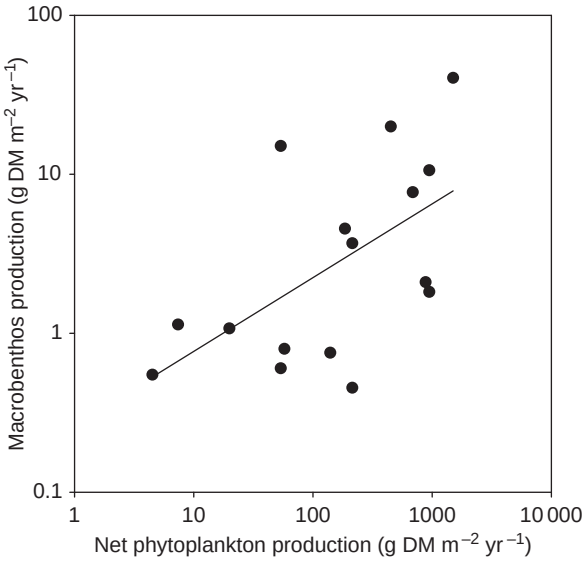

Figure 3 Relationship between production of macrobenthos and production of phytoplankton in a series of lakes ($r^2 = 0.34$, $p = 0.02$). Adapted from data of Kajak *et al.* (1980).

Table 1 Estimates of species richness of the zoobenthos (excluding parasitic forms) in Mirror Lake, a small, unproductive lake in New Hampshire (USA), and typical densities of major phyla in lakes

Phylum	*Estimated number of species in Mirror Lake*	*Typical density in lakes (no. m^{-2})*
Porifera (sponges)	4	NA
Cnidaria (hydras and jellyfish)	2	100–1000
Platyhelminthes (flatworms)	40	1000–50 000
Nemertea (ribbon worms)	1	<100
Gastrotricha	30	100 000–1 000 000
Rotifera	210	10 000–250 000
Nematoda (roundworms)	35	100 000–1 000 000
Annelida (earthworms, leeches)	30	5000–50 000
Mollusca (snails, clams)	6	100–1000
Ectoprocta (moss animicules)	2	<100
Crustacea (water-fleas, seed shrimp, copepods, and relatives)	70	20 000–200 000
Chelicerata (mites)	50	1000–10 000
Tardigrada (water-bears)	5	1000–50 000
Uniramia (insects)	120	1000–50 000

Many lakes around the world contain the same phyla and a comparable numbers of species as Mirror Lake, but have not been so well studied.

animals range from less than a week (rotifers, gastrotrichs) to decades (bivalves). Some species have tough long-lived resting stages (sponge gemmules, ectoproct statoblasts, cladoceran ephippia) that allow populations to reestablish themselves after long unfavorable periods, and assist in passive dispersal between lakes. Various species burrow into the sediments (bivalves, tubificid oligochaetes, *Chaoborus*), glide at the sediment–water interface (gastrotrichs, ploimate rotifers, flatworms), attach (sessile rotifers) or mine (some chironomids in the genus *Cricotopus*) in aquatic plants, or crawl on or attach to solid object such as stones (*Dreissena*, many gastropods).

The zoobenthos includes species that suspension-feed on phytoplankton (many bivalves and some chironomids) or interstitial bacteria (*Pisidium*), graze on benthic algae (gastropods and many rotifers), deposit-feed on sedimented detritus and bacteria (tubificid oligochaetes), are predators on other benthic animals (odonates, tanypodine chironomids, dicranophorid rotifers) or zooplankton (*Chaoborus*), feed on either the leaves (crayfish, chrysomelid beetles) or roots (dorylaimid nematodes, larvae of the beetle *Donacia*) of rooted plants, or shred leaves of terrestrial plants that fall into the water (isopods, caddisflies). Not surprisingly, passive suspension-feeders such as hydropsychid caddisflies and black flies are much rarer in lakes than in flowing waters, presumably because currents in lakes are too slow or undependable to provide them with food.

Benthic animals have several adaptations for dealing with low oxygen concentrations that occur in many benthic environments. Some burrowing animals (chironomids and mayflies) produce currents to bring oxygenated water into the otherwise anoxic sediments in which they burrow. Species in several taxonomic groups (e.g., cladocerans, chironomids, gastropods) produce hemoglobin, which improves oxygen transport under hypoxic conditions. A few species of nematodes, bdelloid rotifers,

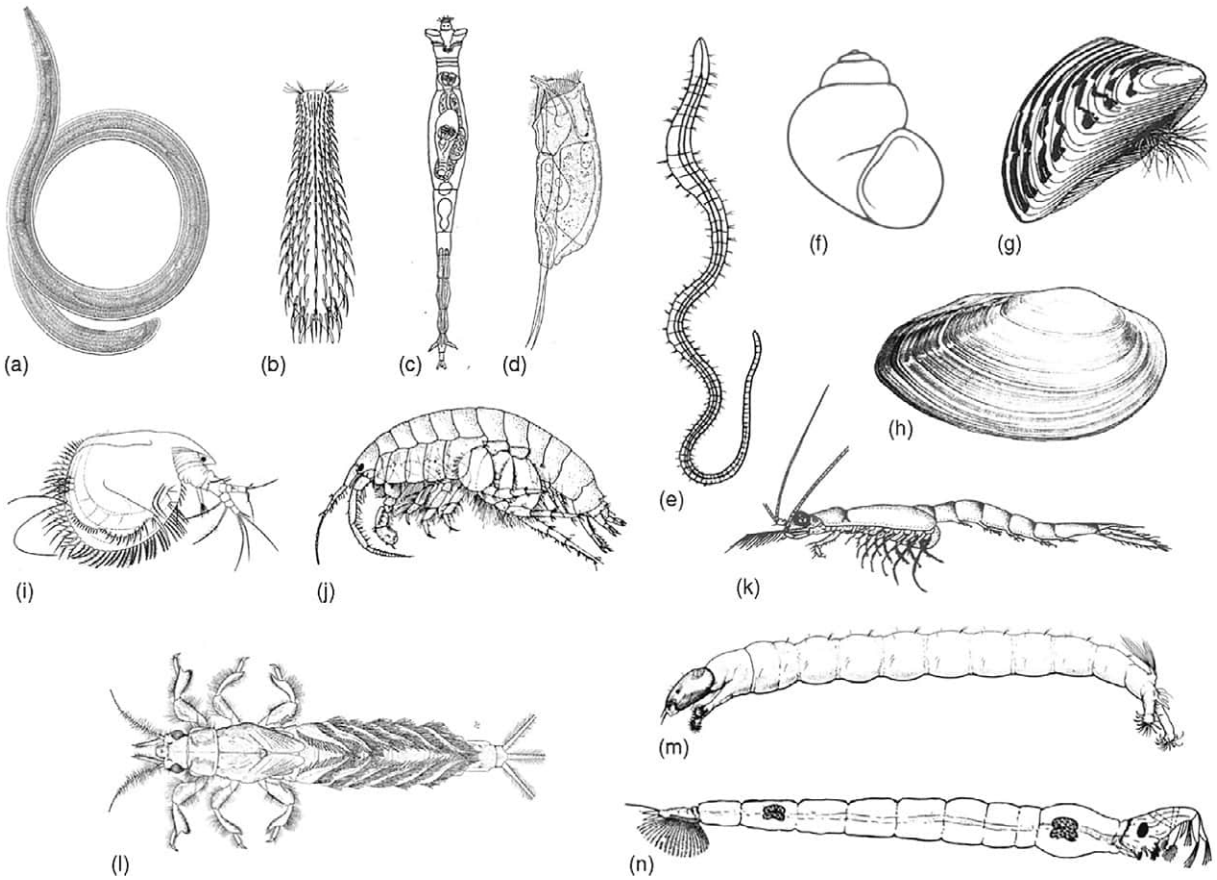

Figure 4 Some important members of the lacustrine zoobenthos. Typical adult body lengths are given in parentheses. (a) a nematode (2mm); (b) a gastrotrich (0.2mm); (c) a bdelloid rotifer (0.5mm); (d) a ploimate rotifer (0.1mm); (e) a tubificid oligochaete (50mm); (f) a hydrobiid snail (3mm); (g) the bivalve *Dreissena* (20mm); (h) a unionid bivalve (75mm); (i) a cladoceran (1mm); (j) an amphipod (10mm); (k) a mysid shrimp (20mm); (l) an ephemerid mayfly (20mm); (m) a chironomid (10mm); (n) the phantom midge *Chaoborus* (10mm).

gastrotrichs, tubificid oligochaetes, copepods, ostracods, and chironomid and chaoborid midges are commonly found in the anoxic profundal sediments of productive lakes. These animals apparently survive extended anoxia either by using anaerobic metabolism of substances like glycogen or by going into extended diapause. Finally, many of the benthic animals (e.g., many insects and pulmonate snails) avoid the problem of low dissolved oxygen altogether by obtaining their oxygen from the air.

Methods of Study

A few members of the lacustrine zoobenthos are large enough to be directly observed in situ (e.g., by SCUBA or mask-and-snorkel), but most species must be collected and brought into the laboratory for study. Scientists have invented a wide range of gear to collect benthic animals (Figure 5). Most often, scientists use grabs, corers, sweep nets, closing bags or boxes, or traps to collect animals or sediments. Often, animals need to be separated from the sediments or plants in which they live. This is usually accomplished by washing the sample through a sieve, most often of 0.1–1-mm mesh, sometimes followed by staining the sample with a dye such as Rose Bengal or examining the sample under a low-power microscope to aid in finding the animals. More or less experimental methods such as density-gradient centrifugation using silica sols (e.g., Ludox®) or application of ice or gentle heat are sometimes used as well.

Variation in the Lacustrine Zoobenthos

One of the chief characteristics of the zoobenthos is its extreme patchiness. The abundance and species composition of the zoobenthos varies within lakes, at scales ranging from centimeters (replicate samples at a single site) to kilometers, as well as among lakes. A number of factors are known to affect the abundance and species composition of the zoobenthos.

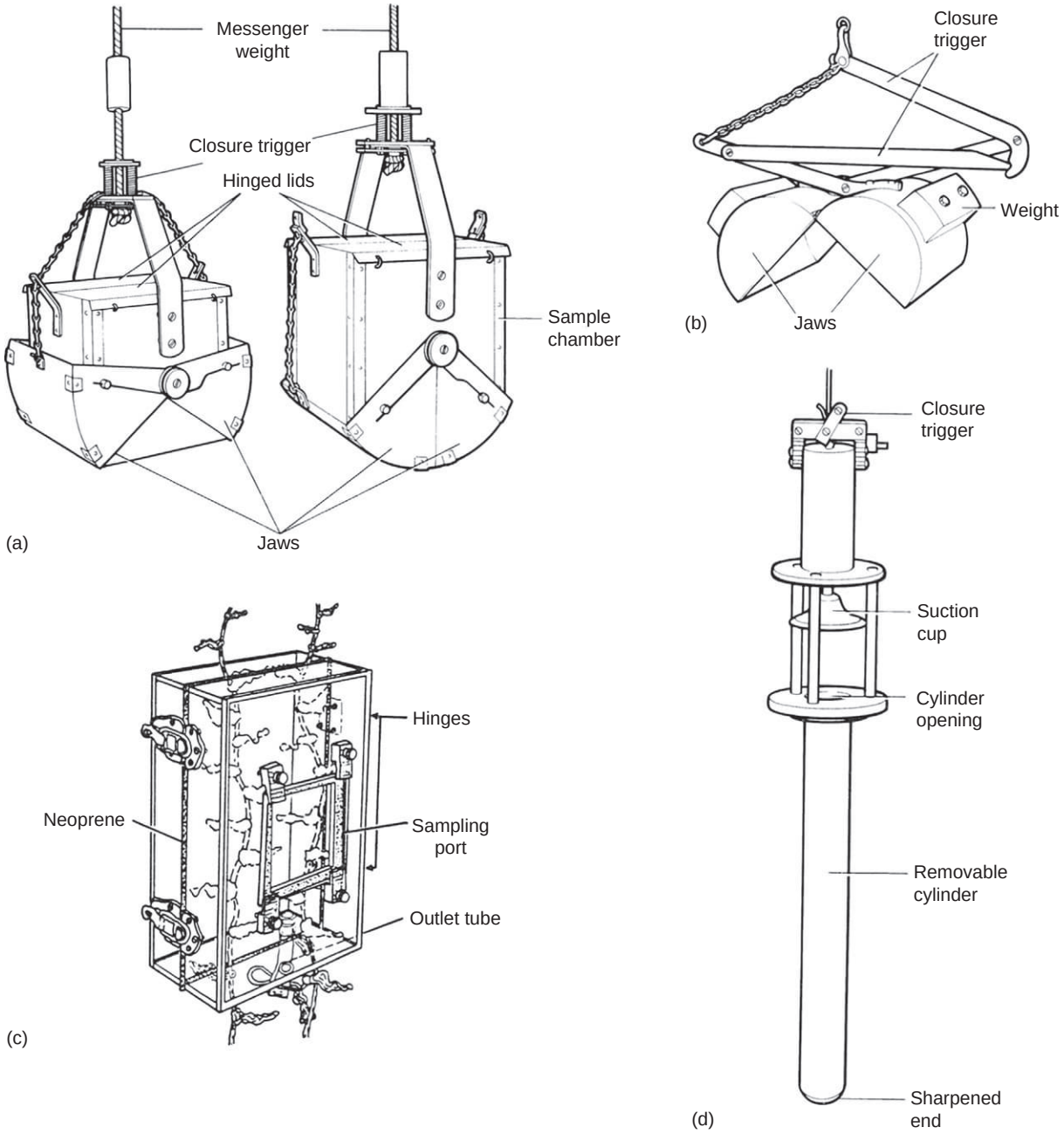

Figure 5 Four samplers commonly used for quantitative studies of the lacustrine zoobenthos. (a) Ekman grab; (b) PONAR grab; (c) Downing box sampler for vegetation-dwelling invertebrates; (d) Kajak-Brinkhurst corer. Adapted from Downing (1984, 1986).

Variation within Lakes

The composition of the zoobenthos almost always varies greatly with water depth within a lake. The abundance of nearly every species in the zoobenthos varies with water depth (Figure 6), and species richness often is much lower in the deep waters of a lake than near the shore (Figure 7). Many studies have also reported variation in the total numbers or biomass of benthic animals with water depth in individual lakes. No single pattern of variation of abundance or biomass with water depth applies to all lakes, because the many mechanisms that link water depth to the zoobenthic community vary in strength across lakes and produce a wide range of patterns in different lakes.

The most important factors that cause zoobenthic composition and abundance to vary with water depth include dissolved oxygen, quantity and quality of organic matter inputs, temperature, sediment grain size and compaction, disturbance, and depth-dependent biotic interactions. The relative contributions of each of these factors and their interactions in driving zoobenthic community structure

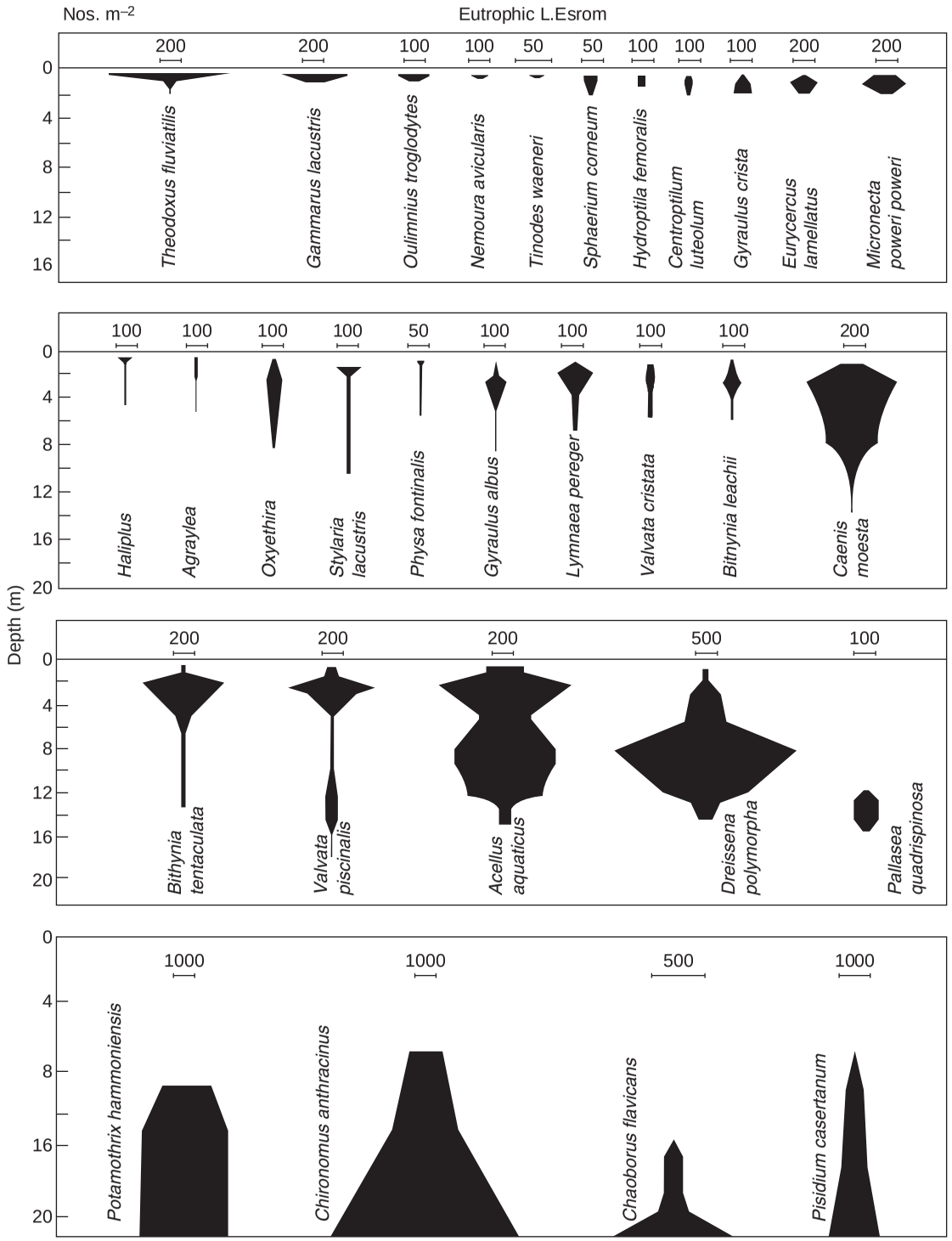

Figure 6 Distribution of benthic animals with water depth in eutrophic Lake Esrom, Denmark. Adapted from Jonasson (2004).

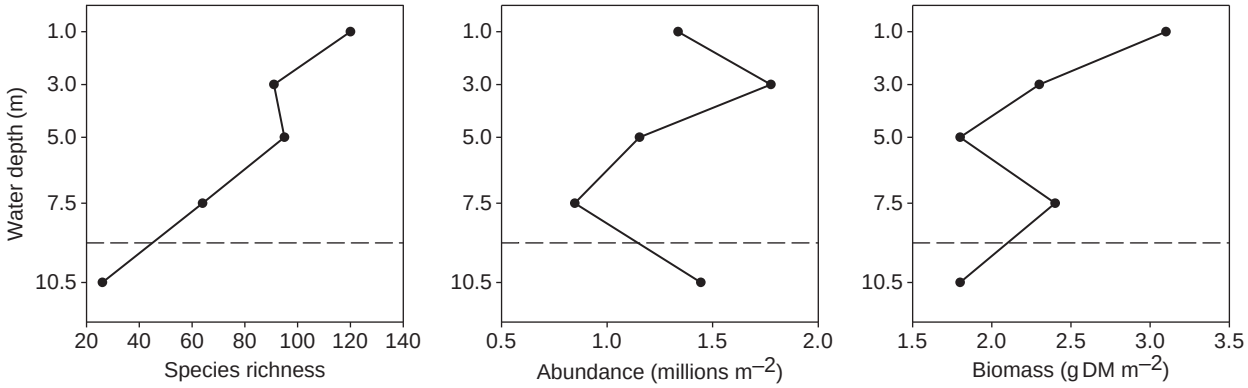

Figure 7 Species richness, abundance, and biomass of benthic animals (including all metazoans) as a function of water depth in Mirror Lake, a small unproductive lake in New Hampshire. The dashed horizontal line shows the depth at which oxygen at the sediment surface falls below 1mg l^{-1} by late summer. Adapted from Strayer (1985).

have not yet been disentangled. In stratified lakes, concentrations of hypolimnetic dissolved oxygen fall through the stratified period, and often reach zero at the sediment surface by the end of the summer. Only a few species of animals can tolerate hypoxic ($<2 mg l^{-1}$) or anoxic conditions for any period of time. The hydrogen sulfide that often accompanies anoxia also is toxic to most animals. Thus, inadequate dissolved oxygen at the sediment surface probably is a major cause of the vertical zonation of the zoobenthos and low species richness in profundal sediments. Nevertheless, declines in richness often occur well above the depth of oxygen depletion (Figure 7), so factors other than oxygen must be important as well. Although few zoobenthic species can tolerate anoxia, these species may be abundant, so low dissolved oxygen does not necessarily reduce zoobenthic density or biomass. Even in unstratified lakes, periods of warm, windless weather may reduce mixing enough to cause short-termdepletion of oxygen at the sediment surface and catastrophic losses of benthic animals. Such ephemeral stratification and oxygen depletion killed nearly the entire population of ~2500 metric tons (dry mass) of the mayfly *Hexagenia* in the shallow western basin of Lake Erie in late summer 1953.

Temperatures in the hypolimnion of a stratified lake are much lower and steadier than in the epilimnion. These low temperatures slow metabolic rates of benthic animals, may not meet thresholds for growth and reproduction of many species, and presumably exclude many species from profundal sediments.

The food base for the zoobenthos changes from the shoreline to the profundal zone. Aquatic plants and attached algae grow only in relatively shallow or clear water. In deep water, freshly settled phytoplankton supplements older detritus washed in from the watershed and littoral zone, and the amount and quality of organic matter reaching the profundal sediments of deep lakes probably declines with increasing water depth. The deposition of this sinking organic matter on the lake bed is highly uneven, depending on wave energy and the slope of the bottom. It seems reasonable to suppose that the quantity and quality of food is usually highest in the littoral zone and in depositional areas, and leads to variation in zoobenthic biomass (Figure 8).

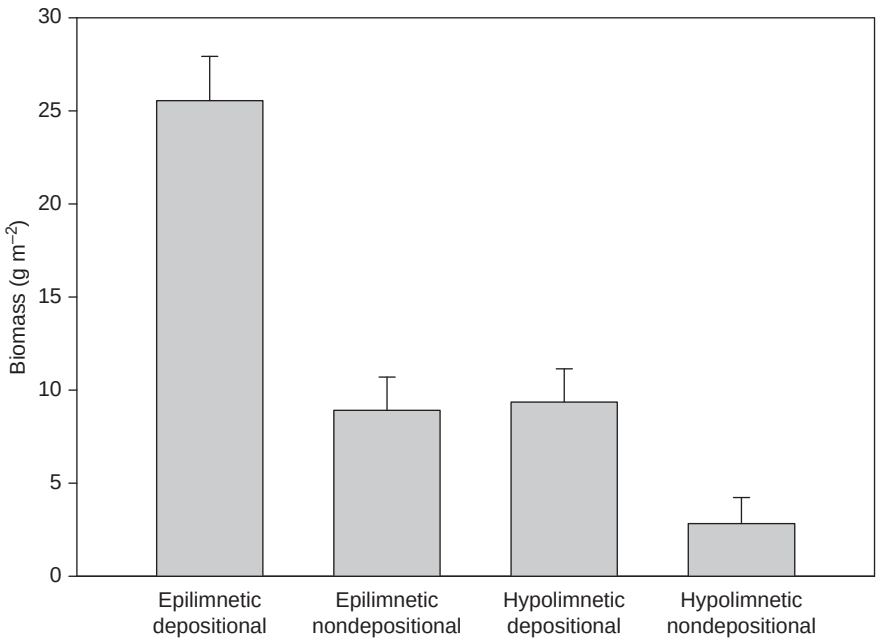

Figure 8 Mean (±1SE) biomass (wet mass) of macrobenthic animals at various sites in Lake Memphremagog, Quebec, as a function of thermal and depositional regime. Adapted from Rasmussen and Rowan (1997).

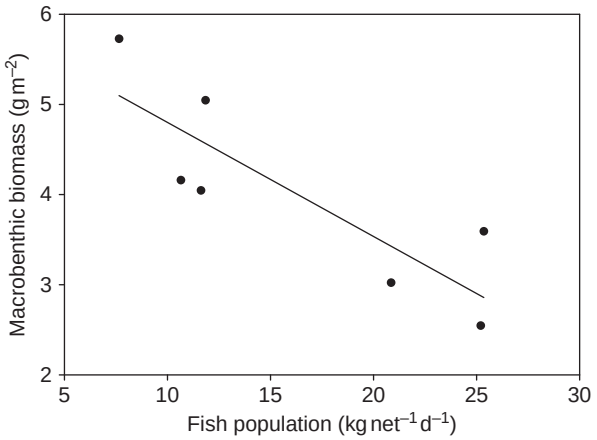

Figure 9 Dependence of macrobenthic biomass (wet mass) on fish predation in the Finnish Lake Pohjalampi. Each point is one year during a long-term experimental manipulation of fish populations. Adapted from Leppä *et al.* (2003).

Sediment grain size and heterogeneity also vary with water depth, typically changing from a highly patchy mosaic of coarse sediments in shallow water to a monotonous plain of fine-grained sediments in the profundal zone. Because of the many mechanisms that link benthic animals to their sediments, this variation in sediments must have a large effect on the kinds of benthic animals that can live at different depths in a lake. High heterogeneity in shallow-water sediments probably is a major cause for the high species richness in the littoral zoobenthos.

Disturbance from wave-wash, ice-push, or fluctuating water levels often causes a zone of markedly reduced zoobenthic density and diversity near the water's edge, particularly in large lakes and reservoirs.

Finally, many of the biotic interactions that affect the zoobenthos are depth-dependent. Fish predation can have very large effects on the number, size, and species composition of benthic animals (**Figure 9**). The numbers and kinds of fish change from the littoral to the profundal zone; indeed, anoxic profundal sediments may be free from fish predation. Likewise, the density and kind of macrophytes, which are important in providing surfaces for attachment, shelter from predation, and food for benthic animals, change markedly with water depth, and can drive major changes in the zoobenthos. Thus, biotic interactions underlie much of the within-lake variation in the zoobenthos.

Most benthic animals are found near the sediment surface (**Figure 10**), presumably because food (benthic algae and sinking phytoplankton) and oxygen are most available there. Nevertheless, animals can be found deeper in lake sediments, sometimes

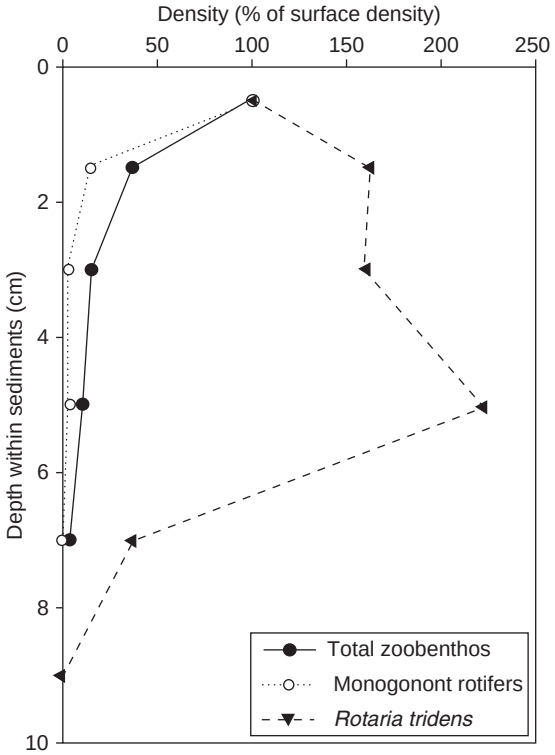

Figure 10 Vertical distribution of benthic animals within the sediments of Mirror Lake, New Hampshire. The three lines show the distributions of all benthic animals, a surface-dwelling taxon (monogonont rotifers), and a taxon that lives deeper in the sediments (the bdelloid rotifer *Rotaria tridens*). Modified from Strayer (1985).

reaching depths of more than 50 cm. Tubificid oligochaetes feed head down in the sediments, so it is easy to understand why they reach deep below the sediment–water interface, but the activities of other benthic animals that live deep within-lake sediments (e.g., some candonid ostracods, midges and bdelloid rotifers) are less well understood.

Variation across Lakes

Organic matter inputs, especially phytoplankton production, affect the numbers and kinds of benthic animals in lakes (**Figure 11**). Typically, lakes with higher organic matter inputs support more benthic animals (**Figures 3** and **11**), although there is some evidence that very high inputs of organic matter may actually reduce numbers of benthic animals, possibly by increasing the area of anoxic sediments. The kinds of benthic animals change with lake productivity as well. Indeed, one of the earliest systems for classifying the productivity of lakes was based on the composition of the profundal zoobenthos.

Lake morphometry has a strong influence on zoobenthic communities. Small, shallow lakes tend to support higher densities of benthic animals than do large, deep lakes. This pattern probably has at least three causes: (1) macrophytes, which support dense and diverse zoobenthic communities, are most abundant in small, shallow lakes; (2) shallow lakes are less likely to stratify than deep lakes, resulting in higher concentrations of dissolved oxygen at the sediment surface; (3) sinking phytoplankton (and other food particles) are less likely to be degraded before reaching the sediment surface in shallow lakes than in deep lakes.

Temperature affects both the number and kinds of benthic animals in lakes. Tropical lakes support different species than do temperate lakes (or arctic lakes), although groups such as chironomids, *Chaoborus*, and oligochaetes are abundant over wide latitudinal ranges. Warm lakes tend to support higher zoobenthic densities than do cold lakes.

Several aspects of water chemistry have strong effects on the zoobenthos. Saline lakes contain distinctive communities of benthic animals. Very salty lakes may contain just a few species of benthic animals, even though overall abundance or biomass of the zoobenthos may not be reduced. Soft water lakes of low pH and low calcium typically contain different species than do hard water lakes, and often are poor in shell-bearing animals (mollusks, ostracods) that need calcium to build their shells. Consequently, the recent acidification from atmospheric deposition has had important effects on the zoobenthos. High concentration of dissolved organic matter in lake water may reduce abundance of benthic animals.

Finally, differences across lakes in biotic interactions can have strong effects on the number and kinds of benthic animals. Only a few examples are well known. Fishless lakes usually contain large, active invertebrates (e.g., swimming or crawling insects) that are

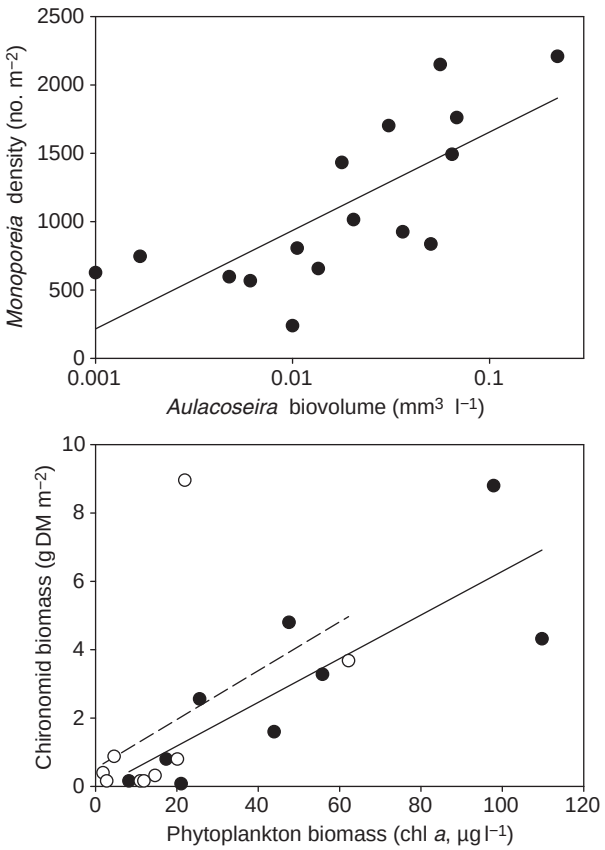

Figure 11 Examples showing the dependence of the zoobenthos on phytoplankton. The upper panel shows the numbers of the amphipod *Monoporeia affinis* in Lake Erken, Sweden, as a function of the amount of the important planktonic diatom *Aulacoseira* in the previous year ($r^2 = 0.54$, $p = 0.0008$). The lower panel shows the biomass of chironomids in April–May at two sites in Lake Balaton, Hungary, as a function of phytoplankton biomass in the previous summer (for black circles, $r^2 = 0.66$, $p = 0.008$; for white circles, $r^2 = 0.20$, $p = 0.23$). Adapted from Johnson and Wiederholm (1992) and Specziár and Vörös (2001).

quickly eliminated if fish are introduced. Crayfish and large bivalves can have strong effects on other benthic animals, as has been shown when invasions of lakes by alien crayfish and *Dreissena* have caused very large changes in benthic animal communities. It seems likely that other unstudied biotic interactions are responsible for variation in the zoobenthos across lakes.

Roles of the Lacustrine Zoobenthos

Secondary production by the zoobenthos in most lakes is modest (Table 2), and energy flow through the zoobenthos certainly is much smaller than that passing through microbial communities. Nevertheless, benthic animals play important roles in lake ecosystems, and even in human affairs. Broadly speaking, the ecological roles of the zoobenthos can be defined as food web or nontrophic roles.

As participants in lacustrine food webs, benthic animals consume phytoplankton, aquatic plants, animals, bacteria, and detritus. Consumption rates can be high enough to control the amount and composition of these food resources. The best-known examples involve the consumption of plankton by benthic animals. Suspension-feeders such as *Dreissena*, sponges, and cladocerans may be abundant enough to reduce phytoplankton biomass, or change its composition (Figure 12). Likewise, benthic animals that eat zooplankton (*Chaoborus*, mysids) can exert strong control on zooplankton communities, with effects that ramify through the ecosystem (Figure 16). Although relatively few benthic animals (crayfish, plant–parasitic nematodes, and some aquatic insects) eat or destroy aquatic plants, they can strongly affect macrophyte biomass and species composition; indeed, benthic animals have been used for biological control of nuisance weeds such as milfoil. Much less is known about the influence of the zoobenthos on attached algae, bacteria, and detritus, although these are the primary foods of most benthic animals. Further, some benthic animals have highly specialized diets and might therefore have selective effects on food resources. Benthic animals probably often control the

Table 2 Secondary production by the macrozoobenthos and zooplankton in several lakes, expressed as a percentage of net organic inputs to the lake

Lake	*Mean depth (m)*	*Net organic inputs (g C m^{-2} yr^{-1})*	*Production of zoobenthos (%)*	*Production of zooplankton (%)*
Tundra pond, AK	<1	26	7	0.8
Marion, BC	2	110	3	0.9
Myvatn, Iceland	2	330	6	1.3
Wingra, WI	3	610	0.4	4
Kiev Reservoir, Ukraine	4	280	6	7
Rybinsk Reservoir, Russia	6	93	0.3	2
Mirror, NH	6	49	12	5
Red, Russia	7	140	1	7
Findley, WA	8	12	6	2
Naroch, Belarus	9	160	0.8	5
Mikołajskie, Poland	11	260	2	21
Esrom, Denmark	12	160	6	7
Pääjärvi, Finland	14	60	3	12
Dalnee, Russia	32	260	1	22

Most benthic data exclude the meiofauna, and are therefore underestimates. Because of methodological differences among studies, data are only approximately comparable. Compiled from many sources.

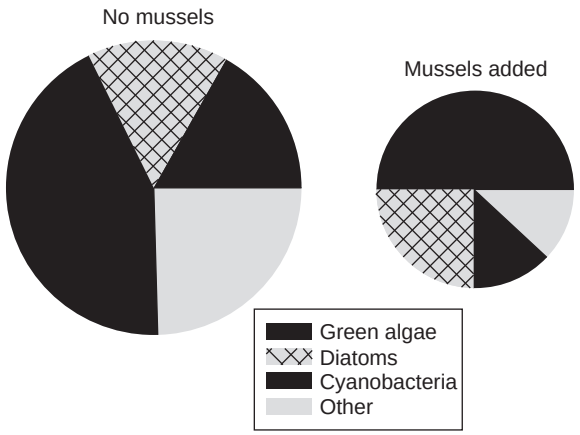

Figure 12 Changes in the amount and composition of phytoplankton in two small Dutch lakes following the experimental addition of *Dreissena polymorpha* to one of the lakes. The area of each circle is proportional to the biovolume of the phytoplankton in each lake. Adapted from data of Reeder *et al.* (1993).

amount and kind of attached algae in lakes, and it seems likely that most particles of detritus pass through at least one benthic animal before being buried in the lake bottom. Thus, there is ample evidence that benthic animals can control the amount and character of food resources in lakes, although we do not yet know how often and under what conditions such strong control occurs.

Benthic animals release nutrients such as inorganic nitrogen and phosphorus when they consume food. Such nutrient regeneration may be important to phytoplankton and attached periphyton in nutrient-limited lakes.

The predominant fate of zoobenthic production is to be eaten, whether by other members of the zoobenthos, fish, or terrestrial predators (**Table 3**). Consequently, the zoobenthos serves as an important link to higher trophic levels. Almost all lake-dwelling fish depend to some extent on zoobenthos, and benthic animals are the primary food of many fish species (**Figure 13**). Large populations of birds, bats, spiders, and other predators may be drawn to lakes or lakeshores to feed on benthic animals, including emerging insects.

Although it has been customary to treat the plankton and the benthos as belonging to separate food webs, many species of the zoobenthos depend either directly or indirectly on the plankton for food, and there are strong reciprocal links between the plankton and the zoobenthos. The pelagic and benthic zones of lake are linked by many strong connections (**Figure 14**), and function as an integrated system.

The major nontrophic role of the zoobenthos is sediment mixing (bioturbation). Three activities are important: (1) feeding, especially by conveyor-belt feeders such as tubificid oligochaetes, which feed in deep layers of the sediments and leave fecal pellets at the sediment surface; (2) burrow construction and ventilation, which are done by ephemerid mayflies and some chironomids; (3) ordinary locomotion by large, active animals such as *Chaoborus* and unionid bivalves. Bioturbation mixes sediments and

Table 3 Estimated fate of zoobenthic production in several lakes

Lake	*Production (gDM m^{-2} yr^{-1})*	*Fate (% of production)*			
		Invertebrate predation	*Fish predation*	*Bird predation*	*Emergence*
Myvatn, Iceland	42	5–52[a]	43	9	48
Mirror, NH	14	80	15	nd	25
Paajarvi, Finland	3.8	50	40	nd	6
Batorin, Belarus	2.6[b]	46	194	nd	nd
Naroch, Belarus	2.6[b]	22	42	nd	nd
Ovre Heimdalsvatn, Norway	2.4[c]	25–28[a]	70	2	3
Myastro, Belarus	0.8[b]	72	272	nd	nd

[a]Estimated by difference.

[b]Growing season only; macrobenthos.

[c]Macrobenthos.

Data are approximate, so percentages do not sum to 100%; nd = not determined. Data are from after various sources.

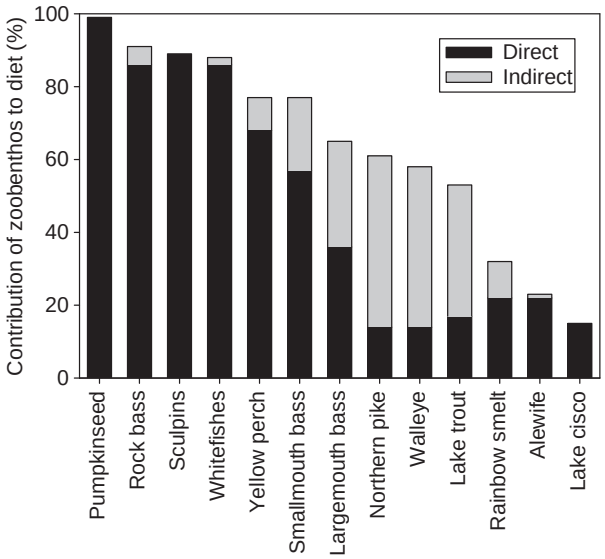

Figure 13 Contribution of zoobenthos to the diets of common species of fish in northeastern North American lakes. 'Indirect' consumption of zoobenthos is consumption of fish that were supported by zoobenthos. Adapted from data compiled by Vadeboncoeur *et al.* (2002).

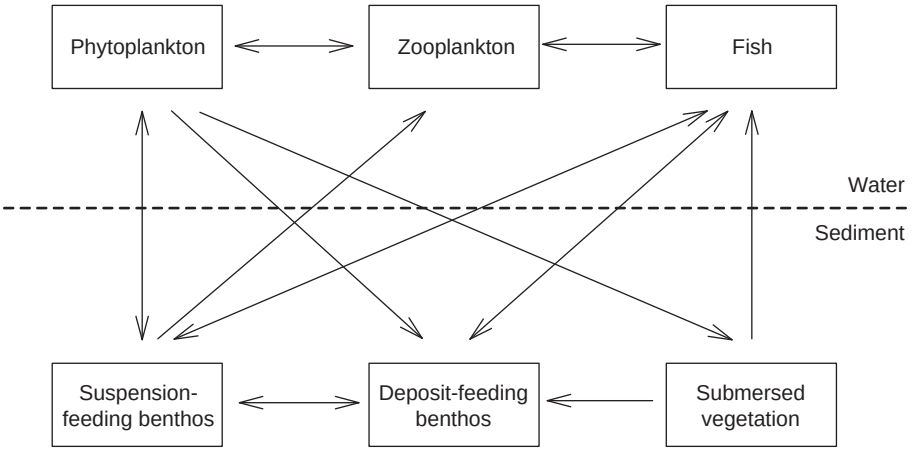

Figure 14 Major interactions between lacustrine communities (Strayer, 2006). Arrows show the hypothesized direction of control; note that many interaction arrows cross between the sediments and the pelagic zone.

increases exchange of dissolved substances (e.g., oxygen, ammonium) between the overlying water and the sediment pore-water. These activities can have large effects on nutrient regeneration and cycling and burial of toxins. In addition, shell-building benthic animals (chiefly large bivalves) can alter the character of benthic habitats through accumulations of their living and dead shells. Such shell accumulations, which can probably reach masses $>1 kg\ m^{-2}$, serve as habitat or spawning sites for other animals, as well as altering biogeochemical transformations at the sediment–water interface.

Applied Issues

Some of the most important diseases of humans and wildlife are carried by benthic animals. Chief among these are diseases caused by trematodes (or flukes), in which freshwater snails, and occasionally decapods, serve as intermediate hosts. In a typical life cycle (**Figure 15**), eggs shed from the definitive host hatch into swimming larvae (miracidia) that seek out and penetrate an aquatic snail. Many species of fresh-water snails serve as hosts for the various trematodes that affect humans, livestock, and wildlife. After undergoing development in the snail, a second free-swimming larval stage (the cercaria) may either enter the definitive host directly when the host is in the water, enter a second intermediate host (a fish or decapod), or encyst on an aquatic plant. The trematode passes from the second intermediate host or aquatic plant into the definitive host when uncooked fish, decapods, or aquatic plants are eaten. Adult trematodes may live in the intestines, liver, blood vessels, or lungs of humans or other vertebrates, and often cause chronic, debilitating diseases. The most important of the snail-borne diseases is schistosomiasis, a debilitating disease caused by the genus *Schistosoma*, which affects ~200 million humans throughout the tropical world. Other significant snail-borne diseases include liver flukes (especially *Fasciola hepatica* and *Opisthorchis sinensis*), which cause large damage to sheep and cattle, as well as affecting millions of people, and various intestinal or lung flukes, which affect many people around the world. Trematodes using freshwater snails as intermediate hosts also affect many vertebrate species other than humans. In fact, cercaria of trematode species that use birds as definitive hosts sometimes burrow into humans. Although such cercariae do not develop normally in humans, they can cause a skin irritation known as 'swimmer's itch' and thereby limit recreational use of lakes. The acanthocephalans are another important group of parasites carried by freshwater benthic animals. Adult acanthocephalans are intestinal parasites of many fishes and other aquatic vertebrates, and benthic crustaceans usually serve as their intermediate hosts.

Human-caused changes to natural habitats sometimes increase disease problems (e.g., impoundments have increased prevalence of schistosomiasis), and ecological interventions (e.g., habitat management, introductions of predators or other biological controls) may be implemented as part of integrated programs of disease control.

Other benthic species are pests. Fouling species such as *Dreissena*, *Corbicula*, and occasionally sponges and ectoprocts block water intakes and may force plant operators to use mechanical cleaning, biocidal chemicals, or pipe coatings to keep water flowing. It appears that large emergences of chironomid midges may be a major cause of 'hay fever' and asthma in some parts of the world. Mass emergences of lake-dwelling insects (chiefly ephemerid mayflies or chironomid and chaoborid midges) may be so large that they cause traffic hazards, produce windrows of dead insects that need to be cleaned up with heavy equipment, and even short-circuit power plants.

Although there has been some interest in biomanipulation to increase the positive impacts of benthic animals, or reduce their negative impacts, such efforts have not proceeded as far as in the pelagic zone, where biomanipulation is now widely practiced. At least three types of biomanipulation have been considered involving benthic animals. Because benthic

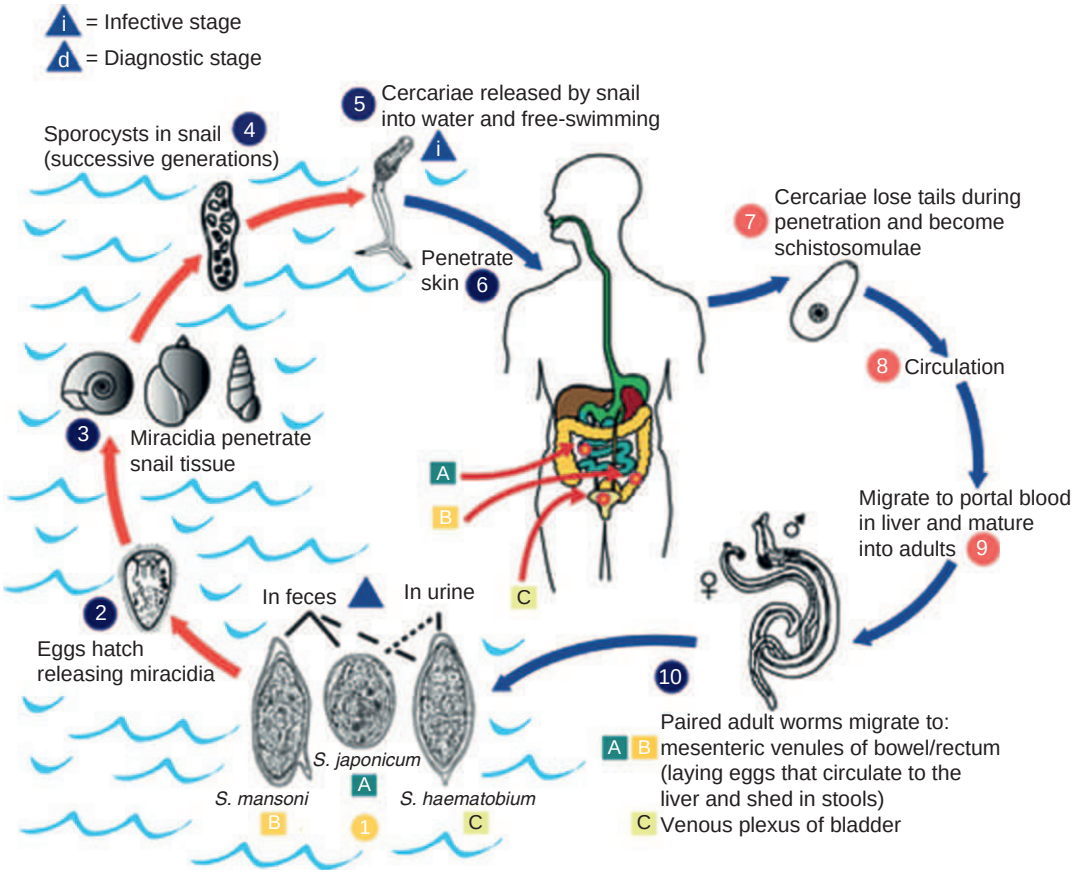

Figure 15 Life cycles of three species of the blood fluke *Schistosoma*. From the Centers for Disease Control.

suspension-feeders may control phytoplankton biomass and composition, some studies have sought to manage nuisance phytoplankton by increasing populations of benthic suspension-feeders (Figure 12). Benthic animals are valuable food for fish, so fisheries managers often have introduced large benthic animals (crayfish and the opossum shrimp *Mysis*) to lakes to increase growth rates or biomass of fish populations. Such introductions rarely have been supported by a careful analysis of likely impacts, and introductions of forage invertebrates sometimes have led to undesirable and unforeseen impacts (Figure 16). Finally, there have been a few attempts to increase populations of benthic animals to control populations of animals that carry diseases. Probably, the most prominent examples have been the additions of predators or competitors of the snails that carry schistosomiasis. Clearly, biomanipulation of lakes using benthic animals is still in its infancy.

Like other freshwater plants and animals, human activities have harmed some species of the lacustrine zoobenthos, which are now extinct or imperiled. Several activities have been especially harmful. Large water diversions have caused some lakes to become excessively salty or even dry up altogether, endangering or eliminating the benthic animals that formerly lived there. Many lakes have been badly polluted by toxins from industry and other sources or sediment from poor land-use practices. Nutrient loading from fertilizers or domestic wastes has increased the productivity of many lakes, leading to anoxic sediments, with obvious consequences for benthic animals. Many of the alien species (sport fish, aquatic plants, and invertebrates) that have been introduced into lakes around the world have had strong effects on benthic animals. An accounting of the summed effects of these harmful activities on benthic animals does not exist, but surely many populations in individual lakes have been imperiled or eliminated. In the case of ancient lakes that support endemic species of benthic animals, local extirpations would translate into global extinctions for the species. Extinctions among the endemic fish species of ancient lakes are well known, and presumably, such extinctions have occurred among the zoobenthos as well.

A few species of benthic animals are harvested from lakes or reservoirs for human use. Important fisheries for wild or cultured populations of various freshwater decapods (crayfishes, prawns, crabs) are scattered in lakes, ponds, and wetlands around the world. Several of the large bivalves have been harvested for millennia for food, pearls, and mother-of-pearl, although the largest fisheries for these animals are in rivers rather than in lakes. Particularly in the nineteenth century, large numbers (>10 million animals/year) of the medicinal leech (*Hirudo medicinalis*) were taken from the wild. Other members of the lacustrine zoobenthos (adult chaoborid midges, eggs and adults of corixid bugs, snails) are harvested in large numbers for human food locally.

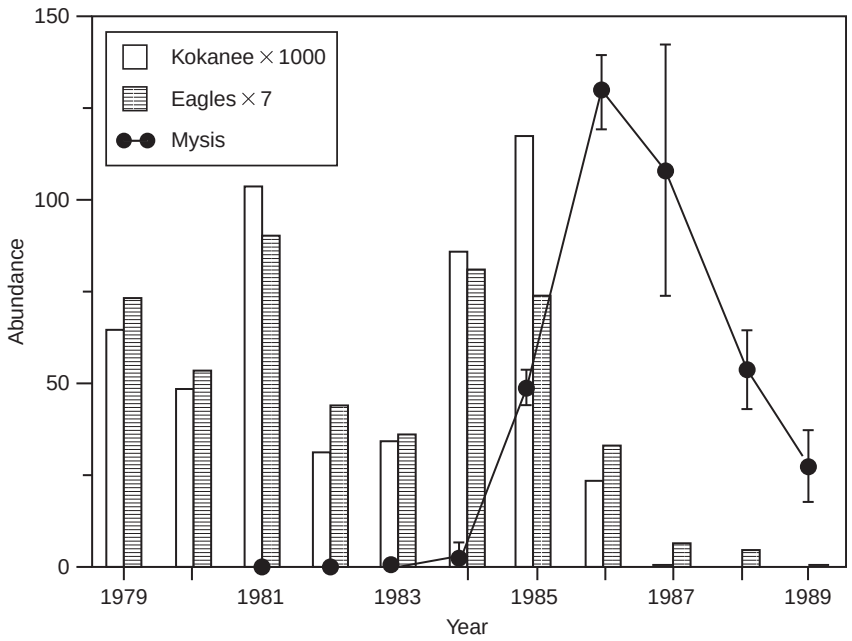

Figure 16 Undesirable effects following the introduction of the opossum shrimp *Mysis* to Flathead Lake, Montana. Data on kokanee salmon and eagles are peak counts from a tributary stream used by the salmon for spawning. Adapted from Spencer *et al.* (1991).

See Also: Structures and functions of Inland Waters - Lakes: Benthic Algae in Lake Littoral Habitats; Structures and functions of Inland Waters - Rivers: Energetics and Food Webs in Large Rivers; Structures and functions of Inland Waters - Wetlands: Benthic Invertebrates of Running and Stagnant Inland Waters

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Zooplankton Diversity and Variation Among Lakes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie-Elodie Perga and Damien Bouffard.

Glossary

Heterotroph An organism that cannot produce its own organic matter (e.g., by photosynthesis), but instead gains nutrition by consuming preexisting organic carbon sources.
Metabarcoding A method that allows the simultaneous identification of multiple species within environmental samples, using variations in the structure of short sections of DNA.
Metacommunity A set of local communities separated in space but that are linked by the dispersal of organisms among them.
Molecular Operational Taxonomic Units (mOTUs) Clusters of DNA sequences that are highly (often 97%) similar to each other, and can therefore be pragmatically considered as belonging to the same species.
Next generation sequencing High-throughput methods for determining the sequence of nucleotides present within sections of DNA.
Parthenogenesis A form of asexual reproduction, where embryos develop without the need for eggs to be fertilized by sperm.
Species richness The number of unique species found in a biological survey. This can be calculated at a single point in space and time, or cumulated.

 https://doi.org/10.1016/B978-0-12-819166-8.00013-X

Introduction

The zooplankton are a diverse grouping of small heterotrophic organisms that live in the open waters of aquatic habitats. They are of great importance for the functioning of aquatic ecosystems, consuming phytoplankton, bacteria and each other, while themselves being consumed by a range of invertebrate and vertebrate predators. As such, the zooplankton are important conduits for the transfer of energy through food webs, they influence water quality, and they sustain life at other trophic levels. Here, as a grounding for later chapters, I introduce some of the major taxonomic groupings of freshwater zooplankton, their traits, and their life cycles. I then address how the diversity and community composition of selected zooplankton groups varies among lakes, as a function of landscape and local lake habitat features. The focus is explicitly spatial (among-lake differences), though there are clearly temporal changes in zooplankton community structure as well.

Taxonomic diversity

Rather than a single, coherent taxonomic group, the zooplankton comprise a variety of multicellular animal taxa in addition to single-celled protists, such as ciliates and flagellates. Here, the focus is on multicellular members of the zooplankton community: the rotifers and planktonic crustacea.

Rotifers

The Rotifera (once known as "wheel animalcules") are a Phylum of small (50–2000 μm), primarily freshwater zooplankton, dominated by two major groupings; the Monogononta and Bdelloidea. Collectively, these groups include an estimated >1900 species capable of inhabiting fresh water, though this may be an underestimate, given incomplete taxonomic knowledge and the likely presence of cryptic species. Many species are very widely distributed at a global scale, though there are some cases of regional endemism. Rotifers can be found across a wide variety of freshwater habitats, from large lakes and reservoirs, to small ponds, temporary puddles, birdbaths, and even the interstitial waters within sediment layers and films of water on mosses and liverworts. Within a specific freshwater ecosystem, rotifers will be found not just in the open water (true zooplankton), but also in littoral and benthic zones. A number of species crawl or attach to substrates, or are sessile: indeed, a relative minority of the total known number of rotifer species are truly planktonic.

Rotifers are highly variable in morphology (Fig. 1), but consistently possess an anterior region of hair-like cilia (called a corona) which is used for food collection and locomotion, a defined pharynx (the mastax), and hardened jaws (trophi) adapted for grasping, piercing, or grinding prey. Most rotifer species exist as single individuals, though colony formation occurs in some cases (e.g., *Conochilus unicornis*).

Cladocera

The Cladocera are a group of microcrustaceans (Phylum Arthropoda), comprising four known Orders: the Anomopoda, Ctenopoda, Haplopoda and Onychopoda. Most species occupy a body size range of 0.2–6 mm. However, the highly-transparent predator *Leptodora kindtii* is considerably larger, approaching 2 cm in length. At a global scale, the number of species has been estimated at 400–500, or even around 620, with a number of regional endemics. However, this is likely to be an underestimate since, as for rotifers, many cryptic species may exist. Cladocerans may be found in a wide range of water body types, including large and small lakes, ponds, and slow-flowing rivers. Some species are truly planktonic, while others live in association with littoral and benthic habitats. For example, *Sida crystallina* (Ctenopoda) may attach to submerged plants while filter feeding, and members of the Chydoridae (Anomopoda) may be observed crawling along strands of filamentous algae as they scrape for food.

A large compound eye (sometimes accompanied by a light-sensitive ocellus) is a conspicuous feature of cladoceran species (Fig. 2). In addition, cladocerans have large second antennae, which are used for swimming or crawling, for pelagic and benthic species, respectively. For many species (those in Orders Anomopoda and Ctenopoda), the body is enclosed in a bivalve carapace. In members of the Onychopoda and Haplopoda, such as *Bythotrephes longimanus*, *Polyphemus pediculus* and *Leptodora kindtii*, this carapace is much reduced to a brood pouch positioned on the thorax.

Copepods

The Copepoda are a Subclass of small crustaceans (Phylum Arthropoda). Although over 2800 known species of copepod inhabit freshwaters, a great many more species are found in marine environments. Freshwater species are found within five Orders, namely the Calanoida, Cyclopoida, Harpacticoida, Gelyelloida, and Siphonostomatoida. Collectively, these species inhabit a very wide range of freshwater habitats, from large lakes to small ponds, groundwater and small pools of water trapped within terrestrial plants (called phytotelmata). Within lake environments, copepod species differ in their habitat use, with some adopting a planktonic, open water existence, while others live in association with submerged plants and surface sediments. Others still are parasitic, particularly on fish and molluscs. Although some species are widely-distributed at a global scale, the overwhelming majority appear to be endemic to single zoogeographic regions, or indeed single (often ancient) lakes.

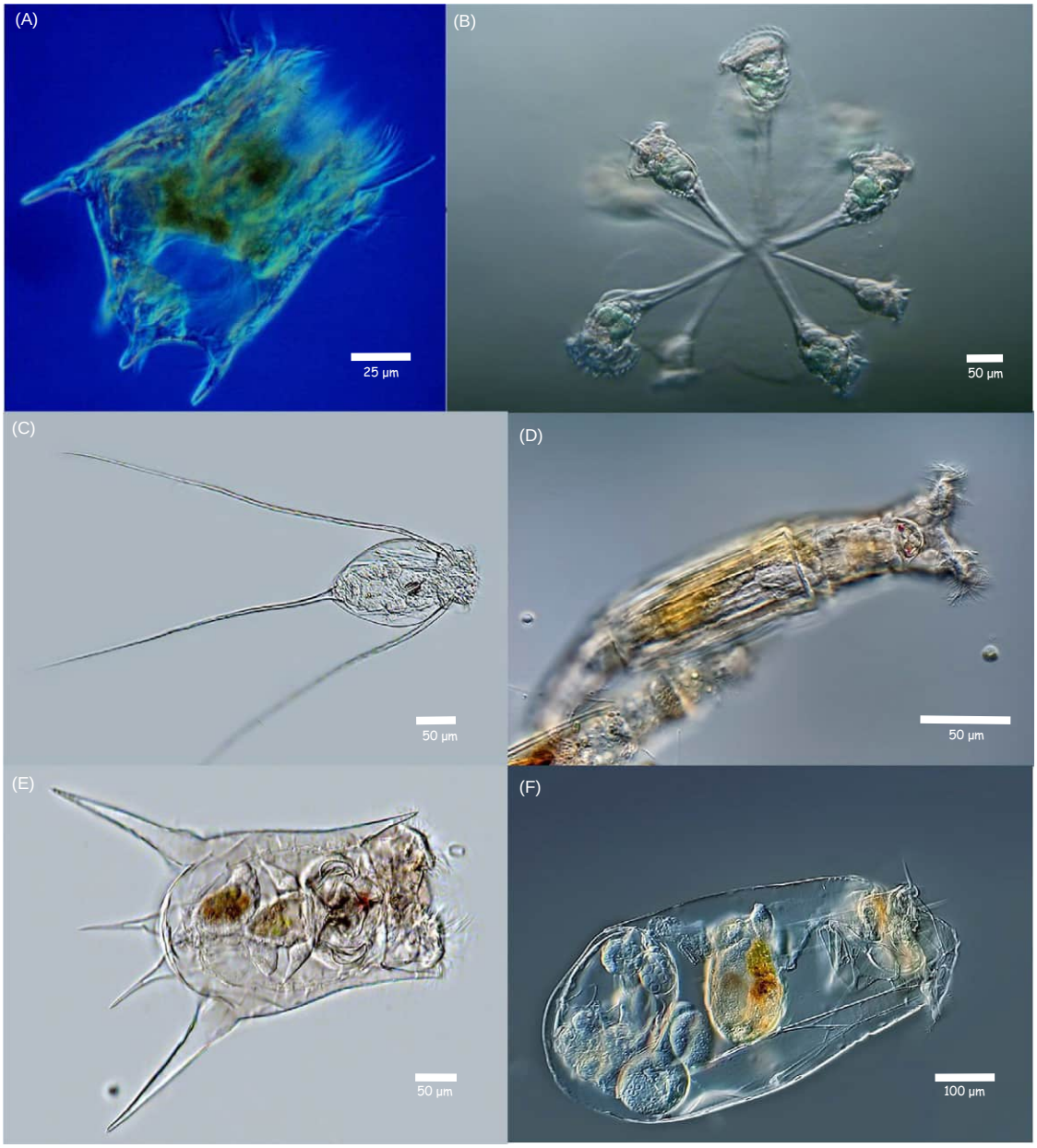

Fig. 1 Examples of rotifer diversity. (A) *Plationus patulus*, (B) *Conochilus unicornis*, (C) *Filinia longiseta longiseta*, (D) *Rotaria rotatoria*, (E) *Brachionus calyciflorus anuraeiformis*, (F) *Asplanchna priodonta*. Note differences in scale. Image credits: (A) Stephanie Hampton, (B–F) Michael Plewka, www.plingfactory.de.

Many freshwater copepod species are of the order of 1–2 mm in size, though some species exceed this. They have jointed appendages and highly-segmented bodies (Fig. 3), which comprise an anterior section (the prosome) and posterior section (the urosome). Thoracic appendages, used for feeding and locomotion, are attached to the prosome. The first antennae of copepods are armed with an array of chemo- and mechanoreceptors that are used to detect potential food items, mates, and predators.

Other members of the zooplankton

Though much research on the environmental drivers of zooplankton diversity has focused on rotifer, cladoceran and copepod communities, it is important to recognize that, in some water bodies, other taxa can contribute to the zooplankton assemblage. These may include other crustaceans, such as freshwater members of the Mysidae (e.g., the opossum shrimp, *Mysis relicta*) and ostracods. Numerous insect species may also join the zooplankton assemblage during their larval and pupal stages (e.g., chironomids). A notable insect addition to the plankton of many lakes is the larval stage of the "phantom midge" (*Chaoborus* spp.); insects that can be voracious and influential predators of other members of the zooplankton community.

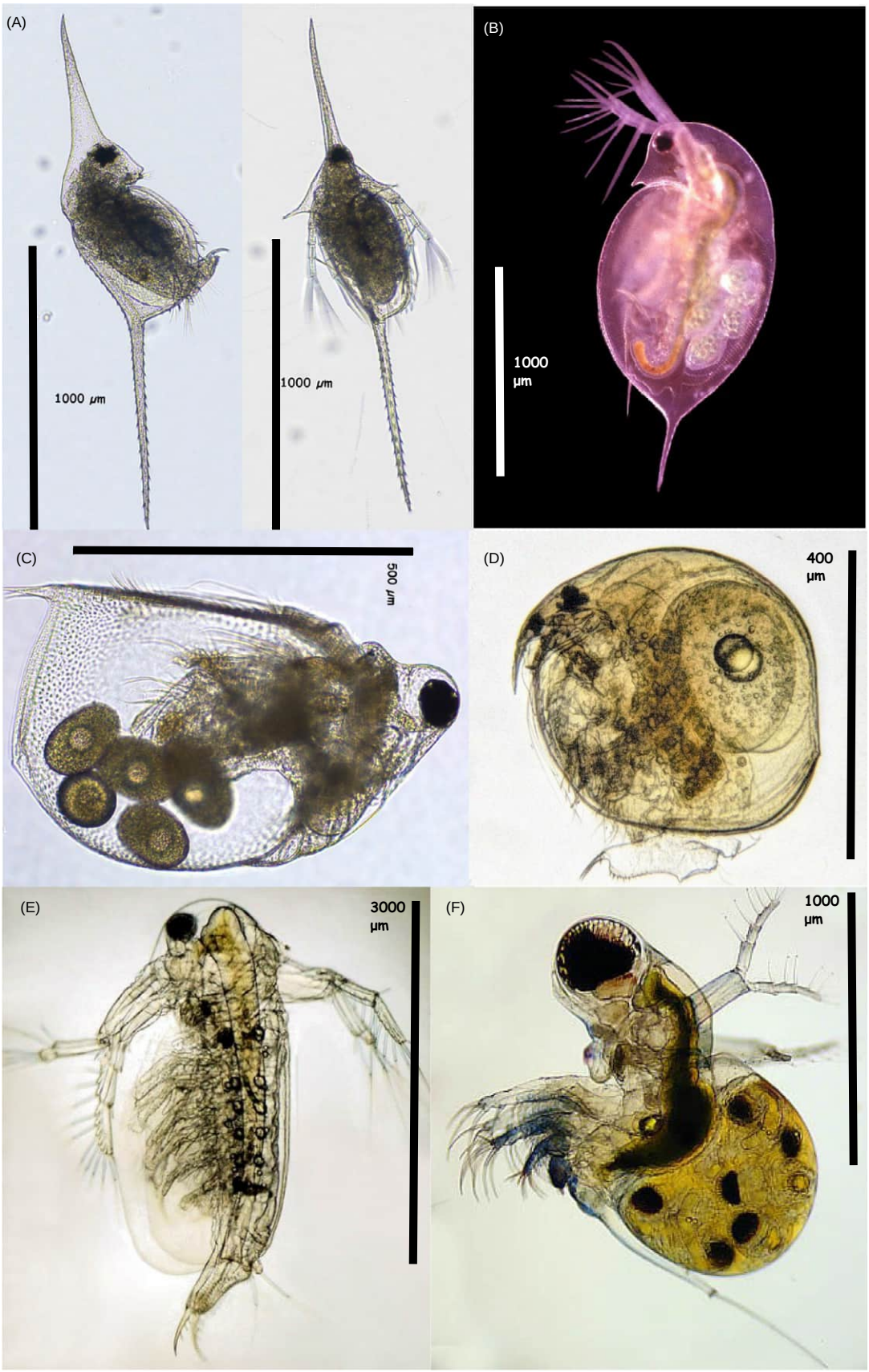

Fig. 2 Examples of cladoceran diversity. (A) *Daphnia lumholtzi*, (B) *Daphnia longispina*, (C) *Scapholeberis* sp., (D) *Chydorus sphaericus*, (E) *Sida crystallina*, (F) *Polyphemus pediculus*. Note differences in scale. Image credits: (A) and (C) K. David Hambright, (B), (D–F) Adrian Chalkley.

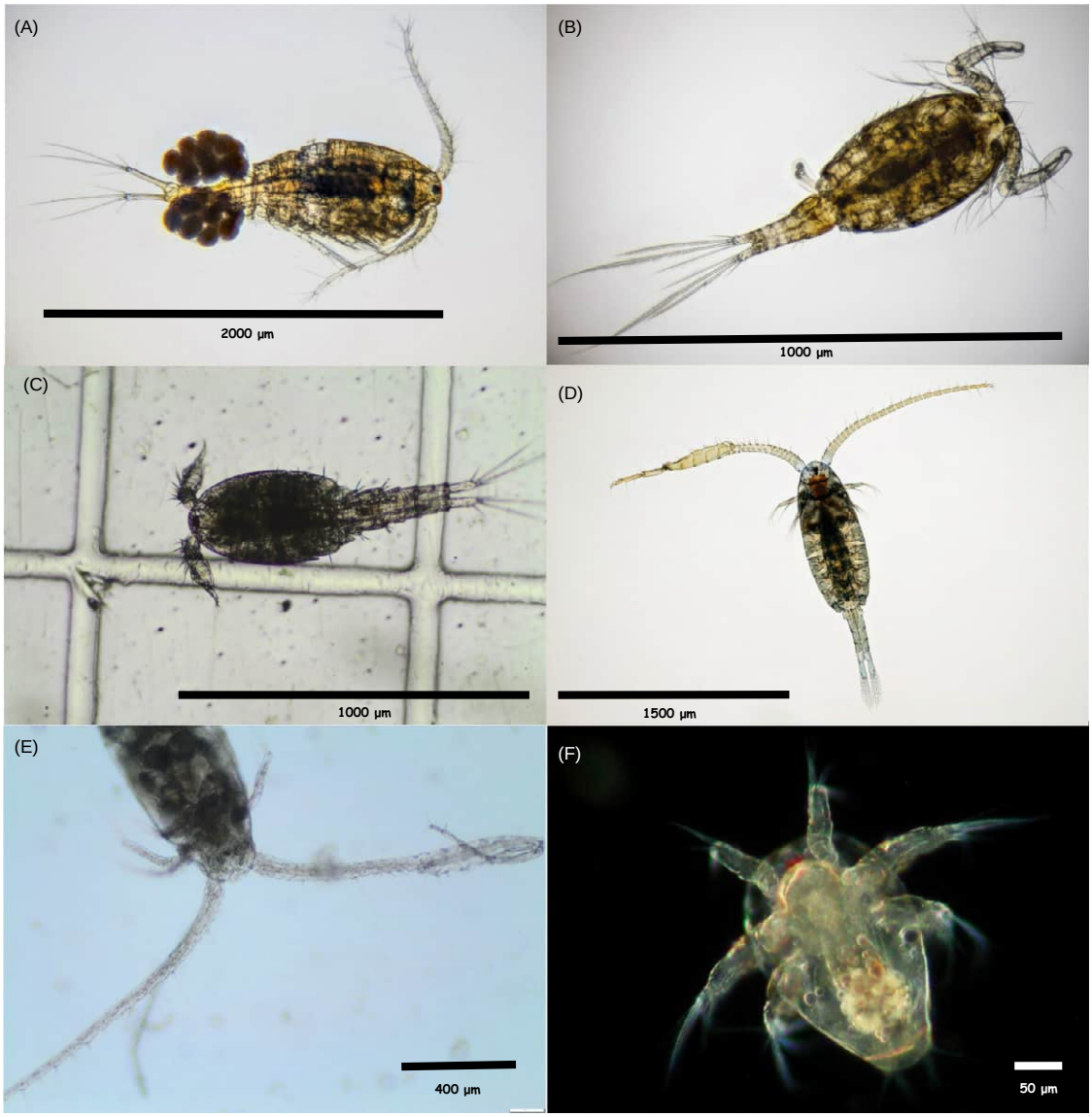

Fig. 3 Examples of copepod diversity. (A) *Cyclops strenuus abyssorum* (female), (B) *Macrocyclops albidus* (male), (C) *Paracyclops fimbriatus*, (D) *Arctodiaptomus wierzejskii* (male), (E) *Eudiaptomus gracilis* (male, close up of antennae), (F) copepod naupliar (juvenile) stage. Note differences in scale. Image credits: (A), (B), (D) Kenny Gifford, (C), (E) Stephen Thackeray, (F) Michael Plewka, www.plingfactory.de.

Life cycle diversity

Different species within freshwater zooplankton communities adopt widely-varying life cycle strategies. These life cycle attributes play an important role in determining the way in which zooplankton respond to environmental conditions, and the time scales over which these responses will manifest.

Cyclic parthenogenesis

Asexual reproduction, without fertilization (parthenogenesis) is commonplace within the rotifers and cladocerans, and may alternate with bouts of sexual reproduction (a pattern known as cyclic parthenogenesis). During the parthenogenetic phase of the life cycle, and under favorable environmental conditions, female individuals produce eggs that develop, without fertilization, into a new generation of adult females. However, certain triggers (e.g., food shortage, overcrowding, change in temperature or day length) can initiate the production of males and sexual reproduction, the result of which is fertilized resting eggs. Resting eggs, often more thick-walled than their unfertilized counterparts, lay dormant (a state known as diapause) until development and hatching are triggered by environmental conditions.

In the case of the rotifers, diploid, amictic females produce diploid eggs by mitosis. Often, a single egg is produced, and is carried by the female, though in some cases these are attached to plants or released freely into the water. In monogononta rotifers, the switch to sexual reproduction is marked by the meiotic production of haploid, mictic eggs that hatch, if unfertilized, into male rotifers. The males, often smaller and much simplified compared to the females, fertilize other haploid eggs, to produce diploid resting eggs.

In many ways, the cladoceran life cycle is similar, with amictic females producing amictic eggs under favorable conditions. However, for cladocerans, the switch to sexual reproduction involves the production of diploid, not haploid, males, which fertilize haploid eggs. As in the case of rotifers, though, the result is the production of toughened resting eggs. These resting eggs are deposited in a hardened pouch, called an ephippium. In the parthenogenetic phase of the cladoceran life cycle, offspring develop from the egg inside the adult female brood pouch, and are released as free-swimming individuals.

Obligate sexual reproduction

Sexual reproduction is commonplace in copepods with both male and female individuals comprising the total population, although a minority of harpacticoids reproduce asexually. There is sexual dimorphism, in that the sexes may differ in body size, as well as in appendage structure. An especially notable feature is that male copepods have major points of articulation on their antennae that allow them to grasp females during copulation. In male cyclopoids, both antennae are modified in this way, whereas in calanoids only the right antennae is typically modified. In the case of calanoids, the right-hand 5th thoracic limb also bears spines that allow the female to be grasped, and sperm transferred, during mating. Fertilized eggs are, for many species, carried in sacs at the rear of the body; typically a single sac for calanoids, and two sacs for cyclopoids. However, some species release their eggs directly into the water, rather than retaining them in sacs. Though eggs frequently develop without delay, some harpacticoid and calanoid copepods can produce resting eggs, which enter a state of diapause. For cyclopoid copepods, diapause typically occurs in sub-adult or adult stages, rather than in the egg stage. In comparison with rotifers and cladocerans the copepod life cycle is complex, comprising six naupliar stages, and five copepodite stages, before adulthood.

Diversity of feeding modes/ecology

All zooplankton face the challenge of obtaining their food from a highly dynamic fluid medium. Approaches to food acquisition vary among species, affecting which prey resources are consumed, how they are located and handled, and the extent to which consumers can actively select for specific prey items. Even species demonstrating the same broad feeding mechanism may feed on different size ranges of particles, or demonstrate a degree of food selectivity based upon factors other than food particle size. These feeding behaviors therefore underpin the way in which zooplankton interact within freshwater food webs, and we can expect that differences in zooplankton diversity and composition will determine the cumulative "grazing" effect that these consumers have upon phytoplankton communities.

Filter feeding

Many cladoceran species filter feed, generating water currents by beating thoracic appendages enclosed within their bivalve carapace. This motion carries particles into a "food groove" between these limbs. The limbs themselves are armed with hair-like setae and setules, and these filters are scraped by other limbs in order to pass food towards the mouth. Filter feeding is considered to be non-selective, though the rejection of non-preferred food items is possible. Cladocerans may reject such items by "kicking" them away from the feeding groove using their post-abdominal claw.

Suspension feeding

Suspension feeding generally involves the generation of water currents that carry small food particles (such as bacteria, protists, microalgae) towards the mouth. In the case of rotifers, these currents are generated by rhythmically beating the anterior cilia. Food items may be ejected by the oral canal or cilia, rather than ingested. Calanoid copepods may also suspension-feed on small particles by vibrating appendages on the prosome in order to create a current that draws food items close enough to the mouthparts that they can be ingested.

Selective and raptorial feeding

Many predatory zooplankton adopt a raptorial feeding mode. This is commonplace within the cyclopoid copepods for which individuals have been observed attacking large prey, such as the larvae of chironomid midges. Raptorial feeding is known for some rotifers, such as the large predatory species *Asplanchna priodonta* which can grasp and ingest smaller rotifers. A number of predatory cladocerans also feed raptorially, such as *Leptodora kindtii*, *Bythotrephes longimanus*, *Polyphemus pediculus* and *Cercopagis pengoi*. This mode of feeding is highly selective, in that individual prey are targeted and consumed, and is generally associated with the consumption of larger prey items than is the case for filter or suspension feeding. Interestingly, calanoid copepods and *Bosmina* can also selectively grasp individual prey items in addition to suspension and filter feeding, respectively.

Scraping

While pelagic species typically employ the feeding mechanisms introduced above, it is noteworthy that many littoral species also scrape the biofilm of underwater surfaces in order to gather food. As an example, such an approach is adopted by certain bdelloidea rotifers (e.g., *Adineta*) and cladocerans (e.g., *Alona* spp.).

Quantifying zooplankton diversity

Before examining the ecological drivers of zooplankton diversity among water bodies, it is worth noting that there are in fact a great number of ways of quantifying diversity itself.

What is diversity, anyway?

In a large number of studies, diversity is expressed in terms of taxonomic (often species) richness; the number of unique taxa found in a defined set of samples. The species complement does indeed appear to vary among water bodies, and in ways that can be at least partially explained by measured ecological factors. However, this measure alone provides no information on the relative abundances of the species involved, and so would be insensitive to situations in which the dominance patterns of species changes, but the species richness does not. To address this issue, some studies have used measures of diversity that account for relative abundance (e.g., Shannon's H). As a single number summary of a community, these measures do not explicitly reveal changes in the identity of the species involved; which particular species are present, and dominate in different communities. Of course, there are analytical approaches that can account for such variation. However, the key point here is that it is important to consider which diversity measurements are most relevant to any given ecological hypothesis or question.

Sampling considerations

When examining patterns in zooplankton diversity, it is also important to recognize that estimates of zooplankton diversity are sensitive to variations in survey design, sampling effort, sample collection, and sampling processing procedures. A diversity of sampling gear and methods are used to collect zooplankton in the field. Net tows are commonly used, though net designs vary among studies. Aspects of net design can fundamentally affect diversity estimates. Nets with coarse mesh sizes will fail to capture small species and life stages, producing samples that give a biased estimate of overall diversity. While finer mesh sizes will, in principle, allow the collection of smaller species, and produce less biased data, they are more prone to clogging by algae and other suspended matter. This will, in turn, reduce net filtration efficiency. Net mouth diameter also has implications for diversity estimates, since larger nets are more likely to capture rare species and minimize net avoidance. Means of deployment also vary; samples may be collected by vertical tows from all or part of the water column, or by horizontal tows. Given the spatial heterogeneity of zooplankton populations, such deployment decisions will also influence diversity estimates.

Other sampling gears are often used. For example, transparent Schindler-Patalas plankton traps are also commonly deployed in place of net tows. In addition, some investigators use pumps to draw samples from different depths, for subsequent filtration. Tube samplers are also used, especially in littoral areas where net sweeps may underrepresent plant-associated species. Among-lake estimates of zooplankton diversity are therefore very likely to be affected by variations in key aspects of the sampling process, for example differences in net mesh size, in the volume of water collected or filtered for a single sample, and in the likelihood that sediment- or plant-associated species are collected alongside true planktonic forms.

Furthermore, one would expect to find more species if searching a large number of samples collected at different locations and depths throughout a water body, and over time, than if analyzing only a single zooplankton sample. This is simply because spatial and temporal sample replication will capture community variation among habitat types within a water body, and as part of seasonal succession. Even within a specific habitat type, such as the pelagic zone, zooplankton communities are patchily distributed due to the effects of water movements, swarming and migratory behaviors, and variability in food concentrations. In addition to this dependence of diversity estimates on sample replication, the number of species "discovered" within any specific sample will vary according to whether the whole sample is searched, or only a sub-sample of it. When comparing diversity among water bodies, methodological inconsistencies are likely to add additional among-water body variation in zooplankton diversity which is not likely to be correlated with environmental drivers, and might partially obscure correlations between diversity and its drivers.

Advances in monitoring zooplankton diversity

Much of our knowledge of the structuring of zooplankton communities is derived from the analysis of samples by light microscopy. However, the toolbox available to freshwater ecologists is ever expanding, and recent methodological innovations promise to deliver high volumes of new, complementary data that will further shed light on zooplankton community dynamics.

It is now becoming possible to use imaging technologies to analyze zooplankton community samples (Fig. 4A). By circulating collected samples through instruments equipped with high speed cameras, it is possible to rapidly gather images of individual organisms, count their abundance, and calculate measures of size and shape. In principle, statistical analysis of the recorded size and

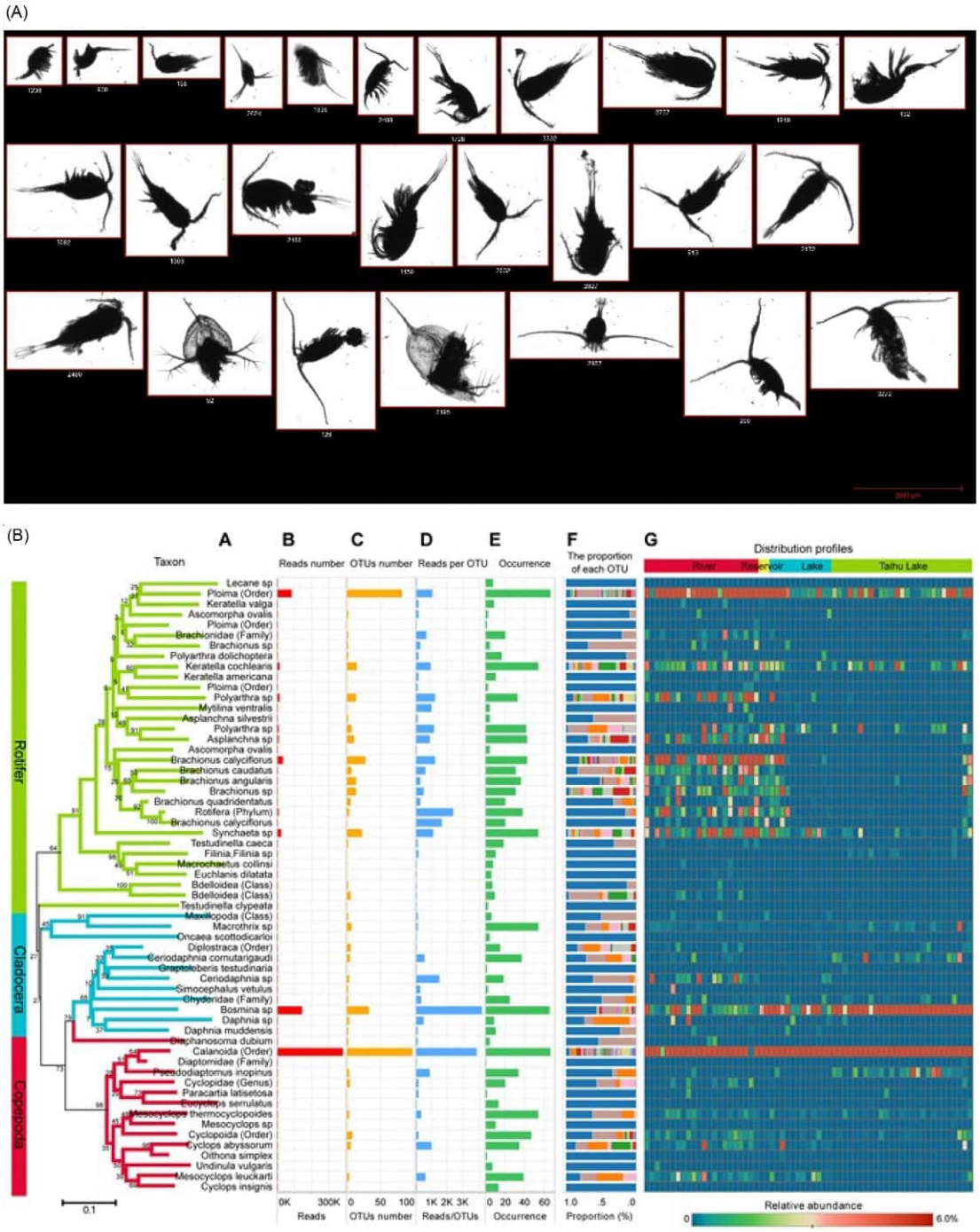

Fig. 4 Examples of modern methods. (A) Images of crustacean zooplankton from a FlowCam® Macro (Yokogawa Fluid Imaging Technologies, Inc.). (B) Molecular analysis of zooplankton diversity. Phylogenetic distribution of assignable components of zooplankton CO1 diversity. (a) A tree diagram of the representative sequence of each taxon. Distance was measured by the number of base substitutions per site, based on the Kimura two-parameter (K2P) method. One thousand bootstrap trials were run using the neighbor-joining algorithm of the Mega 6.0 program. (b) Number of reads of each taxon. (c) Number of OTUs of each taxon. (d) Number of reads per OTU. (e) Occurrences of each taxon in all samples. (f) Proportions of OTUs in the same taxon. Different color represents different OTU, and stacked bar means relative abundance of each OTU. (g) Distribution of each taxon in all samples. The color weighted by relative reads abundance (e.g., 0.01 means the number of reads for this taxon accounts for 1% of total number of reads). (B) Reproduced from Yang J, Zhang X, Xie Y, Song C, Zhang Y, Yu H and Burton GH (2017) Zooplankton community profiling in a eutrophic freshwater ecosystem-lake Tai Basin by DNA metabarcoding. *Scientific Reports* 7: 1773. https://doi.org/10.1038/s41598-017-01808-y.

shape data may allow the automatic identification of taxa in samples based upon their morphological distinctiveness. However, much methodological development is needed to realize this potential. While this continues, images from these instruments can be manually inspected by experienced taxonomists, to allow identification. Interestingly, success in finding rare species by these means is strongly dependent on the abundance of those species and the level of counting effort (the total number of individuals examined), as is the case for traditional light microscopy (Stanislawczyk et al., 2017).

It has been suggested that DNA-based approaches to diversity assessment may overcome some of the uncertainties that can confound traditional, microscopically-derived data, such as inconsistencies in taxonomic identification among analysts, hybridization, and high within-species morphological variability. Furthermore, these approaches potentially allow the rapid quantification of diversity in large numbers of samples, a process that would be time consuming via traditional means. Such methods are based upon metabarcoding of particular gene regions (e.g., the cytochrome *c* oxidase I, COI, region of mitochondrial DNA), following DNA extraction from collected zooplankton samples (Fig. 4B). Using Next Generation Sequencing (NGS) of the extracted DNA, it is possible to identify molecular Operational Taxonomic Units (mOTUs) that are present within that sample, and to subsequently assign these to known zooplankton species using reference databases such as GenBank® and the Barcode of Life Data System (BOLD). This method of diversity assessment shows great promise, delivering data that are consistent with that from more traditional microscopic approaches, and allowing the identification of differences in zooplankton community composition among water bodies (Yang et al., 2017). However, to be effective, DNA-based approaches require careful methodological optimization and, crucially, the inclusion of a wide diversity of zooplankton species sequences in reference libraries. Furthermore, there is active debate regarding the ability of DNA-based approaches to deliver data on species (relative) abundances, in addition to species presence/absence, and thus richness.

Within-species diversity

To date, most research on zooplankton communities has focused on interspecific diversity. However, thanks to DNA-based methods, we now know that, even "within" a species there can exist considerable variation. Populations of the same zooplankton species, but in different water bodies, may be genetically distinct from each other. Such within-species diversity has been demonstrated for a number of species, for example *Daphnia longispina* in the Pyrenees (Ventura et al., 2014) and *Sinocalanus tenellus* in China (Wang et al., 2018). Numerous mechanisms could account for such patterns, including colonization history, dispersal limitation, and local adaptation to environmental conditions. Genetically-distinct lineages of a given species may appear morphologically identical and are sometimes referred to as cryptic taxa. Therefore, without molecular approaches, this aspect of diversity would be invisible to us.

Traits, as well as taxonomy

The majority of existing research into patterns and drivers of zooplankton diversity has adopted a taxonomic approach, where diversity is expressed in terms of the numbers and relative abundances of species, or genera. However, an alternative approach is to consider diversity from a more functional perspective; in terms of the ecological roles that organisms play, and the traits that determine the way in which they respond to, and affect, the wider ecosystem. Functional traits characterize key features of the life-history, population dynamics, and food web interactions of zooplankton taxa, and then permit the delineation of functional groups; sets of species that share similar traits. The excellent paper by Barnett et al. (2007) demonstrates this approach, synthesizing information on body size, habitat use, trophic group and feeding type for 36 North American crustacean zooplankton species, and grouping them into five distinct functional groups. These groupings were not simply a reflection of taxonomy, since the predatory cladoceran *Polyphemus pediculus* was included in the same functional group as a number of omnivorous and carnivorous copepods, while small herbivorous Cladocera were grouped together with herbivorous-omnivorous calanoid and cyclopoid copepods.

Functional approaches to investigating the ecological significance of zooplankton diversity show great potential to clarify links between diversity, ecosystem structure and function. However, important decisions must be made regarding the application of such an approach. For example, investigators will need to consider how many, and which traits are needed to capture the most important aspects of species' ecological roles, and whether these trait data are already available for many species. Furthermore it is important to recognize, and incorporate where possible within-species variation in traits that may arise through growth and development (e.g., juveniles vs. adults), and due to differences in the experimental and field conditions under which they are measured.

Drivers of zooplankton diversity

Zooplankton diversity and community composition vary greatly among water bodies, and these patterns are determined by a range of local and regional scale processes (Fig. 5). While the natural or human-aided dispersal of zooplankton allows species to reach new habitats, the successful establishment of newly arriving species is mediated by physical, chemical and biological features of the recipient water body (Lukaszewski et al., 1999; Shurin, 2000). We must therefore consider zooplankton diversity from a meta-community perspective; as the product of both dispersal among water bodies, and the influence of habitat features that determine which species can survive and reproduce. Here I introduce some of the key habitat features and processes that have been implicated in determining zooplankton diversity though, in reality, there is a great deal of complexity in the way that these factors interact to affect community composition.

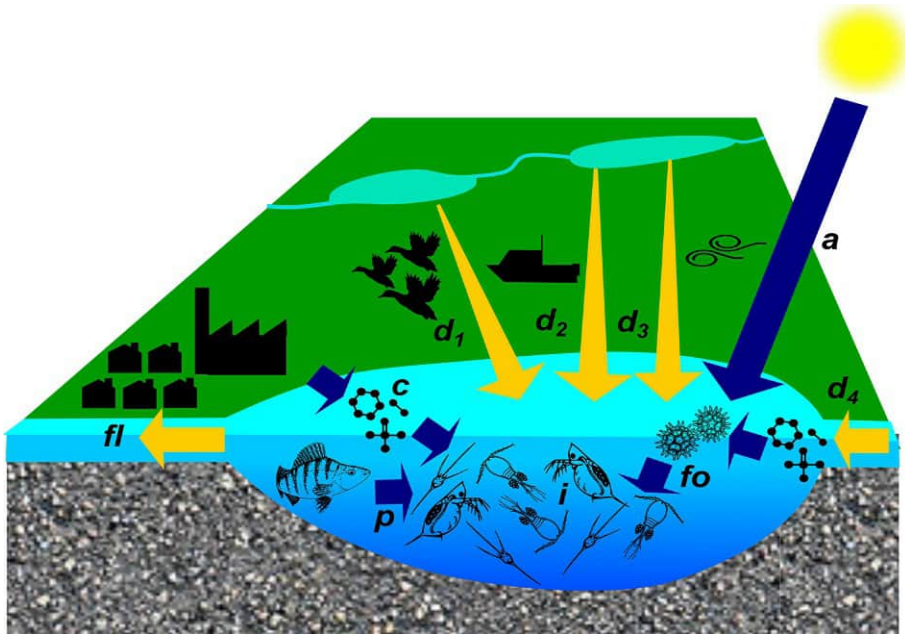

Fig. 5 Example drivers of zooplankton diversity. Local diversity arises as a result of the combined influence of both water body and landscape-scale factors. New species may reach a specific water body through dispersal via other organisms (d_1), human movement among water bodies (d_2), aeolian transport of propagules (d_3), or connections to upstream water bodies (d_4). Local features of the water body environment influence the species that establish; predation (*p*), food quality and quantity (*fo*), interspecific interactions within the zooplankton (*i*), inputs of contaminants (*c*), and flushing (*fl*). Climatic and atmospheric factors (*a*) can also influence diversity through inputs of energy, UV, and acid deposition.

Water body morphometry

Lake morphometry has long been recognized as a correlate of zooplankton community richness. Species richness has often been observed to increase with lake surface area and, sometimes, depth (Dodson, 1992; Merrix-Jones et al., 2013). It has been suggested that this correlation arises because zooplankton immigration rates and lake habitat complexity (the diversity of available niches) increase, while extinction rates decrease, with lake size (Dodson, 1992). However, these patterns are not universally observed (Hessen et al., 2006), possibly because of overriding effects of intrinsic ecosystem properties, and sampling issues. Indeed, it has been suggested that small water bodies might support comparatively high species diversity, if they lack fish (Scheffer and van Geest, 2006). Correlations between lake morphometry and diversity could be mediated by food web structure. Given that deeper, larger lakes tend to have longer food chains (Post et al., 2000), the presence of piscivores reducing planktivore fish feeding pressure could also drive zooplankton communities toward dominance by larger Cladocerans (Carpenter et al., 2001), potentially influencing richness.

Climatic considerations

Zooplankton species richness and composition have been shown to vary with elevation and latitude; patterns that suggest a role for climatic factors in determining diversity. For example, maximal richness values decline at high latitude and elevation across Norway (Hessen et al., 2006), cladoceran species richness declines from south-to-north throughout Canada (Henriques-Silva et al., 2016), and zooplankton compositional change occurs among fishless North American lakes spanning an elevation gradient (Symons and Shurin, 2016). Changes in zooplankton community composition have also been more directly correlated with large-scale temperature and precipitation gradients (Loewen et al., 2019). Lower local or regional-scale species richness in locations with lower temperatures and incoming solar radiation suggest that zooplankton communities may follow the predictions of the species-energy hypothesis, which posits that higher energy inputs support a greater number of species, by stimulating ecosystem productivity, and thereby reducing the chances of species' populations declining to extinction (Pinel-Alloul et al., 2013; Lyons and Vinebrooke, 2016).

It has also been suggested that temperature and diversity may be linked through overlaps in species distributions. This would result in a hump-shaped relationship between species richness and temperature, with maximum species richness at intermediate temperatures, and declines in cooler or warmer systems (Patalas, 1990). The proposed mechanism is that, over the intermediate temperature range, southern warm-water and northern cool-water species would potentially coexist, resulting in a comparatively high diversity. Interestingly, it may not be just average temperature that is correlated with zooplankton species richness, but also temporal variability in water temperature (Shurin et al., 2010). It is thought that lakes that demonstrate strong temperature variation over time allow larger numbers of species to coexist, since those species can occupy niches that occur at different points in time, during periods of either water column mixing or stable thermal stratification.

Additional physical factors

Water flow and availability have clear effects on zooplankton diversity. It has been suggested that differences in water residence time, especially, may act as a potential determinant of the composition of large-bodied crustacean zooplankton communities in reservoirs (Doubek et al., 2019), because taxa with longer generation times (e.g., calanoid copepods) are more likely to be flushed from short residence time systems before completing their life cycles than are short generation time taxa (e.g., cladocerans). This mechanism may underpin observations that zooplankton community composition differs between natural lakes and reservoirs (Merrix-Jones et al., 2013; Doubek et al., 2019).

For temporary ponds, the seasonal timing of flooding or drainage also appears to influence zooplankton communities. In experiments simulating Mediterranean ponds, both the richness and composition of rotifer and crustacean zooplankton varied according to when in the year pond-filling occurred, presumably due to the different environmental conditions that ensue in temporary water bodies that fill at different times of year (Florencio et al., 2020). In an urban setting, winter drainage as part of pond management can also influence community composition (Mimouni et al., 2015).

Research has also addressed the potential role of ultraviolet (UV) radiation in affecting zooplankton diversity and community structure. UV exposure causes DNA damage and mortality in zooplankton, but there are various mechanisms that may allow these organisms to survive under such conditions, including photoenzymatic repair, accumulation of protective pigments and migration away from surface waters. Crucially, species differ greatly in the extent to which they use these strategies, such that high UV can alter the structure of communities. The result is that species richness and diversity can be lower for lakes typified by high UV penetration and exposure, in which only the most tolerant species are likely to survive (Marinone et al., 2006).

Chemical constraints

Many aspects of lake water chemistry may impact upon the diversity of zooplankton communities. Considering the many different potential chemical drivers, the role of pH has received particular attention. Among-lake variability in pH is known to be correlated with crustacean zooplankton species richness, with a decline in species number in more acidic ecosystems (often $<$ approximately pH 6). As well as this effect of average pH, lakes with higher interannual and seasonal variability in pH also support fewer zooplankton species, presumably as a result of higher extinction risks brought about by chemical instability (Shurin et al., 2010). Concentrations of calcium are also known to impact upon zooplankton communities, with relatively Ca-rich *Daphnia* species being less abundant in the communities of lakes with lower Ca concentrations (DeSellas et al., 2011).

Many zooplankton communities are exposed to complex mixtures of environmental contaminants, including pesticides, road salt, detergents, and heavy metals. While diverse communities of rotifers and crustaceans can be supported even in heavily polluted systems, such as wastewater contaminated municipal ponds (Adhikari et al., 2017), contaminants undoubtedly shape community structure. For example, metal (Cu, Ni) contamination of the Sudbury lakes in Canada appears to affect zooplankton community composition, with many *Daphnia* species being particularly sensitive (Valois et al., 2010). However, interactions between contaminant effects and other factors may result in great variability in zooplankton responses. Due to the complexity of ecosystem processes, community-level responses to contamination may be surprising. For example, it is conceivable that diversity would increase in response to pesticide exposure, when competitively superior zooplankton species are selectively eliminated by contamination.

Salinity is a key chemical attribute that influences freshwater zooplankton communities. Studies of South American water bodies undergoing salinization, as a result of climate change, show marked variations in zooplankton composition among lakes of different salinity. While many species struggle to survive under highly saline conditions some are highly tolerant of elevated salt concentrations (e.g., the copepod *Boeckella poopoensis*). Elsewhere, such as in North America, elevated chloride contamination due to road salt application can bring about changes in crustacean zooplankton composition, but the magnitude and nature of the effect varies with exposure history, and might be partially offset by dispersal of species into the contaminated system (Sinclair and Arnott, 2018).

Food quantity and quality

Both the overall availability of food resources, and their nutritional quality, impact greatly upon the growth and reproduction of freshwater zooplankton. This has implications for zooplankton consumer-resource interactions. Here, however, the focus is on relationships between among-lake variations in food availability, and zooplankton community structure.

Previous studies, principally in Europe and North America, have suggested that among-lake variations in crustacean zooplankton species richness are correlated with the availability of food resources, measured as primary production or chlorophyll-*a* concentration. Studies vary with regard to whether this relationship appears to be linear (Hessen et al., 2006) or hump-shaped, with maximum richness at intermediate productivity (Dodson et al., 2000). Such discrepancies may arise as a result of among-study variation in productivity gradient length. In other words, unimodal relationships only become apparent when comparing lakes spanning a very wide productivity range. It has been suggested that the apparent hump-shaped relationship emerges as a result of the balance between more production energetically supporting more species on the one hand, and deteriorating food quality and abiotic conditions, and increasing predation on the other. However, some have challenged this view, suggesting that the pattern may also emerge because intensifying human pressures, that are likely correlated with nutrient loading and productivity (e.g., from contaminant loading),

reduce species richness in highly productive systems (Hoffman and Dodson, 2005). Moreover, it appears that a typical curvilinear relationship between diversity and productivity (using total phosphorus concentration as a proxy) can shift to a linear negative relationship when considering functional, rather than taxonomic, diversity (Barnett and Beisner, 2007). This negative functional trait-based change correlated with a loss of spatial heterogeneity in phytoplankton resources, and a decline in relative food quality. These factors apparently influenced the degree to which functional differentiation could occur in the zooplankton community.

Predation

Zooplankton play an important role in freshwater food webs, and thus ecosystem structure. Here, rather than unpicking these complex dynamics, I present a brief introduction to observed relationships between zooplankton community structure and among-lake variations in predation pressure.

Zooplankton species composition does indeed vary among lakes with and without plankton-feeding fish (Knapp et al., 2001; MacLennan et al., 2015), and species richness may vary with fish community structure (Hessen et al., 2006). For example, Jeppesen et al. (2000) observed that the contribution of *Daphnia* and calanoid copepods to total crustacean zooplankton biomass was lower, while that of small cladocerans and cyclopoid copepods was higher, in Danish lakes with higher planktivorous fish biomass. Studies contrasting the zooplankton communities of lakes that are fishless, and that have been stocked with fish, suggest larger-bodied zooplankton are especially vulnerable to predation by visually-feeding fish (Knapp et al., 2001; MacLennan et al., 2015).

In fishless lakes, invertebrate predators can play an important role in structuring zooplankton communities by suppressing populations of small species. For example, studies into the plankton of Wisconsin bog lakes showed that the insect *Chaoborus* and the copepod *Diaptomus leptopus* can reduce cladoceran, copepod and rotifer populations in the absence of fish (Arnott and Vanni, 1993).

However, discerning the unique effects of predation and other environmental factors on zooplankton community structure can be challenging. In a study of lakes in the Sierra Nevada mountains, Symons and Shurin (2016) demonstrate that zooplankton communities are potentially structured by interactions between these factors. Specifically, the presence of fish suppressed elevational gradients in zooplankton composition, but the strength of the trophic cascade varied with other aspects of the lake environment, such as water temperature and concentrations of dissolved organic matter.

Habitat affinities

Compared to the pelagic zone, the aquatic plants and sediments of littoral zone habitats are structurally complex, and thus are likely to provide a wider range of niches. Numerous studies have shown that these complex habitats can support more diverse, and different assemblages than adjacent open waters. Indeed, researchers have often made a distinction between the "true" zooplankton of the pelagic zone, and purely littoral species, inhabiting only the surfaces of aquatic plants and sediments. However, some have challenged the view that species can be neatly categorized in this way. In a major survey of Norwegian lakes, Walseng et al. (2006) showed that very few crustacean species were found only in open water samples. Many more species were found primarily in littoral zones but, crucially, a great number of cladoceran and copepod species were found in both of these major habitat types. Some microcrustacea can be considered facultatively, or semi-planktonic, and it is possible for littoral zone species to be carried offshore by water movements. As a result, zooplankton diversity estimates, even if based on pelagic samples, will likely be influenced by among-lake variations in the structure and extent of littoral zone habitats.

Dispersal

Zooplankton life cycles typically include stages that permit ready dispersal among water bodies. Rotifers can produce hardened cysts (Monogononta) or desiccation-tolerant forms (Bdelloidea), while cladocera and calanoid copepods produce tough resting eggs, that are readily dispersed by water flow, winds, larger organisms and human activity.

Despite this relative ease of dispersal, many species have restricted geographic distributions. In addition, zooplankton richness is sometimes observed to be greatest for lakes that are less isolated from other water bodies (Dodson, 1992; Merrix-Jones et al., 2013; Lyons and Vinebrooke, 2016), and zooplankton composition may be more similar in water bodies that are close together (Santos et al., 2016) or hydrologically-connected. This apparent influence of other water bodies on local diversity suggests the dispersal of zooplankton among fresh waters. Indeed, such spatial structuring in community composition has been used to infer that dispersal is a limiting factor for local community diversity. This limitation may be especially important for some zooplankton (e.g., copepods), compared to others (e.g., cladocerans), such that typical geographical range sizes differ among major zooplankton groups (Henriques-Silva et al., 2016).

However, zooplankton community structure in any given water body will be a function of both dispersal and local habitat conditions. Although new species may be able to reach a specific standing water body, this alone does not ensure their successful colonization. Shurin (2000) found, through experimentation, that colonization success of new rotifer and crustacean zooplankton can be very low; potentially because interactions with native zooplankton species exclude them. Dispersal effects can also be affected by the previous establishment of non-native species (Sinclair et al., 2015).

Given the importance of recipient ecosystem characteristics in governing colonization success and community structure, it has been suggested that the diversity of local lake communities is only likely to be limited by dispersal when this is occurring over very

large distances (Shurin et al., 2000). Furthermore, the relative importance of dispersal and local species sorting by habitat features may change over time. For newly-formed water bodies, community composition may initially be governed by the dispersal of potential colonist species and then, after this colonization phase, by the influence of local habitat features (Allen et al., 2011).

While human-mediated and natural dispersal may act to increase the richness of local communities, through the introduction of new species, this might not always be the case. In fact, the effects of dispersal depend upon the nature of immigrating species and water body conditions in complex ways. For example, if dispersal introduces new predators or strong competitors to a water body, the local zooplankton diversity might actually decline due to the loss of native species through negative interactions with the newly-established species. The invasion of North American lakes by the predatory cladoceran *Bythotrephes longimanus*, and subsequent declines in the diversity of resident taxa, are case in point. Furthermore, high rates of dispersal could act to homogenize communities across the landscape (i.e., similar community compositions in all water bodies), such that dispersal can no longer increase local water body diversity through the introduction of new species from elsewhere.

Knowledge gaps

- *Resolving both inter- and intraspecific variation in functional traits*. Trait-based approaches to zooplankton community studies promise new insights into the relationship between diversity, ecosystem structure, and ecosystem function. To fully capitalize on this potential at a global scale there is a need to expand the number of taxa for which we have trait-based information, integrate these data, and make them openly accessible. However, in doing so, we need to incorporate and quantify intraspecific trait variation, recognizing that populations and individuals "within" a species are not necessarily functionally-equivalent. We can then begin to ask questions about the relative importance of intra- and interspecific trait variation for zooplankton community structure, and wider ecosystem behaviors.
- *Direct measurement of zooplankton dispersal*. Among water body dispersal is a key process within the metacommunity approach to investigating zooplankton diversity. However, the importance of dispersal is often inferred only indirectly based upon spatial patterns in community similarity among ecosystems. This approach is not ideal, as such patterns could potentially reflect spatial gradients in unmeasured environmental conditions as well. Advances in methods for estimating dispersal via different mechanisms (e.g., through hydrological connectivity, aeolian transport, or by waterfowl) would greatly enhance our understanding of the processes underpinning community assembly.
- *Developing the capabilities of new methods*. We must investigate the capabilities of new methods for measuring zooplankton diversity (e.g., image analysis and DNA-based monitoring), in relation to those of more traditional methods. In doing so we will be able to identify potential complementarities among methods, both novel and established, that allow us to address new questions about the patterns, drivers, and consequences of zooplankton diversity.
- *Zooplankton as indicators of ecosystem state*. The diversity of zooplankton communities is demonstrably sensitive to a wide range of environmental pressures, including contaminants, nutrient enrichment, climate change, and species introduction. As such, these communities are potentially powerful indicators of biodiversity change and ecosystem state change. To operationalize the widespread use of zooplankton as biological indicators, there is a need for research to develop candidate indicators that are sensitive to known pressures, and that can be incorporated into biodiversity monitoring programs.
- *Global tests of theory*. Much of our current understanding of the drivers of freshwater zooplankton communities originates from observations in Europe and North America. We need to understand how scalable and transferable such theory is to other regions and biogeographic provinces, if we are to arrive at a globally-relevant theory of zooplankton community assembly.
- *Diversity and food webs*. Though much valuable work has been done on the diversity of freshwater zooplankton, it would be valuable to expand our understanding of the relationships between zooplankton diversity and food web interactions. Interactions between communities of both fish and invertebrate predators and zooplankton diversity, are worthy of further study, accounting for the different temporal and spatial scales at which these organisms operate and are sampled. A particularly interesting area is the role that diversity and community structure elsewhere in the food web (e.g., phytoplankton, macroinvertebrates, fish) play in affecting zooplankton diversity.

Acknowledgments

I am very grateful to Beatrix Beisner, Stephanie Figary, Marie-Elodie Perga and Thomas Mehner for commenting on an earlier version of this article.

See Also: Emerging methods and topics: Dust and Fog Effects on Inland Waters; Fundamental concepts and theories: Diel Vertical Migration; Structures and functions of Inland Waters - Lakes: Predation on Zooplankton; Structures and functions of Inland Waters - Rivers: Energetics and Food Webs in Large Rivers

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Fish Populations☆

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This is an update of I.J. Winfield, Fish, Populations, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00194-0.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie_Elodie Perga and Damien Bouffard.

Glossary

CPUE Catch-Per-Unit-Effort (CPUE) is the absolute catch of a species standardized with respect to the amount of sampling effort that produced that catch. Units vary greatly, but are frequently some form of numbers (or weight) per time period.
Keystone species Species which have a functional impact on their ecosystem which is disproportionately high in relation to their abundance.
Recruitment/stock/stock-recruitment curves The graphical relationship between the abundance of reproducing adults and the subsequent abundance of resulting young, usually defined with respect to a particular life cycle stage such as end-of-summer juveniles.
R-species Species exhibiting a particular life history strategy involving the production of large numbers of young which subsequently show relatively high mortality. Such species are frequently small, short-lived and can show rapid population growth under appropriate circumstances.
Year-class strength The relative strength of a species' reproduction in a given calendar year.

Introduction

Fish species found in inland waters are extremely diverse, both biologically and taxonomically (Nelson et al., 2016), and are relatively long-lived. Individual longevities of years may be contrasted with the months or even weeks of many other inhabitants of inland waters. Furthermore, fish commonly attain relatively large individual sizes of several kilograms in weight and are usually by far the most abundant vertebrates present in such ecosystems, features which often combine to lead them to act as keystone species with impacts at several trophic levels. The relatively large individual sizes attained by many species have also attracted the attention of humans for millennia (Hart and Reynolds, 2002), initially as a food source in capture fisheries and latterly also as a source of enjoyment in recreational fisheries or even just "fish watching" in ornamental water bodies (Fig. 1).

This historical interest in the fish of inland waters has acted as a major global driver for studies of their populations, particularly in terms of changes in population abundance and individual growth rates. While the underlying science of such studies has much in

☆*Change History:* December 2020. This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie-Elodie Perga and Damien Bouffard.

Fig. 1 Although rarely attaining the density or visibility of these domesticated goldfish (*Carassius auratus*), fish populations play a diversity of roles in the ecological functioning of inland waters and have widespread importance in recreational and commercial fisheries. Photograph by DT Creations.

common with corresponding research on other taxonomic groups, components of it are more specific to the demands of the quantitative study of fish populations. In particular, the diversity of habitats occupied (from fast-flowing upland streams to the bottoms of large lakes), the diversity of individual sizes (from eggs of less than 1 mm in diameter to adults in excess of 1 m in length), the substantial locomotory abilities (with which individuals may undertake migrations in excess of hundreds of kilometers, including temporary or permanent departures from inland waters) and the diverse sensory systems (commonly based not just on vision but also olfaction and mechano-reception) mean that the scientific sampling of the fish populations of inland waters is not a simple matter. To this difficulty must be added the challenges posed to population dynamics theory and understanding by the diversity of life cycle strategies shown by such fish, sometimes even within a single species. With further complications arising from the great longevities of many species, which significantly complicate reproduction dynamics and which may result in a population going through only a handful of complete life cycles during the lifetime of a researcher, the study of fish population dynamics is arguably one of the greatest challenges encountered in the scientific study of inland waters.

This review of the fish populations of inland waters will firstly address in some detail the issue of sampling problems, which as indicated above remain considerable despite the immense collective experience of the world's freshwater fisheries. It will then consider fish population ecology itself using as a framework the equation

$$N_{t+1} = N_t + I - E + R - M$$

where N_{t+1} is future population abundance, N_t is present population abundance, I is immigration, E is emigration, R is reproduction and M is mortality. It will thus take account of the impacts of fish movements through immigration and emigration, both of which are exhibited to a much greater extent than in any other biota of inland waters, before moving to the core features of population ecology, i.e. reproduction and mortality. The combined effects of these diverse factors will then be considered in terms of overall population dynamics. The review will finish with brief conclusions and a personal consideration of persisting knowledge gaps.

Sampling

Almost all readers will have at some time in their life caught a fish. Many will have done this as a young child using a hand-net, quite likely netting a common shiner (*Luxilus cornutus*), a European minnow (*Phoxinus phoxinus*) or some similarly widely distributed species depending on their geographical location. Others may have used rod-and-line with a baited hook or an artificial fly to catch one of many species of fisheries interest such as a bluegill sunfish (*Lepomis macrochirus*) or a brown trout (*Salmo trutta*). However, although it is a simple matter to catch an individual fish, their evasive capabilities, great growth, high longevity and other factors combine to make robust scientific sampling very difficult. On top of this practical challenge, additional complexities are rightly prompted by ethical issues and, paradoxically, by fisheries issues as the owners of local fishing rights are often reluctant to allow others to take "their" fish for scientific study.

As a result of these difficulties, practically every fisheries capture technique has also been used to produce scientific data of varying qualities. Indeed, fishery data themselves are frequently used to give information on relative fish abundance by standardizing catch (e.g. number or weight of fish) with respect to effort (e.g. number of hours fished with a rod or the area of netting used). Although often only approximate and usually relating only to species of specific interest to the fishery (which may be a small fraction of the total species actually present), such so-called catch-per-unit-effort data have the advantages of being relatively readily available for many inland waters and have often been so for many years. However, extensive runs of such data stretching back over several decades are less common. Individual fish samples may also be taken from fisheries catches and, like the products of scientific sampling described below, be examined for a range of biological parameters including the determination of individual age through the detailed examination of their scales or other hard parts such as otoliths.

However, sampling of fish populations is best based on activities undertaken independently of fisheries interests and such scientific effort for monitoring and research is carried out extensively in inland waters (Zale et al., 2013). The methods involved may be broadly categorized into three major groups: passive techniques, active techniques and remote techniques (Fig. 2).

Passive techniques are essentially various forms of traps that rely completely on fish movement. One such method is entrapment, in which fish accidentally find their way into water abstraction systems such as those of reservoirs or power stations. Fish, and other unwanted objects, are removed from the water intake of such operations by meshes before being killed and discarded. If appropriate arrangements can be made with the plant operator, these unwanted fish can be counted and otherwise examined in order to gather basic population data. Although usually biased in various ways which must be taken into account in analysis, entrapment has the great advantages of being typically of long duration and in continuous operation around the clock and throughout the year. True trapping using mesh or netting traps, the latter known as fyke nets, is also frequently undertaken in studies of fish population dynamics, usually with traps set overnight before being lifted. Whether made of mesh or net, the operation of the trap is similar in principle with fish entering through a valve-shaped opening back through which exit is more difficult. A final and by far the most extensively used passive technique is the gill net which comprises a curtain of netting hanging vertically in the water column and which, like traps, is typically set overnight. If the relative sizes of the mesh of the gill net and the cross-section of the fish are appropriate, then only the head of the fish can pass through the mesh and its gill covers prevent it from reversing out. In scientific use, gill nets typically contain several different mesh sizes which allow a range of sizes of fish to be captured by a single net. A significant disadvantage of the gill net is that most captured fish are killed or injured by the operation.

Active techniques are independent of fish movement and, with one notable exception, are essentially scaled-up variations on the hand-net theme. The seine net is a curtain of fine-meshed netting running from the top to the bottom of the water column which is set in a semi-circle from the shore, thus enclosing a known area or volume of water. The two ends of the net are then carefully pulled in, resulting in fish being brought to the shore where they can be transferred to water-filled containers for examination and ultimate release. A second major active technique is the trawl net which is effectively a giant hand-net, typically several meters across, which is pulled horizontally by a powered vessel. Fish are caught in the trawl just as they are in a hand net and, under appropriate conditions, can be brought onboard, examined and released alive. The final active technique considered here is electrofishing (or electric fishing), in which a carefully controlled electrical current is passed into the water to stun temporarily any fish within a radius of typically 1 or 2 m. Stunned fish are caught using an electrically insulated hand net and placed in a water-filled container, from which

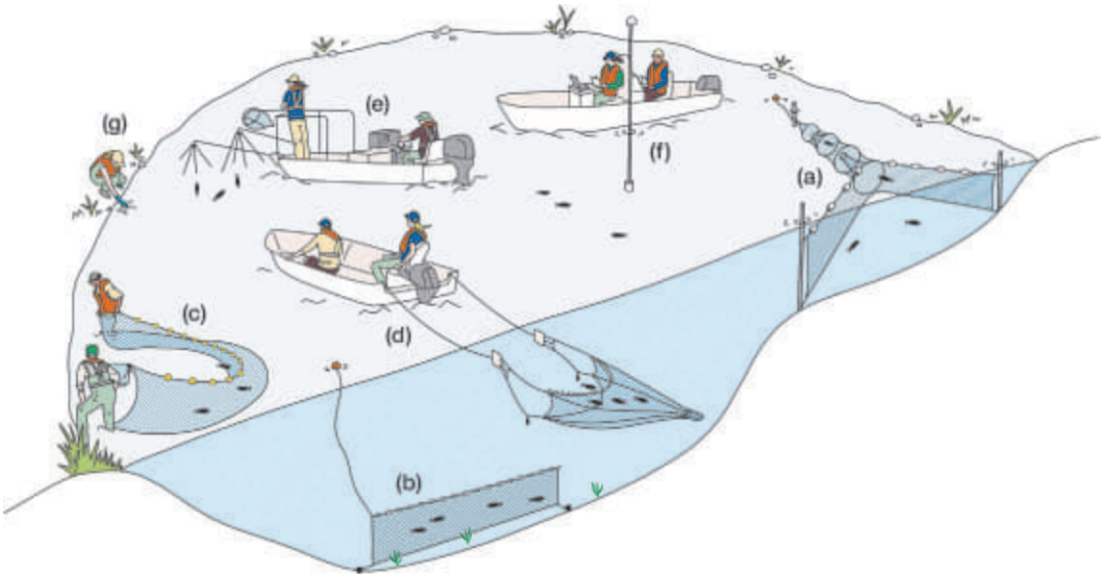

Fig. 2 Scientific sampling techniques commonly used for fish in inland waters include the passive techniques of (a) fyke netting and (b) gill netting, the active techniques of (c) seine netting, (d) trawling and (e) electrofishing, and the remote techniques of (f) hydroacoustics and (g) environmental DNA. Artwork by Rosie C. Winfield.

they can be subsequently examined and released. The major limitation of electrofishing is that its spatial influence is very limited and so it can only be used effectively in small, shallow inland waters or in the shallow littoral zone of larger water bodies.

Remote techniques do not result in the actual capture of fish but instead gather information on them. The most obvious example is visual observation by either diver or by underwater camera, but this approach is usually limited in inland waters by their low water clarities. Alternatively, fish can be counted and their individual size estimated by measuring the disturbances their bodies make to the detectable resistance of the natural electrical environment. Unfortunately, the need to minimize the distance between the fish and the detecting apparatus means that such so-called resistivity counters can only be deployed in shallow habitats and their practical use is largely restricted to detecting the passage of fish along river systems. In contrast, the use of transmitted high frequency (typically 70–400 kHz) sound by an echo sounder to count and to some extent to measure the size of individual fish is a remote technique feasible in all types of inland waters. A relatively recently developed form of such hydroacoustics involves the use of extremely high frequency sound (0.7 or 1.8 MHz) to produce a moving image, much like a monochrome low-resolution video camera but with the benefit of being independent of light and turbidity conditions. Even more recently, there is currently great research interest in the rapidly developing field of environmental DNA (or eDNA) sampling in which DNA is sampled not directly from an organism but from its environment (Rees et al., 2014). This eDNA which has been "shed by an organism or organisms is collected, amplified and then identified through bioinformatics techniques involving extensive species DNA libraries. In addition to the rapid production of fish species lists for inland waters by sampling nothing but water, such use of eDNA can also provide information on the relative abundance of different species (Hänfling et al., 2016). However, the present utility of eDNA in studies of population dynamics is limited because of its inability to estimate age or size distributions.

Immigration and emigration

The substantial locomotory abilities of fish, which result from their relatively large body sizes combined with their sophisticated sensory systems and behavioral repertoires, lead to all species exhibiting directed movements over a range of timescales (from minutes to years) and to many individuals undertaking migrations in excess of hundreds of kilometers, including temporary (e.g. some brown trout known as sea trout) or permanent (e.g. European freshwater eel (*Anguilla anguilla*)) departures from inland waters. Such movements are typically species- and age-specific and may be undertaken along any of the three dimensions of the aquatic environment for a variety of purposes including feeding, predator avoidance and reproduction.

Movements for reproductive purposes, typically referred to as spawning migrations, are often the most dramatic in terms of distance travelled and spectacle. Species which leave inland waters to spawn in the marine environment (termed catadromous) are relatively few in number and are typified by the European freshwater eel, which leaves inland waters to cross the Atlantic Ocean and spawn in the Sargasso Sea. Relatively more species make the converse move, i.e. enter inland waters to spawn having matured at sea (termed anadromous). The best known and arguably most spectacular such species is the Atlantic salmon (*Salmo salar*), which must often overcome substantial waterfalls (Fig. 3) as it migrates up rivers from the coast to headwaters before spawning.

Although such movements may be considered to be on the periphery of population ecology, their resulting immigrations and emigrations have far-reaching consequences for the understanding of local changes in population dynamics. The critical point to

Fig. 3 An Atlantic salmon (*Salmo salar*) leaping a waterfall during its upstream spawning migration. Photograph by Matthew G. Hull.

appreciate is that the local population dynamics of fish in inland waters may be significantly influenced by factors operating distantly. Such distances may vary from just a few tens of meters (e.g. the abundance of young vendace (*Coregonus albula*) in the pelagic zone of a lake may be influenced by oxygen conditions experienced by the previous generation's adults at the bottom of the water column) to thousands of meters (e.g. the abundance of young coho salmon (*Oncorhynchus kisutch*) in the headwaters of a river may be influenced by barriers impeding progress of the previous generation's adults in the estuary).

Reproduction

The reproduction of fish in inland waters has already been referred to in the context of spawning migrations, which are themselves necessary because the habitat requirements of free-swimming fish (whether young or adult) and incubating eggs are usually very different.

Almost all fish species in inland waters are dioecious (i.e. have male and female sex organs in different individuals (Fig. 4)) and the vast majority of them have external fertilization, with only a relatively few species such as the well-known guppy (*Poecilia reticulata*) displaying internal fertilization and development. Outside the tropics, spawning is almost always restricted to a marked seasonal window resulting in the temporally-pulsed production of eggs. Such seasonality follows a general pattern with members of the Order Salmoniformes spawning in winter, those of the Order Perciformes in spring and those of the Order Cypriniformes in summer. The number of eggs produced by females usually numbers in the several hundreds if not thousands and is strongly influenced by individual condition and thus recent feeding history, with important implications for overall population dynamics through the mechanisms of intra- and inter-specific competition for food. Courtship may be elaborate, in some species involving the development of vivid spawning colorations or the construction of a nest of varying complexity, although the act of spawning itself may last only a few minutes. Subsequent parental care ranges between none at all, with many species in captivity readily consuming their own eggs although such cannibalism may be less frequent in nature, through to active nest maintenance and guarding of young. Some species even undertake mouth-brooding in which eggs and young are held within the buccal cavity for up to several weeks. An individual fish may reproduce just once and then die (termed semelparity), or survive to reproduce on at least one further occasion (termed iteroparity).

The relationship between the number of spawning adults and the number of subsequent young produced is of obvious interest to fisheries managers and so has been the subject of considerable research for many decades, at least for those species of commercial importance (Quinn II and Deriso, 1999). Such relationships, which may involve intra-specific competition and predation in the form of cannibalism, are evidently rarely linear but are notoriously difficult to quantify further because of the protracted life cycles and sampling problems reviewed above. In fisheries research these relationships are usually termed stock-recruitment curves, with recruitment essentially being a fisheries term for the production of young fish. This is one of the most important biological relationships requiring statistical description in order to facilitate robust predictions about future population abundance under alternative fisheries management regimes.

To add to this complexity, the stock-recruitment curve is only one contributor to the overall degree of reproductive success shown by any given fish population in any given year. This overall degree of success (commonly referred to as year-class strength) may also be a function of a host of biotic factors including food availability, inter-specific competition and predation (the degree of

Fig. 4 A pair of oscars (*Astronotus ocellatus*), a South American cichlid species which shows elaborate courting behavior and parental care. Photograph by K. C. Blanchett.

each of which may be completely unrelated to the abundance of the population in question), together with abiotic factors including water temperature (including subtle aspects thereof), water flow and water level.

Mortality

Given the highly fecund nature of most fish species, it is not surprising that mortality rates are also relatively high and in life strategy terms they can generally be considered to be classic r-selected species. Survivorship curves for fish of inland waters thus arguably bear more similarities with those of larger macroinvertebrates than they do with those of fellow vertebrates such as birds, mammals and reptiles, although they do share more features with those of amphibians.

The detailed quantification of mortality in fish is notoriously difficult for at least three reasons. Firstly, the determination of mortality rates requires estimates of population abundance over at least two points in time. As noted above, the quantitative sampling of fish populations in all but the smallest of habitats is extremely difficult. Furthermore, in order to assemble a picture of overall population mortality such data have to be collected for each significant life stage transition, for example from egg to larva, from larva to juvenile, and from juvenile to adult. Secondly, apparent individual gains to or losses from a population are often complicated by any immigration or emigration from the study site. As discussed above, such movements are commonplace in the fish populations of inland waters and so require the additional study of migratory behavior before robust mortality measurements can be derived. Thirdly, the relatively great longevities of most fish species mean that the collection of such data usually takes a considerable number of years. Unsurprisingly, density-dependent mechanisms present major and often controversial challenges to our understanding of fish population dynamics (Rose et al., 2001). High quality mortality data exist only for a few populations of a few species, with a stream-based, long-term study of brown trout by Elliott (1994) providing an excellent example of such investigations.

The potential for differing mortality rates to impact fish population age structure is illustrated in Fig. 5 for three modelled (with constant reproduction) populations and one actual population. In the simplest case, Fig. 5a shows the age structure of a population in which each age class suffers an annual mortality rate of 50%. Fish in their first year of life (age 0 years) comprise *c.* 50% of the population and relatively few individuals live longer than 5 years. Such fixed mortality rates are in fact unknown in nature and so Fig. 5b depicts a more common situation in which mortality is 90% during the first year of life, reducing to 20% thereafter. Underyearling (age 0 years) fish now make up *c.* 67% of the population, but more individuals survive to greater ages (in fact to the maximum of 15 years shown in this figure). In Fig. 5c, the mortality scheme is identical with the exception of it returning to 90% after age 5 years to simulate an intense fishery for older fish. As a result, the contribution of underyearling fish to the population increases slightly to *c.* 75% and once again individuals become much rarer after age 5 years. It is important to appreciate that all of these populations are modelled assuming a constant level of recruitment, which is extremely unlikely to occur in nature for reasons discussed above. Finally, Fig. 5d presents the observed age structure of an unfished population of European whitefish (*Coregonus lavaretus*) surveyed using scientific gill nets in Loch Eck, Scotland, United Kingdom. The apparent absence of fish aged 0 and 1 years is probably an artefact of sampling limitations, although it cannot be discounted that recent reproduction has failed. One notable feature is that the abundance of successive age classes clearly does not follow the smooth declines of any of the modelled populations, with the most probable explanation being significant variations in the level of recruitment over the previous decade or so.

A complete explanation of the above observed age structure of European whitefish requires a detailed study of local population dynamics, itself requiring the synthesis of information on immigration and emigration, reproduction, mortality and other factors into quantitative and predictive models of varying degrees of complexity. This challenging area of fish population ecology is considered below.

Population dynamics

The study of population dynamics can be defined as the analysis of the factors that affect the increase, stability and decrease of populations over time. As explained above, in the context of fish populations in inland waters it thus integrates investigations of immigration and emigration, reproduction, mortality and other factors. Such studies are increasingly performed within a framework of quantitative and predictive models of varying degrees of complexity.

As a consequence of their high fecundities and high mortality rates, population abundance in fish generally varies more than in any other vertebrate taxa of inland waters. This variation includes seasonal and long-term components as shown in Fig. 6 for the fish community of a lake monitored by monthly night hydroacoustics surveys over 28 years from 1990 to 2018. Within each year, abundance clearly peaks at the end of the summer as that year's reproduction is completed and results in a several-fold increase in overall fish abundance. Superimposed on this short-term variability is a marked overall increase in abundance from *c.* 2000 onwards.

A brief consideration of this time series, actually recorded from the north basin of the two-basin lake of Windermere, England, United Kingdom, illustrates the potential complexities of fish population dynamics in inland waters, even in the absence of any significant impacts from fisheries. The fish community of this temperate, mesotrophic lake is dominated by the salmonid Arctic charr (*Salvelinus alpinus*), the percid perch (*Perca fluviatilis*), the esocid pike (*Esox lucius*) and, in recent years, the cyprinid roach

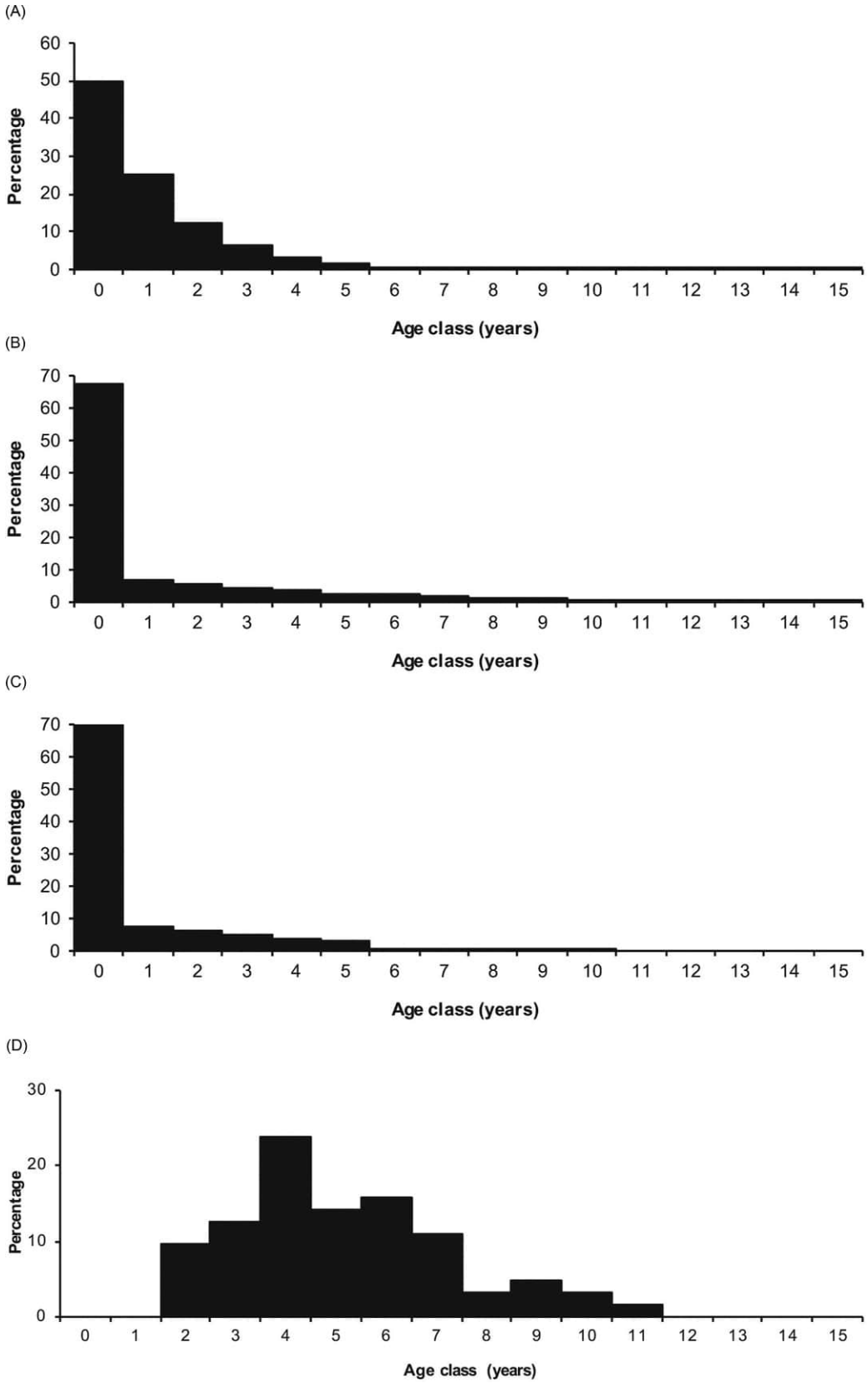

Fig. 5 The impact of differing mortality rates on the age structure of three modelled (with constant reproduction) fish populations and one actual fish population: (a) Modelled population experiencing a fixed annual mortality rate of 50%, (b) Modelled population experiencing a mortality rate of 90% during the first year of life reducing to 20% thereafter, (c) Modelled population experiencing a mortality rate of 90% during the first year of life before reducing to 20% and then returning to 90% after age 5 years to simulate an intense fishery for older fish, (d) Observed age structure of an unfished population of European whitefish (*Coregonus lavaretus*) in Loch Eck, Scotland, United Kingdom. Parts (a) to (c) Author's unpublished data, Part (d) Author's unpublished data reproduced with permission from Scottish Natural Heritage.

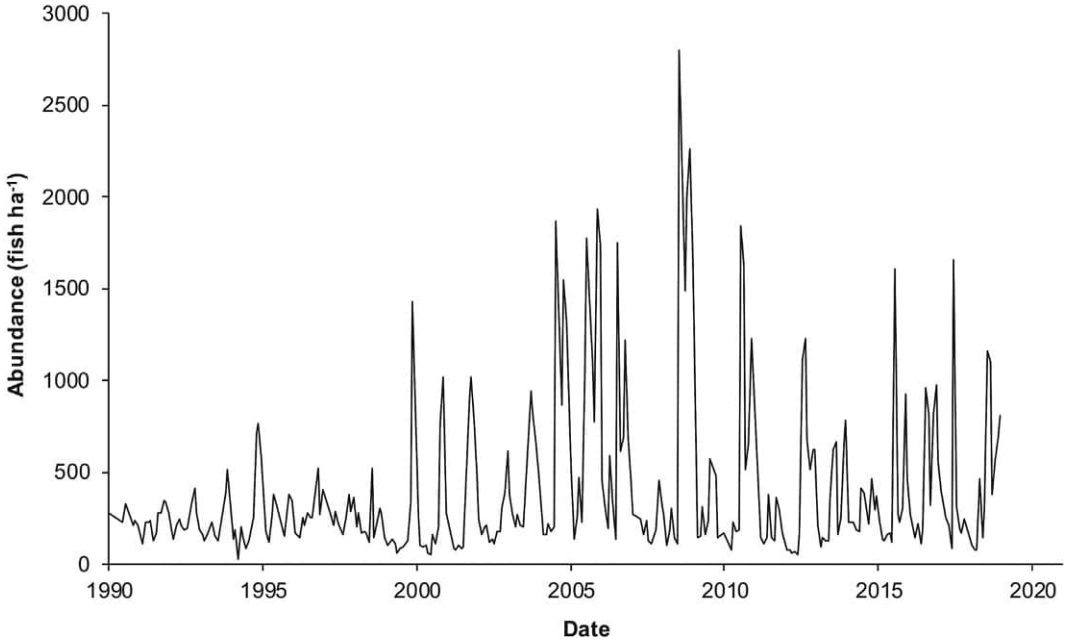

Fig. 6 Seasonal and longer-term variability of the abundance of fish populations exemplified by monthly (January 1990 to December 2018) night-time hydroacoustic surveys of the north basin of Windermere, England, United Kingdom. Author's unpublished data.

(*Rutilus rutilus*). Historical netting studies have shown that the open water of the lake, i.e. the habitat surveyed by the hydroacoustics system, was previously dominated by Arctic charr. Consequently, the changes in fish abundance of the first few years of the present data series have been interpreted in terms of this species and its movements between the two basins of the lake in response to poor oxygen conditions in the hypolimnion of the south basin (Elliott et al., 1996). However, the dramatic increase in fish abundance observed since *c.* 2000 coincides with the spread into the open water of a rapidly-expanding littoral roach population (Winfield et al., 2008). Perch also undoubtedly constitute some fraction of the fish detected during the hydroacoustics surveys, but trapping shows that this species has not shown any marked inter-basin differences in abundance over this time. Pike, in contrast, have shown diverging population biology in the two basins and have made directed movements between them (Haugen et al., 2006), but they are so rare in the open water that their contribution to the hydroacoustic record is negligible.

Using the trapping data referred to above over a longer timescale going back to the 1940s, modelling of the perch populations of both basins of Windermere has been able to explain *c.* 60% of observed variation in recruitment, which was itself strongly synchronous between the two basins (Paxton et al., 2004). Stock-recruitment curves explained a significant component of the annual production of young perch, while the presence of widespread disease and a positive relationship with late summer water temperature were also important factors. Interestingly, water temperature has been consistently higher than the long-term average in recent years and is thought to be a major contributor to the recently increased abundance of roach.

Conclusions

Alongside the provision of potable water and the disposal of selected waste products, the hosting of fish populations is one of the most important ecosystem services provided by inland waters. The importance of abundant and healthy fish populations for commercial and recreational fisheries is self-evident, but these vertebrates are also of great importance to the considerable sector of human society which is not immediately concerned with their capture (Winfield et al., 2018). Whether manifested in the full glory of a spawning run of sockeye salmon (*Oncorhynchus nerka*) or the cosmopolitan distribution of the humble three-spined stickleback (*Gasterosteus aculeatus*), fish populations are often the *de facto* sentinels of the quality of our inland waters. In this context it is reassuring that so much is now known about their populations, while at the same time our currently changing climate challenges us to redouble our research efforts in this complex field.

Knowledge gaps

Sampling young fish

As considered above, fish populations are usually dominated numerically (and often also gravimetrically) by their young stages. Unfortunately, quantitative sampling is particularly difficult for such individuals because their evasive capabilities allow them to

escape samplers designed for invertebrates while their small body size allows them to escape net meshes commonly used for older and larger fish. Limited advances have been made recently in the application of hydroacoustics for the sampling of such individuals, but the need for quantitative biological sampling methods remains.

Sub-population genetic structure

Another issue largely neglected in this review has been the sub-population genetic structure of fish populations. The existence of such diversity has been empirically demonstrated for the vast majority of studied populations, although its implications for overall population dynamics remain poorly understood.

Parasites and diseases

The effects of parasites and diseases on fish populations have been almost completely neglected in the present review, an omission which reflects the scientific literature on which it is based. Although the impacts of parasites and diseases are occasionally obvious even to the casual observer during spectacular outbreaks, their more routine contribution to fish population dynamics in inland waters remains little explored.

Interactions with lower trophic levels

In many lakes, fish populations have been found to exert clear impacts on their zooplanktonic prey, which may in turn have consequent effects for phytoplankton populations. In contrast, in other lakes no such top-down effects are apparent and instead local fish populations appear to be limited primarily by bottom-up effects of prey availability. Such interactions are frequently exploited in the science of biomanipulation in attempts to improve local water conditions, but much remains to be discovered about how the prevailing net directions of such effects are determined.

Endocrine disruptors

In many rivers in the developed world, anthropogenically-generated endocrine disruptors have been found to have demonstrable effects on the reproductive physiology of a variety of fish species. However, the implications for fish population dynamics of endocrine disruptors, and indeed those of many other pharmaceuticals, remain poorly understood.

Microplastics

The use of plastics is near ubiquitous in the modern world, but following their post-use disposal the accumulation of this diverse group of materials in the natural environment is causing increasing concern. Moreover, although plastics typically persist for many years they may be relatively quickly broken down in size (to 5 mm and smaller) by various processes to form microplastics which are themselves small enough to be taken up by a wide range of organisms including fish of all life stages. Little is currently known about the ecological consequences of such processes and this is a very active field of research.

Climate change

In addition to the obvious impact of an increase in water temperature, climate change will also result in fundamental changes to the inland waters inhabited by fish populations through changes in stratification patterns, level fluctuations, flow patterns (including both droughts and floods), period of ice cover, and numerous other features of the abiotic and biotic environments (including deep hypoxia). Considering such impacts within our present understanding of fish population dynamics and becoming able to make meaningful predictions about their effects continues to be a major challenge.

See Also: **Emerging methods and topics**: Electronic Tagging and Tracking of Animals in Inland Waters; Freshwater Ecoacoustics—A New Addition to the Limnologists' Methods Toolkit; **Fundamental concepts and theories**: Bioenergetics; Diel Vertical Migration; The Biomass Size Spectrum; **Human pressures and management of Inland Waters**: Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment; Implications of Climate Change for Freshwater Fisheries; Inland Fisheries Management - Case Studies of Inland Fish; Inland Fisheries Management - Exploitation and Livelihoods; **Social/societal values of Inland waters**: Societal Values of Inland Fishes; The Gender Gap: Women as Authors and Leaders in International Publications in Fisheries Science; **Structures and functions of Inland Waters - Lakes**: Predation on Zooplankton; **Structures and functions of Inland Waters - Rivers**: Energetics and Food Webs in Large Rivers; **Structures and functions of Inland Waters - Wetlands**: Patterns in Freshwater Fish Diversity

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Further reading

EIW: Fish communities in lakes

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Relevant websites

http://www.fao.org/fishery—Fisheries and Aquaculture Department of the Food and Agriculture Organization of the United Nations.

http://www.fishbase.org—FishBase: A global information system on fishes.

https://fisheriesstandardsampling.org—Standard methods for sampling North American freshwater Fish.

http://www.freshwaterlife.org—A freshwater information resource.

https://shoalconservation.org—A partnership aimed at engaging a wide range of organisations to accelerate and escalate action to save the most threatened fish and other freshwater species.

Structure of Fish Communities in Lakes and Its Abiotic and Biotic Determinants

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie_Elodie Perga and Damien Bouffard.

Glossary

Abundance Is the relative representation of a species in a particular community.
Biomass Is the mass of living organisms of a population or a community in a given area at a given time.
Community An ecological community is a group of populations of different species occurring at the same geographical location at the same time.
Evenness An index of numerical equality of species within a community.
Functional diversity A measure of the number of functionally different species within a community.
Functional redundancy Refers to the pattern that multiple species from several taxonomic groups can share similar roles in ecosystem functionality.
Richness Is the number of different species represented in an ecological community.
Size structure The distribution of organismal size (length, mass) within a population or a community.
Taxonomic diversity A measure of the number of taxonomically different species within a community, can also be quantified as the probability that the two randomly taken individuals represent different species.
Trophic cascade Reciprocal effects of predators on prey or of prey on predators that alter the biomass of a trophic level across more than one link in the food chain.

Introduction

To determine factors and processes that generate the structure of local communities is one of the central topics of community ecology. The unified neutral theory of biodiversity and biogeography (Hubbell, 2001) discusses that biodiversity arises at random. In contrast, the niche theory assumes that there are abiotic and biotic determinants that would predict local communities in a deterministic way. Subsequently, we follow the hypothesis of a non-random structure of communities, and elucidate concepts and empirical evidence for abiotic and biotic determinants of fish community structure in lakes.

The structure of fish communities in lakes is a suitable study object for community ecologists because many lakes are spatially isolated and form aquatic islands in the terrestrial landscape. Therefore, first concepts on studying fish community structure referred to the concept of island biogeography (McArthur and Wilson, 1967). In one of the most influential and comprehensive earlier studies, Tonn et al. (1990) developed the concept of hierarchical filters to explain the fish community structure in northern

Wisconsin lakes. These filters ultimately generate local fish species pools from processes operating on different spatial and temporal scales. These authors distinguish between historical and contemporary determinants of species diversity and community composition. Furthermore, they classify the spatial dimension into regional, lake-type and local processes (Tonn et al., 1990).

In this article, we follow the concept of hierarchical filters by covering the main processes and determinants of fish community structure in lakes at varying temporal and spatial scales. At the beginning of the chapter, we include a coarse overview on the global and continental biogeography of freshwater fishes. However, in the subsequent parts we focus in more detail on the contemporary processes determining the composition of fish communities, which operate on lake-type and local scales. Whereas the majority of the studies we refer to have been conducted in the temperate regions of the Palearctic and Nearctic realms, we summarize separately the results of a few studies on lake fish communities in sub-tropical, tropical and Arctic regions. We close the chapter by a list of topics, which are unresolved, and where we expect that future studies will contribute fundamentally new insight to the community ecology of freshwater fishes in lakes.

Methods and key terminology

The exploration of fish community composition in lakes is inherently difficult because fishes cannot be observed visually, except for situations with extremely clear water where visual surveys conducted by divers may inform about species occurrences and numbers. In the majority of cases, however, fishing surveys are used, which shall catch representative parts of the entire fish community to obtain data on community composition and population abundances. Survey fishing gears can be distinguished into active gears (e.g., pelagic or bottom trawls), which are actively moved to catch fish, and passive gears, which rely on the movement of the fish to be caught (e.g., gillnets). A comprehensive overview on fishing gears applied in freshwater ecosystems is provided by Bonar et al. (2009). All survey fishing gears are made of net material with certain mesh sizes, selecting only species and fish sizes that are big enough to be retained by the dimension of the mesh. Accordingly, fishing nets are inherently size- and species-selective. The active fishing by electricity can be applied in particular in shallow water areas, often along the shoreline, but the method is likewise biased towards certain species and size classes of fish that are most efficiently attracted by the electric field. Alternative methods include hydroacoustic devices (echosounders), which are suitable to accurately count fishes and estimate their sizes, but which have severe limits to distinguish species (Simmonds and MacLennan, 2005). More recent developments include the application of environmental DNA (eDNA), which seems to be a reliable tool to obtain qualitative and quantitative information about the fish community composition in lakes (Hänfling et al., 2016; Spear et al., 2020).

To obtain standardized fish catches for evaluating the water quality and ecological integrity according to the European Water Framework Directive, fishing surveys by multi-mesh gillnets in lakes have to follow the European standard (CEN, 2015). This standard defines the number of nets, their distribution to depth zones, the application of benthic and pelagic nets, the duration of net exposure, and the time period during which fishing is recommended. Furthermore, the dimension of the nets and the mesh size and yarn diameter of the panels are exactly described. The application of hydroacoustics (CEN, 2014) and electrofishing (CEN, 2003) for fish community surveys are similarly standardized.

Obtaining accurate coverage of species occurrences and reliable size distributions of fish in lakes is possible only by combining various fishing gears. There are several studies comparing the species or size compositions of fishes in lakes across differing fishing gears (Emmrich et al., 2012; Alexander et al., 2015). A ground-truthing by comparing fish catches from several fishing gears with an accurate census of fish abundance and community composition has been performed only once in a large pond, which could be drained after fishing, enabling to count all fish in this ecosystem (Ravn et al., 2019).

Fishing surveys can deliver several key metrics, which are informative for the fish community composition (see Glossary). First, taxonomic diversity can be expressed as species richness, species diversity and species evenness. Second, species-specific abundances and biomasses can be calculated. For passive gears, relative abundances or biomasses can be derived if a standardisable unit effort (e.g., number of nets, size of nets, number of catching days) can be defined (catch per unit effort). The unit effort is hardly comparable across fishing gears, preventing that relative abundances from different gears (for example, from gill nets and electrofishing) can be combined. For active gears and hydroacoustics, a reference to the fished area or volume is usually possible, and hence true densities (number of fish per area or volume) can be calculated. A third informative metric that can be derived from fishing surveys is the size (length or mass) distribution of fishes, either expressed as size spectrum ignoring taxonomic units, or as species-specific size distributions, reflecting the size- and age composition of populations.

Diversity indices and fish abundance and biomass can be accumulated beyond the taxonomic categories of species or genera. Typical groupings refer to feeding guilds (e.g., planktivores, piscivores, benthivores), temperature preference (cold-water, cool-water and warm-water species), spawning substrates (e.g., lithophils, psammophils, phytophils) and preferred lake habitat (pelagic, littoral, profundal species). By this approach, taxonomic diversity is converted into functional diversity, by assuming that the function of fishes is more important than the taxonomic identity for determining the occurrence of a species within a local community. Functionally dissimilar species usually have low niche overlap, and hence are less affected by interspecific competition. The exact species within a functional groups is, however, strongly dependent on the colonization from the regional species pool, contingent on the hydraulic connectivity of the lake to other aquatic systems. Few systematic comparisons between taxonomic, functional and size diversity have been conducted for fish communities in lakes (but see e.g., Brucet et al., 2018; Lamothe et al., 2018).

There are two different terms in describing all fish within a lake. The term assemblage refers to the species occurring in a lake, without considering interactions between them. In contrast, we use the term community because we demonstrate that species interactions may contribute substantially to forming local fish communities in lakes. When we elucidate potential determinants of

fish community composition in lakes, we will distinguish between effects on taxonomic diversity, effects on functional diversity and redundancy, effects on fish abundances or biomasses, and effects on the size structure of populations or communities.

Historical processes explaining global, regional and local fish species diversity

There are two major processes operating at differing temporal scales, which influence the regional and local occurrence of fish species. First, speciation is the process by which two or more reproductively isolated gene pools are generated from a previously single gene pool. This process includes spatial and geographical, ecological, and sexual components (Bernardi, 2013). Lakes are well-known hot-spots of fish speciation. For example, the African Great Lakes Tanganyika, Victoria and Malawi are all famous for their extraordinarily rich fish fauna dominated by Cichlidae (Fryer and Iles, 1972). The origin of the numerous species is evolution of species flocks from single ancestors, for example by divergent selection on sensory systems (Seehausen et al., 2008), having occurred independently in all lakes. Similar species flocks are described for sculpins (Cottidae) in the Russian Lake Baikal (Kontula et al., 2003), sailfin silversides (Telmatherinidae) in lakes of Sulawesi (Herder et al., 2006) and Midas cichlids in Nicaraguan crater lakes (Barluenga et al., 2006). Evolution of fish species flocks has been described also for temperate lakes in post-glacial landscapes during more recent geological times. Examples are species groups of whitefishes (*Coregonus*) in North and Central European lakes (Ostbye et al., 2005; Hudson et al., 2011) or *Coregonus* ciscoes in the North American Great Lakes (Turgeon et al., 1999). Furthermore, incipient ecological speciation is considered the process generating sympatric morphs of charrs (genus *Salvelinus*) in European postglacial lakes (Jonsson and Jonsson, 2001).

The second historical process is the balance between colonization and extinction. Geologically, the landmasses on earth have changed their position and connectivity (continental drift). Starting from the supercontinent Pangaea about 230 million years ago, the evolution and movements of freshwater fish lineages were affected by the breakup of Pangaea and the subsequently newly formed connections between landmasses. The currently existing configuration of continents has persisted since the Miocene about 15 million years ago. Therefore, colonization of the continents from connected landmasses by the currently existing fish fauna can date back several million years. The most important geological event with respect to the structure of the current fish fauna of the Palearctic and Nearctic realms was the last glaciation during the Pleistocene about 15,000 years ago. Glaciation and de-glaciation altered drainage patterns by change of flow of river systems, and created thousands of moraine and "kettle" lakes in Central and North Europe and in North America. At the glacial maximum, all fishes were extirpated from areas under glaciers or ice shields. Where possible, fishes could move into non-glaciated refuge areas. Re-colonization from refugia after the retreat of the glaciers is seen as the major process explaining the current regional fauna of the northern Palearctic and Nearctic (Griffiths, 2006). Therefore, the lakes formed during the Pleistocene and their fish faunas are geologically very young and hence species-poor, in comparison with the geologically much older and species-rich systems, for example the African Great Lakes.

The current continental and regional occurrence and distribution of freshwater fishes can be ordered along 426 Major Freshwater Ecoregions (Fig. 1) (Abell et al., 2008). An overview of the fish species richness per major freshwater drainage basin is provided by Tedesco et al. (2017). These regional species pools determine the availability of fish species for forming local fish communities in lakes. Large-scale trends of fish species diversity in North America and Europe follow differences in spatial climatic trends, primarily caused by temperature and rainfall, suggesting a strong effect of physiological constraints on species occurrence (Griffiths et al., 2014; Brucet et al., 2013). Europe contains 546 native species of freshwater fish, and there is a clear trend of declining species diversity and number of endemic species from east to west, and from south to north (Griffiths, 2006).

Contemporary processes predicting local fish community composition

Overview

In contrast to the historical processes summarized before, subsequently we cover contemporary processes that contribute to forming lake fish communities. Colonization and extinction contribute to forming both regional and local fish species lists. We further summarize a number of main studies, in which lake fish communities were analyzed at world-wide or continental levels. In the second part of this sub-chapter, we elucidate in more detail the abiotic and biotic predictors of lake fish communities, as obtained from studies at smaller geographical scales, primarily from temperate regions. Finally, we elucidate results from a few studies on lakes in Arctic and tropical regions.

Dispersal and colonization

In lakes, which are hydraulically connected, fish populations and communities can be regarded as forming meta-populations or meta-communities. Dispersal of individuals from a source to a sink population then becomes an important process contributing to formation of local communities. In very large lakes, a meta-population structure can even be found between separate lake basins (Haugen et al., 2006). There is not much known about fish meta-communities across lakes because lakes have been considered primarily as closed systems. However, single studies suggest that the hydraulic connectivity of lakes with their watersheds modifies the fish community structure through dispersal of migrant species (Griffiths, 2017). Furthermore, the pairwise dissimilarity of fish community composition increases with increasing spatial distance between lakes along waterways, attributable in particular to small littoral fish species with a presumed lower capability of long-distance dispersal (Mehner et al., 2014).

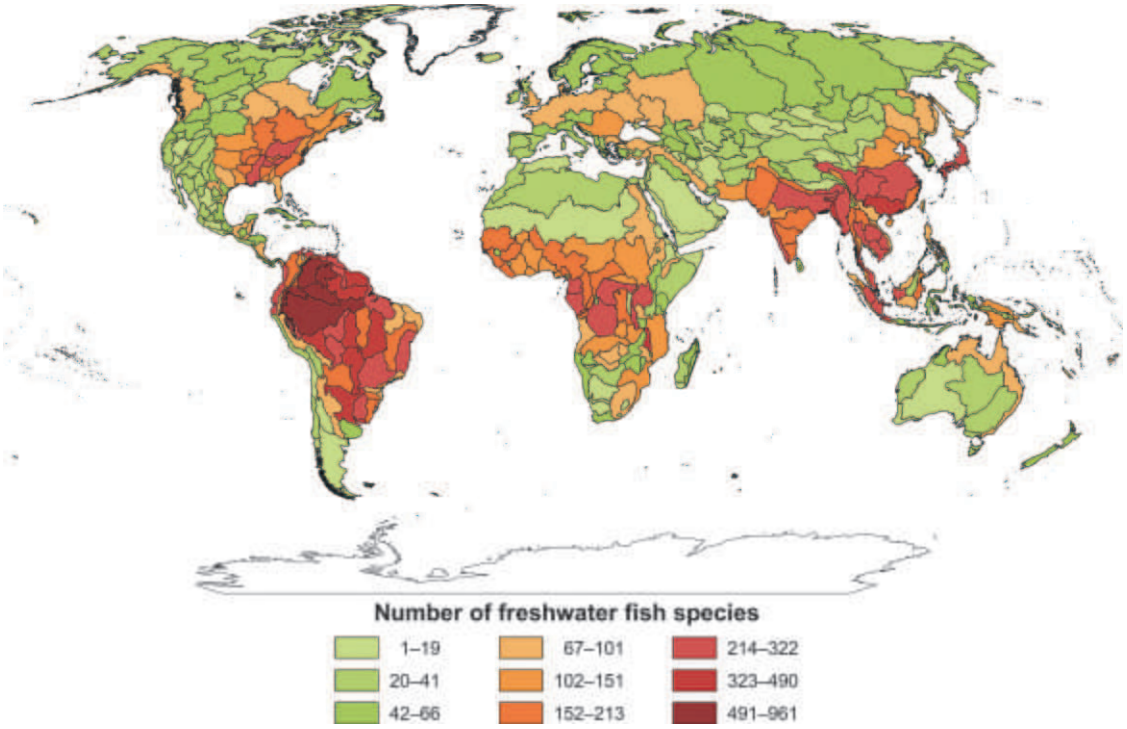

Fig. 1 Fish species richness in the Major Freshwater Ecoregions of the World. Figure reproduced from Abell R, Thieme ML, Revenga C, Bryer M, Kottelat M, Bogutskaya N, Coad B, Mandrak N, Balderas SC, Bussing W, Stiassny MLJ, Skelton P, Allen GR, Unmack P, Naseka A, Ng R, Sindorf N, Robertson J, Armijo E, Higgins JV, Heibel TJ, Wikramanayake E, Olson D, Lopez HL, Reis RE, Lundberg JG, Perez MHS and Petry P (2008) Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. *Bioscience*: 58, 403–414, but richness updated from WWF and TNC. 2015. Freshwater Ecoregions of the World. Available at www.feow.org. Figure re-drawn by Vanessa Bremerich. Richness for the following ecoregions are estimates: Aceh, Indian Ocean Slope of Sumatra & Java, Southern Central Sumatra, Southern Sumatra—Western Java, Central & Eastern Java.

Extinction risk

Freshwater fish species and populations have severely been affected by several threats including destruction or modification of their habitat, water pollution, overexploitation, spread of invasive species, spread of alien parasites and pathogens, salinization, acidification and climate change (Gozlan et al., 2019). In Europe, for example, at least 37% of freshwater fish species are threatened, about 17% of populations are declining, and at least 13 European fish species are globally extinct (Freyhof and Brooks, 2011). The highest number of threatened freshwater fish species is found in the south of the Europe. In central Asia, at least 30 of the 120 fish species that inhabit inland waters are on the Red List (Visconti et al., 2018). In the biogeographical region of North America, the freshwater fish fauna had the highest extinction rate worldwide among vertebrates in the 20th century and the number of threatened freshwater fishes has increased by 25% during the last three decades (Burkhead, 2012). Whereas these data refer to entire freshwater drainage basins, there is a lack of specific data for trends of species richness in lakes. In general, monitoring data for freshwater fish species diversity and abundance are urgently needed worldwide to accurately measure population trends and improve the accuracy of future Red List assessments.

Large-scale studies on lake fish communities

An excellent conceptual overview of approaches and determinants of fish community composition has been published about 20 years ago (Jackson et al., 2001). However, there are also a number of recent studies analysing the effects of abiotic filters and biotic interactions on local fish species richness and composition in lakes at continental or world-wide scales. Strong spatial patterns in structure and functional diversity (as based on trophic niche estimates) were found among 159 fish communities from lakes distributed over almost all continents. There was a complex interplay between external and internal filters, but these patterns may be blurred by anthropogenic species introductions (Comte et al., 2016). A comprehensive overview on almost 2000 lakes in Europe, as based on standardized fishing surveys in the context of the European Water Framework Directive, found strong effects of large-scale climatic differences and abiotic filters on local fish communities (Brucet et al., 2013). The contribution of non-native fish species to these European lake fish communities and its predictors has been explored separately (Trochine et al., 2018). Based on data from almost 7000 Ontario lakes, functional diversity and redundancy of lake fish communities were calculated. Fish communities in larger, deeper and warmer lakes were functionally most redundant (Lamothe et al., 2018). In a similar approach including lakes in Western Europe, taxonomic and functional richness of fishes were strongly correlated, and rare species contributed singular

functions only in rivers and estuaries, but not in lakes, suggesting low sensitivity of lake fish communities to single species loss (Teichert et al., 2017). The size structure of European lake fish communities has been compared by Emmrich et al. (2014). Lakes located in colder European regions dominated by cold-water salmonids were characterized by unimodal or bimodal body-size distributions, whereas lakes in the warmer European lowlands dominated by eurythermic cool- and warm-water species were characterized by almost linear negative log-log abundance-size distributions.

Abiotic predictors of community structure in temperate lakes

Lake morphometry

Lake morphometry has an important effect on the composition of lake fish communities, in particular in interaction with large-scale climatic factors (temperature, rainfall) and productivity (Fig. 2) (Brucet et al., 2013). This has similarly been confirmed for functional diversity of boreal lake fish assemblages (Erös et al., 2009). Lake morphometry affects all horizontal and vertical gradients of abiotic factors in lakes (light, temperature, oxygen concentration, nutrient concentration, pH), and hence creates the within-lake habitat diversity. Accordingly, lake morphometry determines the lake type, which essentially groups lakes into either shallow and polymictic, or deep and monomictic or dimictic types. The logarithm of the lake surface area is a good predictor of the (logarithm of) local species richness (species-area relationship) (e.g., (Griffiths, 1997). Accordingly, lakes with a surface area of <0.001 km^2 (equivalent to <1 ha) may host often only one or two fish species, whereas several hundred species can be found in large (>100 km^2) lakes, for example in the Great Lakes of Africa. Functionally, larger lakes have a greater variety of differing habitats, have a lower probability of local species extinctions and a higher colonization rate. These processes explain why fish species richness increases with lake area.

A comparatively strong effect on local fish community composition is attributable to lake depth. Lake depth is a key determinant for the thermal and mixing regimes of lakes. In temperate and warm regions, only deep (maximum depth $> \sim 12$ m) lakes provide permanent cold-water habitats. Lake depth in combination with turbidity also determines whether light can reach the bottom of lakes. Accordingly, the benthic zone of lakes can be divided into the littoral zone (illuminated) and the non-illuminated profundal zone. Therefore, deep stratified lakes can be inhabited by fishes occurring in either littoral, profundal or pelagic habitats, whereas the fish community composition of shallow and clear lakes consisting only of littoral habitats may be confined to littoral species. The three lake habitats may substantially differ with respect to species richness, diversity and dominant species (Diekmann et al., 2005). The deep-water pelagic and profundal layers of stratified lakes, which are usually cold and naturally well oxygenated, are inhabited by cold-water adapted species, mostly from the order Salmoniformes (genera *Salmo*, *Coregonus*, *Salvelinus*). In turn, there are species bound to the structured littoral areas because of small size, their reproduction relying on macrophytes (phytophils or phytolithophils), or fish species requiring benthic biotic hosts (Unionidae mussels) for their eggs (European bitterling, *Rhodeus amarus*). These littoral species often belong to the thermal guild of warm-water species, and hence cannot propagate into the cold deep-water layers of stratified lakes. Accordingly, fish species richness and diversity of entire lakes can reliably be evaluated only by including fishing surveys in all available habitats.

Further morphometric effects on fish community composition can be expected from shoreline length, shoreline development (length of shoreline relative to perimeter length of an ideal circle of the same surface area) and shoreline slope. With increasing shoreline development and shallower shoreline slopes, habitat variability and complexity of littoral areas usually increase, resulting in higher richness and diversity of the littoral fish communities (Lewin et al., 2014). Finally, the hydraulic connectivity of lakes determines whether lakes are accessible or can be left by moving fish, suggesting that all species with non-resident life styles have a

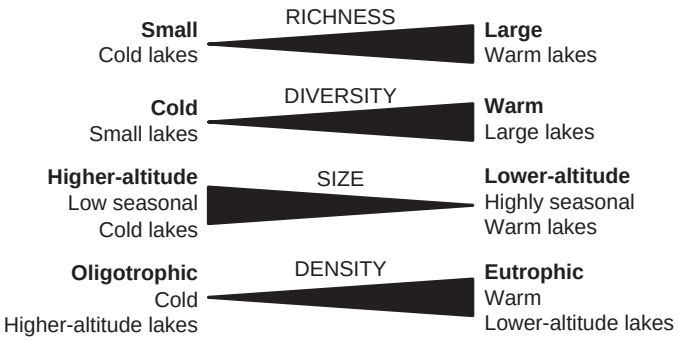

Fig. 2 Scheme showing changes (increase and decrease) for each fish assemblage descriptor in European lakes. Main variables driving changes in each descriptor are given in boldface. Figure reproduced with permission from Brucet S, Pedron S, Mehner T, Lauridsen TL, Argillier C, Winfield IJ, Volta P, Emmrich M, Hesthagen T, Holmgren K, Benejam L, Kelly F, Krause T, Palm A, Rask M and Jeppesen E (2013) Fish diversity in European lakes: Geographical factors dominate over anthropogenic pressures. *Freshwater Biology* 58: 1779–1793.

higher chance to be present in connected lakes. Furthermore, the rates of first colonization and re-colonization are certainly also higher in lakes that are hydraulically connected to other aquatic ecosystems.

There are only few studies demonstrating strong effects of lake morphometry on total fish abundance or biomass and on size distributions. Warm and shallow lakes at lower altitudes usually have higher fish densities than deep lakes with big volumes of cold-water hypolimnetic habitats, and average fish size increases with altitude and declines with temperature and seasonality (Brucet et al., 2013).

Lake productivity

There are several studies showing a strong effect of changing lake productivity on the fish community composition. In the temperate zone of both the Palearctic and the Nearctic, species of the order Salmoniformes (salmon-like species) were replaced by Perciformes (perch-like species), and these have gradually been replaced by species of the order Cypriniformes (carp-like species) with increasing concentrations of phosphorus and nitrogen (lake eutrophication) (Hartmann and Nümann, 1977; Argillier et al., 2013). However, these changes in species dominance are not a direct consequence of the higher nutrient concentrations, but are caused by indirect consequences of the higher lake productivity. Higher nutrient concentrations result in higher phytoplankton densities and biomasses, which make the water more turbid. Lower underwater visibility impairs all fish species, which rely on vision for feeding (e.g., perch *Perca fluviatilis*), whereas species adapted to low illumination (e.g., pikeperch, *Sander lucioperca*) may thrive. Lower illumination of the benthic zones declines the extension of the littoral zone and may ultimately prevent growth of aquatic macrophytes. Hence, all species with a phytophilous spawning mode may become extinct. Furthermore, fine-grain sediment may cover fish eggs deposited at the bottom, hence preventing successful egg development and hatching (Ventlingschwank and Livingstone, 1994).

A second major indirect effect of eutrophication on fish community structure is attributable to the decomposition of the increased amount of organic matter in the deep lake zones, which requires higher oxygen amounts than at the low-productivity situation. If the oxygen deficit cannot be balanced by fresh oxygen from primary production or atmospheric supply, for example in deep-water layers of lakes during the stratification period, layers of low oxygen concentrations may expand and ultimately prevent the occurrence of fish. If the entire deep-water pelagic area of lakes has become inhabitable because of lack of oxygen, also the cold-water habitat is completely lost, and hence species of the cold-water guild can no longer survive in heavily eutrophied lakes. If only the warm-water layer above the thermocline remains habitable, eutrophied stratified lakes resemble shallow lakes, and hence the fish community composition of shallow and stratified lakes becomes more similar with increasing eutrophication (Mehner et al., 2005). Excessive oxygen consumption of lake sediments from decomposition of organic material also impairs successful embryogenesis of bottom-laid fish eggs (Muller and Stadelmann, 2004).

A more direct effect of increasing productivity of lakes is an increase in total fish abundance and/or biomass (Brucet et al., 2013). Primary consumers like pelagic zooplankton and benthic macroinvertebrates respond to higher primary production by increasing biomasses, which then are used by fish consumers to likewise generate higher biomasses. However, the relative increase in fish biomass is often higher than the relative increase in biomass of primary consumers, and hence the per-capita available energy for fishes declines with eutrophication. The consequence is higher competition among the species of the same feeding guild, resulting in slow, so-called stunted growth with a measurable decline of size-at-age in the dominant fish species. These low growth rates are reflected in distorted size spectra, where accumulation of fish in certain size classes becomes obvious as significant residuals from the otherwise log-linear size-abundance relationships (Arranz et al., 2019).

Biotic predictors of community structure in temperate lakes

Predator-prey interactions

Predation by piscivorous (fish-eating) fish on prey fish is considered a strong structuring force for lake fish communities. Time series obtained from small lakes show strong population fluctuations of prey fish in response to drastic declines and subsequent recovery of predator fish, for example after winterkills (Tonn and Paszkowski, 1986). Similarly, the intentional or unintentional stocking or invasion of fish predators (perch; pike, *Esox lucius*) into lakes can induce local extinctions of prey species (Henriksson et al., 2016). The best documented example is the eradication of the native fish fauna composed mainly of small cichlids by introduction of the non-native piscivorous Nile perch (*Lates niloticus*) to the African Lake Victoria (Ogutuohwayo and Hecky, 1991). There are not many studies that report whether certain native predator and prey fish species co-occur less often than by chance, a pattern that would suggest that there is the risk of local extinction of prey in response to the occurrence of the predator. A recent study from more than 700 lakes in Ontario did not find evidence that even large-sized piscivorous species eradicated potential prey fish species from local communities in a systematic and predictive way. Where negative co-occurrences between predator and prey species pairs were found, these were context-dependent and prominent only in a small sub-set of lakes with particular features (MacDougall et al., 2018).

A clearer picture emerges if abundances and biomasses of predator and prey fishes are considered. In response to strong predation by fish predators, substantial declines in prey numbers can be expected. For example, to combat consequences of lake eutrophication, biomanipulation of the fish community was popular to indirectly suppress phytoplankton blooms via a trophic cascade (Mehner et al., 2002). However, the enhancement of piscivorous fish biomass as one of the biomanipulation strategies has often resulted only in a short-term decline of prey fish biomasses in lakes, whereas in the long-term the biomasses of planktivorous and benthivorous fish species recovered despite higher biomasses of piscivores. These results suggest that the piscivorous fish

biomass cannot permanently be enhanced without ongoing maintenance, and the biomass ratios between predators and prey seem to be lake-specific and relatively invariant (Mehner et al., 2002).

To demonstrate the effects of predation by piscivorous fish on prey fish, the structure of fish communities has also been compared among lakes, often from the same regional area. Even by accounting for the effects of differing lake morphometry and productivity on fish communities, the expected negative correlation between predator and prey fish biomasses could not be found (Mehner et al., 2016; Kokkonen et al., 2019). Accordingly, fish-induced trophic cascades by which phytoplankton is suppressed by high predator fish biomasses could not be detected by among-lake comparisons (Mehner, 2010; Bartrons et al., 2020).

Most of fish predators are gape-limited, and hence can swallow prey at once only if the prey fish is smaller than the maximum opening width of the mouth of predators (Hambright, 1994). Typical ratios of predator to prey fish length range between 3:1 and 5:1 (Mittelbach and Persson, 1998), which convert into predator-to-prey mass ratios of about 27–125 (3^3–5^3) (Brose et al., 2006). Accordingly, a strong effect of size-selective predation on the size structure of prey fish communities could be expected. Similarly to the predator effects on prey biomass, time series from single lakes reflected a stronger signal of size-selective predation (Tonn and Paszkowski, 1986) than approaches comparing the size structure of prey fishes among lakes with differing predator size structure (Mehner et al., 2016).

Competition and resource segregation

Interspecific competition has not been a major focus of studies investigating the structure of lake fish communities. We are not aware of a study showing that a certain fish species has become excluded from a local lake community as the consequence of competition with another local fish species, but invasion by non-native species may induce stronger negative effects. In turn, a dominance of positive co-occurrence patterns of species or habitat-specific groups of species among lakes suggests that facilitation and niche similarity structure richness and composition of lake fish communities substantially (Fig. 3) (MacDougall et al., 2018). Mutually negative effects on abundance or biomass of competing fish species are more likely (Eloranta et al., 2016), but systematically negative abundance or biomass correlations between species with similar niches among lakes have not been found (MacDougall et al., 2018). It has to be noted that studies of interspecific competition have to consider the frequent ontogenetic niche shifts in freshwater fishes (Werner and Gilliam, 1984), resulting in a succession of different biotic interactions while fish grow. The effect of competition among species is usually best demonstrated by niche segregation between co-occurring fish species (Genner et al., 1999; McMeans et al., 2020). This process is also considered as a route towards ecological speciation in lake fish communities (Knudsen et al., 2006). However, these young speciation events can be reversed and sympatric species can disappear if anthropogenic influences on lakes destroy the ecological gradients along which niche segregation has been expressed (Vonlanthen et al., 2012).

Stronger effects of competition have been found with respect to size structure of lake fish populations and communities. Interspecific competition modifies the size distribution of lake fish populations, with shifts towards steeper slopes of size spectra where the density of interspecific competitors is high. However, the strongest effect from competition on size spectra is attributable to intraspecific competition (Arranz et al., 2016). The size-at-age declines with increasing density of individuals from the same species, resulting in delayed reproduction and recruitment. Under extreme cases, negative density dependence can induce cyclic population dynamics with alternating strong and weak year classes, e.g., in vendace (*Coregonus albula*) (Hamrin and Persson, 1986) or roach (*Rutilus rutilus*) (Cryer et al., 1986). These results support that biomass and size structure of local fish communities are strongly affected by the available energy provided by autotrophic (phytoplankton, algal biofilms, macrophytes) and heterotrophic (bacteria and fungi) production and the efficiency by which this energy is transferred to the higher trophic levels (Bartrons et al., 2020).

Fish community structure in lakes outside temperate latitudes

Sub-Arctic and Arctic lakes

A few comparative studies have been conducted on the fish communities in Sub-Arctic and Arctic lakes. Lakes in this region respond strongly to the current effects of global warming, and hence comparison of their patterns and dynamics with those from lakes from the temperate zone may shed light on overarching processes and principles of fish community ecology.

The fish assemblages in small Sub-Arctic lakes of northern Alberta (Canada) were structured by species-environment relationships, but also by biotic interactions. Despite a smaller regional species pool, local fish species richness was comparable to similar lakes in the boreal zone (Tonn et al., 2004). Fish species richness in Arctic lakes of Alaska was substantially enhanced by hydraulic connectivity via a permanent channel, primarily caused by higher numbers of restricted species in comparison with non-connected lakes that were dominated by widespread fish species (Laske et al., 2016). The response of fish communities and their trophic interactions to a gradient of productivity and warming was studied in Finnish Sub-Arctic lakes, all located north of the Arctic Circle. In warmer and more productive waters, fish density increased, whereas average fish size declined, most apparent in littoral and benthic habitats (Hayden et al., 2017). The trophic structure of Greenland lakes was strongly determined by the presence of fish and the fish species occurring in the lakes. Fish-induced trophic cascades shifted the zooplankton composition from large taxa towards small-bodied crustaceans, in particular if sticklebacks (*Gasterosteus aculeatus*) were the single fish species present. Invasion of currently fishless lakes by fish will hence substantially modify these lakes (Jeppesen et al., 2017).

Overall, the patterns of fish community structure and the abiotic and biotic correlates in Arctic lakes were very similar to those described for temperate lakes of the Palearctic and Nearctic. Stronger trends of warming and enhanced productivity in Arctic than in

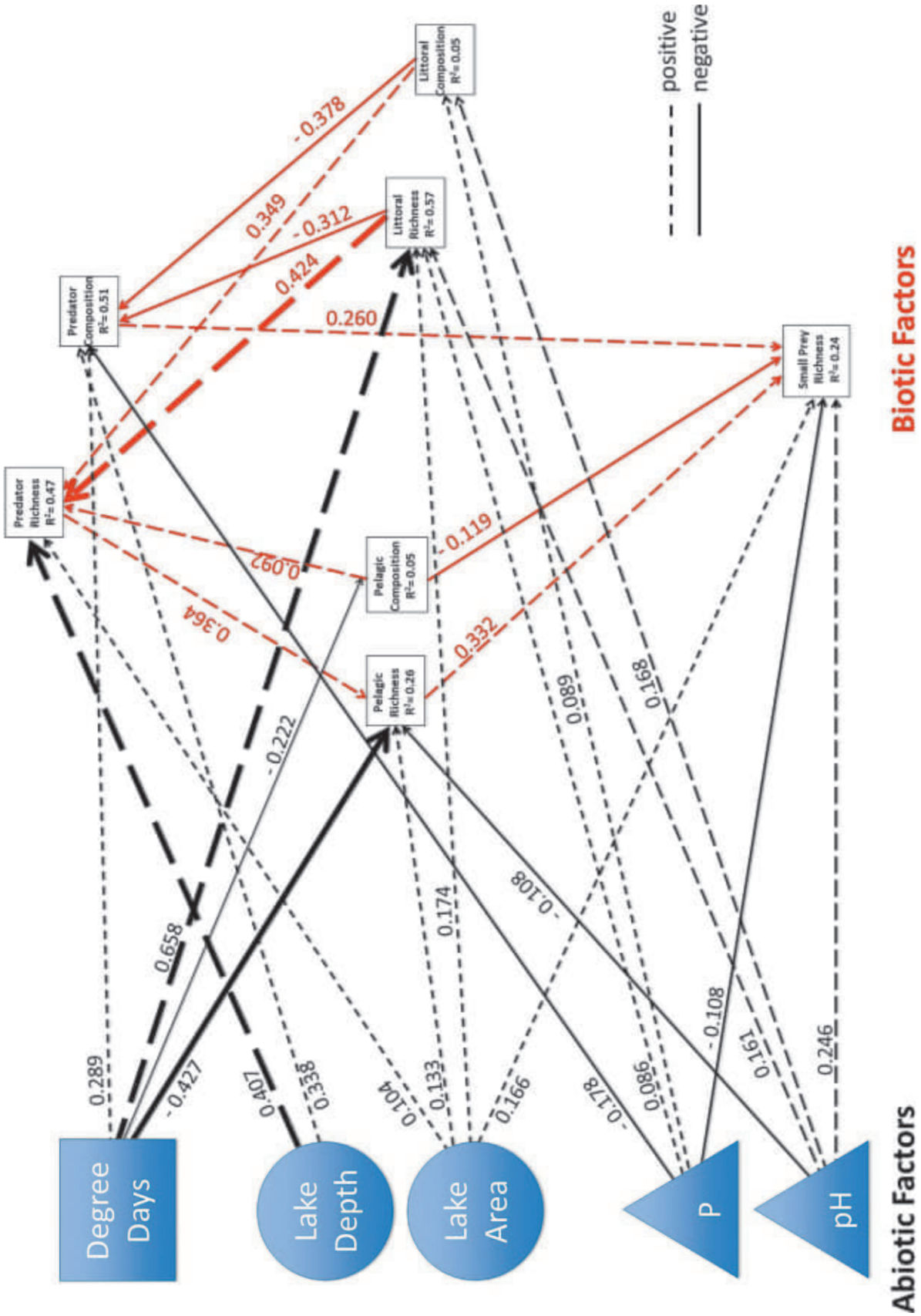

Fig. 3 Direct and indirect drivers of species richness in fish. Structural-equation-model-derived multivariate relationships among integrated abiotic and biotic regulatory factors (blocks = degree days, circles = lake morphometry, triangles = water quality, and biotic factors [red lines]) for the richness and composition of four major fish functional groups in 721 lakes along an 11 degrees latitudinal gradient in Ontario, Canada (SEM integrative model: $n = 648$, MLEST = 4.91, Degree of freedom = 13, $P = .977$). Solid lines indicate negative relationships; dashed lines indicate positive relationships. Arrows indicate the direction of the relationship. Bold lines indicate stronger relationships, arbitrarily assigned as standardized path coefficient values >0.40. Black lines indicate abiotic influences on biotic factors and red lines indicate influences between biotic factors. Functional groups are predator, littoral, pelagic, and small-prey species. Reproduced with permission from MacDougall AS, Harvey E, McCune JL, Nilsson KA, Bennett J, Firn J, Bartley T, Grace JB, Kelly J, Tunney TD, McMeans B, Matsuzaki SIS, Kadoya T, Esch E, Cazelles K, Lester N and McCann KS (2018) Context-dependent interactions and the regulation of species richness in freshwater fish. *Nature Communications* 9: 973.

temperate lakes due to global change will hence increase the similarity in fish community structure between these geographically distant freshwater systems.

Sub-tropical and tropical regions

In contrast to numerous studies from temperate and a few from Arctic and sub-Arctic areas, there is no systematic overview on fish community structures and their predictors in tropical or subtropical lakes. Geologically, most of the lakes in the tropical areas are much older because these areas were not affected by glaciation during the Pleistocene. Freshwater fish diversity in coastal southern Africa lakes and lagoons is a function of historical and present biogeography and salinity, with elements of marine fish communities persisting in lakes which retained a tenuous linkage with the sea. Furthermore, higher fish richness was found in lakes fed by rivers in subtropical than in temperate areas of this region (Whitfield et al., 2017). In tropical and sub-tropical floodplain lakes, the natural flow regime of the river feeding the lakes was most important (Pool et al., 2019). The community structure in floodplain lakes of the Orinoco River in Venezuela was predictably related to transparency, conductance, depth, area and the numerical density of piscivorous fishes (Rodriguez and Lewis, 1997). Fish communities in shallow lakes of the subtropical South America are characterized by higher densities, but smaller average sizes of fish in comparison with lakes at similar productivity in temperate regions (Teixeira-de Mello et al., 2009), and have a higher proportion of omnivorous fish and a lower proportion of piscivorous fish (Gonzalez-Bergonzoni et al., 2012). Therefore, predator fish-induced trophic cascades are less prominent in subtropical and tropical lakes, resulting in higher phytoplankton biomasses than in comparable shallow lakes of the temperature region (Jeppesen et al., 2010). In a large-scale comparison between >1600 temperate Danish and subtropical Florida shallow lakes, a greater control of zooplankton and benthic macroinvertebrates by fish consumers was documented for the subtropical lakes relative to those in Denmark (Jeppesen et al., 2020).

In general, all these results are also important to elucidate potential changes in fish community composition and food-web interactions in temperate lakes in response to global change because the warmer current climate in tropical region may reflect conditions in the temperate regions is a few decades. However, the processes of community formation, predictors of local species diversity and overall fish species richness differ fundamentally between postglacial temperate areas and the geologically older lakes in sub-tropical and tropical regions. Furthermore, the prominent number of floodplain lakes at lower latitudes points to a strong effect of the annual flood regime of the adjacent rivers on the lakes. Patterns and processes of fish community formation in floodplain lakes therefore differ fundamentally from those in the typical moraine lakes of the northern temperate zones. A systematic exploration of fish community composition and their local and regional predictors in tropical and sub-tropical regions in comparison with temperate areas could help identifying general processes at varying temporal and spatial scales that contribute to forming fish communities in lakes.

Future research topics

There are three research areas, in which substantial progress can be expected during the next years. First, the potential of eDNA to generate world-wide fish species inventories is one of the major promises of recent methodological advancements. Although not yet all confounding factors are known, which affect the results of eDNA studies, fish community ecology will massively profit from eDNA sampling because it is substantially less cost- and labour-intensive than the traditional fishing surveys. If (semi)-quantitative analyses as based on eDNA will become possible and will generate reliable results (Spear et al., 2020), even abundance and biomass information for local communities will become available. In combination with remote sensing of lake morphometry and productivity, determination of local predictors for species occurrences and abundances and monitoring of temporal changes in community composition will become possible for thousands of lakes world-wide at less effort than now, revolutionizing the conservation and management of freshwater fish communities in lakes.

Second, community ecology will profit from the finer resolution of empirical trophic networks by new or improved tracer technologies. Stable isotopes, compound-specific stable isotopes, fatty acids, and DNA-based stomach analyses are examples of recently developed or matured approaches. Furthermore, tracking swimming and behaviour of fishes in-situ will facilitate better understanding of contributions from predator-prey and competition interactions to formation of local communities and their temporal dynamics. Host-pathogen interactions and their effects on fish population dynamics and community structure are so far largely ignored, but may likewise change the view on critical processes affecting the presence and persistence of certain species in local communities.

A third important development refers to the statistics of among-lake comparisons of community structure. To evaluate whether interspecific interactions contribute to forming local fish communities in lakes is notoriously difficult. Comparison of patterns among lakes is often hampered by the fact that positive or negative species co-occurrences are caused by similar or dissimilar environmental requirements, respectively, without indicating the effect of interactions. Disentangling between joint occurrences and interaction effects requires recently advanced statistical approaches, for example the hierarchical modelling of species communities (Ovaskainen et al., 2017). These multivariate models allow, by a latent variable approach, to eliminate the effects of spatial configuration of lakes, their environments and phylogeny on species occurrences, making it plausible that the residual variation reflects true interaction effects between species. However, these models have not yet been applied to lake fish communities.

See Also: **Emerging methods and topics**: Electronic Tagging and Tracking of Animals in Inland Waters; Freshwater Ecoacoustics—A New Addition to the Limnologists' Methods Toolkit; **Fundamental concepts and theories**: Bioenergetics; Diel Vertical Migration; The Biomass Size Spectrum; **Human pressures and management of Inland Waters**: Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment; Implications of Climate Change for Freshwater Fisheries; Inland Fisheries Management - Exploitation and Livelihoods; Inland Fisheries Management - Case Studies of Inland Fish; **Social/societal values of Inland waters**: Societal Values of Inland Fishes; The Gender Gap: Women as Authors and Leaders in International Publications in Fisheries Science; **Structures and functions of Inland Waters - Lakes**: Fish Populations; Predation on Zooplankton; **Structures and functions of Inland Waters - Rivers**: Energetics and Food Webs in Large Rivers; **Structures and functions of Inland Waters - Wetlands**: Patterns in Freshwater Fish Diversity

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The Carbon Cycle in Lakes: A Biogeochemical Perspective

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Alkalinity (Acid Neutralizing Capacity, also ANC) A property of water describing its buffering capacity. In most freshwaters, the bulk of the alkalinity results from the bicarbonate and carbonate inputs from the catchment but organic compounds and certain reduction reactions (e.g. sulfate and nitrate reduction) can also contribute.
Carbon burial Process describing the rate of permanent accumulation of carbon in lake sediments. It is larger than the rate of carbon sedimentation because a portion of the deposited can be mineralized (generally to CO_2 or to CH_4) and returned to the water column.
Dissolved and particulate carbon Operationally defined as carbon passing through or retained by a 0.45–0.7 μm porosity filter, respectively.
Gas exchange coefficient (piston velocity, k_{600}) A coefficient linked to the turbulence at the air-water interface describing the exchange rate of gases between the water and the atmosphere.
Inorganic carbon (IC) Consists of the dissolved and particulate phases of the carbonate system. Dissolved inorganic carbon (DIC) refers to the sum of dissolved CO_2 + the bicarbonate anion + the carbonate ion. Particulate inorganic carbon consists only of carbonate in the solid phase in minerals such as calcite, aragonite and vaterite. These minerals can be formed either by chemical precipitation or by the actions of shell-making organisms such as bivalves and snails.
Lake metabolism Refers to the ensemble of processes regulating the balance between primary production and respiration.
Organic carbon (OC) Carbon containing compounds other than inorganic carbon species generally generated or transformed by living organisms. Dissolved organic carbon (DOC) found in lakes typically consists of a mixture of thousands of different organic compounds.
Organic carbon reactivity The rate at which organic compounds are degraded in a sample of lake water, usually expressed as a first-order reaction rate constant. Because lake water typically contains compounds of different reactivities, organic carbon degradation corresponds to a continuum of reactivity.
Primary production The fixation of inorganic C into organic constituents performed by primary producers.
Respiration The conversion of organic matter to inorganic carbon, generally CO_2. Respiration is performed by both autotrophic and heterotrophic organisms.

Introduction

The lake carbon cycle encompasses all the processes that transport, transform, use, exchange or recycle any form of carbon found in lakes. As the common currency of all life, the flow of carbon through lake ecosystems is thus considered a general metric of the intensity of biological activity within, although some carbon transformation also may also occur through abiotic mechanisms. While this biological activity occurs within the lake's shoreline, lake ecosystems are largely a reflection of what they receive and are

inextricably linked with the terrestrial catchment they drain. This paradigm of lakes as receptor funnels and reactors is not unique to carbon and is necessary to account for their observed responses to changes in external loadings, be it of nutrients in the case of eutrophication, or of sulfur or nitrogen oxides for acidification. For carbon, this terrestrial-aquatic linkage is even more pronounced because carbon processing is not only a function of the amount and form lakes receive but also by the input of other substances such as nutrients or, in some cases, of pollutants as well.

At its simplest level, the lacustrine carbon cycle is the study of how lakes react to the external loads of carbon and nutrients they receive from upstream, how the various carbon pools interact with—and are transformed into—one another, and how and in what form they are lost from the lakes, all of which are constrained or augmented by physical, chemical and biological processes. In this chapter, we review the main transformation and transport processes of the largest carbon pools and fluxes and how carbon ultimately leaves the lake at the ecosystem main interfaces: the outflow, the air-water surface and the sediments.

Carbon inputs to lakes: Forms and sources

Carbon in streams, rivers and lakes occurs in a variety of forms that are coarsely distinguished as inorganic (IC) and organic (OC) carbon fractions, each of which can be either dissolved (DIC, DOC) or particulate (PIC, POC). Furthermore, each of these forms is actually the sum of multiple chemical species. In the case of DIC, it comprises three distinct species (dissolved CO_2, bicarbonate and carbonate ions) that are in chemical equilibrium with each other (see details in section below). For DOC, it is composed of thousands of different soluble compounds of varying molecular complexity originating from the leaching and partial degradation or processing of terrestrial organic matter. CH_4 is the simplest dissolved organic compounds but is not normally included in the definition of the DOC pool or inputs, and is nearly always treated separately. Their particulate counterparts, PIC and POC, are generally composed of various carbonate minerals (calcite, aragonite. . .) and small plant or animal organic debris (living or dead), respectively. The four carbon fractions enter lakes mostly via riverine and groundwater inputs but the relative contribution of each of these forms varies enormously between lakes of different regions and even between lakes of the same region (Stets et al., 2009). Nevertheless, some generalities emerge: the dissolved component is generally much larger than the particulate and the riverine load is usually greater than the groundwater load. The partitioning between the organic and inorganic loads is more variable and largely determined by the geological, edaphic and topographic settings of the lake and its catchment. Sedimentary rocks will yield higher inorganic carbon exports than igneous geology while the soil organic content and flat terrains will promote the export of organic carbon. The inputs of inorganic and organic carbon to lakes therefore varies considerably among different regions of the world depending on their topography and local geology (Meybeck, 1987).

Ultimately, both inorganic and organic carbon exports can be viewed as the product of terrestrial primary productivity (Maberly et al., 2013). While this is obvious for the organic fraction, the inorganic carbon export is derived either from the direct transport of soil respiratory CO_2 to the stream channel or by first reacting with various silicate or carbonate minerals to produce bicarbonates through weathering reactions (Viers et al., 2007) such as

$$NaAlSi_3O_8(s) + CO_2(g) + 5\ 1/2\ H_2O \rightarrow Na^+ + HCO_3^- + 2H_4SiO_4 + \text{kaolinite} \quad (1a)$$

and

$$CaCO_3(s) + CO_2(g) + H_2O \rightarrow Ca_{2+} + 2HCO_3^- \quad (1b)$$

In the case of carbonate mineral weathering, only half of the carbon delivered as bicarbonates would be derived from terrestrial primary production and the other half from the mineral itself. Stream surfaces are active sites of gas transfer to the atmosphere and most of the inorganic carbon reaching the lake is in the form of ionic species (HCO_3^- and CO_3^{2-}).

Upon entering the lake, inorganic and organic carbon loads from the catchment constitute an important subsidy to the carbon economy of the lake but not all forms undergo transformation to the same extent. For example, carbonate alkalinity (CO_3^- and HCO_3^{2-} ions) is largely conservative in lakes except in cases where some primary producers (e.g., macrophytes and some algal species) can use bicarbonate ions as inorganic substrates when dissolved CO_2 is scarce (Prins and Elzenga, 1989), or when carbonates precipitate as in marl lakes. Organic carbon inputs however have a much different fate. Most (typically 90%) of the organic carbon enters lakes as dissolved, while the particulate remainder is composed mostly of detrital terrestrial plant and soil material. Although the dissolved organic matter can be quite old and therefore suggestive of a high degree of recalcitrance, the conditions prevailing in aquatic systems are more conducive to its rapid transformation (McCallister and del Giorgio, 2012).

Dissolved inorganic carbon (DIC)

All water, even distilled water, contains some amount of inorganic C in solution. The total dissolved inorganic C content is generally referred to as DIC (total CO_2 by some authors). DIC, however, is made up of several chemical species: the bicarbonate ion (HCO_3^-), the carbonate ion (CO_3^{2-}), and aqueous carbon dioxide, which consists of two pools (dissolved free CO_2 and its hydrated form H_2CO_3, carbonic acid). At equilibrium with each other, H_2CO_3 is about 1/1000th of the concentration of free CO_2. Neither CO_2 nor H_2CO_3 is a charged species; they interchange readily and behave as one pool in chemical reactions. Thus, all of the constants and equations treat $CO_2 + H_2CO_3$ as a single pool and refer to it as either $H_2CO_3^*$ or simply as dissolved or aqueous CO_2.

The concentration of DIC in the oceans is large and within a narrow range (near 2400 μM) and varies with salinity. In inland waters, DIC ranges from <20 μM in acidic soft waters to >5000 μM in alkaline hard waters and even higher in endorheic, saline lakes. In most freshwaters, DIC lies between 100 and 1000 μM in the surface and typically the concentration increases with depth in stratified systems because of the accumulation of respiratory CO_2 (Ducharme-Riel et al., 2015).

Chemical equilibrium of the carbonate complex

When dissolved in water, carbon dioxide ($CO_{2(aq)}$) enters into an equilibrium with the other two carbon species following the bulk simplified reaction

$$CO_{2(aq)} \rightleftharpoons H^+ + HCO_3^- \rightleftharpoons H^+ + CO_3^{2-} \tag{2}$$

with equilibrium constants K_1 and K_2 as:

$$K_1 = \frac{[H^+][HCO_3^-]}{[CO_{2(aq)}]} \tag{3a}$$

and

$$K_2 = \frac{[H^+][CO_3^{2-}]}{[HCO_3^-]} \tag{3b}$$

Neither K_1 nor K_2 are constant; rather their values change slightly with temperature and ionic strength. Values for K_1 and K_2 in dilute waters and equations describing their temperature dependence are given in Table 1. The reaction rates of these protonation/deprotonation between carbonic acid, bicarbonates and carbonates are very fast and can be considered instantaneous. The hydration of CO_2 to carbonic acid (H_2CO_3) is slower but still in the order of a few seconds meaning that for processes that alter any of the three inorganic carbon pools at longer time scales, they can be considered in equilibrium with each other. The partitioning of DIC into its three species is entirely predictable from pH and is expressed by the ionization fractions of each species (α_{sp}), i.e. their fraction of the total DIC pool (thus, the three α's always add up to one):

$$\propto_{CO_2} = \frac{1}{1 + \frac{K_1}{[H^+]} + \frac{K_1K_2}{[H^+]^2}} \qquad \propto_{HCO_3^-} = \frac{1}{1 + \frac{[H^+]}{K_1} + \frac{K_2}{[H^+]}} \qquad \propto_{CO_3^{2-}} = \frac{1}{1 + \frac{[H^+]}{K_2} + \frac{[H^+]^2}{K_1K_2}} \tag{4}$$

Fig. 1 illustrates the relative contribution of the three species to the total DIC pool as a continuous function of pH.

Another important quantity involving DIC is the alkalinity of the water, also known as the acid neutralizing capacity (ANC, expressed in μ- or mequivalents L^{-1}). In older literature alkalinity was often expressed in mg $CaCO_3$ L^{-1} or ppm $CaCO_3$. These units sum up CO_3 and HCO_3 and assume the balancing anion is Ca and then express it as a weight as if it were actually $CaCO_3$. The conversion is 50 mg $CaCO_3$ L^{-1} = 1 mequiv L^{-1} given that carbonate ions are divalent.

Because of the equilibrium described in Eq. (2) the movements between the three species act as the main buffer mechanism in freshwaters, whereby acid additions will displace the equilibrium but with only modest changes in pH, until the ANC is exhausted.

Table 1 Equations describing the temperature dependence of the acid dissociation constants K_1 and K_2 defined in Eqs. (3a), (3b).

$$pK_1 = -126.34048 + \frac{6320.813}{\text{Temp} + 273.15} + 19.568224 \cdot \ln(\text{Temp} + 273.15) \tag{T1a}$$

$$pK_2 = -90.18333 + \frac{5143.692}{\text{Temp} + 273.15} + 14.613358 \cdot \ln(\text{Temp} + 273.15) \tag{T1b}$$

Salinity correction

$$\text{T1c}: \; pK_1' = pK_1 + A_1 + \frac{B_1}{\text{Temp} + 273.15} + C_1 \cdot \ln(\text{Temp} + 273.15) \tag{T1c}$$

where $A_1 = 13.4038 \cdot \sqrt{S} + 0.03206 \cdot S - 5.242 \cdot 10^{-5} \cdot S^2$
$B_1 = -530.659 \cdot \sqrt{S} - 5.8210 \cdot S$
$C_1 = -2.0664 \cdot \sqrt{S}$

$$pK_2' = pK_2 + A_2 + \frac{B_2}{\text{Temp} + 273.15} + C_2 \cdot \ln(\text{Temp} + 273.15) \tag{T1d}$$

where $A_2 = 21.3728 \cdot \sqrt{S} + 0.1218 \cdot S - 3.688 \cdot 10^{-4} \cdot S^2$
$B_2 = -788.289 \cdot \sqrt{S} - 19.189 \cdot S$
$C_2 = -3.374 \cdot \sqrt{S}$

The dissociation constants are usually expressed on a logarithmic scale where $pK_{1\text{ or }2} = -\log_{10}(K_{1\text{ or }2})$. Eqs. (T1a), (T1b) are for dilute freshwaters (Millero, 1979). For estuarine conditions, Eqs. (T1c), (T1d) provide salinity corrections to the freshwater equations (Millero, 2010). Temp is temperature in °C and S is salinity.

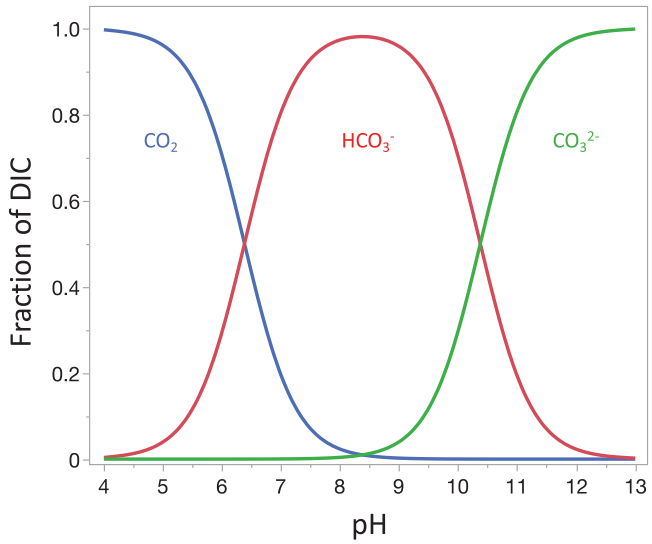

Fig. 1 The fraction of the total DIC pool comprised by CO_2 (blue), HCO_3^- (red) and CO_3^{2-} (green) as a function of pH. This diagram is common in limnology textbooks but has caused some confusion. First, it is actually the proportions of the forms of DIC that regulate the pH rather than vice versa as the diagram might suggest. Second, the *Y* axis is the fraction, not the absolute amount. It is useful to remember that at pH 6.3 the amount of CO_2 and HCO_3^- will be equal and at pH 10.3 the amount of CO_3^{2-} and HCO_3^- will be equal. Values for K_1 and K_2 are not constant but vary with temperature and ionic composition, and are quite different in seawater from the values in dilute freshwater lakes (Table 1).

Carbonate ANC is defined as

$$ANC = \left[HCO_3^-\right] + 2 \cdot \left[CO_3^{2-}\right] + \left[OH^-\right] - \left[H^+\right] \quad (5)$$

While there are other sources of alkalinity in freshwaters (organic acids, sulfate and nitrate reduction, . . .), carbonate alkalinity is by far the most important buffering mechanism. Nevertheless, in very soft waters (<100 μeq L^{-1}), dissolved organic substances can add a non-negligible source of alkalinity (about 1–3 μeq mg C-DOC^{-1}). Since HCO_3^- is generally the main constituent of DIC, it is easy to infer from Eq. (5) that DIC and ANC are generally tightly related. Conversely, Eq. (5) also shows ANC is not altered by the addition or removal of CO_2. This implies that biological processes either producing or consuming CO_2 will not change the alkalinity of the system (unless accompanied by a net change in the base cations). Nevertheless, all of the properties of the DIC complex are intricately related via the equilibrium reactions and the values of ANC, pH and CO_2 concentration form a "triad," whereby knowing any two variables, there can be only one solution for the third. This is very practical because it allows the easy calculation, for example, of CO_2 concentration from pH and Alkalinity (or DIC) measurements (see Stumm and Morgan, 1995). Fig. 2 illustrates the relationship between ANC, pH and pCO_2 at 20 °C, where pCO_2 is the partial pressure of CO_2. Because CO_2 is a gas, it is often expressed as a partial pressure rather than as a concentration. The concentration of CO_2 gas is related to pCO_2 by Henry's law: $[CO_2] = Kh \cdot pCO_2$ (where CO_2 is expressed in μmoles L^{-1}; pCO_2 in μatm and Kh is a constant that varies with temperature). At 20 °C, Kh is about 0.039 μmoles L^{-1} μatm^{-1}. Thus, if the aqueous pCO_2 is 400 μatm (the approximate current value in the overlying atmosphere), CO_2 concentration would be about 16 μM.

The dependence of the ionization fractions (the α's, Eq. 4) on pH alone has sometimes led to the misleading causal inference that it is pH that dictates the concentrations of the constituents. In fact, it is more appropriate to view the CO_2 system as controlling pH. Indeed, even large additions of CO_2 to an aqueous solution of a given alkalinity will induce only a very small shift in the bicarbonate and carbonate concentrations and will instead remain as dissolved CO_2, thereby inducing a substantial lowering of pH. Note that there is a strong asymmetry in this equilibrium process in that removal of CO_2 by photosynthesis or other process can draw a significant amount of CO_2 from the bicarbonate + carbonate pool. Such movements can be important to consider when CO_2 is measured by headspace equilibration (Koschorreck et al., 2021). It is also true that if one adds an acid or a base to lake water, both the pH and the species of DIC will be altered.

Dissolved organic carbon (DOC)

Unlike DIC, dissolved organic carbon is a very heterogeneous mixture of thousands of different organic compounds, the concentrations of which are generally not subject to a chemical equilibrium although some may be. Recent analytical capabilities have revealed that the general order of abundance is highly unsaturated and phenolic compounds > polyphenolic compounds > condensed aromatics > aliphatic compounds, although this order can change upon degradation (Kellerman et al., 2018). The carbon concentration of the bulk DOC pool varies broadly from less than 1 mg to over 300 mg C L^{-1} although the vast majority of lakes fall below 30 mg C L^{-1} (Sobek et al., 2007). In the newer literature, DOC is often expressed in molar units of C, thus the range would be from <80 to >2500 μM. In many freshwater ecosystems, DOC constitutes by far the largest pool of

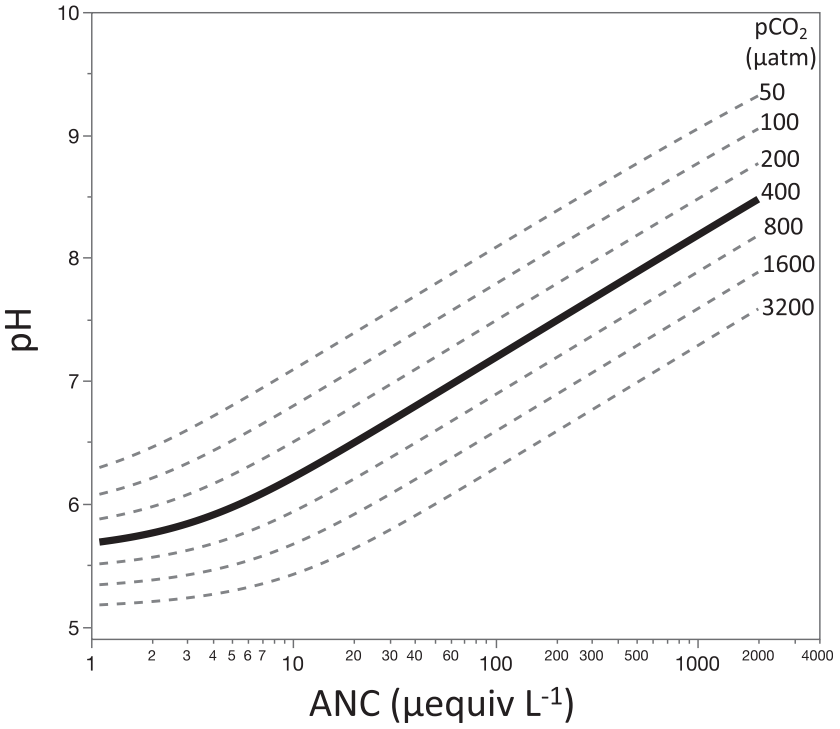

Fig. 2 The triadic relationship between pH, ANC and pCO_2 at 20 °C. Solid line represents atmospheric equilibrium at approximate current levels of 400 µatm (2020).

organic carbon in the water column, exceeding that of phytoplankton except in very eutrophic systems. The nature of the DOC can be characterized in several ways using optical properties, size exclusion chromatography, and more recently, the molecular formula of individual compounds (Stubbins et al., 2014). The colored fraction of the DOC (known as CDOM, m^{-1}) is often a useful metric of its reactivity, particularly with regards to the absorption of light energy. DOC can also be characterized by stable isotopes and both ^{13}C and ^{2}H have been useful. Based on both of these isotopes, DOC in lakes appears to be largely to entirely of terrestrial origin, at least in the small lakes that have been studied (Bade et al., 2007).

Particulate carbon in the water column

In the water column, particles of both organic C (particulate organic C or POC) and particulate inorganic C (PIC) can occur. PIC is a rare and short-lived phenomenon in most lake and generally happens only in those lakes that are both eutrophic and have large amounts of DIC and ANC. During a phytoplankton bloom, CO_2 can be reduced to very low levels thus raising the pH to the point where the solubility of calcium carbonate is exceeded. In Lake Michigan, for example, these "whiting events" occur every few years. In lakes with low DIC, even if there is CO_2 draw down from the atmosphere, there is insufficient carbonate to form a precipitate.

Particulate organic C is defined operationally as those organic particles that are caught on a GF/F filter (about 0.7 µm pore size) but pass through a 63 µm plankton net. Thus, POC in the water column includes living phytoplankton, bacterioplankton, protozoa, and some of the very smallest rotifers as well as detritus. This organic detritus can be the remains of planktonic organisms or detritus of terrestrial origin. The inputs of POC to lakes include phytoplankton primary production, resuspension from the sediments, and inputs of terrestrial particles in streamflow or from the air. The concentrations of POC tend to be much lower than that of DOC, typically about 10-fold lower. Isotopic approaches have shown that POC is a mixture of terrestrial and within-lake sources and this mixture varies along gradients over which these two sources vary.

Carbon transformation processes and lake metabolism

At the broadest level, carbon transformation processes in lakes are the conversion of inorganic carbon to organic forms, and its reverse process, the mineralization of organic compounds to inorganic C, mostly CO_2. These two processes are not regulated by the same drivers and are therefore only loosely coupled. The balance between them is commonly known as the "net lake metabolism" and can be summarized by the general bulk stoichiometric reaction.

$$106\,CO_2 + 106\,H_2O + 16\,NH_3 + H_3PO_4 \underset{\text{Respiration}}{\overset{\text{Primary production}}{\rightleftharpoons}} (CH_2O)_{106}\,(NH_3)_{16}(H_3PO_4) + 106\,O_2 \quad (6)$$

While the fixation of inorganic C in lakes (forward reaction) is essentially performed by primary producers through photosynthesis (micro-algae and macrophytes), the mineralization of organic carbon (backward reaction) can be autotrophic, microbial (heterotrophic respiration) and photo-chemical. In general, microbial respiration accounts for the majority of the mineralization of organic matter in lakes. While this bulk equation (Eq. 6) conforms to the average stoichiometric composition of aquatic biomass (C:N:P = 106:16:1, the Redfield ratio), heterotrophic respiration of organic matter can have different elemental ratios (Berggren et al., 2012). In the broad sense, all biological carbon transformations are either a production or a respiration process, both of which are apportioned among autotrophs and heterotrophs, and can be quantified at any scale: from individual cells to entire ecosystems, or for broad single compartments such as bacteria, phytoplankton, benthic plants, zooplankton, benthos, or fish.

Primary production

Carbon fixation by aquatic primary producers primarily uses dissolved carbon dioxide (CO_2) as the main substrate although many species can use also HCO_3^- ions when ambient dissolved CO_2 is depleted or through various carbon concentrating mechanisms (CCM) (Maberly and Gontero, 2017). At the cellular level, photosynthesis in algae is often described as Monod kinetics whereby rates are limited by the concentration of the main limiting substrate, CO_2. When at equilibrium with the atmosphere, CO_2 concentration in water is around 16 μmole L^{-1} (at 20 °C) which is well below the half-saturation constants of many freshwater algal and macrophyte species (>50 μmole L^{-1}). As a result, rates of aquatic photosynthesis can be enhanced in higher CO_2 concentrations (Jansson et al., 2012). While rates of primary production can therefore be considered limited by inorganic carbon, algal biomass at the ecosystem level is generally limited by a combination of light and nutrients, most notably phosphorus. Inorganic carbon is not considered biomass limiting at this scale because it can be replenished by CO_2 exchange with the atmosphere. It can however strongly affect the composition of the phytoplankton assemblage responsible for pelagic photosynthesis (Low-Décarie et al., 2015).

At the ecosystem scale, primary production occurs in two spatially distinct compartments: benthic and pelagic. Their magnitude is often inversely related and their relative contribution to total lake photosynthesis is usually determined by factors regulating light penetration and by the areal coverage of the littoral zone. Benthic primary production is generally low when phytoplankton abundance is high because of the reduced light penetration to the surface of the sediments. Thus, the contribution of benthic primary producers to the overall production of the lake ecosystem declines with increasing lake trophic status (Vadeboncoeur et al., 2003). Conversely, it can represent most of the lake's productivity, particularly in shallow oligotrophic systems. Among lakes, pelagic primary production spans a very large range, from a few mg C m^{-3} d^{-1} in oligotrophic lakes to >2000 mg C m^{-3} d^{-1} in hyper-eutrophic conditions. Among lakes, differences in both primary production and biomass are thus largely explained by variation in phosphorus concentration although nitrogen is often considered co-limiting. The relationship between algal biomass (expressed as the concentration chlorophyll-*a* in the water column) and phosphorus concentration has served as the basis for the management of eutrophication worldwide (Schindler, 2006). Primary production reaches a plateau in hyper-eutrophic condition when light becomes the limiting factor.

The diurnal cycle in photosynthetic activity induces corresponding variations in the CO_2 concentration of the photic zone of lakes, variations that are used to estimate the magnitude of photosynthesis. The daily amplitude of the CO_2 signal can be quite large and depends on the rates of photosynthesis (Gross Primary Production, GPP) and respiration (R, heterotrophic + autotrophic) as well as on the rate of exchange with the atmosphere (Eq. 7):

$$\frac{d[CO_2]}{dt} = GPP - R \pm Atm.exch. \quad (7)$$

Assuming that R is constant throughout the day and night, estimates of GPP and R can be extracted from time-series of CO_2 (Fig. 3) provided an accurate CO_2 air-water exchange can be obtained (see section CO_2 flux at the air-water interface below). This simple model assumes that, at such short time scales, changes in external inputs and outputs can be neglected. A significant advantage of this approach to quantify aquatic primary production is that it integrates all photosynthetic compartments (algae and macrophytes, pelagic and benthic).

The carbon fixed by photosynthesis has multiple fates. First, it is an important food source for heterotrophic organisms (zooplankton, some rotifers) and thereby sustains a large portion of the whole aquatic foodweb of lakes. As the energy is transferred with various efficiencies to higher components of the trophic chain, organic matter will be lost to respiration in form of the CO_2. Second, upon senescence organic matter (whether of plant or animals) will settle to the sediment floor of lakes where it will undergo either further degradation or be permanently buried (see "Carbon sedimentation" section). Third, all forms of primary production (pelagic and benthic algae and macrophytes) are associated with some release of organic compounds back to the water column (Cole et al., 1982; Demarty and Prairie, 2009; Wyatt et al., 2014). The importance of such autochthonous DOC varies widely among lakes and will fuel further microbial metabolism. In shallow lakes with high coverage of aquatic plants, the release of DOC by macrophytes can exceed allochthonous organic inputs.

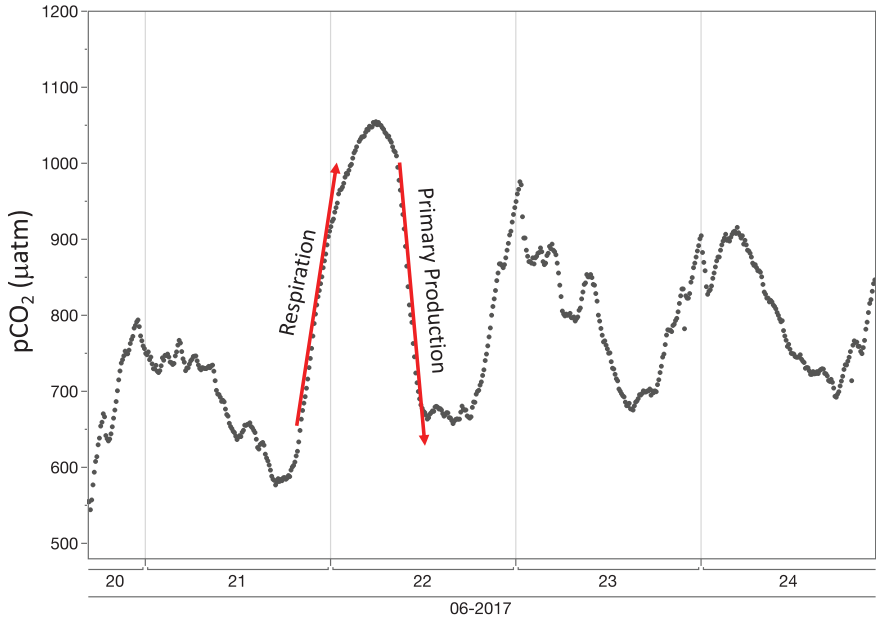

Fig. 3 Diurnal cycle in pCO_2 in L. Croche (Québec) over a period of a few days. Rates of respiration and primary production can be inferred by the pCO_2 oscillations (red arrows) once gas exchange at the air-water interface is taken into account. Irregularities in the diurnal cycles generally originate from intermittent clouds and/or wind-induced changes in gas exchange.

Microbial degradation of DOC

The rate of degradation of DOC by microbes depends on the nature of the organic material as well as on the microbial communities involved. In general, the rate of DOC consumption increases with the concentration and lability of the DOC. While the DOC exuded from autochthonous production (algae and macrophytes) can be consumed rapidly, lake DOC of allochthonous origin has a slower degradation. Further, short-term lake water incubations have shown that the decomposition is not linear in time and is therefore better approximated as a first-order reaction, with decay constants generally in the range of 0.005–0.10 d^{-1}. Decay rates vary according to chemical groups. For example, aromatic compounds tend to have slower decays while simpler molecules such amino acids, proteins and sugars are much more labile. Recent methodological advances using FT-ICRMS have permitted to follow the degradation of the individual organic compounds (or elemental formulas) comprising the DOC and have shown that different compounds decay at very different rates and that some organic molecules are actually generated as a product of microbial metabolism (Mostovaya et al., 2017). This has led to the confirmation of the so-called "reactivity continuum concept" whereby lake DOC cannot be viewed as a single carbon pool of homogenous reactivity but instead as a complex mixture comprising a continuum of reactivities. A popular model (originally developed by Boudreau and Ruddick (1991) for sediment processes) describing the time course of mineralization of a DOC mixture that account for the spectrum of biological reactivities is

$$[DOC]_t = [DOC]_0 \left[\frac{\alpha}{\alpha + t}\right]^{\upsilon} \tag{8}$$

where $[DOC]_0$ and $[DOC]_t$ are respectively the DOC concentrations initially and at time t (in days), and α and ν are parameters describing the probability (gamma) distribution of reactivities within the DOC pool. The α describes the average half-life of the more reactive compounds and ν is a dimensionless shape parameter related to the reactivity of the most abundant species. This model (Eq. 8) is extremely flexible and can accommodate a large range of initial distribution of reactivities of the compounds. Fig. 4 illustrates how the relative distribution of the reactivities will change in time as degradation progresses, with the more reactive compounds disappearing at a faster rate. Accordingly, the same model can be used to illustrate how the apparent decay rate (k_{DOC}, d^{-1}) of the whole DOC pool (the weighted average of the reactivities, dash lines in Fig. 4) will also decrease in time as the more labile material becomes progressively exhausted.

The instantaneous degradation constant at any given time ($k_{DOC\ t}$, in d^{-1}) is given by

$$k_{DOC\ t} = \left[\frac{\upsilon}{\alpha + t}\right] \tag{9}$$

Beyond its simple description of a complex biogeochemical process, the reactivity continuum concept described above has important consequences on our understanding of DOC dynamics of lakes in their landscape. The water residence time of lakes (τ_w), the average time a water molecule spends in the lake before being lost to the outflow, is typically in the order of a few months to a few years, much longer than the degradation time scale of the more labile organic compounds (a few days). Thus, the molecular profile and the biological reactivity of the lake DOC can be quite different from that of the allochthonous DOC fueling the lake

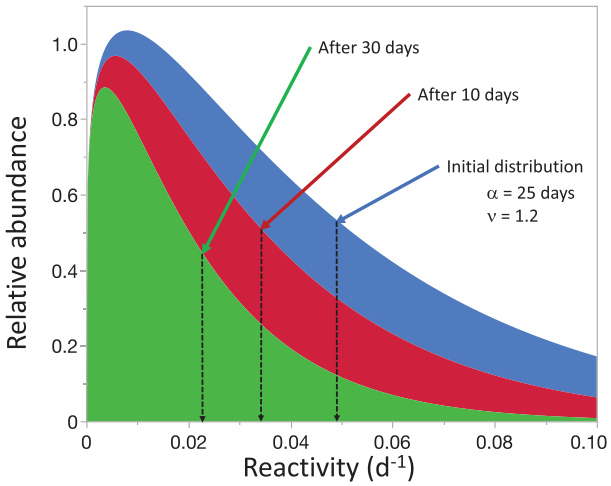

Fig. 4 Illustration of the reactivity continuum concept whereby the abundance of the most reactive compounds (right side of the abscissa) is more rapidly lost, leading to a shift in the distribution of the reactivities (colored surfaces, expressed here as probability density) as time of degradation progresses. Dashed arrows correspond to the average reactivity of the DOC pool ($k_{DOC\ t}$) at different times (initial, 10 days, 30 days) given by Eq. (9).

because the bulk of the easily degradable DOC forms has already been mineralized. Consequently, lake DOC will in general exhibit a much lower apparent decay rate that its main source material (riverine input) and the extent of the decoupling will vary inversely with the water residence time of lake. This implies that even within a region where the nature of the terrestrial DOC is expected to be relatively uniform, lakes with different hydrological regimes will exhibit very different DOC degradation rates.

The effect of hydrology on DOC degradation can be quantified by accounting simultaneously for the continuum of reactivity (α and ν) and for the distribution of water ages within a lake. Assuming for simplicity that fluvial inflows are instantaneously and completely mixed once in the lake, the distribution of water ages about the average water residence time is expected to follow an exponential distribution. Combined with the reactivity continuum parameters, the inverse relationship between organic matter decay constant (k) and lake hydrology can be well approximated by $k = \frac{0.85\ \nu}{\tau_w} \ln\left[1 + \frac{\tau_w}{\alpha}\right]$ (Fig. 5). Nevertheless, lakes with long water residence times will process a larger fraction of the organic carbon load they receive from their catchments even if their overall decay rate is slower. The exact form of the relationship will depend on the reactivity parameters of the source material (insets of Fig. 5) and also of the autochthonous DOC produced (Vachon et al., 2017).

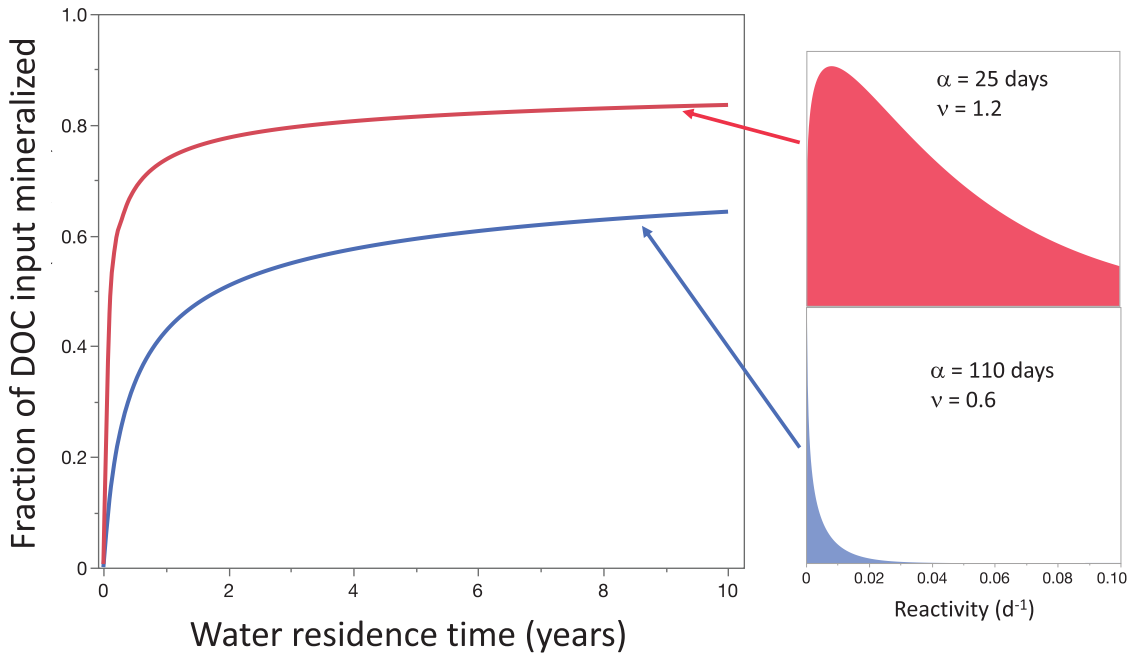

Fig. 5 The influence of water residence time (τ_w, in years) on the fraction of the incoming DOC loads lost annually to mineralization. Depending on the reactivity of the organic material (reactivity distributions on right), the influence of water residence time can be markedly different.

Fate of the organic carbon inputs processed by microbes

For lakes with water residence times greater than 6 months, Fig. 5 shows that a substantial portion of the allochthonous DOC inputs will be processed by microbes. Aquatic microbes are fairly efficient at converting their substrate (DOC) into microbial biomass. In many systems, a bacterial growth efficiency between 10% and 30% is observed but can reach up to 50% in eutrophic systems where a larger fraction of the ambient DOC pool is derived from algal production and associated release of more labile organic carbon. The microbial biomass produced will eventually make its way to higher components of the food web through flagellates and ciliates or through mixotrophic algae. In small DOC-rich lakes, even fish can be construed as being partially composed (up to about 30%) of organic carbon of terrestrial origin and microbes play a central role in this transfer (Pace et al., 2007). In eutrophic lakes, this pathway of energy transfer is less prevalent and mostly consists of algal or macrophyte derived primary production. Thus, most of the organic carbon processed by microbes will be respired to CO_2. In lakes where allochthonous DOC sources constitute a substantial portion of the organic carbon budget, heterotrophic microbial respiration will release CO_2 in excess relative to what is assimilated by primary producers, raising the CO_2 partial pressure above that of the atmosphere and therefore act as a source of CO_2. These lakes have been termed "net heterotrophic" because R > GPP (Eq. 7). As a rule of thumb, lakes with DOC concentrations below and above the threshold value of about 5 mg C L^{-1} are, in general, net autotrophic and net heterotrophic, respectively.

Given that lakes often have DOC concentrations exceeding this threshold (Sobek et al., 2007), net heterotrophy is much more prevalent than net autotrophy. Nevertheless, eutrophic systems routinely exhibit, at least temporarily, CO_2 concentrations well below atmospheric equilibrium and therefore exacerbate the physiological CO_2 requirements of primary producers to function at sub-optimal photosynthetic rates. Reviews of the published literature suggest that the vast majority of lakes (>90%) are oversaturated in CO_2 and are therefore net emitters to the atmosphere (Cole et al., 1994). CO_2 partial pressures in the surface waters of lakes are generally within the 400–2000 μatm (or ppmv) range. If the pCO_2 in the surface water is higher than that in the air (currently about 400 μatm), the net flux of CO_2 will be from the water to the air. We call this condition supersaturation. The converse is called undersaturation. In hypolimnetic waters, pCO_2 can reach much higher values because of isolation from atmospheric exchange but rarely exceeds 10,000 μatm, roughly corresponding to the complete depletion of O_2 from aerobic respiration (Eq. 7, backward reaction). A caveat is that CO_2 excess is not always the result of in situ metabolism but can also originate from other sources, such as inputs of CO_2-rich groundwaters or other geologic processes (Vachon et al., 2016).

Carbon loss processes

At the ecosystem level, there are only three possible fates for carbon: fluvial outflow, outgassing of CO_2 and sedimentation. The relative importance of the loss pathways is very variable among lakes and is still not fully understood. While lakes with very short water residence times will naturally lose most of their carbon through the outflow, the partitioning between evasion and sedimentation is an active area of research and will generally depend on the source and nature of the organic material. In oligotrophic lakes, CO_2 diffusion at the air-water interface will dominate while sedimentation and burial are more important is eutrophic lakes. In this section, we review the processes modulating the magnitude of each of the main loss processes.

CO_2 flux at the air-water interface

Although many carbon-containing gases can exchange, most notably CO_2 and CH_4 but also some volatile organic compounds (VOCs), this section will pertain mostly to CO_2 because CH_4 is treated in other chapters. Carbon dioxide, like all gases, obey basic principles of gas equilibrium (ideal gas law), which states that gases contained in a system with both a gas and a liquid phase are driven to an equilibrium in which their partial pressures in the two phases become equal ($pCO_{2(air)} = pCO_{2(water)}$). In air, the partial pressure of a gas is equivalent to its mole fraction at standard barometric pressure (1 atm). This is because a mole of any gas occupies the same volume at any given temperature and pressure. Thus, partial pressure and concentration in air follows the same relationship for all "ideal" gases. In water however, the relationship between partial pressure and concentration varies between gases because of their different solubilities. For example, if CO_2 and CH_4 are present in lakes at the same concentration of say 200 μmole L^{-1}, the partial pressures exerted by the two gases would be about 5100 and 133,333 μatm at 20 °C, respectively, because CO_2 is much more soluble than CH_4. The relationship between partial pressure and aqueous concentration is given by Henry's law.

$$[Gas] = k_H \cdot pGas \tag{10}$$

where the square bracket represents concentration, p the partial pressure and k_H is Henry's constant for the particular gas at hand. Some gases deviate from this "ideal gas" relationship with partial pressure. For such gases, partial pressure is replaced by fugacity, which corresponds to the effective partial pressure and differs from the mechanical pressure the gas exerts at a given concentration. For CO_2, fugacity and partial pressure are nearly equal in the range of temperature and hydrostatic pressure normally found in lakes and therefore are often used interchangeably. Despite the name, Henry's constants k_H for gases are not constant but are instead dependent on temperature. For CO_2, k_H is about 0.039 at 20 °C but can be estimated for any lake temperatures (0–40 °C) using.

$$\ln k_{H(CO_2)} = -60.2409 + \frac{9345.17}{T + 273.15} + 23.3585 \cdot \ln\left(\frac{T + 273.15}{100}\right) \tag{11}$$

where T is temperature (in °C).

If all lakes were in equilibrium with the atmosphere ($pCO_{2(air)}=pCO_{2(water)}$), they would all exhibit the same concentration of CO_2, except for the temperature effect shown in Eq. (11). However, the mineralization of organic carbon to CO_2 or the consumption of CO_2 by photosynthesis pushes the lake water away from this equilibrium and the water therefore becomes either under or over-saturated with CO_2 with respect to the atmosphere. The ensuing air-water gradient in pCO_2 will initiate a net diffusive transport at the air-water interface of lakes following Fick's first law of diffusion:

$$Flux_{air\text{-}water} = k \cdot k_{H(CO_2)} \cdot \left(pCO_{2(water)} - pCO_{2(air)}\right) \tag{12}$$

which states that the flux (positive is outflux, mmol m^{-2} d^{-1}) is, for a given set of environmental conditions, directly proportional to the air-water concentration gradient $k_{H(CO_2)} \cdot (pCO_{2(w)} - pCO_{2(air)})$ (in mmoles m^{-3}) by a factor k, known variously in the literature as the gas exchange coefficient, exchange velocity or piston velocity (m d^{-1}). To compare the gas exchange coefficients of different gases or of a given gas at different temperatures, k is often standardized to a fixed Schmidt number (Sc). The Schmidt number is the dimensionless ratio of the turbulent transport of momentum to that of mass and therefore depends on the diffusivity of a particular gas and how it varies with temperature. In freshwaters, gas exchange velocities are usually standardized to Sc = 600, which corresponds approximately to the Sc of carbon dioxide at 20 °C and are referred to as k_{600}.

The magnitude of k_{600} depends primarily on the turbulence regime occurring at the air-water interface and is therefore largely driven by wind shear. However, convection whereby cooled surface waters sink to deeper layers also creates turbulence and can significantly contribute to k_{600}, particularly in calm conditions (MacIntyre et al., 2010; Tedford et al., 2014). It is therefore temporally and spatially quite variable and its magnitude generally varies between ≈0.5 m d^{-1} in very calm conditions to >10 m d^{-1} in highly turbulent environments (high winds over large lakes). In average conditions, k_{600} values between 1 and 3 m d^{-1} are often encountered. Several models with different input data requirements exist but a simple empirical formula to estimate k_{600} is given by

$$k_{600} = 0.602 + 0.355\ U_{10} + 0.094\ U_{10} \cdot \log_{10} Area \tag{13}$$

where U_{10} is wind speed (m s^{-1}) at a height of 10 m and Area is the lake' surface area (in km^2) (Vachon et al., 2013). The intercept term of Eq. (13) (0.602 m d^{-1}) is often considered the result of convection-induced turbulence. Since k_{600} is a velocity term that describes the exchange between epilimnetic waters and the overlying atmosphere, values of k_{600} (in m d^{-1}) can be loosely interpreted as the thickness of the epilimnion that can be re-equilibrated with the atmosphere in 1 day. This is informative because it can be compared to the actual depth of the mixed layer to infer the average time a random molecule of CO_2 (or of any gas) stays in the epilimnion before being lost to the atmosphere. This average gas residence time ($\tau_{gas} = \frac{mixed\ layer\ thickness}{k_{600}}$) in the epilimnion of lakes is typically in the order of a few days.

The formulation of the gas flux at the air-water interface in Eq. (12) can accommodate various physical representations of the actual exchange process taking place at the interface. While k is often viewed simply as the empirical exchange coefficient of Fick's diffusion law, it can be also construed as a laminar surface boundary layer of thickness (Z_{BL}) through which CO_2 diffuses strictly by molecular diffusion (D_{CO_2}, about 1.9×10^{-5} cm^2 s^{-1} at 25 °C). In this case,

$$k = \frac{D_{CO_2}}{Z_{BL}} \tag{14}$$

and Z_{BL} is a few hundred microns thick in calm conditions and considerably thinner in highly turbulent periods. Alternatively, k can also be interpreted as resulting from the exchange of small water parcels or elements of various sizes randomly reaching the surface and equilibrating with the atmosphere (Asher and Pankow, 1991). In this so-called *surface renewal model*, k is proportional to $\sqrt{\frac{D_{CO_2}}{\tau}}$ where τ is the average residence time of fluid elements at the water surface and assumed to be the same for all water elements (note that this is τ is distinct and unrelated to τ_{gas} i.e. the average gas residence time in the mixed layer discussed earlier). Further refinements of the surface renewal model have led to more detailed representation of the residence time distribution of the fluid elements at the surface.

For most gases, the choice of physical description of the gas exchange is not particularly important because they ultimately all collapse to the same general expression of gas exchange (Eq. 12). However, in certain situations, the fluxes of CO_2 at the air-water interface need to account for chemical reactions between CO_2 and other ionic species that occur at time scales that are similar to the diffusion process and thereby compete with one another. The physical representation of the exchange process then becomes relevant. While the main CO_2 hydration pathway is with water $CO_{2\ (aq)} + H_2O \rightleftarrows H_2CO_3$, CO_2 also reacts directly with OH^- ions to form bicarbonates and the CO_2 exchange with the atmosphere then becomes a diffusion-reaction system. If CO_2 is able to react chemically during its transport, it will enhance the flux and therefore result in an apparent exchange coefficient (k or k_{600}) that is higher than what would be expected from diffusion alone. The magnitude of this chemical enhancement factor (α) can be expressed as the ratio of the gas exchange coefficient with and without reaction

$$\alpha = \frac{k_{600\ (diff\ +\ reac)}}{k_{600\ (diff)}} \tag{15}$$

and will depend on the time scale of the chemical reaction relative to the time scale of the diffusion process. The faster is the reaction relative to the diffusion, the higher is the chemical enhancement factor. Consequently, chemical enhancement will be highest when the reaction is fastest (high $[OH^-]$, high pH) and diffusion slowest (thicker boundary layer, i.e. calm conditions). Various mathematical expressions have been developed to estimate α depending on the particular physical description of the exchange

process (laminar boundary layer or surface renewal model) but are beyond the scope of this chapter. In most conditions encountered in lakes however, the magnitude of α is close to 1 (no enhancement) but chemical enhancement needs to be accounted for in systems with high pH (generally associated with CO_2 depletion in eutrophic systems) and very calm conditions.

Given the physical and chemical constraints on gas exchange between lakes and the atmosphere described above, research of the past 15 years has shown that the vast majority of lakes are net emitters of CO_2. While some (mostly eutrophic) lakes are net sinks for CO_2 on an annual basis, most are sources. This can only be sustained by allochthonous organic matter that is mineralized in the lake and/or by the direct injection of CO_2-rich groundwater in the water body. The relative contribution of the groundwater source is currently poorly constrained but can very significant. Regardless of the exact source of the lake CO_2 excess relative to the atmosphere, the magnitude of the CO_2 outgassing rate is, while widely variable among lakes, surprisingly large even for the average lake. As a comparison, the amount of CO_2 emitted by a single 1 km^2 lake in 1 day is equivalent to two return trips by car per day between the residences of the two authors of this chapter (a total distance of about 5600 km)! While this natural footprint of lakes cannot be rightfully compared to anthropogenic sources, it serves well to illustrate the intensity of the carbon processing occurring in inland waters. At the larger regional or even global scales, the flux of CO_2 from lakes to the atmosphere is an important but often neglected component of the regional carbon balance (incompletely accounted for by forest carbon models) and is comparable in magnitude to the global CO_2 fluxes absorbed by the combined oceans, despite the huge disparity in areal coverage.

Carbon sedimentation and burial

The loss of carbon from the active pool via sedimentation processes is by far the least well understood part of the lacustrine carbon cycle. Even the source and nature of the sediments is, to a certain extent, only loosely known. While the remains of aquatic organisms (both plants and animals) are an obvious component of sediments, the isotopic signature of sediment carbon often suggests that it is of terrestrial origin. Sediments contain both inorganic and organic forms of carbon and their relative importance is largely determined by the geology of the catchments they drain. Lakes in the boreal regions often harbor very soft waters with little carbonate minerals in the landscapes and sediment carbon will be mostly organic. Although carbon sedimentation often represents a relatively small flux on annual basis, the high preservation of sedimentary organic carbon can lead to large accumulations over millenia (Kortelainen et al., 2004). On the other hand, lakes draining carbonaceous landscapes, such as marl lakes, will be susceptible to calcite precipitation particularly in eutrophic warm waters. The concentration of organic C in sediments is relatively low (3% by weight) in some lakes but can be as high as 30% especially in small lakes with anoxic hypolimnia.

In general, the sedimentary flux of carbon is a function of the amount of particulate material either transported from the catchment or generated within the lake. A significant component of the sedimenting material can also be dissolved organic carbon of allochthonous origin that coalesce into colloidal material to ultimately flocculate and sink down (von Wachenfeldt and Tranvik, 2008). Once sedimented, the material will undergo early diagenetic processes. However, in the time scales relevant to lake functioning, the most important one is the post-depositional mineralization of organic carbon, a process that will decrease through time. The few studies that have examined this directly suggest that after 15–25 years, most of the degradable organic carbon will be lost to mineralization (Gälman et al., 2008) while the remaining mostly terrestrial carbon is permanently buried (Guillemette et al., 2017). This is one of the most striking differences between terrestrial soils and lake sediments. The organic carbon fraction of soils is rarely more than a few hundred years old whereas sediment organic carbon remains for thousands of years and its continued accumulation makes lake sediments a significant stock of carbon even at the landscape level. In the boreal biome, organic carbon buried in soils and lake sediments are of similar magnitude even if lakes occupy a few percent of the terrestrial landscape. An enlightening manifestation of this phenomenon is the realization that the sediments of exceptionally old and deep lakes such as L. Tanganyika in Africa contain more organic carbon than the entire living biosphere! Admittedly this organic carbon can no longer be considered part of the active pool of carbon in these lakes.

The distinction between the carbon flux reaching the sediments (*carbon sedimentation*) and what remains permanently buried (*carbon burial*) is important and is highly variable between lakes. The burial efficiency, i.e. the fraction of the sedimentary influx of carbon that will be permanently buried, ranges from a low of a few percent in lakes when the source of the organic material is largely autochthonous and the sedimented material is exposed to dissolved oxygen, to nearly 100% in lakes receiving mostly allochthonous organic carbon with little oxygen exposure time. Since the oxygen penetration depth in sediments is rarely more than a few millimeters, burial efficiency generally increases with the magnitude of the sedimentation flux because the sediments are rapidly buried by newly sedimented material and therefore does not remain in contact with oxygen very long (Sobek et al., 2009). This process leads to a synergistic effect whereby lakes with higher sedimentary influx will exhibit an even faster carbon burial rate because of the associated increase in burial efficiency.

At the ecosystem scale, the process described above leads to an enormous range in sediment carbon accumulation rates, from a few g C m^{-2} $year^{-1}$ in large oligotrophic lakes to >10 kg C m^{-2} $year^{-1}$ in small agricultural ponds (Downing et al., 2008). In both artificial ponds and natural lakes, the size (surface area) of the ecosystem is one of the prime determinants of burial rate. All else being constant, carbon burial rate generally decreases with increasing ecosystem size. However, the bathymetric shape of the particular system also modulates the rate at which carbon can accumulate. Lakes with high dynamic ratios ($DR = \frac{\sqrt{Area}}{Z}$), i.e. flat lakes, tend to accumulate much less carbon than deeper lakes of the same size because a larger fraction of their surface area is in the littoral zone where degradation proceeds faster (Ferland et al., 2012).

Conclusion

The C cycle has fascinated biogeochemists working on every imaginable ecosystem or biome on Earth and particularly so for the global Terrestrial-Atmosphere-Ocean linkage. At the global scale, CO_2 is a major regulator of climate and the measured rise of atmospheric CO_2 stimulated a great deal of research into the C cycle. Limnologists have been attracted to the C cycle almost since the inception of limnology because of the central role of C in metabolism and the role of the dissolved inorganic C system in regulating both pH and alkalinity. The study of C in lakes is almost a subfield in its own right and has been called "carbocentric limnology" (Prairie, 2008). Lakes had not been thought of in the context of the global C cycle until relatively recently, but they do play a role. The sediments of lakes contain more organic C than the entire rest of the terrestrial part of the biosphere. However, the accumulation rate is slow, so the annual net flux into lake sediments is not particularly large. Further, lakes, taken together, are a modest global source of CO_2 into the atmosphere as a result of both inputs of ground water rich in CO_2 and the catabolism of terrestrial inputs of organic C into lakes.

Lakes, of course, are intimately connected to their terrestrial watersheds and receive terrestrial inputs in stream and groundwater and from the atmosphere. Further, lakes discharge water and C downstream in ground and surface water. At a broader scale each lakes is a node in a terrestrial and stream nexus. So, a chapter like this on the C cycle of lakes tends to underplay these connections. Further, it should be also obvious that there is no such thing as "the carbon cycle" in isolation. The C cycle is closely connected to the cycle of many other elements, notably oxygen, nitrogen, phosphorus, sulfur and hydrogen and calcium as well. While it is possible to focus on the C cycle, biogeochemists usually are studying C and many other elements simultaneously.

See Also: Fundamental concepts and theories: Chemosynthesis; Methane; Nutrient Stoichiometry in Aquatic Ecosystems; Structures and functions of Inland Waters - Groundwater: Biogeochemical Cycling of Carbon and Nitrogen in Groundwater—Key Processes and Microbial Drivers; Karst Groundwater Dependent Ecosystems—Typology, Vulnerability and Protection; Structures and functions of Inland Waters - Rivers: Algae and Primary Production of Streams and Rivers Ecosystems; Ecological stoichiometry in streams; Intermittent Rivers and Ephemeral Streams; Structures and functions of Inland Waters - Wetlands: Carbon Dynamics in Wetlands; Wetland Soils: Physical and Chemical Properties and Biogeochemical Processes

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Lacustrine Phosphorus Cycling

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Bioavailable phosphorus Bioavailable phosphorus is a form that is readily available to be used by organisms to synthesize organic phosphorus molecules.
Dissolved phosphorus Dissolved phosphorus is phosphorus that is in an inorganic aqueous form (e.g., orthophosphate) or part of dissolved organic matter.
External loading External loading is the delivery of phosphorus from the watershed to the lacustrine environment.
Internal loading Internal loading is the release of phosphorus from lacustrine sediments.
Particulate phosphorus Particulate phosphorus is phosphorus associated with particles including incorporated in minerals, sorbed to particle surfaces, and bound in particulate organic matter.
Redox conditions Redox conditions describe the abundance of oxidative or reductant substances in the environment, mainly oxygen, that drive biogeochemical processes.
Sediment-water interface Sediment-water interface is the boundary between the surface of sediments and the overlying water.
Sorption/desorption Sorption/desorption is the process by which phosphate attaches or detaches from the surface of other substances such as clays and mineral oxides.

Introduction

Phosphorus is one of the elemental building blocks of life. It is a component of DNA (deoxyribonucleic acid), the cellular energy molecules ATP and APD (adenosine tri- or diphosphate), the phospholipid bilayer of cell membranes, and the material that forms bones, to name a few examples. Given the importance of phosphorus for so many biological processes, the availability of this element in the environment helps to shape ecological interactions in lacustrine ecosystems. Phosphorus concentrations in the surface waters of lakes can range from undetectable to hundreds of micrograms per liter and are tightly coupled to algal biomass (Dillon and Rigler, 1974), defining the trophic state of the lake (Carlson, 1977). Due to human activities in the watershed, many lakes are becoming enriched in phosphorus making them increasingly likely to suffer from poor water quality, deep water oxygen depletion, and a loss of ecosystem services. Phosphorus's role as a building block of life makes its elemental cycle in lakes a delicate balance between limiting ecosystem functioning when there is too little and a water quality problem when there is too much. The aim of this article is to provide an overview of phosphorus cycling in lacustrine environments including the forms, sources, pools, fluxes, and management of phosphorus in these aquatic ecosystems.

Forms of phosphorus in lakes

Elemental phosphorus is rare in nature. Instead, phosphorus in inland waters usually occurs bound to oxygen in the phosphate molecule (PO_4), which may occur as orthophosphate (PO_4^{3-}) or protonated anions ($H_2PO_4^-$ and HPO_4^{2-}). Phosphate is incorporated into many other molecules that are cycled through the biotic and abiotic components of lacustrine ecosystems. These molecules can be in an inorganic form or as a component of organic matter (Fig. 1). The inorganic form is either particulate—found in minerals or adsorbed to the surface of sediment particles—or dissolved in an aqueous solution. Orthophosphate, a form of dissolved inorganic phosphorus, is the form that is taken up by plants and algae. Organic phosphorus—a term that

 https://doi.org/10.1016/B978-0-12-819166-8.00048-7

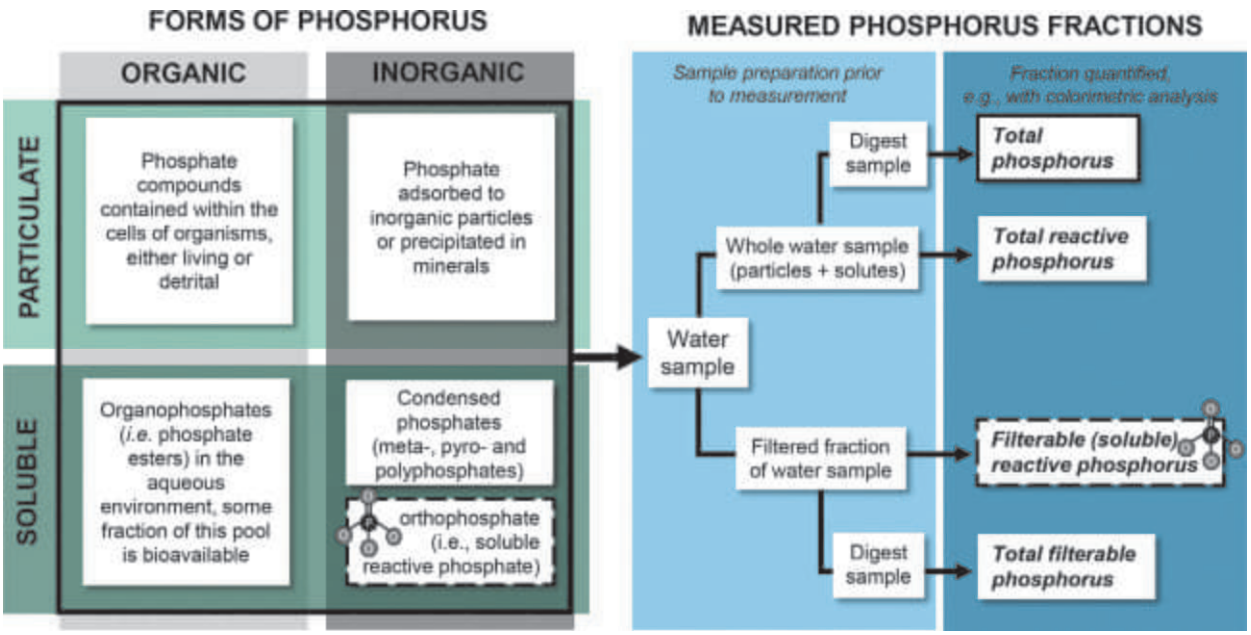

Fig. 1 There are many forms of phosphorus in aquatic environments that can be functionally separated based on whether the phosphorus is in a particulate or soluble form (*green rows*, *left panel*) and if it is part of an organic or inorganic molecule (*gray columns*, *left panel*). A water sample from the environment can contain one, some, or all of these functional forms of phosphorus (*arrow from left to right panel*). The measurement of phosphorus concentration is made from either the whole water (particles + solutes) or filtered fraction (solutes + particles smaller than the filter pore size), on either digested or non-digested samples, yielding the phosphorus fractions and concentrations measured with colorimetric analysis (*right panel*). Total phosphorus (TP; solid outline), which can contain any number of the functional forms of phosphorus, and soluble reactive phosphorus (SRP; dashed outline) are noted with boxes in both panels as they are two of the most frequently reported concentrations from lacustrine ecosystems.

encompasses a complex set of molecules—can also be dissolved in water or particulate, being contained in the living tissues or necromass of microbes, plants, and animals. In addition to the dynamics of phosphate concentrations, bioavailability, and cycling in the water column, sediments are another large pool of phosphorus that can be available for biological uptake (see "Internal Loading" section below). In the sediment, phosphorus also occurs in the particulate, dissolved (in pore water), organic, and inorganic forms (Fig. 1).

One of the most commonly reported measurements of phosphorus in inland waters is the concentration of total phosphorus, which is a measure of all the particulate, dissolved, organic, and inorganic phosphorus contained within a sample (Fig. 1). To measure total phosphorus, unfiltered water samples are digested to convert all phosphorus forms, including the phosphorus bound in organic molecules, into dissolved orthophosphate. Persulfate oxidation is a common digestion technique for samples from the water column, for which a strong acid is used to hydrolyze condensed phosphates and persulfate (an oxidant) is used to separate orthophosphate from organic compounds. The orthophosphate is then measured from the digested sample, often using a molybdenum blue colorimetric method (Murphy and Riley, 1962; APHA, 1988). While the total phosphorus concentration is a measure of all the phosphorus present in a sample, the measurement does not necessarily provide information on the forms or bioavailability of phosphorus present in the ecosystem. Instead, water samples that are filtered to remove particles can be analyzed for dissolved phosphorus fractions, such as the commonly-reported soluble reactive phosphorus. Whether the water sample is filtered prior to analysis and how it is digested determine the fraction that is quantified (Fig. 1). Measurements of dissolved phosphorus reveal more about the abundance and form of potentially bioavailable phosphorus in the environment. By definition, the concentration of dissolved phosphorus cannot be higher than total phosphorus, as it is a fraction of the whole phosphorus pool in the sample.

Soluble reactive phosphorus concentrations are usually low in the epilimnion of lakes and reservoirs even as total phosphorus concentrations are high. This can be caused by the phosphorus present in the epilimnion being bound in algal and microbial biomass or sorbed to inorganic sediment particles suspended in the water column. Repeated measurements of phosphorus concentrations and forms in lacustrine environments can provide insight into the source and dynamic cycling of this element. Ultimately, the source of phosphorus in the water column of a lake is from the watershed, including groundwater (external loading), or from the sediments of the ecosystem (internal loading). As it is the magnitude and timing of phosphorus loading that helps to shape aquatic ecosystem dynamics, particularly algal biomass, understanding the sources of phosphorus in a lake can be key to managing water quality in that ecosystem.

External phosphorus loading

Unlike nitrogen, which can enter ecosystems through fixation of gaseous N_2 into a bioavailable form by cyanobacteria, phosphorus enters aquatic ecosystems through physical transport from the watershed. Phosphate is originally derived from the weathering of

rocks, which forms terrestrial soils. Both climate and surficial geology, interacting with human land use, control the rate of weathering and abundance of phosphate from this process. The inorganic phosphate in soils can then be taken up by plants or microbes, be transported through groundwater or surface water, or sorb to soil particles and be transported through erosive processes. During snowmelt or precipitation events, eroded soil is transported through surface runoff and can enter nearby waters. The magnitude of external loading from soil erosion is mediated by the magnitude of the precipitation event and soil conditions prior to and during the event. Bed and bank erosion in streams during high energy flows will also transport substantial amounts of phosphorus downstream. In addition to runoff-driven soil erosion, wind-driven erosion can mobilize fine particles and deposit them in lakes. Eolian deposition of phosphorus-containing particles can contribute substantially to the phosphorus budgets in distant waterbodies, particularly alpine lakes with few other external inputs.

Phosphorus can also enter aquatic ecosystems as part of an organic molecule. Similar to inorganic forms, detrital particles containing phosphorus can be transported through runoff and deposition from the atmosphere. However, phosphorus contained in dissolved organic matter produced in the watershed is likely a larger source of organic phosphorus in the water column of many lakes. Dissolved organic matter in lakes is often derived from the surrounding terrestrial environment. In undisturbed catchments, exogenous dissolved organic phosphorus can have a large effect on the total phosphorus concentration within a lake. However, in disturbed catchments, high phosphorus concentrations are more commonly the result of human activity.

Global phosphorus and nitrogen cycles have been greatly disrupted by anthropogenic land use and resource extraction, leading to widespread eutrophication of inland and coastal waters. Mining of phosphorus-rich minerals for use in fertilizers has led to phosphorus accumulation in soils globally, particularly agricultural soils, which has increased phosphorus loading to lacustrine environments through surface runoff and groundwater infiltration (Bennett et al., 2001). Agricultural practices like tilling also lead to higher rates of soil erosion, further exacerbating the magnitude of phosphorus loading from the catchment. Practices such as conservation tillage reduce soil erosion, and therefore the flux of particulate phosphorus to receiving waters. Livestock operations are another potential source of agricultural phosphorus pollution. While nonpoint sources of phosphorus from agriculture, urbanization, and other land-use change are pervasive (Carpenter et al., 1998), municipal and industrial effluent can also be substantial point sources of nutrient pollution. A consequence of all these human activities is an increasing amount of phosphorus stored in the watershed that is susceptible to erosion and leaching into surface waters (Kusmer et al., 2019). This pollution threat is further aggravated by changes in precipitation frequency and intensity due to climate change. Once phosphorus has entered a lake from the surrounding watershed, it can be taken up into biomass and cycle through the food web, be transported further downstream, or be stored in the bottom sediments with the potential to be either buried or released back into the overlying water.

Internal phosphorus loading

Internal loading is the release of phosphorus from lakebed sediments to the overlying water column where it is available for uptake by planktonic organisms or export further downstream (Orihel et al., 2017). The sediment phosphorus pool is composed of both organic and inorganic phosphorus, deposited through external loading from the watershed or as detrital particles from internal production. In some lakes, the retention of phosphorus in the sediments through immobilization and burial can be greater than the amount released into the water column, causing the sediments to be a net sink of phosphorus in the ecosystem. Yet in many nutrient-rich lakes, the release of phosphate from the sediments contributes substantially to the bioavailable phosphorus pool in the water column. When sediment-released phosphate reaches the photic zone, it supports phytoplankton blooms that can reach nuisance or even harmful levels. Even with substantial reductions in external phosphorus loading, internal loading of legacy phosphorus from the sediments can continue to fuel algal production, delaying improvements in water quality. As such, being able to predict the timing, location, and magnitude of internal phosphorus loading is key for managing water quality in many lakes. However, the physical, chemical, and biological mechanisms that lead to internal loading vary in both space and time, complicating the prediction of this influential phosphorus flux.

One of the main pathways for internal loading is the movement of phosphate from sediment pore water into the overlying water through diffusion. The phosphate concentration gradient between the pore water and the overlying water column drives the rate of diffusive internal loading (Fig. 2, bottom panel). Numerous processes control the concentration of phosphate in pore water including sorption to and desorption from mineral oxide and clay surfaces, complexing with and dissociation from dissolved organic matter, the formation and dissolution of phosphate-containing minerals, and biological uptake and release through organic matter decomposition and subsequent phosphorus mineralization (Goldberg and Sposito, 1985; Reitzel et al., 2007). Sorption, complexing, precipitation, and uptake processes remove phosphate from the pore water, which decreases diffusive internal loading. Conversely, desorption, dissociation, dissolution, and mineralization release phosphate into the pore water. For example, when conditions at the sediment-water interface or deeper in the sediment profile become anoxic (no oxygen available), iron and manganese oxides will undergo reductive dissolution, which will release any sorbed phosphate. As a result, pore water phosphate concentrations will increase as will the diffusive phosphate flux from the sediments. Phosphorus release due to reductive dissolution under favorable sediment redox conditions was demonstrated early on by Mortimer (1941) studying the sediments of Lake Windermere (United Kingdom). Mortimer's research was foundational to understanding diffusive phosphorus flux from sediments and coupled iron-phosphorus cycles. However, many mechanisms besides redox conditions control sediment phosphate sorption capacity and thus diffusive internal phosphorus loading. These mechanisms include temperature, pH, microbial activity, aqueous phosphate concentrations, sorption site competition, concentrations of alternative electron acceptors, and the geochemical characteristics of the sorbent (Jensen and Andersen, 1992; Caraco et al., 1993; Hupfer and Lewandowski, 2008).

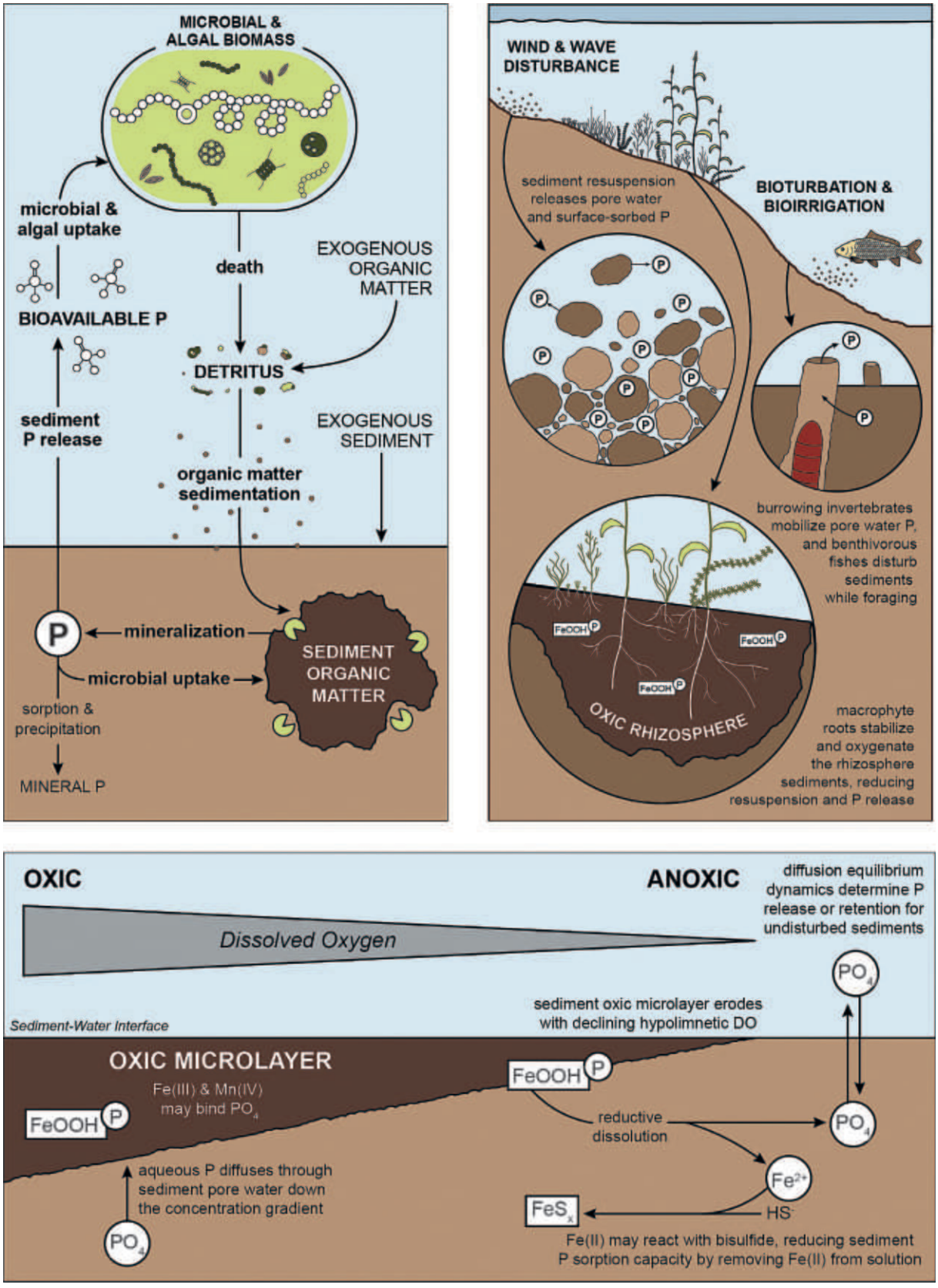

Fig. 2 Phosphorus cycling at the sediment-water interface. Panels focus on the importance of sediment organic matter in biologically-mediated internal phosphorus loading (top left), the role of sediment disturbance and stabilization in internal phosphorus loading (top right), and some of the physical and chemical processes that drive sediment phosphorus dynamics under variable oxygen availability (bottom).

The phosphorus incorporated in organic matter is another active pool of sediment phosphorus. The sedimentation of detritus from the water column, which is a combination of production from within the lake (endogenous) and organic matter from the watershed (exogenous), adds to benthic detritus from biofilms and rooted macrophytes, forming the sediment organic matter pool (Fig. 2, top left panel). Sedimentation of endogenous organic matter is particularly high in nutrient-rich lakes due to the large amount of algal production that escapes consumption. Respiration by heterotrophic microbes leads to the release of the phosphorus bound in sediment organic matter, often leading to increased concentration of soluble phosphorus in pore water (Orihel et al., 2017). Microbes exude phosphatase enzymes that convert less bioavailable forms of phosphorus into the more labile form, orthophosphate (PO_4^{3-}). This biologically-mediated conversion of phosphate can result in high rates of internal loading under aerobic conditions at the sediment-water interface.

Phosphate released into the water column from diffusive flux from sediment pore water will build up in the hypolimnion of stratified lakes. In deeper waters, the hypolimnion is largely aphotic, preventing biological uptake of internally recycled phosphate from the sediments. However, entrainment of deeper water during storm events, internal seiches, or seasonal mixing can make substantial amounts of internally-recycled phosphorus available for uptake by organisms in the photic zone. For example, in Lake Mendota (Wisconsin, United States), internally-recycled phosphorus can become entrained from deeper waters when the thermocline is deepened in the summer following storm events. During a typical year of runoff, entrainment was estimated to be 10 times greater than the external loading of phosphorus to the epilimnion of the lake, whereas it was equivalent to external loading during a year with higher-than-average runoff (Soranno et al., 1997).

In addition to the diffusive flux of phosphorus from undisturbed sediments, internal loading can also occur through advection from physical disturbances. The resuspension of sediment from wind, wave, and gas bubble disturbance leads to the release of pore water phosphorus and potentially the release of loosely bound phosphorus from sediment particles (Fig. 2, top right panel). In general, wind-driven sediment disturbances are episodic, and their spatial distribution in the lake is dictated by both bathymetry and fetch. As such, the contribution of wind-driven disturbances to internal loading is dynamic, likely creating hot spots and hot moments of sediment phosphorus release from shallow sediments. Bioirrigation and bioturbation from organisms such as burrowing invertebrates and benthivorous fishes cause physical sediment disturbance similar to wind. In addition to physical disturbance, burrowing organisms can also modify the redox conditions in the sediment profile, altering the rate of the chemical processes controlling internal loading.

In shallow lakes, aquatic macrophytes play an influential role in internal phosphorus loading dynamics. Macrophyte beds promote the retention of particulate phosphorus in lakebed sediments by limiting resuspension events. Specifically, macrophyte root systems stabilize rhizosphere sediments while the macrophyte canopy reduces turbulent flow above the sediments. However, by reducing turbulent flow, macrophyte beds can also increase local sedimentation rates and organic matter inputs to the sediments. Heightened organic matter accumulation in macrophyte beds may mobilize phosphorus through mineralization or the dissolution of redox-sensitive phosphate minerals if organic matter decomposition consumes all available oxygen at the sediment-water interface. Local, nighttime anoxia has been observed in dense macrophyte beds due to reduced water column mixing and decomposition (Vilas et al., 2017). Few quantitative studies have addressed reduced resuspension versus increased organic matter accumulation in macrophyte beds, so the net effect on internal phosphorus loading remains unclear. The balance of these processes likely varies among different lakes and across seasons in temperature waterbodies.

Macrophytes additionally mediate sediment phosphorus dynamics through radial oxygen loss and root exudates within the rhizosphere. Dissolved oxygen can leak from root tissue into the surrounding sediments, yielding an oxygenated rhizosphere. Radial oxygen loss is associated with phosphorus retention in rhizosphere sediments because oxidizing conditions protect iron and manganese oxides from dissolution, increasing sediment phosphorus sorption capacity (Han et al., 2018). The root exudates of some macrophyte species contain chelating agents that facilitate the dissolution of iron- and aluminum-phosphate minerals, mobilizing any sorbed phosphorus. However, this phosphorus release is tightly coupled with plant uptake and is unlike to release phosphorus directly into the water column (Xing et al., 2018). Although macrophytes are associated with processes that may either enhance or limit internal phosphorus loading, available evidence suggests that macrophytes tend to constrain sediment phosphorus release.

The relative importance of the physical, chemical, and biological mechanisms that control internal phosphorus loading in lacustrine environments is highly dependent on the characteristics of the individual ecosystems and the timescale under consideration. For example, the chemical speciation of iron and phosphorus in the sediments and relative abundance of iron to phosphorus (Fe:P ratio) is a control point for internal loading through the adsorption pathway. Similarly, the abundance of ions that compete with phosphate for sorption sites will also alter internal loading rates (Caraco et al., 1993). Physical characteristics will additionally dictate the spatial and temporal dynamics of internal loading. Shallower lakes may experience frequent episodes of sediment resuspension or brief periods of stratification and mixing which could lead to short pulses of phosphate release. The relative importance of these mechanisms can also change depending on the timescale of interest; physical disturbance may be overwhelmingly important for phosphorus flux on the order of hours or days but less important on an annual basis when compared to other processes such as remineralization or desorption from iron. Timescale is also important when considering the method for quantifying internal phosphorus loading rates in a lacustrine ecosystem.

Measuring internal loading rates

Internal phosphorus loading rates vary considerably among waterbodies. Meta-analyzes of internal loading rates in over 100 lakes and reservoirs around the globe revealed that rates may range anywhere from −27 to 54 mg TP m^{-2} day^{-1} (Nürnberg, 1988; Orihel et al., 2017). Negative rates indicate that sediments retain phosphorus while positive rates signify sediment phosphorus release into

the water column. The relative importance of internal phosphorus loading compared to external phosphorus sources also varies across systems. In some waterbodies the annual internal phosphorus load is masked by large external phosphorus loads; however, in other waterbodies, internal phosphorus loading drives the phosphorus dynamics in the water column (Nürnberg, 1984). Internal phosphorus loading rates are controlled by site-specific mechanisms and basin characteristics and may change dramatically across seasons in temperate waterbodies. As such, it is difficult to predict precise internal loading rates without direct measurements or modeling approaches. However, it is generally assumed that recycling of phosphorus from the sediments is more likely if the hypolimnion is anoxic, although this paradigm is challenged by observations of high release rates from oxic sediments and oligotrophic lakes that experience anoxia with minimal phosphate release (Prairie et al., 2001).

Sediment core incubations, benthic flux chambers, or mass balance approaches are often used to quantify internal loading rates. The appropriate measurement technique should be selected based on research objectives, data availability, and the timescale of interest. Core incubations are performed by removing an intact sediment core with overlying water from the ecosystem and incubating it under ambient or experimental environmental conditions. The rate of change in phosphorus concentration in the overlying water, usually measured every few hours or days, is used to calculate an aerial rate of internal loading. Similarly, deploying benthic flux chambers and measuring the increase of phosphorus concentrations in the overlying water provides a short-term aerial estimate of phosphorus flux. Core and chamber methods have the advantage of allowing investigators to study the variation in rates among sub-habitats, among seasons, or to experiment with environmental conditions to learn more about the mechanisms controlling internal loading rates. However, these methods are also subject to so-called "bottle effects" that can be induced by sealing off the area of measurement from the inputs and dynamics of the surrounding environment.

Mass balance approaches for quantifying internal loading rates do not suffer from bottle effects as these approaches estimate internal loading at the ecosystem scale. In its simplest form, a lake phosphorus mass balance model accounts for the mass of phosphorus in the water column and assumes this mass to be constant. As such, all inputs and outputs of phosphorus from the system must be balanced. Internal phosphorus loading can be estimated from a mass balance model if all other major inputs (e.g., surface and ground water inflows, atmospheric deposition) and outputs (e.g., surface and groundwater outflows) of phosphorus are measured (Mitchell, 1984). Advances in this modeling approach include partitioning lakes into multiple water and sediment compartments and allowing the water column phosphorus mass to be dynamic over time.

Mass balance approaches quantify the net phosphorus exchange between sediments and the water column for an entire lake ecosystem, generally over the course of a year. At this timescale, net loading represents the balance between sediment phosphorus release and retention via sedimentation (Orihel et al., 2017). Although this ecosystem-scale perspective is valuable, estimation of internal phosphorus loading via mass balance cannot reveal when or where sediment phosphorus release is likely to occur or illuminate the underlying mechanisms. Additionally, direct measurements of internal loading rates via core incubations or benthic flux chambers are unlikely to match estimates from mass balance models. This discrepancy arises because it is difficult to scale incubation and chamber measurements to the whole ecosystem and over longer time periods. A better understanding of spatio-temporal variation in internal phosphorus loading is needed to scale direct measurements of loading rates accurately.

Phosphorus use by aquatic organisms

All organisms require phosphorus to support their growth and reproduction. As such, phosphorus availability in the environment, whether from internal or external sources, drives ecosystem dynamics. In particular, primary production in many lacustrine environments is limited by the availability of phosphorus. As a result, phosphorus is mainly bound in the biomass of phytoplankton, heterotrophic microbes, and other organisms when present in the water column of many lakes. The exception to this is most common in hypereutrophic (nutrient-rich) waterbodies where other nutrients such as nitrogen may also limit primary production. However, in most inland waters, when new phosphate is introduced to the ecosystem from external or internal loading in the water column, the uptake rate by phytoplankton and bacteria is rapid. In strongly phosphorus-limited waters, the uptake rates of orthophosphate can be on the order of seconds to minutes (Currie and Kalff, 1984). The strong correlation between phosphorus availability and algal biomass underpins the trophic state classification scheme of lakes and reservoirs (Carlson, 1977).

Trophic state is defined as the total mass of biological material in an ecosystem. Lakes with low biomass are classified as oligotrophic (from the Greek *oligos*, meaning few) and have low concentrations of phosphorus in the water column, limiting productivity. Conversely, those waterbodies with high biomass are classified as eutrophic (from the Greek *eu*, meaning good or well) and have higher concentrations of phosphorus supporting higher rates of productivity (Table 1). In 1977, Carlson proposed a trophic state index that classified lacustrine ecosystems based on either Secchi depth (a measure of water clarity), chlorophyll *a* concentration (an index of algal biomass), or total phosphorus concentrations, due to the strong correlation between these variables (Fig. 3). The trophic state index has been widely adopted by lake managers and policymakers as a tool for classifying waterbodies and predicting the consequences of eutrophication or restoration on aquatic ecosystems (see "Managing The Consequences Of Excess Phosphorus" section below). While the correlation between phosphorus availability and phytoplankton biomass is clear, phytoplankton growth is also dictated by the availability of other essential elements including nitrogen.

Table 1 Trophic state index values from Carlson (1977).

Trophic category	*Trophic state index*	*Phosphorus ($\mu g\ L^{-1}$)*	*Chlorophyll-a ($\mu g\ L^{-1}$)*	*Secchi depth (m)*
Oligotrophic	<1–40	<1–12	<1–2.6	>8–4
Mesotrophic	40–50	12–24	2.6–7.3	4–2
Eutrophic	50–70	24–96	7.3–56	2–0.5
Hypereutrophic	>70	>96	>56	<0.5

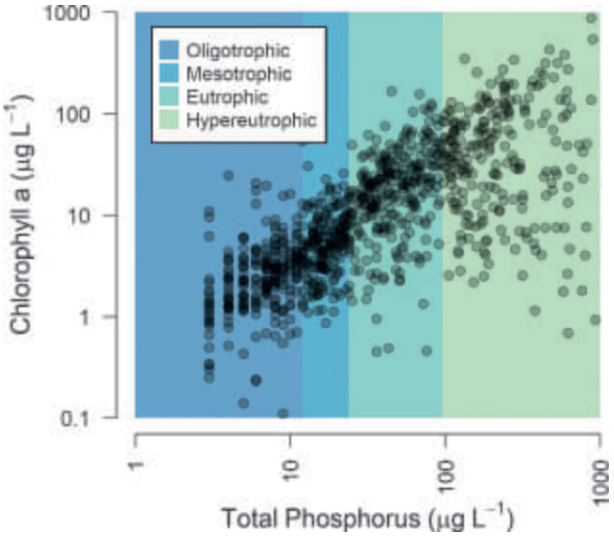

Fig. 3 The relationship between total phosphorus and chlorophyll-a concentrations for 968 lakes in the United States and the trophic state classification for each lake based on the total phosphorus concentration. Data are from the United States Environmental Protection Agency's 2012 National Lake Assessment.

There is considerable variation in phosphorus acquisition strategies and use efficiencies across different macrophyte growth forms. Emergent (e.g., cattails, *Typha* spp.) and floating-leaf (e.g., water lilies, *Nymphaea* spp.) macrophytes primarily obtain phosphorus from sediments and have extensive root and rhizome systems for perennial phosphorus storage. In contrast, submersed macrophytes (e.g., pondweeds, *Potamogeton* spp.) may take up phosphorus from either sediments or the water column, although the importance of foliar uptake varies across species (Granéli and Solander, 1988). Phosphorus use efficiency also differs between emergent or floating-leaf macrophytes and submersed species, especially in temperate lakes. Complex root and rhizome systems allow emergent and floating-leaf species to efficiently use and recycle phosphorus across seasons. Specifically, these macrophytes can translocate phosphorus and other nutrients from their shoots into the rhizomes prior to vegetative senescence in autumn. Unlike emergent and floating-leaf macrophytes, submersed species generally experience continual sloughing of leaves and shoot fragments throughout the growing season. These biomass losses remove a substantial amount of phosphorus from submersed macrophyte beds (Adams and Prenkti, 1982). Although perennial submersed species can translocate phosphorus from shoots to overwintering structures, reduced root systems limit perennial phosphorus storage and thus use efficiency.

While much of the phosphorus contained in the biomass of primary producers in the water column can succumb to sedimentation, a portion of it is lost to consumption by other organisms. Aquatic consumers acquire the phosphorus they need through their diet. The need for essential nutrients such as phosphorus drives ecological interactions among consumers and can shape ecosystem dynamics. For example, the crustaceous zooplankton *Daphnia* are a keystone grazer of phytoplankton in many lacustrine ecosystems. As phosphorus-rich organisms, *Daphnia* need to consume a large amount of phosphorus in their diets which leads to their high grazing rates.

When there is too much phosphorus in a consumer's diet compared to their nutritional needs, they will excrete the excess phosphorus either in a dissolved form readily available for phytoplankton or heterotrophic bacteria uptake or in fecal pellets. The phosphorus in fecal pellets may be lost to the water column through sedimentation or can be dissolved and taken up by primary producers and microbes. The phosphorus that is incorporated into consumers' tissues turns over at a slower rate than the phosphorus in phytoplankton or heterotrophic bacteria due to consumer's longer life span. In general, the longer-lived an organism is in the environment, the slower the turnover of the reservoir of phosphorus in their biomass. When consumers die, the

phosphorus in their necromass is stored in the sediments or recycled back into the water column through mineralization. In some phosphorus-poor lakes, the accumulation of phosphate in the bones and scales of long-lived fishes is an appreciable reservoir of phosphorus in the water column that is not available for uptake by other organisms and turns over slowly.

Managing the consequences of excess phosphorus

Eutrophication is the condition of excessive algal production in waterbodies due to over enrichment of nutrients. Algal blooms can range from an unsightly nuisance to impairing ecosystem services and threatening human health. For example, severe algal blooms can lead to fish kills through the drawdown of dissolved oxygen during senescence. Blooms that are dominated by cyanobacteria can produce dangerous levels of toxins that can harm humans if ingested through drinking water or during recreation. As the production of algae in lakes and reservoirs generally depends on the availability of phosphorus (although some inland waters can experience periods of nitrogen limitation as well), preventing or managing excess phosphorus loads to inland waters is critical for protecting ecosystem services (Schindler et al., 2016).

In 1968, Vollenweider produced a technical report for Organization for Economic Cooperation and Development (OECD) that contained a model describing the relationship between mean phosphorus availability and chlorophyll-a in lakes. He found that the annual index of phosphorus availability in the water column—calculated as a function of external phosphorus inputs, outflows, and the rate of phosphorus loss to sedimentation—was strongly correlated with the mean annual chlorophyll-a concentration among lakes. Simply put, the greater the magnitude of external phosphorus loading to lakes, the greater the algal biomass. The Vollenweider model, along with the seminal whole-lake nutrient enrichment experiments of Schindler (1974) and recovery of Lake Washington after effluent diversion in the 1960s, launched widespread efforts to reduce external phosphorus loading to lacustrine environments in order to mitigate eutrophication. However, eutrophic waterbodies often exhibit a delayed and nonlinear response to declining phosphorus loads. Long-term reductions in external phosphorus loads are not effective at limiting algal biomass and the prevalence of cyanobacteria until in-lake phosphorus concentrations fall below a certain threshold. Similarly, hypolimnetic oxygen depletion due to decomposition of deposited organic matter remains a concern until there are substantial reductions in surface water phosphorus availability (Müller et al., 2019). These hysteretic responses often result from internal phosphorus loading, which can delay or prevent recovery of some lakes even after substantial reductions in external loading. Depending on the size and form of the sediment phosphorus pool and water residence time, it could take decades for the water column to reach equilibrium with surface sediments. The hysteretic response of lakes to reductions in external loading means that management of internal loading may also be necessary to achieve water quality targets in a shorter time frame.

The effective management of phosphorus availability in an individual lake or reservoir is dependent upon an accurate assessment of the mechanisms controlling phosphorus loading in the ecosystem (see table below for examples of phosphorus management case studies). For example, aerating the sediment-water interface to prevent the release of iron-bound phosphate may not have a substantial effect on water column concentrations if there is large pool of labile organic phosphorus that can be mineralized. In fact, the presence of oxygen could have the unintended effect of stimulating aerobic respiration, accelerating the conversion of organic phosphorus to more bioavailable forms. Similarly, phosphate inactivation agents such as alum (aluminum sulfate; $Al_2(SO_4)_3$) that are primarily targeted at improving the phosphorus binding capacity of the surface sediments may be less effective in shallow lakes that experience substantial sediment resuspension, which disturbs the alum "cap" on the sediment surface. The effect of biological communities cannot also be discounted in some ecosystems as excretion of translocated phosphorus by mobile fish can exceed external phosphorus loading for portions of the year. As these scenarios illustrate, predictive models of phosphorus concentrations in lakes that do not provide insight into the mechanisms controlling phosphorus loading are less likely to lead to measurable reductions in eutrophication due to management.

Conclusions

Phosphorus is an essential element, the availability of which shapes the structure and function of lacustrine ecosystems. The form of phosphorus in the water column, whether inorganic or organic, particulate or dissolved, were either transported from the watershed or recycled internally from the sediments. A complex suite of interacting chemical, physical, and biological mechanisms controls sediment phosphorus release including sediment redox chemistry, sediment resuspension via wind mixing or bioturbation, and the structure of macrophyte communities. Internal phosphorus loading mechanisms vary not only between different lakes but also within individual systems. This variability makes internal loading difficult to measure and often challenging to predict. The consequences of widespread eutrophication have created the need to manage phosphorus availability in many lakes to protect ecosystem services. However, effective management hinges on a mechanistic understanding of internal phosphorus cycling in addition to the sources outside of the ecosystem. While substantial gains have been made in our understanding of the pools and fluxes of phosphorus in lakes, better predictive models are needed for more effective lake management, especially as eutrophication is exacerbated by the changing climate in many regions.

Knowledge gaps

- Reliable identification of the magnitude, timing, and mechanisms controlling internal phosphorus loading in individual lakes to guide eutrophication management.
- Phosphorus availability, cycling, and internal loading rates during the winter in lacustrine ecosystems at higher latitudes.
- The bioavailability and cycling of lacustrine dissolved organic phosphorus.
- The importance and role of macrophytes in phosphorus cycling in the sediments.
- Resolving the temporal and spatial complexity of internal versus external phosphorus loading, particularly as it initiates and sustains algal blooms.
- The effect of climate change on the physical, chemical, and biological processes that control phosphorus availability and cycling in lakes.

Case studies of phosphorus management in lakes

Waterbody	*Location*	*Citation*	*Phosphorus Management Strategy*	*Description and Outcome*
Lake Washington	United States	Edmundson (1970)	Sewage delivery to the lake began in 1941 and peaked in 1962. *Diversion* began in 1963. Phosphate concentrations declined 72% but nitrate concentrations only declined by less than 20% by 1969	The mean summertime chlorophyll-a concentrations declined and were closely correlated to mean winter phosphate concentrations from the previous year, indicating that phosphorus was the most important limiting element in the lake
Lake 226	Canada	Schindler (1974)	*Experimental addition* of nitrogen and carbon to one basin of the lake and nitrogen, carbon, and phosphorus to another	An ecosystem experiment was performed by dividing Lake 226 with an impermeable curtain and adding nitrogen and carbon to one half of the lake and nitrogen, carbon, and phosphorus to the other. An algal bloom did not occur in the half with only nitrogen and carbon, but a bloom did occur on the half with phosphorus added. This experiment demonstrated that phosphorus was the key limiting nutrient for algal growth
Lake Dianchi	China	Yan et al. (2019) and Liu et al. (2015)	Enhanced *wastewater treatment* capacity and *sediment dredging* (over 51 million m^3 sediment and 14,800 t phosphorus removed)	Algal blooms in Lake Dianchi are linked to phosphorus availability. Advances in wastewater treatment have reduced external phosphorus loads and sediment dredging has reduced in-lake phosphorus pools. However, internal phosphorus loading remains high due to decomposition of algal detritus and phosphorus mineralization
Lake Tuusulanjärvi	Finland	Horppila et al. (2017)	*Sewage diversion* (reduced mean external phosphorus load by 50.4%, from 1533 to 761 mg P m^{-2} $year^{-1}$) and *aeration* (prevented hypoxia but increased total internal phosphorus load from 432 to 659 mg P m^{-2} $year^{-1}$)	Sewage effluent was diverted from the lake in 1979; however, internal loading delayed water quality improvements. Aeration was used consistently from 1998 to 2010, which prevented summer thermal stratification. The artificial destratification caused total internal phosphorus loading to increase due to warmer bottom water temperatures, enhanced phosphorus mineralization, and sediment resuspension from aeration
Lake Trummen	Sweden	Cronberg (1982) and Bengtsson et al. (1975)	*Sewage diversion* and *sediment dredging* (the top 0.5 m of sediment removed, 50,000 kg phosphorus)	Diverting sewage effluent from the lake in 1959 was not sufficient to reduce algal blooms due to persistent internal phosphorus loading. In 1970–1971 precision, suction dredging was used to remove phosphorus-rich sediments. Coupled management of external and internal loads reduced total algal biomass and the prevalence of cyanobacteria by the mid-1970s
Minneapolis Chain of Lakes	United States	Huser et al. (2016)	*Alum additions* to control phosphorus release from sediments and catchment management to *reduce external loading* (achieved between 1% and 49% across the 4 lakes)	In-lake alum treatments resulted in 4–20 years of water quality improvements in the lakes whereas efforts to manage external loads had a minimal effect on water quality during the same period
Lake Susan	United States	Bajer and Sorensen (2015)	Experimental *removal of common carp* (*Cyprinus carpio*), decreasing biomass from 307.1 kg ha^{-1} to 40.8–64.5 kg ha^{-1}	Carp were removed to reduce bioturbation of sediments resulting in a large increase in aquatic vegetation (+40% in coverage) and early summer water water clarity due to a decline in suspended solids. However, total phosphorus concentrations did not decrease as internal loading not associated with the carp combined with periodic entrainment of hypolimnetic water in this shallow lake maintained high phosphorus concentrations in the water column after carp removal

See Also: Fundamental concepts and theories: Nitrogen; Nutrient Stoichiometry in Aquatic Ecosystems; Human pressures and management of Inland Waters: Agricultural Pressures on Inland Waters; Structures and functions of Inland Waters - Lakes: Phytoplankton Growth and Nutrients; Structures and functions of Inland Waters - Rivers: Ecological stoichiometry in streams; Structures and functions of Inland Waters - Wetlands: Carbon Dynamics in Wetlands

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pH of Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Acid deposition Any form of precipitation that contains acidic components. Carbonic, sulfuric and nitric acid are common acids present in acid precipitation.
Acidity A measurement of the strength of an acid, or the ability of a compound to lose a proton.
Acidification Process by which inland waters become more acidic.
Alkalinization Process by which inland waters become more alkaline.
Acid neutralizing capacity (ANC) The capacity of a water body to buffer against acidification.
Alkalinity The ability of a water body to neutralize acids. Alkalinity is the stoichiometric sum of bases in solution, measured in μeq L^{-1}. *Total alkalinity* refers to the sum of all bases in the solution. *Carbonate alkalinity* is the sum of the number of moles of HCO_3^- + CO_3^{2-} in solution, where 1 mol of HCO_3^- represents 1 M equivalent, and 1 mol of CO_3^{2-} is 2 M equivalents, due to charge differences. Since bicarbonate and carbonate are the most abundant ions in aquatic ecosystems, alkalinity is often estimated through the measurement of carbonate alkalinity alone.
Basicity A measurement of the strength of a base, or a compound's ability to accept protons.
Buffering capacity Measurement of a water body's ability to resist changes in pH. Defined as the number of moles of acid or base required to change the pH of the water by 1 unit. A lake with a high buffering capacity would require more acid or base to shift its pH.
Cation exchange Refers to the process by which one cation is replaced by another. This can occur on soil particles, or across biological membranes, and usually refers to the replacement of specific biologically-important cations (e.g., Ca^{2+}) with protons from an acid source.
pH The negative of the base 10 logarithm of the concentration of free hydrogen ions.
Salinization syndrome The observation of increasing salinity in inland waters through the landscape loading of salts, acceleration of weathering, and the increased use of concrete and lime. Often associated with increasing lake pH.

Introduction

The dissociation of water molecules to H^+ and OH^- ions determines the pH of water, which is defined as the negative (or inverse) of the base 10 logarithm of the concentration of free hydrogen ions ($-\log_{10}[H^+]$).

pH is a fundamental property of inland waters that is well understood chemically, and has profound and complex ecological implications. Measuring pH is relatively straightforward and as a result has been assessed in inland waters since the inception of limnology. This ease of measurement has led to a great abundance of pH measurements, revealing that surface freshwaters typically range between pH 6 to 9, with values of 2 to 12 observed in more extreme environments. The pH of the aquatic environment is an important driver of physical, chemical, and biological properties, which both regulates, and responds to ecosystem functioning. Human activities have dramatically shifted the pH of many inland waters, from a trend of acidification beginning in the late 1960s,

 https://doi.org/10.1016/B978-0-12-819166-8.00045-1

to a more recent trend of widespread alkalinization. The magnitude and direction of these pH shifts vary regionally, as they are dependent on many interacting factors, including underlying geology, land use, and climate. To anticipate and mitigate further impacts of anthropogenic pH change on inland waters, we require a comprehensive understanding of the biogeochemical and physical drivers of pH change, and ecological impacts on freshwater ecosystems.

This chapter outlines an understanding of the drivers underlying the natural range of pH of inland waters, provides an overview of the natural and anthropogenic factors that cause deviations from baseline values, and describes the implications of these perturbations for ecological community structure and functioning.

Measurement of pH of inland waters

Comprehensive overviews of methodologies underlying pH measurement in aquatic environments for both the field and the laboratory are available from the US Geological Survey (Ritz and Collins, 2008) and the US Environmental Protection Agency (USEPA, 2017), and many other authorities. Briefly, standard measurement requires a probe consisting of ion selective reference- and measurement electrodes connected to a digital visualization interface (Ritz and Collins, 2008). Most pH meters include an internal temperature sensor that automatically adjusts pH measurements based on ambient conditions. Where ambient temperature is not directly measured, direct temperature measurements must be made, and pH values adjusted accordingly. Current potentials generated between measurement and reference electrodes are converted to pH with the ideal Nernstian response, which links the electrical response to activity of H ions (59.16 mV per unit pH), and if present, the built-in temperature correction factor (Ritz and Collins, 2008).

Controls of pH

Natural pH range

The pH of pure water is given to be neutral (7.0). Most inland waters lie within a pH range of 6–9, because of buffering with the carbonic acid system, described below. Many systems deviate dramatically from this range, and can have pH values as low as 2 to as high as 12 in extreme environments (Langmuir, 1997; Wetzel, 2001). The pH of inland waters can be altered when water interacts with basic or acidic substances originating in the atmosphere, the terrestrial environment, within ground- and surface waters, and aquatic sediments.

Buffering capacity

The ability of inland waters to resist changes in pH (**Buffering capacity**) is primarily accounted for by the equilibrium of the carbonate system (Eq. 1, Fig. 1).

$$CO_{2(g)} + H_2O \rightarrow H_2CO_{3(aq)} \leftrightharpoons H^+_{(aq)} + HCO_3^-{}_{(aq)} \leftrightharpoons 2H^+_{(aq)} + CO_3^{2-}{}_{(aq)} \quad (1)$$

Here, CO_2 dissolves in water and forms carbonic acid (H_2CO_3). This carbonic acid equilibrates with bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}). Increases or decreases of any of the compounds from this equation (Eq. 1) can cause shifts to the left or right. Together, the sum of $CO_{2(g)}$, $H_2CO_{3(aq)}$, $HCO_3^-{}_{(aq)}$ and CO_3^{2-} is known as dissolved inorganic carbon, or DIC.

The buffering capacity of inland waters is typically measured through estimates of alkalinity, which is estimated by adding acid to a sample and measuring the resulting changes in pH. Alkalinity is a functional measurement that encompasses the sum of all acids and bases in the sample. In natural waters, it is often assumed that alkalinity arises entirely from carbonate alkalinity, which is

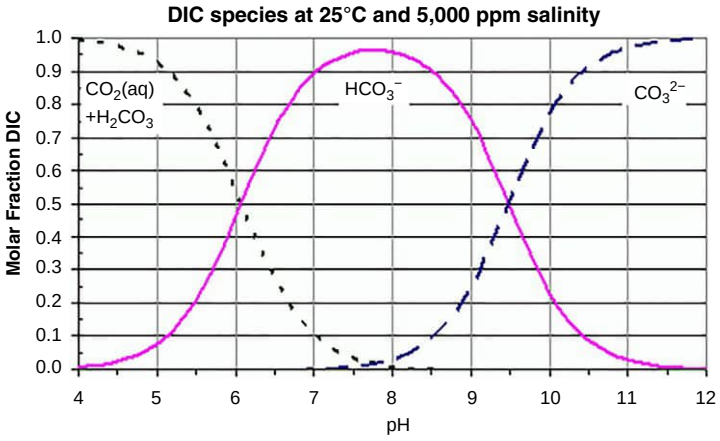

Fig. 1 Carbonate equilibrium showing the relative proportion of carbon species ($CO_2 + H_2CO_3$, HCO_3^-, and CO_3^{2-}) in relation to the pH of water. This diagram demonstrates that at high pH values, most inorganic carbon is in the form of CO_3^{2-}, while most inorganic carbon is present as CO_2 at low pH.

the sum of bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}), as these are the most common ions in aquatic ecosystems. Carbonate alkalinity is calculated by summing the molar quantity of bases, where 1 mol of HCO_3^- is 1 M equivalent, and 1 mol of CO_3^{2-} is 2 M equivalents, so carbonate alkalinity in molar equivalents = (moles HCO_3^-) + 2 × (moles CO_3^{2-}). The different molar equivalents of HCO_3^- and CO_3^{2-} refer to the moles of protons that are produced in the equilibrium as seen in Eq. (1). Thus, for example, a system with more carbonate will be better able to withstand inputs of protons, as Eq. (1) will shift to the left. The carbonate equilibrium is also often represented graphically (Fig. 1), which shows the relative proportion of inorganic carbon species at varying pH.

New inputs of CO_3^{2-} or other sources of alkalinity via precipitation, runoff, and groundwater delivery increase the acid buffering capacity of aquatic ecosystems. Internal production of solutes can also alter the balance of acids and bases in a system, and thus the alkalinity (Schindler et al., 1985). Evapoconcentration can lead to increased concentrations of all acids and bases and thus increase pH of basic systems, or lower the pH of acidic systems. The bulk of the alkalinity linked to inorganic C ultimately comes from chemical weathering processes in terrestrial landscapes that mobilize bicarbonate and carbonate, and thus is strongly influenced by underlying geology. However, microbial reduction of oxidized compounds of C, N, S, Fe, and other elements also generates alkalinity through both assimilatory and dissimilatory pathways (Kelly et al., 1995). In extremely dilute, soft-water lakes, the internal biological generation of alkalinity through processes such as sulfur oxidation and nitrification can actually account for the largest sources of alkalinity to the system (Schindler et al., 1985).

Biological controls of pH

pH can vary significantly over multiple timescales. On shorter timescales (hourly to seasonal), temporal fluctuations are directly related to the consumption and production of CO_2 from photosynthesis and respiration, which can increase and decrease ecosystem pH, respectively, through associated shifts in the balance of the inorganic carbon system (see Eq. 1). Changes in the balance of the rates of photosynthesis and respiration can therefore generate both spatial and temporal variability in pH within a water body. Temporally, pH varies over both diel and seasonal scales to match patterns in primary production, where pH is often lower at night than it is during the daytime (Maberly, 1996), and can match seasonal trends in algal production with mid-summer peaks when algal concentrations are also peaking (Kratz et al., 1987). pH also tends to be dramatically lower during winter in ice covered lakes as respired CO_2 accumulates under ice (Kratz et al., 1987; Finlay et al., 2015). Interannual and decadal-scale variability in pH for a given system can range widely, from 0.8 to 1.3 units (Maberly, 1996; Finlay et al., 2015), owing to shifts in factors affecting the balance of primary productivity and respiration such as nutrient loading and temperature. Spatially, one of the most obvious pH gradients in productive lakes occurs where pH values are high in the photic zone due to the predominance of primary production and lower in the hypolimnion due to intense heterotrophic respiration (Wetzel, 2001), a pattern which inversely tracks variations in dissolved inorganic carbon concentrations (Wetzel, 2001). These differences in productivity can also explain cross-ecosystem patterns of pH, as lakes with higher productivity often have higher pH than do those with lower productivity.

Chemical controls of pH

In general, the pH of aquatic systems is a result of the "dynamic interplay between natural acids and bases, with extreme pHs found when either dominates" (Langmuir, 1997) (Fig. 2). As summarized by Langmuir (1997) and shown in Fig. 2, systems with low pH ($< \sim 3$) are often dominated by inputs of acid rain or weathering products of pyrite (FeS_2). Therefore, extremely low pH can be found in regions of volcanic activity and watersheds composed of pyrite rocks and clay soils, which export sulfuric acid to surface waters. Ecosystems with intermediate pH of ~4.5–10 often reflect respiration-derived carbonic acids or organic acids (dominant in

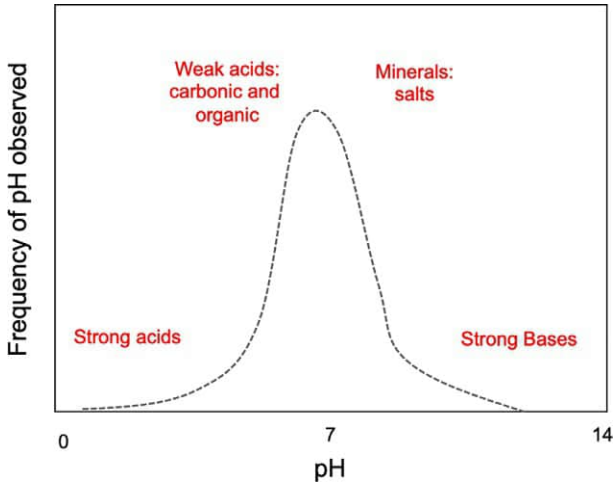

Fig. 2 The general distribution of pH values observed in natural aquatic ecosystems, and the corresponding acids and bases that often dominate in the general range of corresponding pH. Figure adapted from Langmuir D (1997) *Aqueous Environmental Geochemistry*. Englewood Cliffs: Prentice-Hall, Inc., 601.

systems with pH < 7), or mineral byproducts of bedrock (silicate, alumino-silicate, and carbonate) weathering (in systems with pH > 7) (Langmuir, 1997; Fig. 2). Moderately alkaline systems typically have elevated carbonate and are well buffered above pH of 8 (Wetzel, 2001). Accordingly, surface water pH has been shown to increase in response to enhanced catchment weathering and export of base cations, and following decreases in the delivery of organic acids from land (e.g., Tibby et al., 2003). Aquatic systems with extreme pH > ~10 are often dominated by the dissolution and evapoconcentration of minerals rich in HCO_3^- and CO_3^{2-} such as calcite (Langmuir, 1997; Fig. 2). With a lack of outflow, lakes in the continental interior in endorheic basins experience evapoconcentration of salts delivered from the watershed, and are accordingly also typically saline. The pH of lakes is therefore often high in endorheic regions where the watershed contains high levels of alkali salts, such as $NaCO_3$ and $CaCO_3$.

Calcite ($CaCO_3$) precipitation and dissolution is a common process in hardwater lakes that has profound impacts on lake pH, owing to the following equilibrium:

$$CaCO_{3(s)} + CO_{2(aq)} + H_2O \leftrightharpoons Ca^{2+}{}_{(aq)} + 2HCO_3^-{}_{(aq)} \quad (2)$$

Whiting events can be observed when calcite precipitates out of solution, seen as a milky turquoise cloud forming surface water (Fig. 3). When calcite becomes oversaturated, it can precipitate out of solution, generating CO_2 and reducing pH following Eq. (1) above. Specifically, these triggers include warming temperatures in spring and summer which lead to reduced $CaCO_3$ solubility, the removal of CO_2 and elevation of pH due to increasing rates of photosynthesis, causing a shift in Eq. (2) to the left, and an increased presence of nucleation sites (algal cells or other small particles) that provide a substrate for the formation of calcite crystals (Wetzel, 2001).

Physical controls on pH

Climate-driven hydrologic shifts over multiple timescales are often an important driver of aquatic pH. Precipitation typically has a pH between 5 and 5.6, due to dissolution of CO_2 and other N, S, and C trace gases that are oxidized in the atmosphere (Schlesinger and Bernhardt, 2020). Owing to the low pH of snow and rain (Baas Becking et al., 1960), precipitation patterns can drive temporal variations in pH. In response to acidic rainfall and snowmelt inputs, changes in surface water pH can range from 0.4 to 3.2 units (Maberly, 1996). Snowmelt and runoff flowing via surface or subsurface paths can pick up CO_2 and organic acids from soils, causing a further decrease in pH (Buffam et al., 2008).

Surface water pH is often very low (~3) in bog systems, where inputs of weathering products from the catchment are minimal, rain and snowfall are quantitatively important (Baas Becking et al., 1960), or where *Sphagnum* moss in the watershed actively exchanges cations, releasing H^+ into the water (Wetzel, 2001). Therefore, landscapes dominated by bogs tend to have bog-fed headwater streams with low pH.

Acidification can also occur through changes in climate. For example, drought conditions can reduce delivery of alkaline groundwater with high acid neutralizing capacity (ANC), reduce lake ANC, and lead to a decline in surface water pH (Webster et al., 1990). Warmer winters can lead to alkalinization through shorter ice cover, causing reduced accumulation of respiratory-derived CO_2 under ice in winter and elevated pH in spring (Finlay et al., 2015).

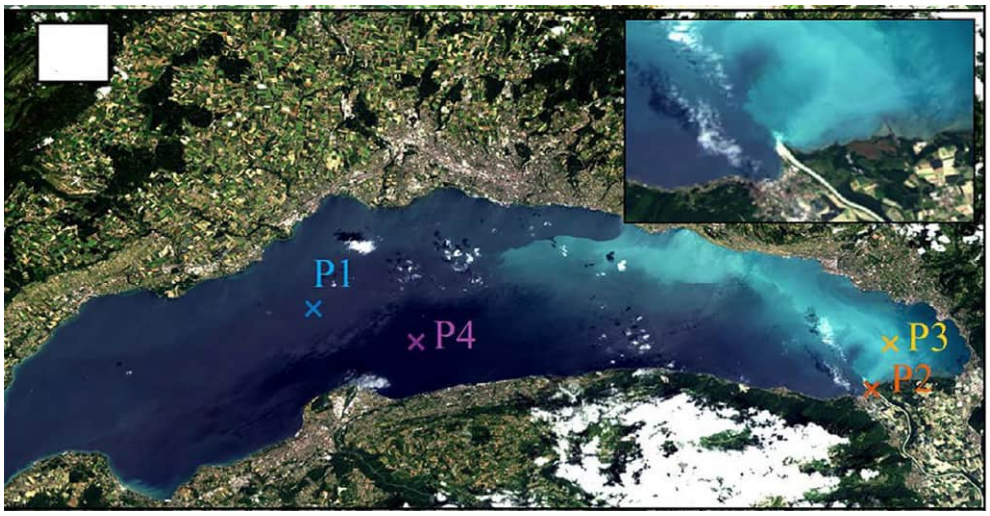

Fig. 3 Remote sensing photograph of a whiting event in Lake Geneva. Whiting events occur when calcium carbonate precipitates out of solution From Nouchi V, Kutser T, Wuest A, Muller B, Odermatt D, Baracchini T, Bouffard D (2019) Resolving biogeochemical processes in lakes using remote sensing. *Aquatic Sciences* 81: 27. https://doi.org/10.1007/s00027-019-0626-3.

Human impacts on pH: Acidification and alkalinization

Around the globe, distinct shifts in human activities have resulted in dramatic and non-linear changes in surface water pH over decadal- to millennial timescales. Therefore, we emphasize a need for caution when attempting to define natural, baseline pH of most aquatic systems. For example, Renberg et al. (1993) show that Swedish lakes have undergone four periods of pH change since the last glaciation (Fig. 4). First, a long-term acidification period from 12,000–2300 BP demonstrated decreasing pH from ~7.0 to 5.5 resulting from a decline in base cation concentrations in catchments (region I, Fig. 4). This period was followed by an anthropogenically induced alkalinization period (2300 BP–1900 AD) when land use changes resulted in increased nutrient (causing increased primary productivity) and base cation loading to lakes, thereby increasing pH to above 6.0 (region II, Fig. 4). Next, the more recent acidification period, from 1900 AD to present, corresponded to the period of widespread industrialization and combustion of fossil fuels (region III, Fig. 4, described below). The fourth period started in the 1970s and corresponds to the liming activities initiated by the Swedish government (region IV, Fig. 3, Renberg et al., 1993). This localized case study highlights two critical concepts relevant to any watershed: First, that "background" pH in aquatic networks varies through time, and second, that sequential shifts in dominant human stressors can lead to unique temporal trajectories of pH.

Acidification

A dramatic acidification of inland waters across North America and Europe started in the late 1960s and early 1970s as a result of widespread fossil fuel combustion and smelting of sulfide ores. Sulfide ore smelting and gasoline and coal burning release sulfur dioxide (SO_2) into the atmosphere where chemical reactions produce sulfuric acid. Nitrogen oxides (NO_x) are also produced through smelting and gasoline and coal burning and similarly react in the atmosphere to produce nitric acid. These acids are removed from the atmosphere through acid rain and acidify inland waters, most notably in regions of hard bedrock in the north-eastern United States, south-eastern Canada, and Scandinavian countries. The extent of this acidification was significant: between 25% and 35% of the lakes in the Adirondack region (New York, United States) were found to have acidified, and those with low alkalinity and ANC were much more strongly affected than were those with higher ANC (Cumming et al., 1992). Similarly, over 50% of lakes in southern and central Sweden experienced pH levels below 6.0, and 22–36% were lower than 5.0, with dramatic impacts on diatoms and other phytoplankton, zooplankton, and fish (Almer et al., 1974). Similar multidecadal observations of declining pH have been recorded in other industrialized regions (Tibby et al., 2003). The impacts of acidification on aquatic ecosystems are widespread, and are discussed in detail below.

Pollution generated from diverse mining activities has caused acidification of many streams and rivers worldwide (Dold, 2008). The phenomenon of acid mine drainage (AMD) arises largely due to the unearthing of previously buried minerals, which are oxidized by microbes after atmospheric exposure. This mechanism generates sulfuric acid during the oxidation of sulfide minerals, the dominant form of which is pyrite (FeS_2) (Herlihy et al., 1990). AMD is exported from mine sites through groundwater and overland flow (Dold, 2008), and in some cases during catastrophic events such as breaching of the walls of tailings ponds. AMD export can cause pH declines in weakly buffered streams to values <4 (Herlihy et al., 1990; Dold, 2008). By using a survey of acid-sensitive streams throughout the eastern United States, Herlihy et al. (1990) demonstrated that up to 2% of streams had been impacted by AMD, with AMD acidifying up to 10% of streams in sub-regions that were intensely impacted by coal mining. Yet where mine tailings consist of alkalic materials that are low in S and rich in calcite (Kennedy et al., 2016), mine drainage can remain neutral to alkaline, and can have little long-term effect on aquatic ecosystem pH in well buffered catchments (Herlihy et al., 1990; Kennedy et al., 2016), or even increase the pH in sediment layers receiving settled tailings materials. Therefore, mining activities do not exert a uniform effect on the pH of downstream ecosystems, but depend on underlying geology of the region.

Surface water acidification may be further exacerbated by land use change (Renberg et al., 1993; Erlandsson et al., 2011). The recovery of previously deforested lands in Europe and North America may have contributed to lake acidification, where soil

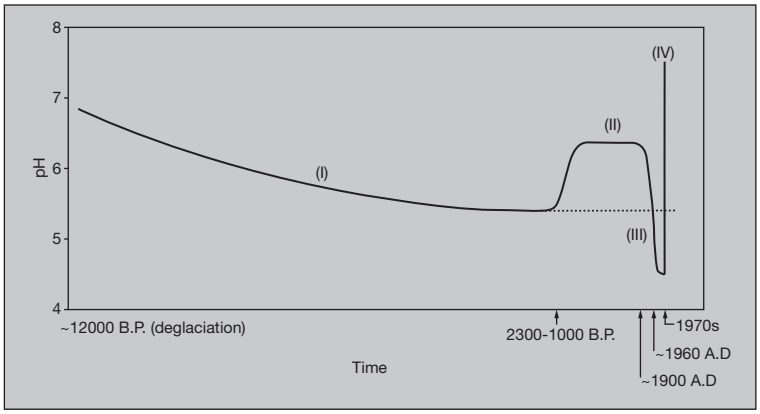

Fig. 4 Schematic diagram of the pH development in acidic lakes in southern Sweden during the postglacial period, with the four periods discussed in the text (I = the natural long-term acidification period, II = the anthropogenic alkalinization period, III = the recent acidification period, IV = the liming period). From Renberg I, Korsan T, and Anderson NJ (1993) A temporal persepective of lake acidification in Sweden. *Ambio* 22(5): 264–271.

development allowed for accumulation of organic matter on the terrestrial landscape, enhanced soil microbial activity, and therefore export of organic acids and CO_2 to downstream water bodies. Because reforestation and sulfate deposition were both occurring at the same time in the early- mid- 20th century, and both primarily affect hard-bedrock and thin-soiled regions, it is often difficult to differentiate between the two drivers.

In general, the impacts of acid rain on inland waters have been dramatically reduced since the 1990s, when regulations were implemented to scrub sulfur and nitrogen oxides from smelters and coal burning plants, and vehicle exhausts were regulated in North America and Europe (Driscoll et al., 2001). Additional efforts to mitigate acidification have been enacted in western Europe (e.g., Sandøy and Langaker, 2001 and references therein). In Sweden, the National Swedish Board of Fisheries has limed lakes through the addition of limestone, or dolomite, directly to the lakes. These additions began in 1976, have been applied to >7500 lakes, and continue to this day, with costs exceeding 360 million Euro. This liming has been effective in increasing "the pH of lakes" in Sweden by an average of ~0.8 units, has resulted in increased biodiversity, and has prevented the loss of endangered flora and fauna (Svenson et al., 1995).

Ecosystem recovery from acidification depends on many factors beyond chemical restoration of water bodies to pre-impacted levels. Other important processes include other vectors of water quality, the presence of a regional pool of colonizing species, and a consideration of other community-level ecological interactions, which are highly complex and often difficult to predict (Yan et al., 2003). As a result, biological recovery of lakes is often slower than chemical recovery (Arnott et al., 2006).

While the release of N and S oxides have been greatly reduced in the past decades, and acid rain is much less of a concern than it once was, there are some current trends in acidification, particularly through the process of brownification, the increased loading of colored organic matter from the catchment (Erlandsson et al., 2010). Here, increasing mobilization of terrestrially-derived organic acids to inland waters can lower pH directly, and has caused an increase in respiration of allochthonous organic matter, causing elevated CO_2 and thus depression of pH (Erlandsson et al., 2010). Further, increasing atmospheric pCO_2 linked to human emissions may increase the concentration gradient and enhance the rate of ingassing of CO_2 into inland waters, thus lowering pH. Yet the vast majority of inland waters remain supersaturated with pCO_2 at levels well above atmospheric content.

Alkalinization

Interestingly, recent exploration of decadal water quality trends in many regions show an increase in alkalinity, salinity and often the pH of many inland waters, termed the "salinization syndrome" (Kaushal et al., 2018). Alkalinization results from increased inputs of basic molecules such as base cations or bicarbonate which can result from a number of processes. These include changes to the hydrologic cycle of river basins, changing land use patterns, or the addition of weatherable material like lime and concrete. Alkalinization is not always associated with increasing pH, but, broadly speaking, the rate of change of pH tends to be inversely proportional to the initial conductivity of the river (Kaushal et al., 2013).

Alkalinization and pH increase are widely reported for inland waters. While alkalinization in some regions is the direct result of recovery from acidification, other regions that did not experience acidification are now becoming more alkaline. Recent studies have shown that >60% of streams in the United States have seen increases in pH, with stronger trends observed in more heavily populated areas (Kaushal et al., 2013, 2018). Carbonate lithology was the primary cause of increasing alkalinity in rivers of the eastern United States (Kaushal et al., 2013), and recovery from acidification combined with increasing agricultural lime usage to alkalize soils caused alkalinization in rivers of the conterminous United States (Stets et al., 2014). Following European settlement and watershed development, a centuries-long increase in pH has occurred in an Australian Floodplain lake (Tibby et al., 2003). Significant alkalinization of 134–185% has also been demonstrated in large Russian Arctic rivers between ~1980 and 2020, attributed to factors including higher temperatures and precipitation, anthropogenic activity, thaw of permafrost (perenially frozen) soils, changes in hydrology, vegetation shifts and decreased acid deposition (Drake et al., 2018). Another example of alkalinization has been demonstrated in mountain streams in northeastern China, which have demonstrated, on average, an increase of nearly 1.5 pH units (from 7.08 to 8.49) between the 1970s and the 2010s, linked to mining activities and agricultural fertilization (Zhao et al., 2019). Collectively, these studies point to the widespread alkalinization and pH increase linked to human impacts in watersheds worldwide.

The impacts of pH change on ecosystem properties

The effects of pH change on aquatic ecosystems are varied and often can be difficult to tease apart from other drivers of environmental change, namely climate change and watershed development. Moreover, pH change is often the response to, not the cause of different environmental changes, such as changing CO_2 concentrations linked to metabolic shifts. Often, acidification or alkalinization of inland waters occur in concert with other sources of perturbation, so changes to pH are seldom the sole driver of variation in ecosystem structure and functioning. Here, we establish how pH drives variability in ecosystem functioning and note specifically where other factors may contribute to ecosystem change. As such, we summarize the influence of pH on ecosystems broadly, while emphasizing the myriad additional factors that interact with water chemistry to affect ecosystem change.

Physical properties of inland waters, pH, and ecosystem change

Changes in pH of inland waters impact UV penetration and lake stratification depth. In the Experimental Lakes Area of Ontario, Canada, a 20-year experimental acidification study demonstrated that acidification increased rates of dissolved organic carbon DOC photo decomposition processes, and in combination with climate change (notably increasing temperatures and reduced

precipitation) contributed to reduced DOC concentrations (Schindler et al., 1996). This reduced DOC concentration caused increased UV penetration with cascading effects on lake biota (see below, Schindler et al., 1996).

Biogeochemistry

Variability in pH is an important regulator of biogeochemical functioning in aquatic environments, with shifts in either direction reflecting *responses* to both aerobic and anaerobic biogeochemical processes (Wetzel, 2001). Wetzel (2001) notes that a change of 1 pH unit under standardized conditions induces a far greater change in the oxidation-reduction (redox) potential (58 mV increase per increase in pH unit) than do modest and environmentally-relevant changes in dissolved oxygen concentrations or water temperature. Therefore, patterns of chemical speciation in aqueous environments are summarized as a function of both the gradient of proton- (pH) and electron availability (pE, or electrical potential). A detailed exploration of these relationships for individual elements is beyond the scope of this chapter, but can be found in many geochemical and biogeochemical textbooks (e.g., Stumm and Morgan, 1995; Langmuir, 1997; Schlesinger and Bernhardt, 2020).

Organic matter and nutrient cycling

Organic matter (OM) cycling in aquatic ecosystems is complex and depends on a multitude of factors that regulate its concentration and chemical composition. Changes in pH thus have a variable, and typically secondary influence on dissolved aquatic OM (DOM) properties, relative to other environmental changes such as land use, hydrology, and other factors (Spencer et al., 2007). In a controlled lab setting, in vitro modification of pH from 2 to 10 demonstrated modest changes in OM light absorbance and fluorescence at intermediate pH adjustment, and more pronounced changes at both pH extremes (Spencer et al., 2007). Changes to pH can also impact how OM interacts with nutrients and bioreactive metals. The capacity for the dissolved fraction of organic matter to bind bioreactive elements such as Fe decreases dramatically as pH increases from ~4.5 to 7 (Neubauer et al., 2013). Pace et al. (2013) showed that increases in pH from 7 to >10, alongside increased base cation availability, may cause polymers and colloids in the dissolved OM pool to expand in size, exposing chromophoric OM to sunlight that transforms and photo-bleaches the OM pool. This mechanism may alter the light climate of alkaline surface waters, where light-attenuation by the OM pool is reduced.

Changes in pH can also impact aquatic nutrient cycling. Where photosynthetic CO_2 uptake leads to pH increases to ~8 to 9.2, sediment P absorption can be slowed, and eventually reversed to cause sediment P desorption and release (Fisher and Wood, 2004). Such moderate increases in pH may have less impact on ecosystem P recycling than do other drivers such as biological organic P recycling or wind-driven mixing (Fisher and Wood, 2004). In systems with extreme autotrophic growth or large inputs of alkaline solutes, pH increases to >10 can generate much higher rates of sediment P desorption and release, where hydroxide and other ions may replace phosphate at binding sites on oxidized iron precipitates (Fisher and Wood, 2004 and references therein). Aquatic nitrogen cycling is also importantly mediated by environmental pH. Sediment nitrification rates in temperate US streams showed a unimodal response to pH changes, and were highest at pH ~7 to 7.5 (Strauss et al., 2002).

Carbon cycling

In many systems, the tight coupling between pH and inorganic carbon speciation (Eq. 1 and Fig. 1) yields a direct correlation between pH and the concentration of CO_2, an important greenhouse gas. Lake acidification has been demonstrated to increase aqueous CO_2 in several studies. For example, acidification of two shallow tropical lakes resulted in large emissions of CO_2 (Marotta et al., 2010). In contrast, alkaline lakes can often act as CO_2 sinks due to CO_2 undersaturation relative to atmospheric concentrations (Finlay et al., 2015). Yet, this undersaturation is dependent on dissolved inorganic carbon concentration in the water, where highly saline lakes, with elevated DIC can still act as CO_2 sources, despite pH levels above 9.0 (Duarte et al., 2008). This pattern can be explained by the equilibria between carbonate species with pH (Fig. 1). Elevated pH can additionally impact CO_2 flux and alter exchange with the atmosphere through chemical enhancement of CO_2 flux, whereby flux rates are accelerated at higher pH levels than would be seen without enhancement (Wanninkhof and Knox, 1996).

As is often the case when describing the chemical environment of lakes, it can be difficult to determine causal pathways: do changes in pH impact CO_2, or do changes in CO_2 impact pH? The answer is usually "both." Metabolic CO_2 cycling directly controls pH on shorter timescales (hourly, to daily and weekly) (e.g., Maberly, 1996); intermediate timescales of pH change (e.g., seasonal) can be shaped by inputs of external water masses with distinct pH due to different content of CO_2, organic acids, bases, and nutrients (Buffam et al., 2008); over years to centuries, natural and human driven changes can regulate the influx of acids and bases to aquatic networks via catchment weathering, atmospheric deposition, direct loading of nutrients, acids, and bases from point sources, and climatic shifts that restructure ecosystems and drive solute evapoconcentration and alkalinization (e.g., Tibby et al., 2003; Finlay et al., 2015; Kaushal et al., 2018).

Metals and metal toxicity

The pH of aquatic ecosystems exerts an important influence over metal exposure and toxicity. Whether natural or linked to human activities such as mining and AMD (reviewed by Gray, 1997; Dold, 2008), acidified water interacts with the surrounding geology to liberate metals and other elements, and induce potentially toxic effects on aquatic food webs. Metal toxicity effects are exerted on organisms both directly, and indirectly through biomagnification or bio accumulation (Gray, 1997). Metals typically become more toxic to biota at low pH because of cation exchange in biological membranes, where H^+ competes with metal cations for exchange sites, and because pH affects metal speciation (Peterson et al., 1984). Conversely, as pH increases above 4.5 iron speciation shifts

from predominantly organic-bound, to the formation of iron (oxy)hydroxide precipitates that increase in size, and are thus more prone to deposition, as a function of pH and redox conditions (Neubauer et al., 2013). At low pH, Cd and Cu inhibit P uptake by algae, which causes increased metal toxicity in acidic conditions (Peterson et al., 1984). The increasing bioavailability of metals in low pH waters results in increasing bioaccumulation of methylmercury, Cd, and Pb in fish. At elevated levels, these heavy metals become increasingly toxic when Ca^{2+} concentrations are low, which increases the permeability of biological membranes to the metals (Spry and Wiener, 1991).

Community ecology

The pH of inland waters has considerable impacts on community ecology, through all levels of the food web. Species have optimal pH ranges and these biological tolerances are one factor that can initially structure the aquatic community, a fact that has led to the recreation of lake pH over time using paleolimnological analyses of diatom valves in sediment cores (e.g., Cumming et al., 1992). Many additional environmental factors frequently interact and contribute to the effect of pH on organisms and ecosystem functioning (Schindler et al., 1996). The following section provides illustrative examples of the responses of biological communities to changing pH, but is not intended to be an exhaustive evaluation of the extensive research which has been conducted on this topic.

Plankton

Limited studies on the impact of lake water pH on bacterial community structure and function have demonstrated a few interesting trends. Like other biota, bacterioplankton exhibit maximal growth at taxa-specific optimal pH (Bååth and Kritzberg, 2015). In lakes of the Mackenzie Delta in northern Canada, bacterial community respiration and production declined during rapid (hourly to daily) increases in pH arising from an macrophyte growth. These reductions in bacterial community metabolism recovered after a few days when the bacterial community composition shifted to adjust to the new lake pH (Tank et al., 2009).

The impact of changing pH on the phytoplankton community is complex and involves many interacting factors including not only pH, but also DOC, DIC and other components of the food web (Fig. 5, Leavitt et al., 1999), and algal communities have consequently experienced dramatic changes through lake acidification and recovery. In one study conducted at the Experimental Lakes Area, total algal biomass increased 200–400% under mild acidification (from pH 6.6 to 5.0), but then declined to near-baseline levels under severe acidification (pH 4.5, Leavitt et al., 1999).

Zooplankton species richness, diversity, and abundance all were reduced by acidification. Calcium-rich zooplankton species, including *Daphnia* are often dramatically affected by acidification and reductions of calcium to <1.5 mg L^{-1} can reduce population growth rates through inhibition of reproduction and clutch sizes (Jeziorski et al., 2008).

Zooplankton recovery after lake pH recovery from acidification has been demonstrated to be slow, owing to the varying recovery rates of predators in the system causing a top-down trophic cascade. The slow return of catchment derived Ca^{2+} can also delay the recovery of *Daphnia* species and other calcium-rich biota (Jeziorski et al., 2008). The slow recovery of fish populations (see "Fish" section below), resulted in elevated invertebrate predator populations (the beetle *Graphoderus liberus*) which maintained low calanoid and cladoceran zooplankton population sizes through predation (Arnott et al., 2006).

Macroinvertebrates

Acidification and associated reductions in Ca^{2+} were found to reduce populations of oligochaetes, mayflies and some chironomids, but increased odonata, trichoptera, other chironomids and *Crangonyx* (amphipod) (Stephenson et al., 1994). *Chaoborus punctipennis* populations doubled in an experimental acidification study in Little Rock, Wisconsin, United States. This increase in *Chaoborus* numbers was attributed to a decline in an invertebrate predator (*Mesocyclops edax*) on early stages of *Chaoborus*, rather than an increase in food availability or reduction in fish predation (Fischer and Frost, 1997). The impact of acidification on macroinvertebrates has also been attributed to varying metal toxicity, where cadmium toxicity decreased, but aluminum toxicity was much higher when pH was reduced (Wren and Stephenson, 1991).

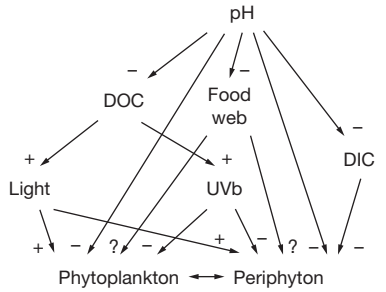

Fig. 5 Main potential direct and indirect effects of lake acidification on algal abundance. Effects of acidification either inhibit (–) or stimulate (+) response variables. Effects of food-web changes on algae depend on complex food-web interactions and are not predictable (?). From Leavitt PR, Findlay DL, Hall RI and Smol JP (1999) Algal responses to dissolved organic carbon loss and pH decline during whole-lake acidification: Evidence from paleolimnology. *Limnology and Oceanography* 44: 757–773.

Fish

Lake acidification has had dramatic impacts on fish populations and communities, reducing fish diversity at low pH (Driscoll et al., 2001). Scandinavian lakes lost entire fish populations, and acidification was determined to be the cause of the most devastating fish losses recorded in Scandinavian history (Muniz et al., 1984). After a few years of fluctuating population sizes of fish in Lake 223 of the ELA, lake trout (*Salvelinus namaycush*), white sucker (*Catostomus commersonii*), fathead minnow (*Pimephales promelas*) and slimy sculpin (*Cottus cognatus*) all showed a reduction in survival to adulthood (Mills et al., 1987). At low pH (<5 or 6) reproductive failure and extirpation of populations can occur (Magnuson et al., 1984). The reduction in DOC concentrations with acidification can cause increased UV-B penetration and changes to epilimnetic depth (see "The impacts of pH change on ecosystem properties" section), with consequences to the fish community. An increased epilimnion depth and increased exposure to UV-B penetration might cause a reduction in habitat, limiting fish to a narrow vertical layer where UV-B limits their survival above, and low oxygen limits them below (Schindler et al., 1996).

Conclusions

The pH of inland waters can range widely (2–12), but is typically well buffered, such that most systems naturally lie within the circumneutral range (6–9). Surface water pH is not static, but can change on hourly to much longer (multidecadal, centennial) timescales as a result of both abiotic and biotic processes operating both within and outside a waterbody's physical boundaries (e.g., in watershed soils, or in distant landscapes that are connected by atmospheric transport of materials).

Aquatic ecosystems have undergone changes (in many cases, extreme) in pH due to human activities that have dramatically intensified since the onset of the industrial revolution. The consequences of these activities are complex, and vary from system to system and process to process, such that both acidification and alkalinization of aquatic systems are observed in different environments. These large, directional changes in pH (both natural and human-induced) have dramatic impacts on the structure and functioning of aquatic ecosystems, which can restructure communities from bacteria up to fish and other vertebrates.

Lotic and lentic aquatic systems can recover from human disturbances to their baseline pH. Case studies show how intensive government-led initiatives can mitigate negative impacts of acidification and allow for the recovery of biota in impacted systems. These examples highlight the important role that science-guided policies can have in remediating pH levels in aquatic ecosystems, but also note the importance of a comprehensive understanding of the long-term (centennial- to millennial-scale) patterns in pH if the goal is to reach "baseline" values. Moreover, despite these accomplishments, we have not entirely curtailed anthropogenic pH change in aquatic ecosystems, and in many cases it is now the non-point influences that are driving acidification and alkalinization of watersheds worldwide.

Knowledge gaps

- Alkalinization is much less studied than acidification, and remains less well understood.
  - In many cases, we can learn from lessons related to recovery from acidification, but new challenges are expected with alkalinization
- Differentiating between underlying causes of acidification and alkalinization will be important for mitigation efforts
- Determining baseline pH of lakes in a historical context is crucial for determining whether mitigation is required

Important case studies

Name of site	*Country*	*Coordinates*	*Main topic*	*Key reference*
Swedish lakes	Sweden	~56°–67°N ~11°–16°E	Remediation from acidification	Renberg et al. (1993) and Erlandsson et al. (2011)
Mountain streams	China	40°30′–42°30′N 122°0–125°0′E	Salinization and Alkalinization	Zhao et al. (2019)
Adirondak lakes	United States	44° 06′N 73° 55′W	Acidification	Cumming et al. (1992)
Experimental Lakes Area	Canada	49° 66′N 93° 72′W	Experimental acidification, impacts on ecosystem function	Schindler et al. (1996) and Peterson et al. (1984).
North-western Ontario lakes	Canada	46° 23′N 81° 02′W	Recovery from acidification	Yan et al. (2003) and Arnott et al. (2006)
American rivers and streams	United States	~25°–49°N ~125°–75°W	Salinization syndrome	Kaushal et al. (2013)
Russian rivers	Russia	~47°–53°N ~89°–107°E	Alkalinization	Drake et al. (2018)
Hubbard Brook Experimental Forest	United States	43° 09′N 71° 72′W	Long-term effects of acid rain on forest and aquatic ecosystems	Likens et al. (1996)

See Also: Structures and functions of Inland Waters - Lakes: Lacustrine Phosphorus Cycling; The Carbon Cycle in Lakes: A Biogeochemical Perspective

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Ecological Zonation in Lakes

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This is a reprint of W.M. Lewis, Ecological Zonation in Lakes, Editor(s): Gene E. Likens, Encyclopedia of Inland Waters, Academic Press, 2009, Pages 416-422, ISBN 9780123706263, https://doi.org/10.1016/B978-012370626-3.00209-X.

Glossary

Aphotic – **Without light, generally interpreted limno-logically as receiving less than 1% of solar irradiance reaching a lake surface.** Epilimnion – **The uppermost and warmest layer (also called the mixed layer) of a lake that experiences density stratification induced by seasonal warming at the lake surface.** Euphotic – **That portion of a lake receiving sufficient solar irradiance to support photosynthesis (typically more than 1% of full solar irradiance).** Hypolimnion – **The most dense, deepest, and coolest layer of a thermally stratified lake. The hypolimnion does not support photosynthesis, because it lacks solar irradiance, and in many cases shows partial or complete depletion of dissolved oxygen.** Littoral – **Near the shore of a waterbody, where irradiance reaching the bottom is above 1% of solar irradiance at the water surface.** Metalimnion – **A layer of transitional density and temperature that connects the epilimnion to the hypolimnion.** Pelagic – **Beyond the littoral zone of a lake.** Benthic – **The zone of a lake extending a few centimeters above and below the bottom of the lake.**

Introduction

Lakes show many kinds of spatial variation in both vertical and horizontal dimensions. Variation can be chemical, physical, or biotic, and is important to the understanding of ecosystem functions. Although some types of variation are unique to specific classes of lakes, others are common to most lakes, and correspond to an obvious spatial organization of the biota in lakes. The existence of certain common types of spatial organization in lakes has led to the naming of specific zones that have distinctive ecological characteristics.

A complete list of all zones that have been named by limnologists would be lengthy and complex (Wetzel, 2001). Complex nomenclatures have been abandoned by modern limnologists, however. Modern limnology focuses on simple zonation systems that are easily applied by limnologists and others interested in lakes. Table 1 gives a summary of zonation systems that are currently in broad use.

Horizontal Zonation: Littoral and Pelagic

The nearshore area of a lake (littoral zone) differs from the offshore shore area (pelagic zone). The only group of autotrophs in the pelagic zone is the phytoplankton, which consists of very small algae that are suspended in the water column. The littoral zone also has phytoplankton (which move freely between littoral zone and pelagic zone), but also has two other categories of autotrophs (Figure 1): aquatic vascular plants (aquatic macrophytes), and films of attached algae (periphyton). Periphyton grow on the leaves of macrophytes and on other solid surfaces such as mud, sand, rocks, or wood.

The outer margin of the littoral zone, beyond which is the pelagic zone, is the point at which significant growth of macrophytes and periphyton becomes impossible because of darkness. This boundary corresponds approximately to the location at which the amount of solar irradiance reaching the bottom of the lake is $<1\%$ of surface irradiance. At bottom irradiances $<1\%$, there is little or no net photosynthesis, which prevents growth of the attached autotrophs (macrophytes and periphyton) that are typical of the littoral zone.

For a lake of a given size and shape, the width of the littoral zone depends on transparency of the water as well as shoreline slope (Figure 2). In oligotrophic lakes, which have low nutrient concentrations and therefore develop very small amounts of the phytoplankton biomass that could shade the lower water column of lakes, the littoral zone extends to depths of 4–20m or even

Table 1 Summary of the four major zonation systems for lakes.

Zonation	*Temporal variability*	*Description*
Horizontal	Stable	
Pelagic zone		Offshore (bottom irradiance $<1\%$)
Littoral zone		Nearshore (bottom irradiance $\geq 1\%$)
Vertical	Stable	
Water column		Water extending from lake surface to bottom
Lacustrine sediments		Lake-generated solids below the water column
Benthic zone		Interface of water column and lake bottom
Vertical	Seasonal	
Epilimnion	(mixed layer)	Uppermost density layer (warm)
Metalimnion		Middle density layer (transition)
Hypolimnion		Bottom density layer (cool)
Vertical	Dynamic	
Euphotic zone		Portions of a lake with $\geq 1\%$ light (photosynthesis)
Aphotic zone		Portions of a lake with $<1\%$ light (no photosynthesis)

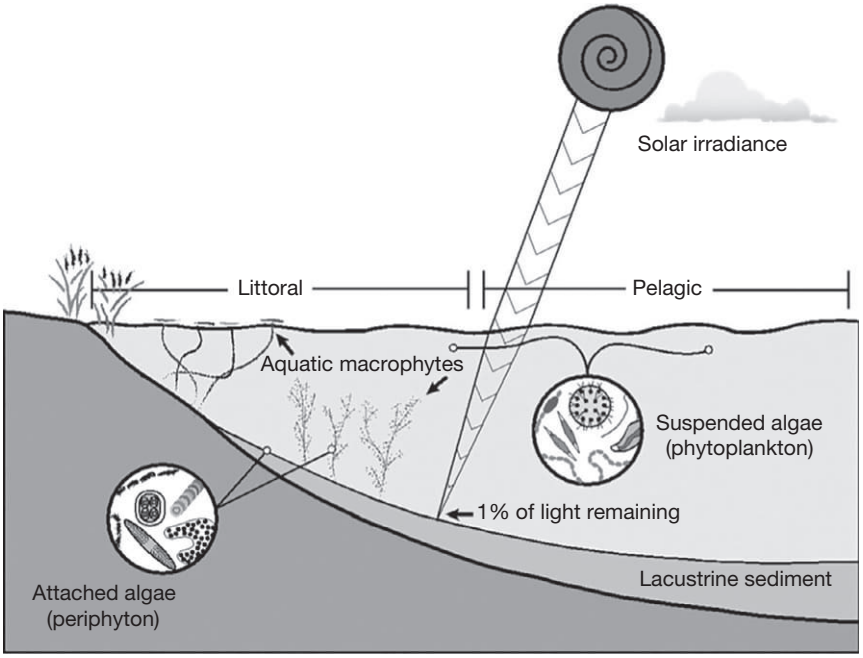

Figure 1 Depiction of the littoral and pelagic zones of a lake. The littoral zone extends outward from the shoreline to approximately the location at which the solar irradiance at the bottom of the lake corresponds to about 1% of the solar irradiance at the top of the water column. Within the littoral zone, growth of aquatic macrophytes and attached algae (periphyton) is possible. The pelagic zone begins at the outer margin of the littoral zone. Phytoplankton are exchanged freely between the littoral and pelagic zones as well.

more, depending on transparency of the water. In the eutrophic category, the depth of 1% irradiance ranges between 0.1 and about 2 m, and the mesotrophic category spans ~2–4 m. In the most extreme cases of eutrophication (lakes highly enriched with nutrients), where the depth of 1% light corresponds to only a few centimeters, the littoral zone as defined by light is virtually absent, and the littoral zone may be defined instead by the zone of influence for traveling waves and corresponding disturbance of the bottom (0.5–1.5 m). In general, small lakes have a higher percentage of surface area in the littoral zone than do large lakes (**Figure 2**), although some large, shallow lakes have large littoral zones (e.g., Lake Okeechobee, Florida).

Although littoral zones are most easily defined on the basis of macrophytes and attached algae, a littoral zone can also be distinguished from a pelagic zone by its distinctive heterotrophic communities and by its food-web structure. Because littoral zones provide shelter, whereas pelagic zones do not, littoral zones often support dense populations of organisms that thrive when protected from predation. Larval and juvenile fish, for example, seek shelter within the littoral zone from predation by larger fish. Large invertebrates, such as dragonfly larvae or crayfish, typically are most abundant in littoral zones, where they are least likely to be consumed by fish. The littoral zone also has invertebrate communities that specialize in the consumption of attached algae by nipping or scraping the algal coatings on macrophytes or other solid surfaces. In the pelagic zone, there is no food source comparable to the periphyton of a littoral zone. In general, the communities of a littoral zone are more diverse than those of the pelagic zone, and the key species of the two zones differ.

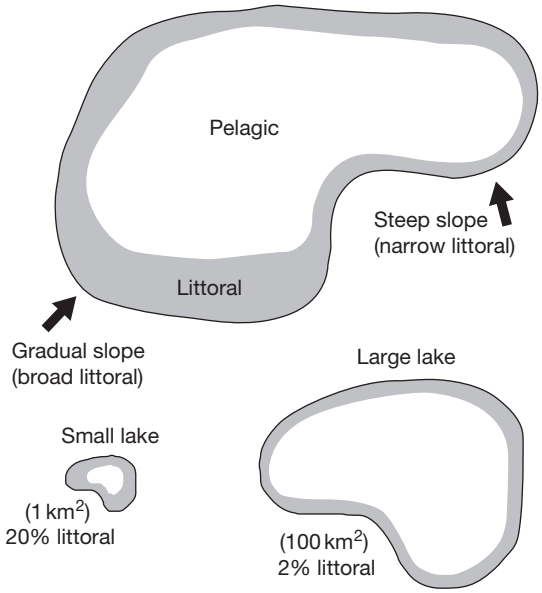

Figure 2 A plan view of the littoral and pelagic zones of lakes, illustrating variation in the width of the littoral zone associated with changes in slope along the margin of any given lake, and the tendency of smaller lakes to have a higher percent areal coverage of littoral zone for the total lake area.

In the pelagic zone of a lake, the autotroph community is composed of phytoplankton (**Figure 1**), which are adapted for life in an environment that is free of solid surfaces. Consumers, such as zooplankton, living and reproducing in the pelagic zone must escape predators by avoiding the upper, illuminated part of the water column during the day, or must be agile or so small as to be impractical as a food for many predators.

Vertical Zonation: Water Column, Sediments, and the Benthic Interface

Lakes have a vertical zonation consisting of the water column, underlying lacustrine sediments (lake sediments), and the benthic zone, which occupies a few centimeters above and below the sediment–water interface (**Figure 3**). The water column extends across both the pelagic and littoral zones. The water column of the pelagic zone is driven by wind-generated currents into the littoral zone

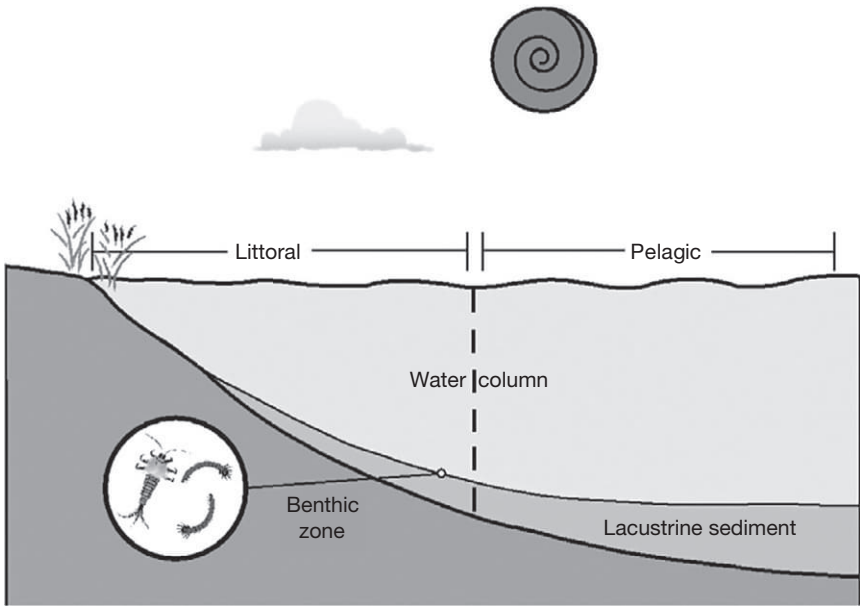

Figure 3 Illustration of the division of a lake into three vertical components: water column, lacustrine sediments, and the boundary between the water column and sediments (benthic zone).

where water is displaced from the littoral zone into the pelagic zone. Thus, water-column constituents such as dissolved gases, dissolved solids, suspended solids, and suspended organisms are constantly exchanged between the pelagic zone and the littoral zone whenever there are currents in the top few meters of a lake. Chemical differences between the top few meters of the pelagic zone and the littoral zone may develop under the influence of biological processes, however, when currents are weak.

Although the water column is shared by the pelagic zone and the littoral zone, lacustrine sediments always underlie the pelagic zone but may or may not cover all of the littoral zone. Sediments are produced by the settling of mineral and organic matter that is derived from the watershed of a lake, and from organic matter consisting of fecal pellets, organic debris (detritus), and skeletal fragments of organisms derived from the lake itself. A constant sedimentation of this fine mixed solid material occurs over the entire lake. Disturbance of sediments by moving water occurs primarily in shallow water, where most of the energy of wind-generated currents and traveling waves are expended against the bottom of the littoral zone. Thus, energy near the shore may cause fine sediments, such as those that are characteristic of lakes, to be swept to deeper water. For this reason, lacustrine sediments may not accumulate in all parts of a littoral zone. Alternatively, in lakes that are small or strongly sheltered from wind, and thus not subjected to extremes of wind-generated disturbance, lacustrine sediments may occupy most or all of the littoral zone.

Lacustrine sediments are capable of supporting eukaryotic organisms (algae, protozoans, invertebrates, vertebrates) only when they are oxic. When the hypolimnion is oxic, the top few millimeters of sediment often (but not always) will be oxic. Below the top few millimeters, there typically is a decline in oxygen because microbial respiration supported by organic matter in the sediments leads to the depletion of oxygen, but some oxygen (e.g., 50%) may persist because invertebrates in the sediment pump oxygen through small tunnels into the sediment to as much as 10–20 cm within the sediments. Almost all of the deeper sediments (>10–20 cm) in lakes, which may be many meters thick, are anoxic and can support only microbes that are capable of anaerobic metabolism. When the water of the hypolimnion is anoxic, the entire sediment profile is anoxic, and can support only anaerobic microbes. There are many such microbes, and anoxic sediments show strong evidence of their metabolism, including accumulation of reduced substances such as ferrous iron, sulfide, and methane. At progressively greater depths in sediments, however, the metabolism of microbial anaerobes slows because the easily used portions of organic matter are exhausted or because oxidizing agents such as sulfate or nitrate may be depleted. Thus, there is a decline in microbial metabolic rate from the upper sediments to the deepest sediments, which are almost inert biologically.

The interface between the water column and the lacustrine sediments carries its own name ('benthic zone') because it is exceptionally important from the ecosystem perspective, despite its narrow dimensions. Organisms that live on the sediment surface or just below it (down to about 20 cm) carry the name 'benthos'. In sediments below the pelagic zone, the benthos does not include autotrophs because there is no light reaching these sediments. The benthic zone is rich in invertebrates, provided that it is oxic at the surface, which is not always the case. Oxic benthic zones often support a number of important invertebrates, most of which are embedded within the sediment, as necessary to avoid predation. Examples include midge larvae and the larvae of other insects (**Figure 3**). Certain fish species (e.g., catfish) may be associated closely with the benthic zone, in that they are adapted to find and consume the embedded invertebrates by chemosensory means, without using vision. Oxic benthic zones also support protozoans and bacteria conducting oxic metabolism, including especially the oxic breakdown of organic matter. Anoxic benthic zones only support anaerobic bacteria and a few specialized protozoans.

The benthic zone extends not only across the bottom of the pelagic zone but also across the bottom of the littoral zone (**Figure 3**). The benthic component of the littoral zone includes not only the interface between lacustrine sediments and the water column but also between the water column and any parts of the littoral zone that happen to be swept free of lacustrine sediments. Thus, the entire solid surface at the bottom of a lake lies within the benthic zone.

Seasonal Zonation: Vertical Layering Based on Density

Because the temperature of water affects its density, it is common for lakes to develop layers of different density corresponding to temperature differences across the layers. At temperate latitudes, all but the shallowest lakes develop a density stratification during spring that typically persists until late fall. Similar seasonal stratification is also common in subtropical and tropical lakes, but the duration of stratification is longer and the nonstratified period (mixing period) does not contain an interval of ice cover, as it often does at temperate latitudes.

Density stratification causes an ecologically important vertical zonation of lakes (**Figure 4**). An upper layer, which contains the air–water interface, is the epilimnion of a stratified lake; it may also be referred to as the 'mixed layer'. The epilimnion is the warmest and least dense of the three layers. Its thickness is strongly influenced by the size of the lake, in that larger lakes show a higher transfer of wind energy to water currents, which thickens the mixed layer during its period of formation. In sheltered water bodies, mixed layers may be as thin as two meters, but in larger (>10km^2), windswept water bodies, they may be as thick as 15–20m. In addition, the thickness of a mixed layer in a given lake increases over the fall cooling period, during which the bottom of the mixed layer erodes the layer below.

The mixed layer often shows sufficient irradiance throughout its full thickness to support photosynthesis. Even in lakes that have very low transparency, the uppermost portion of the mixed layer is well illuminated.

The mixed layer extends continuously across the pelagic zone and littoral zone. Only in highly transparent lakes does the littoral zone extend below the mixed layer. Within the pelagic portion of the mixed layer, zooplankton herbivores feed vigorously on phytoplankton, but may move downward out of the mixed layer during the day in order to avoid predation. Other small

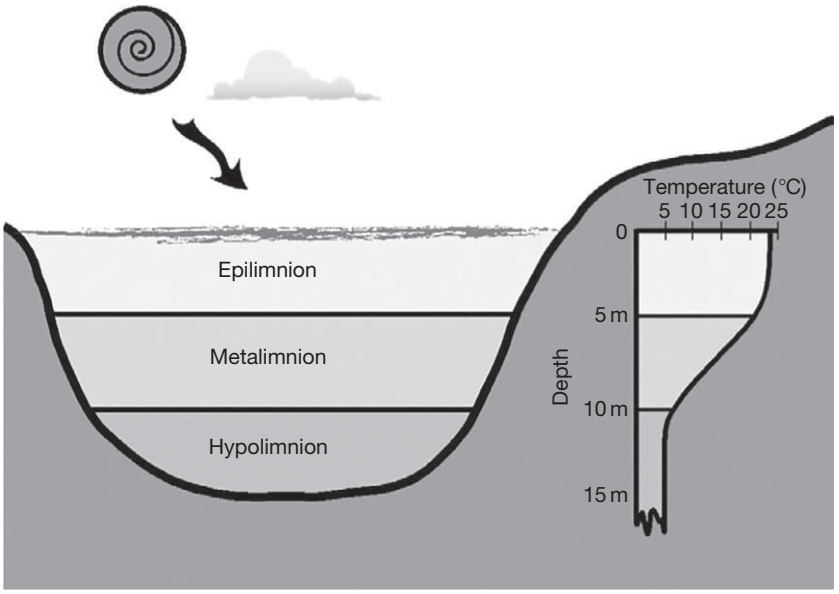

Figure 4 Illustration of the three density (temperature) layers determined by seasonal stratification of a water column.

invertebrates often migrate out of the mixed layer during daylight hours as well. Most of the energy of wind transferred to water is dissipated within the mixed layer; this energy contributes to the high degree of uniformity in the mixed layer at small to intermediate distance scales (up to 10km or more), except during extended calm weather.

Below the mixed layer of a stratified lake is a thermal gradient, corresponding to a density gradient. The gradient makes a transition in temperature and density between the mixed layer and the coolest layer, which lies in contact with the bottom of the lake. The thermal transition is referred to as the thermocline, but the layer within which the thermocline lies is best referred to as the metalimnion (Figure 4). The metalimnion may or may not receive sufficient irradiance to support photosynthesis. In lakes that are quite transparent, phytoplankton often grows in the metalimnion, whereas lakes of low transparency seldom show growth of autotrophs in the metalimnion. In the pelagic zone, phytoplankton growing in the metalimnion of a transparent lake may be of different species composition than phytoplankton growing in the mixed layer. Some mass transfer occurs between the epilimnion and the metalimnion, the amount of which is dependent on the amount of turbulence at the interface of the two layers. The thickness of the metalimnion varies a great deal among lakes. It is seldom thinner than 2 m, and may be as thick as the mixed layer or even thicker.

The deepest seasonal layer in lakes is the hypolimnion. The temperature and density of the hypolimnion typically reflect conditions that occur when seasonal stratification becomes established. It is common for stratified lakes at temperate latitudes to have hypolimnetic waters that are near 4 °C, the temperature at which water is most dense, or slightly above 4 °C, reflecting the prevailing water temperature at the time of spring stratification. At lower latitudes, the minimum temperature increases, until it reaches approximately 24 °C within 10° latitude of the equator. Thus, a stratified lake might have a hypolimnion of 4 °C in Wisconsin and 24 °C in Venezuela.

The hypolimnion, in contrast to the mixed layer, has a very low degree of turbulence, is too dark for photosynthesis, and is isolated from the surface. Also, except at low latitudes, it is much cooler than the mixed layer (Figure 4).

Because of its physical isolation from photosynthesis and from atmospheric oxygen, the hypolimnion typically loses oxygen during the period of stratification. The loss of oxygen depends on the size of the hypolimnion, its temperature, the duration of stratification, and the amount of organic matter coming down to it from above, which is a byproduct of the trophic status of the lake. In lakes that are just deep enough to support stable stratification (e.g., 10–20 m), the hypolimnion may be absent, as the metalimnion reaches the bottom of the lake. In deeper lakes, the hypolimnion may equal the volume of the epilimnion, and in very deep lakes (e.g., >100 m), the hypolimnion may be much larger than the epilimnion. Lakes with a very large hypolimnion often maintain hypolimnetic oxygen throughout the stratification season, especially at temperate latitudes where the hypolimnion is cool. Lakes with a very small hypolimnion typically lose most or all of their oxygen, even if they have low productivity, because the sediments of a lake contain enough organic matter to demand most or all the oxygen from a small hypolimnion. Oxygen concentration in lakes with a hypolimnion of intermediate size is quite sensitive to trophic state. Eutrophic lakes typically lose most or all of their hypolimnetic oxygen, thus producing an anoxic benthic zone, whereas lakes of lower productivity may retain an oxic hypolimnion overlying a benthic zone that has an oxidized surface.

Loss of oxygen is of great importance to the metabolism of a lake because eukaryotes (most protozoa, invertebrates, fish, algae) cannot live in anoxic waters. Thus, loss of hypolimnetic oxygen excludes nonmicrobial components of the biota from the deep waters of a lake.

Zones with Dynamic Dimensions: Euphotic and Aphotic

Photosynthesis in the water column of lake is dependent on the availability of photosynthetically available radiation (PAR, wavelengths 350–700 nm). PAR, which corresponds closely to the spectrum of human vision, is removed exponentially as it travels through a water column. The availability of PAR is high during daylight hours at or near the surface of the water column. If nutrients are present, rates of photosynthesis are likely to be high near the surface. A progressive decline in PAR with depth is paraleled by a decline in rates of photosynthesis with depth. At a depth corresponding to ~1% of the surface irradiance, net photosynthesis reaches zero, which is a threshold beyond which accumulation of plant biomass is not possible. At depths below the 1% level, photosynthetic organisms (e.g., phytoplankton) lose mass and either die or become dormant unless they are returned to the surface by water currents, which commonly occurs in the mixed layer but not in the metalimnion or hypolimnion.

The depth between the water surface and the depth of 1% irradiance is referred to as the euphotic zone (Figure 5). Below the depth of 1% irradiance is the aphotic zone. The euphotic zone may not occupy the entire epilimnion of a lake, or may extend to the full thickness of the epilimnion. In some cases, the euphotic zone may extend into the metalimnion, but its extension into the hypolimnion of a lake is unlikely.

The thickness of the euphotic zone is dependent on transparency of the water, which in turn is influenced by dissolved color (colored organic acids from soils), inorganic suspended matter (silt and clay), and living organisms, and especially those that contain chlorophyll, an efficient absorber of light. Because the concentrations of each of these constituents can vary on relatively short time scales (e.g., weekly), the thickness of the euphotic and aphotic zones is dynamic; it is subject to both seasonal and irregular change over time.

The thickness of the euphotic zone may be small at times of high runoff, when suspended inorganic material and colored organic compounds enter lakes in the largest quantities. Other times when the euphotic zone may be thin it coincides with algal blooms, which can produce sufficient chlorophyll to reduce the transparency of the water column substantially. Conversely, the euphotic zone may thicken substantially when nutrients are exhausted because phytoplankton biomass is likely to decline, thus increasing transparency of the water. Also, strong grazing by zooplankton may thicken the euphotic zone by removing phytoplankton biomass.

The euphotic zone extends across an entire lake, including both pelagic and littoral zones. In fact, the mean thickness of the euphotic zone determines the outer boundary of the littoral zone because of its effect on the attached vegetation that is characteristic of littoral zones.

Overview

The four sets of zones shown in Table 1 define distinctive habitats within lakes that are associated with specific categories of organisms and biogeochemical or metabolic processes. The zones reflect some of the most important physical and chemical factors

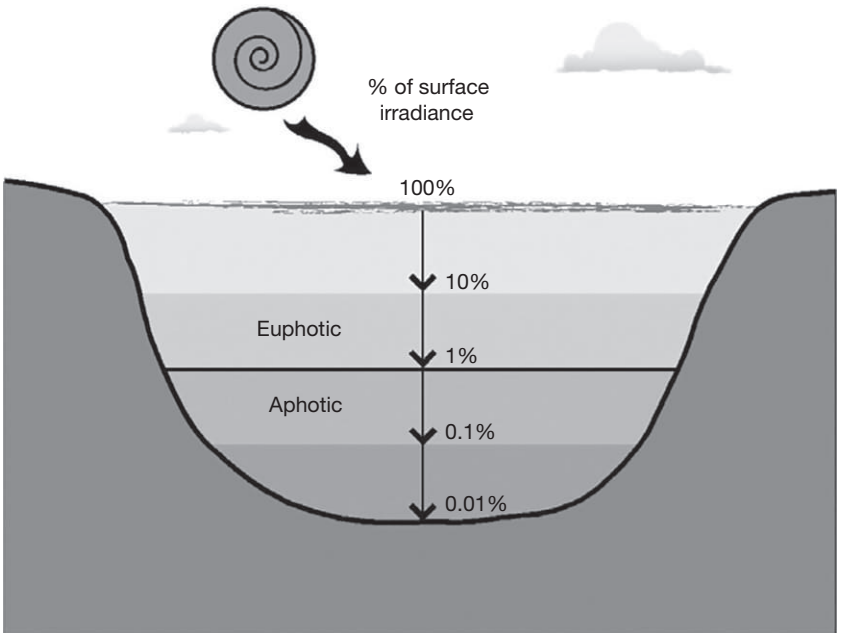

Figure 5 Illustration of the division of a lake into euphotic and aphotic zones. The euphotic zone, which is the lake volume within which positive net photosynthesis can occur, corresponds approximately to the depth at which ≥1% of incoming irradiance is found. Portions of the lake below this boundary have negative net photosynthesis or negligible total photosynthesis.

that control biotically driven processes and biotic community structure. Zonation, although generally a qualitative rather a quantitative concept, reflects accumulation of experience and measurements across lakes of many kinds. Therefore, knowledge of zonal boundaries in a lake allows some general predictions to be made about the kinds of organisms and rates of biogeochemical processes that will occur in a given lake, and the spatial distribution of these organisms and processes.

See Also: Fundamental concepts and theories: Ecosystem Engineers in Freshwater Ecosystems; Structures and functions of Inland Waters - Lakes: Lake Food Webs; Structures and functions of Inland Waters - Rivers: Riparian Zones; Structures and functions of Inland Waters - Wetlands: Benthic Invertebrates of Running and Stagnant Inland Waters

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Phytoplankton Growth and Nutrients☆

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This is an update of J.A. Raven, S.C. Maberly, Phytoplankton Nutrition and Related Mixotrophy, in Encyclopedia of Inland Waters, Edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00138-1.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Catchment The land and water area that drains into a given inland water. It is defined at its perimeter by the watershed, and is synonymous with the drainage basin.
Cell quota The amount of a particular element in a cell.
Eutrophication The process, often driven by human activities, that increases productivity usually as a result of increased nutrient load and causes a series of consequent changes to the ecosystem.
Michaelis-Menten/Monod kinetics A kinetic response curve with the form of a rectangular hyperbola characterized by a large increase in rates of activity (Michaelis-Menten) or growth (Monod) at low substrate concentrations and no further increase in rate at high, saturating, substrate concentrations.
Mixotrophy The ability to use a combination of both inorganic and organic sources of nutrients and energy.
Osmo-organotrophy The ability to use dissolved organic compounds as sources of nutrients and energy.
Phago-organotrophy The ability to ingest living or dead organic particles as sources of nutrients and energy.
Photoautotrophy (=photolithotrophy) involves the photoproduction of ATP, and NAD(P)H with an inorganic electron source, and the consumption of ATP and NAD(*P*)H to convert CO_2 to reduced organic C using an autotrophic CO_2 fixation pathway.
Stoichiometry The relative amounts of different elements, usually expressed on an atomic basis.

Introduction

Phytoplankton form the base of the pelagic food web in inland waters. Unlike rooted plants with access to nutrients in the sediment, phytoplankton depend on the open water as their sole direct source of minerals. Phytoplankton comprise cyanobacteria and phylogenetically diverse eukaryotic algae that convert light energy and mineral nutrients into organic matter. Many species also exploit the elements and energy within dissolved organic compounds and particles produced in the catchment or within the water. Here, we describe the nutrient requirements of phytoplankton, their different modes of nutrition, the mechanisms they employ to acquire nutrients and the ecological consequences of their varying ability to exploit an often scarce and spatially and temporally variable resource. When nutrients are abundant, often as a result of human disruption of nutrient cycles, phytoplankton productivity, and often biomass, increases to the point that it causes a range of ecological consequences that reduce the value of the water resource for mankind.

☆*Change History:* October 2021. SC Maberly, DB Van de Waal, JA Raven are involved in preparing this update. The chapter has been completely rewritten with no common figures/ tables, etc.

Nutrient requirements and cellular composition

Phytoplankton take up and assimilate nutrients with the use of light as an energy source. Although carbon is not always thought of as a nutrient, we include it here since it is a major element in most phytoplankton cells, typically comprising around 50% of ash-free dry weight. Nutrients are assimilated into a range of biochemicals, including carbohydrates, lipids, amino acids and nucleotides. These serve as structural compounds, are involved in energy and nutrient capture and storage, and the transfer of genetic information. A large range of elements are required including, in (approximate) order of atomic abundance: H, C, O, N, P, K, S, Mg, Ca, Cl, Fe, Mn, Cu, Zn, Ni, Co and for some heterokonts such as diatoms, Si.

In the 1930s, the American oceanographer, Alfred Redfield, analyzed depth profiles in the ocean and showed that nutrients and phytoplankton had an average atomic ratio of 106C: 16 N: 1P (Redfield, 1934). Subsequent refinements to the ratio have been produced (Geider and La Roche, 2002), but it is widely used to represent the approximate stoichiometric requirements of exponentially growing, nutrient replete marine and freshwater phytoplankton for these three important elements. Trace elements are required, in smaller amounts, and are involved in many processes. For example: sulfur is contained in some amino acids and redox-signaling compounds, the oxygen-evolving complex of Photosystem II requires Mn, the electron transport chain between photosystems II and I involves Fe and sometimes Cu, the nitrogenase enzyme in cyanobacteria able to fix N_2 requires Fe and usually Mo (rarely V), different aspects of nitrogen assimilation involve Mo and Ni, the extracellular hydrolysis of organophosphates involves Zn or Co, and while carbonic anhydrase normally requires Zn, other elements including Co, Cd or Mn are present depending on the sub-type of the enzyme or as replacements when Zn is unavailable (Morel et al., 2020). Using algal cultures of marine and freshwater phytoplankton, (Quigg et al., 2011) showed that the average trace element atomic stoichiometry was 18 Fe: 2.8 Mn: 1.34 Zn: 0.50 Cu: 0.11 Co: 0.11 Cd to 1000 mol P. However, there were consistent differences among evolutionary groups. For example, the green plastid lineage had higher Fe, Cu and Cd to P ratios and lower Mn to P ratios than the red plastid lineage. Growth limitation or yield limitation by P, N and C has been demonstrated in freshwater phytoplankton populations, and Si can limit diatom at certain times of the year. There is also evidence for limitation by trace elements including K, Co, Cu, Fe, and Mo in some lakes.

The nutrient content of phytoplankton cells will vary, between bounds, depending on nutrient availability. The minimum cell quota (Q_{min}) occurs where the growth rate is zero and increases with cell volume in a similar way for marine and freshwater phytoplankton (Edwards et al., 2012). Many phytoplankton indulge in "luxury consumption," storing nutrients in excess of the cell quota to permit growth when external nutrients are depleted. For example, the commonly limiting nutrient phosphorus can be stored as polyphosphate granules and used as a reserve of P and energy (Sanz-Luque et al., 2020).

Modes of resource acquisition

The typical mode of nutrition in phytoplankton is photoautotrophy, with inorganic carbon (CO_2 or HCO_3^-) as the C source. For photosynthesis, inorganic carbon (as CO_2) is fixed, where H_2O acts as the reductant source, and photons in the wavelength range 400–700 nm as the energy source, and O_2 as the by-product (Eq. 1):

$$CO_2 + 2H_2O^* + \geq 9 \text{ photons } 400 - 700 \text{ nm} \rightarrow CH_2O + H_2O + O_2^* \quad (1)$$

where the * on the oxygen of H_2O is to emphasize that the oxygen in O_2 comes from H_2O. The minimal photon requirement for photosynthesis with diffusive CO_2 uptake saturating the carboxylating enzyme ribulose-1.5-bisphosphate carboxylase-oxygenase is 9 photons per CO_2 molecule. This mode of nutrition relies on the flux of photons and inorganic carbon to the cells being adequate to permit net photosynthesis to exceed losses caused by processes such as phytoplankton respiration, loss of dissolved organic carbon, sinking, grazing, parasitism and hydraulic removal.

Oxygenic photoautotrophy only occurs in cyanobacteria among extant prokaryotes, and was transferred to eukaryotes through endosymbiosis with genetic integration in the ancestor of the Archaeplastida around 1600 million years ago, and independently around 60–140 million years ago in the ancestor of the phototrophic rhizarian *Paulinella*. In inland waters, phytoplankton of the dominant members of the Archaeplastida are the chlorophyte and streptophyte green algae, although some red algae phytoplankton also exist. Secondary endosymbiosis of an excavate with a chlorophyte alga yielded photosynthetic Euglenophyceae, while secondary endosymbiosis involving one or more phagotrophic eukaryotes and (a) red algal endosymbiont(s) produced the basal photosynthetic Dinophyta, the Cryptophyta and the Ochrophyta, including the important inland water Bacillariophyceae and Chrysophyceae and Synurophyceae. These endosymbioses, with some horizontal gene transfer, yielded organisms with Form IB and Form ID ribulose bisphosphate carboxylase-oxygenase (Rubisco) and light-harvesting pigments. In inland water Dinophyta there have been losses of photoautotrophy, in some cases regained by tertiary endosymbiosis of cyanobacteria or eukaryotic algae.

Osmo-organotrophy involves the uptake of dissolved organic matter as a source of energy, carbon and other essential nutrients, and occurs in some inland water planktonic Chlorophyta, Dinophyta and Euglenophyta. Phylogenetic analysis, and the presence of variously reduced, non-photosynthetic, plastids, shows that this trophic mode is a derived condition among these algae. Osmo-organotrophs can grow in the dark or very low light and so can occur where obligately photoautotrophic algae cannot grow.

The phago-organotrophic mode of nutrition involves the ingestion and digestion of dead or living organic particles. It is very likely that a particle ingestion mechanism is ancestral in eukaryotic algae, having been involved in the endosymbiosis of a

cyanobacterium that became chloroplasts of the Archaeplastida and, by secondary and tertiary endosymbiosis, other algae. Phago-organotrophic nutrition occurs in freshwater Cryptophyta, Dinophyta and Euglenophyta.

Another organotrophic mode of nutrition in freshwater microalgae is parasitism; a freshwater dinoflagellate infecting fish is an ichthyoparasite. Whether the parasite can be considered as planktonic could be debated, but it at least has a planktonic dinospore phase in its life-cycle.

The first three trophic modes of freshwater plankton are not mutually exclusive: there are planktonic mixotrophs (mixoplankton) that combine two, or all three, trophic modes (Jones, 2000). In marine phytoplankton, mixotrophy is widespread (Flynn et al., 2019) and this is likely also to be the case for freshwater phytoplankton. Osmo-mixotrophs combine photoautotrophy with osmo-organotrophy. The mere capacity to take up and metabolize dissolved organic compounds does not necessarily mean that the cells can grow exclusively on dissolved organic carbon. Phago-mixotrophy combines photoautotrophy with phago-organotrophy. Constitutive phago-mixotrophy, i.e., with both the photoautotrophy and phago-organotrophy components encoded in the nuclear genome and, in part for photoautotrophy, the plastid genome occurs in the Chrysophyceae, Cryptophyta, Dinophyta and Euglenophyta. There are large variations in the fraction of the maximum possible growth rate that can be achieved relying on organic carbon, with Cryptophyta toward the photoautotrophic end of the spectrum and *Dinobryon* (Chrysophyceae) requiring light to perform phagotrophy, and many members of the Chrysophyceae at the phago-organotrophic end. An alternative mode of phago-mixotrophy involves kleptoplasty, i.e., retention of plastids from food items ingested by a phago-organotroph in a form that allows continued photosynthesis. Kleptoplasty is known from some freshwater dinoflagellates. Since most of the genes needed for plastid repair are encoded in the nucleus of the ingested phototroph, the longevity of the ingested plastid will be limited unless appropriate genes have been incorporated into the host genome from previous ingestion events, or retained from the current food item. This second alternative verges on a photosynthetic symbiosis, a form of constitutive phago-mixotrophy, e.g., in "dinotoms."

Mechanisms of inorganic and organic nutrient acquisition

Nutrients include the chemicals supplying essential elements and, for mixotrophs, energy, and also, in many cases, compounds such as vitamins that are mainly enzyme cofactors that the alga is unable to synthesize. Emphasis is placed here on the nutrients that contribute most to limitation of phytoplankton photosynthetic productivity and those that contribute to eutrophication and harmful algal or cyanobacterial blooms, with some consideration of chemo-organotrophy.

From a global biogeochemistry perspective, the ultimate growth rate-limiting element for photoautotrophic growth is phosphorus, however in the short term in particular locations other elements such as (combined) nitrogen, carbon, sulfur and trace elements may be limiting. Uptake involves nutrients crossing the lipoprotein plasma membrane. Ions, and neutral solutes with a molecular weight >50–100 kDa, have very limited permeability. Permeability is defined at the uncatalysed rate at which a solute crosses a unit area of membrane for a given driving force. The driving force is the concentration difference for neutral solutes, and, for ions such as many nutrients, the electrochemical potential difference involving both concentration difference and electrical potential difference that is inside-negative except in acidophiles. Catalysis involves transmembrane proteins that allow solute-specific energetically downhill flux of nutrients through channels or transporters, and energy-coupled flux of the solute. The energy for this process comes from energetically downhill flux of some other solute, or exergonic biochemical reactions. Maintaining the electrical potential difference across the plasma membrane involves active efflux of electrogenic H^+ and Na^+ by ATPases.

The concentration of the nutrient solutes containing carbon, nitrogen and phosphorus is low relative to the half-saturation value for the assimilating enzyme in the cell in many (relatively) anthropogenically uninfluenced inland water bodies or during blooms in more impacted waters as a result of high nutrient demands. For CO_2, where there is the possibility of diffusive entry through the lipid component of lipoprotein membranes, lack of saturation of the enzyme could be offset by increased content of the assimilatory enzyme Rubisco, although at a large cost in protein synthesis, given the low specific reaction rate of the enzyme. This is exacerbated by restriction on transport by aqueous diffusion boundary layers and, in eukaryotes, plastid chloroplast membranes. Some inland waters are naturally enriched in CO_2 relative to atmospheric equilibrium as a result of runoff from the catchment containing CO_2 from root respiration (Maberly et al., 2013) or in situ mineralization of organic carbon from terrestrial productivity. However, many eukaryotic phytoplankton organisms, and all cyanobacteria, have CO_2 concentrating mechanisms (CCMs). These catalyze the energized accumulation of CO_2 at the active site of Rubisco relative to the concentration in the medium. These generally involve active influx of HCO_3^- at one of the membranes between the medium and Rubisco in eukaryotes and at the plasma membrane of cyanobacteria, or CO_2 influx followed by energized conversion of CO_2 to HCO_3^- in cyanobacteria. In all these cases, carbonic anhydrase activity is essential to interconvert CO_2 and HCO_3^- rapidly at particular locations within the cell. Since CO_2 is the C species assimilated by Rubisco, there is a requirement for H^+ influx/OH^- efflux for internal acid-base regulation when HCO_3^- enters the cell.

Other inorganic solutes containing major nutrient elements bearing a negative charge are NO_3^-, $H_2PO_4^-/HPO_4^{2-}$ and SO_4^{2-}. The assimilation of NO_3^- and SO_4^{2-}, with carbohydrate from photosynthesis, produces an array of organic compounds that bearing a much smaller negative charge per element than do the nutrient anions plus OH^-, and charge balance and acid-base regulation requires influx of H^+ or efflux of OH^-. As well as their electrical charge, the low affinity for their anionic substrate of the assimilatory enzymes, and the low external concentrations in many inland waters, especially for NO_3^- and $H_2PO_4^-/HPO_4^{2-}$, mean that active influx is needed (Raven et al., 2008). Environment concentrations of NH_4^+ are often also low; as a cation the inside-negative electrical

potential difference across the plasma membrane favors entry. However, again based on the affinity of the assimilatory enzyme for its substrate, and the magnitude of the electrical potential difference across the plasmalemma, NH_4^+ entry frequently needs active transport. Since the products of final organic products of NH_4^+ assimilation have a slight negative charge per N, H^+ efflux/OH^- influx is needed for acid-base and charge balance. At high pH and NH_4^+ concentration there is sufficient external NH_3 to allow its unregulated diffusive entry, and toxicity.

The important signaling ion Ca^{2+} enters cells by specific channels, and active efflux involves a Ca^{2+} ATPase. Trace element transport in freshwater phytoplankton has been best investigated in the unicellular green alga *Chlamydomonas* for Cu^{2+}, Fe^{2+}, Mn^{2+} and Zn^{2+} (Blaby-Haas and Merchant, 2012). The inside-negative electrical potential difference across the plasma membrane provides a greater driving force for entry of doubly charged than singly charged cations. The cytosol concentration of these free ions is believed to be very low, for example because free Fe^{2+} and Mn^{2+} generate the very damaging hydroxyl radical by the Fenton reaction. An external Fe^{3+} reductase allows external Fe^{3+}, the dominant species of iron in oxic environments, to be acquired by cells.

For the entry of osmo-organotrophs and osmo-mixotrophs, organic solutes generally require active transport, e.g., H^+-glucose cotransport has been characterized in *Chlorella*. However, acetate entry seems to involve entry of undissociated acetic acid. There is growing evidence that organic forms of nitrogen and phosphorus are bioavailable to riverine phytoplankton (Mackay et al., 2020). This is an overlooked but potentially important source of nutrients since in some inland waters, concentrations of organic nutrients exceed that or inorganic nutrients. These nutrients may be taken up directly, e.g., active influx of amino acids in *Chlorella*, while others depend on the facultative production of exoenzymes such as acid or alkaline phosphatases allowing influx of phosphate derived for organic phosphate precursors, or rely on external metabolism by microbial consortia to produce inorganic ions. Some freshwater algae require exogenously supplied vitamins. In some cases the supply depends on close association of the algae with bacteria that produce the vitamin(s) while phago-mixotrophy can supply such vitamins directly.

Competition for nutrients

Phytoplankton growth is often constraint by nutrients, in oligotrophic systems with low nutrient loads as well as in eutrophic systems when phytoplankton biomass build-up is high and has stripped nutrients from the water (e.g., during blooms). In the latter case, light can also become a limiting resource due to self-shading. The outcome of resource competition depends on the balance between rates of growth and loss, and on resource acquisition traits. For nutrients, the concentration where growth rate equals the loss rate is referred to as Tilman's R^* (Fig. 1; Tilman, 1982), and reflects the overall competitive strength of a species for a given resource based on a number of physiological processes (Fig. 1A; Eq. (2); Litchman et al., 2015). Specifically, higher maximum growth and acquisition rates (μ_{max} and V_{max}), lower half-saturation concentrations ($K_{1/2}$), lower minimal cellular quota (Q_{min}), and lower loss rates (L) will lead to a stronger decrease in resource concentrations and thereby a lower R^*. The species with a lower R^* will be the better competitor for a particular resource as compared to species with a higher R^*, because under these resource levels growth rates of the weaker competitor becomes lower than the loss rates (Fig. 1B).

$$R^* = \frac{K_{1/2}\,\mu_{max}\,Q_{min}\,L}{V_{max}\,(\mu_{max} - L) - \mu_{max}\,Q_{min}\,L} \tag{2}$$

While R^* originally described competition for nutrients such as nitrogen, phosphorus and silicon, similar relationships have been produced for inorganic carbon and light (Ji et al., 2017). For some elements, including inorganic carbon and nitrogen,

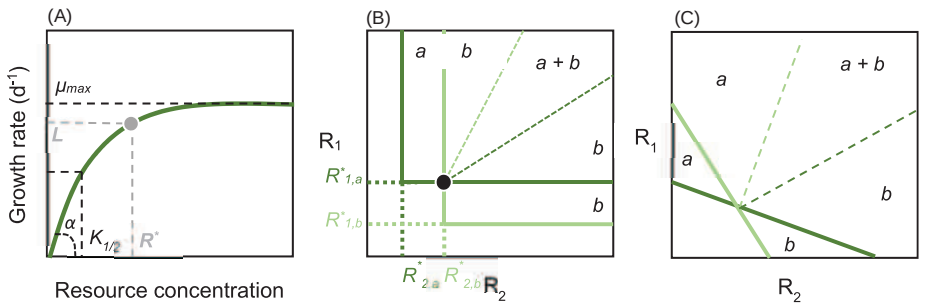

Fig. 1 Schematic overview on the coupling of physiological processes to resource competition. Growth (μ) depends on resources following a Monod function (sensu Michaelis-Menten enzyme kinetics), with maximum growth rates μ_{max} achieved under highest resource concentrations, and the half-saturation concentration $K_{1/2}$ of the limiting resource at half the maximum growth rate (A), and the affinity α as indicated by the initial slope (i.e., $\mu_{max}/K_{1/2}$). When inducing a fixed loss rate (*L*, gray dashed line), for example representing the dilution rate in a chemostat, the species will deplete resources until reaching a stable equilibrium (gray circle), where μ equals *L* at its respective R^* value. The R^* thus represents the concentration of a resource (i.e., R_1 or R_2) that allows zero net growth. When species *a* (dark green lines) and *b* (light green lines) exhibit different R^* values for different resources (B), their zero-net growth isoclines (i.e., lines where μ equals *L*) intersect. This can lead to a stable equilibrium when the better competitor for R_1 (species *b*) more rapidly takes up R_2, and vice versa, and is reflected by the ratio at which R_1 and R_2 are taken up (dashed vertical lines). For substitutable resources (C), the zero net growth isoclines intersect with the axes. In these cases, the outcome of competition depends on the slopes of the zero net growth isoclines in combination with the ratio at which R_1 and R_2 are taken up.

phytoplankton can compete for different chemical forms (i.e., CO_2 and HCO_3^-, or NO_3^-, NO_2^- and NH_4^+). While competition for these substitutable resources will also depend on the various physiological processes, including the ratio at which resources are taken up, there is no single R^* for each resource (Fig. 1C). Rather, competition depends on the ability of species to compete for either substitutable resource in the absence of the other (i.e., the points where the zero net growth isoclines cross the axes in Fig. 1C). The acquisition of one resource may also depend on the availability of other resources, which will change the trajectory of the zero net growth isoclines (i.e., to a non-linear relationship), with consequent shifts in the competitive outcomes. Moreover, the acquisition of nutrients such as N and P may be influenced by other factors, such as light, CO_2 concentrations and temperature, and thus also alter competitive outcomes (Van de Waal and Litchman, 2020).

Trade-offs are typically involved in nutrient acquisition by phytoplankton. For instance, fundamental catalytic constraints restrict processes with a high maximum rate from having a high affinity and vice versa. Small cells have a high surface area to volume ratio that maximizes uptake rate but limits the capacity to process and store nutrients. Limited space on the plasma membrane for transporters will produce trade-offs in the nutrients taken-up. Trade-offs within and among resource acquisition traits prevent dominance of a limited number of species, and can thereby mechanistically explain coexistence of multiple species under a limited set of resources. Moreover, species with differences in specific resource acquisition traits may exhibit comparable R^* values, and thus not be able to outcompete each other, thus following the neutral theory of biodiversity (Hubbell, 2001).

Alternative resource acquisition strategies such as N_2 fixation and mixotrophy increase the competitive ability of species for resources. The facultative ability of diazotrophic cyanobacteria to fix N_2 allows them to grow under combined nitrogen-deprived conditions, while phagotrophy and osmotrophy by mixoplankton allows growth under general resource deprived conditions (Flynn et al., 2019). When competing for inorganic resources, species with alternative resource acquisition strategies can maintain growth when the original resources are absent. They will thus be superior competitors under these conditions, provided that organic resources are available. Competition for inorganic resources is furthermore affected by direct species interactions, referred to as interference competition, such as the synthesis of allelochemicals that inhibit growth or cause increased mortality of competing species, as well as intraguild predation shown by some mixoplankton.

Nutrient acquisition traits (V_{max}, $K_{1/2}$, α), as well as nutrient demands (Q_{min}), depend on cell size, and competitive ability for resources therefore also will change with cell size. Due to their smaller surface area to volume ratio, larger phytoplankton can have a lower overall affinity for a resource and thereby decrease their competitive ability (i.e., increasing R^*; see also Eq. 1). At the same time, their larger cell volumes lead to higher minimum cellular quota, which will also reduce their competitive ability (i.e., increasing R^*; see also Eq. 1). Larger cells can contain more cellular machinery to acquire nutrients, such as pigments or food vacuoles, yet they are also hampered by stronger self-shading (i.e., package effect). Generally, smaller phytoplankton are found to be better competitors for inorganic resources, while larger phytoplankton have beneficial traits to acquire organic resources, experience lower grazing losses, and show higher plasticity toward changing environmental conditions (Van de Waal and Litchman, 2020).

Stoichiometric considerations

The overall elemental composition of phytoplankton is linked to the biochemicals within the cells and in the cell walls. For example, lipids are rich in carbon, proteins in nitrogen, and nucleotides contain relatively high amounts of nitrogen and, particularly, phosphorus while silicon is essential for diatom cell walls. The phytoplankton elemental composition thus reflects their biochemical make-up, and the relative balance of these elements (e.g., C:N, C:P, N:P and C:Si) can potentially be linked to dedicated functions (Geider and La Roche, 2002; Sterner and Elser, 2002).

The elemental stoichiometry of phytoplankton varies as phytoplankton acquire their nutrients through separate pathways, and because elements can be effectively stored in molecules such as carbohydrates, polypeptides, and polyphosphates. Such plasticity supports phytoplankton growth under resource deficient conditions as it reduces the minimum quota (Q_{min}; see section "Competition for nutrients"), while effective storage provides an extended supply of elements when a resource is temporarily limiting. Because phytoplankton species differ in their biochemical make-up, they can also exhibit a distinct elemental stoichiometry. The optimal N:P stoichiometry of phytoplankton has been defined as the ratio between minimum quota for N and P (i.e., $Q_{min,N}$: $Q_{min,P}$), reflecting the ratio where cells shift from N to P limitation (Klausmeier et al., 2004). Alternatively, the optimal ratio can be considered as the N:P ratio at μ_{max} under prevailing environmental conditions (Hillebrand et al., 2013). Following this latter approach, differences have been observed across phytoplankton phyla, with generally consistent lower optimal N:P ratios in diatoms and a tendency to higher N:P ratios in cyanobacteria and chlorophytes (Hillebrand et al., 2013).

Taxonomic differences in optimal N:P ratios are difficult to couple directly to distinct cellular structures of the phytoplankton phyla, except for higher N:P ratios in cyanobacteria which may reflect the ability of various species to fix N_2. When considering other elements, clear functional differences can be expected. Among the clearest examples are diatoms that require large amounts of Si for their silica frustules, and calcareous phytoplankton, mainly found in the ocean, that have higher demands for Ca to produce their calcite liths or plates that are involved in their cell wall structure. Moreover, phytoplankton superfamilies have distinct differences in their composition of various trace metals (see section "Mechanisms of inorganic and organic nutrient acquisition"). Regulation of trace metal composition also closely interacts with shifts in the composition of macroelements such as C, N and P (Twining and Baines, 2013). The whole suite of elemental changes is reflected by the ionome (i.e., the elemental composition of an organism), which reveals physiological shifts that are linked to overall cellular metabolism including the acquisition and assimilation of limiting and non-limiting resources (Jeyasingh et al., 2017).

Role of nutrients in controlling ecosystem structure and function

Nutrient concentrations in inland waters are a function of diffuse or point source inputs from the catchment, hydrological losses and exchange with the atmosphere, the sediment and the biota. Lakes can be divided into different trophic types based on their productivity, assessed primarily by the amount of phytoplankton, but also sometimes supported by secondary effects such as on light or oxygen concentrations (see below). Lakes are categorized into oligotrophic (or ultra-oligotrophic) for the least productive through mesotrophic and eutrophic to hypertrophic for the most productive. A widely-used classification uses a numerical "trophic state index" based on phytoplankton biomass (chlorophyll *a* concentration), Secchi disk depth and total phosphorus concentration as surrogates of productivity and stresses that productivity is a continuous gradient (Carlson, 1977). The natural gradient in lake trophic state from oligotrophic to eutrophic is controlled largely by the transfer of nutrients from the catchment to water. In addition, anthropogenic nutrient addition, caused primarily by diffuse leaching of fertilizers added to the catchment to boost production, and release of domestic, agricultural, and industrial waste often as point-sources, cause nutrient enrichment of inland waters. In contrast to lakes, there is not a widely-used trophic-state scheme for streams and rivers.

The dilute concentrations of major nutrients in many inland waters, especially in areas with low anthropogenic impact, results in widespread nutrient limitation of phytoplankton primary productivity and growth. Large-scale relationships between the availability of P and N and phytoplankton biomass, as the concentration of chlorophyll-*a*, were first established by Vollenweider (1968). This, along with pioneering work by David Schindler and his group on lakes in the Experimental Lakes Area of the Canadian Shield, where addition of phosphate to whole lakes, or parts of a lake, stimulated large phytoplankton populations (Schindler, 1977) helped to establish the importance of P as a potentially limiting nutrient. More recently, N has been more fully recognized as a co-limiting or solely limiting nutrient in inland waters and other environments (Elser et al., 2007). An analysis of a dataset of over 1000 European lakes showed the effects of both P and N in supporting phytoplankton populations, partly because they tend to co-vary and also because the phytoplankton themselves contribute to the total nutrient concentrations (Fig. 2; Phillips et al., 2008).

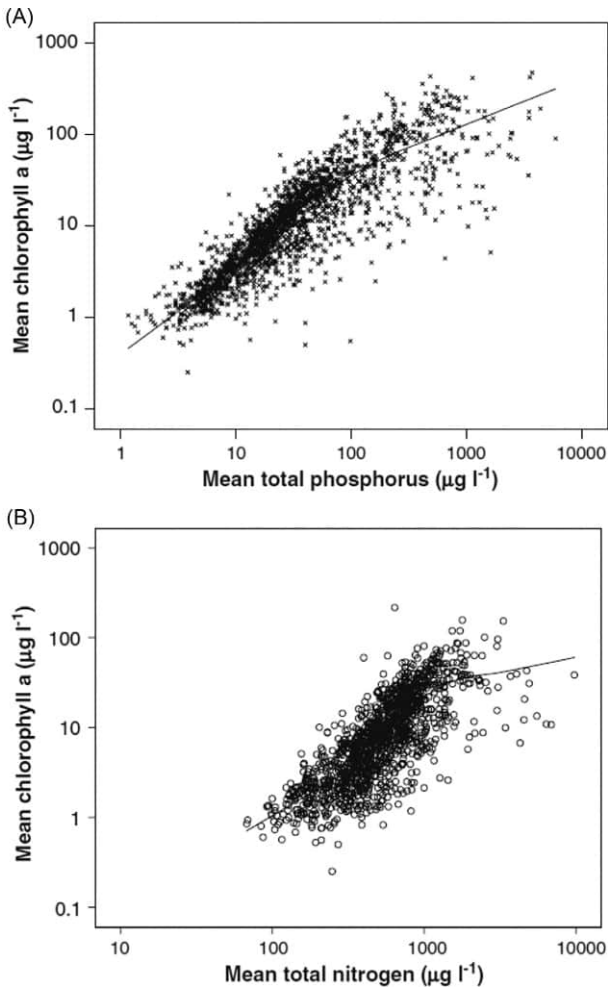

Fig. 2 Relationship between growing season chlorophyll-a concentration and (A) total phosphorus concentration and (B) total nitrogen concentration. The solid line is the LOESS fitted curve (Phillips et al. 2008).

They also showed that at high nutrient concentrations, increases in nutrient no longer increased phytoplankton populations, presumably because the nutrient is no longer limiting, and that deep lakes generate less phytoplankton chlorophyll-*a* per unit nutrient than other lakes which is likely to be caused by greater light limitation. Interestingly, there is evidence that anthropogenically-driven atmospheric deposition of N has pushed phytoplankton away from native N limitation toward P limitation (Bergstrom and Jansson, 2006).

The ecology of naturally eutrophic or anthropogenically eutrophic (cultural eutrophication) lakes is very different from oligotrophic lakes. Decomposition of the larger amount of organic material that is produced can often lead to oxygen-depletion at depth during seasonal stratification (Foley et al., 2012). This has important consequences for re-release of P (and N) from the sediment to the overlying water with the obvious risk of causing further eutrophication. At the same time, oxygen-depletion may promote denitrification, causing dissolved N concentrations to decrease by loss of N_2 to the atmosphere, and which may lead to seasonal N limitation. Oxygen depletion also restricts the distribution of other forms of life and can limit depth-refuges from warming surface water and can cause fish-kills. The higher phytoplankton biomass intercepts more light in the surface water, increasing surface warming and strengthening stratification and reducing the penetration of light to depth and consequently reducing the maximum depth of rooted higher plants. More widely, the competitive balance between the two main types of photoautotrophs, phytoplankton and higher plants, is pushed toward phytoplankton as nutrient availability increases with the potential to switch from a clear water, plant-dominated state to a turbid, phytoplankton-, dominated state (Janssen et al., 2021; Scheffer et al., 1993).

The species composition of the phytoplankton community is affected by nutrient availability (Reynolds et al., 2002). A common symptom of nutrient enrichment is the summer-dominance by cyanobacteria (also referred to as blue-green algae), many of which have the facultative ability to produce a range of toxins, primarily neurotoxins and hepatotoxins (Svirčev et al., 2019) and can form "scums" at the water surface (Fig. 3). Green algae (chlorophytes) also often benefit from nutrient enrichment while cryptophytes and chrysophytes are often reduced.

Cultural eutrophication is widespread and is probably the greatest cause of anthropogenic change to inland waters worldwide (Carpenter et al., 2011). Many mitigation measures have been implemented, although often with relatively modest success (Søndergaard et al., 2007) and have focussed more on P than N. These include reducing nutrient loads to the inland waters from point sources, use of buffer strips adjacent to water to reduce diffusive nutrient input from fields, and reducing fertilizer application to fields. A second approach applies agents to the water to bind P chemically, reduce its release from anoxic sediments and to kill phytoplankton directly. A third approach, more applicable in reservoirs than natural lakes, alternately de-stratifies the water and

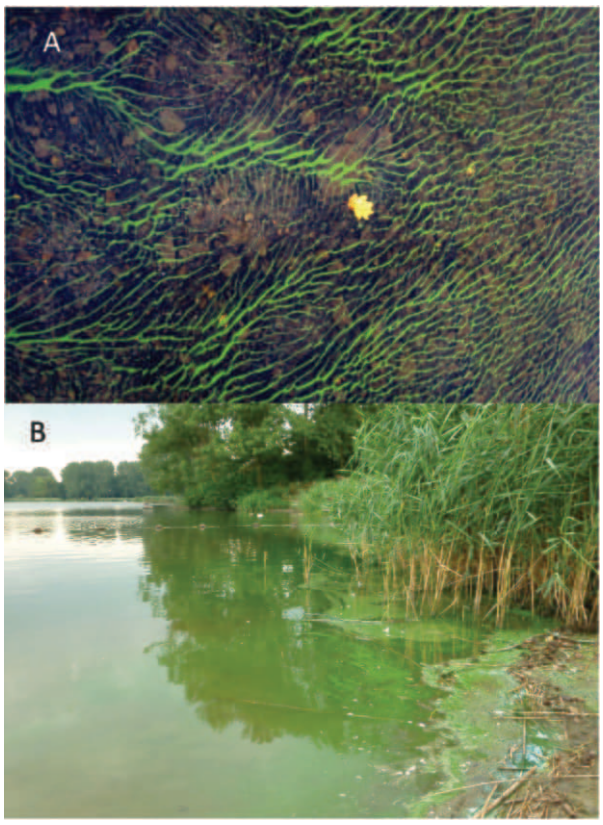

Fig. 3 Cyanobacterial blooms. (A) Cyanobacteria blooming under ice in Loweswater, UK. (B) Cyanobacterial bloom at "De Grote Plas," The Netherland. (A) Photo courtesy of Prof John Macfarlane. (B) Photo courtesy of Dedmar van de Waal.

allows stratification to form so that neither species that favor stratified nor unstratified conditions can produce large populations. A fourth approach promotes the density of zooplankton by manipulating the food-web to reduce the population of planktivorous fish (Søndergaard et al., 2007). Nevertheless, there is some evidence for reduction in nutrient loads as a result of mitigation actions and reversal of eutrophication effects at some lakes (Jeppesen et al., 2005).

Problems caused by nutrient enrichment are exacerbated by multiple stressors, particularly climate change (Moss et al., 2011). Since climate change is a global problem that cannot be solved locally, reduced nutrient loading to inland waters will need to be increased even further to mitigate the adverse effects of cultural eutrophication. This exposes a potential tension between water and food security that is yet to be resolved. A largely unknown aspect is the extent to which dissolved organic forms of P and N can substitute for inorganic nutrients and support phytoplankton populations in natural conditions.

Conclusion/Synthesis

Freshwater phytoplankton extract a large range of essential elements from often low concentrations in water. The stoichiometric requirements for different elements are broadly similar but vary among different phylogenetic groups. Phytoplankton exploit inorganic chemicals, dissolved organic compounds and organic particles to satisfy their nutrient and energy requirements, often involving mechanisms that require energy. Nutrient availability often limits the productivity and biomass of phytoplankton in inland waters. Species with superior kinetic uptake characteristics, diverse sources of supply, high storage capacity and low rates of loss will tend to outcompete other species. Human activity has caused a widespread increase in the supply of nutrients to inland waters. This "cultural eutrophication" has increased productivity and phytoplankton biomass, with a consequent cascade of secondary effects that frequently reduce the value and availability of water resources to mankind.

Knowledge gaps

1. The availability and ecological role of organic forms of nutrients.
2. Mechanisms of acquisition and assimilation of nutrients in a wider range of phytoplankton taxa.
3. Studies of uptake and assimilation of nutrients at the transcriptomic and proteomic level.
4. How interaction among environmental factors affect nutrient uptake and competition.
5. The role of mixotrophy in affecting competitive interactions
6. The role of trace elements in controlling phytoplankton productivity and diversity.

See Also: **Emerging methods and topics**: Dust and Fog Effects on Inland Waters; **Fundamental concepts and theories**: Comparative Primary Production; **Human pressures and management of Inland Waters**: Agricultural Pressures on Inland Waters; The Role of Wetlands in Mitigating Impacts From Diffuse Agricultural Loads; **Structures and functions of Inland Waters - Lakes**: Benthic Algae in Lake Littoral Habitats; Currents in Stratified Water Bodies: Internal Waves; Measurement and Variability of Lake Metabolism; Phytoplankton Productivity; **Structures and functions of Inland Waters - Rivers**: Algae and Primary Production of Streams and Rivers Ecosystems; **Structures and functions of Inland Waters - Wetlands**: Wetland Soils: Physical and Chemical Properties and Biogeochemical Processes

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Relevant websites

https://www.algaebase.org/about/—AlgaeBase
https://www.ceh.ac.uk/services/lake-ecosystem-models-assessing-phytoplankton—PROTECH model/Phytoplankton responses to environmental change.

Phytoplankton Productivity

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This is an update of M.T. Dokulil, C. Kaiblinger, Phytoplankton Productivity, In Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00140-X.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie-Elodie Perga and Damien Bouffard.

Nomenclature

E_k	Light-saturation parameter ($E_k = P_m/\alpha$)
F_0	Fluorescence at a baseline value
F_m	Maximum fluorescence when all traps are closed
F_V	Variable fluorescence
GPP	Gross primary productivity (production)
NPP	Net primary productivity (production)
NPQ	Nonphotochemical quenching. Defined as a mechanism to protect from the adverse effects of high light intensity
optical depth	One-unit O.D. is equal to a halving of light intensity
P/E	Photosynthesis (production) versus energy (light) curve
PAR	Photosynthetic active radiation (typically 400–700 nm)
PET	Photosynthetic electron transfer
P_G	Gross photosynthesis
P_m	Production at light saturation level at which photon absorption exceeds steady state electron transport
P_N	Net photosynthesis
PQ	Photosynthetic quotient (volume O_2 released in photosynthesis as a proportion of the volume of CO_2 used in that process)
PSI	Photosynthetic unit I
PSII	Photosynthetic unit II
PSU	Photosynthetic unit
qP	Photochemical quenching (decrease of fluorescence reflecting photosynthetic activities)
R_C	Community respiration
R_P	Respiratory loss
z_c	Compensation depth (the depth where daily GPP = R_P per day)

z_{cr}	Critical depth (depth where daily integral NPP = integral R_P per day)
z_{eu}	Euphotic zone (equal to the depth of 1% light intensity)
z_{mix}	Mixing depth (water column which is mixed by wind)
α^*	Chlorophyll-a specific light absorption (production per unit chlorophyll-a)
$\sigma_{(\lambda)}$	Optical absorption cross section calculated from $\frac{2.3 - \left(Ln\frac{E_\lambda}{E_{0\lambda}}\right)}{Chl-a}$ and σ^* integrated over PAR, with E_λ is transmitted irradiance for wavelength, $E_{0\lambda}$ is incident irradiance and Chl-a is the chlorophyll-a concentration, all per unit area
σPSII	Functional absorption cross section (Dimension: area per unit of compound), Defined as the in vivo cross section of the light harvesting system absorbing photons by wavelength dependent probability
Φ_m	Maximum quantum yield (maximum of an event per photon absorbed by the system)

Introduction

This chapter intends to provide a theoretical and practical introductory fundament for the understanding of phytoplankton primary production in freshwater by students, novices in the field, practitioners and any interested person. Text and associated graphs highlight concepts, measurements techniques, models and physiology of plankton photosynthesis. Additional information on the production ecology of other autotrophic producers in freshwaters can be gained from "Comparative primary production."

Concepts related to production

Production of new organic matter from inorganic nutrients using sunlight as energy source, known as photosynthesis, is an essential prerequisite for life on earth. The organsims carrying out photosynthetic processes to build cellular material are therefore called autotrophs. Marine and freshwater algae contribute about half of annual primary productivity on the planet. Clarifying the processes contributing to the drawdown of inorganic carbon (CO_2) is crucial for understanding carbon cycling and functioning of global ecosystems.

In its early phase, studies on the energy flow through aquatic systems revealed by estimates of primary productivity largely rested on the ecosystem concept (Goldman, 1968). The 50 year aniversary of invention of the radioactive carbon-14 method triggered a new interest in productivity measurements (Williams et al., 2002), boosting techniques (Fahey and Knapp, 2007) and concepts (e.g. Falkowski, 2012). New concepts were developed such as the "active pipe" concept for the global quantification (Tranvik et al., 2018), nutrient stoichiometry (Maranger et al., 2018) and integrative understanding (Hotchkiss et al., 2018; Seekell et al., 2018) of carbon metabolism. Advancements in carbon acquisition and concentrating mechanisms have been reviewed by Griffiths et al. (2017). Dokulil and Qian (2020) provide an article reviewing the history of photosynthesis, carbon acquisition and primary productivity.

Photosynthesis in algae

All autotrophic oxygenic organisms carrying the pigment chlorophyll-a, both prokaryotes and eukaryotes, share the same fundamental reaction equation of photosynthesis using light as energy source:

$$2H_2O + CO_2 + \text{Light} \overset{\text{Chl-a}}{\rightarrow} (CH_2O) + H_2O + O_2 \quad (1)$$

In this equation, chlorophyll-a catalyzes a reaction, or a series of reactions whereby light energy is used to oxidize water producing molecular oxygen:

$$2H_2O + \text{Light} \overset{\text{Chl-a}}{\rightarrow} 4H^+ + 4e + O_2 \quad (2)$$

This partial reaction starting with light absorption is one of the two core reactions in oxygenic photosynthesis. The second reaction is the reduction of CO_2 which can proceed in darkness as well as in light and can be described as

$$CO_2 + 4H^+ + 4e^- \rightarrow CH_2O + H_2O \quad (3)$$

These two reactions require an intermediate reducing compound (not shown here) because free electrons normally do not occur in biological systems (Falkowski and Raven, 2007).

Impinging light is processed in two photosynthetic reaction centers (RCs) by two electron acceptors: a quinone, in type II, and an Iron-Sulphur cluster in type I. These two RC-types called Photosystem II (PSII) and Photosystem I (PSI), work in tandem, produce oxygen and lead to linear electron transport, delivering electrons to carbon dioxide fixation and other mechanisms. The common

basic photosynthetic equation (1) shown above has gained complexity during algal evolution in terms of photosynthetic structures, pigments, and metabolic differences to cope with a multitude of light climates and ecological niches (Falkowski et al., 2004).

While photosynthetic structures in cyanobacteria are internal membranes called thylakoids, all algal phyla have specialized organelles, called plastids or chloroplasts which themselves contain thylakoids. Primary plastids were most likely acquired from primary cyanobacterial endosymbiosis by the Glaucophyta (glaucophyte algae), the Rhodophyta (red algae), and the green algae. These linages share a two-membrane bound photosynthetic plastid organelle (Table 1; Bellinger and Sigee, 2010). After primary plastids were established in ancestors, they disseminated into other phyla such as Bacillariophyta (diatoms), dinoflagellates, cryptophytes, haptophytes and euglenophytes through multiple secondary and tertiary endosymbiosis. These divisions have plastids surrounded by 3–4 membranes and have 1–2 flagella, at least in reproductive cells (Table 1).

Photosynthetic organisms are frequently exposed to changes in light quality and quantity to which they have to acclimate or even adapt. They need to collect light energy efficiently particularly when light is limiting. Consequently, different algal divisions have distinctive accessory pigmentation in terms of chlorophyll and carotenoid species (Table 1). In case the capability of the photosynthetic apparatus is exceeded, organisms must also be able to dissipate light energy absorbed in excess.

Light harvesting

Photosynthesis begins with photo-absorption by pigments located in the thylakoid membranes. The only pigment present in all oxygen producing phytoplankton is chlorophyll-a and it is the essential pigment required for photosynthesis. Most light absorption, however, is due to accessory pigments such as other chlorophyll species and carotenoids as well as phycobilinproteins which are found in Cyanobacteria, Glaucophyta, red algae and Cryptophyta. Major differences in pigment composition among higher taxonomic groups can significantly affect the ability of phytoplankton to absorb light (Table 1). Chlorophyll-a specific light absorption is not only affected by the pigment complement, but also by cell size and intracellular pigment concentration.

Photosynthetic electron transfer (PET), located in large membrane complexes harboring Photosystem I (PSI) and Photosystem II (PSII), allows considerable versatility in electron flow to match varying requirements of nutrient transport, photo- and biosynthesis. The ratio of the two photosystems remains ambiguous because of the variability among algal divisions and environmental conditions. In Heterokontophyta the ratio can exceed 2, whereas in Cyanobacteria it is typically 0.25–0.5. The ratio can also change with growth, irradiance, or nitrogen starvation (Larkum, 2016).

Carbon reduction

Net carbon fixation in photosynthesis involves a cycle of reductions, referred to as the Calvin-cycle, in the plastids of algal cells or in the cytoplasm of Cyanobacteria. At the heart of this cycle is the carboxylation of ribulose 1,5-biphosphate (RuBP) catalyzed by the enzyme RUBISCO, a monophyletic enzyme existing in two forms. The Form I enzyme is found in cyanobacteria and all eukaryotes, except for some peridinin-containing Dinophyta which contain the Form II enzyme. The activity of the enzyme is low compared to other carboxylases. RUBISCO accounts for a sizeable fraction of the cell (1–10% of cell carbon or about 2–10% of total protein), with the amount dependent on ambient light conditions. Under high irradiance, RUBISCO can account for up to five times as much cell mass as chlorophyll-a (Raven et al., 2012; Bracher et al., 2017).

Table 1 Algal divisions (phyla): Pigmentation, origin of chloroplasts by endosymbiosis, fine structure of chloroplasts and flagella in vegetative cells and gametes (reproductive cells = rep. cells). Isokont—equal length, heterokont—unequal length.

Phylum	*Pigmentation*		*Endosymbiont*	*Chloroplast fine structure*		*Flagella*
	Chlorophylls	*Carotenoids*		*Membrans*	*Thylakoids*	
Cyanobacteria	a	β	–	0	0	0
Rhodophyta	a, d	α, β	Cyano 1°	2	0	0
Glaucophyta	a		Cyano 1°	2	0	0
Chlorophyta	a, b	α, β, γ	Cyano 1°	2	2–6	0-many isokont
Euglenophyta	a, b	β, γ	Chloro 2nd	3	3	1–2 emergent
Dinophyta	a, c_2	β	Rhodo 2nd–3rd	3	3	2 heterokont
Cryptophyta	a, c_2	α, β	Rhodo 2nd	4	2	2 isokont
Xanthophyta	a, c_1, c_2	α, β	Rhodo 2nd	4	3	2 heterokont
Chrysophyta	a, c_1, c_2, c_3	α, β, ε	Rhodo 2nd	4	3	2 heterokont
Paeophyta	a, c_1, c_2, c_3	β, ε	Rhodo 2nd	4	3	2 hetero -rep. Cell
Bacillariophyta	a, c_1, c_2, c_3	β, ε	Rhodo 2nd	4	4	1 -rep. Cell

Modified and combined from Bellinger, E.G., Sigee, D.C., 2010. Freshwater algae: identification and use as bioindicators. John Wiley & Sons, Chichester. ISBN 978-0-470-05814-5 (Table 3.1) and Larkum, A.W.D., Grossmann, A.R., Raven, J.A. (Eds.), 2020. Photosynthesis in Algae: Biochemical and physiological mechanisms. Advances in Photosynthesis and Respiration including Bioenergy and Related Processes 45, Springer Nature Switzerland AG, Cham. https://doi.org/10.1007/978-3-030-33397-3.

Understanding the role of RUBISCO in phytoplankton ecophysiology is essential to determine whether RUBISCO or PET limit light-saturated photosynthesis and to estimate the concentration of CO_2 needed to support a specific photosynthetic rate. This has implications for assessing the inhibition of carbon fixation by oxygen and the role of a CO_2-concentrating mechanism. Activity of the enzyme is regulated in vivo by a multitude of mechanisms and external factors best studied in chlorophytes and Cyanobacteria. Under low light and/or low CO_2, RuBP is saturating and the rate of CO_2 fixation is limited by RUBISCO activity. However, under conditions of high light and/or high CO_2, carbon fixation is limited by the regeneration of RuBP, a process known as sink limitation.

Photorespiration

Photorespiration is the oxygenation of RuBP by RUBISCO followed by photorespiratory glycolate metabolism. Competition between O_2 and CO_2 reduces the rate of carbon assimilation, energetic efficiency of photosynthesis, and may reduce the photosynthetic quotient (PQ = O_2 produced/CO_2 assimilated). Values of PQ of 1.2–1.8 are representative for protein and lipid synthesis. Values of PQ as low as 0.75 can be obtained from photorespiration and glycolate excretion at the CO_2 compensation point where CO_2.uptake equals CO_2 evolution. PQ values below 0.75 can only be explained if unbalanced growth conditions where respiration contributes to net gas exchange are considered.

Evidence that photorespiration influences net photosynthesis and is linked to photoinhibition stems from the effect of oxygen concentration on the rate of ^{14}C assimilation. The observed reduction in particulate ^{14}C is accompanied by an increase of excreted dissolved organic carbon (Hagemann and Bauwe, 2016).

Carbon-concentrating mechanisms (CCM)

Most of the understanding of the biophysical CCM is based on studies of Cyanobacteria and chlorophytes. Bacillariophyceae and peridinin-containing dinophytes have less efficient CCM. Direct evidence for a CCM comes from intracellular CO_2 levels exceeding those in the suspending medium. The CCM is associated with the carboxysomes, microcompartments in Cyanobacteria; in chlorophytes and other eukaryotes it is associated with pyrenoids containing highly varying amounts of RUBISCO.

Estimation of what fraction of the global net primary production is mediated by pyrenoid-possessing algae and what fraction derives from pyrenoid-less eukaryotic algae and cyanobacteria requires knowledge of species abundance. The figure of one quarter to one third of global carbon fixation being mediated by pyrenoid-possessing families has been proposed but there are still unsolved questions (Mackinder et al., 2016; Meyer et al., 2017).

An alternative to biophysical CCM is C_4 photosynthesis, still a controversial issue in algae. The confusion over C_4 metabolism arises because the enzymes present in C_4 photosynthesis are present in algae as well. These enzymes are present in different algal groups in different amounts and are not sensitive to oxygen like the Calvin cycle enzyme RuBP. The best cases so far have been reported for two marine organisms.

Other pathways for C-acquisition

Besides the Calvin cycle, carbon may also be gained via two other pathways, β-carboxylation and mixotrophy. Carboxylation occurs in the dark and does not generally result in a net increase in carbon fixation. Alternatively, carbon can be acquired through mixotrophy. Several algal groups have been shown to be facultatively mixotrophic, heterotrophic, or may utilize dissolved organic compounds osmotrophically. The substitution of autotrophy and the regulation of mixotrophy are not well understood (Beardall and Raven, 2016). See chapter by Raven/Maberly.

More detailed insights into recent advances in the complex photosynthesis of Cyanobacteria and eukaryotic algae, recent discoveries in pigmentation, and the differentiations among algal divisions provide Borowitzka et al. (2016), Pessarakli (2016) and Larkum et al. (2020).

Response of phytoplankton productivity to environmental variability

Instantaneous rates of photosynthesis are controlled by external factors. Understanding how the environment influences chlorophyll-a specific light absorption (α^*), the ratio Chl-a:C and the parameters of the P/E curve are essential to evaluate, model, and predict primary productivity. The rate of photosynthesis is controlled by the efficiency of light utilization to drive the ensemble of photosynthetic reactions. As a first approach, the light dependency can be described as:

$$P_E = E_a \, \Phi_E \tag{4}$$

where P_E is the photosynthetic rate at incident irradiance E, E_a is the light absorbed by the organism (in quanta m^{-2} $time^{-1}$), and Φ_E is the quantum yield at irradiance E (moles O_2 produced or C fixed per moles photons absorbed). The absorbed light is calculated from incident spectral irradiance $E_{0(\lambda)}$ and averaged optical absorption cross section σ^*:

$$E_a = E_{0(\lambda)}\ \sigma^* \tag{5}$$

(for description and units of σ^* refer to the section on abbreviations and definitions above).

The *photosynthesis-irradiance response* (P/*E*-curves) is commonly obtained from oxygen or carbon based rates per hour normalized to chlorophyll-a (α^*), versus irradiance E. Typically three distinct regions, namely a light-limited region, a light saturated region, and a region of photoinhibition can be distinguished (Fig. 3). Photosynthetic rates are linearly proportional to irradiance at low light levels because the rate of photon absorption determines the rate of steady-state electron transport from water to CO_2. The initial slope of this light limited region is commonly denoted by the symbol α or α^B when normalized to chlorophyll-a. This initial slope of the P/E curve is not a photosynthetic rate; rather it is a time independent measure of efficiency indirectly related to the maximum quantum yield Φ_m.

As irradiance further rises, photosynthetic rates become increasingly nonlinear and approach a saturation level P_m at which photon absorption exceeds the steady state electron transport. Light saturated photosynthesis is explicitly time dependent with dimensions of O_2 production or CO_2 fixed per unit chlorophyll per unit time. The curvature can be described by the light-saturation parameter E_k which is never actually directly measured; rather it is derived from the intersection of α and P_m (Fig. 3):

$$E_k = P_m/\alpha \tag{6}$$

At supra-optimal irradiance beyond light saturation a reduction in photosynthetic rate may occur. This reduction is dependent on intensity of the light and the duration of exposure and is called photoinhibition. This modification of P_m is brought about by either a reduction in the number of photosynthetic units or by an increase in the maximum turnover time. The degree of inhibition can be estimated from the parameter β which is derived similarly to α from the P/E curve (Fig. 3). Corresponding to E_K, a light intensity E_I can be inferred describing the onset of inhibition. Several further light intensities can be deduced from P/E curves as indicated in the caption to Fig. 3. Most notable is the compensation irradiance (E_C) when net gas exchange becomes zero because respiration equals gross primary productivity (GPP). The compensation irradiance can be related to α^{Chl} and chlorophyll normalized respiration:

$$E_C = R^{Chl}/\alpha^{Chl} \tag{7}$$

The irradiance at the compensation point is not fixed but varies primarily with respiration and to a lesser extent with α^{Chl}, both of which depend on environmental conditions.

Physiological acclimation of the P/E curve α^{Chl} appears to follow several simple rules under conditions of balanced growth. As a first approximation α^{Chl} can be considered constant, with changes to the carbon-specific light saturated rate (P_m^C) inducing changes in the ratio Chl-a:C. At constant temperature and when cells are nutrient-replete, maximum carbon specific rate is largely independent of irradiance, but is highly correlated with maximum specific growth rate μ_m and temperature because temperature affects enzymatic reactions. The light saturated rate often is also determined by CO_2 availability.

Several empirical mathematical descriptions of the photosynthesis—light response curve P/E exist. The various formulations mainly differ in the abruptness of the transition from light-limited to light saturated photosynthesis. Some models include photoinhibition.

One simple mechanistic interpretation using the terms and notations mentioned above is the exponential function:

$$P^{Chl} = {P_m}^{Chl}\left[1 - \exp\left(-\alpha^{Chl}\, E/{P_m}^{Chl}\right)\right] \tag{8}$$

Defining productivity

Ecologists favor the term phytoplankton productivity although what is usually measured are photosynthetic rates. Moreover, the term productivity is frequently confused with production. It has therefore been argued to abandon one of the two terms or to replace it by activity. Strictly speaking, there is a clear difference. *Productivity* is a time dependent process; it is a rate with dimensions of mass per unit area or volume per time. *Production* is a quantity, with dimensions of mass.

Biological processes perceive and adjust to changes in the external environment. Many regulatory processes occur rapidly to allow photosynthesis to track instantaneously changes in the surrounding medium (Fig. 1). In nature, photosynthetic processes are therefore constantly modified. Regulation describes adjustments of catalytic or energetic efficiency which involve slight structural modifications. Physical, biochemical or physiological response on a short time scale, within the life span of individual organisms or assemblages, are collectively called acclimations which are nonlinearly related to temporal variations in irradiance, temperature and nutrients. Ecological or evolutionary adaptations by assemblages through selection of phenotypic traits occur on a longer time scale. Associated changes in community structure affect photosynthetic rates.

Terminology

Conceptually, photosynthesis or productivity is defined as an instantaneous rate of biomass change over time (dB/dt) over infinite time intervals which cannot be measured. Typically, integral rates over time are obtained. Estimation by fluorescence techniques however comes closest to instantaneous rates.

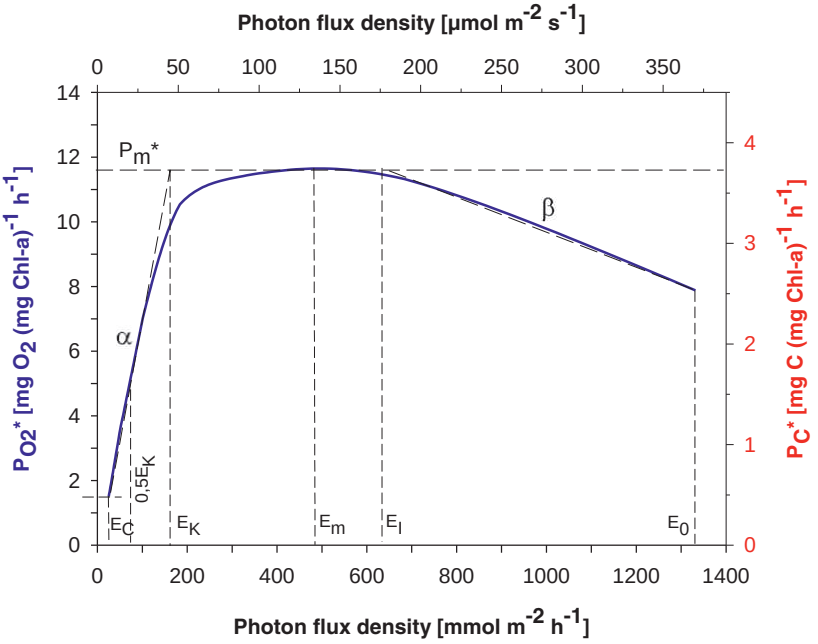

Fig. 1 Example of a photosynthesis-irradiance response curve (P/E) expressed both as chlorophyll specific oxygen evolution (P^*_{02}, left Y-axis) and carbon uptake (P^*_C, right Y-axis) versus photon flux density. The two axes are shifted by PQ = 1.16. P^*_m = Maximum chlorophyll-specific rate of photosynthesis; α = slope of the light limited region; β = slope of the region of photoinhibition; E_0 = subsurface photosynthetic active radiation (PAR); E_I = photon flux density at onset of inhibition; E_m = photon flux at P^*_m, E_K = photon flux density at the onset of saturation; $0.5E_K$ = 50% of E_K used in certain types of column integration calculation; E_C = Photon flux density at the compensation point.

Gross photosynthesis (P_G) is defined as the light dependent rate of electron flow from water to the terminal electron acceptors (e.g. CO_2) in the absence of any respiration losses. This process is directly proportional to linear photosynthetic electron transport and hence, gross oxygen evolution. Therefore, gross photosynthesis should be defined based on oxygen production rather than carbon fixation. This distinction is essential, especially when photorespiration is high. *Respiratory losses* (R_P) in photosynthetic organisms are rates of electron flow from organic carbon to O_2 with the concomitant production of CO_2, including photorespiration. The difference of these two processes is called *Net Photosynthesis* (P_N):

$$P_N = P_G - R_P. \tag{9}$$

Gross primary production is identical to gross photosynthesis. Net primary production, however, denotes organic carbon produced by photosynthetic processes within a specified time period available to other trophic levels.

In natural aquatic environments, direct measurements of primary production are virtually impossible to obtain because it is difficult to determine the contribution of algal respiration to total respiratory losses. Measurements of respiration include the metabolic contribution of heterotrophs, and therefore reflect *Community Respiration* (R_c). In fact, net primary production values, when reported, are usually confused with net photosynthesis.

Estimating photosynthesis in aquatic ecosystems

According to Eq. (2), measurements of photosynthetic rates for autotrophic plankton organisms in aquatic ecosystems are usually based on rates of either *oxygen production* or *inorganic carbon uptake*. Various modifications and alternatives of the basic techniques exist. In addition, fluorescence and remote sensing techniques became increasingly important. Measurements are performed either as in situ incubation or as simulations in the laboratory. A variety of mathematical models describe photosynthetic rates in space and time and their acclimation to environmental conditions.

The O_2-technique (Gaarder and Gran, 1927)

The rate of oxygen evolution is usually quantified from chemical, electro-chemical or opto-chemical methods. Because absolute changes in oxygen concentration are usually small and the background concentration of the gas in most situations is very large, precise data are relatively difficult to obtain. Moreover, even if done precisely, evolution of oxygen in the light represents net community photosynthesis, and fluxes of oxygen in the light and dark include total community respiration. Adding dark respiratory

losses to light dependent oxygen evolution gives a measure of gross photosynthesis. Estimates of net photosynthesis in natural aquatic ecosystems based on measurements of oxygen fluxes are more uncertain than measurements of gross photosynthesis.

Recent advances in sensor techniques allow high frequency estimation of oxygen profiles. The acquired data can be used to estimate metabolism (net ecosystem production) from free water oxygen changes (Staehr et al., 2010, 2016; Obrador et al., 2014). This method is based on the seminal paper by Odum (1956) estimating dissolved oxygen changes in free water basically from.

$$\Delta O_2/\Delta t = GPP - R - F - A \tag{10}$$

with $\Delta O_2/\Delta t$ the change in dissolved oxygen concentration, GPP gross primary production, R ecosystem respiration, F exchange of O_2 with the atmosphere, and A all other processes leading to changes in oxygen.

The technique can equally well be used for both lakes and streams (Izagirre et al., 2007; Demars et al., 2015) and may be combined with estimates from a similar diel CO_2 technique (Peeters et al., 2016). Hoellein et al. (2013) provide a synthesis of metabolic results from various ecosystems. The complex calculations necessary to obtain reasonable results can be facilitated using Lake Metabolizer in R (Winslow et al., 2016).

The ^{14}C-method (Steemann Nielsen, 1952)

For more than half a century, the method most commonly used was based on the rate of incorporation of radioactive ^{14}C in the form of inorganic carbon into acid-stable (usually particulate) organic carbon. Assuming that over some finite time period, the change in concentration of total dissolved inorganic carbon in the bulk water is small relative to the photosynthetic rate of the cells, and the addition of a small amount of radioactively labeled inorganic carbon does not perturb the concentration of the dissolved inorganic carbon, then the rate of incorporation of radioactivity into organic material obeys the rules of tracer analysis. These conditions are met in many environments, but care must be taken in freshwaters having low total concentrations of inorganic carbon.

The rational for the ^{14}C-based tracer method is that the light-dependent rate of incorporation of the radioactively labeled carbon into organic material is quantitatively proportional to the rate of incorporation of nonradioactive inorganic carbon

$$^{12}C_{uptake} : {}^{12}C_{available} = {}^{14}C_{uptake} : {}^{14}C_{available} \tag{11}$$

From Eq. (12) follows that carbon uptake is

$$^{12}C_{uptake} = \left({}^{14}C_{uptake}/{}^{14}C_{available}\right) x\, {}^{12}C_{available} \tag{12}$$

Because ^{14}C is heavier than the stable natural isotope ^{12}C, there is an isotopic discrimination of about 5% against the radioactive isotope during carbon fixation which is accounted for by a factor of 1.05. More recently, tracer-based techniques substituted the use of the radioactive isotope (which incorporation was measured by liquid scintillation counting) by a stable isotope tracer (^{13}C), which incorporation is measured by isotope-ratio mass spectrometry. The basics of the techniques however remain similar.

Over short periods of time, before a significant fraction of organic carbon becomes labeled, the method gives a reasonable estimate of gross photosynthetic rates. As the exposure time continues, the organic carbon pool becomes increasingly labeled, ultimately reaching equilibrium with the isotope in the bulk water. A fraction of the labeled carbon is then respired, and the incorporation of the tracer begins to approximate the rate of net photosynthesis.

The rate at which equilibrium labeling is approached is dependent on the growth rate of the organism(s). The faster the growth rate is, the faster the equilibrium will occur. Thus, the interpretation of radioactive carbon incorporation as gross or net photosynthesis is generally somewhat ambiguous and is complicated by the duration of the experiment in relation to the growth rate. In nature, the latter parameter is usually unknown and numerous discussions have emerged concerning the validity, accuracy and interpretation of the method.

Fluorescence techniques

One of the major problems of the methods mentioned above is the timescale. Photosynthetic rates obtained by in situ incubation techniques are average values over a given time period. To overcome these problems, bio-optical models have been developed in oceanography to extrapolate photosynthesis vs. irradiance curves (P/E). In bio-optical models, it is assumed that the P/*E*--relationship does not depend on the incubation time, which is not true. Most of the short-term physiological adjustments of plankton species are expressed in changes of the functional absorption cross section (σPSII). To keep the timescale short, rapid measurement techniques based on in vivo fluorescence have been developed. Recent active fluorescence techniques opened the possibility to quantify small-scale, rapid changes in physiology and hence provide estimates of primary productivity with a temporal resolution of seconds (review in Hughes et al., 2018).

Fluorescence is a phenomenon which is based on the absorption of light by photosynthetic pigments and its re-emittance at a longer wavelength. When light energy (photons) reaches the light trapping antenna-pigments of a photosynthetic unit (PSU), the Chl-a molecule is excited. In order to return to the ground state, the Chl-a molecule needs to release energy, most of which is lost as heat. What is left is used to "close" the reaction center or is re-emitted as fluorescence. Chlorophyll-fluorescence is very much dependent on the wavelength and intensity of the incoming light. Either photosynthesis or thermal dissipation influence

fluorescence resulting in photochemical quenching (qP) or nonphotochemical quenching (NPQ), respectively. While high light conditions can cause nonphotochemical quenching, weak light which is continuously applied is correlated to in vivo chlorophyll. When phytoplankton is in a dark-adapted state (e.g. during night or when the light is very weak), all reaction centers are in an active, open state and the fluorescence yield is minimal. In this state, fluorescence is at a baseline value F_0. When all the traps are closed the maximum fluorescence level (F_m) is reached. Variable fluorescence is obtained by subtracting F_0 from F_m ($F_v = F_m$-F_0). The potential yield of the photochemical reaction is therefore given by F_v/fm, which is quantitatively related to the photochemical efficiency of PSII. Based on these parameters a wide variety of modifications of fluorometric methods have been developed.

Delayed Fluorescence, DF (Goltsev et al., 2009) most commonly records the decay of fluorescence in the dark after a single turnover flash or after continuous light excitation.

Pump-and-Probe (P&P)-Fluorometry (Falkowski and Kolber, 1990) uses an intense "pump"-flash to close the reaction centers of natural phytoplankton assemblages to reach F_m. After a decay of 80-100 μs, a weak "probe"-flash is induced to re-open the traps to yield F_0. By controlling the intensity of the pump flash and the time delay between the pump- and probe flashes, more physiological information can be retrieved.

Pulse-Amplitude-Modulation (PAM)-*Fluorometry* is a variant of the Pump-and-Probe technique and was introduced to distinguish between photochemical and nonphotochemical quenching. Repeated intense flashes are used against a background of low light to obtain F_m and F_0. PAM as well as P&P-fluorometry are methods which are based on multiple turnover rates. However, both methods have limitations. PAM-fluorometry provides variable fluorescence only and some features of the PSU such as the functional absorption cross section (σPSII) cannot be described, while P&P-fluorometry is too slow to follow the dynamic changes in PSII.

Fast Repetition Rate Fluorometry (FRRF) has been developed to overcome the deficiencies of its predecessors (Kolber and Falkowski, 1992). The instrument is based on high frequency emission of blue light flashes at sub-saturating energy which gradually saturates the PSII reaction centers within a single turnover. The rate required to saturate the PSII reaction center is proportional to the functional absorption cross-section of PSII (σPSII). After reaching the saturation level (F_m), relaxation flashes with longer inter-flash delay are emitted to re-open the reaction center. The rate of relaxation is related to the turnover rate of PSII (τ). FRRF instrumentation has recently been expanded to more than one wavelength to improve the detection of cyanobacteria (Houliez et al., 2017).

Primary productivity estimates can be derived from variable fluorescence. Introducing the photosynthetic quotient (PQ) in the equation, the rate of carbon fixation can be obtained to qualitatively predict photosynthetic rates from changes in the quantum yield of fluorescence.

Remote sensing

Measures of primary production have always been complemented by calculations such as depth, time or wavelength integrated models (Behrenfeld et al., 2002). Similar algorithms became increasingly important as remote sensing, particularly from satellites developed and sensor technologies improved. Initially measurements from space were designed for global marine productivity estimations but can as well be used for larger aquatic systems (Bresciani et al., 2011; Hestir et al., 2015; Boucher et al., 2018). Present

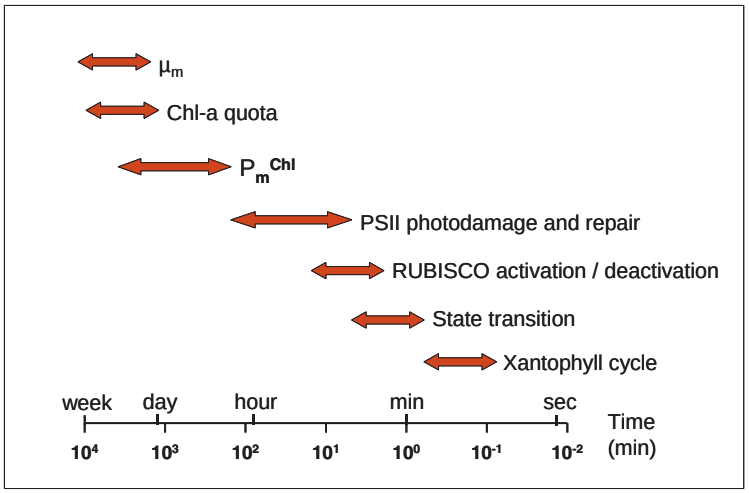

Fig. 2 First order time constants for acclimation of algal photosynthesis to step changes in photon flux density. Modified from Raven, J.A., Geider, R.J., 2003. Adaptation, acclimation and regulation in algal photosynthesis. In Larkum, A.W.D., Douglas, S.E., Raven J.A. (Eds.), Photosynthesis in Algae. Advances in photosynthesis and respiration, vol. 14, pp. 385–412. Springer, Dordrecht. https://doi.org/10.1007/978-94-007-1038-2_17 in Larkum, A.W.D., Douglas, S.E., Raven, J.A. (Eds.), 2003. Photosynthesis in Algae. Advances in Photosynthesis and Respiration, vol. 14, Kluwer, Dordrecht, p. 407. https://doi.org/10.1007/s10811-005-0461-x.

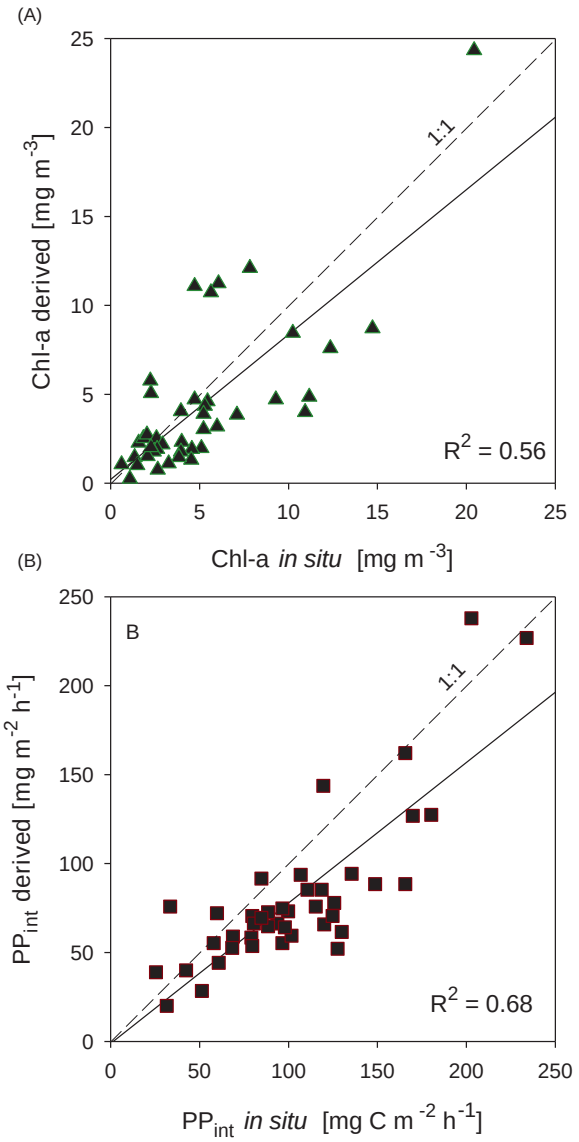

Fig. 3 Comparison of (A) satellite-derived (MERIS) and in situ sampled Chl-a and (B) satellite-based and in situ integrated primary productivity (PPint) in Lake Geneva. Modified from Soomets, T., Kutser, T., Wüest, A., Bouffard, D., 2019. Spatial and temporal changes of primary production in a deep peri-alpine lake. Inland Waters 9, 49–60. https://doi.org/10.1080/20442041.2018.1530529.

day algorithm estimate chlorophyll which is then used to calculate primary productivity using a variety of models (Fig. 2; Raven and Geider, 2003). Recently, image data derived from remotely piloted aircraft systems (or drones) are under investigation (Joyce et al., 2017) (Fig. 3; Soomets et al., 2019).

Productivity in the "real" world

Let us now consider photosynthesis in a planktonic system in a water column, a planar representation of surface area projected to a depth z. Light (E) incident on the water surface is attenuated with depth, approximately following an exponential function (Fig. 4). We define a depth z_{eu} equal to the 1% light intensity as the base of the euphotic zone. This is the portion of the water column supporting primary production in most instances. In some cases, extremely light adapted assemblages can survive at much lower photon flux densities. The euphotic depth is often confused with the compensation depth (z_c), defined as the depth where daily gross productivity balances respiratory losses over a day. Above z_c, net photosynthesis is possible, below the result of oxygen production and consumption is negative. The average compensation depth is dependent on the surface light intensity E_0 and can be highly variable; it may, however, frequently correspond to the euphotic depth. If the portion of the water column which is mixed by

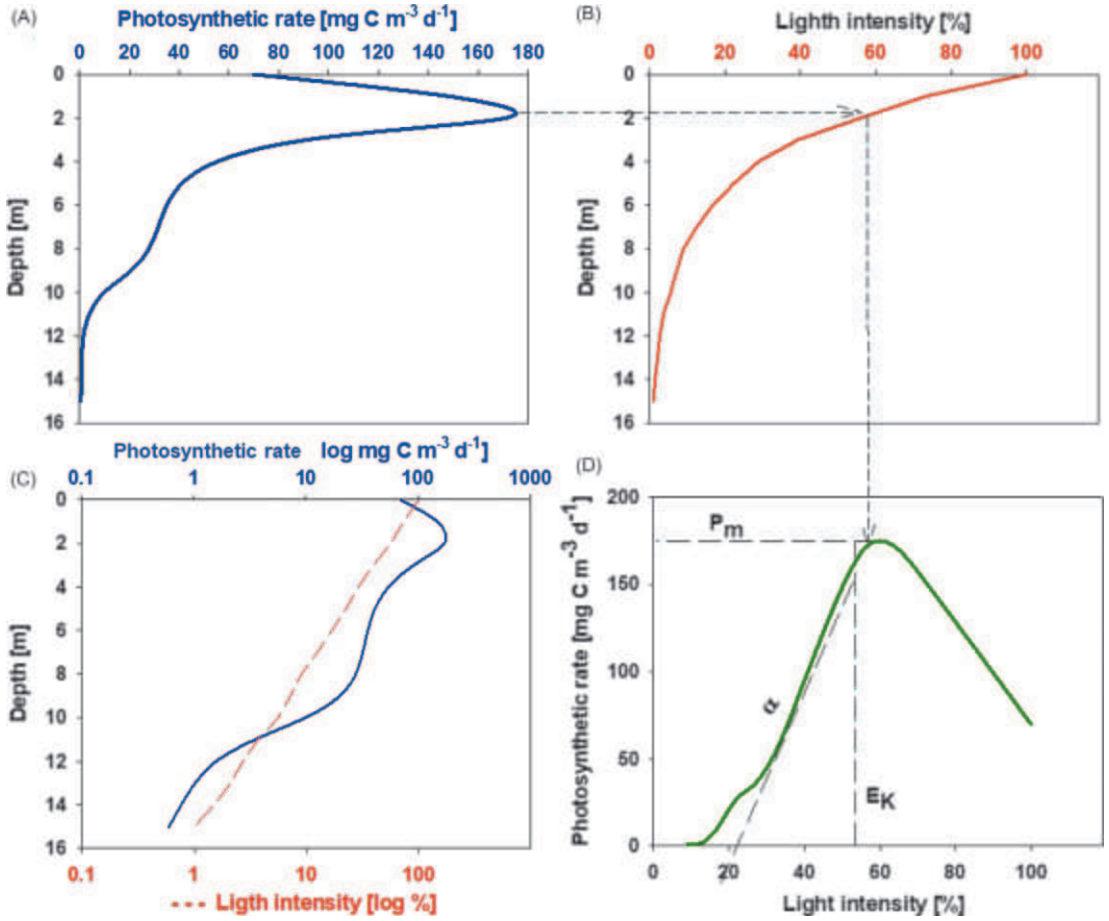

Fig. 4 Example how to convert a measured profile of photosynthetic rates (A) and vertical light attenuation (B) into a P/E curve (D). In addition, the profiles in (A) and (B) are combined into a semi-log plot (C) to indicate the similar decay of both variables with depth.

wind (z_{mix}) extends beyond the euphotic zone, a critical depth (z_{cr}) can be defined where integral net photosynthesis balances integral respiratory losses (Fig. 4).

In Fig. 4, an idealized daily integrated profile of photosynthetic rates is presented with algal biomass assumed to be homogeneous over depth, and therefore unimportant to the shape of the curve. At the surface, photosynthetic rates are typically depressed as a manifestation of photoinhibition which, at least partly, is an artifact of in situ methodology. Common methods keep algae constantly at high irradiance over prolonged periods of time which otherwise would float freely through the light gradient. Rates rise to P_m lower in the column and then decline monotonically as light becomes limiting, representing the low irradiance-dependent region of the P/E curve. Respiration losses (R_P) are assumed to be constant throughout the water column which has recently shown to be far from typical (Mantikci et al., 2019). Traditionally, respiration of the photoautotrophs has been assumed to be 10% of the maximum photosynthetic rate, and independent of irradiance. Many freshwater studies indicate that respiratory losses relative to P_m are variable. Additionally, the euphotic zone is influenced by temperature, supra-optimal light levels, nutrient limitations, nonhomogenous distribution of phytoplankton biomass, or even compositional changes of the assemblage within the water column. Plankton respiration on average increases with chlorophyll-a, total phosphorus (TP), and dissolved organic carbon (DOC) concentrations. Accurate measurement of R_P is one of the biggest challenges in estimations of primary production and will also affect the determination of the compensation depth as well as the critical depth.

A real vertical photosynthetic profile and light attenuation is exemplified in Fig. 4A and B, indicating also the approximate corresponding exponential decrease of both (Fig. 5C). Using the data in Fig. 5A and B, Fig. 5D indicates how to construct a P/E curve from real data.

Depending on the composition and vertical distribution of phytoplankton biomass, vertical profiles of phytoplankton productivity can substantially deviate from the schematic profile shown in Fig. 4. Three examples are depicted in Fig. 6. Deep chlorophyll maxima of various types of algae, such as picoplankton, Cyanobacteria etc., can produce secondary peaks of productivity at a greater depth. Turbid shallow lakes often do not show photoinhibition at the surface and have steep, compressed vertical profiles. High-mountain lakes may have profiles reaching P_m near the sediment because motile phytoplankton species dominate which tend to avoid large UV doses associated the high photon flux at such elevations (Fig. 6). Such "irregular" types of vertical profiles cannot be transferred to P/E curves; hence, physiologically meaningful parameters are extremely difficult to deduce. Moreover, these profiles cannot be described in simple mathematical terms, and modeling therefore is complicated if not impossible.

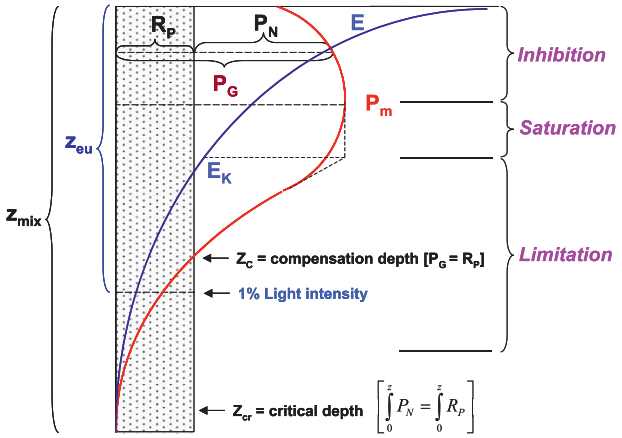

Fig. 5 Conceptual diagram showing a schematic vertical profile of gross photosynthesis (P_G), phytoplankton respiration (R_P), and attenuation of irradiance (E) in a hypothetical lake. Maximum photosynthetic (P_m) and net-photosynthetic rates (P_N) are indicated. The regions of photoinhibition, light saturation and light limitation are indicated on the right-hand side. The depth of the euphotic zone (z_{eu}), equal to 1% light intensity, the compensation depth (z_c) and the critical depth (z_{cr}) as well as the mixing zone (z_{mix}) are given.

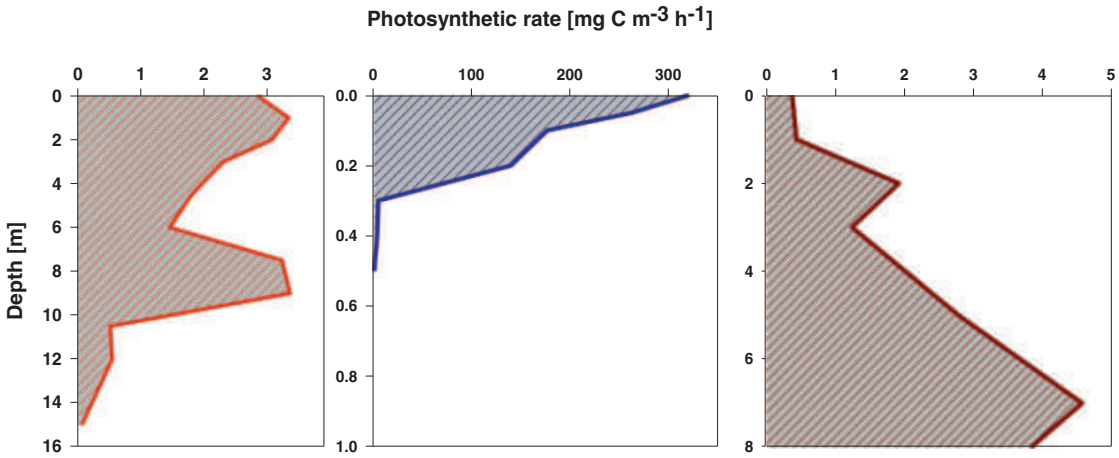

Fig. 6 Examples of nonregular vertical productivity profiles. Left Panel: Profile with a 2nd maximum at depth from a deep living low light acclimated population or assemblage (e.g. *Planktothrix rubescens*). Middle panel: Profile typically for turbid shallow lakes or turbid rivers as well as in highly eutrophic, algal bloom situations- Right panel: Maximum photosynthetic rate occurring at greater depth (often near the bottom). Typically for clear water, high-mountain lakes when UV-light penetrates deeply.

In essence, interpretation of productivity measurements in fresh-waters is often difficult, dependent on the technique used, and further complicated by the complex and variable composition of natural algal assemblages.

Daily, seasonal and inter-annual variability of production

One of the major determinants of variability in photosynthetic response is the daily variation in irradiance. Both the light-saturated and the light-limited chlorophyll specific photosynthetic rates are generally elevated during the photoperiod. The correlation between these two parameters suggests an increase either in the number of active reaction centers or in their turnover rate. The diel irradiance cycle is the natural synchronizing agent for algal populations in the environment constraining growth rates. Algal assemblages must cope with short-term changes in irradiance during a day and acclimate photosynthetic rates to variations from day to day.

Superimposed is the annual cycle of solar radiation which depends on latitude and altitude. Depending on the geographical position, annual variation of irradiance ranges from moderate near the equator to very pronounced at high latitudes. Accordingly, the magnitude of primary production strongly varies with climatic regions (Table 2). It must be emphasized that production continues at exceptionally low light intensities even under ice (Reitner et al., 1997; Dokulil and Herzig, 2009; Dokulil et al., 2014).

Table 2 Ranges of average daily and annual net-productivity in ecosystems of the world. Combined from various authors and sources.

Ecosystem	*Mean daily production (mg C m^{-2} d^{-1})*	*Average annual production (g C m^{-2} yr^{-1})*
Tropical lakes	100–7600	30–2500
Temperate lakes	5–3600	2–950
Arctic lakes	1–170	<1–35
Antarctic lakes	1–35	1–10
Alpine lakes	1–900	<1–250
Temperate rivers	<1–3000	<1–650
Tropical rivers	<1–24.000	1–5000

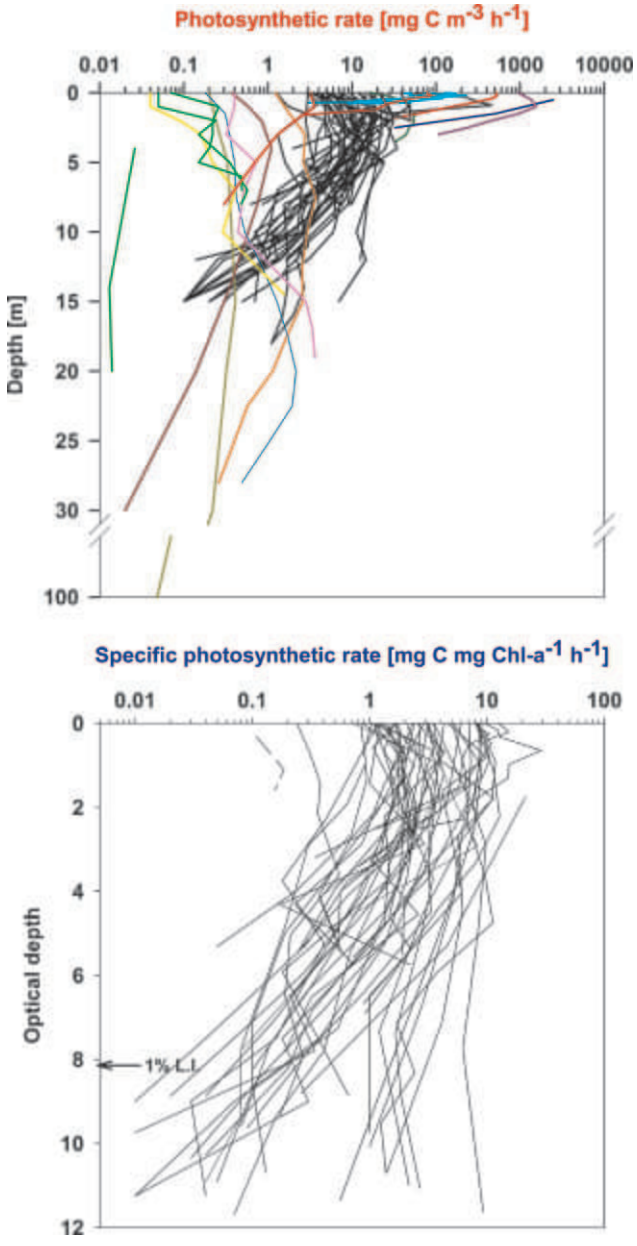

Fig. 7 One hundred vertical profiles of carbon fixation as a function of physical depth (A) and normalized to chlorophyll-a and optical depth (B). One unit of optical depth is equal to a halving of light intensity (Dokulil and Kaiblinger, 2009).

Table 3 Primary production, biomass, chlorophyll-a and dominant algal groups for the trophic categories observed in freshwaters (Dokulil and Kaiblinger, 2009).

Trophic level	*Primary production (mg C m^{-3} d^{-1})*	*Biomass (mg C m^{-3})*	*Chlorophyll-a (mg Chl-a m^{-3})*	*Dominant algal group(s)*
Ultra-oligotrophic	<50	<50	0.01–0.5	Chrysophyceae
Oligotrophic	50–300	10–100	0.3–3.0	Cryptophyceae Bacillariophyceae
Mesotrophic	250–1000	100–300	2–15	Dinophyta
Eutrophic	600–2500	250–600	15–30	Cyanobacteria
Hypertrophic	>2500	>600	> 30	Chlorophyta Euglenophyta
Dystrophic	<50–500	<50–200	0.1–10	

Assessment of primary production at the global scale

Several thousand vertical profiles of daily integrated photosynthetic rates have been obtained world-wide from many different freshwater ecosystems. Vertical profiles of photosynthetic rates from many lakes using different measurement techniques are summarized and expressed as volumetric carbon uptake per day in Fig. 7A. The profiles display a high degree of variability from as low as 0.1 mg C m^{-3} d^{-1} to way over 1000 mg C m^{-3} d^{-1}. The range of photosynthetic rates therefore is at least four orders of magnitude in freshwaters while it is only three in the sea. This is not surprising, considering the wide variety of lake types from extremely nutrient poor (ultra-oligotrophic) to nutrient rich (hypertrophic), from very shallow lakes (<2 m) to deep lakes (>200 m). Similarly, average daily column productivity (ΣΣP) ranges from 50 mg C m^{-2} d^{-1} to greater than 2500 mg C m^{-2} d^{-1} (Table 3).

The major source of variation in photosynthetic rates in aquatic systems is related to the amount and distribution of photoautotrophic biomass. To put it simply, under any irradiance condition photosynthetic energy flow is dependent on population density of the photosynthetic machinery. Since photosynthetic reaction centers are causally related to the concentration of photosynthetic pigments, normalization to chlorophyll-a, which is universally contained in all algal classes should lead to a reduction in variance. When carbon uptake rates from Fig. 7A are normalized to chlorophyll-a and plotted versus optical depth which is independent of physical depth, the magnitude is largely reduced (Fig. 7B). Chlorophyll-specific carbon uptake rates range from less than 1 to over 10 mg C mg Chl-a^{-1} h^{-1}, like observations in the sea (Falkowski and Raven, 2007).

Global gross primary production (GPP) of lakes was assessed as about 54 Tmoles C y^{-1} equivalent to 0.65 Pg C y^{-1} (Pace and Prairie, 2005). The amount of carbon produced in lakes is rather small relative to the 108–128 Pg C y^{-1} produced globally by plants (Walker et al., 2017).

Conclusions

The last 100 years and particularly the 20th century can be entitled as the "century of ecology" (Worthington, 1982) and perhaps equally as the century of productivity investigations. Measurements of photosynthetic rates and primary productivity have been much elaborated in detail on regional, global and temporal or seasonal basis over the last almost hundred years of expertise. A multitude of techniques and methodological refinements were established, and further development is still in progress. The rise in understanding subtle details of photosynthetic metabolism caused essential improvements in models of production, making estimations via remote sensing possible. Several open questions however remain (Hughes et al., 2018).

Knowledge gaps

- Conversion of electron transfer rates to equivalent rates of C-fixation
- Environmental influence of the electron requirement for C- fixation (Φe, C) as well as effects of phytoplankton composition and physiology
- Higher resolution and improved algorithms for remote sensing (Satellite) models
- Improved primary production estimates from high frequency measurements
- Central data repository

See Also: Emerging methods and topics: Dust and Fog Effects on Inland Waters; Fundamental concepts and theories: Comparative Primary Production; Regime Shifts and Tipping Points; Structures and functions of Inland Waters - Lakes: A Diversity of Primary Producers in Lakes; pH of Inland Waters; Phytoplankton Growth and Nutrients; Structures and functions of Inland Waters - Rivers: Algae and Primary Production of Streams and Rivers Ecosystems

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Biophysical Interactions in Phytoplankton

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Biophysical interactions Examining the interactions of biology and physics to shape the environment.
Convection Movement caused by differences in density between two parcels of water.
Eddy A circular movement of water.
Epilimnion The surface layer of a classically stratified water column, lying above the thermocline; it tends to be the same temperature throughout.
Extinction coefficient A measure of how easily light can penetrate into water.
Hypolimnion The deepest layer of a classically stratified water column, lying below the thermocline; it tends to be the same temperature throughout.
Internal seiching Subsurface movement of water along the thermocline generated by a standing wave oscillating through a waterbody. Frequently caused by the displacement of water upwind during wind forcing, which returns once the forcing is relaxed, setting up the oscillation.
Metalimnion The middle layer of a classically stratified water column, usually coinciding with the region of the thermocline.
Mixed layer The surface layer in a lake, in contact with the atmosphere, it is assumed to be fully mixed.
Phytoplankton A collection of microscopic bacteria, protists and plants which inhabit our open waters, capable of obtaining energy via photosynthesis.
Thermal structure, stratification The vertical temperature variation in a column of water affecting its density. For example, where different water depths have different temperatures, the density difference of these depths results in the water column becoming stratified.
Thermocline The region of rapid temperature change in a stratified water body.
Turbulence Unstable motion characterized by irregular, chaotic movement with rapid changes in velocity.

Introduction

Phytoplankton, the collection of microscopic bacteria, protists and plants which inhabit our open waters, are both shaped by and alter their physical water environment. These interactions occur across a range of spatial and temporal scales from length scales of micrometers and timescales of seconds in turbulent flow to whole lake basins (kilometers) and seasonal patterns reflecting changes in stratification and mixing. Physical interactions at the smallest scales help to shape the form and function of phytoplankton and contributes to shaping the dominant species in the community at any point in time. These biophysical interactions occur through the vertical water column of lakes, where phytoplankton can alter their physical environment through heat absorption and density alteration and the physical environment can structure the extent and intensity of mixing experienced by planktonic organisms and their access to the nutrients essential for survival. Across horizontal gradients in lakes, physical processes of convection, wind mixing and seiching generate gradients in nutrients, patches of surface phytoplankton and subsurface accumulations of phytoplankton which both determine and are determined by the types of phytoplankton present in the community. These accumulations have

 https://doi.org/10.1016/B978-0-12-819166-8.00158-4

implications for understanding patterns in biogeochemical processing and determining spatial patterns in water quality that can impact shoreline recreation or water draw-off. The aim of this chapter is to introduce the main concepts of biophysical interactions in phytoplankton. It provides an overview of different scales of biophysical interactions in phytoplankton over vertical and horizontal dimensions in lakes.

Small-scale interactions

The physical water environment of lakes exerts a fundamental control on the form and function of phytoplankton. At a basic level this is because, according to Stokes' Law, large objects sink faster than small objects of the same density, assuming they have the same shape and drag effects. Reynolds (1998) suggests that this offers an advantage to smaller cell sizes compared to larger ones, as small cells will not sink out of photic layers as quickly and be more likely to remain entrained within moving water, enabling carbon acquisition and cell division to occur. He goes on to hypothesize that the minimum eddy size in a lake places an upper size limit on the phytoplankton form size that can be sustained, which is determined by the balance between the shear or friction velocity of the water (u^*) and the settling velocity of the phytoplankton (ws) (Reynolds, 1998). Where $u^* > ws$, the phytoplankton cell will be entrained within the water motion and where $u^* < ws$ the cell will be dis-entrained resulting in sinking, floating or swimming movements dominating the movement of the organism. In practice, turbulent velocities are usually between one to six orders of magnitude larger than sinking velocities, which results in phytoplankton being continuously redistributed in the turbulent water column (Naselli-Flores et al., 2020). Deeper water columns dissipate energy more slowly than shallower water columns. This is the case where the water may be shallow because of the lake bathymetry or because the lake is stratified and mixing is restricted to the surface mixed later. This difference in water column depth results in larger minimum eddy sizes in a deep lake like Lake Constance, 2.9–1.5 mm, versus a shallow lake like Lough Neagh, 0.7 mm (Reynolds, 1998). In order to stay entrained within the water column and able to access light required for growth, Reynolds suggests that phytoplankton need to be smaller than the eddies likely to be generated in their lifetimes, which is why most planktonic algae are <200 μm in size and colonies <2 mm, the latter being only likely to dominate in very calm or stratified water.

Owing to their small size, phytoplankton experience turbulence as a shear flow, where different fluid volumes flow past each other at different velocities. This difference in velocities generates a torque in the water which results in a constant rotation of organisms (Wheeler et al., 2019). The interaction of turbulence with motility traits has been shown to differ depending on whether species are motile, such as dinoflagellates, or non-motile, such as diatoms, with the result that patchiness may be more pronounced for motile species (Durham et al., 2013). Where the destabilizing effect of torque overcomes stabilizing effects related to cell morphology, such as a pear-shaped morphology with a 'heavy' bottom, cells are deflected from their preferred orientation. This deflection due to turbulence can cause cells to become trapped in high shear regions, resulting in accumulations of cells and patchiness at the mm scale (Durham et al., 2013). These patches can persist for hours to weeks and can often represent ecological hotspots.

The concentration of phytoplankton cells can result in opportunities for enhanced predation but it may also offer some advantages to the organisms, particularly in terms of enhanced encounter rates for phytoplankton with a sexual stage and increasing the concentration of allelopathic compounds which may be used to deter other organisms and reduce predation (Wheeler et al., 2019). Phytoplankton have also been found to exhibit behavioral responses to cues from flow through an ability to change shape and alter swimming behavior. This response is thought to enable motile phytoplankton to escape from physiologically harmful areas of high turbulence, counteracting the destabilizing effects illustrated above (Wheeler et al., 2019).

The physical environment and turbulent mixing play a key role in determining the availability of light energy and nutrient resources to phytoplankton cells (Reynolds, 1998). The ability of individual cells to access the resources required for growth is determined by cell size, where larger surface areas to volumes can confer an advantage in uptake rates. The diffusion boundary layer is the region around a phytoplankton cell which is chemically altered by its presence. In the case of nutrients, this region is depleted due to cell uptake. Turbulence and cell motility both have the action of making this layer thinner, which enhances transport to and from the organism (Wheeler et al., 2019). This passive or active movement around the cell reduces the nutrient uptake advantage of small cell size, because boundary layers around larger cells are more strongly deformed by the movement. This deformation increases the nutrient concentration gradient near the cell and results in more nutrient rich water being brought into the boundary layer enhancing nutrient uptake (Wheeler et al., 2019).

The effect of turbulence on resource acquisition then has implications for the evolutionary adaptation of phytoplankton species and selection for species in different environments. Chain formation in diatoms and dinoflagellates, for example, may in part be explained by the presence of flow and turbulence, since the oscillation of shear flow allows for a greater thinning of boundary layers in chain morphologies than it would for a single cell (Wheeler et al., 2019). At a community level, in nutrient poor environments, pico- and nano-plankton dominance may, in part, be explained by their relatively higher uptake rates than those for larger phytoplankton without exposure to strongly turbulent conditions (Reynolds, 1998). In contrast, nutrient depleted conditions in stratified eutrophic systems, are likely to select for larger cells or colonies, which may be motile and able to dis-entrain from weak turbulence and vertically migrate to access nutrient resources (Reynolds, 1998).

Vertical interactions

Phytoplankton as mediators of their physical environment

Lake thermal structure

A proportion of incoming solar radiation, unlike the other surface heat fluxes, penetrates beneath the surface of a lake. The rapidity of its absorption with depth can vary substantially between lakes and is strongly influenced by phytoplankton concentrations. Thus, these organisms have the potential to influence the thermal structure of lakes.

The relationship between light absorption and depth is parametrized by the light extinction coefficient, k (m^{-1}), in the equation,

$$I_z = I_0 \, e^{-kz},$$

where I_0 is the solar radiation penetrating the surface of the lake and I_z is the solar radiation at a depth z (negative downwards). The higher the extinction coefficient is, the more that light is absorbed nearer the surface (Fig. 1). So, for example, with an extinction coefficient of $k = 2.0$, more than 98% of the light is absorbed in the top 2 m, while for $k = 0.2$ less than 35% of the light is absorbed in the top 2 m. With $k = 0.5$, nearly 2% of the light still reaches 8 m depth, while for $k = 0.2$, the same amount reaches as far down as 20 m (Fig. 1). As the solar radiation is absorbed it heats the water, so for small extinction coefficients the heat from the sun penetrates much deeper into the water column than when the extinction coefficients are large. The profound differences in where the heat is being absorbed in the water column shapes the thermal response. Pure water itself absorbs light, as do a variety of chemical constituents such as humic material, while absorption is further increased by phytoplankton in the water. Extinction coefficients can, therefore, be estimated as a background value, which would depend on the dissolved chemical constituents, and a value proportional to the phytoplankton concentration. For example, for a background extinction coefficient of 0.2 m^{-1}, and an optical cross-section of chlorophyll of 0.015 m^2 mg^{-1} (Kirk, 1994) then extinction coefficients of 0.5 m^{-1} and 2.0 m^{-1} would correspond to chlorophyll *a* concentrations of 20 and 120 mg m^{-3}, respectively.

Lake surface area is a major determinant of the impact of extinction coefficients on thermal structure, with the influence of extinction coefficients being commonly evident in smaller lakes, while being less obvious in larger lakes (Fee et al., 1996). The relationship with lake surface area is, in part, a result of mixed depths typically being deeper in large lakes than in small ones (Fee et al., 1996) and the impact that has on the ratio of mixed depth to photic depth. If the mixed depth is deeper than the photic depth then virtually all the light would be absorbed within the mixed layer and, in theory, the heat would then be distributed throughout that layer, so changes to extinction coefficient would have relatively little impact (Fee et al., 1996; Persson and Jones, 2008). Thus, given the variation in light extinction curves (Fig. 1), a lake with surface area sufficient for a mixed depth of, say 10 m, should be negligibly impacted by a change in extinction coefficient from 2.0 to 0.5 m^{-1}, as for either coefficient nearly all the light is already absorbed by 10 m, but thermal characteristics could be influenced by a change from 0.5 to 0.2 m^{-1}. In comparison, a smaller lake with a mixed depth of only 2 m would be influenced by a change in extinction coefficient from 2.0 to 0.5 m^{-1} as well. Thus, for any lake there would be a sub-range of extinction coefficients which would have an influence on lake thermal characteristics depending on whether all light was being absorbed within the mixed layer or not. Likewise, changes to small extinction coefficients tend to produce bigger effects, while changes to very high values, for example above 2 m^{-1}, tend not to matter too much to thermal structure for all but the shallowest epilimnia (Fig. 1). Hence, small lakes and relatively clear lakes tend to be more susceptible to changes in extinction coefficient than relatively large turbid lakes.

One of the most observed influences of extinction coefficients (Mazumder et al., 1990; Fee et al., 1996; Persson and Jones, 2008) is on thermal length-scale metrics, such as thermocline depth or mixing depth. Typically, these are found to be several meters shallower in lakes with higher extinction coefficients than those with lower extinction coefficients, at least for small to moderately sized lakes. Similarly, long-term changes in extinction coefficient in a lake have been observed to be accompanied by long-term changes in these thermal metrics.

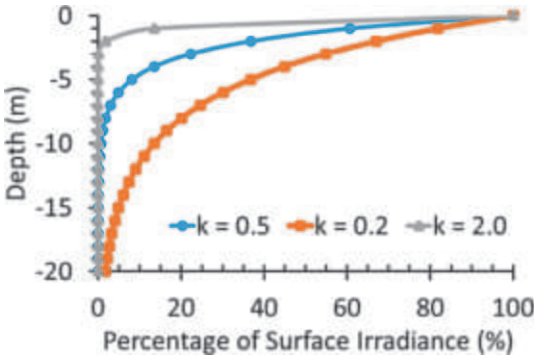

Fig. 1 Percentage of surface solar radiation reaching different depths for three different extinction coefficients, *k*: 2.0 (gray triangles), 0.5 (blue circles), 0.2 (orange squares).

Lake temperatures can also be affected by changes to extinction coefficient, although the most striking impacts are typically observed in the metalimnion and hypolimnion, rather than the epilimnion. In smaller lakes, field and modelling studies of extinction coefficient impacts have consistently shown comparatively cooler deeper water in less transparent lakes, and often by several degrees. For example, Mazumder et al. (1990) studying lakes and enclosures with and without planktivorous fish, the former with fewer zooplankton, more small phytoplankton, and shallower Secchi depths than the latter, showed metalimnetic waters several degrees cooler where the fish were present and the extinction coefficient greater, as the solar radiation was not penetrating to the deeper waters.

Studies are equivocal on the impacts on surface temperature, though. A comparison between two large neighboring enclosures, one with high phytoplankton concentration and one with low, showed the one with the greater concentration to have higher surface temperatures of about 0.5–1.0 °C (Jones et al., 2005). On the other hand, the opposite effect has been observed (e.g. Mazumder et al., 1990) with slightly higher surface temperatures in the clearer lakes, possibly owing to increased backscattering of incoming solar radiation by small phytoplankton. Modelling studies have shown that there is a temporal consideration, with less transparent lakes having comparatively warmer surface temperature at the start of stratification, but then a lower surface temperature later in the summer. The initial comparative rise in surface temperature is moderated by the consequential increase in surface cooling from outgoing longwave and sensible and latent heat fluxes associated with a warmer surface (Jones et al., 2005). Subsequently, the concurrent sizeable decrease in metalimnetic water temperature ultimately leads to cooling from below later in the stratified season when chillier metalimnetic waters gradually entrain into the deepening mixed layer (Persson and Jones, 2008). When the average effect on surface temperature has been studied over the whole stratified period it has been found to be rather small, generally less than 1 °C.

The effect of a marginal increase on surface temperature and a simultaneous significant comparative decrease in temperature of deeper water in less transparent lakes also impacts stratification. Stratification is usually found to be comparatively stronger and comparatively longer in lakes with higher extinction coefficients (Persson and Jones, 2008). Again, the morphology of a lake, and the range of extinction coefficients experienced, will be key to how large the effect could be, but for particular morphologies, the extinction coefficient can make sufficient difference to determine whether a lake is polymictic or dimictic (Shatwell et al., 2016). The temporal consideration of seasonality of phytoplankton growth is also important, with the timing of blooms, when extinction coefficients will be higher, and clearwater phases, when extinction coefficients will be lower, potentially influencing stratification and destratification of polymictic lakes (Shatwell et al., 2016).

Bioconvection

Physical processes generally dominate in controlling the environment experienced by phytoplankton where there is active turbulence. However, there are circumstances, under low turbulent mixing, when microorganisms can induce convective mixing processes, thus altering the physical conditions they experience. This is achieved through alterations to the density of the water due to their presence in high concentrations, and is a phenomenon termed bioconvection. Upward swimming and the aggregation of cells increases the density of the surrounding water above that of the water below it; this results in instability and convective mixing of the cells downwards. The mixing is therefore continued while the organisms continue their active upward swimming behavior. Despite the potential for bioconvection to occur in phytoplankton, particularly actively motile groups, evidenced in laboratory experiments (Bees and Hill, 1997), observations of bioconvection in lakes are currently limited to motile bacteria (Sommer et al., 2017). The relative importance of this process in mixing in lakes is therefore poorly understood at present.

The influence of the physical vertical structure of lakes on phytoplankton communities

Phytoplankton require light and nutrients for growth and each have a heterogenous vertical distribution within the water column (Klausmeier and Litchman, 2001). Light availability reduces with depth with the gradient of attenuation depending on water color and the concentration of suspended solids, including phytoplankton (Kirk, 1994). Photosynthetically active radiation (PAR) is available to phytoplankton until it reaches roughly 1% of its surface value, which is defined as the photic depth; below this depth light levels are generally considered too low for photosynthesis (Kirk, 1994).

The vertical distribution of nutrients and phytoplankton are determined by the depth of surface mixing. During lake stratification, a vertical density gradient inhibits the whole water column from mixing, restricting mixing to surface waters. The depth of surface mixing is important for phytoplankton growth as it determines the light levels and nutrient concentrations that phytoplankton are exposed to. When a lake is stratified, nutrients can be at their highest levels below the mixed layer and scarce within the mixed layer as they are used rapidly by the phytoplankton (Klausmeier and Litchman, 2001).

Phytoplankton resources can therefore have opposing vertical gradients of irradiance and nutrients (Fig. 2). Therefore, vertically, there are narrow bands of space that are suitable for phytoplankton growth which fluctuate depending on the position of the mixed depth (Klausmeier and Litchman, 2001). This led to the development of the "critical depth" hypothesis whereby phytoplankton growth can only be maintained if the surface mixed layer is shallower than some critical depth (Sverdrup, 1953). This theory suggested that if mixing was sufficiently shallow then the light conditions will be favorable for photosynthesis and therefore phytoplankton populations can be maintained (Sverdrup, 1953). This did not explain, however, how phytoplankton blooms can form in the absence of stratification or during times of weak stratification which led to the idea of "critical turbulence" (Huisman et al., 1999). If turbulent mixing was less than a critical value then phytoplankton populations can be maintained as growth exceeds sinking losses (Huisman et al., 1999).

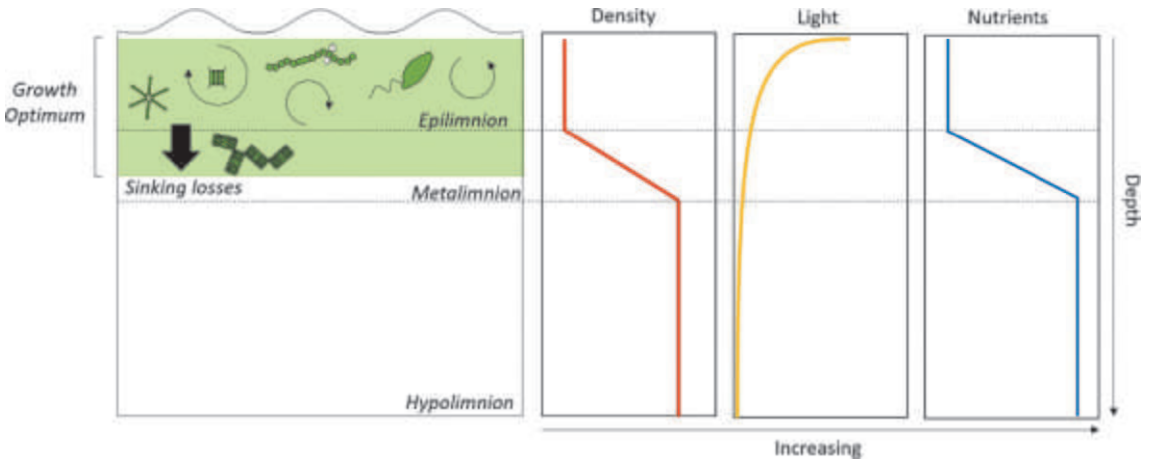

Fig. 2 Vertical gradients in density, light and nutrients create varying optima for phytoplankton growth.

The vertical distribution of phytoplankton in the water column is further complicated by the different resource requirements, sinking rates and levels of motility between phytoplankton taxa (Naselli-Flores et al., 2020). At times of full water column mixing, phytoplankton are mixed throughout the water column and they are roughly exposed to the same light levels and nutrient concentrations (Huisman et al., 1999). Under these conditions, diatoms are often abundant as higher turbulence overcomes the relatively higher sinking velocities of diatoms compared to other taxa, which combined with the low light adaptation of these species, enables them to persist during deep mixing (Reynolds, 2006). These conditions, coupled with the abundance of silica (required for the formation of diatom frustules), mean that diatoms are often the first phytoplankton to bloom in spring in temperate systems (Reynolds, 2006).

As stratification strength increases and vertical mixing becomes weaker, different phytoplankton taxa can occupy different depths according to their specific resource requirements and levels of motility which can lead to vertical niche partitioning (Beisner and Longhi, 2013). Some species of cyanobacteria such as *Dolichospermum* sp. have small air sacs called vesicles which enable them to rise to the surface and form large blooms (Huisman et al., 2018). These blooms have become a major water quality hazard for many lakes and reservoirs globally due to their potential toxicity and other negative ecosystem impacts (Huisman et al., 2018). Mixing induced either by storm events or via an artificial mixing system (Visser et al., 2016) can break up surface blooms as deeper mixing can result in light limitation. In some instances mixing can result in increased pressure deeper in the water column, which can cause the collapse of gas vesicles, preventing buoyancy (Walsby, 1994). Persistent mixing can result in cyanobacteria being replaced by chlorophytes, flagellates or diatom taxa which are adapted to the lower light conditions associated with deeper mixed depths (Visser et al., 2016). The critical role of mixing and mixed depth in determining phytoplankton community composition is illustrated by the rapid community changes induced by short term changes in lake physical structure (Jöhnk et al., 2008). However, these changes can be transitory, with a return to high stratification strength and shallow surface mixing following a mixing event leading to surface blooms of cyanobacteria re-forming.

Phytoplankton biomass can also peak at depths below the surface forming a deep chlorophyll maximum (DCM). This can occur in lakes when the euphotic depth is deeper than the mixed depth (Leach et al., 2018). Phytoplankton occupying this position can access the higher nutrient concentrations in the metalimnion and they can persist due to their adaptation to low light conditions and/or their ability to migrate between areas of favorable nutrient and light levels (Arvola et al., 1991). Taxa associated with deep water biomass peaks include low light adapted cyanobacteria such as *Planktothrix* sp., motile cryptophytes and occasionally diatoms as the cool dense water at deeper depths can slow their sinking rates. Some motile phytoplankton such as the cryptophyte *Cryptomonas* sp. and the dinoflagellate *Ceratium* sp. undergo daily migrations, occupying the upper layers of the water column during the day to access higher light levels and migrating to the metalimnion at night to access nutrients (Arvola et al., 1991).

Horizontal interactions

Spatial patterns in phytoplankton distribution are a common feature of lakes, the drivers of which have been related to physical mixing and water movements, chemical gradients and biological interactions (Pinel-Alloul, 1995). Physical drivers of these patterns are related to convective, advective and seiching processes driving waves and current formation which move phytoplankton around a lake basin. Since physical forcing is rarely constant in time or space, the continual changes in the strength, direction or extent of these drivers and the subsequent relaxation of forcing when the wind drops, for example, result in the formation of phytoplankton patchiness over a range of spatial scales from basin level > 1 km to microscale effects within turbulent eddies.

In lakes, there are a number of convective processes which act on the waterbody that may influence the movement and aggregation of phytoplankton. Differential heating and cooling occurs because water columns of different depths warm and cool

at different rates and to different extents. This affects the spatial development of vertical stratification across areas like the littoral and pelagic zone or in sidearms of lakes and reservoirs. The result is the creation of horizontal density gradients across these areas, setting up a 'thermal siphon' of water movement (Monismith et al., 1990). These convective movements are likely to develop in the absence of other horizontal mixing processes, which would act to equalize the density gradient; therefore they tend to form under low wind speeds and in wind-sheltered locations, frequently at night. Night time horizontal convection has been found to transport nutrients from littoral zones into offshore areas, acting as an internal nutrient source (James and Barko, 1991).

In addition to horizontal patterns established by thermal convective transport, the development of advective movement through wind-derived waves and currents can also act to create horizontal variability in phytoplankton concentrations at a range of spatial scales. At a basin level, wind-induced circulation, wind mixing processes, upwelling and downwelling associated with thermocline tilting and the effect of lake inflows will dominate in determining the spatial distributions of phytoplankton communities (Pinel-Alloul, 1995). Wind field strength and its persistence have been found to be important factors in the accumulation of phytoplankton across scales of greater than one kilometer down to tens of meters (Pinel-Alloul, 1995). The propensity for phytoplankton to form patches or accumulations depends in part on their physical characteristics, with positively buoyant, neutrally buoyant and negatively buoyant species all showing different relationships under different wind forcing (Cyr, 2017). Phytoplankton motility or buoyancy characteristics interact with these physical drivers, with evidence for downwind advective movement of positively buoyant species and upwind movement of negatively buoyant species resulting in high concentrations in areas of upwelling under consistent wind forcing (George and Edwards, 1976). Laboratory studies identified a threshold in wind speed of 2–3 m s^{-1}, for buoyant species, below which surface accumulations may form under low wind speeds and above which more turbulent mixing would result in entrainment into deeper waters (Webster and Hutchinson, 1994). Downwind concentrations have been reported under conditions of higher but steady wind speeds (Cyr, 2017).

Wind exposure and persistence of wind direction can affect how phytoplankton patches form and the extent and duration of phytoplankton patches. Lakeshore morphometry can create sheltered areas of a lake, setting up heterogeneity in wind exposure over the lake surface. This differential wind exposure can set up the development of gyre circulations, with algal patches forming and persisting within them (Schernewski et al., 2005) (Fig. 3). Circulation patterns and the effect on phytoplankton populations will differ over time as a result of changing wind direction. For example, a concentration of algal cells resulting in a surface bloom can occur at times coincident with the prevailing wind direction, as a result of the circulation pattern, compared with times when winds are perpendicular to the main axis of a lake, which results in multiple circulation cells occurring and no bloom (Schernewski et al., 2005). Long-term reductions in wind speed have also been associated with increased extent and duration of cyanobacterial blooms, as cells are not mixed away from the surface or dispersed laterally (Wu et al., 2015).

Fig. 3 Surface phytoplankton bloom following basin scale circulation patterns in Lake Atitlan, Guatemala, 2009. From NASA Earth Observatory image by Jesse Allen, based on data from the NASA/GSFC/METI/ERSDAC/JAROS, and U.S./Japan ASTER Science Team https://earthobservatory.nasa.gov/images/41385/harmful-bloom-in-lake-atitlan-guatemala.

In addition to the surface effect of wind on algal populations, in stratified lakes, internal waves, caused by the oscillation of the thermocline can also drive patch formation in phytoplankton through direct and indirect effects. Internal waves form following thermocline tilting due to wind stress thickening of the upwind epilimnion, which can oscillate once the wind stress is released. These waves interact at the edges of the lake basin where waves can break and result in episodic vertical transport of nutrients from the hypolimnion to epilimnion. Where thermocline tilting is strong, regions of upwelling water at the downwind area of a lake can mix deeper phytoplankton layers to the surface (George and Edwards, 1976). In addition, internal waves can also affect the horizontal distribution of sub-surface accumulations of phytoplankton, such as the cyanobacterium *Planktothrix rubescens*, altering the vertical and horizontal position of the maximum biomass over the course of several days (Cuypers et al., 2011). The accumulation of phytoplankton into patches has implications for the location of biogeochemical cycling in lakes and the potential for hazardous species to impact on ecosystem services provided by the lake. For example, the accumulation of cyanobacteria scums around drinking water draw-off points or along bathing beaches can detrimentally affect the provision of freshwater and amenity use.

Methods for quantifying turbulence and phytoplankton

Technological developments over recent years are enabling improved observations of both the physical properties of water, including turbulence and mixing, and the vertical and horizontal distribution of phytoplankton to be captured at finer scales. As turbulence is so varied over both time and space, fully characterizing turbulence in lakes is very challenging. Measurements of turbulence can be made using highly sensitive instruments such as microstructure profilers, which typically measure temperature, conductivity and shear many times per second as they descend through the water column. These measurements can be used to calculate the dissipation rate of turbulent kinetic energy, which provides a measure of the turbulence of the water. An alternative approach, which is frequently adopted in lake systems, is the use of moored Acoustic Doppler Current Profilers (ADCPs). These instruments can provide measures of water current velocity and the dissipation rate of turbulent kinetic energy and modes of seiching, depending on their configuration (Simpson et al., 2011). Accurate measurements of water temperature over a vertical profile, using for example, thermistor strings, can also provide a means of calculating vertical eddy diffusivity for heat, K_z, which can be used as a measure of vertical water column mixing below the surface layer, where other processes are assumed to be negligible (Jassby and Powell, 1975).

The advent of increasingly sophisticated sensors for measuring biological components of lake systems is leading to an improved resolution of measurement of vertical and horizontal planes in lakes. The deployment of vertical profiler systems with multi-parameter sonde attachments capable of measuring chlorophyll *a* or phycocyanin is providing sub-daily resolution data on the vertical distribution of phytoplankton and even distinguishing broad algal groups based on pigment fluorescence. This high frequency measurement over monthly and longer time periods enables the interactions between physical changes in the water column and interactions of the phytoplankton to be characterized in greater detail. Across horizontal dimensions the increasing use of Earth Observation through satellites and drone technology is enabling the spatial extent and spatial dynamics of algal blooms to be tracked at daily and sub-daily frequency. Linking short term spatial observations of algal movements with two-dimensional and three-dimensional physical models driven by weather predictions is starting to be used to predict bloom movements and enable the forecasting of their potentially hazardous accumulation.

Conclusion/synthesis

This chapter introduces the key features of biophysical interactions in phytoplankton. It considers how interactions occur and manifest themselves at different temporal and spatial scales. Biophysical interactions occur at the microscale as a result of the size and strength of turbulent eddies and swimming or sinking behavior of individual cells. These interactions can have macroscale effects on lake thermal structure, the vertical distribution of phytoplankton cells in response to their resource environment and result in horizontal patch formation at the lake basin scale. Phytoplankton are both structured by and, in some cases, structure their physical environment. These interactions drive community changes, species interactions and the provision of ecosystem services like drinking water and recreation amenity.

Knowledge gaps

- The role of physical mixing in inducing behavioral, physiological and morphological responses in phytoplankton
- Understanding the importance of bioconvection as a mixing process in lake ecosystems
- Process-based links between physical mixing processes and spatial patch formation and dissipation in phytoplankton
- The extent of backscattering of incoming solar radiation by phytoplankton
- The influence of climate on how light attenuation impacts thermal structure
- Detailed high frequency in-situ data on phytoplankton species and morphology

Case studies

Lake	*Topic*	*References*
Lake Cadagno	Bioconvection	https://aslopubs.onlinelibrary.wiley.com/doi/full/10.1002/lno.11702
Lake Superior	Deep chlorophyll maxima	https://www.sciencedirect.com/science/article/pii/S0380133004703901?via%3Dihub https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lno.10656#:~:text=The%20vertical%20distribution%20of%20chlorophyll,deep%20chlorophyll%20maximum%20(DCM)
Esthwaite Water	Horizontal patterns in phytoplankton	https://www.jstor.org/stable/2259185?seq=1#metadata_info_tab_contents https://www.cabdirect.org/cabdirect/abstract/20113227230
Rotorua Lakes Region	Horizontal patterns in phytoplankton derived from satellite images	https://www.sciencedirect.com/science/article/pii/S0303243421002543?via%3Dihub

See Also: **Emerging methods and topics**: Dust and Fog Effects on Inland Waters; **Fundamental concepts and theories**: Comparative Primary Production; **Structures and functions of Inland Waters - Lakes**: Benthic Algae in Lake Littoral Habitats; Currents in Stratified Water Bodies 1: Density-Driven Flows; Currents in Stratified Water Bodies: Internal Waves; Phytoplankton Productivity; Saline Lakes; Small-Scale Turbulence and Mixing: Energy Fluxes in Stratified Lakes; Surface Mixed Layers in Lakes; **Structures and functions of Inland Waters - Rivers**: Algae and Primary Production of Streams and Rivers Ecosystems

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Measurement and Variability of Lake Metabolism

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Anabolism Metabolic pathways that synthesize complex molecules from smaller molecules.
Attenuation The gradual loss of light intensity through the water column.
Autochthonous Material produced within the lake itself.
Autotrophic Organism producing its own organic matter from inorganic carbon (CO_2), using light or inorganic chemical reactions as an energy source.
Benthic Region of the lake including the sediment surface and shallow sub-surface layers.
Catabolism Metabolic pathways that breakdown complex molecules into smaller units.
Catchment Area of land where precipitation collects and drains towards a lake.
Ecotone The transitional area between two adjacent ecosystems.
Heterotrophic Organism that cannot produce its own organic matter, rather obtains organic materials from living organisms or detrital organic matter.
Hydraulic retention time Average length of time that a water molecule remains in the lake.
Lake metabolism The sum of anabolic and catabolic pathways in a lake.
Littoral Near shore area where light penetrates to the bottom of the lake.
Pelagic Open water area where light does not penetrate to the bottom of the lake.
Photooxidation Oxidative degradation caused by light (this article focuses on photooxidation of dissolved organic matter).
Stoichiometry Relationship between the relative quantities of substances forming a compound or material, typical expressed as a ratio.
Stratification Separation of water into distinct lake layers caused by different water densities.

Lake metabolism

Lake metabolism represents the collective breakdown (catabolism) and synthesis (anabolism) of molecules within a lake. Organismal metabolic rate, from bacteria to fishes, is influenced by organism size and a few key constituents, namely light, nutrients, temperature, and organic matter. The influence of these constituents on organismal metabolism ultimately governs metabolism at the whole-lake scale (i.e., lake metabolism) and can influence whether a lake is a net source or sink of carbon. Estimates of lake metabolism provide insight into energy flow within the lake, measures of trophic status, and how a lake contributes to broad-scale biogeochemical cycling. Variations in constituents that influence lake metabolism result in differences in metabolic rates across lakes and also within lakes both spatially (vertically or horizontally) and over time. The first estimates of

lake metabolism were made several decades ago based on diel measurements of dissolved gasses within freshwater systems (Odum, 1956). With recent advancement in sensor technologies, estimating lake metabolism has become much more accessible, providing unique opportunities for addressing fundamental questions of energy transformation within lakes. In this article, we describe the key drivers of within and across lake variability in lake metabolism including nutrient and light availability, temperature, and organic matter concentration and how these drivers shape lake metabolic patterns across Earth's biomes.

Most metabolic reactions in lakes use oxygen since it is a favorable electron acceptor for organisms. There are several energy pathways utilized by lake organisms that do not involve oxygen, such as iron reduction, acetoclastic methanogenesis, denitrification, and anoxygenic photosynthesis. Although these metabolic processes that utilize electron acceptors other than oxygen are less energy efficient, they can contribute significantly to total lake metabolic rates in some instances. However, much of the focus of lake metabolism studies have been on oxygenic processes, such as aerobic respiration and oxygenic photosynthesis, and this article will cover methods for estimating and constraints on these oxygenic processes. From here on, when we refer to lake metabolism or metabolism in this article, we are referring to oxygenic metabolic processes.

Methods of estimating lake metabolism

Overview

Estimating whole-lake metabolism requires approximating processes that influence the production and consumption of organic carbon by organisms within the lake. Understanding a few key processes and main components of lake metabolism allows researchers to estimate whole-lake metabolism or metabolism at certain locations within a lake. Estimating aerobic metabolism involves measuring molecules produced or consumed in photosynthesis and respiration (Eq. 1). Primary production and respiration are often highly correlated in lakes and span a wide range of metabolic rates (Hoellein et al., 2013; Fig. 1).

$$\begin{aligned} &\text{Photosynthesis}: 6CO_2 + 6H_2O \overset{\text{light}}{\rightarrow} C_6H_{12}O_6 + 6O_2 \\ &\text{Respiration}: C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O \end{aligned} \quad (1)$$

Bottle bioassay method

Photosynthesis only occurs in the presence of light while respiration is a continuous process and occurs in both the presence and absence of light. This key difference between the two processes allows researchers to estimate these fundamental components of lake metabolism by measuring oxygen or carbon dynamics using paired light and dark bottles. With this method, the researcher incubates lake water in two separate bottles, one that is clear and exposed to natural or artificial light regime, the "light" bottle, and another that is sealed off from the light by wrapping the bottle in foil, paint, or another method, thereby shutting off photosynthesis, the "dark" bottle. Changes in carbon fixation or dissolved gasses (O_2 or CO_2) are then measured over a certain time period (e.g., several hours to a day) to estimate the rate of metabolism for specific lake depths, which could be used to estimate metabolic rates for an integrated water column. Carbon fixation can be measured by adding radioactive carbon isotopes, such as ^{14}C, into the bottles, sampling the bottles over time to measure how much carbon has been incorporated into algal cells. Dissolved gas concentrations within the bottles can be measured with dissolved gas probes or the Winkler titration method. The dark bottle gives an estimate of lake respiration (R, table 1), while the light bottle gives an estimate of lake net ecosystem production (NEP, Table 1) since both photosynthesis and respiration occur in the light bottle (Fig. 2). Adding the dark bottle oxygen production rate (should be negative since respiration consumes oxygen) to the light bottle oxygen production rate (could be negative or positive) yields an estimate of gross primary production (GPP, Table 1). Although the light and dark bottles are simple to implement, they

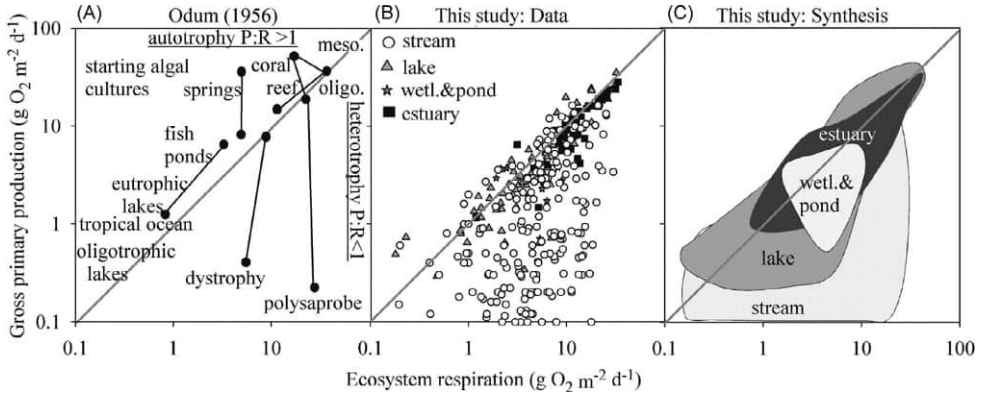

Fig. 1 Rates of gross primary production and ecosystem respiration for several aquatic ecosystems including lakes. From Hoellein TJ, Bruesewitz DA and Richardson DC (2013) Revisiting Odum (1956): A synthesis of aquatic ecosystem metabolism. *Limnology and Oceanography* 58: 2089–2100. https://doi.org/10.4319/lo.2013.58.6.2089.

Table 1 Lake metabolism terms.

Abbreviation	*Term*	*Explanation*
GPP	Gross Primary Production	Total photosynthesis from all autotrophic organism within the lake
R	Total Respiration	Total respiration from autotrophic and heterotrophic organisms within the lake
R_h	Heterotrophic Respiration	Respiration from heterotrophic organisms
R_a	Autotrophic Respiration	Respiration from autotrophic organisms
NEP	Net Ecosystem Production	Net balance of photosynthesis and respiration in the lake (GPP – R)
NPP	Net Primary Production	Net organic carbon produced from autotrophic organisms (GPP – R_a)

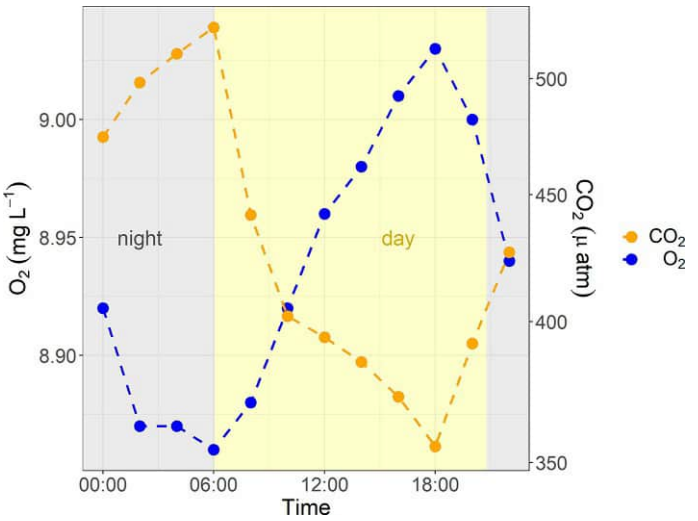

Fig. 2 Example of O_2 and CO_2 cycle within a lake upper mixed layer (epilimnion). During the day, gross primary production outpaces lake respiration resulting in a net production of O_2 and consumption of CO_2. Later in the day when solar radiation is reduced and during the night when there is no light, respiration still occurs in the absence of gross primary production resulting in net consumption of O_2 and production of CO_2. Data for this figure are from Harp Lake on August 1, 2014 (Vachon et al., 2020). By Ludmila S. Brighenti and Jacob A. Zwart—Created and shared by Ludmila S. Brighenti and Jacob A. Zwart to be uploaded to Wikimedia., CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=97281590.

can be limited in their inference of whole-lake metabolism since estimates of metabolism from the bottle would need to be extrapolated to the entire lake, which often does not capture the spatial heterogeneity of metabolism vertically or horizontally within a lake.

Whole-lake carbon budget method

To better assess metabolism at the whole-lake scale, researchers can measure all the inputs, outputs, and accumulation of either organic or inorganic carbon to a lake over a season or year, also known as a whole-lake carbon budget. Typically, the most important carbon inputs to a lake include surface water and groundwater inflows and litterfall, while the most important outputs include surface water and groundwater outflows and carbon gas emissions. Lakes also accumulate carbon in the water column and lake sediments. This labor-intensive method can be used to estimate NEP. Since NEP is the difference between gross primary production and respiration (NEP = GPP – R), it can be viewed as the net biological conversion of inorganic carbon to organic carbon (and vice versa; Eq. 1) and can thus be determined through whole-lake mass balance of either inorganic or organic carbon (Stets et al., 2009).

Free-water method

Measurement of diel changes in dissolved gasses within the lake, also known as the "free-water" method, has quickly become one of the most common methods of estimating lake metabolism since the wide adoption of autonomous sensors used to measure dissolved oxygen and carbon dioxide in water (Fig. 2). The free-water method is particularly popular since many daily estimates of lake metabolism can be collected relatively inexpensively and can give insights into metabolic regimes during difficult-to-observe time periods, such as during storm events. Measured changes in dissolved oxygen and carbon dioxide within a lake represents the sum of all organismal metabolism from bacteria to fishes, after accounting for abiotic changes in dissolved gasses such as atmospheric gas exchange and advection (Fig. 3). This concept is similar to the light and dark bottle method but at a much larger measurement footprint. Since photosynthesis does not occur without light, changes in O_2 or CO_2 during the night represents lake

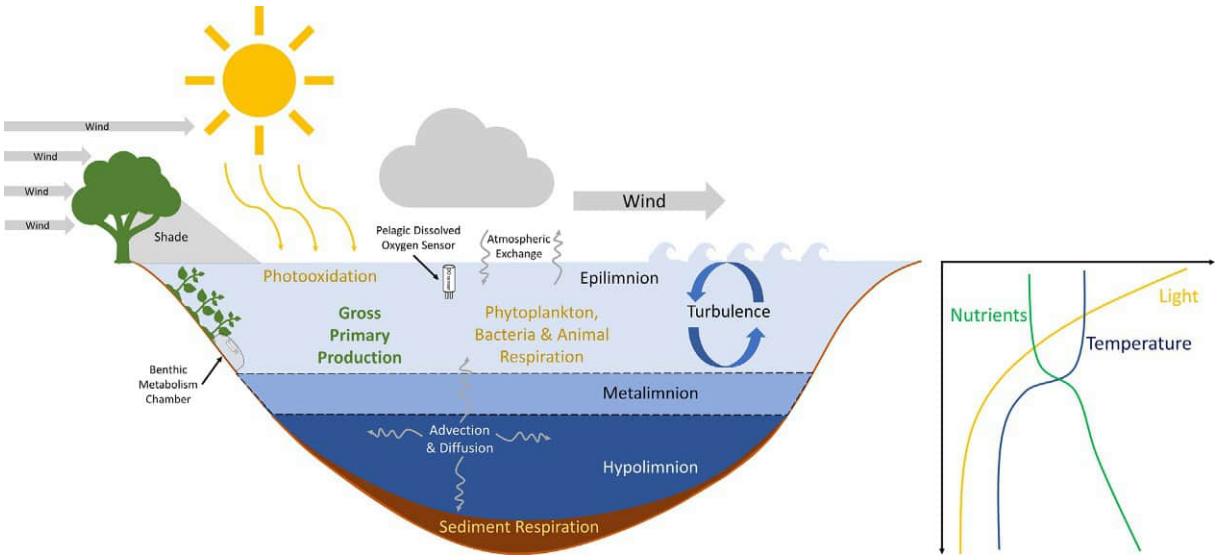

Fig. 3 Lake cross-sectional diagram of the factors influencing lake metabolic rates and concentration of dissolved gasses within lakes. Processes in gold text consume oxygen and produce carbon dioxide while processes in green text produce oxygen and consume carbon dioxide. Physical processes can both increase or decrease dissolved gas concentration, for example atmospheric gas exchange can increase or decrease lake dissolved oxygen depending on whether the lake is undersaturated or oversaturated in dissolved oxygen compared to the atmosphere, respectively. The panel on the right shows how light, temperature, and nutrients tend to change with depth for a stratified lake, which in turn results in variation in metabolic rates vertically within a lake. By Ludmila S. Brighenti and Jacob A. Zwart—Created and shared by Ludmila S. Brighenti and Jacob A. Zwart to be uploaded to Wikimedia., CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=91461560.

ecosystem respiration (R). Measuring the net change in O_2 or CO_2 over a 24-h period yields an estimate of net ecosystem production (NEP), and adding NEP and R together gives an estimate of GPP. The changes in lake dissolved oxygen concentrations (DO) is represented as:

$$DO_{t+1} = DO_t + GPP_t - R_t + F_{atm,t} + F_{dv,t} \quad (2)$$

where DO_{t+1} and DO_t are the dissolved oxygen concentrations (mg L^{-1}) at times t + 1 and t; $F_{atm,t}$ is the flux of O_2 between the lake and the atmosphere; and $F_{dv,t}$ is the flux of O_2 between water masses driven by advection, turbulent diffusivity, and differences in O_2 concentrations (diffusion). Dissolved oxygen concentrations are usually measured with a oxygen probe, either by a researcher visiting the lake and manually measuring oxygen concentration or via an automated sensor. Gas fluxes between the lake and atmosphere can be measured via floating chambers or eddy covariance methods but are more typically estimated using numerical models relating gas flux to surface water turbulence stemming from wind and changes in lake water temperature. Likewise, diffusive flux of gasses within the lake are typically estimated with numerical models but can be measured with specialized instruments.

Extracting a high signal-to-noise ratio is key to obtaining good estimates of lake metabolism from the free-water technique. Estimates of lake metabolism can be optimized by adequate consideration of the data collection and analysis methods used such as: location of dissolved gas collection (typically in the surface mixed layer); number of sensors vertically and horizontally (Obrador et al., 2014; Van de Bogert et al., 2012); frequency and duration of data collection; and, modeling methods (Staehr et al., 2010a). Extrapolating site or depth specific measurements to the entire lake can be problematic, especially if there is high spatial variability within a given lake. Multiple sensors in the lake, either horizontally or vertically distributed, or targeting different environments (e.g., benthic vs. pelagic metabolism), can help resolve some of the heterogeneity issues when estimating whole-lake metabolism. Correctly accounting for physical processes of dissolved gas dynamics is needed to achieve good estimates of lake metabolism using the free-water method. For example, differing models of gas exchange with the atmosphere can lead to widely varying estimates of lake metabolism (Dugan et al., 2016), and thus, researchers should carefully consider which gas exchange method is most appropriate for their study site. The free-water technique often requires programming skills and knowledge of many equations to convert sensor data to estimates of lake metabolism. Luckily, there are open-source, community-built tools that reduce these analytical barriers, such as the R software package *LakeMetabolizer* (Winslow et al., 2016).

As mentioned above, aerobic processes are most commonly considered in lake metabolism studies in which it's assumed that anaerobic processes contribute negligibly to O_2 and CO_2 dynamics. However, paired O_2 and CO_2 sensors have shown that these dissolved gasses can deviate from the assumed 1 to −1 line (Vachon et al., 2020), meaning that there can be processes not accounted for in lake metabolism studies if only aerobic processes are considered.

Benthic metabolism

In addition to pelagic metabolism, benthic metabolism from periphyton and sediment organisms can sometimes account for a significant portion of whole-lake metabolism. Analogous to the light and dark bottle methods described above ("Bottle bioassay method" section), lake sediment cores can be collected and changes in dissolved oxygen or carbon fixation can be used to estimate rates of primary production and respiration. Recent methods describe isolating the sediment-water interface with transparent domes and measure changes in dissolved oxygen in situ (Godwin et al., 2014), which is a hybrid between the free-water method and light-dark bottle method (Fig. 3).

Constraints on lake metabolism

In the following section, we describe the relationship between constituents that influence organismal and ecosystem-level metabolism, focusing on light, organic matter (OM), nutrients and temperature. Although relationships between organisms and individual constituents are well-established, interacting effects of constituents on metabolic rates from organisms to lake ecosystems makes predicting changes in metabolism across lakes or within lakes through time difficult. Here, we discuss how these basic constraints affect lake metabolism and in "Variable metabolic responses to atmospheric forcings" section we show some examples of how some of these factors and confounding effects can affect lake metabolism at various space and time scales.

Light

Light is one of the primary drivers of primary production since it is essential for the conversion of carbon dioxide and water into organic matter through photosynthesis (Eq. 1). Experimental studies of light dependency of primary production typically show a non-linear relationship. The initial linear increase of primary production with increasing light availability is interpreted as conditions where primary production is mostly light-limited. As light intensity continues to increase, primary production is considered 'light-saturated' when primary production does not increase with light, but rather is limited by other constituents, typically nutrients and temperature. Different species of primary producers have different light utilization efficiencies and different optimum light for growth (Schwaderer et al., 2011). Moreover, the light utilization efficiency of phytoplankton increases with increasing nutrient availability and is higher under low light conditions due to the optimization use of light through physiological and structural adaptations (Girdner et al., 2020). These different responses at the organismal level propagate to influence whole-lake metabolism (Staehr et al., 2016; Zwart et al., 2015). Nevertheless, a linear response of GPP to light remains often a good approximation indicating light-limitation of primary production (Hanson et al., 2008), even in lakes with low nutrient availability (Karlsson et al., 2009). This has typically been explained by self-shading within the algal community and by the vertical distribution of light throughout the water column, where the upper part of the water column may be exposed to light-saturated conditions, whereas deeper depths are light limited.

Light is unevenly distributed vertically through the water column, due to light attenuation (Fig. 3). Thus, GPP rates are also unevenly distributed and restricted to the photic zone of the lakes (i.e., uppermost layers of the water body where light is above 1% of the surface light). In a stratified lake, the vertical distribution of GPP depends highly on the balance between nutrient and light availability throughout the water column. Typically, nutrients increase in concentration from the top to the bottom lake layers while light decreases (Fig. 3). These opposing gradients of nutrient and light availability can lead to a chlorophyll peak in intermediate depths, called the deep chlorophyll maximum. Although more common in oligotrophic lake, in which a peak in dissolved oxygen accompanies the deep chlorophyll maximum, it can also occur in eutrophic and dystrophic lakes (Leach et al., 2018).

Seasonal variations in light levels are important drivers of seasonal variations in lake metabolic rates, especially in high-latitude lakes, where seasonality in light is more pronounced (Fig. 4). For a typical high-latitude lake, high incoming light during summer and spring and longer day length enhance GPP and stimulate R. Respiration rates are increased due to higher autotrophic biomass, but also due to more bioavailable organic matter (OM), coming from increased algal production and photooxidation of recalcitrant OM. Although less pronounced, higher photooxidation of recalcitrant OM during summer and spring also occurs in low-latitude lakes (Amaral et al., 2013). As day length becomes shorter and incoming solar radiation decreases during autumn and through winter, metabolic rates decrease and GPP becomes more light-limited. For many of the world's lakes, ice and snow cover during winter blocks out incoming solar radiation and contributes to light-limitation in the water column (Song et al., 2019). Due to sampling difficulties, under-ice estimations of metabolic rates are scarce and dissolved oxygen depletion is poorly understood (Obertegger et al., 2017). In tropical lakes, seasonality due to differences in light through the four astronomical seasons (spring, summer, autumn, and winter) is less marked than in high-latitude lakes and usually follows annual changes in rainfall and water column stratification and mixing dynamics.

Organic matter

Consumers in lakes require organic matter to maintain organismal function, growth, and reproduction. Often, organic matter in lakes, whether particulate or dissolved, increases rates of respiration as consumers convert the organic matter to cellular growth and organismal maintenance. Indeed, surveys of respiration rates across lakes along an organic matter gradient often exhibit a positive

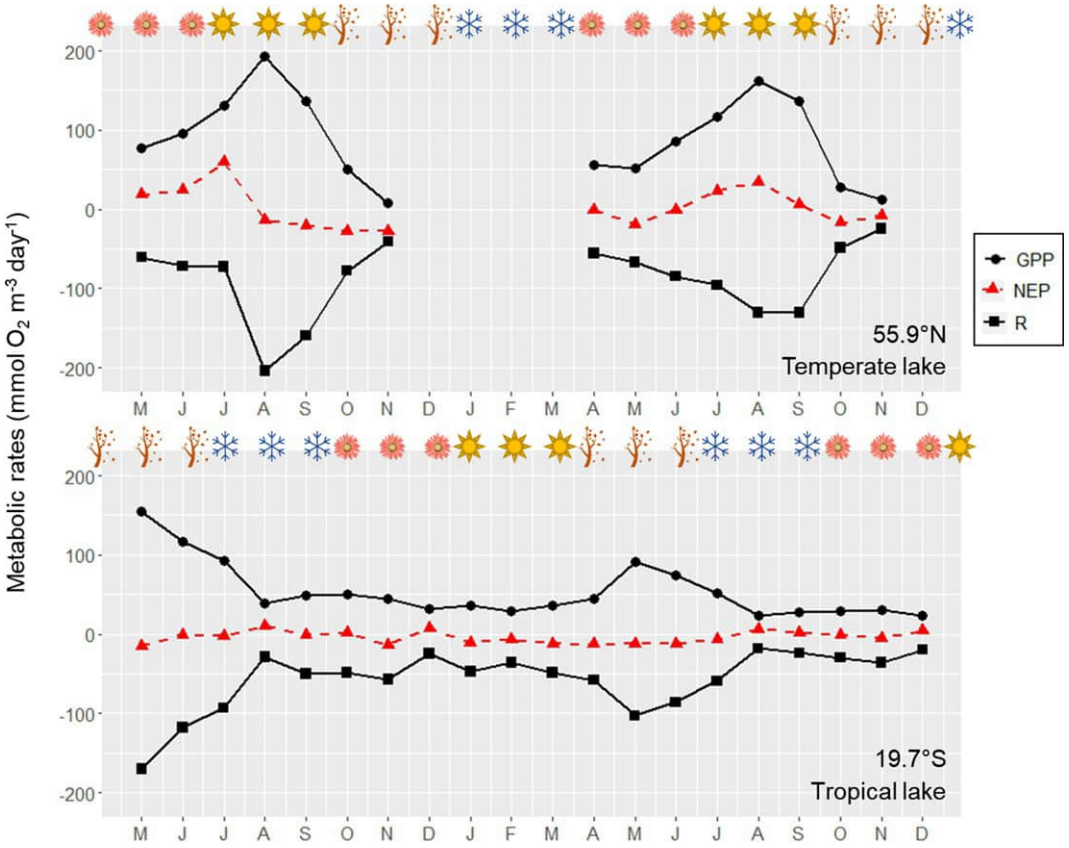

Fig. 4 Seasonal variations in metabolic rates during 20 months (from May to December) in a Danish temperate eutrophic lake (A) and in a Brazilian tropical mesotrophic lake (B). Symbols represent astronomical seasons (autumn—tree, winter—snowflake, spring—flower and summer—sun). Data for the temperate lake was digitized from Fig. 7 in Staehr and Sand-Jensen (2007) and data for the tropical lake is the monthly average of metabolic rates in Brighenti et al. (2015). By Ludmila S. Brighenti and Jacob A. Zwart—Created and shared by Ludmila S. Brighenti and Jacob A. Zwart to be uploaded to Wikimedia., CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=97325463.

relationship between organic matter concentration and respiration (e.g., Hanson et al., 2003). Often, the excess respiration rate due to high concentration of organic matter exceeds the rates of primary productivity, resulting in a negative NEP. The negative NEP means that more CO_2 is produced than fixed within the lake, indicating that these lakes are likely net emitters of CO_2 to the atmosphere. Highly stained dissolved organic matter can cause an even greater negative NEP due to high attenuation of incoming light, thereby limiting primary production while sustaining ecosystem respiration. Hanson et al. (2003), in a study with 25 high-latitude lakes in the United States, found a positive correlation between R and dissolved organic carbon (DOC), and a negative correlation between NEP and DOC (Fig. 5). However, there is a lack of consensus on the literature regarding the straightforward positive relationship between DOC concentrations and R (Solomon et al., 2013). These varied findings highlight the complexity regarding effects of DOC on lake processes, such as differences in DOC quality and the shading effect of DOC, that can reduce GPP and respiration rates from primary producers (R_a, table 1).

Nutrients

Organisms need different elements to compose biological structures (e.g., enzymes, nucleic acids, cell walls) and maintain biological processes (e.g., photosynthesis, cellular respiration). These elements are called nutrients, and their availability and rate of assimilation control the rate of metabolism from the cellular to the ecosystem level. In lakes, phosphorus (P) and nitrogen (N) are the most common limiting nutrients to primary production and ecosystem respiration. Although P is often referred to as the main limiting nutrient in lakes, lake metabolism can be limited by N or co-limited by P and N (Elser et al., 2007).

Temporal and spatial variation in nutrient availability and its stoichiometry are important drivers of temporal and spatial variations in lake metabolic rates. For example, temporal changes in the catchment (e.g., between seasons and years) affect metabolic rates by altering nutrient and organic matter inputs to the lake, light attenuation and mixing dynamics. Regarding changes in nutrient availability due to changes in the catchment, land use conversions to croplands, pasturelands, and urban areas are associated with increased input of nutrients to the water bodies (Delkash et al., 2018), leading to eutrophication and enhanced GPP and R.

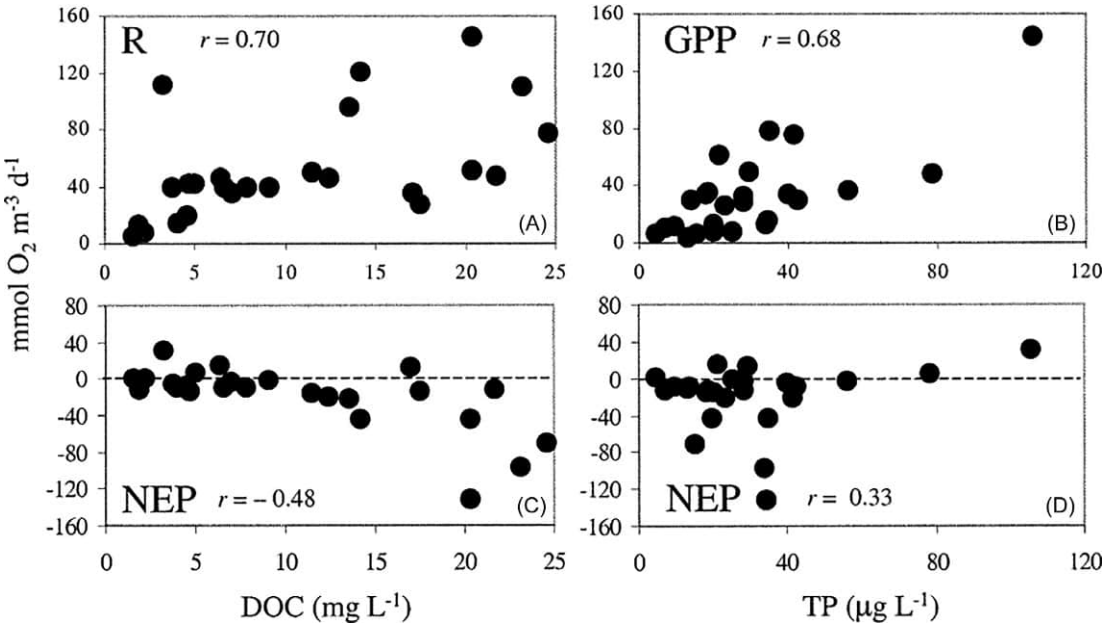

Fig. 5 Relationship of metabolic rates with dissolved organic carbon (DOC) and total phosphorus (TP) concentrations in 25 lakes in Wisconsin and Michigan (USA). From Hanson PC, Bade DL, Carpenter SR and Kratz TK (2003) Lake metabolism: Relationships with dissolved organic carbon and phosphorus. *Limnology and Oceanography* 48: 1112–1119.

Spatially within lakes, nutrients availability can differ laterally from the littoral to the pelagic zone as well as vertically in the water column (Fig. 3). Littoral areas are more prone to receive nutrient inputs from the catchment and also to internal loading from the sediments than pelagic zones. Moreover, littoral areas are more complex and heterogeneous due to high sediment-to-water volume ratio, presence of macrophytes, and due to the water-terrestrial ecotone. Therefore, metabolic rates are usually higher and more variable in the littoral area compared to the open water pelagic zone (e.g., Van de Bogert et al., 2007).

Lakes with different trophic status (i.e., differences in nutrient levels) have different metabolic rates, usually following the gradient from a lower GPP and R in oligotrophic lakes to a higher GPP and R in eutrophic lakes. However, the variation of NEP with trophic status is not so straightforward. Research has shown a weak correlation between NEP and phosphorus concentration (Fig. 5; e.g., Hanson et al., 2003; Solomon et al., 2013), that can be partially explained by the balance between nutrient availability, stimulating primary production, and organic matter availability, stimulating heterotrophic respiration. In a study of 25 globally-distributed lakes, Solomon et al. (2013) reported that although GPP and R increased with increasing total phosphorus (TP), NEP was higher in lakes with higher TP and moderate DOC levels.

Temperature

Temperature influences not only the spatial distribution and the occurrence of organisms, but also the rates of biological activities, physiological processes, and biochemical reactions. Metabolic rates have a hyperbolic relationship with temperature, increasing exponentially, and decreasing at high temperatures outside of organismal optimal ranges. However, thermal stress is not often documented within the temperature ranges experienced by most organisms in their natural sites.

The temperature-dependence of R differs from the temperature-dependence of GPP due to the higher activation energy of aerobic respiration compared to oxygenic photosynthesis (Fig. 6). Thus, R increases more rapidly with increasing temperature than GPP, which influences the metabolic balance of the lakes and can determine whether lakes are net sources or sinks of carbon. Theoretically, with all other factors affecting metabolic rates held constant, warmer lakes are more likely to be net heterotrophic (negative NEP) than similar lakes with colder water. Moreover, temporal variations in temperature drive temporal variations in metabolic rates, especially on respiration rates. On a daily scale, R is largely affected by changes in water temperature due to the day-night cycle (Yvon-Durocher et al., 2012) and affected across days due to changes in weather conditions and inflow of groundwater or surface water masses of different temperatures than the lake. Seasonally, lower temperatures during winter months lead to lower metabolic rates compared to summer months, and this difference is more pronounced in high-latitude and high-altitude lakes that freeze during the winter. Notably, a majority of lakes in the world are at higher latitudes meaning that most lakes' metabolism is significantly influenced by seasonal changes in temperature (Obertegger et al., 2017). However, seasonal dynamics of metabolic rates are complex because seasonal variations encompass multiple factors, including temperature, incident light, and nutrient and organic matter availability.

In addition to temperature, organismal size and community structure can also influence rates of lake metabolism at the ecosystem scale. The Metabolic Theory of Ecology predicts that metabolic rates should vary with body size and temperature

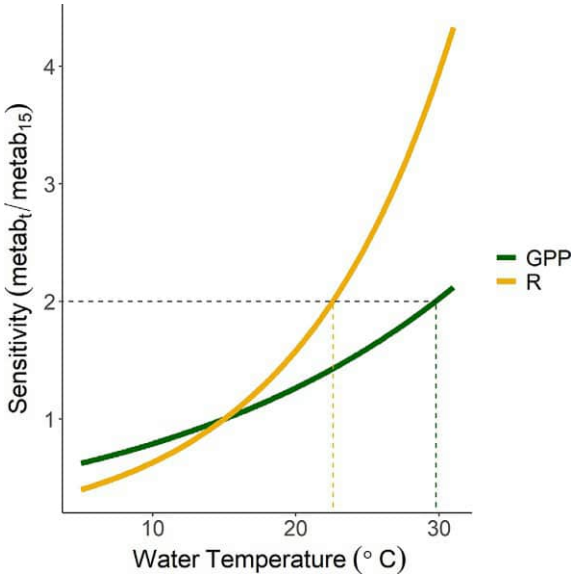

Fig. 6 Temperature sensitivity of gross primary production (GPP) and respiration (R) based on average activation energies reported in Yvon-Durocher et al. (2012). As water temperature increases, R increases more rapidly than GPP due to the higher average activation energy for R. In this figure, GPP and R temperature responses are reported as relative to GPP and R rates at 15 °C. A doubling of metabolic rates compared to metabolic rate at 15 °C (horizontal dashed line) occurs with just a 7.6 °C increase for R but requires a 14.8 °C increase to double GPP. By Ludmila S. Brighenti and Jacob A. Zwart—Created and shared by Ludmila S. Brighenti and Jacob A. Zwart to be uploaded to Wikimedia., CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=97281589.

(Brown et al., 2004; Enquist et al., 2003), where organisms with smaller body sizes should have a higher metabolic output per unit body mass. This means that if an aquatic community is made up of primarily small organisms, then this community is predicted to have a higher metabolic rate per total biomass at a given temperature compared to a community that is comprised of mostly large organisms. There is some experimental support for these theoretical predictions as well, where aquatic communities with relatively small organisms had a higher temperature-corrected metabolic output (Yvon-Durocher and Allen, 2012).

Variable metabolic responses to atmospheric forcings

Interacting effects of constituents on metabolic rates makes predicting changes in lake metabolism across lakes or within lakes through time a challenging task (e.g., Olson et al., 2020). Understanding these complex interactions on metabolic rates is important given the multiple environmental factors that are expected to change under climate and land use change in the coming decades, including rising water temperatures, changing water column stability, and changing nutrient loading rates. Improving our understanding of how interacting drivers affect lake metabolism will help predict how lakes fit into global biogeochemical cycles and is essential to understand when trying to predict how the world will respond to future perturbations in climate and land use. In the following section, we highlight a couple of scenarios where interacting drivers have complex effects on lake metabolism.

Storm effects on lake metabolism

Storm events that bring strong winds and heavy precipitation affect the balance between light and nutrient availability and in turn affect lake metabolism. However, not all storms affect lake metabolism in the same way for all lakes; for example, some storm events increase net ecosystem production while others decrease. The response of lake metabolism to storm events is related to several interacting factors including the storm characteristics (e.g., duration, intensity, amount of rain), lake morphometric characteristics (e.g., lake depth), and landscape surrounding the lake (e.g., agricultural fields, forests) (Stockwell et al., 2020). Storms that are accompanied by strong winds deepen the mixed layer of lakes which can increase nutrient supply into the upper mixed layer from more nutrient-rich deeper lake layers (Giling et al., 2017). Nutrients can also come into lakes following storm events with heavy rain through increased stream and groundwater inflows to the lake (Zwart et al., 2017). This increase in nutrient supply often leads to increased GPP in the upper mixed layer several days following the storm.

Although storms can relieve primary producers from nutrient limitation, they can also increase light limitation through increased turbidity or loading of colored dissolved organic matter. Storms accompanied with heavy rain flush soil organic matter from the lake's surrounding landscape which increases light attenuation within the lake and can limit GPP despite the increase in nutrients. The increased organic matter load can increase respiration rates within the lake as bacteria and other organisms break down the organic matter and convert it to inorganic carbon (Eq. 1). These complex and interacting effects of storms on GPP and R

can cause some lakes to increase in NEP (GPP > R) while other lakes decrease in NEP (GPP < R) following the storm events. The storm characteristics influence whether lakes increase or decrease in NEP, but lake characteristics can also influence metabolic response. For example, lakes with very long hydraulic retention times show little metabolic response to storm events while lakes with short hydraulic retention times exhibit stronger metabolic responses (Zwart et al., 2017). However, extremely short hydraulic retention times following storms (e.g., 1 day or less) can cause scouring and complete flushing of organisms within the lake or reservoir, which can greatly reduce metabolic activity (Williamson et al., 2021).

Global warming effects on lake metabolism

Temperature is an important regulating factor of lake metabolism, either directly through temperature dependence of physiological rates of respiration and photosynthesis, or indirectly through effects on lake physical processes such as mixing dynamics of the water column.

As described in "Temperature" section, metabolic rates increase exponentially with temperature. Temperature dependence of metabolism is affected by the kinetics of molecules through the activation energy, or the proportion of molecules with enough kinetic energy to start the metabolic reaction. However, this temperature dependence differs between R and GPP due to the higher activation energy of aerobic respiration compared to photosynthesis (Fig. 6). Thus, it is predicted that as temperature increases with global warming, R will increase more rapidly than GPP, in turn leading to a higher heterotrophy of lakes globally. This hypothesis has been corroborated by a manipulative experimental study, which showed that a long-term increase in water temperature causes a shift in experimental ponds from carbon-sink to carbon-sources, reducing carbon sequestration (Yvon-Durocher et al., 2017). These can lead to positive feedback to global warming due to enhanced emissions of greenhouse gasses from lakes, such as carbon dioxide and methane.

Warming temperatures can also influence the size spectrum of the organisms that make up the lake community, which can influence rates of ecosystem metabolism as predicted by the Metabolic Theory of Ecology (Brown et al., 2004; Enquist et al., 2003). Artificial warming experiments have shown that increases in water temperature increase the prevalence of small organisms in the phytoplankton community (Yvon-Durocher et al., 2011). The reduced average size of organisms with increased warming can, in turn, increase the metabolic output per unit biomass independent of direct temperature effects on cellular metabolism (Yvon-Durocher and Allen, 2012).

In regard to the indirect temperature effects on metabolism, some lakes' metabolic rates are strongly influenced by the dynamics between mixing and stratification of the water column. Studies have shown a trend overall the past decades with a warming of surface water and more stable water columns in lakes around the globe, which can potentially affect the mixing and stratification dynamics of lakes (Pilla et al., 2020), thus affecting temporal dynamics of lake metabolism. During mixing events, nutrients, organic matter, and organisms such as bacteria, which were concentrated in the aphotic zone are made available for the euphotic zone of the lake, often stimulating primary production and respiration. However, mixing events and a less stable water column can also cause a decrease in water transparency, which can limit primary production in some environments or at certain times of the year. Whether or not GPP rates increase will depend on a balance between increasing nutrient availability and decreasing light availability (Fig. 7).

In lakes where primary production is mainly limited by light, as in some temperate (e.g., Staehr et al., 2010b) and subtropical lakes (e.g., Tonetta et al., 2016), it is common that, during the mixing season, GPP rates decrease due to less light availability. For example, in a two-year study in a eutrophic temperate lake in Denmark (Staehr and Sand-Jensen, 2007), GPP and NEP increased

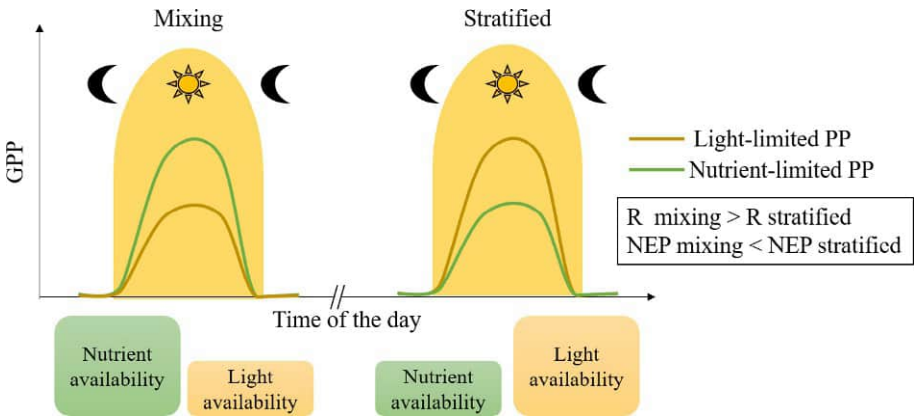

Fig. 7 Conceptual figure of the effects of mixing and stratification dynamics on gross primary production (GPP) in two different situations: one with light-limited primary production (PP) and other with nutrient-limited PP. During the mixing period, nutrient availability is increased, while light availability is decreased. During the stratified period, light availability is increased and nutrient availability is decreased. The scales at the bottom of the figure represent the balance between nutrient and light availability during the mixing and stratified period. R = ecosystem respiration; NEP = net ecosystem productivity. By Ludmila S. Brighenti and Jacob A. Zwart—Created and shared by Ludmila S. Brighenti and Jacob A. Zwart to be upload to Wikimedia commons., CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=91667821.

during summer stratification (Fig. 4), when temperature, light availability, and chlorophyll-a concentrations were higher and nutrient availability and mixing depth were lower. The increased GPP and NEP rates were highly associated with an increase in light availability. However, periods with relatively high R in comparison with GPP coincided with mixing events of the water column during autumn, due to the greater availability of organic matter, leading to a negative NEP.

In lakes where primary production is mainly limited by the availability of nutrients, mixing events are generally associated with an increase in GPP. For example, in a tropical mesotrophic lake (Brighenti et al., 2015), where light availability was high throughout the year, mixing events that occured in the dry and colder periods (autumn and winter) were associated with an increase in GPP (Fig. 4). In this case, the decrease in light availability was offset by an increase in the availability of nutrients. However, as respiration rates were also increased during the mixing period, NEP tended to remain in balance or slightly heterotrophic ($NEP \leq 0$).

In addition to direct and indirect thermal effects, global warming also influences changes in nutrients and organic matter inputs to lakes, lake water residence time, and lake hydrological balance. Thus, global warming consequences on lake metabolism are not straightforward and strongly interact with land use (Adrian et al., 2009). Differences in lake morphometry (e.g., lake size and shape), catchment properties (e.g., land use and drainage area), and water residence time will affect how metabolic rates differ between lakes and how they may respond to different environmental drivers, such as changes in rainfall regimes and land use. For example, Hayes and others (2015) studied phytoplankton nutrient limitation across 42 lakes in different watersheds. Their study reported a climate and land use interaction, affecting the occurrence and shifts from phosphorus-limitation to nitrogen-limitation in lakes with agricultural-dominated watersheds, whereas phytoplankton in lakes in forest-dominated watersheds were consistently nitrogen-limited.

Knowledge gaps

Recent methods and statistical techniques for estimating lake metabolism are providing insights into the complex relationship between lake metabolic rates and characteristics that control these rates. Often, these new insights are showing that these relationships are more complex and nuanced than previously thought, indicating that a holistic view of the effects on metabolism is the most appropriate approach. Understanding these complex interactions on metabolic rates is important given the multiple environmental factors that are expected to change under climate and land use change in the coming decades, including rising water temperatures, changing water column stability, and changing nutrient loading rates. Improving our understanding of drivers of lake metabolism will help predict how lakes fit into global biogeochemical cycles and is essential to understand when trying to predict how the world will respond to future perturbations in climate and land use. Several outstanding knowledge gaps remain that would help us understand current and future lake metabolism patterns, including:

- Improve accounting for benthic contribution to whole-lake metabolism.
- Test new hypotheses related to interacting effects of light and nutrient limitation on lake metabolism.
- Increase number of estimates of lake metabolism under ice.
- Increase number of estimates of lake metabolism studies for tropical lakes, especially African lakes.
- Improve methods to model physical processes when estimating metabolism using the free-water method.
- Increase number of estimates of horizontal and vertical variability in lake metabolism.

See Also: Fundamental concepts and theories: Chemosynthesis; Lakes as Ecosystems; Structures and functions of Inland Waters - Lakes: The Carbon Cycle in Lakes: A Biogeochemical Perspective; Structures and functions of Inland Waters - Rivers: Algae and Primary Production of Streams and Rivers Ecosystems; Energetics and Food Webs in Large Rivers

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https://github.com/GLEON/LakeMetabolizer—LakeMetabolizer.

Ecological Consequences of Climate Extremes for Lakes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie_Elodie Perga and Damien Bouffard.

Glossary

Aquatic hypoxia Reduction of the dissolved oxygen concentration in water to the point where it is detrimental for organisms living in that system.
Brunt Väisälä (BV) buoyancy frequency A metric of the stability of water column thermal stratification
Ebullition Bubble formation and loss.
Hypolimnion The lower layer of a stratified lake beneath the thermocline.
Resilience The capacity of a system to prevent a shift to an alternative state.
Schmidt stability The resistance to mechanical mixing due to the potential energy inherent in the stratification of the water column.

General introduction

Weather and longer term climatic cycles are fundamental drivers of change in lake ecosystems. This control is manifested in strong diel and seasonal cycles that are well recognized and described in lake thermal structure, biochemical cycling and biological processes. The climatic cycles that drive in-lake change also include decadal and longer-scale phenomena such as the North Atlantic Oscillation (NAO) and the El Niño/Southern Oscillation (ENSO). All of these cycles will, by definition, have periods of higher and lower values relative to average conditions. Any given lake ecosystem will be adapted to these recurring highs and lows. Recently, however, there has been an increasing research focus on the effect of extremes in both weather and climate on lakes, events which are projected to become even more intense and frequent due to the impacts of global warming. Such extreme events include not only more intense heatwaves and subsequent droughts, but also increases in the frequency and magnitude of, for example, storms. Sudden events like storms are difficult to predict. They result in pressures on lakes that can, in turn, have unexpected and even unprecedented consequences. Understanding how all these weather and climate related pressures subsequently cascade through lake ecosystems will be essential if we are to manage lakes and reservoirs in the future. The aim of this article is to provide an overview of current knowledge on the shorter and longer term effects of extremes in weather and climate on lake ecosystems. We review the definition of extreme weather and climatic events generally and in relation to lakes, describe how such events are propagated through catchments and within lakes, and more specifically how they affect lake physics, lake biogeochemistry and lake biota. We conclude by highlighting gaps in our current knowledge which need to be addressed to ensure that appropriate action can be taken to protect lakes and reservoirs and the services that they provide.

 https://doi.org/10.1016/B978-0-12-819166-8.00027-X

The definition of extreme events: Issues and challenges

While weather describes the atmospheric conditions as a certain location and time, climate refers to how the weather behaves on average over a more prolonged period or over a defined area. Both weather and climate can have extremes. This article will follow the Intergovernmental Panel on Climate Change (IPCC) (Seneviratne et al., 2012) and use the term climate extremes to collectively refer to both extreme weather events and extreme climate events. There is, however, no universally accepted definition of such events, either in relation to weather and climate extremes (Seneviratne et al., 2012) or in relation to the study of ecosystems, including lakes. In fact, the term extreme climatic event (ECE) has become more commonly used in ecological studies recently to include both weather and climate events and their impacts (van de Pol et al., 2017). Extreme events are usually defined (1) statistically, for example, by how frequently they occur or whether they exceed a particular threshold, or (2) based on the impacts they exert (van de Pol et al., 2017). Hydrologists also commonly define extremes in stream discharge using top and bottom percentiles (for example, the Q05 statistic representing the top 5% of stream flow rates), or return periods (for example, a 1-in-200 year flood event).

The IPCC have defined an extreme weather (or climate) event as "the occurrence of a value of a weather (or climate) variable above (or below) a threshold value near the upper (or lower) ends ("tails") of the range of observed values of that variable" (Seneviratne et al., 2012). One issue of note with this type of percentile or threshold approach is that the absolute values will differ depending on location. An assessment of the effects of storm events on a lake on the exposed Atlantic coast of Ireland, for example, used a definition of storms which included those times when mean hourly wind speed was higher than 97.5% of the dataset (the top 2.5%), corresponding to a wind speed threshold of 10.6 m s^{-1} (Andersen et al., 2020). In contrast, a study based in Lake Muzelle in the French Alps used the top 3% of values at that site and had a wind speed threshold of 3.0 m s^{-1} (Perga et al., 2018). In addition to such differences related to location, the temporal span of any dataset that is used to define the percentiles will also affect the magnitude of a change that is considered to be extreme. The use of set value thresholds can also be problematic for defining heatwaves. While there is a general acceptance that heatwaves are periods of extremely high temperatures, again there is no internationally accepted definition (McCarthy et al., 2019). Any defined threshold will again result in different absolute values depending on location, with heatwave thresholds at lower latitudes generally being higher than those at higher latitudes. This can also lead to anomalies even within national borders. For the island of Britain, for example, a heatwave has been defined using a threshold value of 25 °C for most of the island, but with the threshold increasing in increments up to 28 °C in the southeast (McCarthy et al., 2019). In general, studies of lakes have used a heatwave definition based on such locally used climate based thresholds, although more recently, lake heatwaves have been defined using thresholds based on in-lake temperature data, allowing assessment at a global scale (Woolway et al., 2021).

The second approach to defining extreme events in ecological studies, including those on lakes, focuses on the impacts of the events rather than the climatic drivers. Jennings et al. (2012), for example, used the term episodic events (which included extreme in-lake events but also events of a lower magnitude), which they defined as "an increase in magnitude relative to more regular, stable conditions." They presented events where there were clear responses for in-lake variables to a change in climatic conditions without those changes being based on any set percentile or threshold. It could be argued, however, that there are events that regularly recur within the annual cycle in lakes that would be considered as extreme if such a response-based approach were used. These include high inflows in spring following annual snowmelt, and the onset and breakdown of stratification each year, events which can happen rapidly and lead to extreme changes in lakes over days or even hours. If possible, therefore, any comparison of extremes based on in-lake data should place these events in the context of a longer-term record, such as the study of de Eyto et al. (2016) where the effects of an extreme flood that took place over several hours were set in the context of data for the lake over a 5-year window. Given the issues outlined above, and in the absence of universal agreement, studies of extreme events should be careful to at least ensure that any definition used is clearly and comprehensively described.

The propagation of climate extremes through the catchment-lake continuum

Climate extremes have the potential to have large impacts on lake ecosystems, but the extent and nature of any effect will depend on both the timing of the event, and on lake and catchment characteristics. The magnitude of changes in stream discharge, for example, will depend on rainfall or snowmelt, but also on catchment geology, topography, soil type and depth, and on vegetation cover. The increase in discharge for a given quantity of rainfall is dependent on water use by catchment vegetation and therefore will be much higher in winter than in summer, a time when more rainwater will be lost through evapotranspiration. The timing of snowmelt, which results in large springtime flows in some catchments, also depends on both current and prior air temperatures and on the extent of the accumulated snowpack. Climate extremes can also impact processes within a lake by more than one mechanism. The sudden pulse of water flowing into a lake during floods may carry loads of dissolved and particulate material which can lead to changes in the chemical composition of the water column, but may also result in a physical disturbance of the lake. Some high rainfall events may not be accompanied by any extreme in wind speeds, such as the 1-in-250 year rainfall event described for Lough Feeagh, Ireland (de Eyto et al., 2016) (Fig. 1). However, stronger wind speeds do often accompany high rates of precipitation during

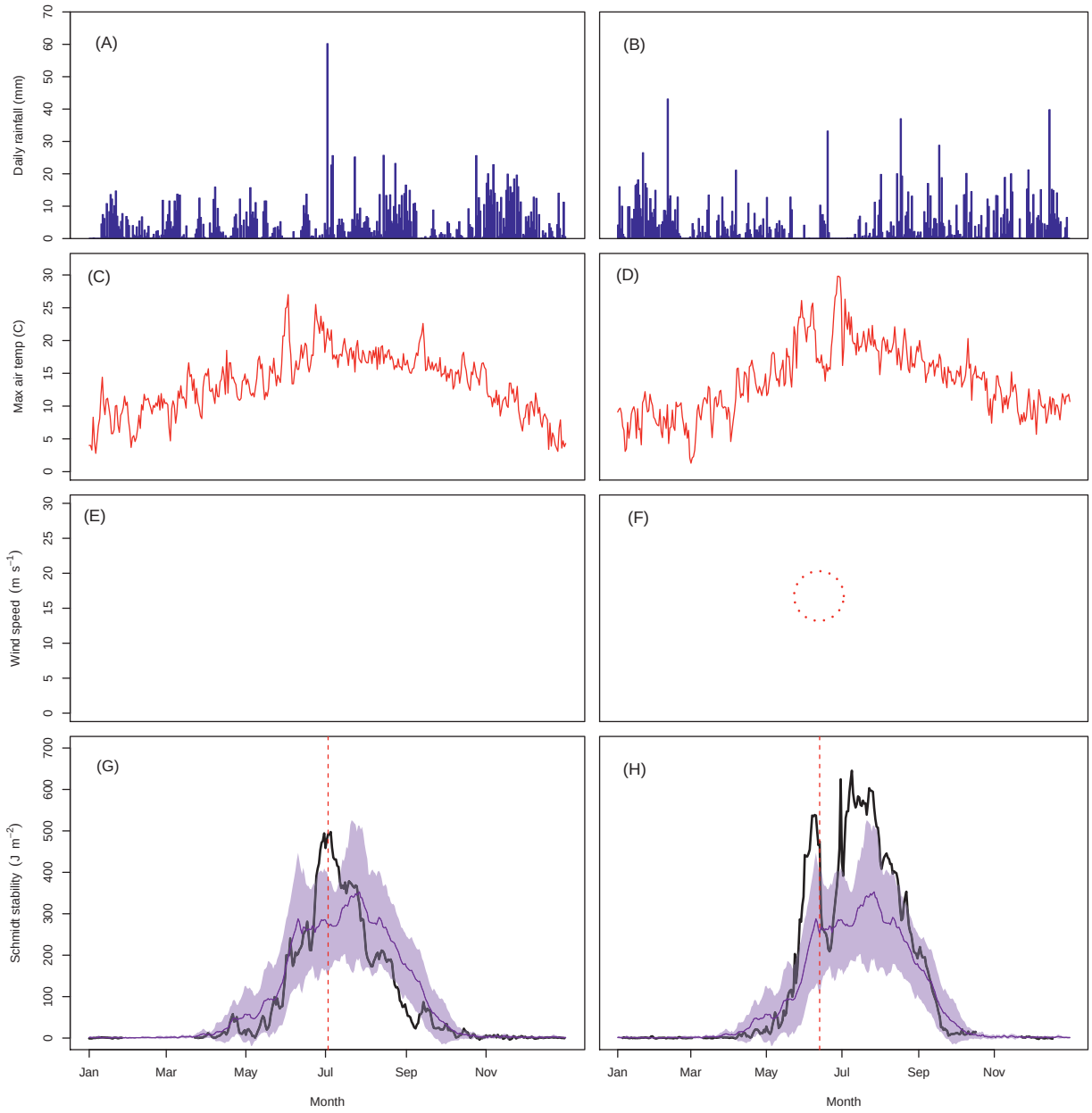

Fig. 1 Data for years with extreme climatic events (left 2009, right 2018) for Lough Feeagh, Ireland: (A and B) daily total rainfall; (C and D) mean daily air temperature; (E and F) highest 10 min mean wind speed (m sec^{-1}); (G and H) lake Schmidt stability. The red dashed lines indicate a 1-in-250 year precipitation event in July 2009 which was accompanied by relatively low wind speeds (de Eyto, et al., 2009) (G), and Storm Hector in 2018 (H), which had a mean daily wind speed of 8.9 m sec^{-1} on June 14th 2008, with gusts of 26 m sec^{-1} (red dashed circle). The purple area and line in (G) and (H) represent the mean and standard deviation for Schmidt stability for the period 2005–18.

storms, and both of these will contribute to mixing and therefore possible resuspension of material from lower waters within the lake. Dissolved substances which are washed out from the catchment may also originate from the atmosphere. Episodic acidification events associated with washout of atmospheric pollutants during high rainfall, for example, have been an important water quality issue in many regions. The impacts of any climate extreme on lake biogeochemistry can also affect other downstream water bodies. Following Storm Ophelia in 2017, there was an upwelling of cold and low-oxygenated waters at the southern-end of Windermere in the United Kingdom lake district which led to a decrease in dissolved oxygen (DO) concentrations by approximately 48% in the main outflow from the lake (Woolway et al., 2018).

Monitoring the effects of climate extremes in lakes

Because of the short timescales of many extreme events, especially high stream discharge events and wind-induced mixing, high frequency monitoring is usually required to discern their effects. This is especially true for storms which are generally short-lived. Few studies have quantified the nature and extent of multiple climate extremes over many years in the context of lakes. A recent detailed analysis of 13 years of storm duration and occurrence for a lake in Ireland found that storm duration based on wind speed was an average of 54.0 h in winter, with a range of 9.0–186 h, and an average of 46.4 h in summer, with a range of 15–94 h (Andersen et al., 2020). Pulses in the export of dissolved and particulate substances from the catchment and in-lake mixing during such storms can, therefore, often take place over relatively short time periods. The deployment of sensors which measure many of the relevant dissolved chemical species, however, have until recently been unreliable and such data are still relatively scarce for many variables. Of the sensors that are commonly used in lakes, those for temperature, conductivity and DO are the most widely deployed, and there are now datasets for these parameters that cover several decades from some sites. Such DO data are also commonly used to calculate estimates of lake metabolism, i.e., the balance between gross primary production and respiration within the lake. Data from in situ monitoring systems can also be used to investigate the impacts of climate extremes on lakes at a regional level, such as the study by Klug et al. (2012) where the effects of Hurricane Irene were tracked across multiple lakes in the eastern United States. However, sensors for many of the parameters that would be needed to comprehensively describe the effects of climate extremes in lakes are still scarce. High frequency data from CO_2 sensors, for example, are only recently becoming available. Such information is increasing knowledge of the processes that drive change in CO_2 cycling and emissions from lakes, information that is critical for quantifying the role of lakes in global greenhouse gas emissions estimates. Both absorbance and fluorescence-based sensors are now commonly used to monitor chlorophyll levels and as proxies for dissolved organic matter (DOM), while sensors for nitrate and ammonium-nitrogen, using UV absorbance, have also become more common. Automated sensors that reliably measure dissolved phosphorus at the low levels required for most lakes are still not available. Similarly, high frequency sensor-based datasets for lake methane (CH_4) concentrations and emissions, another powerful greenhouse gas, are scarce.

Effects of climate extremes within lakes

Effects on lake physics

Climate extremes can have substantial effects on lake physics, and therefore on biogeochemical cycles, however, the magnitude of such effects will also be dependent on the prior thermal conditions. Storms may be associated with extremes in wind, rainfall, or both. Some storms may also induce colder than normal weather conditions promoting additional convective mixing. Overall, storms typically have the effect of decreasing light availability, depressing surface temperatures, increasing mixing, and deepening the thermocline (Stockwell et al., 2020). The extent to which a lake is already warmed or stratified when hit by a storm will mediate the physical impact of the storm on lake dynamics. A recent study of changes in epilimnetic temperatures during storms in the stratified period found, however, smaller changes than had been hypothesized (Doubek et al., 2021). The decreases were on average −0.28 °C across the 18 study lakes during the strongest windstorms, and −0.15 °C after the heaviest rainstorms. Storms with extreme winds will also increase mixing in a lake, thereby weakening stratification and deepening the mixed layer. An increase in cloud cover and decrease in air temperature, often associated with summer storms, would typically also increase cooling fluxes from a lake (Andersen et al., 2020), weakening stratification further and increasing any reduction in surface temperature. The effects of extreme rainfall on lake physics are affected by catchment and lake characteristics, and antecedent weather conditions as described above. Depending on the catchment and its vegetation, extreme rainfall could induce dramatically increased river flow. The extent that this would affect a lake in part depends on the lake residence time, with greater effects happening at shorter residence times. The impact will also depend on the difference in temperature between inflowing water and lake surface water. Often summertime river flow is a cooling flux, so extreme inflows in lakes with a short residence time can reduce lake surface temperature and in-lake stability as well as providing extra energy for mechanical mixing (Strasškraba and Hocking, 2002). Lake water level would also be increased. Furthermore, storms that induce increases in turbidity in rivers can increase light attenuation in a lake. This, in turn, can increase lake surface temperature and lake stability while causing deeper lake waters to cool, as solar heating at depth is reduced (Persson and Jones, 2008). Such impacts on turbidity may mitigate some of the direct effects of increased river flow, but potentially cause longer lasting effects on the lake thermodynamics than the direct impact of the storm (Perga et al., 2018).

Heatwaves can lead to periods of extreme warm surface air temperature, and can have a considerable influence on the physical environment of lakes. The primary physical response of lakes to atmospheric heatwaves is an increase in surface water temperature, with knock-on effects on the vertical temperature profile and on vertical mixing (via buoyancy forces). Air temperature extremes during a heatwave will generally result in a shoaling of the upper mixed layer of the water column, steeper vertical temperature gradients (thus enhanced lake thermal stability), and a cooling of the hypolimnion (Jankowski et al., 2006). The impact of a heatwave on lake physical structure can be more severe when air temperature extremes are accompanied by anomalous conditions in other components of the lake surface energy budget, notably solar radiation and wind speed (Woolway et al., 2020), which influence not only important air-water energy fluxes (i.e., sensible and latent heat in the case of wind speed) but also vertical mixing and heat storage. Specifically, higher than average solar radiation and lower than average wind speed during a heatwave, such as in Europe in 2018, can lead to extraordinary lake surface warming (Fig. 2). These atmospheric variables can even have a greater

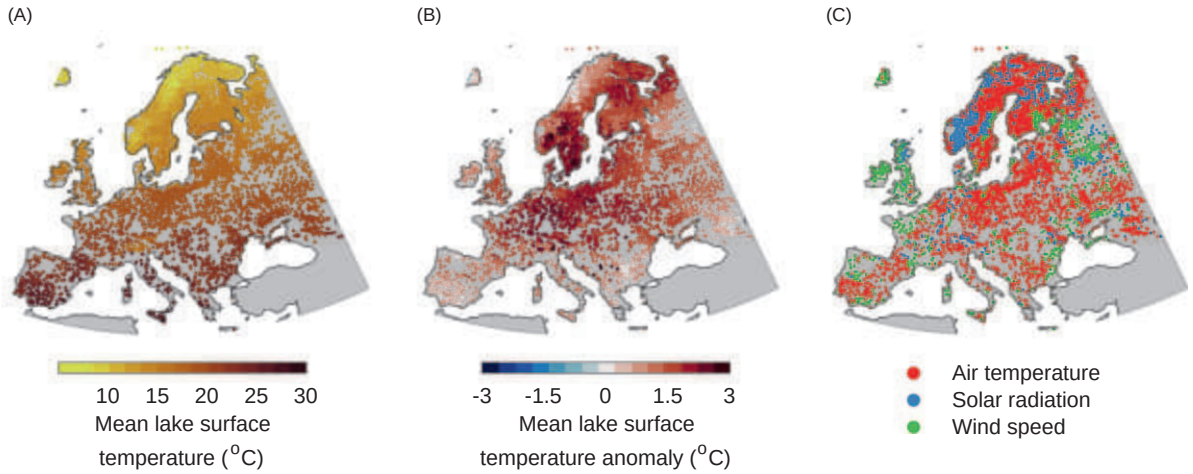

Fig. 2 Simulated surface water temperatures for 46,557 lakes during the 2018 European heatwave. Shown are the variations in May-October (A) mean lake surface water temperature; (B) mean lake surface water temperature anomalies (relative to the 1981–2010 average), and (C) results from an attribution analysis which explored the main drivers of lake surface temperature change. Different colors in panel (C) represent the atmospheric variable (air temperature, solar radiation, wind speed) that had the greatest influence on lake surface temperature anomalies during the 2018 heatwave. Data from Woolway RI, Carrea L and Jennings E (2020) Impact of the 2018 European heatwave on lake surface water temperature. *Inland Waters* 1–11. doi: 10.1080/20442041.2020.1712180.

influence than air temperature on lake surface temperature extremes in some regions (Fig. 2). Periods of extreme lake surface water temperature, recently described as "lake heatwaves," are expected to become more intense and longer lasting during the 21st century (Woolway et al., 2021). Moreover, many lakes worldwide will likely reach a permanent heatwave state, relative to historic conditions, resulting in a substantial departure from the "normal" lake thermal conditions that have shaped lake ecosystems in the past towards a new norm. The occurrence of climate extremes may also be concurrent, or consecutive. Storm Hector, for example, came in from the Atlantic to the west coast of Ireland during the 2018 European heatwave (Fig. 1). Before the storm, the Schmidt stability within the lake was higher than was usual due to lower wind speeds and high temperatures. This stability value decreased dramatically during and following the storm, but then quickly reestablished to pre-storm levels as the heatwave continued.

Effects on lake biogeochemistry

The chemical species in any lake at any given time will include dissolved gases and ions, molecules, and a range of smaller and larger particulate material. The export of substances to lakes, and the processes that lead to their formation within lakes, can be directly influenced by climate extremes. But the effects may also be indirect, with changes related to a cascade of impacts that are propagated through the physical, chemical and biological processes within the lake (Fig. 3) (Jennings et al., 2012). High winds and precipitation associated with Tropical Storm Fay at Lake Annie (United States) resulted in a shallowing of the thermocline and a decline in stability (measured as buoyancy frequency), which in turn resulted in a decline in surface DO levels as deoxygenated water was recirculated from depth (Fig. 3A, D and G). In contrast, a similar storm at Lough Feeagh (Ireland) resulted in only a slight immediate decline in surface water DO (Fig. 3B, E and H). Lake waters can also become supersaturated with oxygen as a result of high levels of photosynthesis during and following algal blooms. The first of two mixing events in Slotssø (Denmark) began during such a bloom (Fig. 3C, F, and I). Dissolved oxygen concentrations did decrease following a first mixing event, but since phytoplankton biomass was still relatively high, they returned to supersaturated levels within 3 days. In contrast, the lake became fully mixed during the second event in October and DO remained low.

Likewise, while increases in lake DOM concentrations often occur following large inflows during storms, they can also have a direct biological cause, such as the decomposition of phytoplankton cells within the lake following periods of high primary production. Where changes in dissolved or particulate substances result from a cascade of linked processes that has been initiated by a climate extreme, they can be considered a consequence of that event. The resultant cascade of impacts can involve many biological, chemical and physical processes. For example, Kasprzak et al. (2017) described a very complex set of events related to a summer storm in Lake Stechlin (Germany). A mean daily wind speed of 7.7 m s^{-1} led to a tilting and deepening of the thermocline, and the release of cyanobacteria that had previously formed a deep chlorophyll maximum into the mixed layer above. The subsequent increase in cyanobacterial photosynthesis raised the pH of the water and induced massive calcite precipitation to levels not previously recorded at the site. As a consequence, the lake then became turbid for several weeks.

Extreme discharge events will only carry a high load of particulate and dissolved substances into a lake or reservoir when those substances are actually available within the catchment hydrological network. The extent of this store of material will itself be governed by antecedent weather. A prior drought in catchment soils, for example, has been shown to affect the magnitude of the export of DOM (Jennings et al., 2012) and sediment (de Eyto et al., 2016; Perga et al., 2018). The load of substances exported will

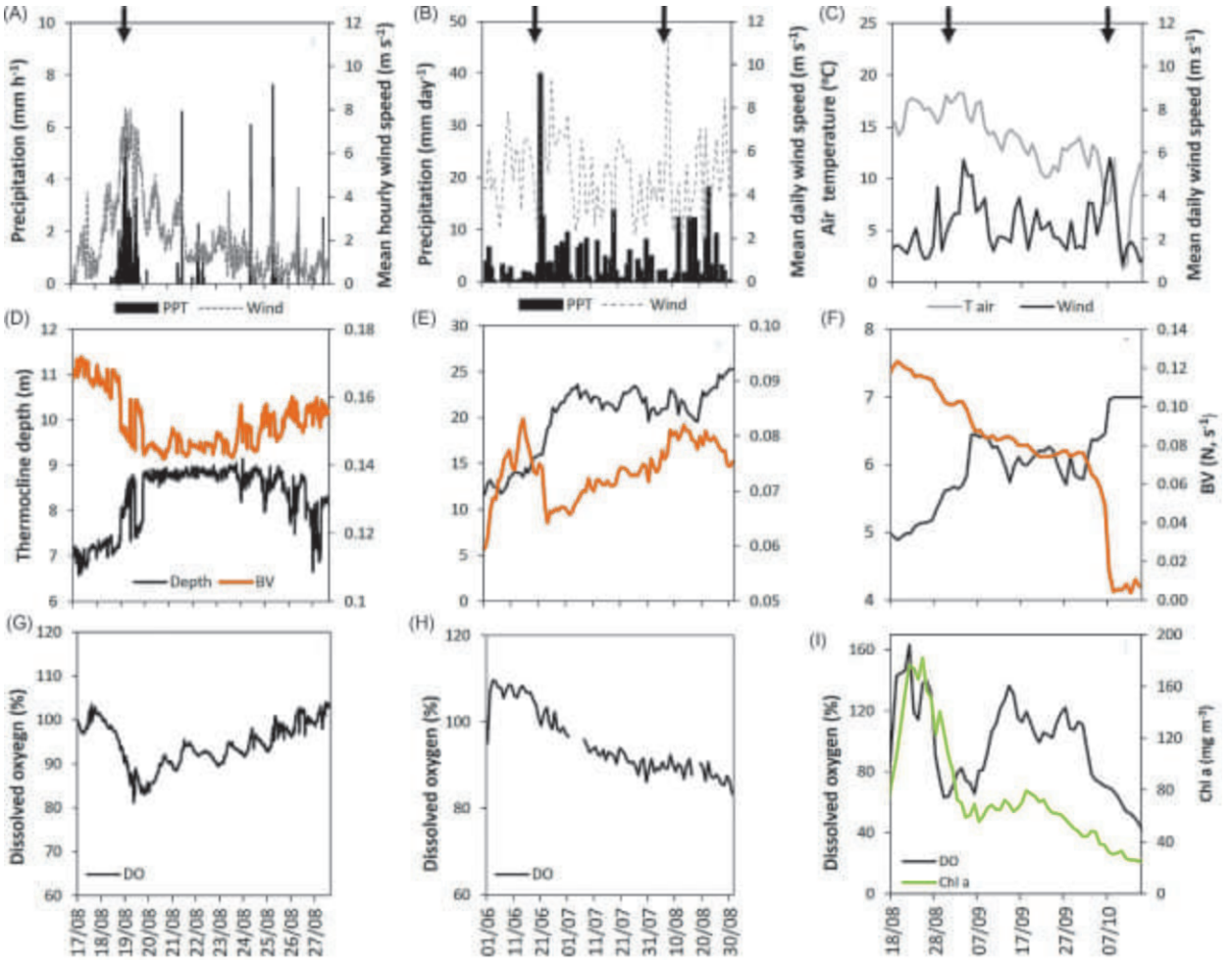

Fig. 3 In-lake responses to extreme changes in wind and precipitation at Lake Annie (United States) (A, D and G), Lough Feeagh (Ireland) (B, E and H), and Slotssø (Denmark) (C, F and I); main meteorological drivers (A–C), Brunt Väisälä (BV) buoyancy frequency and thermocline depth (D–F), dissolved oxygen (DO) levels and chlorophyll *a* concentrations (Slotssø only) (G–I). Black arrows indicate timing of change in meteorological driver. After Jennings E, Jones S, Arvola L, Staehr PA, Gaiser E, Jones ID, Weathers KC, Weyhenmeyer GA, Chiu CY and De Eyto E (2012) Effects of weather-related episodic events in lakes: An analysis based on high-frequency data. *Freshwater Biology* **57**(3): 589–601.

also vary depending on the activation of differing flow pathways through the catchment soils during high precipitation. Gases are lost from the lake surface through ebullition (bubble formation and loss) and diffusion to the atmosphere. Extreme summer rainfall events have been shown to alter CO_2 and CH_4 fluxes in southern Finish lakes, with the systems switching from being a net sink to a net source of CO_2 to the atmosphere (Ojala et al., 2011).

Wind induced mixing of the water column will also result in changes in the concentrations of both dissolved and particulate chemical species. Some of these extreme in-lake mixing events can also be related to long-term extremes in climatic cycles. A major springtime resuspension plume (25-year high) in southern Lake Michigan, for example, was triggered by atmospheric and water column instability in an El Nino year, which temporarily altered the dynamics of autotrophy and heterotrophy in the lake (Cotner et al., 2000). The effects of a sudden in-wash of nutrients or DOM to a lake will also depend on the quality of that material, and whether it is labile and therefore easily decomposed. Farjalla et al. (2006) reported that while flood pulses brought high loads of DOM to the Amazonian Lake Batata, bacterial growth and DOM bioavailability were higher during low-water periods when decomposition of phytoplankton was the main source of organic matter.

Heatwaves can also have dramatic effects on the concentrations and processes controlling chemical species in lakes. It is well recognized that heatwaves, which usually result in stronger and more intense stratification, can promote algal blooms. However, they can also alter the rates of nutrient and gas cycling. The dominant CH_4 emission pathway in a shallow productive lake, for example, shifted from gas ebullition to diffusion following high CH_4 release from sediments that was driven by colder hypolimnetic temperatures during a heatwave, and concurrent high release rate of CH_4 from the lake sediments (Bartosiewicz et al., 2016). Such events will also have longer-term effects and in this case, the release of gases that had accumulated in the hypolimnion during the heatwave resulted in a further high release rate of CH_4 when the lake overturned in the autumn. The impacts of heatwaves and other

climatic extremes can affect the availability of nutrients, for example, lower hypolimnetic oxygen concentrations and higher hypolimnetic nutrient concentrations (Wagner and Adrian, 2011).

The ecological consequences of climate extremes for lake plankton dynamics

While numerous drastic short-term effects have been observed in lake responses to climate extremes, such as exceptionally mild winters, summer heatwaves, extreme storms or heavy rainfall events, the longer term changes in plankton communities and subsequent changes in ecosystem functioning as a result of such events are still unclear (Stockwell et al., 2020). The responses in lakes are complex and inherently variable depending on the severity, frequency, duration and timing of the events and particularly the antecedent conditions, and lake and catchment type (Jennings et al., 2012; Perga et al., 2018; Stockwell et al., 2020). Entrainment from run-off during extreme precipitation events, or entrainment of, for example, hypolimnetic DOM and nutrients, have caused algal biomass and biodiversity to either reduce in some cases or increase in others (Jennings et al., 2012; Kasprzak et al., 2017; Stockwell et al., 2020). The once in 250-year flood event in 2009 in oligotrophic Lough Feeagh (Ireland) caused the water column to destabilize, and was followed by a reduction in primary production (de Eyto et al., 2016). In contrast, an extreme rainy period in 2000 caused a strong increase in external organic carbon loading to Lake Mälaren, a large lake in Sweden, which was followed by a doubling of spring Cryptophyte biomass (Weyhenmeyer et al., 2004). There is also evidence that bacterial communities are more resilient to the effects of storms on the lake environment than the phytoplankton community are. For example, Jones et al. (2008) reported that bacterial communities recovered quickly after typhoons in a small freshwater humic lake in Taiwan, while phytoplankton did not recover in a predictable way.

Heatwaves are likely to promote cyanobacterial blooms as these species exhibit optimal growth at high temperature and profit from stable thermal stratification. However, two extreme hot summers (2003 and 2006), during which water temperatures were above average to the same extent in Müggelsee (Germany), resulted in a cyanobacteria bloom in 2006 but a record low cyanobacteria biomass in 2003. This difference was attributed to the fact that the lake thermal stratification pattern was critically intense only in 2006 (Huber et al., 2012). Heatwaves will also often increase the length of thermal stratification. This effect resulted in a shift towards a higher proportion of buoyant cyanobacteria capable of N-fixation (*Aphanizomenon*, *Anabaena*) and a decline in diatoms because of high temperature, exceeding their upper lethal limit and sedimentation losses (Wagner and Adrian, 2011). Zooplankton species with high thermal tolerances (i.e., *Thermocyclops oithonoides*, *Thermocyclops crassus*) and/or those that grow quickly at high temperatures (i.e., rotifers) became more common (Wagner and Adrian, 2011). Not all climate extremes, however, will have a biological effect. An extreme wind event may have little impact on phytoplankton in a lake that was previously already fully mixed. Conversely, storm effects on phytoplankton communities may be compounded when lakes are not yet recovered from a previous storm, or if periods of drought alternate with periods of intense precipitation, potentially eroding ecosystem resilience (Stockwell et al., 2020).

The ecological consequences of climate extremes for fish populations

Many fish species have low tolerance to high water temperatures because warm water has a low solubility of oxygen. Hence, it is difficult to disentangle the effects of high temperature from the effects of low DO concentrations for fish. Heatwaves, leading to anomalously high water temperatures, and associated aquatic hypoxia, can cause huge problems for lake fish populations, particularly when heatwaves occur over lakes which are already at risk from algal blooms, which, in themselves, can further lower oxygen levels as phytoplankton cells decompose. This chain of events often leads to massive fish kills, as seen in the large shallow Lake Peipsi, on the border of Estonia and Russia. Here, large fish kills of smelt, *Osmerus eperlanus m. spirinchus (Pallas)*, and vendace, *Coregonus albula* (*L.*), have been reported in years when summer water temperatures have exceeded 20 °C for several days in a row (Kangur et al., 2013). As the lake is shallow and well mixed during the summer, these extreme temperature events lead to hypoxia throughout the water column, even impacting the more tolerant bottom dwellers such as ruffe, *Gymnocephalus cernuus (L.)*. This phenomenon has increased in frequency over the last number of decades and has been exacerbated by increasing eutrophication of the lake.

The manifestation of the risk due to the heatwave very much depends on the resident fish species, which will be locally adapted and well suited to their natural habitat. For example, the fish communities of oligotrophic mountain lakes are adapted for life in cold, nutrient poor conditions, while those of shallow eutrophic lakes, such as coarse fish, are probably eurythermal (capable of withstanding a wide range of temperatures) and can thrive even in water with low levels of oxygen. These two differing communities will have varying levels of resistance to sharp increases in temperature and resulting hypoxia. For example, the aforementioned fish community of Lake Peipsi has shifted from a mainly coregonid fish community to one dominated by cyprinids as the frequency of extreme warming events has increased.

Storms bringing high winds can also pose a significant risk to fish populations, particularly those living in highly stratified lakes. High winds can cause sudden overturns of the water column, and the introduction of potentially toxic substances from the sediment water interface into the water column, or the rapid mixing of anoxic waters into the epilimnion. Massive fish kills of tilapia, *Oreochromis mossambicus*, and croaker, *Bairdiella icistia*, have been recorded in the Salton Sea, a coastal lake in California (Marti-Cardona et al., 2008). These fish kills occurred immediately after episodic wind driven upwellings of hypoxic hypolimnetic

water, mixing high concentrations of hydrogen sulfide and ammonium throughout the entire water column, thereby eliminating any refuge for the fish. The severity of this type of impact may be mitigated by the ability of populations to move out of the danger zone quickly. This is often not the case for short lived events that can happen very quickly. In addition, lakes are often used for highly productive aquaculture operations, with fish confined to certain portions of the water body. In these cases, rapid unpredicted overturns can have enormous economic consequences. Cages of Tilapia, *Oreochromis niloticus*, are farmed in Lake Buhi in the Philippines, and fish kills related to extreme climate events including typhoons and hurricanes have been estimated at 322.1 million PhP (~5.6 million euro) between 1998 and 2018 (Nieves et al., 2020). Finally, physical disturbance of habitat resulting from short lived storm events is a considerable risk to fish populations, especially in shallow littoral areas. Massive storms along the coast of Lake Victoria (Africa) caused the death of 2400 t of *Lates niloticus* and *Oreochromis niloticus*, an effect that was attributed to disturbance of the littoral zone causing increases in turbidity and sediment resuspension. The gills of the dead fish were found to be clogged by detritus and algae (Ochumba, 1990).

Longer term effects of climate extremes on lakes

Climate extremes may also have longer-term effects in lakes, although the evidence for this is sparser. Multi-year effects on water chemistry will be more likely in lakes with multi-year retention times (Jennings et al., 2012). In lakes where there is a strong recurring seasonal cycle, biological effects may also be reset during the normal autumn-winter-spring transition (e.g., de Eyto et al., 2016). However, climate extremes may also act as a tipping point and trigger a fundamental shift in the functioning of a lake ecosystem with a transition of one state to another, often referred to as a regime shift. Lake Apopka in Florida (United States) serves as a well-studied example of how long-term stressors and extreme events interact in causing and subsequently maintaining a dysfunctional stable state. Lowe et al. (2001) concluded that hurricanes accelerated a regime shift to a turbid state in that lake, but this was only made possible by a long-term increase in nutrient loading. Before eutrophication, the clear water state was capable of resisting a regime shift and coped well with the damage caused by extreme events.

An additional aspect of the longer-term effects of climate extremes on lakes is the projected increase in their frequency and intensity due to global warming. Quantifying these future impacts requires not only an understanding of historical trends and potentially new theory on the more stochastic impacts within lake ecosystems (Stockwell et al., 2020), but also the use of dynamic models that adequately replicate in-lake responses. Current and projected changes in stratification during heatwaves have been well-captured by lake physical models (Woolway et al., 2021). These physical models have also been shown to capture the effects of short-lived storms on thermal structure (Mesman et al., 2020). As illustrated above, however, the responses for lake biogeochemistry and biota to climate extremes can be complex. Moreover, they can also be strongly affected by processes in the surrounding catchment, interactions between species, and antecedent conditions within a given lake. While there are now many commonly used lake biogeochemical models that can simulate in-lake responses, challenges still remain for adequately quantifying projected changes in climate extremes with the required degree of uncertainty.

Conclusion

Climate extremes, including storms, floods, heatwaves, and droughts, are projected to increase in frequency and magnitude in the coming decades as global warming progresses. Understanding the effects of these extreme events on lakes and reservoirs is crucial if appropriate management is to be planned and implemented. Using high frequency and longer-term monitoring, the effects of storms and heatwaves on lake physics are now relatively well understood. We also now have some detailed examples of how complex the lake ecosystem response to climate extremes can be, involving many trophic levels and feedbacks through linked biogeochemical cycles. Much remains to be learnt, however, in relation to many of the chemical and biological impacts. In particular, we need to increase our understanding of why some lakes seem to have an inherent ecosystem resilience to these extreme climatic events and how this resilience is compromised by otherhuman pressures. Gaining more insights into these effects will inform both lake management and the modelling studies that will be required to assess the impacts of future climate change.

Knowledge gaps

1. More lake studies are needed on the effects of climate extremes on the cycling and emissions of CO_2 and CH_4 and on their role in the global carbon cycle.
2. Whole system studies are required that use high frequency monitoring to explore shifts in nutrient concentrations and plankton communities, during and following climate extremes.
3. New theory and conceptual models which include both trends in climate extremes and in in-lake conditions can be used to predict both linear and more complex whole-system responses and therefore inform dynamic modelling of lake ecosystems.

Important case studies.

Name	*Country*	*Coordinates*	*Main topic*	*Key references*
Feeagh	IE	53°56.44′ N 9°34.40′ W	1. 1-in-250 year rainfall event 2. Analysis of physical impacts of storms over a 13 year period	1. de Eyto et al., 2016 2. Andersen et al., 2020
Stechlin	DE	53°10′ N 13°02′ E	Storm-driven cascade of events	Kasprzak et al., 2017
Muzelle	FR	44°57.04′ N 6°5.85′ E	Role of antecedent conditions on impacts of storms on turbidity	Perga et al., 2018
Multiple sites	United States	NA	Effects of Hurricane Irene across a network of eastern United States lakes	Klug et al., 2012
Müggelsee	DE	52°60′N, 13°90′E	Critical thresholds in thermal stratification determined contrasting responses in algal mass in two heat wave years Heat waves enhance the risk of cyanobacteria blooms	Huber et al., 2012 Wagner and Adrian 2011
Peipsi	EE	58°39′ 7″ N 27°27′ 23″ E	Heat wave causes summer fish kills	Kangur et al., 2013

Acknowledgments

We acknowledge the support of the staff of the Marine Institute, Newport, Ireland, in the collection of the data in Fig. 1. Fig. 3 is based on Jennings et al. (2012) using data for Lake Annie, Lough Feeagh and Slotssø only. Data for gross primary production for Slotssø are also omitted here. We thank the editors for their insightful and useful comments.

See Also: Emerging methods and topics: Remote Sensing of Inland Water Quality; Human pressures and management of Inland Waters: Implications of Climate Change for Freshwater Fisheries; Structures and functions of Inland Waters - Groundwater: Anthropogenic Pressures on Groundwater; Karst Groundwater Dependent Ecosystems—Typology, Vulnerability and Protection; Structures and functions of Inland Waters - Lakes: Lakes as Recorders of Earth Surface Dynamics From Yearly to Plurimillennial Time-Scales; Structures and functions of Inland Waters - Rivers: Climate Change and Extreme Events in Shaping River Ecosystems; Ecological and Evolutionary Consequences of Disturbance in Freshwater Ecosystems; Flood Plains of Large Rivers; Hydrology and Classification of Rivers for Management; River Resilience; Structures and functions of Inland Waters - Wetlands: Wetlands Under Global Change; Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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Relevant Web-Based Resources

https://serc.carleton.edu/eddie/enviro_data/activities/lake_mixing.html—Project EDDIE Lake Mixing Module.
https://serc.carleton.edu/eddie/enviro_data/activities/lake_mixing.html—Project EDDIE Macro-scale Feedbacks Module.
http://www.flake.igb-berlin.de/model/run—FLake-Global.
http://eprints.dkit.ie/id/eprint/530—NETLAKE toolbox for the analysis of high-frequency data from lakes

Nutritional Constraints on Zooplankton

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This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Cholesterol The predominant sterol in animal tissues.
Co-limitation Simultaneous limitation by multiple nutrients.
Ecological stoichiometry Balance between chemical elements in ecological interactions.
Incipient-limiting level (ILL) Concentration of food or of a food quality constituent above which consumer growth is not anymore limited by food quantity or the specific quality component under consideration.
Long-chain polyunsaturated fatty acids (LC-PUFA) Fatty acids with more than 18 carbon atoms and more than one double bond (unsaturation) that are required as membrane components and as precursors for other bioactive molecules (eicosanoids). Many consumers cannot synthesize LC-PUFA in quantities covering their physiological demands.
Phytosterols Sterols found in plants and algae.
Seston Sum of living and non-living particles suspended in water.
Sterols Lipid-like compounds that are required as membrane components and as precursors for steroid hormones and other bioactive molecules. Arthropods cannot synthesize sterols *de novo* and thus rely on dietary supply.
Threshold elemental/biochemical ratios Ratio between e.g., two elements or between a fatty acid and carbon in the diet at which the element or fatty acid of concern may become limiting.
Trophic upgrading Upgrading of a nutritionally inadequate food by a consumer (e.g., by providing LC-PUFA) for subsequent use by higher trophic levels.

Introduction

Zooplankton is of central importance for material and energy fluxes in aquatic food webs. Nutritional constraints at the phytoplankton-zooplankton interface can thus have severe consequences for ecosystem functioning and services. For example, zooplankton nutritional constraints might limit zooplankton capacity to control algal blooms, as well as fish production. The taxonomic diversity of potential food organisms of zooplankton is analogous to a wide diversity in traits of food organisms, such as size, mineral and biochemical contents, morphological and behavioral defenses, or toxin production, which co-evolved in equally diverse assemblages of zooplankton consumers differing in breadth of resource use, demand for nutrients, and biochemical machinery. Zooplankton may be constrained by the overall quantity of food and/or its quality. The food quantity, i.e., its energy content, is generally equated with the carbon concentration within the size range edible for zooplankton species, whereas the quality of food is usually expressed relative to food quantity, i.e., carbon content. The distinction between quantity and quality limitation is, however, not clear-cut. For example, phytoplankton morphological adaptations reducing edibility are often

considered as quality components, but reduce the food quantity available for the zooplankton (Ger et al., 2016). Likewise, low food quality might be associated with energetic costs due to increased resting metabolism in consumers (Ruiz et al., 2021).

This chapter starts with an overview of controlled laboratory experiments examining various aspects of nutritional constraints, including food quantity and quality limitation, co-limitation by multiple food constituents, as well as the interaction between nutritional constraints and ambient temperatures. We then continue with the complexity of zooplankton nutrition in a food web context, and present evidence about nutritional constraints of zooplankton *in situ*, e.g., during seasonal plankton dynamics in lakes of different trophic status. Finally, the adaptive responses of zooplankton to nutritional constraints will be discussed.

Zooplankton nutrition—Laboratory experiments

In this chapter we will address how laboratory experiments have contributed to our understanding of zooplankton nutritional constraints. We discuss food quantity constraints and several aspects of food quality constraints such as deficiencies of elements, fatty acids, sterols, amino acids and the presence of harmful metabolites in zooplankton diets. Then we examine simultaneous limitation by several diet compounds and how water temperature interacts with both food quantity and food quality to influence zooplankton growth and reproduction.

Food quantity

The dependence of zooplankton growth and reproduction on food quantity can be described using functional responses. Along a food quantity gradient, zooplankton growth rates increase with increasing food availability up to a critical threshold food concentration (Fig. 1A). Below this threshold food concentration, food availability is insufficient to balance metabolic losses, eventually resulting in a decrease in body mass or, on the population level, in a decrease in population density (Lampert, 1987; Sterner and Schulz, 1998). Threshold food concentrations and thus food quantity requirements differ among zooplankton species, but general principles are difficult to extract from the available literature. Threshold food concentrations have been reported to decrease with body size across *Daphnia* species (Gliwicz, 1990), to increase with body size across rotifers (Stemberger and Gilbert, 1985), and to show no relationship with cell size across ciliates (Weisse, 2006). Ciliate threshold food concentrations strongly overlap with those of *Daphnia* and small rotifers (Weisse, 2006). Above the threshold food concentration, growth rates increase further with food quantity until the growth response curve approaches its maximum. The food concentration at which growth is no longer limited by food quantity is often referred to as the incipient limiting level (ILL).

The edible size range, and thus food quantity, can be reduced because of morphological defenses of food organisms interfering with ingestion rates, e.g., formation of filaments, colonies, and spine formation, or assimilation rates, e.g., thickened cell walls and mucous sheets that may allow passing the zooplankton gut unscathed (Lürling, 2021). A well-documented example of morphological properties hampering ingestion is the inducible defense reaction of the green alga *Scenedesmus*. In the presence of a kairomone (i.e., a signaling molecule) released by *Daphnia*, *Scenedesmus* cells form colonies consisting of up to eight cells of which the peripheral cells may express long spines. Inducible morphological defenses can interfere with the filtration process of filter-feeding zooplankton, thus reducing the efficiency with which phytoplankton species are exploited. Another example of morphological properties reducing food uptake is filament formation, which occurs in various phytoplankton groups, especially among cyanobacteria (Lürling, 2021).

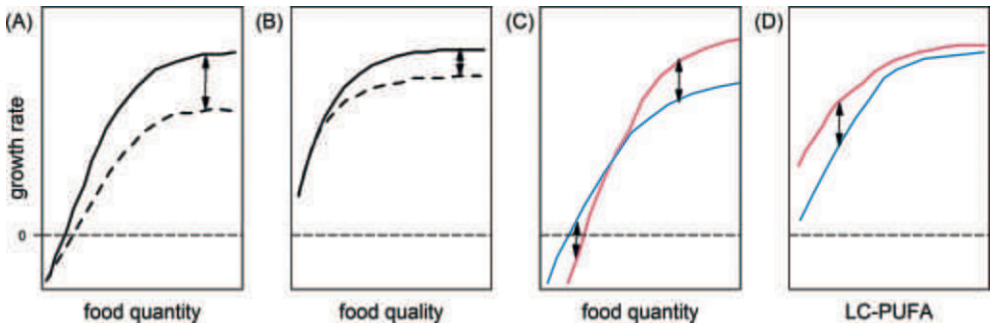

Fig. 1 Zooplankton growth rates as a function of (A) food quantity with food of different quality, (B) food quality in the presence and absence of a second limiting nutrient, (C) food quantity at two different temperatures, and (D) LC-PUFA contents at two different temperatures. In (B) and (D), food quantity is non-limiting. Arrow in (A) denotes the food quality effect on growth rates, in (B) the effect of a co-limiting food quality component, in (C) and (D) the effect of water temperature. Note that in (C) the effect of water temperature on growth rate at low food concentration is opposite to the effect of water temperature on growth rate at high food concentrations.

Food quality

Besides food quantity, the growth of zooplankton can be limited by food quality. The shape of functional response curves and thus threshold food concentrations and ILLs are influenced by food quality. Typically, food quality effects become most pronounced at high food concentrations, causing strong differences in maximum growth rates (Fig. 1A). Poor food quality can be either due to dietary deficiencies impairing growth and/or reproduction, or due to harmful secondary metabolites potentially resulting in severe intoxication. Dietary deficiencies may result from imbalanced supply of elements, or certain biochemicals, which are required for growth and reproduction but cannot be synthesized *de novo* from low molecular precursors. Biochemicals considered to be essential can be found among the polyunsaturated fatty acids (PUFAs), sterols, amino acids, and vitamins. The actual requirements for a particular nutrient, however, may differ between animal taxa, species or even clones of the same species. In recent years, aquatic food quality research has increasingly focused on assessing the physiological and ecological consequences associated with dietary element, PUFA, sterol, and—more recently—amino acid deficiencies, as well as harmful secondary metabolites. In comparison, the role of e.g., vitamins in determining food quality has been poorly addressed.

Elements

All animals require a set of elements to cover their physiological demands, most notably carbon (C), nitrogen (N) and phosphorus (P). The stoichiometry of these elements, i.e., their quantitative relationships, and its significance for trophic interactions has been extensively studied in past decades (Sterner and Elser, 2002). Carbon is the most abundant element in organic matter; it typically represents 40–50% of the dry biomass of most organisms, and thus is used as a surrogate for food quantity. Zooplankton growth has been shown to be crucially affected by the availability of dietary N and P, more specifically by the C:N and the C:P ratio of their food. Compared to most other zooplankton taxa, *Daphnia* contain high amounts of P, which is most likely linked to their high growth rates, and thus are more susceptible to P limitation than taxa containing less P and achieving lower growth rates, such as *Bosmina* or calanoid copepods (Sterner and Elser, 2002). However, copepod nauplii may also have low C:P ratios (Villar-Argaiz and Sterner, 2002), which suggests that juvenile life stages even of calanoid copepods may be sensitive to stoichiometric constraints. The Growth Rate Hypothesis (GRH) proposes positive relationships between growth rate, body P and ribonucleic acid (RNA) content. More than 25% of the overall biomass P content is implemented in RNA, suggesting that protein biosynthesis is sensitive to dietary P supply and that P demands increase with growth rate. The GRH is a central component of the ecological stoichiometry concept and provides a mechanistic explanation of P-limited growth responses (Sterner and Elser, 2002). Zooplankton consumers also require other elements in their food to cover their physiological demands. Nitrogen is a central component of amino acids and dietary deficiencies in N may potentially impair zooplankton growth (Hessen, 1992). Other elements that serve as obligate constituents of macromolecules may similarly impair the performance of zooplankton consumers but our knowledge of elemental nutrient limitations other than those mediated by P and N is still scarce.

Fatty acids

As in other organisms, fatty acids play an important role in zooplankton physiology. They are indispensable components of cell membranes and as such involved in e.g., temperature acclimation (Hazel and Williams, 1990), and they serve as precursors for eicosanoids, which are important mediators in reproduction, the immune system, and ion transport physiology (Stanley, 2000). Animals are typically incapable of synthesizing long-chain PUFAs *de novo*, i.e., from low-molecular-weight precursors, and thus must acquire these essential nutrients from their diet. Five PUFAs are commonly considered to be physiologically important: the three ω-3 (n-3) PUFAs α-linolenic acid (ALA, 18:3n-3), eicosapentaenoic acid (EPA, 20:5n-3), and docosahexaenoic acid (DHA, 22:6n-3), and the two ω-6 (n-6) PUFAs linoleic acid (LIN, 18:2n-6) and arachidonic acid (ARA, 20:4n-6). The long-chain (>C18) PUFAs, EPA, DHA, and ARA, are conditionally essential because some animals can synthesize these long-chain PUFAs from their respective precursors ALA and LIN via elongation and desaturation or via retro-conversion from dietary PUFAs with longer carbon chains. However, the conversion rates at which these metabolic processes occur are typically low and often insufficient to meet physiological needs, i.e., dietary supply is still required to maximize growth and offspring production (Martin-Creuzburg et al., 2010; Taipale et al., 2011; Von Elert, 2002). Several PUFAs have been shown to support *Daphnia* growth. Which of these PUFAs actually becomes limiting under natural conditions may change with dietary PUFA availability. In general, however, EPA and ARA seem to be most effective in supporting growth and especially reproduction of *Daphnia* (Becker and Boersma, 2003; Ravet et al., 2003). Dietary DHA tends to be retro-converted to EPA in the metabolism of *Daphnia*, suggesting that the reported positive effects of DHA supplementation on *Daphnia* performance are in fact due to an increased availability of EPA (Martin-Creuzburg et al., 2010; Von Elert, 2002).

Sterols

Experimental evidence suggests that rotifer and crustacean zooplankton are incapable of synthesizing sterols *de novo* and thus require a dietary source of sterols to meet their physiological demands (von Elert et al., 2003; Wacker and Martin-Creuzburg, 2012). Sterols are indispensable structural components of all eukaryotic cell membranes. They modulate and refine membrane fluidity, permeability, and the functioning of various membrane proteins, serve as precursors for steroid hormones, such as the molt-inducing ecdysteroids in arthropods, and are required as signaling molecules during embryonic development (Martin-Creuzburg and von Elert, 2009). In contrast to plants and most algae, which contain a large variety of different sterols

(phytosterols), cholesterol is the predominant sterol in most animal tissues including crustaceans, but not in rotifers (Wacker and Martin-Creuzburg, 2012). Herbivorous crustaceans typically use dietary phytosterols to synthesize cholesterol. However, not all phytosterols found in algae are suitable as cholesterol precursors. Thus, in addition to low dietary sterol levels, the quality of dietary sterols may affect the performance of zooplankton (Martin-Creuzburg and von Elert, 2009).

Experimentally modifying the availability of dietary sterols revealed a strong impact of dietary sterols on various life history traits of *Daphnia*; somatic growth rates, offspring production, and the probability of survival were all significantly reduced with decreasing dietary sterol supply (Martin-Creuzburg et al., 2005b). Rapidly growing animals may have particularly high dietary sterol requirements because sterols are needed for the biosynthesis of new cell membranes and as precursors for the molt-inducing ecdysteroids, implying that an adequate dietary supply with sterols is particularly important for juvenile somatic growth (Martin-Creuzburg et al., 2009). However, sterols are presumably also important for ovarian maturation and egg production.

Amino acids

Amino acids are the structural units of proteins and peptides and dietary deficiencies in certain amino acids may thus interfere with protein biosynthesis. Nine amino acids are commonly considered essential: phenylalanine, valine, threonine, tryptophan, isoleucine, leucine, methionine, lysine, and histidine. Other amino acids, such as arginine, cysteine, and proline, are described as 'conditionally essential', as they are required only under certain circumstances or life stages. Reports on amino acid requirements of zooplankton are scarce. The amino acid content of animals tends to be regulated homeostatically, i.e., changes in the amino acid content of consumers are rather low despite considerable changes in the availability of dietary amino acids (Müller-Navarra, 2008). This might result in amino acid limitation if specific amino acids are underrepresented in zooplankton diet. Currently, there are hardly any studies providing experimental evidence for amino acid limitation of zooplankton growth. However, population growth of the rotifer *Brachionus calyciflorus* has been shown to be limited by leucine and isoleucine in laboratory supplementation experiments (Wacker and Martin-Creuzburg, 2012).

Harmful metabolites

Toxicity is another important food quality constraint that can severely impair zooplankton performance (Wilson et al., 2006). Many cyanobacteria are known to produce a variety of potentially harmful secondary metabolites such as microcystins, cylindrospermopsins, anatoxin-*a*, and various protease inhibitors. Also mixotrophic and heterotrophic flagellates of the genera *Ochromonas* and *Poterioochromonas* have been shown to produce various metabolites, i.e., chlorosulfolipids, that are toxic to zooplankton (Bedke and Vanderwal, 2011; Boenigk and Stadler, 2004). Microcystin-LR, the best studied of the various microcystins, has been shown to be toxic to zooplankton, most likely through inhibition of phosphatases (DeMott et al., 1991). However, detrimental effects of cyanobacteria on zooplankton performance could often not be linked to microcystin toxicity (Tillmanns et al., 2008; Wilson et al., 2006). Instead, other cyanobacterial peptides came into focus that have been shown to inhibit digestive proteases in zooplankton (Rohrlack et al., 2004; Von Elert et al., 2005). The diversity of potentially harmful metabolites found in cyanobacteria suggests that synergistic or additive effects among metabolites must be considered for improving our understanding of cyanobacteria-grazer interactions. It should be noted, however, that toxicity varies among species and even strains and that not all cyanobacteria are necessarily toxic to zooplankton.

Multiple nutritional constraints

Some food organisms may pose several challenges for their zooplankton consumers. For example, several cyanobacteria species may be inadequate food for zooplankton because of either filament or colony formation, production of harmful metabolites, and sterol and/or PUFA deficiency. Supplementation experiments with *Daphnia magna* feeding on different cyanobacteria species suggest that somatic growth rates are limited along a hierarchy of low ingestibility due to filaments, toxicity, sterol deficiency and PUFAs deficiency (Martin-Creuzburg et al., 2008).

Laboratory experiments revealed that zooplankton growth can be limited by multiple nutrients simultaneously. In respect to sterols and EPA (Sperfeld et al., 2012) as well as sterols and phosphorus (Lukas et al., 2011), somatic growth of *Daphnia* has been shown to be limited simultaneously by two diet components (Fig. 1B). Likewise, amino acids and sterols may co-limit rotifer population growth (Wacker and Martin-Creuzburg, 2012). Somatic growth rates of zooplankton in a multi-nutrient limitation setting can be described using the multiple limitation hypothesis (MLH, Gleeson and Tilman, 1992; Sperfeld et al., 2012), which considers interactions between co-limiting nutrients and predicts smooth transitions from a limitation by one nutrient to a limitation by another. Whereas co-limitation of somatic growth of *Daphnia* has been observed only for a certain range of resource concentrations, resulting in small effect sizes (Sperfeld et al., 2012), co-limitation of population growth of *Daphnia* may be more pronounced due to the differences in effect sizes of sterols and PUFAs on somatic growth and reproduction, respectively. While somatic growth seems to be primarily constrained by a low dietary sterol content, reproduction seems to be more affected by a low dietary LC- PUFA content (Martin-Creuzburg et al., 2010). As population growth requires both individual somatic growth and reproduction, there is a high possibility of co-limitation.

Temperature resource interactions

Zooplankton in lakes outside the tropics experience large seasonal changes in temperatures, which will strongly affect their metabolic rates and consequently their nutritional requirements in terms of food quantity and quality. As metabolic rates scale exponentially with temperature (Gillooly et al., 2001), nutritional demands increase with temperature, likely resulting in increasing ILLs with increasing temperatures (Giebelhausen and Lampert, 2001) and thus increasing food quantity effects with increasing temperatures (Fig. 1C)—as long as temperatures do not exceed the optimum temperature for growth. At low food concentrations, an increase of temperature might even have negative consequences for growth. Likewise, the effects of food quality also depend on ambient temperatures. The C:P ratio of food has been found to have a large effect on *Daphnia* growth at 25 °C, whereas there was hardly any effect at 10 °C (Persson et al., 2011). Also, sterol requirements increase with increasing temperature (Martin-Creuzburg et al., 2012; Sperfeld and Wacker, 2009). In contrast, PUFA requirements decrease with increasing temperature, i.e., temperature affects growth more strongly on a low PUFA diet (Fig. 1D) (Martin-Creuzburg et al., 2012; Sperfeld and Wacker, 2012), as more PUFAs are required to maintain membrane fluidity at low temperatures. Hence, temperature will influence both food quantity and quality constraints simultaneously possibly resulting in complex interactions that make it difficult to distinguish between temperature effects on quality versus quantity nutritional constraints. Such interactions must also be taken into account in experimental work. For example, studies analyzing temperature dependencies of growth in respect to food quantity or stoichiometric constraints might have incorrectly assumed that LC-PUFAs were not limiting in low-temperature treatments. Hence, LC-PUFAs might have acted as a hidden treatment in some experiments, which would result in an overestimation of the temperature dependency of growth in respect to e.g., food quantity or phosphorus supply.

Zooplankton nutrition in a food-web context

Freshwater zooplankton is a taxonomically and functionally diverse assemblage of organisms, consisting of unicellular protists, such as heterotrophic flagellates and ciliates, as well as metazoan grazers, most notably rotifers and crustaceans (see chapter on zooplankton diversity and variation between lakes). These taxa range in size from few micrometers (μm) for large flagellates to several centimeters for large crustaceans (Fig. 2). Zooplankton differ in the size range of food organisms they can exploit, resulting in group-specific predator-prey size ratios. These average predator:prey size ratios (in equivalent spherical diameters) range from 3:1 for flagellates towards 100:1 for cladocerans (Hansen et al., 1994), with yet extreme values. For instance, the predator:prey size ratio for raptorial crustacean consumers might be as low as 1:1 while it can reach 1000:1 for filter-feeders.

The food organisms of zooplankton change along the size gradient from prokaryotic cells, which dominate the food sources up to a size of 1 pg C, towards eukaryotic phytoplankton, which dominate from 1 pg C towards 4 ng C, and zooplankton from ~10 ng C onwards (Fig. 2). Within this range of zooplankton food sizes, there is a partial covariation between size and food quality. This covariation is caused by physical/physiological and taxonomical constraints. The surface-to-volume ratio increases with decreasing cell size, which is thought to result in higher nutrient affinities and consequently higher cellular elemental contents of small cells. While prokaryotes (bacteria and cyanobacteria) are potentially important providers of elements (phosphorus) for zooplankton, the majority of prokaryotic taxa lacks the biochemical machinery to build sterols and LC-PUFAs. Thus, while food

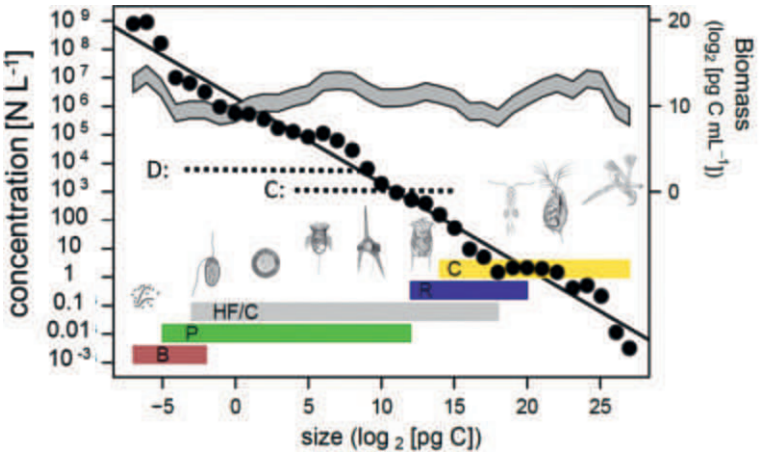

Fig. 2 Size spectrum of the pelagic community of Lake Constance. Shown is the overall biomass in each size range (grey polygon) and the concentration of organisms in each size range (black dots). Size ranges of organism groups are shown as horizontal bars (B: bacteria, P: phytoplankton, HF, C: heterotrophic flagellates and ciliates, R: rotifers, and C: crustaceans). The horizontal dotted lines indicate the size range of food items of a copepod (C) with a size of 0.5 μg carbon and a *Daphnia* (D) with a size of 4.2 μg carbon. Figure modified from Güde H and Straile D (2016) Bodensee—Ökologie und anthropogene Belastungen eines tiefen Voralpensees. *Limnologie Aktuell* **15**: 1–271.

cells below a size of 1 pg C may represent an important source of energy and enrich zooplankton diet with elements, a high percentage of small prokaryotic cells in the diet may dilute its LC-PUFA and sterol content. Within the whole size-range occupied by phytoplankton (Fig. 2), also zooplankton organisms, i.e., heterotrophic flagellates and ciliates, are present. For zooplankton feeding on prey sizes of 1 pg to 10 ng C, approximately 1–10% of available carbon is represented by heterotrophs. Small zooplankton taxa, especially heterotrophic flagellates and ciliates, feed on low quality bacteria, thereby converting low quality bacterial food into higher quality protozoan food that is then available to larger zooplankton. Such trophic upgrading of food particles by protozoans may be due to the repacking of otherwise poorly ingestible food particles to more easily accessible food particles, and/or biosynthesis of essential biochemical nutrients by the intermediary protozoan grazers. However, protozoan taxa might differ in their capacity to upgrade food for higher trophic levels. Heterotrophic flagellates, for instance, are capable of synthesizing sterols *de novo* (e.g., Bec et al., 2006), whereas ciliates might lack this capacity (e.g., Martin-Creuzburg et al., 2005a).

In contrast to mineral and biochemical content, there seems to be no toxicity gradient along the bacteria-phytoplankton size range. Toxic constituents are known from bacteria (Matz et al., 2004), cyanobacteria (Wilson et al., 2006), as well as mixotrophic and heterotrophic flagellates (Hiltunen et al., 2012).

Seasonal and lake trophy differences in zooplankton nutrition

Based on phytoplankton concentrations and composition, zooplankton nutritional constraints in terms of food quantity and quality are expected to vary seasonally (Sommer et al., 1986) and between lakes of different trophic status (Watson et al., 1997). A large amount of high quality food, i.e., diatoms and cryptophytes, is available to zooplankton during the spring bloom of phytoplankton in most lakes, suggesting that neither food quantity nor food quality constraints are relevant during this time of the year. Furthermore, low temperatures during spring suggest that growth rates are strongly temperature limited. In contrast to the spring bloom, the summer phytoplankton bloom is often dominated by inedible algae (Sommer et al., 1986), and the low concentration of edible algae suggests that zooplankton might be limited by food quantity. In addition, food quality is predicted to decrease during the season as the contribution of algae deficient in LC-PUFAs and/or suitable sterols, e.g., green algae or cyanobacteria, increases. The fraction of in-edible algae as well as the fraction of low to moderate food quality algae (cyanobacteria and chlorophytes) increases with increasing trophic status in summer phytoplankton (Watson et al., 1997), suggesting that the seasonal shift from edible to in-edible algae and from high to low quality food is getting larger with increasing trophic status.

Laboratory experiments provide threshold elemental or biochemical ratios (TER, TBR) for nutritional constraints of consumers, which can be related to seston elemental or biochemical ratios to infer nutritional constraints *in situ*. Most estimates for TER and especially for TBR have been established for *Daphnia* (but see Frost et al., 2006), which relates to the key role of *Daphnia* in freshwater food webs. However, as *Daphnia* is a non-selective consumer, TER and TBR estimates for *Daphnia* may be considered as upper bounds for TER and TBR for more selective consumers, because they might be able to select for higher-quality food. *Daphnia* are expected to be P limited when the P content of its food is <8.6 μg P mg C^{-1} (molar C:P ratio of >300; e.g., Urabe et al., 2018). In a compilation of 576 measurements from 285 lakes, roughly 20% of seston molar C:P ratios were found to exceed 300, suggesting P limitation of *Daphnia* (Sterner et al., 2008).

The proposed growth saturation thresholds for EPA depend on temperature (Sperfeld and Wacker, 2011). For example, an EPA content within a bootstrapped range of 0.7–2.0 μg mg C^{-1} was necessary to achieve 75% of the maximum somatic growth of *Daphnia* at 20 °C, whereas approximately twice (bootstrapped range: 1.6–4.9 μg mg C^{-1}) the EPA content was necessary to achieve 75% of maximum growth at 15 °C (Sperfeld and Wacker, 2011). These thresholds suggests that a moderate EPA limitation frequently occurs *in situ* (Sperfeld and Wacker, 2011).

It has been reported that sterol limitation is likely if prokaryotes contribute more than 40–50% to edible biomass (Martin-Creuzburg et al., 2011), which seems possible during cyanobacterial blooms in eutrophic lakes or in humic lakes in which, due to large amounts of allochthonous material, heterotrophic bacteria can account for a major fraction of suspended particulate organic carbon (Hessen, 1985). However, supplementation experiments revealed *Daphnia* ILLs in a range of 3.5–34.4 μg mg C^{-1} using 10 different phytosterols (Martin-Creuzburg et al., 2014), suggesting that the eukaryotic species composition also needs to be considered when assessing potential sterol limitations *in situ*.

While a comparison of seston concentrations with TER and TBR may point to potential nutritional constraints, there are three types of evidence for the actual occurrence of nutritional constraints of zooplankton *in situ*: (1) correlative studies comparing seston nutrient concentrations with zooplankton growth characteristics, (2) comparative studies, and (3) supplementation studies exploring potential nutrient limitations experimentally. Correlative studies suggested that zooplankton performance can be limited by food quantity as well as by several aspects of food quality. For example, clutch size of *Daphnia* has been shown to be tightly related to particulate organic carbon concentration in the edible size fraction (e.g., Lampert, 1978). Likewise, somatic growth rates of *Daphnia* that were reared on natural seston were found to be correlated with the concentration and/or content of EPA (Müller-Navarra et al., 2000), ALA (Wacker and von Elert, 2001), and sterols (De Lange and Arts, 1999). Correlative studies are limited in deepening our insights in the causal relationships, nor do they allow a straightforward estimation of the relative importance of food quantity versus food quality effects. The latter might be achieved via comparing zooplankton growth rates observed when feeding on seston ((g(seston)) with a) growth rates when feeding on a standard laboratory food alga, such as the green alga *Scenedesmus*, at a similar carbon concentration ((g(Scen)) and b) with growth rates when feeding at non-limiting concentrations ($g(Scen_{max})$) (Fig. 3). A food limitation index (FL-I = $g(Seston)/g(Scen_{max})$) can be calculated which is the product

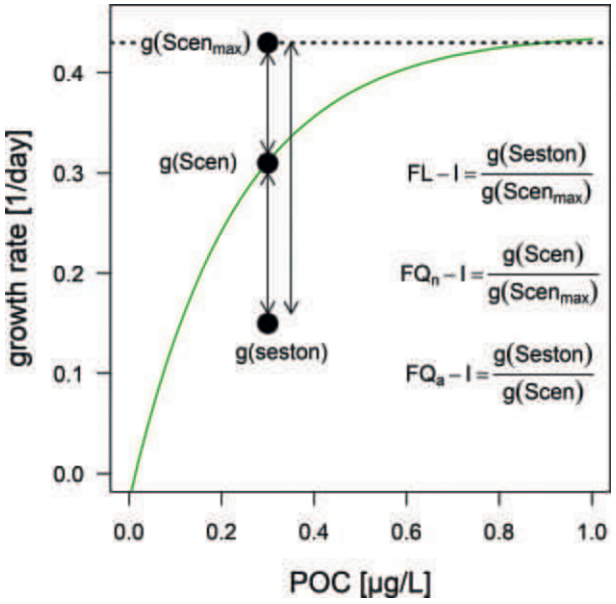

Fig. 3 Estimation of the strength of overall food limitation (FL-I), and of the effects of food quantity (FQ_n-I) and food quality (FQ_a-I) for zooplankton somatic growth on natural seston (g(seston)) relative to growth on standardized food (e.g., the green alga *Scenedesmus*, g(Scen), green line) at a similar concentration of particulate organic carbon (POC), and to maximum growth on standardized food ($g(Scen_{max})$). FL-I can be calculated as the product of FQ_a-I times FQ_n-I.

of a Food Quantity Limitation Index (FQ_n-I = g(Scen)/$g(Scen_{max})$) and a Food Quality Limitation Index (FQ_a-I = g(seston)/g(Scen)) (Fig. 3). Data for the calculation of such indices are scarce, but were reported during a seasonal course in mesotrophic Schöhsee (Müller-Navarra and Lampert, 1996), and at two different trophic conditions (mesotrophic and oligotrophic) in Lake Constance (Hartwich et al., 2012; Wacker and von Elert, 2001).

In mesotrophic conditions (Schöhsee and mesotrophic Lake Constance), FL-I values approached one during spring and autumn, implying no food constraints during these periods (Fig. 4A). This supports correlative studies, suggesting that *Daphnia* growth during spring is mainly controlled by temperature (Straile et al., 2012) and not by nutritional constraints (Straile, 2015). Strongest food constraints were observed around May and June, i.e., during the clear-water phase and intermediate food constraints during summer. In oligotrophic Lake Constance, FL-I was lower especially during spring and the clear-water phase. However, in all three studies, food constraints were never strong enough to stop *Daphnia* growth. FQ_n-I reached higher values in Schöhsee compared to the two study years in Lake Constance, and varied between 0.6 and 0.8 during most parts of the summer (Fig. 4B). FQ_a-I varied considerably between the three studies during spring and early summer with values approaching or even exceeding one in mesotrophic conditions (i.e., seston quality approaches or exceeds the quality of *Scenedesmus*), and lowest values in oligotrophic Lake Constance (Fig. 4c). During summer, FQ_a-I varied between 0.6 and 0.8 in all lakes/conditions. The ratio FQ_a-I/FQ_n-I gives a measure of the relative importance of quantity versus quality constraints (Fig. 4D). Values above one indicate the predominance of quantity constraints, whereas values below one suggests predominantly quality constraints. The ratio was close to one in all three studies around July and August, suggesting co-limitation by food quantity and quality, and that quantity and quality constraints on juvenile growth were of similar magnitude during this time of the year (Fig. 4D). Dominance of quantity constraints during spring may result from true quantity constraints in oligotrophic lakes, but also from FQ_a-I values exceeding one.

The high seston quality in spring (FQ_a-I >1) is presumably a result of the algal taxonomic composition, i.e., the dominance of PUFA-rich diatoms and cryptophytes during the spring bloom, but also due to low *in situ* water temperatures during spring, resulting in higher PUFA production of algae (Piepho et al., 2012). Thus, FQ_a-I values exceeding one point to an important limitation of this approach, the ignorance of food x temperature interactions. *Daphnia* growth rates in the three studies were determined at 20 °C, which is close to *in situ* temperatures during summer, but not during spring and autumn. Consequently, the use of 20 °C, instead of lower *in situ* temperatures, as experimental temperatures might have caused underestimation of FQ_n-I (= overestimation of food quantity limitation) and overestimation of FQ_a-I (= underestimation of food quality limitation) during spring and autumn.

Finally, direct evidence of quantity and quality limitation can be achieved via supplementation studies (DeMott et al., 2001, 2004; Hartwich et al., 2012; Santer and Lampert, 1995). One of the few studies available, which did not work with *Daphnia*, showed that nauplii of cyclopoid copepods are unable to develop during summer on natural seston collected from Lake Schöhsee, but were able to do so upon supplementation with the green alga *Chlamydomonas reinhardtii* (Santer and Lampert, 1995). This study provides strong evidence that also selective feeders, such as copepods, experience nutritional constraints within sensitive life stages, but does not allow distinguishing between food quantity and quality constraints. This was achieved, at least partially, in *Daphnia* studies in hypereutrophic ($P > 50$ µg L^{-1}) Dutch lakes (DeMott et al., 2001), eutrophic (P ~ 25 µg L^{-1}) and oligotrophic lakes ($P < 10$ µg L^{-1}) in Michigan (DeMott et al., 2004), and in oligotrophic (P < 10 µg L^{-1}) Lake Constance (Hartwich et al., 2012). In the latter study,

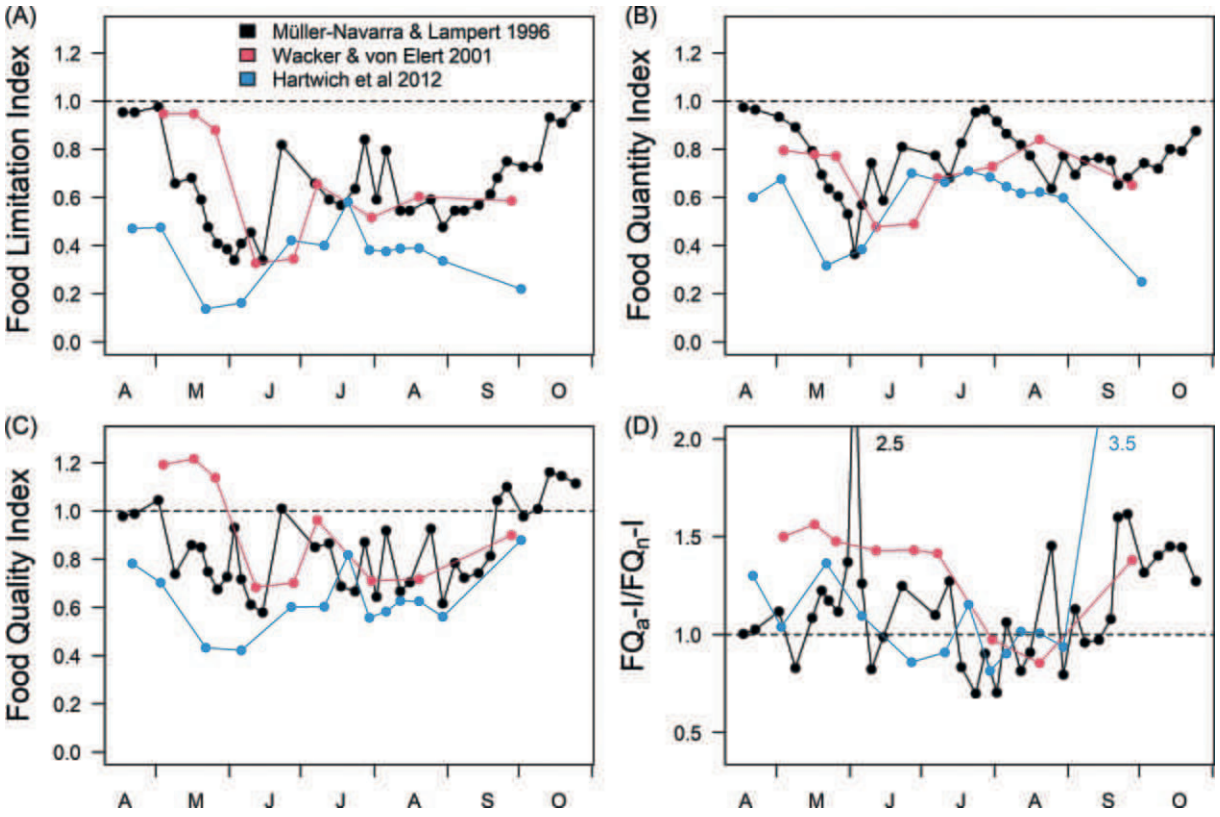

Fig. 4 Seasonal changes in the (A) food limitation index, (B) food quantity index, (C) food quality index, and the ratio of the two indices in three studies quantified using the somatic growth rate of juvenile *Daphnia* as shown in Fig. 3. Note that all indices are based on growth experiments conducted at 20 °C using the green algae *Scenedesmus* as reference food. Hence, all indices ignore the food X temperature interactions and underestimate the role of food quantity limitation, i.e., overestimate the food limitation Index, the food quality Index, and the ratio FQ_a-I/FQ_n-I, i.e., as food algae of higher quality compared to *Scenedesmus* do exist.

the cyanobacterium *Synechococcus* was used to test for food quantity limitation, in addition phosphate and LC-PUFAs were supplemented to natural seston to assess P and PUFA limitation, respectively (Fig. 5). The largest increase of *Daphnia* somatic growth rates was obtained by adding *Synechococcus* to the diet, suggesting food quantity constraints. As *Synechococcus* does not contain LC-PUFAs and sterols, but is rich in phosphorus, this increase indirectly suggests that LC-PUFAs and sterols were not limiting. However, it does not exclude the possibility of a co-limitation by food quantity and phosphorus. In most of the experiments documented in the literature (DeMott et al., 2001, 2004; Hartwich et al., 2012)—with the exception of experiments conducted in two out of the three Dutch lake—phosphate supplementation (Fig. 5B) stimulated growth less than *Synechococcus* supplementation suggesting that in one Dutch lakes, the Michigan lakes and in Lake Constance, food quantity constraints were more important. Likewise, growth rate increase via EPA and ARA supplementation in Lake Constance was small relative to *Synechococcus* supplementation (Fig. 5C and D).

The rather small increases of growth rates observed after phosphate and LC-PUFA supplementation (median increases all <10%) contrasts with a rather low FQ_a-I of 60–80% in comparative studies (Fig. 4); i.e., in order to balance such FQ_a-I values, growth rates should have increased 25–67% upon supplementation. One possible explanation would be that food quality constraints, as indicated by FQ_a-I values, are unlikely due to single dietary compounds, pointing towards co-limitations and interactive effect mediated by multiple food compounds. For example, algal P limitation enhances the digestion resistance of some green algae, thereby increasing food quantity limitation of *Daphnia* (DeMott and Van Donk, 2013). In addition, harmful algae might additionally have contributed to growth limitation of zooplankton (see above).

Zooplankton adaptive response to food constraints

Supplementation experiments testing the quality of *in situ* seston are usually performed using neonates of consumers produced under standardized conditions. Such an approach may overestimate nutritional constraints as only phenotypic responses to nutritional constraints taking place during the consumer growth period, but not maternal effects or rapid evolutionary responses of consumers are considered. Many studies have shown that zooplankton adapt physiologically and evolutionary to temporal and spatial changes in food quantity and quality. For example, *Daphnia* and rotifers cultured at low food concentrations will have lower

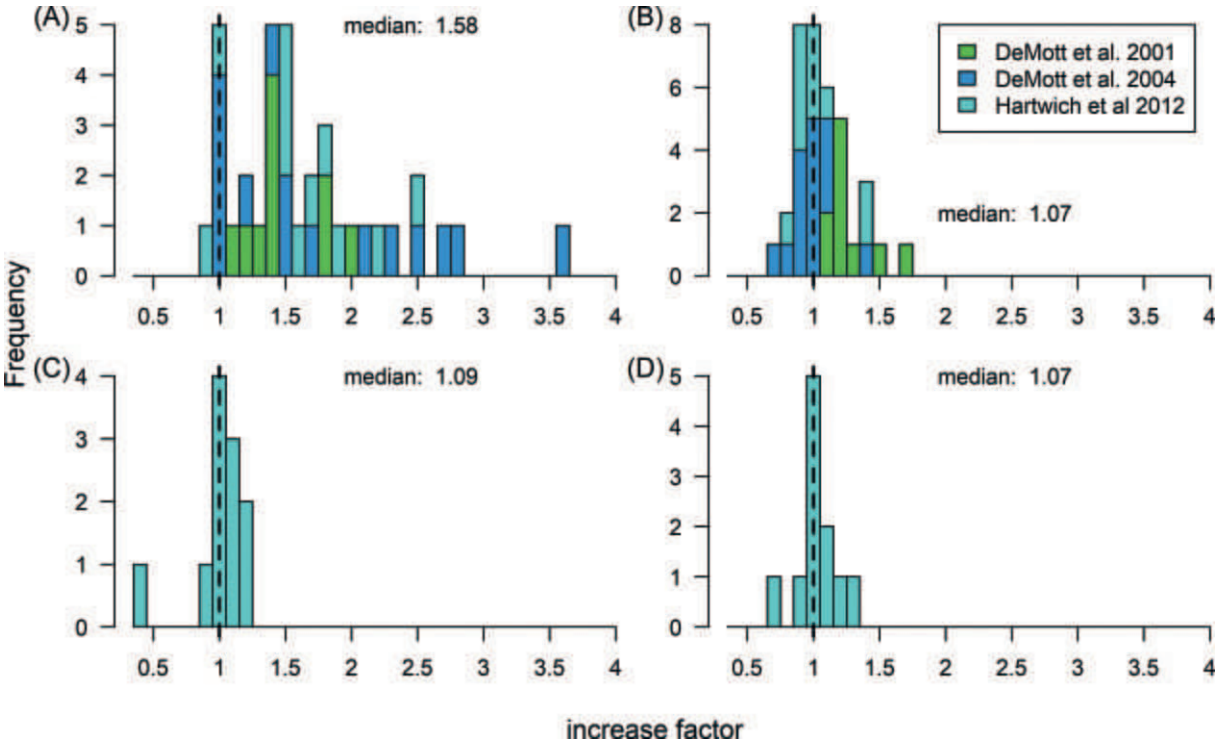

Fig. 5 Frequency of growth increases in supplementation experiments from three studies supplementing lake seston with (A) the cyanobacterium *Synechococcus*, (B) phosphate, (C) EPA and (D) ARA. One experiment from DeMott et al. (2004) was excluded, as close to zero growth on seston resulted in extremely high growth increases for *Synechococcus* and phosphate supplementation.

threshold food concentrations compared to *Daphnia* and rotifers of the same clone cultured at high food concentrations (Rothhaupt and Lampert, 1992). In *Daphnia*, such phenotypical adaptation is due to phenotypic plasticity, i.e., formation of larger filter areas and smaller mesh sizes of filters, which will allow them to filter a larger amount of water and smaller particles in a given amount of time (Lampert and Brendelberger, 1996). Likewise, phenotypic response to cyanobacteria can result in tolerance to cyanobacterial microcystins, e.g., via the regulation of transporter gene expression (Schwarzenberger et al., 2014). Microevolutionary adaptation of *Daphnia* to the presence of toxic cyanobacteria has been observed during two decades of lake eutrophication (Hairston et al., 1999), but also during one seasonal course of plankton succession (Schaffner et al., 2019). There is also clonal variability of *Daphnia* in respect to phosphorus (Weider et al., 2004) and PUFA limitation (Brzeziński and Von Elert, 2007), suggesting that *Daphnia* populations may also show microevolutionary responses to changes in seston C:P ratios or LC-PUFA contents. However, microevolutionary adaptation to lower food quality and quantity likely seems to involve costs when food is abundant and of higher quality, which prevents an evolutionary fixation of these traits. For example, lake oligotrophication resulted in a microevolutionary loss of *Daphnia* tolerance to cyanobacteria that had previously evolved over three decades of eutrophication (Isanta-Navarro et al., 2021).

Knowledge gaps and perspectives

1) Our understanding of nutrient limitations under controlled laboratory conditions has improved significantly in recent years. However, our understanding of zooplankton nutritional constraints *in situ* is still limited. We need more seston supplementation experiments in lakes of varying trophic state, degree of autochthonous production, and mixing depth to unravel the relative roles of food quality versus food quantity limitation, as well as the role of co-limitation of various food quality compounds. Such work may be accompanied by studies examining the nutritional phenotype (Frost et al., 2014), i.e., the molecular and biochemical status of experimental and sampled zooplankton in order to improve our ability to infer the strength and type of nutritional constraints *in situ*.
2) Our understanding of the role of temperature x food constraints interactions is still limited. Changes in both food quantity and quality requirements of zooplankton with temperature requires careful design of laboratory experiments to prevent hidden treatments. Likewise, field studies are needed which explicitly address the interaction between temperature and both food quantity and quality constraints on zooplankton.
3) Zooplankton will respond to nutritional constraints phenotypically, via maternal effects, and evolutionary. The relative role of these responses *in situ* for the mitigation of nutritional constraints is insufficiently understood.

4) Due to the central position of *Daphnia* in lake food webs and its suitability as a laboratory model organism, research on zooplankton nutritional constraints is primarily centered on *Daphnia*. More work on the nutritional constraints of other zooplankton taxa is urgently needed.
5) Finally, the availability of genomic information for aquatic consumers opens new avenues to explore the molecular basis of zooplankton responses to nutritional constraints and to link physiological responses to these constraints. Applying recently developed high-throughput" -omics" tools (transcriptomics, proteomics, metabolomics) to reveal molecular patterns of resource acquisition and exploitation at various environmental conditions may now rapidly advance our understanding of how zooplankton respond to nutritional constraints.

Acknowledgment

We thank Alexander Wacker and the editors for comments on the manuscript.

See Also: Emerging methods and topics: Dust and Fog Effects on Inland Waters; Fundamental concepts and theories: Diel Vertical Migration; Structures and functions of Inland Waters - Lakes: Predation on Zooplankton; Zooplankton Diversity and Variation Among Lakes; Structures and functions of Inland Waters - Rivers: Energetics and Food Webs in Large Rivers

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Predation on Zooplankton

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Glossary

Benthic Organisms living at the bottom of aquatic ecosystems.
Community In ecology is used to define an assemblage of interacting individuals belonging to different species at a given place or region.
Lentic Relative to freshwater systems lacking a directional current such lakes and ponds.
Meta-analysis Statistical approach allowing to make a global analysis of the outcome of different studies.
Phylogenetic Relative to the evolutionary relationships among living organisms.
Population In ecology is used to define an assemblage of individuals belonging to the same species at a given place or region.
Seston Pool of living (e.g. phytoplankton) and non-living particles (e.g. detritus) suspended in the open water.
Zoochory Dispersal mediated by animals.

Introduction

Freshwater zooplankton can be found in a wide array of habitats, ranging from temporary pools to permanent ponds and large lakes. Because of this variability and their relatively high dispersal potential, they are thus exposed to an extremely large range of environmental conditions including different levels of predation pressure from both vertebrates and invertebrates. Nearly all fishes have at least one early stage feeding on zooplankton and zooplanktivory is an essential step for most of them. In response to this strong selective pressure, zooplankton has evolved a large array of adaptations, ranging from changes in life-history traits to rapid anti-predator behavioral responses.

Predation has profound effects on zooplankton at many levels, from the individuals to the community. Examples of such effects include higher mortality of more conspicuous zooplankters, consequent changes in the size structure of both populations and communities, with potential effects on zooplankton diversity. These changes have the potential to affect both ecosystem functioning and the associated ecosystem services, because of the huge potential impact of zooplankton to graze phytoplankton. An increase in the predation pressure on large-bodied filter-feeding zooplankton could in fact translate into an increase of phytoplankton with negative consequences for the quality of the water (e.g. reduced transparency).

The aim of this chapter is to give an overview of the state-of-the-art of the studies about the mechanisms of predation itself, the effects of most widespread to less common predators feeding on zooplankton in inland waters and on the most important anti-predator adaptations found in the different zooplankton groups.

 https://doi.org/10.1016/B978-0-12-819166-8.00123-7

Planktivory

Feeding modes

Zooplanktivory has evolved in many orders of freshwater fishes (Lazzaro, 1987) as well as in many invertebrate taxa such as insect larvae (e.g. phantom midge and dragonfly), crustaceans (both carnivorous copepods and cladocerans), rotifers and even carnivorous plants (e.g. bladderwort). In both cases, zooplanktivory could be either facultative or obligate. In the case of invertebrates, besides the presence of some obligate predators (e.g. the rotifer *Asplanchna*), many cyclopoid copepods, for example, feed on algae and protozoa at the larval stage, but can predate on other zooplankters (including their own conspecifics) while still consuming large algae when adults. Whereas some specialized fishes such as paddlefish (*Polyodon spathula*) are obligate planktivores during their whole lifetime, many others are facultative because they can integrate zooplankton to their diet by switching, say, from zooplankton to benthic invertebrates depending on their relative availability. Ontogeny has another important impact on the ability of fish to capture prey since most species are gape-limited. Whereas zooplankton prey are relatively small for most adult fish, fish larvae might be constrained by gape-limitation to feed only on the smaller zooplankters. Thus, planktivorous fishes vary their selectivity and their potential effects on zooplankton during their ontogeny.

Most invertebrate zooplanktivores such as copepods and phantom midge larvae (*Chaoborus* spp. Diptera) are tactile predators which use mechanical stimuli produced by prey to locate and attack them. Tactile predators are grasping-feeders which capture and handle their prey with specialized appendages (Fig. 1D). As fish larvae, most are gape-limited and select relatively smaller

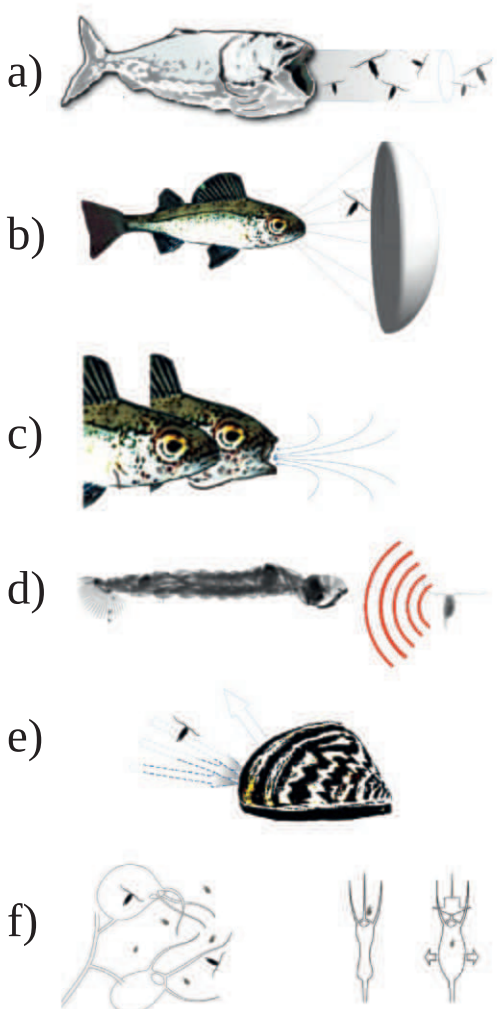

Fig. 1 Types of zooplanktivores. (A) Filter-feeder: the cylinder describe the "search volume"; (B) Particulate-feeder: the section of the sphere represent the visual field with the reaction distance (RD) represented by lines; (C) Particulate-feeder using its protrusible jaw to capture a prey; (D) Tactile predator: a phantom midge larvae reacting to the vibrations of a nearby zooplankton prey; (E) Current-feeder: a zebra mussel entraining in its current a small prey; (F) Trap-feeder: bladderwort. On the left are illustrated two bladders attached to the carnivorous plant, whereas on the right is shown a bladder before and after the prey's capture. (A) Based on a frame captured from a video online: Filter-Feeding Menhaden | Caught On Camera: https://www.youtube.com/watch?v=WhprcLcGGBs from: https://myfishingcapecod.com/filter-feeding/. (E) Modified from a picture of Dreissena taken at: https://serc.carleton.edu/eyesinthesky2/week5/getting_to_know_myworld.html. (F) (Left) Petr Dlouhý (2008) public domain https://en.wikipedia.org/wiki/File:Utricularia_traps_(sketch).svg. (Right) Petr Dlouhý - Image: Utricularia trap expansion.gif, Public Domain, https://commons.wikimedia.org/w/index.php?curid=987701.

zooplankton individuals compared to adult fish (Riessen, 2015). Benthic sessile organisms could also feed on zooplankton as shown by (i) current-feeders such as mollusk bivalves (e.g. zebra mussel) which can capture small zooplankters by entraining them with the continuous current generated by their ciliated gills (Fig. 1E) or by (ii) carnivorous aquatic plants (e.g. bladderwort) which use bladder-like traps activated by trigger hairs to capture and digest zooplankters and other small invertebrates (Fig. 1F).

Among planktivorous fishes, two different types of feeding are typically distinguished: particulate and filter feeding (Lazzaro, 1987; Fig. 1A and B). In the first case, fish predate on zooplankters by locating them visually and pursuing/attacking them individually. To increase their efficiency in particle capture, many teleost fish have evolved jaw protrusibility, which enhances their capacity of engulfing a relatively large volume of water in a very short lapse of time (Fig. 1C). Some filter-feeding fishes can use this mechanism to draw zooplankters into their oral cavity (pump filter-feeding), whereas others capture zooplankters by ram swimming with their mouth agape (tow-net filter-feeding) (Lazzaro, 1987) (Fig. 1A). In both cases, filter-feeders do not spot individual preys, but retain all the particles above a given size by using their gill rakers and other oral structures.

Whereas these structures were formerly thought to function as dead-end sieves (like a kitchen food strainer; Fig. 2A), it has been shown that the main water flow runs parallel, rather than perpendicular, to the filter surface, and that only small flows of water pass through the sieve openings (Sanderson et al., 2016; Fig. 2B). More recently it has been shown that the presence of closely-spaced small ribs in the fish oral cavity generate small turbulences at their backward-facing step which entrap particles and direct them toward the gut while reducing clogging to a minimum (Sanderson et al., 2016; Fig. 2B). Such mechanism, named "vertical cross-step filtration" has been demonstrated to hold for ram filter-feeding fishes such as paddlefish and is expected to work also for other filter-feeding organisms (Sanderson et al., 2016).

Whereas paddlefish represent a typical case of tow-net filter-feeding, its mode of detecting preys is peculiar compared to more common planktivores. This species uses in fact electrolocation to track zooplankton swarms when adult and individual zooplankters when juvenile. These latter use a particular mechanism of electrolocation named stochastic resonance, which could be seen as a form of enhancement of the signal-to-noise ratio when spotting a weak electrical signal emitted by an individual prey over a background of electrical white noise (as the one produced by a zooplankton swarm; Freund et al., 2002).

Several differences exist between particulate and filter feeding, including the geometry of the "search volume" of water within which the fish capture its prey. Whereas for filter-feeders such volume is the product of the distance traveled while ram-swimming agape by gape area, for particulate feeders this latter parameter is replaced by the fish visual field (Fig. 1A and B), which is function of the distance at which the fish detects its prey (the "reaction distance", RD; Eggers, 1977). Given that different factors such as predator species, prey size and light levels can affect RD (O'Brien, 1979), the efficiency of particulate-feeders has the potential to vary more with varying environmental conditions than that of filter-feeders, whose "searched volume" is mostly dependent on their anatomy and swimming speed. Whereas in both cases there is a certain degree of prey selectivity, visually-oriented particulate feeders are typically more selective, by eliminating efficiently more conspicuous individuals such as larger or more pigmented ones, together with those bearing eggs (Lazzaro, 1987; but see Gliwicz, 2002 for a more complete discussion).

Switching between the two feeding modes have been observed for certain fish species, either to adapt to ontogenetic changes or to cope with varying environmental conditions. The efficiency of zooplanktivores is in fact a function, among other things, of their feeding mode and of prey abundance. For example, the food intake of a typical filter-feeder is supposed to increase proportionally with zooplankton abundance for a given prey size (a so-called Type I functional response; Fig. 3). In contrast, particulate feeders are

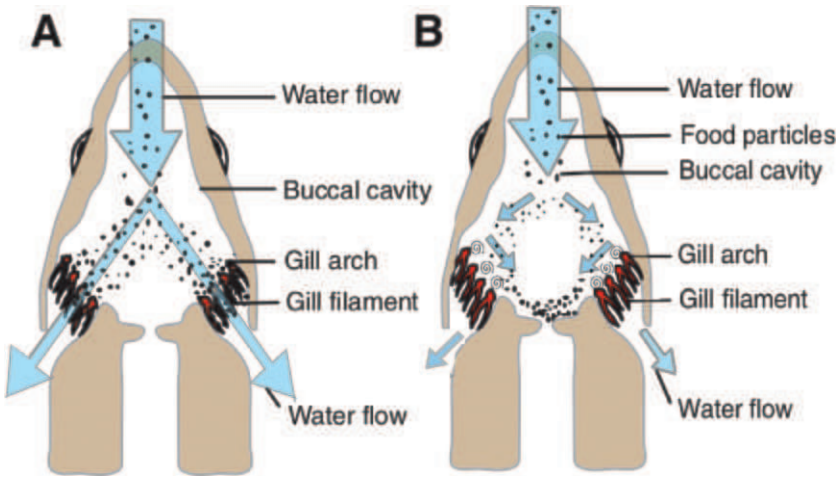

Fig. 2 Models of particle retention by filer-feeding fishes. (A) Dead-end sieve filtration. Particles are sorted by the filter formed by the branchial structures and then are directed toward the esophagus, with the mainstream flow running perpendicular to the filtering surface; (B) Vertical cross-step filtration. When the mainstream flow, which runs parallel to filtering surface, encounters backward-facing steps formed by gill structures it creates vortices which lead the water to pass between the gills, thus allowing particles to be retained without clogging the gills. Modified from Fig 1 in: Paig-Tran, E. M., Bizzarro, J. J., Strother, J. A., and Summers, A. P. (2011). Bottles as models: predicting the effects of varying swimming speed and morphology on size selectivity and filtering efficiency in fishes. *Journal of Experimental Biology* 214(10): 1643–1654.

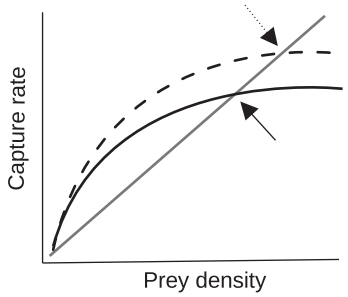

Fig. 3 Linear (type I; grey line) vs. asymptotic (type II; continuous black line) functional responses of predators to varying abundances of prey. Filter-feeding and particulate feeding conform, respectively, to types I and II functional responses. The black arrow indicates the point at which a switching is expected from particulate- (more efficient at low prey density) to filter-feeding (more efficient at high prey density) when prey density increases. By enhancing RD, increased light levels (and/or temperature) can push the switching point to the right (dotted arrow) by changing the shape of the type II functional response (dashed line).

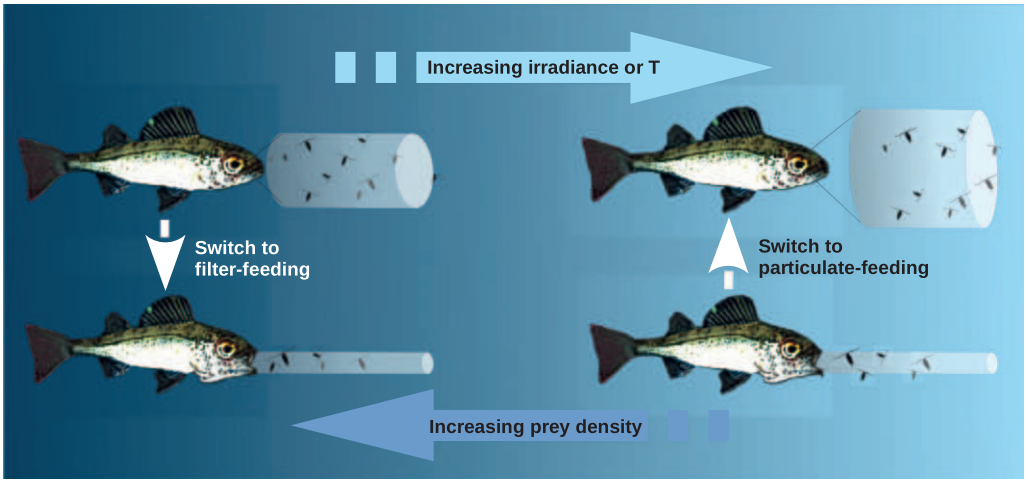

Fig. 4 Expected responses to light, temperature (T) and prey density of both particulate (above) and filter-feeders (below). In this simplified view, particulate feeders "scan" a conical portion of the water mass in front of them, characterized by a radius equal to the so-called "reaction distance" (RD), which increases with both irradiance and temperature. By moving forward, the fish detect and eventually capture individual zooplankters with directed fast pursuits aimed at the prey within an ideal cylinder of radius RD and of length S (the distance moved by the fish); As they move forward agape, filter feeders "scan" a cylindrical portion (the "search volume") of the water in front of them, with the radius of the cylinder determined by the gape width. The white arrows indicate the direction of the switch when either prey abundance or light levels/temperature change. Modified from Fig 2 in Stautland IT (2019). *Modelling the Switch between Bite-Feeding and Filter-Feeding in Planktivorous Fishes*. Master's Thesis. The University of Bergen.

more efficient than filter-feeders at relatively low prey densities, but become limited by prey handling time when prey abundance became too high, with their efficiency reaching a plateau (a so-called Type II functional response; Fig. 3). This could have important consequences not only on the issue of competition between particulate- vs filter-feeder species with varying prey abundance, but could also determine a switch between feeding modes in those species capable of a flexible feeding behavior (Fig. 4).

Effects of environmental factors on predation efficiency

Besides levels of visible light and prey abundance, other factors could affect predation efficiency on zooplankton. Ultraviolet radiation (UVR) has a potential role to play in this sense in clear-water systems, where it could improve the efficiency of those visual predators able to see in these wavelengths (Leech et al., 2009). By affecting light levels, turbidity is also expected to reduce the efficiency of visual predators. Despite in some cases the effects of visually-oriented zooplanktivorous fish have been shown to be similarly strong in clear vs turbid waters, a recent meta-analysis clearly showed that turbidity has clear negative effects on particulate-feeding fish in the majority of cases (Ortega et al., 2020). Surprisingly, the same study showed that filter-feeding fish were also negatively affected by turbidity, showing the potential weight that this driver can have on predator-prey interactions. All these results suggest together that the actual widespread human-driven increase in turbidity might have critical effects on predator-prey dynamics in lakes across large scales.

Temperature has also potential important consequences on predator-prey interactions since it can affect both encounter rates of zooplankters with predators (both vertebrate and invertebrate) and RD in particulate-feeders because of increased visual acuity.

Whereas in both cases an increase in temperature might cause an increase in predation risk for zooplankton, a recent experimental study has shown that warming can increase predation risk for zooplankton exposed to visual predator fish more due to increased RD than due to increased encounter rates (Gliwicz et al., 2018).

By increasing the structural complexity of the habitat and thus reducing fish attack rate, submerged aquatic vegetation (SAV) is also known to reduce predation risk for zooplankton. Therefore, SAV beds are key in maintaining both higher biomass and diversity of zooplankton in lakes. However, since SAV also offers shelter to large numbers of benthic invertebrate predators such as dragonfly larvae, these habitats are in some cases riskier than the open area and the relative risk of these two habitats should be considered when assessing predation risk for zooplankton.

Finally, the role of zooplankton behavioral traits should also be considered when predicting the outcome of predation since very large differences exists between taxa in their ability to flee predators and/or avoid encounter with them. Copepod nauplii, for example, are able to jump away very fast when a predator is approaching (speeds up to 130 body lengths sec-1) whereas slow-moving waterfleas (*Daphnia*) are easy targets. It has been shown that taking into account such traits can help explaining the outcome of predation on zooplankton by fish with different selectivity in freshwater ecosystems (Vincent et al., 2020).

The consequences of predation

From the individual to the community level

In ecology there has been a long-lasting debate about the relative roles of bottom-up (i.e. resource-driven) vs. top-down (i.e. predation driven) forces in determining both the success of individuals and the shape of the communities in which they are embedded. It is currently acknowledged that the interplay of predation and competition for resources can have profound effects on zooplankton, from the individual to both the population and community level (Gliwicz, 2002). Whereas their roles differ on prey populations, in both cases body size has been shown to be a key trait in determining their impact on zooplankton. This trait determines in fact both zooplankton vulnerability (larger individuals are more exposed to fish predators, while smaller ones are more exposed to invertebrate ones) and their efficiency as competitors (in most cases, larger zooplankters outcompete smaller ones because they better tolerate starvation).

Seminal work made in the 1960s revealed these huge effects that fish predation could have on zooplankton community structure in natural systems (Hrbáčkek et al., 1961). Selective predation by fish is in fact able to eliminate larger individuals/taxa, thus entirely re-shaping the zooplankton community (Fig. 5). In general, predation is considered to be responsible of zooplankton mortality at a higher degree compared to starvation, disease and parasitism whereas competition is expected to drive mostly the reproductive output and the efficiency of energy transfer from the base of the food web (Gliwicz, 2002). In a nutshell, whereas competition is expected to drive the rates at which processes take place, such as growth, birth, and food assimilation, predation is expected to control state variables such as abundance, body size and biomass, thus having a more visible impact on more easily measurable

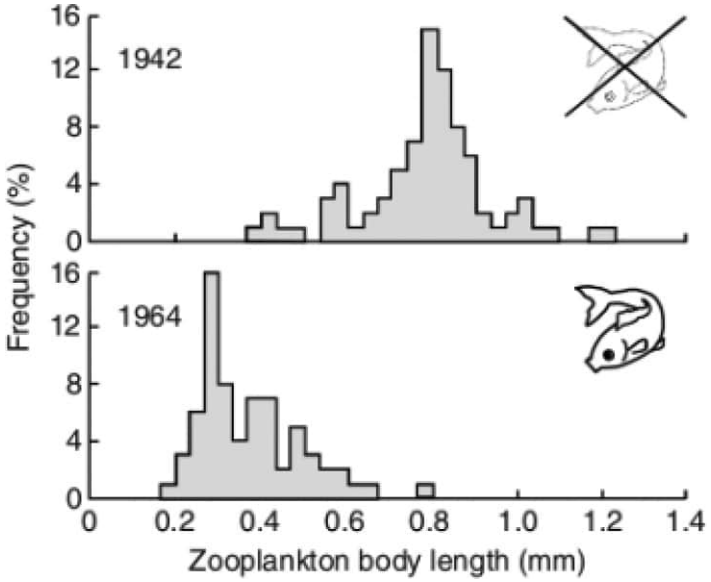

Fig. 5 Origin of the 'size–efficiency hypothesis': Large-bodied species, superior in competition for resources, dominate the zooplankton community in a lake in New England sampled in 1942 (top), but are absent in 1964 due to their inferiority in evading predation by a visually oriented planktivorous fish (bottom). The change in size distribution of the zooplankton occurred between 1942 and 1964, following the establishment of a landlocked population of *Alosa pseudoharengus* in the lake. Adapted from Fig. 4 in Brooks JL and Dodson SI (1965) Predation, body size and composition of plankton. *Science* 150: 28–35, with permission from the American Association for the Advancement of Science.

traits of the community (Gliwicz, 2002). The effects of competition can be seen among zooplankton taxa when predators are absent and food is limiting, where the lower food thresholds of larger zooplankters favor their dominance over smaller ones by increasing their birth rate relatively to the latter (Gliwicz, 2002). In the presence of predators, the effects of competition are not expressed at the level of population abundance since this latter is controlled by predation. It has been shown for example that a given level of predation usually leads to relatively stable abundances in zooplankton prey independently of food limitation (Gliwicz, 2002). The relationship between RD and prey size can help explain the fact that this effect seems to be size-specific. An individual fish can in fact perceive the abundance of a large zooplankton species as equal to that of a smaller, but more abundant one, simply because the RD for these latter is smaller, leading to an underestimation of their abundance relatively to the former (Fig. 6). Given that the mortality imposed by visual predators is proportional to the relative abundance of preys perceived by their retina, predation by a given size class of fish (of a given species) is expected to lead to species-specific prey abundances due to differences in their body size (Gliwicz, 2002).

In addition to body size, any other trait increasing conspicuousness of zooplankters are counter-selected in the presence of visual predators. Both pigmentation and the presence of eggs, for example, increase the vulnerability to visually-oriented predators. The presence of epibiotic organisms such as ciliates or euglenoids attached on zooplankton can also alter their conspicuousness exposing heavily burdened individuals to stronger fish predation. In general, transparency seems to have evolved in zooplankton to maintain a low conspicuousness to visual predators despite the varying degrees of contrast and lighting levels in the open water. Evasiveness also contribute to determine the issue of predation, with adult copepods and nauplii being less exposed to fish predation than slow-moving cladocerans such as large *Daphnia* (Vincent et al., 2020).

Both mesocosms and whole-lake experimental studies have confirmed the role of predation in shaping both taxonomic composition and size distribution of zooplankton communities. Thus, selective predation by fish tends to eliminate first the large bodied cladocerans such as large *Daphnia*, whereas smaller zooplankters (e.g. rotifers) suffer proportionally less mortality. The consequent release of competition allows these latter to increase in abundance and dominate the community in the presence of predators (Gliwicz, 2002). The combined result of size-selective predation and competition on zooplankton communities is known as the *size-efficiency hypothesis* (Brooks and Dodson, 1965; Fig. 5). The presence of invertebrate predators of zooplankton (themselves prey of fish) within the zooplankton community is expected to reinforce this pattern by exerting a selective predation pressure on small zooplankton when planktivorous fish are absent. However, some studies have challenged this view by revealing that in some cases invertebrate predators such as phantom midge larvae, carnivorous cladocerans such as spiny flea (*Bythotrephes longimanus*) and *Leptodora kindtii* can have unexpected strong impact on zooplankton, similar or even stronger than the one exerted by zooplanktivorous fishes (e.g. Walsh et al., 2017). The presence of such strong predators within the zooplankton community itself is thus key to understand the balance between vertebrate and invertebrate predators. Instead of taking into account only the presence/absence of fish, a more realistic view integrating gradients of fish predation pressure might give a more precise idea of the role of invertebrate predators in shaping zooplankton communities. This is shown for example in boreal lakes, where predation on zooplankton could result from unspecialized zooplanktivores fishes or from very efficient invertebrate predators such as large (>1 cm) predacious phantom midge larvae in fishless lakes. In many boreal lakes of Eastern North America, for example, the only planktivory from fish is due to the generalist brook charr (*Salvelinus fontinalis*), which exerts a relatively weak predation pressure on zooplankton, while it efficiently controls large-bodied phantom-midge larvae (e.g. Drouin et al., 2009). Within this context, predation pressure on zooplankton is larger in the absence, rather than in the presence of fish, as predicted by the classic paradigm, resulting in an increase in zooplankton body size distribution from fishless to fish lakes (Fig. 7).

Resilience to predation of zooplankton communities

Short-term variations in predation pressure are commonplace in freshwater systems due for example to the seasonal synchronization of fish hatching in temperate lakes. Whereas an increase in predation pressure can have rapid effects on zooplankton communities, the reverse might take more time. Despite short generation times and plasticity in anti-predator defenses can allow

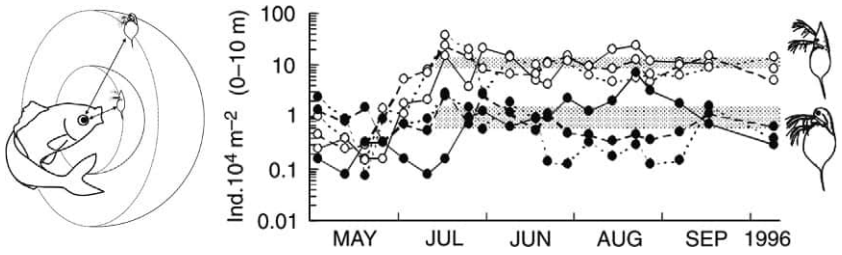

Fig. 6 Diagrammatic representation of the differences in reaction distance (RD) for two *Daphnia* species differing in body sizes (left panel) and the temporal evolution of their population densities in a lake with a visual planktivorous fish (right panel). Despite the fact that the smaller prey species has a larger population abundance (right panel), the smaller reaction distance of this species relatively to the larger one (left panel) leads to the perception of similar abundances by their common predator. This latter thus exert a stronger pression on the largest species despite its lower abundance, thus stabilizing the population abundance of the two species at different population densities. From (Left) Fig 9 and (Right) Fig 8 in Gliwicz MZ (2002) On the different nature of top-down and bottom-up effects in pelagic food webs. *Freshwater Biology* 47(12): 2296–2312.

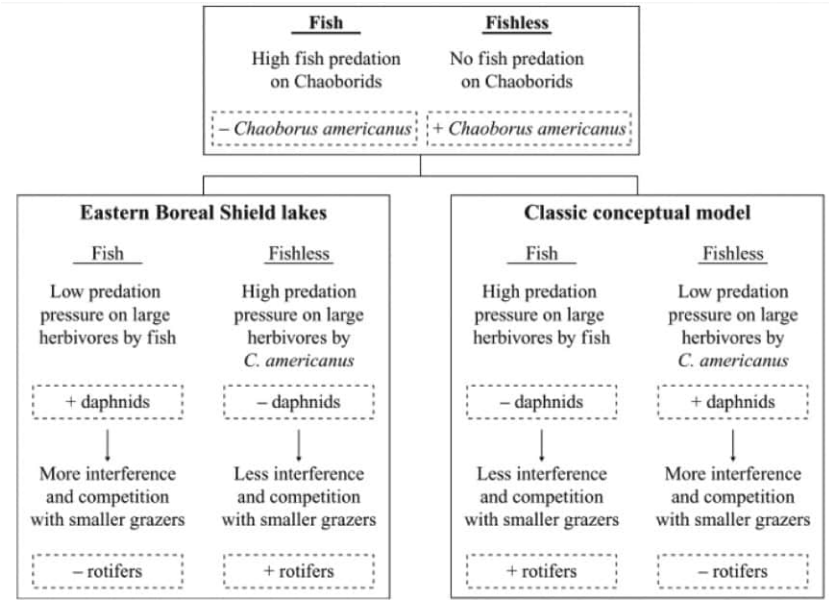

Fig. 7 Conceptual model of the top-down control of zooplankton communities in the eastern Canadian Boreal Shield lakes and in classic studies (e.g. Brooks and Dodson, 1965). From Fig 4 from Drouin A, Sirois P, and Archambault P (2009) Discriminating zooplankton communities in lakes with brook trout (Salvelinus fontinalis) and in fishless lakes. *Ecoscience*, 16(3): 271–281.

zooplankton to cope with transient regimes of predation, it has been showed that planktivorous fish, even if present only for a short period of time, can have long-lasting effects on zooplankton communities (Ersoy et al., 2019). Several studies had in fact showed that, when re-colonization is limited because of depletion of the resting stage (e.g. eggs) bank in the lake sediments, the recovery from the effects of predation might take several years. The consequences of resting stages depletion might be particularly important for copepods since these crustaceans reproduce only sexually and have to find a mate to rebuild a population, which could be limiting at very low population densities. In contrast, cladocerans, which are able to go through either sexual or asexual reproduction, can re-build a population faster by reproducing clonally. Because of the high dispersal potential of their flying adult stages, key invertebrate predators such as phantom midge larvae can overcome these limitations and easily recolonize lakes and ponds after fish removal without being dependent on recruitment from resting stages banks.

Positive effects of predation on zooplankton populations

Whereas fish can impose a severe mortality on zooplankton populations, they can have at the same time both direct and indirect positive effects on them. In addition to induce an earlier reproduction in many zooplankton species (see below), which could compensate for the toll imposed by predation, the overall reduction of zooplankton grazing on phytoplanktonic algae translates into a reduced competition and overall greater availability of resources for herbivorous zooplankton itself. Therefore, by releasing competition for the resources, predation can lead to higher growth and fecundity rates and thus increase the zooplankton reproduction potential. Moreover, many zooplankton species have eggs with thickened shells (e.g. ephippia in cladocerans) whom have been demonstrated to be resistant to digestion in the fish gut. Since females bearing dark pigmented ephippia are more conspicuous, they suffer heavier predation from visually-oriented fishes which could also mean that they are potentially dispersed more easily by these latter across the watershed. Unfortunately, invasive species also benefit from this adaptive mechanism (a form of zoochory) as have been demonstrated for the spiny water flea (*Bythotrephes cederstroemi*), an invasive predator cladoceran introduced recently in North America (Taylor Jarnagin et al., 2000). Since these invertebrate predators can have themselves profound impacts on the zooplankton communities, the net effects of this predation-mediated dispersal on the zooplankton community are difficult to predict.

Food-web and ecosystem level

Cascading effects on primary producers

Since the 1960s the idea that consumers can control the biomass of primary producers has sparked interest for the role of predation in the functioning of the ecosystems (Hairston et al., 1960; Brooks and Dodson, 1965). The "green world hypothesis" (Hairston et al., 1960), for example, suggested that the biomass of plants in our planet is high because herbivores are controlled by predation (a so-called *"trophic cascade"*). Applied to lakes, the basic idea is that (i) planktivores can trigger an increase of phytoplankton by

reducing the biomass of filter-feeding zooplankton such as large *Daphnia*, and (ii) piscivorous predators can reverse this pattern by reducing the abundance of planktivorous fish. Based on these simple ideas, the biomanipulation concept became thus popular in the 1980s, when numerous attempts have been made to control the effects of eutrophication by the manipulation of the biomass of planktivorous fish. At the end of the 1990s it has been demonstrated that these effects are effective in the medium term (<10 years) but that in the long term they have to be accompanied by a reduction of nutrient sources to be maintained (Hansson et al., 1998).

This area of research attracted since then a large interest, stimulating theoretical work together with experimental approaches at both the mesocosm and the whole lake level. Whereas the simplest form of the trophic cascade hypothesis is based on a linear food chain rather than a more realistic food web and does not take into account the full realism of aquatic communities and lake ecosystems, many studies gave support to its overall predictions, suggesting that in many cases the trophic cascade concept is a heuristics which can help explain natural patterns in many lake food webs despite it fails to take account some key biotic interactions.

Effects on the biogeochemical cycles

Predation could also affect element cycling (e.g. C, N and P) via its impact on zooplankton grazers. The increase in phytoplankton primary production following an increase in predation on zooplankton has for example the potential to affect the carbon cycle. Whereas many oligo-mesotrophic boreal lakes tend to be net sources of carbon to the atmosphere since they receive relatively large amounts of carbon of terrestrial origin, an increase in pelagic primary production can shift the balance between autotrophy and heterotrophy and cause them to be net sinks of carbon of atmospheric origin (Schindler et al., 1997). This effect might be seen as somewhat counterbalancing the negative effects of planktivores on water quality due to a trophic-cascade from grazers to phytoplankton.

Another potential intriguing effect of predation on zooplankton might be mediated by the relative ability of different zooplankton taxa in retaining and recycling different nutrients. Freshwater zooplankton is in fact known to have the potential to modify the stoichiometry of the seston because their needs in terms of C, N and P differ among species. *Daphnia* and Copepods have a very distinct stoichiometric composition, with the former being more P-enriched than the latter (lower C:P and N:P ratios; Fig. 8A). Given that the seston in lakes is typically enriched in both C and N relatively to P, this food source is imbalanced relative to the *Daphnia* nutritional demands (Fig. 8A), suggesting a potential P-limitation for this key zooplankter relative to copepods. Therefore, in *Daphnia*-dominated systems, not only phytoplankton is under a stronger top-down control than in copepod-dominated systems, but there is also a potential consumer-driven P-limitation due to a reduced recycling of P relative to N by *Daphnia*. Therefore, the tendency of *Daphnia* to sequester relatively high amounts of P to maintain its homeostasis could contribute to maintain low phytoplankton biomass via nutrient limitation. In lakes, phytoplankton growth has been showed to shift from P- to N-limited when the zooplankton community shifts from *Daphnia* to copepod dominance (Sterner and Elser, 2002). It has been showed (Sommer and Sommer, 2006) that such stoichiometric effect of predators is less likely to occur in marine systems because the difference in N:P ratio between seston and grazers does not suggest nutrient imbalance (Fig. 8B). Since body size is another factor potentially affecting nutrient recycling, fish predation can have an additional potential effect on this ecosystem property by shaping the size structure of the zooplankton community. Since smaller organisms have relatively higher metabolic rates per unit biomass than larger ones, the elimination of larger zooplankters by selective predation should increase the potential of the zooplankton community to recycle nutrients.

Predation can also affect the transport of nutrients by zooplankton organisms moving across habitats (e.g. taxa performing vertical migrations) and across ecosystems (e.g. planktonic larvae of emergent aquatic insects). By reducing the numbers of planktonic phantom midge larvae, for example, fish predation has the potential to reduce the cross-ecosystem export of essential fatty acids from aquatic to terrestrial systems (Martin-Creuzburg et al., 2017). It is in fact known that preys of aquatic origin may

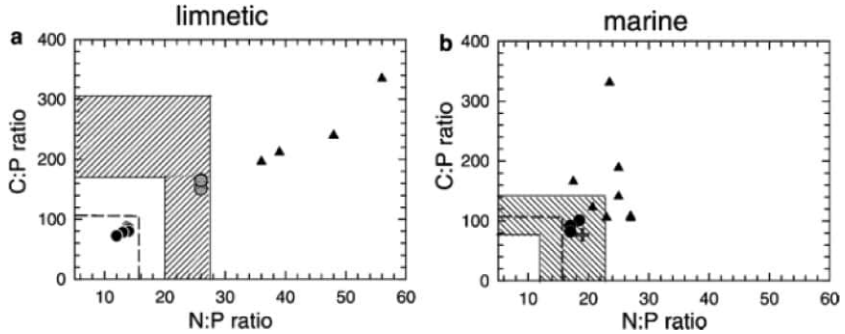

Fig. 8 Stoichiometry of zooplankton and seston in freshwater (A) and marine (including brackish water) systems (B). Hatched area: range of mean values for seston stoichiometry; broken line areas represent mean values for zooplankton and seston, respectively. Broken line represents the Redfield ratio (C:N: $P = 106:16:1$), which is the average elemental ratio consistently found in many phytoplankton species and is often assumed as a reference; Zooplankton symbols: (A) black circles *Daphnia* spp., grey circles *Bosmina* spp., triangles copepods. (B) Circles *Evadne* spp., triangles copepods, cross *Oikopleura dioica*. From Fig 6 in Sommer U and Sommer F (2006) Cladocerans versus copepods: the cause of contrasting top–down controls on freshwater and marine phytoplankton. *Oecologia*, 147(2): 183–194.

have superior food quality for terrestrial consumers given their high content in good quality poly-unsaturated fatty acids (PUFA). Moreover, predation, by forcing some zooplanktonic organisms to move between the hypolimnion to the epilimnion (see below), could increase their potential to transfer nutrients and contaminants from one habitat to the other, as it has been demonstrated for methylmercury transported from the bottom to the top of the water column by migrating *L. kindii* (Hall et al., 2020).

Anti-predator defenses

Constitutive vs inducible defenses

In response to the strong selective force represented by predation, zooplankton have evolved a large array of anti-predator defenses, either constitutive (i.e. fixed over ecological times) or inducible (i.e. plastic). Within the former category we could cite the fact that (i) some species evolved long spines or gelatinous sheaths reducing their vulnerability to predators without increasing their conspicuousness (e.g. the spiny flea and *Holopedium* spp.;), (ii) most zooplankters have evolved body transparency, (iii) the life cycles of some taxa include a period of suspended development which allows them to avoid the pelagic habitat (e.g. the diapause allows some copepods to stay buried in the sediments during long periods) or (iv) the strong swimming abilities of some zooplankters allowing them to flee when a predator is attacking (e.g. copepod nauplii). Besides these relatively fixed traits (some of them might eventually be modulated in response to varying predation risk), other anti-predator defenses are expressed only in the presence of a cue from a predator. Among freshwater zooplankton species we have the most striking examples of inducible defenses such as changes in morphology, pigmentation, life-history traits and behavior (e.g. Kruppert et al., 2017; Ekvall et al., 2020). This phenotypic plasticity likely reflects the need for these organisms to rapidly respond to the potentially varying predation risk found in freshwater ecosystems.

Induced anti-predator morphological defenses have been largely studied in freshwater zooplankton boosted by the demonstration that cyclomorphosis (i.e. a seasonal variation in body shape), a widespread phenomenon known in limnology since the 19th century, was not due to seasonal variations in abiotic variables as previously thought, but to a varying predation pressure on certain zooplankters such as some rotifers (e.g. *Keratella* and *Brachionus*) and *Daphnia* spp. (Diel et al., 2020).

Not only it has been demonstrated that these morphological changes are adaptive in a context of a varying predation pressure, but also that they are mediated in most cases by chemical cues ("*kairomones*") released by the predators. For example, chemical cues released by phantom midge larvae have been shown to induce variations in both body shape and carapace stiffness in *Daphnia* (Kruppert et al., 2017). By interfering with predator efficiency in capturing and handling prey, respectively, these changes have the potential to reduce *Daphnia* vulnerability to its predator. Some *Daphnia* species can reduce the predation by tactile predators such as tadpole shrimps (*Triops cancriformis*) by inducing a "crown of thorns" (Petrusek et al., 2009) whereas others develop a "neckteeth" in response to phantom midge larvae (Kruppert et al., 2017). Among the inducible defenses observed in *Daphnia*, there is also the first case mentioned that the bilateral symmetry by *D. barbata* in the presence of tadpole shrimps is abandoned. The so-obtained twisted carapace is thought in fact to interfere with the feeding apparatus of this benthic predator and reduces its efficiency in handling prey (Herzog et al., 2016). More common examples include the formation of spines or "helmets" to reduce capture rate by gape-limited predators (Lass and Spaak, 2003).

A phenomenon similar to what was found in *Daphnia* has been observed with *Holopedium glacialis* (*H. gibberum*) whose gelatinous sheath embedding its carapace (ca. 2–3 times larger its body length) can significantly increase in size when exposed to phantom midge larvae (Stenson, 1987). Given the transparency of the gelatinous sheath, this strategy reduces predation from gape-limited tactile predators while not increasing conspicuousness to visual predators. This example in interesting since the gelatinous sheath could have also a role in reducing prey palatability by diluting prey nutritional quality due to the high water content of the sheath, thus probably reducing its attractiveness to predators. Besides this, there are only few examples of reduced palatability or use of distasteful/toxic substances in freshwater zooplankton.

One of the most studied case of behavioral anti-predator defense in freshwater zooplankton is the diel vertical migration (DVM) which is considered one of the most massive migration phenomena on earth. When performing DVM, individuals spend the night feeding in surface waters and descent to deeper (and colder) waters at dawn to avoid predation and/or UVR risk in well lit-waters (Diel et al., 2020). The opposite pattern is also known in some taxa (inverse DVM) and it is probably due to invertebrate predators such as phantom midge larvae performing DVM in the presence of fish (Diel et al., 2020). State-of-the-art labelling techniques based on fluorescent nanoparticles have recently allowed to follow experimentally the behavioral response of individual zooplankters to kairomones from different predators in the laboratory. This innovative approach showed that *Daphnia* spp. can adjust both their swimming speed and their vertical position in the water column depending if the predation risk was due to a fish (cyprinid) of from an invertebrate (dragonfly larvae) (Ekvall et al., 2020).

Costs of induced defenses

Whereas the reversibility of induced defenses in the absence of predators is usually used as a demonstration of the presence of a cost of predator-induced phenotypic plasticity, direct estimation of such costs is not always straightforward to obtain. The costs associated to non-consumptive effects of predators via changes in prey behavior (e.g. DVM) can be understood as the consequences on fitness associated with the use of sub-optimal habitats. For example, the lower temperature found in the refuge from predator relative to the feeding habitat could cause a reduction in growth and reproductive rates, with potential large consequences in terms

of population abundance, as shown from both laboratory and time-series studies on natural systems. Another potential cost associated with the use of sub-optimal habitats is an increased disease risk, as it has been shown for *Daphnia* because of an increased risk of encountering parasites such as fungi when migrating to bottom layers (Decaestecker et al., 2002). Other trade-offs concerning anti-predator defenses deserves attention, such as those cases involving multiple predators. Whereas in some cases prey may experience a net benefit in terms of mortality if different predators interfere with each other, it is possible that adopting a given induced defense for a given predator would increase its predation risk relative to other predators. This has been suggested for zooplankton performing DVM in the presence of both vertebrate and invertebrate predators (Fiksen et al., 2005). Given that many anti-predator induced defenses are often specific to one or few predators, it cannot be excluded that the overall predation rate from multiple predators could be higher than could be predicted by summing the predation rates estimated for each predator separately.

Demonstrating the cost of other types of defenses (e.g. morphological) has been proven more challenging since the direct cost associated to forming and maintaining a given morphological defense might be only a minor part of the total cost a prey has to assume. In some cases, changes in life-history traits are necessary for the defense to be effective, thus changing the total cost for the prey.

Freshwater vs marine zooplankton

Whereas freshwater and marine zooplankton share many features, some of their specificities are helpful to understand their differences in terms of response to predators. One of the differences between freshwater and marine zooplankton concerns the relative broader phylogenetic spectrum of organisms found in marine systems relative to inland waters. Moreover, marine zooplankton is composed of both taxa spending their entire life cycle in the pelagic realm (the so-called "holoplankton"; e.g. ctenophorans) and, to a large extent, to taxa such as mollusks and sponges spending only their larval phase as planktonic organisms (the so-called "meroplankton") but their juvenile/adult phase as benthic organisms. In freshwaters, only some organisms such as the larvae of trematodes (miracidia and cercariae) and of some mollusk bivalves (e.g. zebra mussel veligers) are considered as equivalent to marine meroplankton.

Whereas freshwater systems lack many of the predaceous taxa that consume zooplankton in marine systems, such chaetognats and jellyfish (whereas insects, well represented in freshwater systems, virtually are lacking in the marine ones), the relative proximity of the pelagic realm to the littoral zone (due to relatively small size of most inland systems) implies an increased likelihood for zooplankton to be predated by carnivorous benthic organisms such as dragonfly larvae, backswimmers and even carnivorous plants.

Plasticity in anti-predator defenses is apparently less present in the marine realm, where zooplankton communities are exposed to less variable predator regimes. Marine zooplankton is known to adopt non-plastic morphological (spines), nutritional (gelatinous bodies or sheaths) and behavioral (DVM) adaptations to predation. The fact that meroplankton is relatively more abundant in marine relative to freshwater zooplankton probably explains partly this difference. The diversity of freshwater zooplankton is in contrast due nearly entirely to holoplankton, within which phenotypic plasticity in response to predation had probably more occasions to evolve.

The presence of highly efficient and plastic grazers such as *Daphnia* itself (and cladocerans in general, relatively rare in the marine realm) is another peculiarity of the freshwater lentic ecosystems, which could explain why the impact of herbivory on phytoplanktonic algae is particularly strong in freshwaters relative to the marine systems, whose holoplankton is dominated by calanoids copepods.

Conclusion/synthesis

The results of a vast body of research had illustrated many aspects of how predation can shape zooplankton populations and communities. Understanding the differences between types of predators is not only relevant to those interested in natural history, but has deep consequences to forecast for example the impact of a given predator on a natural freshwater system and its water quality. Moreover, studying the strategies adopted by freshwater zooplankton to cope with the pervasive effects of predation allows not only to refine our predictions about the impact of this key biotic factor, but also offer a glimpse on the extraordinary complexity of the evolutionary solutions adopted by zooplankton to reduce the toll of predation.

Knowledge gaps/*future needs*

- Better understanding of the interactions between predation and other environmental factors (e.g. UV radiation risk).
- Direct and indirect costs associated to inducible defenses.
- Better taxonomic resolution of functional traits relevant to predation other than body size.

See Also: Fundamental concepts and theories: Diel Vertical Migration; Structures and functions of Inland Waters - Lakes: Zooplankton Diversity and Variation Among Lakes

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Productivity of Fish Populations: Environmental and Ecological Drivers☆

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Marie Elodie Perga and Damien Bouffard.

Nomenclature

a	Relative cost of producing new individuals to replace those lost through mortality
$\mathbf{B}$	Total population biomass
$\mathbf{B_j}$	Biomass of new individuals that recruit to the population at age j
$\mathbf{E}$	Mean activation energy of cellular respiration
$\mathbf{g}$	Instantaneous rate of biomass increase, includes both somatic growth of existing age groups and recruitment of new individuals to the youngest age group
$\mathbf{i_0}$	Normalization constant
$\mathbf{k}$	Boltzmann constant
$\mathbf{K}$	Population carrying capacity
L_{act}	Population rate of energy expended on interactions with the environment
$\mathbf{L^a_{act}}$	Population rate of energy expended on attacking prey
$\mathbf{L^s_{act}}$	Population rate of energy expended on searching for prey
$\mathbf{L_{inf}}$	Asymptotic length
$\mathbf{L_m}$	Population rate of energy expended on basal maintenance costs
$\mathbf{L_R}$	Population rate of energy loss to propagule (eggs/sperm) release
$\mathbf{L_z}$	Population rate of energy loss to mortality
$\mathbf{M_{ind}}$	Individual metabolic rate
$\mathbf{M_{pop}}$	Average routine metabolic rate of individuals in a population that is at its carrying capacity.
$\bar{N}_i$	Average abundance of a cohort over its $[i+1]^{th}$ year of life.
$\mathbf{P}$	Tissue production
P_{cc}	Production of a population at its carrying capacity.
P_F	Population rate of energy acquired from foraging
$\mathbf{P^{max}_{\varepsilon}}$	Maximum rate of energy acquisition
P_{ε}	The rate of energy flow from the environment through a population
ρ_F	Proportion of energy available in forage that is acquired by population members

☆*Change History:* January 2022. BJ Shuter updated every section in this chapter. Figs. 2,5, and 7 have been updated.

ρ_R	The degree to which the energy of propagules released to the environment is augmented, over early life, to generate the energy of older individuals recruiting to a population.
R	Population rate of energy acquired from addition of newly recruited individuals
r	Proportion of adult body weight that is released as propagules at each breeding period.
s	Relative cost of synthesizing somatic tissue
t	Time
T	Environmental temperature (°K)
W_i	Weight of an individual
$\bar{W}$	Mean weight of individuals in a population that is at its carrying capacity.
$\mathbf{W_{ind}}$	Individual somatic weight
$\mathbf{W_{inf}}$	Asymptotic weight
z	Instantaneous mortality rate; rate of biomass loss through mortality.

General introduction

Freshwater fisheries are essential economic, cultural and subsistence resources in many countries around the world, with freshwater fish harvests supplying enough food protein for an estimated 158 million people globally (McIntyre et al., 2016; Funge-Smith and Bennett, 2019). It has long been recognized (e.g., Leach et al., 1987) that sustainable harvests are determined by the capacity of natural populations to produce new biomass—their rates of biomass production. Historically, fisheries conservation was achieved mainly through focused efforts on fisheries regulation. More recently, the negative effects of anthropogenic stresses (i.e., climate change, habitat degradation, pollution, invasive species) on the fundamental processes supporting the viability of fish at both the individual and population level have been recognized, leading to an expansion of conservation efforts to include protection of both the quantity and quality of fish habitat (Sass et al., 2017).

Fishes are dynamic in time and space. They are influenced by a range of species-specific abiotic and biotic factors and require a minimum amount of usable habitat to be viable, resulting in both population abundance and production varying directly with the quantity and quality of available habitat (Fig. 1). Countries like Canada have recognized legislatively that the productivity of fish populations and communities are inextricably linked to habitat availability and have implemented policy requirements and

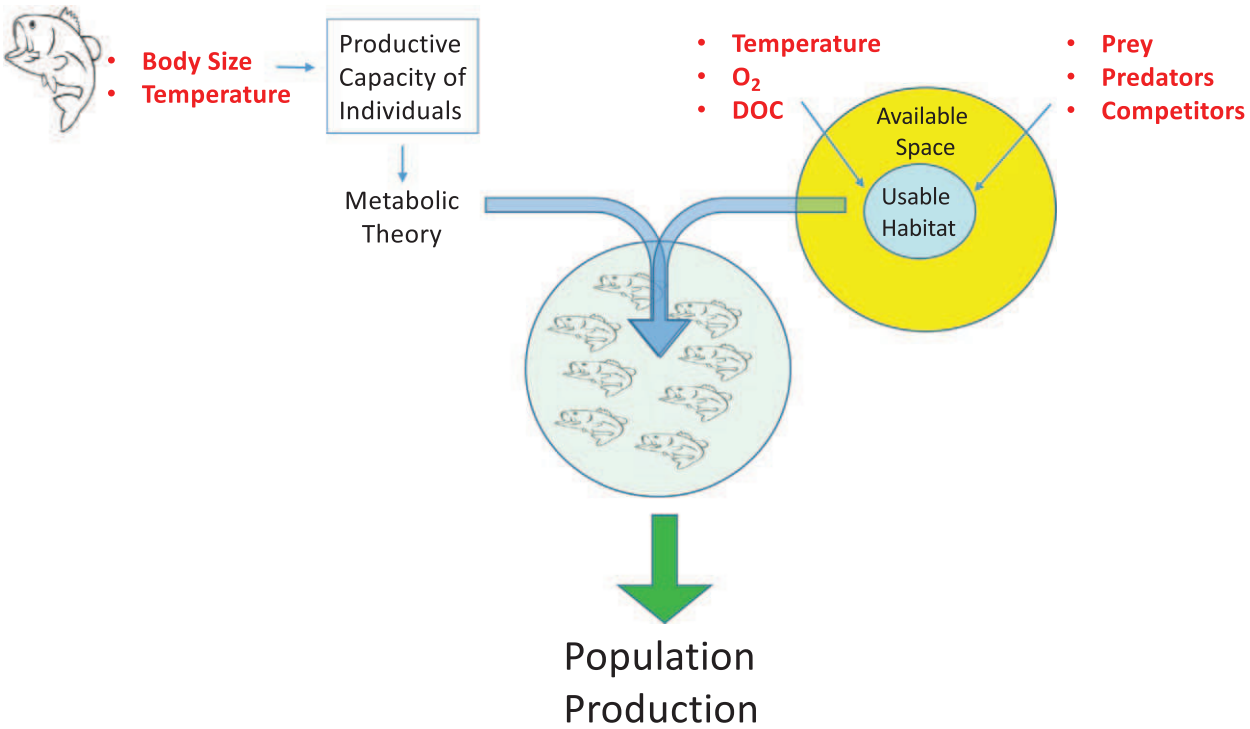


Fig. 1 Body size and temperature preference are the dominant traits that determine the capacity of an individual from a particular species to synthesize new biomass from its environment. The physical space available (e.g., lake size, river width/length) sets an upper limit on realized production. The degree to which realized production reaches that upper limit is determined jointly by the fraction of the available space that is usable as habitat by the target species, and the "quality" of that habitat space. This, in turn, is determined by: (i) the abiotic characteristics of the available space that define the fraction of that space that is usable = the relative amount of space that supports tolerable temperatures and water chemistry for the target species; (ii) the degree to which abiotic conditions in the usable space match species-specific optimal performance traits = the quality of the usable habitat (iii) the relative abundance of prey, competitors and predators that inhabit the usable habitat.

scientific approaches that focus on sustaining production through habitat conservation using regional productivity benchmarks (DFO, 2016). However, the effectiveness of this approach hinges on developing a sound understanding of the environmental and ecological forces that shape the productivity of freshwater fish populations in their natural environments. Currently our understanding of these forces is limited, due mainly to the time and cost of the field studies required to quantify how production varies among wild populations of limnetic and riverine fish.

Production at the population level is defined as the amount of tissue elaborated in the population over a time period (Δt), regardless of whether that tissue survives to the end of that period (Waters, 1977). Production is expressed as biomass elaborated per unit space per unit time (e.g., kg ha^{-1} year^{-1}). It is determined by the three separate processes that add or subtract new biomass to that segment of the population (i.e., typically older juveniles to the oldest adults) that can be accurately tracked with existing technologies. Those processes are (i) tissue growth, which causes the weight of existing population members to increase from W_t to $W_{t+\Delta t}$; (ii) reproduction, which causes new individuals to recruit to the population as members of the youngest observable group; and (iii) mortality, which causes the number of older population members to decrease. We illustrate the fundamental way in which these separate processes interact to generate production as follows. Assume that: (i) the overall increase in population biomass, associated with both tissue synthesis and reproduction, can be approximated by a single value (g) representing the instantaneous fractional rate of biomass increase; and that (ii) the loss in population biomass associated with mortality can be approximated by a single value (z) representing the instantaneous fractional rate of biomass decrease. Therefore, the instantaneous rate of change in biomass (dB/dt) can be expressed as:

$$\mathrm{dB/dt} = (\mathrm{g} - \mathrm{z}) * \mathrm{B} \tag{1}$$

and the production generated over the interval Δt equals (see Gillespie and Benke, 1979 for a demonstration):

$$P_{\Delta t} = [B_{t+\Delta t} - B_t][\mathrm{g}/(\mathrm{g} - \mathrm{z})] \tag{2}$$

where B_t is the initial biomass density (kg ha^{-1}) at time t.

For a population at its carrying capacity (i.e., B is constant and therefore $\frac{dB}{dt} = 0$), growth (including both tissue synthesis and recruitment) and mortality rates must be equal and therefore, $g^*B = z^*B$, from Eq. (1). While Eq. (2) is undefined for $g = z$, Gillespie and Benke (1979) demonstrated that, P_{cc}, the production of a population at its carrying capacity, can be computed as

$$P_{cc} = g * B = z * B \qquad \text{when } (\mathrm{g} - \mathrm{z}) \to 0 \tag{3}$$

In nature, g and z are dynamic and sensitive to changes in both environmental conditions and population biomass. However, Eq. (3) should hold, provided B, g and z vary randomly around relatively constant mean values.

Ideally, production estimates are based on extended time series of comprehensive demographic information (i.e., abundance, biomass, growth and mortality; Dolbeth et al., 2012; Rypel et al., 2015) and hence are logistically demanding. However, the high value of population production estimates compensates for their cost since: (i) they provide direct measures of the degree to which individual populations extract energy from their supporting ecosystems (Downing et al., 1990; Downing and Plante, 1993); (ii) they provide indirect measures of sustainable harvest at the population level (e.g., Leach et al., 1987); and (iii) they provide the empirical basis for advancing our understanding of the forces that drive variation in production in the natural world (Downing and Plante, 1993). This last role is of value since it is fundamental to the development of new and better models for predicting the responses of production both to environmental changes, and to the management actions designed to mitigate those changes. In this chapter, we begin by first reviewing the standard methods used to estimate production in the field. We then go on to (i) review the fundamental bioenergetic processes that support production at the population level, (ii) summarize current knowledge regarding the sensitivity of those processes to changes in both abiotic and ecological conditions, (iii) identify recent methodological advances that promise to increase the precision and accuracy of production estimates, and (iv) suggest promising directions for increasing our knowledge of how production is determined in the wild.

Estimating production

Traditional methods

Production is typically estimated first within a given size-class or age-cohort. These results are then aggregated across classes or cohorts to give an overall estimate of production for the population or community of interest. A variety of estimation methods exist and the choice of method is largely dictated by the data available to calculate the estimate. In the simple situation where age-specific growth and survival rates are constant over time, the following elaboration (patterned after Benke and Huryn, 2017, assuming a time unit of 1 year) of Eq. (1) captures the basic information alluded to, or directly used, in all of these methods:

$$P = B_j + \sum_{i=j}^{i=n} \overline{N_i} * \Delta W_i \tag{4}$$

where:

- P is the production of new biomass generated by the entire population over 1 year,
- $\{j,n\}$ is the range of ages for which both abundance ($\overline{N}_i$ = the average abundance of a cohort over its $[i + 1]^{th}$ year of life) and size at age (W_i and $\Delta W_i = [W_{i+1} - W_i]$) are known, and
- B_j is the biomass of new individuals that recruit to the population when they reach age j.

If $j = 0$, then this equation provides an unbiased estimate of production for the entire population. If $j > 0$, then B_j represents the accumulated tissue growth of individuals surviving from age 0 to age j; this equals the annual production of those age groups only in the unrealistic situation where all individuals survive from age 0 to age j. In the real world, where significant mortality occurs in early life, B_j underestimates the production of early age groups and thus P is underestimated. If B_j is omitted from the result, then P is an unbiased estimate of production over the age range $[j, n]$: the range of ages that can be effectively monitored. If the growth and mortality rates for a population are relatively constant over time, data from a point-in-time sample can be used in Eq. (4) to estimate the value of P that is typical for that population. If growth and mortality rates vary widely from year to year, consecutive annual samples are required to provide the year-specific estimates for $\bar{N}_i$ and ΔW_i that are needed to generate annual values for P over the time interval of interest. When applying any of the methods listed in Table 1, sampling programs need to be designed to minimize the biases in estimates of both $\bar{N}_i$and ΔW_i that typically arise from such factors as size/age selectivity of sampling gear, variation in sampling efficiency across habitat types, life cycle complexity (e.g., migration or developmental changes in habitat), and, consequently, the completeness of sampling coverage of the population or community of interest.

While production estimation methods follow the basic concepts outlined above, accepted methods in the literature for calculating production estimates vary based on the data available. The Instantaneous Growth Rate (IGR) method (see Table 1) remains the most widely accepted and popular method for production calculations due to its greater precision. However, the price for this precision is the high data demand of the method (Hayes et al., 2007). While the size-frequency method is based on length-classes and does not require aging data, it too requires at least two consecutive sampling periods to calculate a single estimate. Older and less frequently used methods include the Allen curve and Summation (Removal and Increment) methods. The Allen curve is a graphical extension of the IGR method and is based on cohort-specific growth-survivorship curves. However, it is rarely implemented now because it lacks a variance estimator. Summation methods are based on estimates of the gain or loss of tissue by a population over time: removal summation focuses on estimating the loss rate of individuals, while increment summation focuses on estimating the tissue growth of individuals. Variance estimators for the removal summation method are also unavailable (Hayes et al., 2007). There are numerous worked examples for each of these methods in the literature, and a selection for each is listed in Table 1.

Recent refinements

Five of the seven methods listed in Table 1 require characterization of the life-time growth patterns of typical population members. Growth is a sensitive component of production estimates that offers insight into the state of a population. However, growth

Table 1 Overview of fish production calculation methods, examples, and data requirements.

Method	*Summation (removal and increment)*	*Allen curve*	*IGR (instantaneous growth rate)*	*Simplified IGR*	*P/B ratios*	*Size-frequency*	*IGR modified with cohort-fitted growth curves*
Examples	Newman and Martin (1983)	Waters (1977)	Newman and Martin (1983), Hayes et al. (2007), and Rypel et al. (2015)	Embke et al. (2019)	Newman and Martin (1983), and Randall and Minns (2000)	Garman and Waters (1983)	See "Recent refinements"
Data required							
For estimating rate of change							
Two or more time periods	Y	Y	Y	N	N	Y	Y
Cohort size-at-age	Y	Y	Y	Y	N	N	Y
Size composition (weight, length; no age data)	N	N	N	N	Y	Y	N
For estimating abundance							
Cohort density (number, biomass)	Y	Y	Y	Y	Y	Y	Y

Y denotes data types required for the estimation method, N denotes data types that are not required for the estimation method.

calculations within production estimation methods are often a significant source of error. Error introduced through growth calculations can arise from the under-sampling of age groups that is common in fisheries surveys: when few (e.g., <5) individuals are captured, weight data for age-cohorts or size-classes will be quite inaccurate. By replacing estimated weights for under-sampled age classes with predicted weights from growth curves fitted to individual cohorts, error will be reduced and the overall precision of production estimates will be increased.

Additional refinements include a simplified IGR method from Embke et al. (2019) that allows for the calculation of production estimates without consecutive annual measurements, while incorporating biomass lost to harvest. However, this method relies on simplifying assumptions that should be recognized (i.e., subsamples of ages and lengths determine relative age-class densities; age-specific mean weights are determined from ecosystem specific age-length keys). This method offers the opportunity to explore conservative "snap-shot" estimates of production based on limited data, particularly from harvested populations.

The bioenergetics of fish production

Seminal empirical work has shown that freshwater fish production is correlated with total phosphorus, primary production (Downing et al., 1990), standing biomass and mean body-mass of fishes, annual mean air temperature, latitude, and species richness (Downing and Plante, 1993). Since these associations are largely consistent with expectations generated from the Metabolic Theory of Ecology (MTE: Brown et al., 2004; Savage et al., 2004), we will use the MTE explicitly in our account of how individual-level bioenergetic processes support population-level production in wild freshwater fish populations (Fig. 1).

General principles: The Metabolic Theory of Ecology

The Metabolic Theory of Ecology (MTE) contends that the primary factors that shape the energy metabolism of individuals (i.e., body size and temperature) also shape the rates of energy gain and loss that determine the flow of energy through a population in the wild. This focus of the MTE makes it particularly relevant to the study of production since it is the flow of energy through a population that must underlie the rates of biomass gain and loss (g and z in Eq. 1) and therefore also determine population production. This is seen most clearly through the relationship that defines production for a population at its carrying capacity. From Eq. (3), at carrying capacity, production equals g^*B. Given that the synthesis of new biomass requires the input of new energy, changes in mass-specific production rates (i.e., changes in g) must reflect changes in energy flow. Hence, understanding the forces that drive changes in energy flow will lead directly to a deeper understanding of the forces that drive changes in production. What follows is a brief summary of the MTE, focusing on its relevance to understanding the forces that drive production in the wild.

For most ectotherms, basal metabolic rate (M_{ind}, the flow of energy required to sustain life in an individual) is given by:

$$M_{ind} = i_0 W_{ind}^{3/4} e^{-E/kT} \tag{5}$$

where M_{ind} is individual metabolic rate, W_{ind} is the somatic weight of the individual, T is the environmental temperature (°Kelvin) the individual is experiencing, i_0 is a constant that is specific to each species, E is the mean activation energy of cellular respiration (0.60–0.70 eV) and k is the Boltzmann constant ($8.62\ 10^{-5}$ eV/K; Brown et al., 2004; Gillooly et al., 2001). The routine and maximum metabolic rates typically seen in the wild roughly follow simple multiples of this basic equation (Peters, 1983).

Now that we have a bioenergetic description of individual metabolism (Eq. 5), we show how it can be used to describe the flow of energy through an entire population. Following Savage et al. (2004), the flow of energy through a population that is maintaining itself at its carrying capacity within its supporting habitat can be derived as follows:

(i) replace individual somatic weight (W_{ind}) in Eq. (5) by the average weight of individuals ($\overline{W}$) when the population is at its carrying capacity (K),

(ii) energy flow ($P\varepsilon$) through the population under an environmental temperature (T) is then given by:

$$P\varepsilon = (1 + s + a) * M_{pop}(\overline{W}, T) * K(\overline{W}, T) \tag{6}$$

where $M_{pop}(\overline{W}, T)$ is the basal metabolic rate of individuals in the population, s and a augment basal metabolism to account for costs associated with generating new somatic and reproductive tissue, respectively, at the rates required to maintain the population at its carrying capacity, and $K(\overline{W}, T)$ is the numerical abundance at carrying capacity.

(iii) the bracketed first term in Eq. (6) explicitly identifies the processes that underlie the growth term (g) in Eq. (3): tissue maintenance (1), somatic growth (s) and reproduction (a). It also clarifies how body size and environmental temperature (through $M_{pop}(\overline{W}, T)$ as defined by Eq. 5) act together with abundance to determine overall energy flow and consequently production.

Now, if we replace population abundance $[K(\bar{W}, T)]$ in Eq. (6) with its biomass equivalent $[K(\overline{W}, T)^*\overline{W}/\overline{W}]$ and expand M_{pop} with the temperature and weight effects from Eq. (5), then Eq. (6) becomes:

$$P_\varepsilon = (1 + s + a) * \left[K(\overline{W}, T) * \overline{W}\right]\left[i_0 * e^{-\frac{E}{kT}} * \overline{W}^{3/4}/\overline{W}\right] \tag{7}$$

and this simplifies to:

$$P_{\varepsilon} = (1 + s + a) * [population\ biomass]\left[i_0 * e^{\frac{E}{kT}} * \overline{W}^{-1/4}\right] \tag{8}$$

where i_0 is the normalization constant from Eq. (5). Note that, since $\overline{W}/\overline{W}$ is equal to 1, multiplying Eq. (6) by $\overline{W}/\overline{W}$ to get Eq. (7) does not alter the validity of either equation. Given that production (P) must be supported by energy flow (P_{ε}), it is reasonable to expect that production will also follow Eq. (8). This expectation is supported by the fact that there is a qualitative and quantitative match between Eq. (8) and the empirical analysis of production presented by Downing and Plante (1993). These authors showed that the statistical links between population production and standing biomass, temperature and mean body-mass are consistent with the form of Eq. (8) and that the fitted exponent for body weight (−0.17) in their analysis is similar to the expected value of −0.25.

Another important production metric is the production to biomass ratio (P/B). The P/B ratio is an expression of population growth that is linked to the productive capacity of a population's habitat (Randall and Minns, 2000) and has been used in a variety of contexts to estimate production when data intensive methods cannot be applied (e.g., Sprules and Stockwell, 1995; Shuter and Ing, 1997; Randall and Minns, 2000). By simply dividing both sides of Eq. (8) by population biomass, we arrive at:

$$\frac{P\varepsilon}{[population\ biomass]} = (1 + s + a) * \left[i_0 * e^{\frac{E}{kT}} * \overline{W}^{-1/4}\right] \tag{9}$$

which highlights the role of both temperature and somatic weight in determining the P/B ratio.

Support for the MTE rests on general summaries of empirical data on the performance of various plants and animals in the wild. Data on marine and freshwater fish populations have also played a supporting role in these analyzes, indicating that it is a relevant framework for considering the production of fishes. The following section provides a more detailed demonstration of the degree to which current knowledge of fish bioenergetics matches expectations from the MTE.

MTE and freshwater fish—Examining the role of body size and temperature in detail

The acquisition and allocation of energy towards biomass production occurs simultaneously with energy losses to maintenance and activity (L_m and L_a respectively), individual mortalities (L_z) and propagule release (eggs and sperm; L_R). Assuming that P is roughly proportional to P_{ε}, this implies that:

$$P \propto\ P\varepsilon = [\rho_F * (\text{available forage}) + \rho_R * \mathrm{L_R} - (L_m + L_{act}) - L_z - L_R] \tag{10a}$$

which simplifies to:

$$P \propto [\mathrm{P_F} + R - (\mathrm{L_m} + \mathrm{L_{act}}) - \mathrm{L_z} - \mathrm{L_R}] \tag{10b}$$

where $\boldsymbol{\rho}_F$ is the proportion of available forage energy that is acquired by population members (i.e., foraging efficiency), $\mathrm{P_F}$ represents total energy acquired by the population from foraging, $\boldsymbol{\rho}_R$ is the degree to which energy released to the environment as propagules accumulates during offspring development to return to the monitored segment of the population as newly recruited individuals, and R is the product of $\boldsymbol{\rho}_R$ and $\mathrm{L_R}$ (Fig. 2). Notably, the degree of energy allocated towards propagule production is a positive reflection of the size and health of the individual and this, in turn, will contribute directly to the degree to which energy released as propagules returns to the population as newly recruited individuals ($\boldsymbol{\rho}_R$; e.g., Venturelli et al., 2009, 2010).

From the MTE, we would expect these processes of energy acquisition and recruitment to vary predictably with body size and temperature, following the allometric Arrhenius weight-temperature functional form defined in Eq. (5), with individual somatic

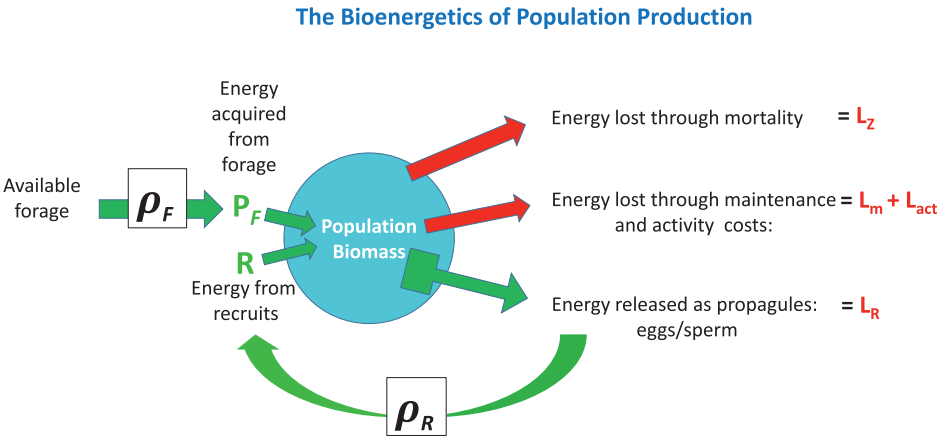


Fig. 2 Over any time period, realized production by the older individuals in a population derives from several different flows of energy through those individuals: For a population in equilibrium with its environment [dB/dt = 0], the following relationships should hold: (i) the production of new biomass (somatic tissue + reproductive tissue) is determined by the net gain in energy from foraging ($= \mathrm{P}_{\boldsymbol{F}} - (\mathrm{L_m} + \mathrm{L_{act}})$) where $\mathrm{P}_{\boldsymbol{F}}$ depends on the amount of prey available in the environment and the foraging efficiency ($\boldsymbol{\rho}_F$) of a typical individual. (ii) the increase in biomass from new individuals recruiting to the population is determined jointly by the biomass released as propagules ($\mathrm{L_R}$) and the degree to which that biomass is augmented over early life ($\boldsymbol{\rho}_R$) by the combined effects of individual growth and mortality. (iii) the total gain in biomass from growth and recruitment = losses from metabolic costs, propagule release and mortality.

weight replaced by the population mean somatic weight (Eqs. 6–8, following Savage et al., 2004) and the proviso that T does not exceed the tolerance range of the species in question. Thus, maintenance losses can be described as:

$$L_m = i_{\mathrm{m}}\, \overline{W}^{\beta m} \tag{11a}$$

the maximum rate of energy acquisition, P_{ε}^{max}, as

$$P_{\varepsilon}^{\ max} = i_{\varepsilon max}\, \overline{W}^{\beta_{\varepsilon max}} \tag{11b}$$

losses to mortality as:

$$L_z = i_z\, \overline{W}^{\beta z} \tag{11c}$$

and losses to propagules as:

$$\mathrm{L_R} = \mathrm{r} * \overline{W} \tag{11d}$$

where:

$$\beta_m \approx \beta_{\varepsilon max} \approx 3/4 \tag{11e}$$

$$\beta_z \approx -1/4 \tag{11f}$$

and $[i_m,\ i_{\varepsilon max}]$ exhibit the temperature dependence evident in Eq. (5), i_z increases with temperature and r is a species-specific constant. For individuals, there is good empirical support for Eqs. (11a), (11b), (11d) (Fig. 3A and B) regarding maintenance losses and energy acquisition: (i) estimates of bioenergetic performance parameters for 58 fish species described in the fish bioenergetics model FB4 (Deslauriers et al., 2017) are consistent with the allometric form; (ii) typical values for β_m and $\beta_{\varepsilon max}$ are close to the expected value of ¾ (Eq. 11e); and (iii) over species-specific thermal tolerance ranges (Savage et al., 2004), the effect of temperature on i_m and $i_{\varepsilon max}$ is consistent with the Arrhenius relationship (Fig. 4A and B; Deslauriers et al., 2017).

For populations, there is also good empirical support for Eq. (11c) regarding losses to mortality (McCoy and Gillooly, 2008; Fig. 3C): the allometric form is followed, the exponent has a value close to the expected value of −1/4 (Eq. 11f), and i_z shows the expected increase (vertical offset) with increasing environmental temperature. In Eq. (11d), energy lost to reproductive activity ($r * \bar{W}$) is assumed to be proportional to somatic weight. This is consistent with the typical metric used in field studies for this quantity (i.e., GSI = gonad weight/body weight). For fish generally, values of r for mature females can range from 0.2 to 0.6 (Lester et al., 2004b).

The variable L_{act} (Fig. 2) measures the energetic cost to the individual of interacting with its environment and is often dominated by foraging costs. These separate into the cost of search (L^s_{act}) and the cost of attack (L^a_{act}). There is strong theoretical (Weihs, 1977; Ware, 1978) and empirical (Videler and Nolet, 1990; Ryan et al., 2015) support for asserting that search velocity in the wild will match the velocity that maximizes distance traveled per unit swimming cost. Travel at this velocity varies with (body length)$^{0.45}$ with a metabolic cost, at the level of the individual, that is roughly proportional to basal metabolism. It then follows that the overall activity cost needed to provide a population with a fixed daily ration of prey biomass will vary with the overall attack cost (L^a_{act} = [# attacks]*[cost/attack]). This will increase with the number of prey required to meet that ration and, all else being equal, that number and the overall attack cost will decrease as prey size increases. This effect of prey size on foraging cost has been observed in many natural populations (Paloheimo and Dickie, 1966; Kerr and Ryder, 1977; Sherwood et al., 2002a; Giacomini et al., 2013).

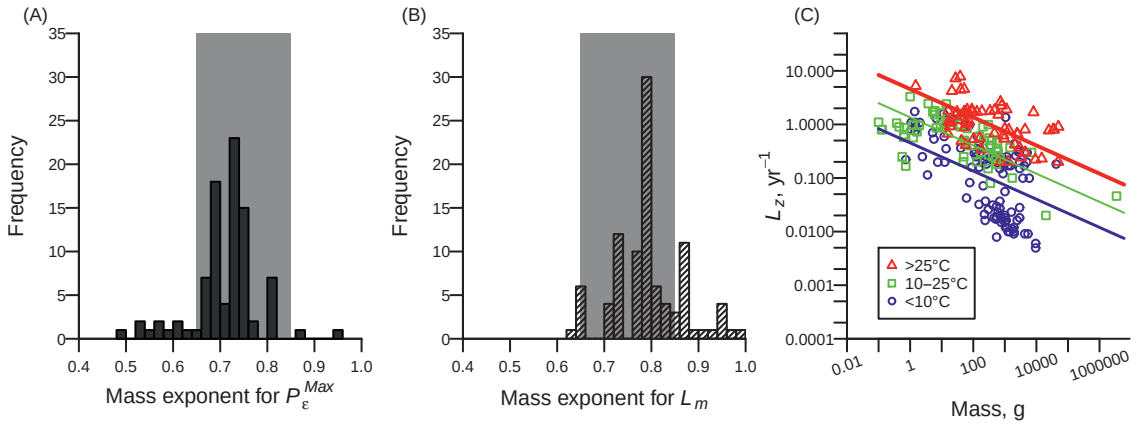


Fig. 3 Relationships of fish consumption (Panel A), metabolism (Panel B) and mortality (Panel C) with body mass. Histograms of fish mass exponents for consumption (Panel A, as g food per day) and metabolism (Panel B, as g O_2 consumption or energetic units per day) both approximate 0.75. The median values for consumption and metabolism are 0.73 and 0.79, respectively and the shaded region highlights density of observations between 0.65 and 0.85. Instantaneous mortality (Panel C) scales negatively with body mass among fishes occupying cold, cool and warmwater habitats: the common slope across habitats approximates −0.25 (estimated slope = −0.263; note log scales on axes). Panels A and B: Data FROM Deslauriers D, Chipps SR, Breck JE, Rice JA, and Madenjian CP (2017) Fish bioenergetics 4.0: An R-based modeling application. *Fisheries* 42:586–596; Panel C: Data from McCoy MW and Gillooly JF (2008) Predicting natural mortality rates of plants and animals. *Ecology Letters* 11:710–716.

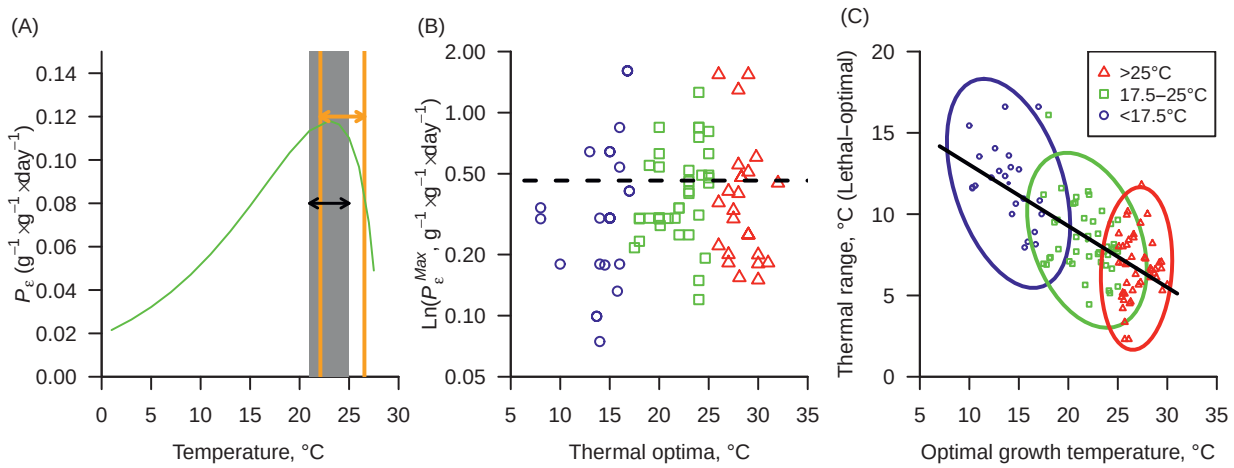


Fig. 4 Influence of thermal range on individual performance in fishes. Panel A: In fishes, both consumption and basal metabolism increase with temperature to a peak value and then decline rapidly, with death occurring at a critical maximum temperature. The green curve shows the thermal response of consumption for Walleye (*Sander vitreus*) when prey are abundant. The temperature range supporting optimal performance is characterized by the fundamental thermal niche (after Magnuson JJ, Crowder LB, and Medvick PA (1975) Temperature as an ecological resource. *American Zoologist* 19: 331–343, in gray) of 4 °C around the optimum temperature. The overall shape of the basal metabolism vs temperature curve is similar to that in Panel A but shifted to the right by 2C. For temperatures below the optimum, the pattern of increasing rates with increasing temperature approximates the Arrhenius temperature relationship in the MTE. This holds for both consumption and basal metabolism. Panel B shows that the peak consumption observed at the species-specific optimum temperature does not vary systematically across thermal guilds. Each point refers to a particular species; points are colored by thermal guild, where guild membership is set by optimum growth temperature (OGT, from Hasnain, SS, Escobar MD and Shuter BJ (2018) Estimating thermal response metrics for north American freshwater fish using Bayesian phylogenetic regression. *Canadian Journal of Fisheries and Aquatic Sciences* 75:1878–1885): cold-blue OGT < 17.5; cool-green OGT falls between 17.5 and 25.0; warm-red OGT > 25. The mean peak consumption rate across all guilds $= 0.46$ g^{-1} g^{-1} day^{-1}. Panel C shows that thermal range (the difference between the optimal growth and lethal temperature, shown in orange in Panel A) narrows significantly from cold to cool to warmwater fishes. Data in panels A and B from Deslauriers D, Chipps SR, Breck JE, Rice JA and Madenjian CP (2017) Fish bioenergetics 4.0: An R-based modeling application. *Fisheries* 42:586–596; panel C data from Hasnain, SS, Escobar MD and Shuter BJ (2018) Estimating thermal response metrics for north American freshwater fish using Bayesian phylogenetic regression. *Canadian Journal of Fisheries and Aquatic Sciences* 75:1878–1885.

For a particular species, individual metabolic rates are relatively insensitive to temperature over a specific thermal range (Fig. 4A) where performance is optimal in regards to activity, feeding, growth, and reproduction (Fry et al., 1947; Pörtner, 2002; McMeans et al., 2020). This optimal range has been dubbed *the fundamental thermal niche* (Magnuson et al., 1979). The diversity of temperature constraints that have shaped ecological performance of freshwater fish has produced wide diversity in realized thermal niches, with species-specific optimal performance temperatures ranging from 5 °C to 30 °C (Hasnain et al., 2018). The center of the fundamental thermal niche has been used to group freshwater fish species into three discrete thermal guilds (McMeans et al., 2020): cold-water—optimal temperatures <17 °C; cool-water—optimal temperatures ranging from 17 °C to 25 °C; and, warm-water—optimal temperatures >25 °C (Fig. 4B and C). Although the peak feeding rate at the optimal temperature is similar across guilds (Fig. 4B), the width of the thermal niche declines progressively as the optimal performance temperature increases (Fig. 4C). Within a thermal guild, feeding rate (Fig. 4A) and basal metabolic rate respond in a similar way to temperature differences: for temperatures below the thermal niche, both rates approximate the Arrhenius temperature relationship; for temperatures above the thermal niche, both rates decline rapidly following rapid declines in enzymatic efficiency (Fry et al., 1947; McMeans et al., 2020; Pörtner, 2002).

The impetus for an individual to seek its optimal operating temperature shapes its habitat use and consequently its realized growth and mortality risk (e.g., Cruz-Font et al., 2019). This, in turn, shapes its productive capacity and, thus, the productive capacity of the population to which it belongs. Empirical data suggests that functioning at temperatures exceeding the preferred range can lead to energetic inefficiencies (e.g., metabolic costs increase faster than ingestion rates) that reduce population productive capacity (Gorman et al., 2016). However, at temperatures within and below the preferred range, temperature differences can promote variation in production in at least three ways:

(I) By promoting changes in the overall abundance of new forage through changes in factors like primary production (e.g., Cross et al., 2015; Junker et al., 2020) and growing season length (Shuter and Ing, 1997; Gorman et al., 2016).
(II) By promoting higher feeding rates on existing forage supplies: for freshwater fish, temperatures below optimal have similar exponential effects on both maximum consumption rates and metabolic costs (Deslauriers et al., 2017; Fig. 4A), therefore, temperature increases at the lower end of the tolerance range can promote higher net energy gain by promoting higher feeding rates on existing forage resources.
(III) By promoting changes in the availability of existing forage supplies: for example, temperature change (e.g., seasonal warming or cooling in boreal lakes) can extend/limit the opportunities for a particular consumer to forage in some habitats by driving ambient habitat temperature into/out of the consumer's tolerance zone (Guzzo et al., 2017).

When forced to forage in habitats outside of their optimal thermal niche, reduced foraging efficiencies (Fig. 4A) and additional energetic costs reduce the net energy available for production of new tissue. Ultimately, this can impact fitness through impaired survivorship and/or reproductive success (Quince et al., 2008; Guzzo et al., 2017; Cruz-Font et al., 2019).

The role of habitat

Ecosystem size ultimately dictates the habitat available to support fish production. Additional characteristics such as light (Lester et al., 2004a), oxygen (Plumb and Blanchfield, 2009), and temperature (Guzzo and Blanchfield, 2017) determine the amount of habitat that is actually useable by that population (Fig. 1). These characteristics can then be further modulated by nutrients, such as dissolved organic carbon (DOC; Ask et al., 2009). Thermal habitat constraints on fishes have been thoroughly discussed in Section "MTE and freshwater fish—Examining the role of body size and temperature in detail", thus, our attention below turns specifically to the constraints set by space, oxygen and nutrients.

The role of habitat: Spatial limits

Production is often quantified on a per unit habitat basis (e.g., Downing and Plante, 1993; kg ha^{-1} year^{-1}) with the implicit assumption that this value is independent of lake or river size. However, physical boundaries (e.g., lake shoreline, riverbanks) clearly limit fish population function in most freshwater ecosystems. In rivers compared to lakes, home ranges are smaller for a given fish size (Minns, 1995), while P/B ratios are larger (Randall et al., 1995). This is likely due to the greater role of throughput (i.e., more allochthonous than autochthonous inputs) in rivers. Similarly, since the fraction of littoral zone surface area typically decreases with lake size, allochthonous nutrient inputs and littoral benthic production often make a greater contribution to overall production in small lakes than in large lakes. This is important as ecosystem size can limit food chain length, and consequently top predator size, in both terrestrial and aquatic systems (Schoener, 1987). These effects are particularly evident among top predators living in lake ecosystems (Vander Zanden et al., 1999; Post et al., 2000, 2002). Simple energetic arguments and empirical findings (outlined below) support the contention that these effects will influence fish population production.

Given that:

- Metabolic demand increases with body size (Eq. 5), and
- Hydrodynamic constraints ensure that the metabolic cost of areal search is proportional to basal metabolism ($L^s_{act} \sim L_m$; Ware, 1978; Videler and Nolet, 1990).

It follows that:

- Foraging space, which is approximated by home range size, should increase with body size;
- Large piscivores will be absent from very small ecosystems;
- The adult size of piscivores will tend to be larger in the longer food chains that are common in larger systems; larger systems tend to support longer food chains because foraging spaces are larger, food web diversity is higher and forage species tend to be larger (e.g., Sherwood et al., 2002a; McGarvey et al., 2016).

Fig. 5 illustrates this congruence between individual capabilities (e.g., areal search rate), metabolic need (e.g., home range size), increased foraging opportunities (e.g., presence/absence of pelagic forage fish) in larger systems and population traits (e.g., mean adult size). Data used to generate the black and blue lines are from the Lake Trout (*Salvelinus namaycush*) life history data base documented in Lester et al. (2021). Here "Body Length" is typical adult body size, estimated as the mean of length at maturity and maximum length.

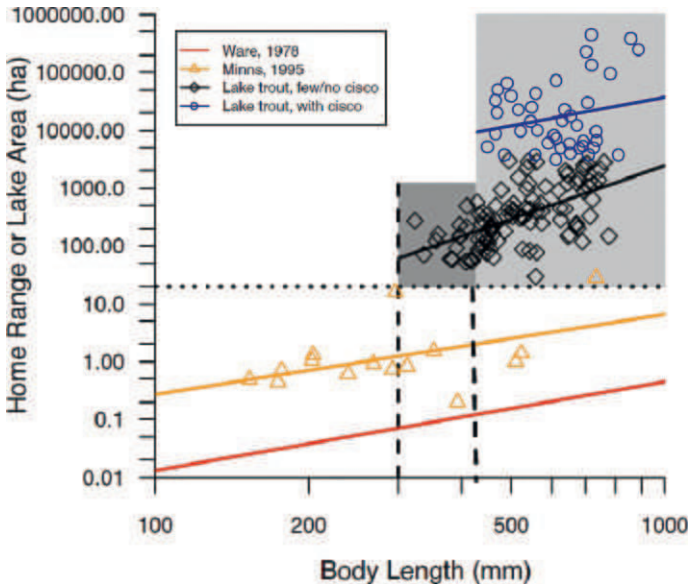


Fig. 5 Similarities across spatial scales of how body size influences the use of space by fish: (i) The lowest (red) line: the relationship (Ware, 1978) linking fish body size to prey search rate (ha time^{-1}), (ii) the orange line: the relationship (Minns, 1995) linking home range size to fish body size (ha) in lakes, (iii) The black line: the relationship linking lake size (ha) to adult body size for populations of Lake Trout (*Salvelinus namaycush*) where pelagic piscivory is negligible, (iv) The highest (blue) line: the relationship linking lake size (ha) to adult body size for populations of Lake Trout (*S. namaycush*) where pelagic piscivory is dominant.

All four relationships exhibit very similar slopes. Lakes below the horizontal dotted line are too small to support a top predator like Lake Trout (*S. namaycush*). The range of small body sizes marked by the two vertical dashed lines are only found in small lakes where pelagic piscivory is absent (dark gray rectangle).

In aquatic systems (freshwater and marine—Sprules and Barth, 2016) both numerical and biomass abundance (per unit habitat) decline as body size and trophic position increase (Andersen, 2019). Therefore, changes in prey size will affect the net benefit to predators through changes in both prey abundance and predator foraging efficiency. Eqs. (6), (8) and (9) can be used as guides to generate predictions of how these diverse effects will impact predator production *per individual* (Eq. 6) and predator production *per unit predator biomass* (Eqs. 8 and 9). They also identify the central role that overall population abundance (numerical and biomass) plays in determining total population production and consequently production *per unit habitat*. Eq. (10a) explicitly identifies the primary roles that available forage (i.e., forage *per unit habitat*) and predator foraging efficiency play in determining production *per unit habitat*.

Population biomass production (per unit habitat) should vary inversely with adult size (Eq. 8; Downing and Plante, 1993) and hence be higher in smaller ecosystems. Lester et al. (2021) quantified this effect for North American Lake Trout (*S. namaycush*) populations, showing that the equilibrium rate of biomass production (including growth and recruitment) among adults in unexploited populations was an allometric function of adult size ($\sim W_{inf}^{-1.63}$)—a result consistent with the theoretical work of Andersen and Beyer (2006). Here, and in other studies, the measure of adult size is the weight or length (W_{inf}, L_{inf} respectively) typical of the largest adults in the population. For two well studied Lake Trout populations (Lake 373: 27 ha, $L_{inf} = 425$ mm; Lake Opeongo: 5800 ha, $L_{inf} = 603$ mm; Cruz-Font et al., 2019), this implies that biomass production per hectare for Lake 373 is approximately five times the production for Lake Opeongo. This drop in production is roughly consistent with the drop in trophic efficiency (e.g., Andersen, 2019 p. 36) expected, given that Opeongo Lake Trout are feeding on pelagic fish, one trophic level higher than Lake 373 Lake Trout, which feed on zooplankton (Vander Zanden et al., 1999).

The role of habitat: Oxygen limitation

The physiological performance of ectotherms depends strongly on aerobic metabolic rate, which varies with both oxygen concentration and temperature. At high temperatures or during times of intense activity, oxygen supply can exceed demand, and the metabolic rate approaches a limit (Fry et al., 1947; Pörtner, 2002; Rubalcaba et al., 2020). The difference between basal metabolism and this metabolic limit represents the aerobic scope (i.e., the energy available) for fitness-enhancing activities such as movement, feeding, digestion, growth, and reproduction. From Eq. (5), we expect metabolic oxygen demand to increase with higher temperatures within the liveable thermal boundaries of fishes, and this expectation has strong empirical support (e.g., Rubalcaba et al., 2020). In the aquatic environment, oxygen and temperature act together to define the oxythermal habitat space that supports optimal performance by individuals of a particular species (Fig. 1). The size and positioning of this space within the larger habitat will vary with climate/latitude, with implications for behavior patterns, activity costs and, ultimately, population productivity. Behavioral telemetry studies have found that Lake Trout (*S. namaycush)* reduced their use of littoral regions due to shorter spring and longer summer seasons (Guzzo et al., 2017). This was accompanied by (i) loss of optimal oxythermal habitat; (ii) reduced access to littoral prey resources; leading to (iii) reduced individual growth rates and body condition. These findings are particularly important within the context of climate change, where warmer, longer summer seasons can lead to significant decreases in oxythermal habitat for cold-water fish and increases for warm-water fish (Guzzo and Blanchfield, 2017).

The role of habitat: Nutrient limitation

Nutrient limitation of ecosystem productivity is an important theme of freshwater ecology and this limitation is implicit in the population abundance terms in Eqs. (6)–(9): increased nutrient inputs are expected to increase production at lower trophic levels, promoting increased population abundance, and consequently higher production at higher trophic levels. Many studies have identified phosphorus as a correlate (Downing et al., 1990) and a driver (Mills, 1985; Rennie et al., 2019; Hecky and DePinto, 2020) of both fish biomass and production. This is nicely demonstrated in several whole lake experimental lake studies (Schindler 1990, Bristow et al., 2008) that involved nutrient additions and increases in total phosphorus concentration in small oligotrophic lakes. In one experiment, the production of the resident top predator (*Coregonus clupeaformis*), rose and fell with the initiation and cessation of nutrient additions (Mills 1985). These changes in production were the combined result of parallel increases in abundance, recruitment, and somatic growth (Mills 1985). In another experiment (Rennie et al., 2019), the abundance of both small forage fish (i.e., minnows) and the resident top predator (*S. namaycush*), rose and fell with the initiation and cessation of nutrient additions. The increases in top predator abundance were accompanied by parallel increases in somatic growth and maturation size and a parallel decrease in age at maturation.

Beyond the direct effects of nutrient levels on ecosystem productivity, other components of water chemistry (e.g., pH—Mills et al., 2002a,b; Schindler 1990) can indirectly modulate fish production through bottom-up effects on nutrient and habitat availability. For example, DOC attenuates light and thus can alter vertical temperature profiles (Pilla et al., 2018), primary productivity (Ask et al., 2009) and oxythermal habitat availability (Knoll et al., 2018). Increases in DOC can be accompanied by decreases in fish abundance (Seekell et al., 2018), growth (Benoît et al., 2016), and biomass production (van Dorst et al., 2019). Such effects are of immediate concern since DOC concentrations are increasing in aquatic ecosystems due to climate change and altered precipitation cycles (Solomon et al., 2015).

The role of community: Prey and competitors

Like production (as outlined earlier in Sections "General principles: The Metabolic Theory of Ecology" and "MTE and freshwater fish—Examining the role of body size and temperature in detail"), the life history of a population emerges from the bioenergetic processes that determine the amount of energy allocated to fitness-enhancing traits such as somatic growth and reproduction (Lester et al., 2004b; Shuter et al., 2016). As discussed in Section "MTE and freshwater fish—Examining the role of body size and temperature in detail", these bioenergetic processes are strongly dependent on prey availability and quality (Giacomini et al., 2013). Prey quality, and particularly prey size relative to predator size, (the predator/prey size ratio; Andersen and Beyer, 2006; Brose et al., 2006) can be just as important as prey availability in determining the energy budget of individual fish and populations (Fig. 6A). The net energetic benefit associated with acquiring a unit biomass of food typically increases as prey become bigger (e.g., Kerr, 1971; Shuter et al., 2016)—even if the biomass density of small prey is high, many individual prey captures are needed to meet the energy needs that arise with increasing predator size (Cruz-Font et al., 2019). The high attack costs that result can create a bioenergetic bottleneck where the value of reaching larger adult size (i.e., increased fecundity with larger size; Giacomini et al., 2013; Cruz-Font et al., 2019) is offset by the energetic cost of reaching and maintaining that size (Sherwood et al., 2002a,b). Life history theory dictates that this trade off will shape both the size-at-maturity and post-maturation growth pattern of the predator (Jensen, 1996; Charnov and Gillooly, 2004; Lester et al., 2004b): when larger prey are available, fitness is maximized by an increase in adult size and a reduction in reproductive allocation (Fig. 7A). These differences feed back, through their effects on adult size and somatic growth, to exert a strong influence on population production (Eq. 8).

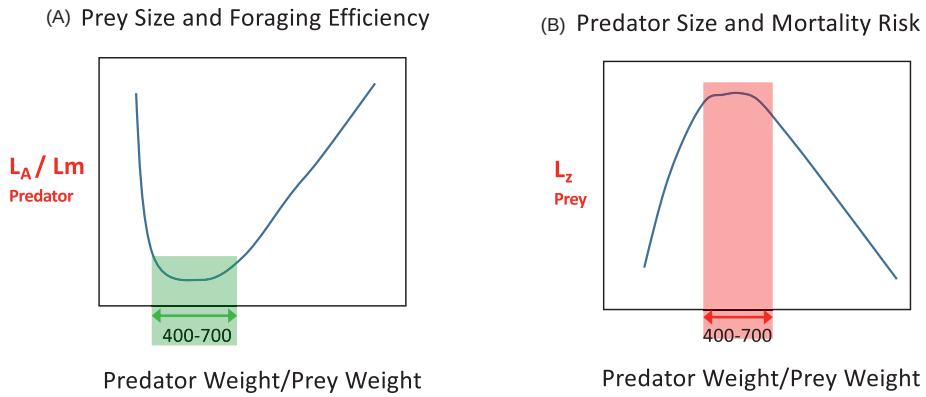


Fig. 6 Forces affecting the balance of energy flow (gains vs losses) through a population when the overall supply of prey resources is fixed. (A) Relative prey size determines foraging costs for predators: very large prey are very costly (if not impossible) to capture; as prey become smaller, the cost per capture declines but the gain per capture also declines—acquisition of a fixed amount of biomass is accompanied by increasing activity costs; the net result of this tradeoff is that relative feeding costs reach a minimum (and feeding efficiency reaches a maximum) when the predator/prey weight ratio lies in the range [400,700]— Andersen, 2019. (B) Relative predator size determines mortality on prey. The relationship between predator benefit and prey size evident in panel A has a parallel effect on prey mortality risk. For the prey, mortality risk rises and falls with increasing predator size. Since predator feeding efficiency on very large and very small prey is low then, all else being equal, the mortality risk for prey should be correspondingly low, with highest risk associated with predators that are 400–700 times larger (by body weight) than prey.

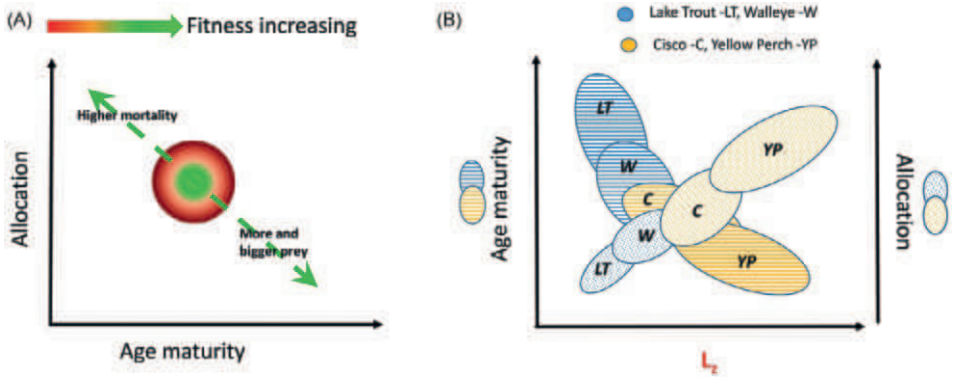


Fig. 7 Prey availability and predation risk act together to determine the timing/extent of reproductive allocation and hence the lifetime growth pattern of a typical individual. Panel A: the theoretical relationships linking optimal life history traits (allocation of energy to reproduction and age at maturity) to both variation in prey size and mortality. Panel B: the observed relationships (after Fig. 3 in Shuter et al. (2005) linking life history traits to trophic position and mortality (L_z) for a sample of fish populations from freshwater lakes (number of populations: 14 Lake Trout *(Salvelinus namaycush)*, 17 Walleye *(Sander vitreus)*, 10 Cisco *(Coregonus artedi)*, 15 Yellow Perch *(Perca flavescens)*).

Competition for prey can also drive population production, with production decreasing as species richness increases (Downing and Plante, 1993). In particular, invasions of non-native species can alter fish production in potentially unpredictable ways. When introduced, Northern Pike (*Esox lucius*) often negatively impact native species (DeBates et al., 2003; Haught and von Hippel, 2011)—in some cases eliminating prey species, leaving pike monoculture lakes (Regmi, 2012; Nicholson et al., 2015). In lakes without an offshore prey fish population, the invasion of non-native Smallmouth Bass (*Micropterus dolomieu*) can negatively impact Lake Trout (*S. namaycush*) dramatically by reducing their access to larger nearshore prey (minnows), forcing an increased reliance on offshore zooplankton (Vander Zanden et al., 1999) leading to slower growth rates and reduced production. From an ecosystem perspective, it is currently unclear as to whether the production of invasive fishes can ultimately offset the loss of native fish production in invaded ecosystems such as these.

The role of community: Predator pressure

Trade-offs between predation mortality and growth are common in fishes, since mortality losses are driven by the relative size of predator and prey (Fig. 6B). Growth can provide an escape from predation, with prey fish (or, in cannibalistic species, juvenile life stages) growing rapidly and maturing earlier to exceed predator gape (Day et al., 2002; Biro et al., 2005; Urban, 2007). Ironically, the increased foraging required to achieve rapid early growth rates often leads to increased exposure to predation. However, this comes with the benefit of reaching an invulnerable size faster (Urban, 2007). Alternatively, if refuges (spatial or temporal) are available, fish may modify their behavior to avoid predation, but this may force a decrease in foraging opportunities (e.g., Peacor, 2003). Linked changes in both overall activity and foraging can generate wide variation in growth trajectories (Abrams and Rowe, 1996). In Yellow Perch (*Perca flavescens*), maximum size, size at maturity, growth rate and growth efficiency all increased with increased predation risk, despite negative correlations with consumption and activity (Rennie et al., 2010). These results suggest that increased use of refuges in these populations permitted increased growth when risk of predation was high.

This trade-off between mortality and growth impacts life history decisions in ways that are similar to the trade-off between prey size and growth (Fig. 7A). The value of reaching larger sizes through allocating most available energy to somatic growth is offset by the increases in mortality that accompany higher foraging rates. Life history theory dictates that individuals will reach a point where the benefits of growth will be outweighed by the risk of mortality and all surplus energy should be allocated to reproduction (Jensen, 1996; Charnov and Gillooly, 2004). This will lead to earlier maturity and reduced post-maturation somatic growth under high mortality, with consequences for production through changes in both adult size and somatic growth. This set of joint differences in mortality, growth and maturity schedules is typical of the differences observed between forage fish and top predators (Fig. 7B).

Future directions and conclusions

It should be clear now that bioenergetic theory provides a unified paradigm for developing explicit hypotheses regarding the forces driving variation in production in wild populations of freshwater fish. However, the empirical work needed to explicitly test these ideas has lagged behind theory development. In the 2017 summary of currently available data provided by Rypel and David (2017), less than 30% of production estimates were based on direct estimates of production and over 60% of these were published prior to 2000. This highlights the need for new direct empirical estimates of fish production to refine our understanding of how drivers like habitat limitation, temperature/climate change, and prey size/foraging efficiency shape production in the wild. In addition to new empirical studies, a wider application of methodological refinements and further development of logistically simpler predictive models of fish production are needed, both to extend our understanding of production and to develop more effective, evidence-based strategies for conserving fish productivity.

Addressing costs of reproduction in production estimates

In most fish species, energy assigned to biomass synthesis shifts significantly at sexual maturity from somatic tissue to the predominate production of energy dense reproductive products (i.e., propagules; Gunderson and Dygert, 1988; Henderson et al., 2000). This shift in energy allocation leads to significant changes in the growth curve of individuals and populations: (i) prior to maturation, body weight increases steadily as biomass production accumulates; (ii) after maturation, body weight increases prior to spawning but then declines suddenly at spawning with the expulsion of propagules (Fig. 8A). Failure to account for these changes in weight and energy allocation to reproduction can generate age-specific bias in production estimates (Fig. 8B and C, Box Fig. 1).

Biphasic growth models capture these energy shifts particularly well and have been widely accepted since they were first proposed (Charnov et al., 2001; Lester et al., 2004b), with empirical work demonstrating their efficacy in providing accurate descriptions of lifetime growth (Shuter et al., 2005; Quince et al., 2008). These models explicitly recognize the landmark change in energy allocation that occurs with sexual maturity (Fig. 8A) through depicting (i) pre-maturation length growth as a linear function of age and (ii) growth at, and post-maturation, as an abrupt switch to an asymptotic form that is consistent with the von Bertalanffy equation. These models are then able to quantify traits that are critical in determining individual fitness (i.e., age at first reproduction, reproductive investment; Charnov et al., 2001, Shuter et al., 2005). This provides the opportunity to test hypotheses regarding how age-at-maturity and reproductive allocation (and hence lifetime growth pattern) should change with changes in mortality rate, prey availability (Fig. 7) and other environmental and ecological factors. Lastly, biphasic model fits can provide an

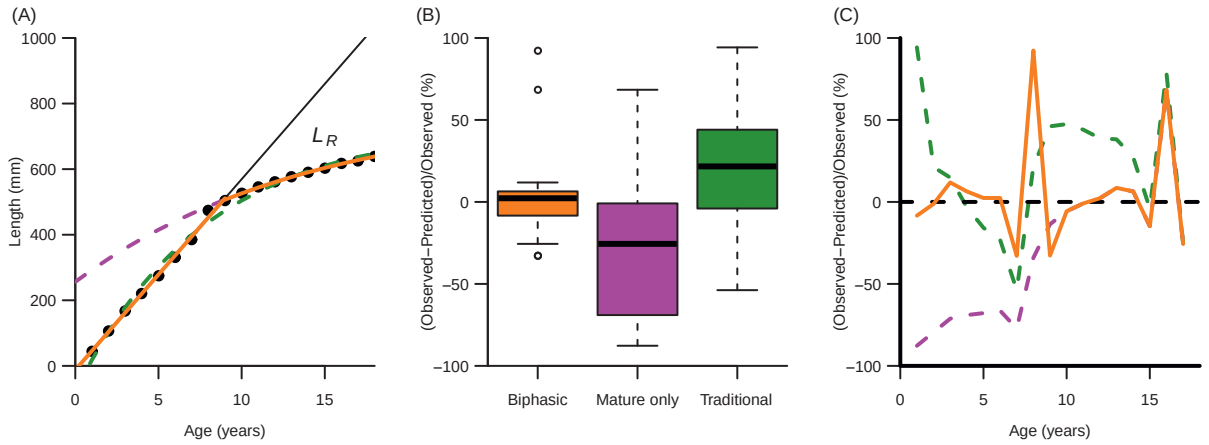


Fig. 8 Growth in fishes is often approximately linear when immature, but slows following maturity once allocation to reproduction (L_R) is initiated (Panel A, size at age of Lake Opeongo lake trout). The deviation from the initial linear pattern increases progressively with higher allocation of energy to reproduction. This growth pattern can be characterized by a von Bertalanffy growth function (Green dashed line), but more recently bi-phasic models of growth (orange) that explicitly recognize linear immature growth are more common. Absence of information on immature fish (common in commercial fisheries; shown in purple) can lead to overestimation of immature fish size if the growth curve for older ages is extrapolated to younger ages. When these growth curves are used to measure instantaneous growth (as they are in common production estimation methods), the bi-phasic model more accurately describes observed growth on average (Panel B). Growth curves fit to only mature fish are variable relative to observed growth (Panel B) and tend to greatly overestimate immature growth (Panels B and C). The traditional von Bertalanffy fit to all age classes is also variable and tends to underestimate instantaneous growth (Panel B), especially at the smallest age classes and immediately post-maturation (Panel C). (A) Data from Shuter BJ, Giacomini HC, de Kerckhove D and Vascotto K (2016) Fish life history dynamics: Shifts in prey size structure evoke shifts in predator maturation traits. *Canadian Journal of Fisheries and Aquatic Sciences* 73:693–708.

indirect estimate of reproductive energy allocation Shuter et al. (2005) that can be used to scope the magnitude of potential bias in empirical studies that do not cleanly allow for its cyclic gain and loss over a typical growing season. For example, the biphasic fit to the data in Fig. 8A generates an estimate of annual reproductive investment by females that is equivalent to ~23% of body weight.

This highlights the importance of ensuring that the production that is allocated to reproductive tissue is accounted for in production calculations, as well as the production allocated to somatic tissue. This requires:

- Accounting for the greater energy density of reproductive tissue (particularly eggs—see summaries in Gunderson and Dygert, 1988; Shuter et al., 2005) over somatic tissue;
- Scheduling field sampling to allow for the fact that seasonal patterns of reproductive allocation can exhibit accelerated allocation just prior to spawning and that most reproductive tissue is expelled when spawning ceases.

Failure to recognize these issues can lead to significant underestimates of population production—as illustrated in Box 1.

Refining the P/B ratio approach

The P/B ratio method for estimating production is founded on statistical regression models that summarize patterns in observed population production data. It is simple to apply, requiring only estimates of biomass and mean fish size for a given population, community, or ecosystem. Further development of this method along the following lines is needed both to confirm its reliability and broaden its applicability to a wider range of ecological contexts:

- Challenge the basic P/B model with new empirical data on how the relationship between production and biomass is affected by cofactors such as climate, food web diversity, habitat type (e.g., lake vs. river), and habitat size and complexity (e.g., Minns, 1995; Randall et al., 1995);
- Include size composition data in a weighted mean P/B and compare resultant production estimates with those derived from more data-intensive methods (such as the IGR method—Table 1);
- Use estimates of (dW/dt)/W from individual growth models (e.g., biphasic models) to derive species or stock-specific P/B ratios and compare with those derived directly from empirical data;
- Evaluate whether key life history parameters (e.g., growth coefficients), along with phylogenetic and environmental variables, can be used to derive species- and site-specific P/B values (see Thorson, 2020).

Currently, there is limited appreciation of how basin-wide production is shaped by scale and habitat factors (Oberdorff et al., 2011); recent work with Alaskan Pacific Salmon (*Oncorhynchus tshawytscha*) populations (Brennan et al., 2019) suggests that the integration of biocomplexity across large spatiotemporal scales can act to stabilize production basin-wide. Development of a more diverse and precise set of P/B models may provide the tools needed to design logistically feasible studies of variation in production across entire watersheds. The new knowledge of basin-wide patterns in production, obtained from such studies, could provide the empirical foundation needed for developing more effective, evidence-based strategies for assessing fisheries and conserving productivity at broader spatial scales (e.g., Rypel and David, 2017; Jarvis et al., 2020).

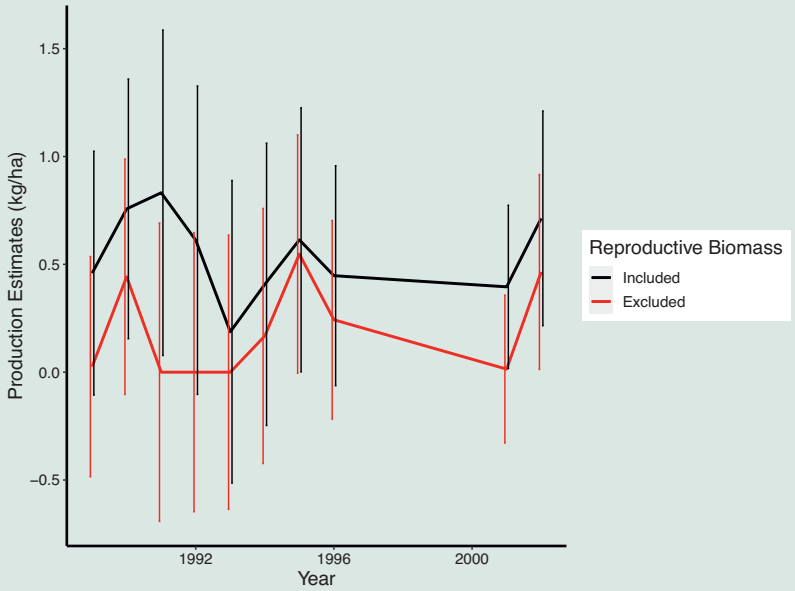
Box 1 Consequences of missing reproductive biomass in production estimates.

Access to prey resources and habitat suitability can exert a strong influence on the age or size at which an individual begins to allocate acquired energy to reproduction (Shuter et al., 2016). This key life-history trait is important to the overall productivity of a population since it dictates both adult maximum size and life-time fecundity. Current production estimation methods do not explicitly account for the energy or biomass lost through propagules (eggs/sperm) during spawning. By not accounting for loss of reproductive tissue, such estimates may underestimate the overall productivity of a population. This is of particular concern if field sampling occurs at times that do not coincide with spawning events, when investment in gametes is highest prior to release.

We aimed to assess the extent to which sampling of non-spawning individuals could underestimate overall production by failing to account for the production of reproductive tissue. Using long-term Lake Trout size-at-age data from Lake 375 in the IISD-Experimental Lakes Area (ELA), we calculated production estimates using the IGR method from 1989 to 2002 under population scenarios reflecting different sex ratios (50:50 and 80:20 females:males; the latter represents an extreme case of potential biomass allocation to gametes). Reproductive investment scenarios were set by the GSI (gonad weight expressed as a percentage of body weight: 15% for females, 5% for males) values observed for Lake Trout in Lake Opeongo in Algonquin Park, Ontario (Pazzia et al., 2002).

Since ELA Lake Trout data were collected in the fall during spawning, we felt justified in assuming: (i) our observed weight-at-age values included the full weight of tissue allocated to reproduction, and therefore (ii) these data provided the ideal dataset for evaluating potential bias as outlined below. A weighted average for population gonadal investment was calculated using female and male GSI values (0.1 and 0.13 for 50:50 and 80:20 females:males populations, respectively). These values were then multiplied against the weight of all aged individuals greater than 6 years of age, under the assumption that fall spawning Lake Trout *(Salvelinus namaycush)* spawn for the first time at the end of their 6th growing season. These amounts were then subtracted from the age class specific mean weight of all mature individuals, simulating spawning losses in the population. This allowed us to determine the degree to which we would underestimate production if our sampling occurred outside of the spawning period. Production estimates that excluded reproductive tissue were up to 50% lower than estimates based on the full observed weight of individual fish at spawning (Box Fig. 1; $t_{18} = -3.7628$, $P < .001$), with little difference between the 50:50 and 80:20 scenarios.

We demonstrate that underestimates of production may be substantial when reproductive biomass is not captured through appropriately timed sampling. This highlights the need to carefully consider the timing of field surveys such that reproductive energy allocation can be included when developing field sampling protocols designed to estimate production, or components of production.



Box Fig. 1 Comparison of annual production estimates that include reproductive biomass versus estimates that exclude reproductive biomass. Estimates are based on Lake *(S. namaycush)* Trout from lake 375 at the IISD-Experimental Lakes Area. A female:male sex ratio of 50:50 was assumed and reproductive biomass was estimated using sex specific mean values for the ratio of gonad weight to body weight (the GSI). Error bars represent estimate variance.

Conclusions

Our summary of current knowledge suggests that the primary drivers of production in freshwater fish populations can be divided in two distinct categories:

1. Forces that drive food availability:
   (i) Production at lower trophic levels sets the level of available food;
   (ii) The presence of competitors reduces available food through sharing;
   (iii) The presence of predators limits access to available food by imposing additional mortality risk.
2. Forces that shape life history and hence determine adult size:
   (i) Temperature, as a modulator of growth rates through its effects on both foraging efficiency and basal metabolic costs;
   (ii) Ecosystem size;
   (iii) Relative prey size, through its effects on foraging efficiency;
   (iv) Predation-induced mortality.

The fundamental link between environmental temperatures and foraging as it relates to production is worth stressing here. The empirical findings and theory discussed earlier demonstrate that bottom-up influences—which control prey resource availability—appear to be critical drivers of fish production. This is consistent with other theoretical work suggesting that prey resources may often be the primary factor driving animal production, overriding direct effects arising from temperature and/or metabolic limitations (Cross et al., 2015; Junker et al., 2020).

On this basis, we offer the following testable hypotheses to guide future research:

1. Given that prey body size is a main determinant of predator body size, an increase in prey body size in the absence of changes in prey trophic level and abundance should lead to an increase in both predator foraging efficiency and predator size, with the following consequences for production: *increases* in both predator production per unit habitat area and predator production per individual (as per Eqs. 10a and 6); a parallel *decrease* in predator production per unit biomass, as per Eq. (8). The fact that the predicted direction of change depends very much on the units used to measure production highlights the importance of clearly defining those units.
2. As habitat size increases, top predators tend to occupy higher trophic levels. This is accompanied by the following changes in the dominant prey species: *increases* in both trophic level and individual size; *decreases* in both numerical and biomass abundance (Sprules and Barth, 2016, see chapter on the Biomass Size Spectrum, Andersen, 2019). The consequences for predator production will be diverse: at the population level, production per unit habitat will decrease (assuming increased foraging efficiency cannot compensate for the overall reduction in prey abundance), production per unit biomass will also decline (as per Eq. 8) but production per individual will increase (as per Eq. 6).
3. P/B ratios can be used as logistically simpler surrogates of detailed fish population production estimates, particularly for population and community production estimation on larger regional scales such as watersheds and lake regions.
4. Oxythermal habitat loss as a consequence of climate change will decrease production in stenothermic predators.
5. As DOC increases, light limitation increases, reducing the overall productive capacity of freshwater ecosystems, with negative consequences for fish production.

Fish production has long been recognized as the ideal metric for understanding the state of fish populations since it is the outcome of a major pathway of energy flow (Waters, 1977). Establishing the mechanisms that drive fish production within freshwater ecosystems through exploring the hypotheses we have laid out above will advance current knowledge in useful ways by: (i) answering fundamental questions around freshwater ecosystem function, and (ii) promoting the development of the practical management tools needed to mitigate future stresses on these systems from climate change, human development, invasive species, and exploitation.

Knowledge gaps

- New and defendable empirical estimates of production from a diversity of freshwater systems
- A better accounting for reproduction costs in production and MTE approaches
- How the relationship between production and biomass is affected by cofactors such as climate, food web diversity, habitat type (e.g., lake vs. river), and habitat size and complexity
- Refine the upscaling of individual growth models to population levels
- Accounting for phylogenetic diversity in production models

Further reading

- Bioenergetics and energy budgets
- The biomass size spectrum
- Benthic algae and food webs
- Fish populations
- Fish communities
- Lake food webs
- Inland Fisheries Management—Exploitation and Livelihoods
- Societal values of inland fishes

See Also: **Emerging methods and topics**: Electronic Tagging and Tracking of Animals in Inland Waters; Freshwater Ecoacoustics—A New Addition to the Limnologists' Methods Toolkit; **Fundamental concepts and theories**: Bioenergetics; Diel Vertical Migration; The Biomass Size Spectrum; **Human pressures and management of Inland Waters**: Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment; Implications of Climate Change for Freshwater Fisheries; Inland Fisheries Management - Case Studies of Inland Fish; Inland Fisheries Management - Exploitation and Livelihoods; **Social/societal values of Inland waters**: Societal Values of Inland Fishes; The Gender Gap: Women as Authors and Leaders in International Publications in Fisheries Science; **Structures and functions of Inland Waters - Lakes**: Fish Populations; Predation on Zooplankton; **Structures and functions of Inland Waters - Rivers**: Energetics and Food Webs in Large Rivers; **Structures and functions of Inland Waters - Wetlands**: Patterns in Freshwater Fish Diversity

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Lake Food Webs

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This article was reviewed by Section Editors, Marie Elodie Perga and Damien Bouffard.

Glossary

Food web A description of the feeding relationships among organisms in an ecosystem.
Trophospecies A group of species that use the same resources and/or occupy the same trophic level (sometimes referred to as a "trophic guild").
Omnivory A feeding preference wherein an organism feeds on multiple prey or trophic levels.
Benthic energy pathway Resources originating from the bottom substrates of a lake.
Pelagic energy pathway Resources originating from the open-water area of a lake.
Bottom-up control The case in which nutrients regulate the biomass and community of primary producers, with effects that propagate to higher trophic levels to structure the ecosystem.
Top-down control The case in which predators regulate the abundance and/or size structure of their prey, with subsequent effects on the abundance and/or size structure of lower trophic levels to structure the ecosystem.
Trophic cascade The propagation of predation-driven, indirect changes in the abundance and/or community composition of trophic levels in a food chain, sometimes driven by the addition or removal of a top predator.
Biomanipulation Deliberate modification of an ecosystem by adding or removing species, usually predators.
Microbial loop Food web pathway in which dissolved organic matter is returned to the classical metazoan food web via food web linkages involving bacteria, protists, and crustaceans.
Biomagnification The process of the accumulation of contaminants in consumers at successively higher trophic levels.
Benthification A shift in energy production from the pelagic to benthic habitat.

Introduction

The study of food webs is the study of feeding or trophic relationships among species in an ecosystem. Interest in studying food webs stems from the fact that no species exists on its own. Rather, each species is embedded in a network of predator-prey interactions. These predator-prey interactions are of interest themselves and food web studies often provide a description of the feeding relationships among species within an ecosystem. Yet it has become clear that food webs have far-reaching consequences for ecosystems. Food web interactions greatly affect the abundance and dynamics of species. Food webs also have implications for ecosystem-level processes such as nutrient cycling and energy flux. Thus the study of food webs bridges population, community, and ecosystem ecology. At a foundational level, food webs provide a powerful framework for evaluating a collection of organisms as an ecological system.

It is critical to recognize that food web studies can encompass an exceptionally broad range of approaches and types of studies. Here, we identify three major approaches to studying food web study. A *connectance* (also known as topological or structural) food web is the binary (presence/absence) of predator-prey links among species in a community (Fig. 1A; Martinez, 1993, Dunne et al., 2002). *Energetic* food webs aim to represent the pathways and flows of energy through the food web, where links are weighted according to their energetic importance (Fig. 1B). Finally, *dynamic* (also known as functional) food webs focus on the factors that structure the abundance of different organisms and trophic levels, with emphasis on how the effect of predation cascades throughout food webs (Fig. 1C).

Food webs in nature are exceptionally complex. Studies of food webs inevitably involve simplifying this vast complexity into something more manageable. Examples include lumping similar species into 'trophospecies' (e.g., trophic guild), simplifying the ecosystem into discrete trophic levels or steps in a food chain, and ignoring taxa and habitats that are not considered important.

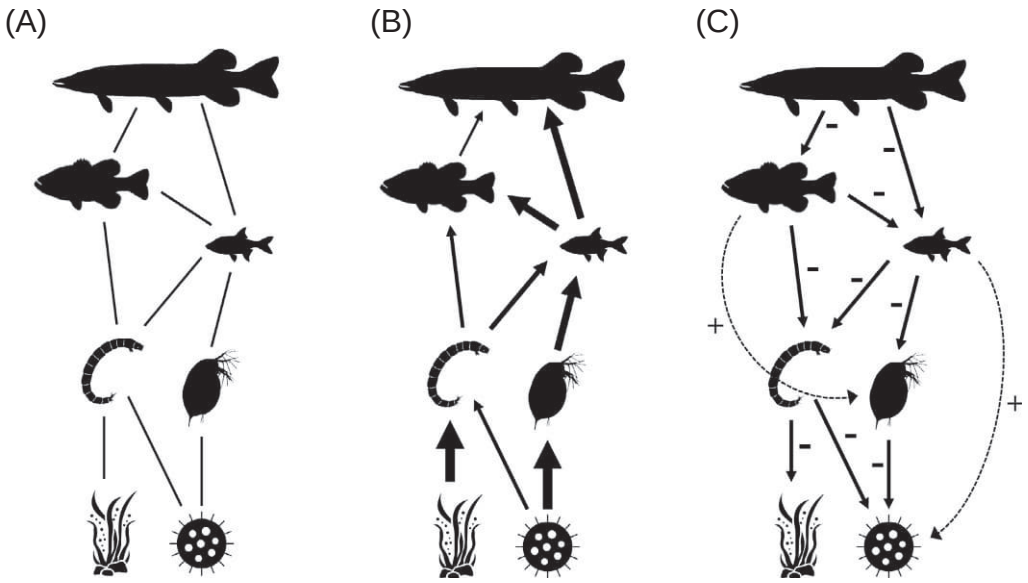

Fig. 1 Conceptual illustration of three approaches to the study of food webs: (A) connectance webs represent predator-prey links in an ecosystem, (B) energetic webs include information about the energetic importance (fluxes and flows) of food web links, (C) dynamic webs represent the linkages important for regulating abundance, including indirect and direct effects. In panel B, the size of the arrow indicates the magnitude of energy flow between trophic levels. In panel C, dashed arrows represent indirect interactions. Sign (– or +) represents the effect of the interaction.

Given the complexity of food webs, it is important to think carefully about what information is being described in a food web diagram or study.

The goal of this chapter is to provide a broad overview of lake food webs and highlight current areas of research interest. Lakes occupy a small portion (<2%) of the earth's surface, but are a vital source of freshwater to humanity, and provide a diversity of exceptionally valuable ecosystem services (Wilson and Carpenter, 1999). Studies have demonstrated that shifting food webs can have important implications for lakes and the ecosystem services they provide (Walsh et al., 2016). Moreover, several foundational advances in ecology emerged from studying lake food webs, including Lindeman's tropho-dynamic concept (Lindeman, 1942) and the concept of trophic cascades (Carpenter et al., 1985). One reason that the study of lake food webs has made broad contributions may be that lakes have well-defined boundaries, making them amenable to ecosystem study. While early ecologists viewed lakes as self-contained microcosms, researchers now recognize that there are strong inter-connections between lakes and their surrounding watersheds.

We divide this chapter into four sections. The first briefly addresses *connectance food webs*. While we do not expand broadly on this perspective, we offer multiple references for further reading. The second section focuses on food web studies taken from an energetic approach (*energetic food webs*). These studies tend to be 'bottom-up' in nature and emphasize how resources or energy at the base of the food web are transferred to higher trophic levels, as well as identifying the resources and energy pathways supporting higher trophic levels. The third focuses on *dynamic food webs*. These studies emphasize the effects of predators on their prey, and the interaction between 'bottom-up' and 'top-down' controls in structuring lake food webs. The fourth and final section highlights *integrative and applied perspectives* on food web studies including areas of emerging research interest in the study of lake food webs.

Connectance food webs

Connectance food web studies examine broad-scale patterns across collections of empirical food webs. These food webs are based on information about the presence/absence of trophic linkages. Connectance food webs are essentially network diagrams (Martinez, 1993; Dunne et al., 2002). Broad patterns can be examined - for example the number of observed trophic links can be related to the number of species, leading to a measure of food web connectance (Cohen and Briand, 1984; Paine, 1988). Connectance studies have also evaluated the relationship between the number of links in a food web and how many predators and prey occur (Cohen and Briand, 1984). Although connectance food webs can provide information about a system, many have critiqued this approach based on the arbitrary and poor quality of the data, as it fails to go beyond simple presence/absence of food web linkages (Paine, 1988).

Energetic food webs

Food chain concept—While natural food webs are characterized by vast complexity, many food web studies simplify matters by grouping functionally similar organisms. When considered in energetic terms, organisms are often combined into trophic levels – groups of species that are thought of as comprising a single step in ecosystem energy transfer. Photosynthetic organisms are considered primary producers (Λ1) and are the foundation of the food web. They are consumed by herbivores or primary consumers (Λ2), which are in turn consumed by secondary consumers (Λ3), and in many cases, tertiary consumers (Λ4). At each step, energy is lost, ultimately limiting the number of trophic levels in the food chain (Fig. 2). This fundamental concept of energy flow through successive trophic levels and concurrent energetic loss at each trophic level was presented by Elton (1927) and later Lindeman (1942) in his study of Cedar Bog Lake, Minnesota. While the transfer of energy from one discrete trophic level to the next is undoubtedly an oversimplified depiction of real food webs, the food chain concept has proven to be an exceptionally useful heuristic for conceptualizing energy flow in ecosystems.

Embracing complexity – the food web concept—Observational studies of feeding relationships generally reveal that the food chain concept with its simple trophic levels is a gross oversimplification of nature. Many species are 'omnivorous,' feeding on multiple

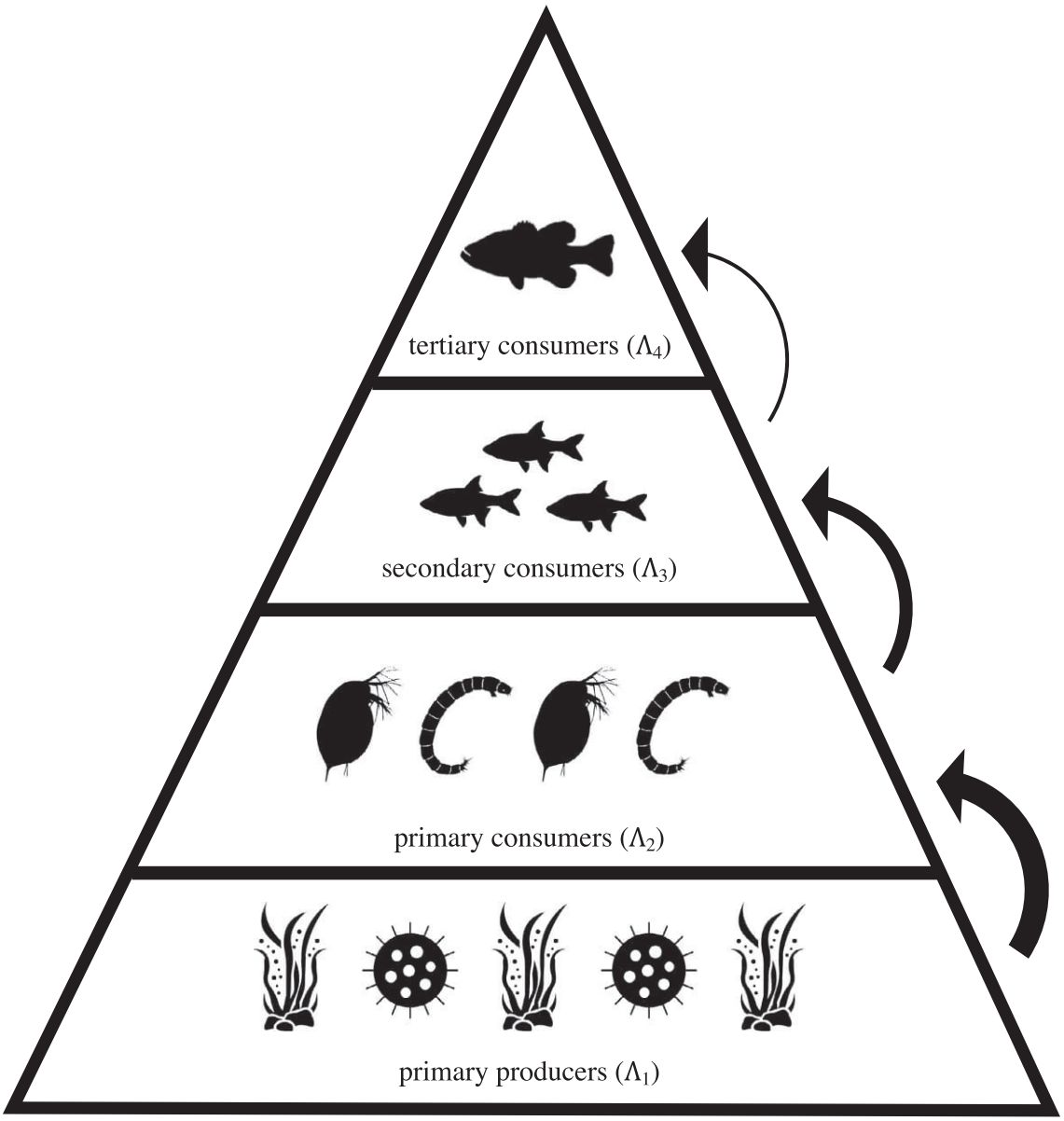

Fig. 2 Trophic pyramid showing energy flow across four trophic levels (Λ1, Λ2, Λ3, Λ4). Pyramid highlights the decrease in production at successive trophic levels. Arrow width indicates the magnitude of energy flow.

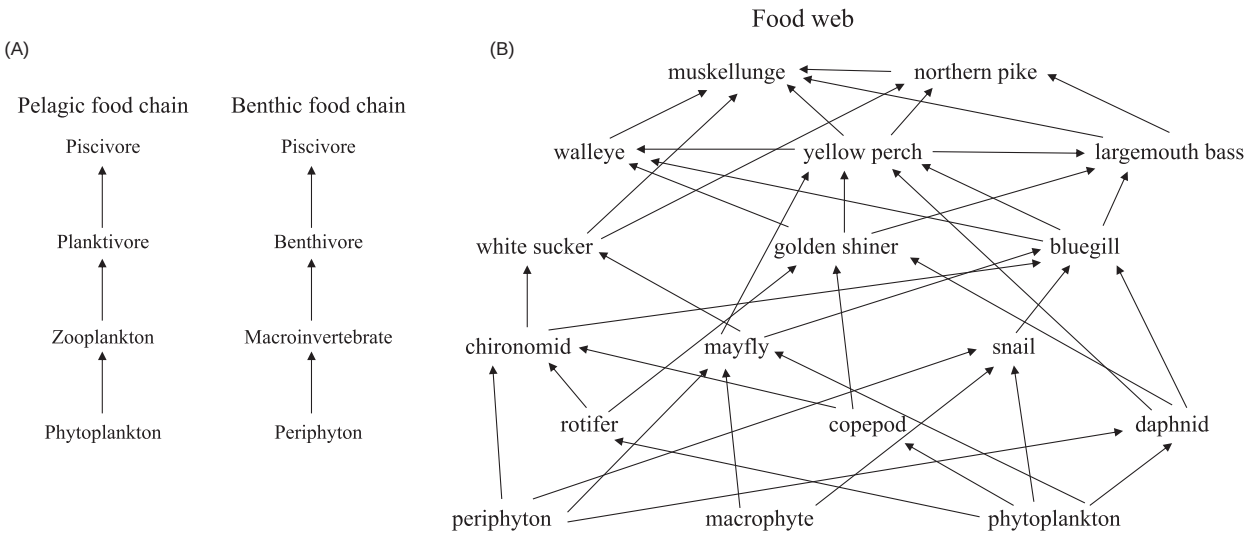

Fig. 3 Two idealized, linear food chains from pelagic and benthic habitats (panel A), as well as a simplified reticulate food web of a north temperate lake (panel B). Adapted from Rudstam LG, Allen Y, Johnson BM, Luecke C, Post JR, and Vanni MJ (1992) Food web structure of Lake Mendota. In: *Food Web Management*, pp. 233–242. New York, NY: Springer.

prey or trophic levels. Diets can vary among individuals of a trophic level, and shift during the ontogeny of a species, adding further complexity. Food web diagrams, sometimes comprised of numerous food chains (Fig. 3A), can be used to represent these more reticulate and complex food web relationships (Fig. 3B). But even these still tend to be an oversimplification of actual feeding relationships. The concept of trophic position incorporates some of this complexity. Though conceptually analogous to trophic level, trophic position is non-integer in nature and reflects the weighted average of the various feeding pathways supporting a consumer. Trophic position can be estimated from diet data. In recent decades trophic position has been estimated using stable nitrogen isotope ratios sampled from organismal tissues. Stable nitrogen isotope ratios become enriched between prey and predator tissues, thus providing a measure of consumer trophic position (Cabana and Rasmussen, 1996; Fry, 2006).

What basal energy sources support lake food webs?—Lake food web studies in the past decades have focused on identifying the trophic basis of support for higher consumers. These studies have revealed new insights into energy flow pathways in lakes. One important area of research has examined the energy (carbon) sources supporting higher trophic level production. Studies examining organisms' diets and stable carbon isotopes have found benthic (bottom) algae-based production pathways to be especially important in supporting higher consumers such as fish (Vander Zanden and Vadeboncoeur, 2002). This was surprising, as benthic production and trophic pathways have traditionally received little attention in limnology. An important implication is that fish play a central role in coupling benthic and pelagic production pathways in lakes.

Studies have also reported an important role of terrestrial-derived carbon in supporting higher trophic levels in lakes (Pace et al., 2004). This is especially the case in small lakes with high levels of terrestrially-derived dissolved organic carbon (DOC). This work reveals the potentially important role of heterotrophic bacterial food web pathways in supporting the production of metazoan consumers. Heterotrophic bacteria are known for their role in decomposition of organic matter. More recent work reveals that microbial food chains involving flagellates, protozoans, and rotifers funnel bacterial production (albeit with varying efficiency) back into classical metazoan food webs, ultimately supporting higher consumers such as fish. The presence of terrestrially-derived DOC plays a critical role. It reduces light penetration, and thus limits lake primary production. It also fuels heterotrophic bacterial production, and the microbial food web pathways described above (Karlsson et al., 2009).

Cross-habitat linkages—It has long been recognized that the structure and function of lakes is strongly influenced by their surrounding landscape. Due to their low-lying position in the landscape, organic matter and nutrient runoff from the land readily make their way into waterways and ultimately into lakes. Expanding agricultural and urban land use have dramatically accelerated nutrient inputs. Land use is the dominant driver of lake and coastal eutrophication (i.e., nutrient enrichment of a waterbody), a global problem that has led to the degradation of lakes worldwide.

More recently, studies have identified the importance of lake-to-land linkages wherein lake-derived productivity fuels or influences adjacent terrestrial ecosystems (Gratton et al., 2008). Lakes support the early life stages of many invertebrates, which then emerge and continue their lives in terrestrial environments. Emergent insects transport nutrients from lake-to-land, sometimes resulting in a significant flux of nutrients and prey to terrestrial systems. Riparian predators rely on emergent aquatic insects as a food source. The export of aquatic production to terrestrial ecosystems is common and can alter the functioning of terrestrial food webs through a nutrient fertilization effect, and by providing prey subsidies to terrestrial consumers.

Dynamic food webs

Drivers of food web structure—What ultimately controls the abundance of organisms at different trophic levels in an ecosystem? This is a central question of dynamic food web studies. Energy flow in ecosystems is unidirectional, moving from lower to higher trophic levels. So it is perhaps obvious that lower trophic levels influence higher trophic levels as a result of this direct energetic reliance. But predators also influence their prey, and the implications can be far-reaching. Dynamic food web studies attempt to understand the controls that structure organismal abundance across different trophic levels. Two predominant paradigms arose: bottom-up and top-down, leading to a debate over the relative importance of these controls. For decades, scientists emphasized the importance of bottom-up factors. In lakes, this was supported by that fact that there is a strong relationship between nutrient loading or nutrient concentration and algal biomass (Schindler, 1974). More recently, the structuring role of consumers, or top-down controls have been investigated in lake food web studies. Today it is well recognized that both bottom-up (nutrients) and top-down (consumers) forces interact to structure lake food webs, and that complex interactions yield a much richer range of dynamics than would be the case with simple linear food chains (Zaret and Paine, 1973; Carpenter et al., 1987; Knight et al., 2005; Koel et al., 2019).

Trophic cascade concept—The influential role of predators in structuring prey communities in lakes has been known for many decades. In response to variability in phytoplankton biomass that could not be explained by nutrients, it was proposed that changes in top predators could propagate to lower trophic levels through what is now known as a trophic cascade (Carpenter et al., 1985). Through whole-lake manipulations, it was established that while potential phytoplankton biomass is set by nutrients, realized biomass is influenced by the reciprocal effects of predators on prey transmitted through the food web. In these experiments, the removal of top predators (piscivores) resulted in the increased abundance of zooplanktivores, decreased grazer abundance, and higher algal biomass (Fig. 4).

Behaviorally mediated effects—Many studies emphasize the effects of direct, lethal predation in creating cascades in lake food webs, but predators also greatly influence prey behavior, which indirectly alters community interactions. In the presence of predators, prey may reduce activity or change their use of habitat, thereby altering prey diets and interactions in food webs. For example, the presence of piscivorous largemouth bass (*Micropterus salmoides*) altered the habitat use of juvenile sunfish (*Lepomis* spp.), leading to behaviorally-mediated cascading effects on benthic macroinvertebrates (Werner et al., 1983). Without largemouth bass, juvenile sunfish prefer the pelagic zone, but in the presence of largemouth bass, sunfish change habitat to the vegetated littoral zone where

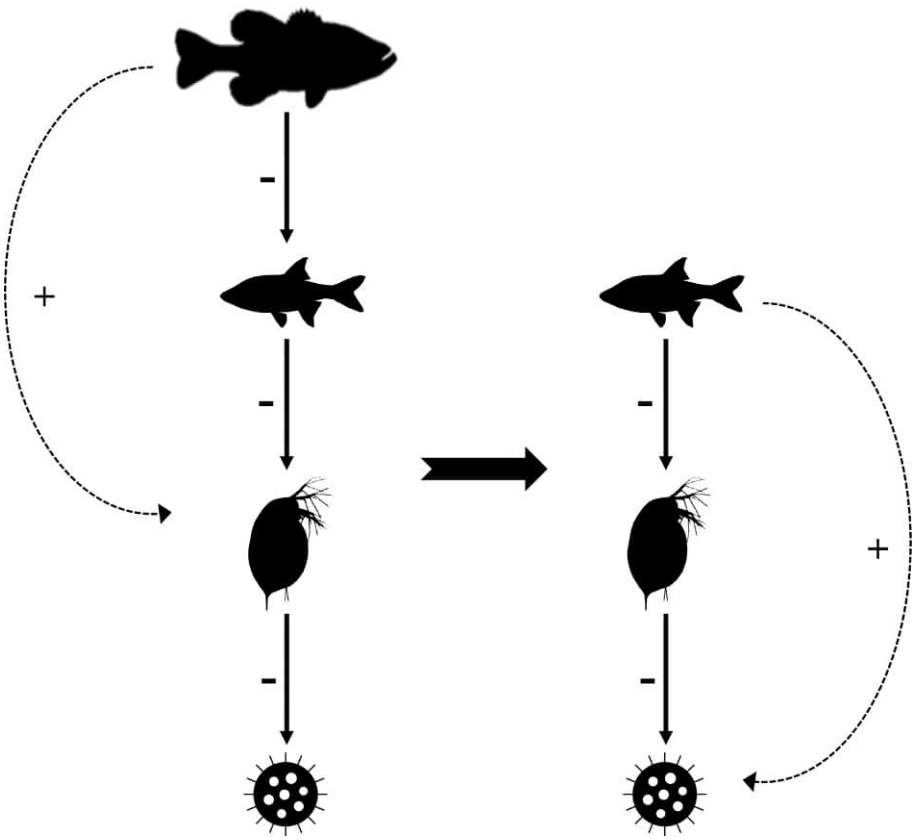

Fig. 4 A simplified dynamic pelagic food web consisting of four trophic levels. Solid arrows indicate direct interactions. Dashed arrows represent indirect interactions. Sign (– or +) represents the effect of the interaction. The horizontal arrow indicates an ecosystem shift wherein the top piscivore predator is removed.

they increase feeding on benthic macroinvertebrates, leading to reduced macroinvertebrate densities. It is clear that predators can have significant indirect effects on lake food webs by causing behavioral shifts in intermediate consumers.

The importance of indirect food web interactions is now well documented in a variety of contexts. This includes responses to the introduction of invasive species, situations involving cross-habitat linkages, and dynamics that play out over long time scales. In addition to providing a useful framework for assessing the role of top-down and bottom-up factors in structuring food webs, the trophic cascade concept also informs efforts to improve water quality in lakes (Hansson et al., 1998). Food web manipulations ('biomanipulations') such as stocking piscivores or removing coarse fish, are commonly employed to improve lake water quality, particularly where further nutrient reductions are not possible.

Structuring role of macrophytes—Macrophytes (i.e., aquatic plants) are an important group of primary producers in lakes that can play a role in regulating food webs. Beyond serving as a food source for certain lower level consumers, they also play an important structuring role in food webs. Macrophytes provide habitat for many species, serve as a predation refuge for invertebrates and fish, and greatly influence animal communities in a variety of ways (e.g., spawning, feeding habitat). By shaping predator-prey interactions, their effects can propagate through food webs. In this way macrophytes play a central role in the coupling of pelagic and littoral zones (Jeppesen et al., 1998).

Alternative stable states—Ecosystems exposed to changing environmental conditions, such as climate change or nutrient loading, may respond in different ways. Some systems change gradually, while others may abruptly shift between alternative states over a range of environmental conditions. An ecosystem exhibits 'alternative stable states' when the system response is not continuous given gradual changes in an environmental variable but instead shifts abruptly between two alternative equilibria (Scheffer et al., 1993). This theory was established from the study of shallow lakes in response to varying nutrient loading. Researchers observed that lakes displayed two equilibria: a clear state dominated by aquatic vegetation and a turbid state characterized by high phytoplankton biomass. Characteristic of alternative stable states, the lakes remained in their respective regime and a change in nutrient loading was insufficient to reverse states. Instead, considerable effort or a severe perturbation, such as intensive removal of zooplanktivorous fishes (biomanipulation) was needed to "push" the system back to the alternative state.

Food web stability—A topic of long-time interest to food web ecologists centers on how food web structure and complexity influences ecosystem stability. Stability can have different meanings, but often refers to susceptibility to runaway variation in species' abundances. Historically it was argued that complex food webs were buffered against strong dynamics and thus likely to be more stable. But theoretical analyses by May (1972) found that complexity tended to destabilize food webs. The most recent work reveals that if most food web linkages are weak, complexity tends to confer stability to food webs (McCann et al., 1998). Weak links serve to reduce fluctuations between consumers and producers, thereby maintaining populations further away from collapse. Studies of natural lake communities reveal that food webs are largely composed of weak interactions and few strong interactions. Today, food web stability and interaction strength in lakes continues to be a topic of great interest.

Integrative and applied perspectives

Lake food webs are characterized by complex biotic interactions. Food web interactions in lakes can also be influenced by external physical, chemical, and biological drivers. While the primary paradigms for how organisms interact and regulate one another are well established, the study of lake food webs is interdisciplinary and draws upon multiple realms of knowledge. As a result, there are many other approaches used to further our understanding of lake ecosystems that ultimately inform the use and management of lakes. Here we highlight several integrative and applied perspectives that demonstrate the cross-disciplinary approaches taken in the study of lake food webs.

Incorporation of microbial components—Historically studies of lake food webs largely overlooked microbial components of the ecosystem. But even with traditional food web approaches, many observed that the energy produced by phytoplankton was not enough to explain the productivity of higher trophic levels, prompting recognition of the importance of the 'microbial loop'. Heterotrophic bacteria are well known for their role in the decomposition of organic matter in lakes. There is a more recent recognition that bacteria form the basis of a pelagic microbial food web involving organisms such as heterotrophic flagellates, ciliates, and rotifers that ultimately links to the traditional metazoan food web (crustacean zooplankton, fish). The degree to which this microbial loop is an energetic 'link' or 'sink' in lakes is highly context dependent. Incorporation of the microbial loop provided new insights into energy flow in lakes.

Stoichiometric approach – "you are what you eat"—Everything in ecosystems is made up of chemical elements, such as carbon (C), nitrogen (N), and phosphorus (P). The study of the ratios among these chemical elements is called stoichiometry, which has become particularly influential in aquatic ecology with the field of ecological stoichiometry. Ecological stoichiometry considers the relative contribution of nutrients (e.g., C, N, P) as structuring agents of food webs (Sterner and Elser, 2002). This approach stems from the finding that a consumer's chemical composition reflects the chemical composition of its food, or in other words, "you are what you eat." Although ecological stoichiometry is applicable to any element, most studies focus on C, N, and P as they are the dominant components of organisms and often growth limiting (especially N and P). In aquatic systems, the ratio between C, N, and P (C: N: P) in the water is used to assess which of these nutrients is limiting for primary producers and thus higher trophic levels. In this view, relative nutrient concentrations provide the fuel for potential ecosystem productivity and animals represent large pools of nutrients that interact to structure lake communities (Sterner and Elser, 2002).

In addition to storing nutrients in their bodies that may be made available as they die and decompose, animals also have important indirect effects on lake stoichiometry. Higher level consumers, such as fishes, excrete and translocate nutrients within ecosystems, providing a substantial portion of phytoplankton nutrient demand (Vanni, 2002). For example, when zooplanktivorous fish become abundant they reduce grazing pressure by zooplankton (top-down effect), but they also promote phytoplankton growth by increasing available phosphorus through excretion (indirect bottom-up effect). Through direct and indirect impacts on ecosystems, consumers act as sources and sinks of nutrients and can impact lake community interactions.

Contaminants—The study of food webs has also made contributions to our understanding of contaminants in lakes. For contaminants such as methyl mercury, Polychlorinated biphenyls (PCBs), and dichloro-diphenyl-trichloroethane (DDT) that are transferred up food chains from prey to predator, the trophic position of a consumer is a strong determinant of contaminant levels (Cabana and Rasmussen, 1994). For these toxins, higher contaminant concentrations are found in progressively higher trophic levels, accumulating as they move up the food chain in a process known as 'biomagnification.' Food chain biomagnification can have noteworthy impacts, especially when highly contaminated prey are eaten by fish-eating birds and mammals, and toxins are passed on to adjacent ecosystems (Blais et al., 2007). Recent work has also identified concern over neonicotinoid insecticides. These chemicals are widely used in agriculture and have toxic impacts on planktonic and benthic invertebrates. The decimation of the food base due to neonicotinoids has led to fishery declines and is an emerging area of research (Yamamuro et al., 2019).

Biomanipulations with unintended consequences—Natural resource managers have often intentionally introduced species to achieve management objectives. Such efforts have involved the introduction of predatory fish to elicit a trophic cascade to increase water clarity (Hansson et al., 1998). Others have aimed at supplementing the forage base. These species introductions can have unintended consequences that ripple throughout the food web. One example involves the opossum shrimp (*Mysis relicta*), a predatory zooplankter that has been introduced into lakes of western North America and elsewhere to augment the food base for salmonids. Opossum shrimp introductions have led to sharp declines in large zooplankton species (e.g., *Daphnia*) and a shift to smaller zooplankton taxa, often leading to fishery declines. Specifically, in Lake Tahoe (CA-NV, USA), opossum shrimp were introduced in the 1960s, which led to significant declines in large zooplankton, reduced water clarity, and declines in Kokanee salmon. In Flathead Lake (MT, USA) the effect of introduced *Mysis* was similar in that zooplankton declined. In addition, this introduction bolstered populations of the non-native piscivore, Lake Trout. This increased predation on Kokanee salmon, thereby leading to their collapse. Further, these shifts redirected ecosystem energy flow, limiting resources available to nearby ecosystems and causing declines in terrestrial top predators (e.g., bald eagles; Ellis et al., 2011).

Fish species are commonly introduced to lakes to satisfy fishery management objectives but can have unexpected food web consequences. In some instances, the introduction of non-native species can have effects that cascade through the food web and adjacent ecosystems. For example, following the stocking of non-native lake trout (*Salvelinus namaycush*) in Yellowstone Lake (WY, USA), highly valuable endemic Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) declined significantly (Koel et al., 2019). But it is not only non-native species that cause concern. Stocking of native fishes has also resulted in unintentional effects. In many lakes in North America and Europe, fishes of recreational interest are stocked annually. This practice can homogenize fish faunas, reduce genetic variation, and alter community composition as a result of higher predator populations than may occur naturally (Eby et al., 2006). In summary, intentional efforts to manipulate biotic composition in lakes often has unexpected effects that can ripple through multiple trophic levels and even into adjacent ecosystems (Koel et al., 2019).

Invasive species impacts on food webs—The introduction of non-native species can have profound effects on lake food webs. The Laurentian Great Lakes, with >180 introduced non-native species, have experienced so many food web disruptions that it can be difficult to interpret. One exception has been the invasion of Dreissenid mussels (*Dreissena* sp.). In 1988, Dreissenid mussels were discovered and quickly spread throughout much of the Great Lakes. Dreissenids are effective filter feeders and excrete organic material to the benthic substrate they inhabit. Given the rapid expansion and population growth of Dreissenid mussels in the Great Lakes, water clarity increased. This resulted in widespread 'benthification' wherein energy production shifted from pelagic to benthic regions, leading to an ecosystem-wide shunt from pelagic to benthic food web pathways (Mayer et al., 2013). The invasion of Dreissenid mussels greatly modified physical habitat with far-reaching effects on lake food webs.

Climate change impacts on food webs—As climate changes, food webs may experience strong perturbations resulting in unexpected consequences if interacting species respond differently to shifting environmental conditions. In Lake Washington (WA, USA), it was shown that increasingly warmer springs over the past 40 years have led to the uncoupled timing of phytoplankton and zooplankton blooms (Winder and Schindler, 2004). The spring diatom bloom no longer synchronized with the keystone herbivore (*Daphnia*) hatching period due to climate warming, resulting in long-term declines in *Daphnia*. Beyond the effects of climate change on the phenological coupling of trophic levels, climate change is expected to dramatically alter species interactions in lakes, though there is still much uncertainty regarding what the future will look like given the potential for unexpected results.

Social and economic change as a result of food web shifts—Food webs can change as a result of many drivers including biomanipulations, invasive species, and climate change. Structural food web changes can have drastic impacts on lake ecology itself, but these shifts can also ripple throughout human communities reliant on these ecosystems for nourishment, suitable water quality, as well as employment/tourism opportunities causing dramatic social and economic changes. One of the most pronounced examples of this occurred in Lake Victoria, Africa when a large-bodied piscivore, Nile perch (*Lates niloticus*), was introduced in the 1950s. Nile perch have transformed the lake food web as they rapidly consumed native fishes, specifically causing the extinction/near-extinction of numerous endemic cichlids (Balirwa et al., 2003). As a result of the disrupted native ecosystem, many locals were displaced from traditional occupations in the fishing trade or bought into the cash economy to purchase nets capable of catching adult Nile perch. The introduction of Nile perch ushered in a robust commercial fishery, leading to a novel international trade economy that has

further impacted social dynamics in the region. Beyond drastically altering the lake food web, the Nile perch fishery has led to further deforestation in the region, increased conflicts over fish exportation, and has rippled into the illegal trade of wildlife (e.g., bushmeat) as fishery catches fluctuate. Given the demand and reliance on Nile perch, this species has been overfished, which in combination with other ecosystem changes (e.g., water quality declines, nearshore human population growth) has led to further food web shifts and socio-economic changes (Balirwa et al., 2003). People are highly reliant on lakes for numerous services, including nutrition, employment, and recreation. Perhaps it should not come as a surprise that changing food webs can have dramatic consequences for human societies and well-being.

Conclusion

Food webs are a way of representing predator-prey relationships, energy flow, and multi-trophic level interactions in ecosystems. While food webs show the pathways of energy flow in ecosystems, predator-prey interactions simultaneously influence this flow of energy and cycling of nutrients, thereby shaping the productivity and abundance of organisms across multiple trophic levels. The structure of food webs is influenced by both internal and external drivers. Despite their relatively small global coverage, lakes provide disproportionately valuable ecosystem services to humans, which are highly influenced by food web interactions. Many different approaches and perspectives are used to understand lake food webs, including connectance, energetic, and dynamic approaches. In combination with other disciplines, these approaches highlight how food web structure affects community and ecosystem properties of lakes, including the ecosystem services that benefit humans.

Knowledge Gaps

- How can we simplify the vast complexity of natural food webs into something more manageable to inform our understanding and management of these ecosystems?
- How does food web structure and food web complexity in particular influence ecosystem stability and resilience?
- What are the causes and consequences of abrupt shifts in lake ecosystem states?
- What are the consequences of invasive species for lake food webs?
- How do shifting external drivers such as climate interact with changing food webs?
- What are the implications of changing lake food web for the multitude of ecosystem services provided by lakes?
- What is the role of adaptation and evolution in species interactions, and what are the broader food web consequences?
- How do parasitic interactions affect lake food webs?

Case Studies.

Site name	*Country*	*Coordinates*	*Topic/concept*	*Key reference*
Cedar Bog Lake	USA	45.4105, –93.1991	Tropho-Dynamic Concept	Lindeman (1942)
Peter, Paul and Tuesday Lakes	USA	46.2522, –89.5040	Trophic cascade	Carpenter et al. (1987)
Peter and Paul Lakes	USA	46.2522, –89.5040	Terrestrial support	Pace et al. (2004)
Lake Mývatn and 7 nearby lakes	Iceland	65.5975, –17.0029	Cross-habitat linkages	Gratton et al. (2008)
Great Linford Pits and Ponds	UK	52.0698, –0.7571	Alternative stable states	Scheffer et al. (1993)
Flathead Lake	USA	47.8999, –114.1165	Biomanipulation	Ellis et al. (2011)
Laurentian Great Lakes	USA	42.1159, –81.4271	Invasive species effects (benthification)	Mayer et al. (2013)
Lake Victoria	Kenya, Uganda, Tanzania	–0.595261, 33.462087	Socio-economic effects	Balirwa et al. (2003)

See Also: Fundamental concepts and theories: Parasites in Aquatic Food Webs: How and Why Environmental Gradients Influence Epidemics and Their Implications; Trophic Dynamics and Food Webs in Aquatic Ecosystems; Structures and functions of Inland Waters - Groundwater: Trophic Interactions in Subterranean Environments; Structures and functions of Inland Waters - Lakes: Predation on Zooplankton; Structures and functions of Inland Waters - Rivers: Aquatic Food Webs In Rivers; Ecological and Evolutionary Consequences of Disturbance in Freshwater Ecosystems; Energetics and Food Webs in Large Rivers; Secondary Production in Streams

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Section Introduction: Structures and Functions of Inland Water – Rivers

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Rivers are ubiquitous features of the Earth's landscape. They are carved by the runoff from precipitation moving by gravity downhill to the oceans or inland terminal basins. As they flow, they transport sediment (and wood) via erosion, creating dynamic networks of channels and floodplains in which aquatic and riparian species evolve and thrive. Although rivers and streams comprise less than 0.005% of the freshwater on land, they host a greater species diversity per unit area than terrestrial or marine ecosystems. These diverse, dynamic systems provide innumerable goods and services to support human economic activities and societal wellbeing. The future of rivers in a human-dominated world requires that we better understand how they function and what management interventions can contribute to their sustainability.

In this "Streams and Rivers" section of the EIW2, we have collected 36 excellent chapters that help the reader understand rivers as complex and diverse freshwater ecosystems that vary across the landscape due to differences in climate, surficial geology, catchment topography, land cover and evolutionary history of the organisms that comprise these dynamic ecosystems.

These chapters present a variety of perspectives from authors who are experts on the particular chapter content. General conceptual foundations of whole river systems are presented in terms of how river ecosystem structure and function change along the longitudinal profile of a river system (Dodds and Maasri), and how nutrients move from upstream to downstream via water flow and biological uptake and release (Webster, Newbold and Thomas). Rivers also extend periodically outside their normal channels laterally onto with the adjacent land to support riparian ecosystems (Merritt) and diverse and productive floodplains in large rivers (Hamilton). Streams and rivers also have a vertical dimension, with surface water moving into the streambed to the subsurface "hyporheic" zone, where special fauna and important nutrient transformations occur (Lewandowski, Müller and Schulz). The habitats within a river or riparian zone are strongly influenced by the physical nature of the streambed and the dynamic flux of water and sediment, as described in the excellent chapter on fluvial geomorphology (Kondolf and Bizzi). The dynamics of streamflow through river channels, the sources of that variability and how differences in streamflow among rivers can be generalized are treated in a chapter on hydrology (McManamay). Some types of rivers are relatively distinct due to hydrologic or climatic harshness, and examples of these are covered in chapters on high latitude streams (Lento and Culp), alpine streams (Khamis, Brown, Milner, Hannah, Fell), dryland rivers and streams (Compson, Allen, Gao, Hong, Sarremejane, Ruddell, Delvecchia, Burrows, Monk), and intermittent and ephemeral streams (Datry and Stubbington).

Many chapters are included that describe basic biological processes in river systems. For example, algae capture solar energy and convert that, along with dissolved nutrients, via primary production into a fundamental basal food and energy resource (Stevenson). This algal production, along with detritus imported from the terrestrial realm, drives production of consumers and overall ecosystem productivity (Whiles and Patrick). Aquatic organism production can be strongly constrained by the balance between nutrients available and those needed for growth, as described in the chapter on the growing field of stoichiometry (Atkinson, Halvorson, Evans-White, Hopper, Vanni). The interactions between organisms in streams and rivers are often viewed through the lens of communities of species interacting in a food web in streams to mid-size rivers (Thompson) and in large rivers (Thorpe). These interactions may also be mediated through dynamic environmental variation caused by disturbance of the habitat due to hydrologic variation or streambed movement (McIntosh and Barrett). Streams or rivers can recover after disturbance, even catastrophic disturbance, through a process of succession (Milner).

New insights into stream and river ecology over the last decade emphasizes the importance of habitat connectivity in the context of river networks, allowing distant local populations to be connected via dispersal to create metapopulations or metacommunities (Cathay and Brown). This macrosystem perspective (Thorpe) or viewing local system in a regional (network) context is also critical for understanding the resilience of streams and rivers to landscape fragmentation and environmental change (Van Looy, Fuller, Gilvear, Thoms, Wolter).

Streams and rivers suffer many impacts from human activity, often in terms of degraded water quality (Bohenek and Sullivan), and these are covered in chapters on the effects of dams (Schmidt), mining (Clements), and multiple stressors from a variety of pollutants (Birk), including novel stressors such as pharmaceuticals (Rosi). A chapter on urbanization (Walsh) discusses dominant impacts on streams and rivers caused by the world's growing population. Additional threats to river biota and ecosystems are covered in chapters on the spread of non-native species in rivers (Olden, Chen, Garcia-Berthou, King, South, Vitule) and on the growing concerns about climate change and its attendant increase in extreme event frequencies (Tonkin).

To guide management of rivers, the extent of stress or pollution on modifying biological integrity is typically quantified though biomonitoring methods (Hawkins and Carlisle), including novel approaches using "environmental DNA" collected from stream water (Baird, McGee, Compson, Hajibabaei, Robinson, Porter). Many chapters discuss various management actions, including stream restoration in general (Palmer and Laub) and modifying flow releases from dams to obtain partial restoration via "environmental flows" (Arthington). The growing science of dam removal is also presented (Bellmore and Duda), as this avenue of river restoration is increasingly being used. These actions are often grounded in the concern over species loss, as discussed in a chapter on biodiversity conservation in rivers (Linke and Hermoso) and a chapter on the "ecosystem services" provided by rivers (Jähnig, Jardine, Pusch, Wantzen, Dehnhard, Scholz, Tharme, Langhans, Podschun) that are at risk of loss by many human activities.

In sum, these 36 chapters provide the reader of the EIW2 with both a broad and a detailed view of streams and rivers that will advance society's understanding of these complex and ubiquitous inland freshwater systems. On a personal note, I wish to offer my personal thanks to all the contributors to this section—the last 2 years have presented especially challenging circumstances that complicated personal and professional lives. Nonetheless, the authors of these chapters persisted and completed their contributions, with the result being an excellent compilation of contemporary perspectives on stream and river science that speak to the urgency of better managing our inland fresh waters toward a resilient future and for the continuation of all the benefits and opportunities — economic, social, cultural and spiritual — they provide to humanity.

The River Continuum Concept

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Allochthonous Carbon produced outside the stream in the terrestrial habitat, which falls or washes into the stream.
Autochthonous Carbon produced by primary producers in the stream or river.
Collector-gatherers Animals that collect small organic particles (living or dead) for food.
Ecosystem respiration (ER) The sum of respiration (i.e., the process involving the intake of oxygen and the release of carbon dioxide from the oxidation of organic substances) by all heterotrophs and autotrophs in an ecosystem. Units are in mass per area per time or mass per volume per time.
Filter feeders Animals that collect particles in suspension in the water column.
Functional feeding groups Classification of organisms based on their ecological role, particularly their trophic position in a food web. Often used to classify animals.
Gross primary production (GPP) The total carbon fixation in an ecosystem. It can also be represented by dissolved oxygen flux. Units are in mass per area per time or mass per volume per time.
Invertivores Animals that feed on invertebrates.
Macrophytes Aquatic plants that have adapted to living in aquatic environments.
Net Ecosystem Production The gross primary production (GPP) minus the ecosystem respiration (ER) that indicates net carbon gain in a system. It is sometimes represented as GPP/ER where net carbon gain is represented by values greater than one.
Periphyton The complex film of algae and other organisms attached to solid surfaces in freshwater environments.
Piscivores Animals that feed on fishes.
Planktivorous Animals that feed on plankton, including zooplankton and phytoplankton.
Riparian zone The zone near the edge of a river or stream.
Scraper-grazers Animals that scrape biofilms from solid surfaces, usually periphyton (i.e., attached algae). Also refers to animals that eat macrophytes (aquatic plants). Grazer implies consumption of photosynthetic organisms.
Shredders Animals that break down leaves or wood for nutrition.

Introduction

The River Continuum Concept (RCC, Vannote et al., 1980) is almost a half-century old, and as of September 2021 Google Scholar counts over 12,000 citations and the more restrictive Web of Science lists over 6300 citations. At the core of this concept is the idea that at each specific location in a watershed, inputs from upstream interact with the local terrestrial riparian habitat to control ecosystem characteristics. These interactions then shape river ecosystem metabolism, energetics, and biological communities. Whether considered a milestone in stream ecology that shaped stream ecology research or a concept that needs revision, it has the merit of spurring considerable research, conceptual advance, and debate in stream ecology. Here, we explain the RCC, and how

it has evolved over the years since first proposed by Vannote et al. (1980), including support and critiques. We end with ideas of how researchers might use the concept into the future.

The original concept centered on the continuous connection from a temperate forested high elevation stream flowing through ever-bigger channels into a large lowland river (Fig. 1). The organic material entering from nearby riparian vegetation, the organic material transported from upstream, and the light entering the flowing water driving photosynthesis are the factors that control the sources of carbon and their identity. In small streams with dense canopy cover, the light is low for much of the year, so primary production (autochthonous carbon) is limited and most carbon enters the system in the form of terrestrial leaves, dissolved organic carbon, and other detritus (allochthonous carbon). This leads to a system dominated by heterotrophic respiration (mostly microbial) that relies upon the organic material. In this case, gross primary production (GPP) is low, ecosystem respiration (ER) is high, net ecosystem production is negative, and GPP/ER is less than one. In the middle-sized streams further down the continuum, the stream widens, and light can stimulate productivity. While the light promotes primary production, allochthonous carbon also enters the stream from nearby riparian vegetation and washes in from the small streams above. In this case, GPP rates balance ER, and net ecosystem production approaches or is greater than zero. Note the original paper suggested GPP/ER greatly exceeded one in middle- sized streams, but subsequent research suggests it rarely does by much. Once the flow reaches large rivers, the system is almost completely dependent upon carbon transported from above or gross primary production by any primary producers in the water if turbidity is low enough so that ample light can be transmitted into the river.

This basic pattern in carbon and light supply then controls function and composition of the communities of invertebrates and fishes. The relative dominance of invertebrates is categorized by their functional feeding groups. These include (1) shredders that consume large organic detritus, (2) collector-gatherers that filter or collect smaller particles, (3) scrapers-grazers that consume periphyton or macrophytes, and (4) predators. Changes along the continuum are driven mainly by relative availability of allochthonous and autochthonous carbon sources. In small streams, invertebrate communities rely heavily on allochthonous particulate organic matter, such as leaf litter, decomposed detritus, pollens, and other organic debris, or the microbes on this organic matter. Communities of small streams are, therefore, predicted to be dominated by shredders and collector-gatherers. Shredders process primarily coarse particulate organic matter (>1 mm diameter), while collector-gatherers process the finer fraction of this particulate matter. Both shredders and collector-gatherers depend upon microbial biomass and the byproducts of microbial metabolism for their nutrition. In middle-sized streams, communities shift to dominance by collector-gatherers and scraper-grazers. The development of periphyton as more light reaches the stream in a relatively open canopy characterizing middle-sized streams drives increased relative abundance of grazers. Farther down the continuum, an increase in water turbidity and a sharp reduction of relative importance of locally produced allochthonous detrital coarse particulate carbon are expected. The concept predicts that associated invertebrate communities in these larger systems will be dominated by collector-gatherers including filter feeders.

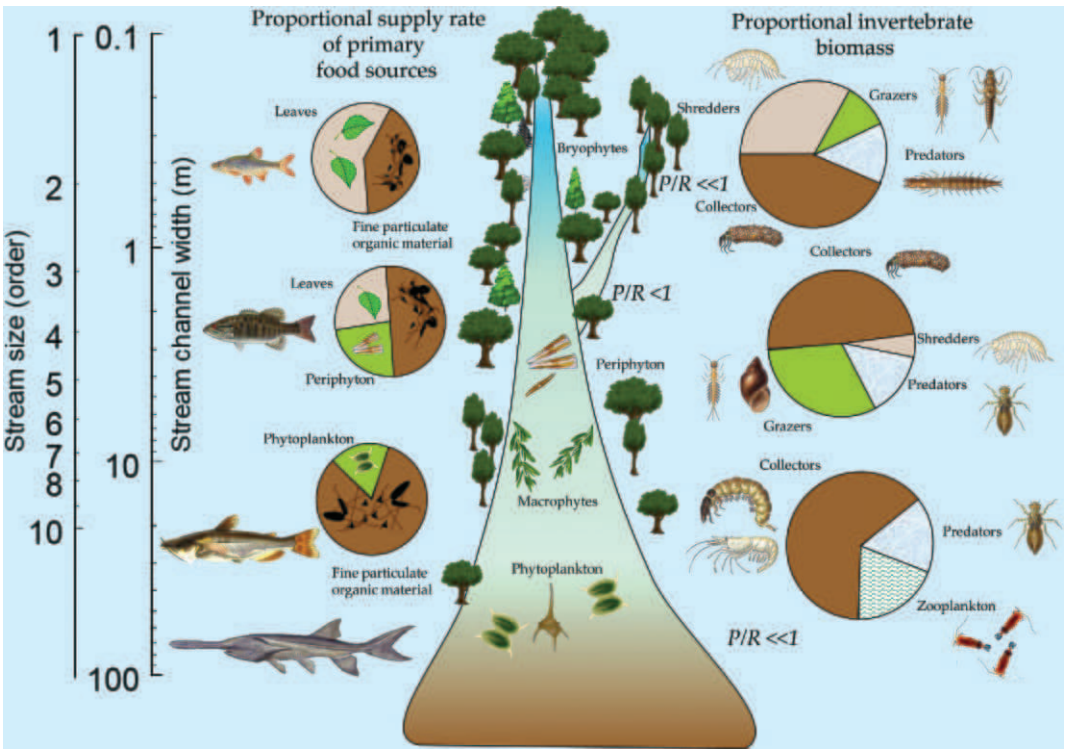

Fig. 1 A diagram of the River Continuum Concept. Modified from Vannote RL, Minshall CW, Cummins KW, Sedell JR and Cushing CE (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130–137.

The original paper, therefore, argues that the longitudinal pattern in invertebrate communities reflects an adaptation to optimize energy use. Thus, energy in the form of organic carbon that is not used in the upstream parts of the stream moves downstream and the downstream community benefits from it. Stated differently, the invertebrate communities have evolved to efficiently use the balance of organic carbon generated locally (either allochthonous or autochthonous) and that being transported from upstream.

The concept predicts fish communities will be dominated by invertivore species in small streams and headwaters, by invertivores and piscivores in middle-size streams and further downstream along the river continuum. In the largest sections of the river, often associated with low slope, planktivorous species will become more prevalent reflecting the semi-lentic (i.e., lake-like) nature of such waters. Many of the species in large rivers are adapted to high turbidity/low light conditions. The original concept also states that this shift in fish communities reflects changes in affinity to water temperature. Headwater and small stream communities exhibit low diversity and affinity to cool water, while further along the continuum, fish communities are more diverse with increasing affinity to warmer water.

The original concept

The RCC used five components to describe how it should apply to stream ecosystems. Here, we discuss components that "went forward" or received substantial attention in the scientific community, as well as those that were "set aside" or were less commonly examined.

Components that went forward and why

In general, these components went forward because they provided easily testable hypotheses. They are also simpler to understand, so they form the basis of teaching efforts and appeal to a wide range of types of scientists. The common image associated with the RCC found in many textbooks is based on these components (e.g., Fig. 1).

Stream size and ecosystem structure and function

This component is, by far, the most widely examined and has shaped much of the stream ecology research subsequent to the RCC. It stipulates that based on stream size (expressed as stream order) a longitudinal shift in loadings of carbon shape communities of invertebrates and fishes. The ratio of stream GPP/ER characterizes the longitudinal change in carbon inputs. When photosynthesis is the dominant pathway of incoming carbon the GPP/ER is expected to be greater than 1. This component has been tested in multiple ecoregions and on different types of rivers spanning temperate and tropical ecosystems (see, table of supporting case studies below, Table 1). Researchers have also thoroughly examined changes in community composition of fishes and invertebrates and shifts in their trophic guilds to validate the predictions of the RCC. The bioenergetic influences along the river continuum are also widely considered by stream researchers.

Ecosystem processing along the continuum

This component stipulates that unused or partially processed materials in a river ecosystem will be transported downstream where communities are structured to capitalize on the so-called "inefficiencies" of upstream processing. The fate of unprocessed material and the examination of retention, leakages, and downstream adjustments are topics often researched in the context of watershed functioning as a whole.

Table 1 A few important case studies.

Site	*Country*	*Latitude*	*Longitude*	*Main topic covered*	*Reference*
North Carolina	United States	35.05977°	−83.43022°	Regulation of stream detritus dynamic by macroinvertebrates	Wallace et al. (1982)
Pennsylvania	United States	39.752086°	−75.775300°	Organic matter inputs and turnover	Minshall et al. (1983)
Michigan	United States	42.405863°	−85.344884°	Organic matter inputs and turnover	Minshall et al. (1983)
Oregon	United States	44.232134°	−122.190617°	Organic matter inputs and turnover	Minshall et al. (1983)
Idaho	United States	44.123941°	−114.870759°	Organic matter inputs and turnover	Minshall et al. (1983)
Pennsylvania	United States	39.752086°	−75.775300°	Shift in metabolism from net heterotrophy to primary production downstream	Bott et al. (1985)
Michigan	United States	42.405863°	−85.344884°	Shift in metabolism from net heterotrophy to primary production downstream	Bott et al. (1985)
Oregon	United States	44.232134°	−122.190617°	Shift in metabolism from net heterotrophy to primary production downstream	Bott et al. (1985)
Idaho	United States	44.123941°	−114.870759°	Shift in metabolism from net heterotrophy to primary production downstream	Bott et al. (1985)
Quebec	Canada	50.384993°	−65.315187°	Carbon flux and standing stocks	Naiman et al. (1987)
North Carolina	United States	35.0598622°	−83.430618°	Invertebrate secondary production	Grubaugh et al. (1997)
Idaho	United States	44.123941°	−114.870759°	Invertebrate diets	Rosi-marshall et al. (2016)
Tennessee	United States	36.350833°	−85.565000°	Food webs	Curtis et al. (2018)

Components that were set aside

In general, these concepts are more difficult to understand than those that went forward. They are not as easily tested, as they require long periods of time (e.g., geomorphological change or biological evolution) or space for time substitutions for confirmation. They are not simple to explain graphically and thus have seen less interest in the research and teaching communities.

River ecosystem stability

This component stipulates that ecosystem stability may be viewed as the tendency to reduce fluctuation in energy flow and other variables of the physical system while the structure and function of the biota are maintained. We note that river ecologists and geomorphologists have developed a differing view of "stability" than in some other branches of ecology (e.g., Connell and Sousa, 1983). In general, the idea of a dynamic equilibrium in geomorphology suggests an overarching stability in the face of continuous change that can include catastrophic events such as intense floods (Schumm and Lichty, 1965). This view of a dynamic equilibrium suggests a sort of stability at longer periods used by river geomorphologists that strongly influenced the framers of the RCC. Ecosystem stability is therefore achieved by a dynamic interplay between physical and biological components that change along the river ecosystem from low to high stream orders. In highly fluctuating environments (e.g., fluctuation in temperature, dissolved oxygen concentrations, or water discharge), the biota may assume a critical role in stabilizing the energy flux through an entire system, whereas in highly stable environments the role of the biota in ecosystem stability will be reduced. Only more recently have stream ecologists approached system stability through the concepts of thresholds and alternative stable states (e.g., Dodds et al., 2010). Furthermore, most stream research on stability and disturbance does not directly reference the RCC. Finally, until recently ecologists have not considered stability or dynamic equilibria in the face of global climate change and the prevalence of invasive species that may come to dominate energy flows and change the predictions of the RCC.

Temporal adjustments in maintaining an equilibrium of energy flow

This component stipulates that stream ecosystems will tend towards uniformity of energy flow on an annual basis. Synchronized change in biological communities to temporal patterns of energy sources over an annual cycle controls uniformity of energy flow. Thus, biological systems move towards equilibrium by a trade-off between a tendency to optimize the use of energy inputs and a tendency towards a uniform rate of energy processing throughout the seasons. While this principle has been validated in streams of temperate forested regions (Minshall et al., 1983; Bott et al., 1985), little attention has been given to examining this principle in streams of other biomes. In general, most stream researchers do not produce annual budgets of carbon flux, so few data are available to test this idea. However, longer-term carbon flux estimates are becoming available (e.g., Roberts et al., 2007; Uehlinger, 2006), but only a few are available for larger rivers on an annual basis (e.g., Dodds et al., 2013), and these are not paired with estimates of production by different functional groups of animals. Factors that disrupt systems such that the species evolved in a particular area are no longer as well suited for the habitat (e.g., anthropogenic disturbances, directional climate change, species invasions) will interfere with this "equilibrium."

The invariance and the absence of succession in stream communities

This temporal equilibrium component stipulates that biological systems of each stream order are in equilibrium with the physical system at that point of the continuum. Temporal succession is not explicitly considered under the framework of the RCC, instead, biological systems present only a spatial shift along the continuum. Losses and gains of species occur primarily in low probability cataclysmic events and in response to evolutionary channel development. The lack of observation of successive biological stages is attributed to communities being a continuous heritage of species rather than an isolated temporal composition of species within a sequence of discrete successive stages. Thus, slow evolutionary processes shaping stream channel development are the main drivers of this invariance (or absence of succession) of stream communities at a non-evolutionary period. Little research has examined this principle to date, the main obstacles being the availability of extensive temporal data, and the numerous major alterations that have affected river ecosystems globally in the last century making it challenging to dissociate the contributions of natural and anthropogenic changes to the succession in stream communities.

Critique and support

The conceptual framework of the RCC received both critiques and support since its publication. Several papers supporting the overarching predictions of the RCC appeared soon after the original paper (see table of supporting case studies, Table 1). Minshall et al. (1983) documented the greatest inputs of allochthonous materials in headwaters in four stream networks across the United States. Bott et al. (1985) documented decreases in the relative importance of heterotrophic metabolism relative to primary production in four watersheds across the continental US as predicted, but noted that seasonal variation and that the shift happened at different stream orders. Rosi-Marshall et al. (2016) visited the same Idaho sites used in the previous two studies and re-sampled invertebrates. They found, as the RCC predicts, the greatest amount of reliance on leaf litter in headwaters. However, the authors also noted that there were substantially more autochthonous materials in the guts of stream invertebrates than predicted in the lower order streams. Lately, Curtis et al. (2018), tested the RCC predictions by explicitly linking consumer groups and found that the RCC predictions are integrated into the food webs, transcending, therefore, assemblage boundaries.

The main critiques can be grouped into four major divisions: (1) The limited applicability of the concept arguing that it was developed only for temperate river systems with forested headwaters and rivers flowing in relatively undisturbed landscapes, ignoring, therefore, the complexity of river systems globally. Many argued that the concept applies only to one type of river system excluding, just to cite a few, intermittent rivers, grassland rivers with reduced woody riparian, endorheic rivers, and tropical rivers. (2) The concept failed to integrate lateral habitats and floodplains and their contributions to both river functioning and biodiversity. Critics argued that the relative contribution of lateral connectivity becomes more and more important with increasing stream order and the contribution of lateral habitats in meandering and braided river sections, for example, cannot be ignored when conceptualizing river ecosystems. (3) geomorphological patterns and others that form the template for habitat often do not reliably follow the upstream-downstream continuum of the RCC and local processes may depend more heavily on local conditions than transport from upstream. (4) The concept did not account for the general framework of meta-community theory and identified only local environmental heterogeneity as the main driver for changes in the composition of stream communities.

The first critique, that the RCC only covers temperate forested headwater streams and does not apply to other biomes, is somewhat unfair. The Vannote et al. (1980) paper explicitly said that "At higher elevations and latitudes, and in xeric regions where riparian vegetation is restricted, the transition to autotrophy may be in order 1". This statement acknowledges that the authors understood that the patterns they were describing were potentially biome-specific. However, several critiques and modifications have addressed this issue. Soon after the original publication, Winterbourn et al. (1981) criticized the RCC by showing the limited applicability of the concept to New Zealand river systems with unpredictable rainfall patterns and low forest biomass. Barmuta and Lake (1982) responded to this critique that the lack of invertebrates following the expected patterns in New Zealand rivers could have been related to unusually high disturbance rates in the rivers studied by Winterbourn et al. (1981). Dodds et al. (2004) modified the RCC for application to grassland streams, and this approach was taken further subsequently, to predict the way that biomes modified the predictions of RCC (Dodds et al., 2015). Greathouse and Pringle (2006) studied freshwater invertebrates in tropical streams of Puerto Rico. They found that predators, scrapers, and shredders followed the prediction of the RCC patterns, but that filterers and omnivorous freshwater shrimps did not. They suggested that spatially restricted predation on the shrimps by fishes could explain part of the deviation from the patterns expected by the RCC. Tomanova et al. (2007) found patterns of invertebrate structure and function mostly followed the RCC in Bolivian streams once the corrected for altitude.

The second avenue of criticism, that the RCC failed to integrate lateral habitats and floodplains and their contributions to both river functioning and biodiversity has been discussed by several researchers. Sedell et al. (1989) noted the RCC did not predict the importance of side habitats (e.g., backwaters and weakly connected oxbow lakes) connected to large rivers that are vital habitats for fishes and important locations of high ecosystem productivity. Junk et al. (1989) formalized the idea that large rivers experience high flows that connect lateral habitats to the main channel, further developing ideas of ways that large rivers are not completely explained by the RCC. However, materials carried into lateral habitats can originate from upstream.

The third avenue of criticism, that geomorphological patterns that form the template for habitat often do not reliably follow the upstream-downstream continuum of the RCC, and that local processes may depend more heavily on local conditions than transport from upstream has also received consideration. This avenue relates to the second avenue discussed in the last paragraph. Minshall et al. (1985), further refined by Montgomery (1999), suggested a "process domain" framework could allow the application of geomorphological considerations at various scales to make the RCC more broadly predictive. Thorp et al. (2006) took this idea further in their Riverine Ecosystem Synthesis (RES). They viewed streams as nested hierarchies of patch mosaics, with ecosystem dynamics resulting from a composite of intra and inter patch processes. Functional process zones, as identified in the RES, controlled therefore local processes. They stressed the non-equilibrium processes that result in "quasi-equilibrial metastable states". This synthesis led to 14 predictions on ecological characteristics in streams. This synthesis allows for upstream linkages upon which the RCC depends, but it focuses much more heavily on local conditions and views ecological processes in rivers and streams as substantially more insular than the RCC does. The degree to which local processes dominate relative to control by position in the watershed and location on a continuum from headwaters to large rivers is still an active area of research in stream ecology. More recently, Maasri et al. (2021) and Collins et al. (2018) have shown that despite considering rivers through a discreet model like the RES, the longitudinal and progressive downstream gradient of responses to abiotic and biotic features will be observed in communities and processes, thus forming a partial biotic continuum as predicted by the RCC.

The idea of breaks in the RCC as spawned a number of publications on the river "discontinuum" For example, when a tributary enters a stream, the discharge downstream is abruptly greater (Poole, 2002), and such tributaries create unique habitats above and below the main channel (Benda et al., 2004) disrupting the concept of a smooth continuum. Natural features such as beaver dams (Burchsted et al., 2010), lakes (Jones, 2010), and subsurface stream flow (Di Lorenzo et al., 2013) have all been described as discontinua. These researchers present a view that is closer to the RES than the RCC.

The fourth, and most recent, avenue of criticism states that the RCC failed to integrate the contribution of the theoretical framework of meta-community ecology in explaining changes in communities along the continuum (see review by Doretto et al., 2020). This avenue needs to be considered with respect to the relatively recent rapid development of research in meta-community theory. Meta-community theory postdates the RCC (see, Hanski, 1994, Leibold, 1995, or Leibold et al., 2004), with only a few exceptions referring to the role of dispersal limitation or stochasticity as drivers of ecological communities that can be dated to the early 20th century (Chase and Myers, 2011).

Some further modifications to the RCC have been proposed in addition to the four areas of criticisms to broaden the applicability and scope of inference of the RCC. Statzner and Higler (1985) proposed to simplify the concept and reduce its theoretical ballast by excluding components that are either unexpected, unsupported by evidence, or restricted to particular

geographic areas. Those components dealt mainly with the absence of succession in stream ecosystems, the temporal sequence of species replacement, or longitudinal patterns of biodiversity, shifting, therefore, the RCC towards an energetics based concept, with emphasis on photosynthesis, respiration, and on the status of organic matter and corresponding organization of communities. This suggested simplification was prescient, and Statzner and Higler (1985) suggested dropping the components that we listed above as "not going forward"; it appears that the stream research community has taken this recommended approach for the most part.

The RCC developed in a time when ecologists often focused on "natural" conditions and abiotic and biotic drivers of stream networks as relatively constant over time (e.g., no climate change or invasive species). However, human impact has increased substantially as we move into the Anthropocene. Dams are ubiquitous in watersheds of most areas with human inhabitation, and Stanford and Ward (2001) modified the RCC by considering how human-constructed impoundments disrupt the continuum. While reservoirs strongly influence the continuum, other features can as well. Anthropogenic influences can disrupt or enhance connectivity by activities such as water abstraction drying stream channels, channelization of flows, and construction of impoundments.

Additionally, deforestation, row crop agriculture, and urbanization can lead to large disruptions in the expected continuum by altering flow, riparian conditions, and natural sediment regimes. The RCC does at least provide a framework under which to understand some implications of these changes to river ecosystems.

Conclusion

The RCC has received great attention, in part, because it took a landscape view of how position in the watershed influenced stream ecosystems. River ecologists were primed to receive this view because of the obvious influence of the watershed on aspects such as water quality, discharge, flood intensity, and biotic components (Hynes, 1975). These types of ideas still have relevance. For example, the meta-ecosystem framework (Loreau et al., 2003) was proposed as a new avenue for landscape ecology, but the RCC already fits into that framework in that it includes multiple linked systems that are spatially distributed and have specific interactions based on how they are linked. The second reason that the RCC has been successful is that the components that went forward are conceptually simple and based on obvious abiotic properties such as the fact that stream channels generally get wider further down in the watershed and flow moves materials downstream. The RCC provides testable hypotheses, and they are easy to modify as new approaches have arisen. Even if some of the specifics do not hold (e.g., streams are not all in the temperate biomes originally considered), it is easily modified based on basic geomorphological and ecological principles (e.g., riparian canopies can intercept light, the balance of metabolism in ecosystems, functional adaptations of stream invertebrates) to provide a new framework applicable to local conditions.

Knowledge gaps

- How does the continuum vary with the biomes that rivers and streams are embedded in?
- What is the relationship of the continuum with local processes such as floodplain dynamics and functional processing zones?
- What is the influence of humans on the expectations/predictions of the RCC, including land cover/land use change, climate change, and eutrophication?
- Does biogeography influence the RCC (e.g., do areas with functional groups of organisms with different evolutionary history display different patterns)?
- Do any of the less studied predictions of the RCC hold (e.g., can paleoecology get at the idea of animals in ecosystem optimizing energy flow)?
- How does the RCC relate to meta-community concepts?

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The Nutrient Spiraling Concept

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Spiraling length The sum of uptake length and turnover length, that is, the total distance a nutrient atom travels as it completes a cycle from mineral form to organic form and back to mineral form. **Turnover length** The average distance a nutrient atom travels in organic form before being mineralized. **Uptake length** The average distance a nutrient atom travels in dissolved, inorganic (mineral) form in the water column before being immobilized by autotrophic or heterotrophic processes.

Introduction

Nutrient spiraling in streams refers to the coupling of nutrient cycling and hydrologic transport. Nutrients do not really "spiral," but the analogy is a useful way to study the dynamics of nutrients such as nitrogen and phosphorus in streams. The concept was introduced by Webster (Webster 1975; Webster and Patten 1979) with the idea that the intensity of nutrient cycling in a stream, or the "tightness" of the conceptual spiral, reflects the activity of streambed biota in capturing, using, and recycling nutrients that otherwise would be carried downstream with the current. Newbold and colleagues (Newbold et al., 1981; Elwood et al., 1983) proposed that this intensity could be expressed as the downstream distance required for a nutrient atom to complete one loop of the spiral, which they termed the spiraling length, S, and which consists of the sum of an uptake length, S_W, and a turnover length, S_B (Fig. 1). In any ecosystem, nutrients in bioavailable forms are used by organisms, pass through food web components, and return to bioavailable forms through excretion and decomposition, thus completing a conceptual nutrient "cycle." In a stream, the flow of water ensures that a nutrient atom on completing a cycle is transported some distance downstream, so that its flow through the ecosystem may better be conceptualized as a spiral, or helix, stretched in the downstream direction.

In all but the largest rivers, most of the biological activity occurs on or in the streambed. Uptake of nutrient from the flowing water by bottom-dwelling organisms slows or even stills the downstream journey of the nutrient. Where a limited nutrient supply supports an active streambed biota, spiraling length is short and nutrient atoms cycle many times within a reach or river network. A large nutrient supply and/or low nutrient demand yields long spiraling lengths and little recycling. The most common practical use of the spiraling concept lies in measuring the portion of the spiraling length termed the uptake length. From a measurement of uptake length, the assimilation of a nutrient by streambed biota can be calculated. Less common in the literature are estimates of turnover length, although notable exemptions exist, many associated with organic carbon turnover (e.g., Newbold et al., 1982; Minshall et al., 1992). This chapter presents the equations underlying the spiraling concept, then turns to the practicalities of measuring spiraling, its application to the modeling of nutrient dynamics, and finally to challenges for future work.

Stream spiraling metrics

For idealized conditions, stream spiraling metrics were defined as follows (Newbold et al., 1983; Newbold, 1992):

Uptake length, S_W, is the distance traveled by a nutrient atom in dissolved, inorganic (or mineral) form before uptake (biological assimilation) and is given by

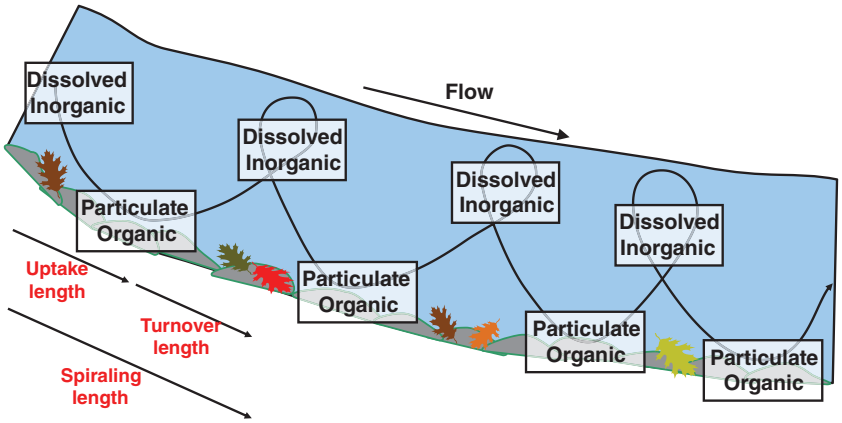

Fig. 1 Nutrient spiraling in streams consists of uptake length and turnover length, which together make up the spiraling length.

$$S_W = F_W/(U * w) \tag{1}$$

in which F_W is the downstream transport of nutrient in a dissolved mineral form available for uptake, U is the uptake flux per unit bed area of stream, and w is the stream width.

Turnover length, S_B is the average distance traveled in biological form, including passage through the food web, prior to mineralization via excretion or decomposition, and is given by:

$$S_B = F_B/(R * w) \tag{2}$$

in which F_B is the downstream transport of nutrient in living or dead organic matter, and R is the flux per unit area of nutrient mineralization, i.e., the return to available form.

The total downstream transport, F, *is* $F_W + F_B$. If we assume that the stream is in steady state and is without lateral losses and gains, then $U = R$ and, combining Eqs. (1) and (2), the spiraling length, S, becomes:

$$S = S_W + S_B = F/(U * w) \tag{3}$$

Eq. (3) expresses the basic idea that spiraling length is the distance of stream in which all of the transported nutrient is cycled, on average, one time.

The simplifying assumptions behind Eqs. (1)–(3) are, in addition to steady state ($R = U$) and the absence of lateral losses and gains, that all of the measured nutrient actively cycles and that all of the uptake, U, is supplied by nutrient in inorganic form. The constraints of these assumptions, together with a number of measurement challenges, have limited experimental measurement of total spiraling length to a single study (Newbold et al., 1981, 1983) in which it was possible to trace injected radioisotope through the food web. This study found that the uptake length accounted for 87% of the spiraling length, suggesting that uptake length alone provides an approximation to spiraling length. However, this study did not quantify storm-related transport of particulates, which would likely have increased turnover length if estimated as a long-term average. However, this work was conducted in a first-order, spring-fed stream and turnover length may account for an increasing proportion of spiraling length as stream size and/or seston concentrations increase. Global budgets suggest that a significant portion of nitrogen and phosphorus exported from rivers to the ocean occurs in particulate forms (e.g., Meybeck, 1982) supporting the hypothesis that turnover length may become increasingly important along the river continuum.

Measuring nutrient spiraling in streams

The uptake length of a single inorganic compound or ion, such as PO_4^{-3}, NH_4^{+1}, or NO_3^{-1}, can be measured by adding the nutrient or an isotopic tracer to the stream and observing its loss from the water column as it travels downstream. Assuming that the nutrient in the water column is well mixed and that uptake by streambed biota removes a constant fraction of the over-lying nutrient per unit distance traveled downstream, the longitudinal loss of added nutrient or tracer, M, can be described by a simple exponential loss function:

$$\frac{dM}{dx} = -k_L M \tag{4}$$

which, upon integration yields:

$$M_x = M_0 e^{-k_L x} \text{or } \ln M_x = \ln M_0 - k_L x \tag{5}$$

where M_X and M_0 are the quantity of added nutrient or tracer x meters downstream and at the addition site, respectively, and k_L is the longitudinal loss rate in units of inverse length. Uptake length (S_W) is equivalent to $1/k_L$.

The uptake flux (U) is calculated from S_W as:

$$U = \frac{QC}{wS_W} \tag{6}$$

where Q is stream discharge and C is the nutrient concentration in the stream water. Of the metrics used to describe cycling in streams, the uptake flux is the most generic descriptor in that equivalent terms exist for all ecosystems.

S_W is often converted to a third spiraling metric, the vertical transfer velocity, using:

$$v_f = \frac{Q}{wS_W} \tag{7}$$

The resulting parameter, a mass transfer coefficient often referred to as the uptake velocity (v_F), describes a theoretical velocity at which nutrients "move towards" locations of assimilation (e.g., stream bed). Solving Eq. (6) for S_W and substituting into Eq. (7) illustrates the relationship between v_F, U, and C.

$$v_f = \frac{Q}{w}\frac{wU}{QC} = \frac{U}{C} \tag{8}$$

Because Eq. (8) indicates that v_F reflects the relative magnitude of biotic use (as represented by U) to nutrient availability (C), some have referred to v_F as a descriptor of retention efficiency (e.g., Davis and Minshall, 1999).

Together, these three terms (S_W, v_f, and U) form what has been referred to as the "metric triad" of dissolved nutrient dynamics (Webster and Valett, 2006). Each metric has its utility in the study of nutrient cycling in streams. U represents a stream's use of nutrients on an areal basis, which facilitates cross-ecosystem comparisons. S_W quantifies the spatial scale associated with nutrient assimilation. Lastly, v_F represents the relative efficiency with which a stream takes up nutrients to which it's exposed. Clearly, no one variable is best suited for the suite of questions surrounding nutrient spiraling and each member of the metric triad has its place in examining solute dynamics in streams.

The simplest method for measuring nutrient uptake is to do a short term nutrient addition. (e.g., Stream Solute Workshop, 1990). For large streams, researchers have used a pulse release technique (e.g., Tank et al., 2008) where a slug of nutrient is added and followed downstream. The problem with both the injection and pulse release techniques is that they raise the nutrient concentration, and if nutrient uptake is a function of concentration, then uptake is not the same as under ambient conditions (Mulholland et al., 1990, 2002; Dodds et al., 2002). It is likely that both methods often saturate uptake. Payn et al. (2005) developed a method of injecting nutrient at different levels and then extrapolating back to the ambient level, but this method had not been used very successfully (e.g., Earl et al., 2006). Covino et al. (2010b) also suggested a method that used the varying concentrations from a slug release, but the downstream concentrations do not reflect the actual concentrations passing over the streambed.

Alternative methods of measuring nutrient spiraling are to use radioactive or stable isotopes. The use of these tracers results in negligible changes in the ambient nutrient level. The problems with isotope methods are the hazards of using radioactive materials and the high cost of obtaining and analyzing stable isotopes. Examples of using these techniques are described below.

Case studies of nutrient spiraling in streams

Elwood, Newbold, Mulholland, and their colleagues used radioactive isotopes (^{32}P and ^{33}P) to measure phosphorus spiraling in Walker Branch, TN (Newbold et al., 1983; Mulholland et al., 1985, 1990). By combining the results from their field studies with a computer model, they quantified phosphorus fluxes through the food web and found that spiraling length varied seasonally, being shortest after autumn leaf fall when decomposing leaves exerted the greatest P demand.

Mulholland et al. (1997) also used radioactive phosphorus to compare the role of hyporheic zones in nutrient dynamics in Walker Branch and Hugh White Creek, NC. As far as we know, this was the last study to use field additions of radioactive materials to study stream nutrient spiraling, although more recent studies have used ^{14}C labeled particles to estimate particle transport distance (e.g., Thomas et al., 2001).

The spiraling concept was the basis of the Lotic Intersite Nitrogen eXperiments (LINX). In LINX1, researchers used 6-wk additions of ^{15}N-labeled ammonium to compare nitrogen processes in 11 predominantly undisturbed headwater streams extending from Alaska to Puerto Rico and spanning desert to tropical forest ecosystems (Peterson et al., 2001; Webster et al., 2003). They found that small streams play an important role in nitrogen removal from the water column and that nitrogen uptake is dominated by biological processes, either heterotrophic or autotrophic.

In the second LINX study (LINX2), ^{15}N-labeled nitrate was used to compare nitrogen processes in 72 streams across multiple biomes and with undisturbed, agricultural, and urban land use (Mulholland et al., 2008). Results showed that nitrate uptake was largely related to instream photosynthesis and that denitrification was related to heterotrophic activity (Hall et al., 2009; Mulholland et al., 2009). Both biotic uptake and denitrification increased with stream nitrate concentration, but the efficiency of uptake

and denitrification declined as concentration increased, reducing the proportion of in-stream nitrate removal. Land use was an important control on nitrate uptake and denitrification, primarily due to its effect on nitrate concentration. Greater agricultural and urban land use also resulted in higher in-stream photosynthesis and consequent greater nitrate uptake.

Models of nutrient spiraling

Studies of stream nutrient spiraling have demonstrated the importance of linking computer models with field research. Civil engineers have long been using models that incorporate biological processes with downstream transport (Streeter and Phelps, 1925). The following are just a few examples of nutrient spiraling models of stream ecosystems. The first stream ecosystem models were used to calculate components of stream dynamics. Webster (1983) used a spiraling model to determine the role of stream insects in detrital processes, and Newbold et al. (1983) developed a model that they used to estimate uptake and turnover lengths of phosphorus. In their study of the Kuparuk River (AK), Wollheim et al. (1999) demonstrated the importance of coupling modeling and field research. Similarly, McKnight et al. (2004) and Gooseff et al. (2004) coupled field studies with computer models to study nutrient dynamics in Antarctic streams. As part of the LINX2 study, Mulholland et al. (2008) used a spiraling model to demonstrate the relative roles of small versus large streams as nitrate sinks. Lin and Webster (2012) fit a model, which included concentration dependent uptake, to the data from the Snake River slug release (Tank et al., 2008). They concluded that fitting release data to a fully dynamic model may be a useful way to understand nutrient dynamics in streams. Recently, Webster et al. (2016) developed a spiraling model, which included nitrogen, phosphorus, and carbon. They used this model to make predictions about nutrient competition and mutualism between stream autotrophs and heterotrophic microbes.

Challenges of stream nutrient spiraling studies

1. Developing methods that are less hazardous and less expensive than radioactive and stable isotopes.
2. Finding tools to study important nutrients, such as base cations and sulfur. Essentially all spiraling research has been with nitrogen and phosphorus, though the original idea for spiraling came from a study of calcium and potassium (Webster, 1975).
3. Separating biotic and non-biotic processes such as sorption to inorganic surfaces and chemical precipitation. For example, Covino et al. (2010a) suggested that physical retention dominated nitrogen retention in a stream in Idaho.
4. Finding ways to separate surface and hyporheic processes (Mulholland et al., 1997). Nutrient retention in a stream may be significantly influenced by hydraulic retention (Valett et al., 1996), which occurs when water leaves the main water column and enters flow that moves more slowly (Morrice et al., 1997). Flow paths of this type extend residence times by prolonging contact between sediment biota and transported materials. Several studies have shown greater nutrient retention is streams with more surface water—hyporheic water interaction (e.g., Martí et al., 1997; Mulholland and DeAngelis, 2000). Thomas et al. (2003) developed a method called the Ratio Partitioning Method to estimate the amount of nutrient cycled through the hyporheic zone.
5. Understanding and modeling the relationship between biotic uptake and stream water concentration. The relationship is probably linear under very low concentrations but follows some saturation function as concentration increases. Lin and Webster (2012) used a Monod function for uptake, and Webster et al. (2016) used a similar function for algal nutrient uptake but modified it with an internal stores limitation (Droop 1973, 1974).
6. Recognition that nutrient spiraling is not as simplistic as defined above. Some nutrients can exist in multiple mineral forms (e.g., nitrate and ammonium), which can have different uptake lengths. Also, nutrients exist in various organic forms, and incorporating the various turnover processes into stream dynamics, including turnover by higher organisms (insects, fish), is a major challenge to stream nutrient studies. While the downstream velocity of nutrients bound in organic particles may be very slow, turnover time can be very long. As a result, turnover length can be long and a major component of total spiraling length (e.g., Dodds et al., 2000).

Conclusions

Streams are longitudinally structured ecosystems connected by the downstream flux of water, solutes, particles, and organisms. Advancing our understanding of stream ecology will require studies that directly address the unique template of stream ecosystems. At the same time, streams are examples of open ecosystems in which questions of general ecological theory can be addressed. The nutrient spiraling concept provides a powerful tool for meeting these challenges.

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Stream Geomorphology

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This is an update of J.P. Bravard, F. Petit, Geomorphology of Streams and Rivers, in Encyclopedia of Inland Waters, edited by Gene E. Likens, Elsevier inc., 2009, https://doi.org/10.1016/B978-012370626-3.00043-0.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Alluvial channel Channel of stream flowing through erodible alluvium (i.e., river transported sediment).
Bankfull flow The flow that just fills the morphological channel up to the banks (sometimes conflated with the flow that occurs as an annual peak every 1.5 years, which is not necessarily equivalent).
Bedrock channel River flowing over fixed bedrock.
Channel incision Erosion of the riverbed and consequent channel lowering.
Channel pattern Form of the river channel as viewed from above.
Effective discharge The flow that transports the most sediment over time.
Episodic channel A channel in Mediterranean or other semiarid climate that goes many years without experiencing channel forming flow, but occasionally experiences a powerful flash flood that is capable of rearranging the bed and banks.
Longitudinal profile Plot of streambed elevation over distance.
River's trajectory The geomorphological river changes that occur over time.
Sediment budget A compilation and accounting for the magnitude and spatio-temporal distribution of sediment sources, sediment transport processes and deposition in a river network.
Sediment caliber The size of sediment particles (clay, silt, sand, gravel).

Water and sediment flow shape rivers

Stream (or "fluvial") geomorphology refers to the forms of rivers and streams, and the processes that create and maintain them. Stream channels and their floodplains are formed by the flow of water and the sediment it transports, both acting on the landscape through which they flow. Streams carry the water and sediment derived from a drainage area or catchment, and the drainage area is the most commonly used measure of the scale of a stream. Streams may also be ranked within the river network by their "stream order," which is determined by the relative number of tributaries that join together to form the stream. A small headwater stream would be a first-order stream, while downstream, a large river might be of fourth or fifth order. A plot of streambed elevation over distance (like a longitudinal slice along the river) is known as a longitudinal profile, while a transect through the river perpendicular to the flow direction is a cross section. Channel pattern refers to the shape of the channel as viewed from above, such as meandering or braided channels, described below.

We can distinguish first between two broad categories of streams: those that flow over bedrock, termed "bedrock channels" and those that flow through erodible alluvium (river transported sediment), termed "alluvial channels," usually flanked by regularly inundated flat surfaces termed "floodplains." The dimensions and shape of alluvial channels depend upon patterns of flow and sediment transport, including the volume and sizes of sediment moved (Church, 2006). Because changes in flow or sediment load can result in changes to alluvial channels, these channels have attracted most attention from researchers and managers. However, many alluvial channels have occasional bedrock outcrops, which can exert strong influence on the channel.

The quest for the channel-forming flow

One of the driving questions in fluvial geomorphology in the latter half of the 20th century was determining the flow that corresponded to the "bankfull" channel, i.e., the flow that just fills the morphological channel up to the banks. The underlying concept of effective discharge was established by Wolman and Miller (1960), who argued that geomorphic work could be estimated as the product of magnitude and frequency. That is to say, we know a big flood can erode, move, and deposit more sediment than a moderate flood, but the moderate floods occur more frequently. So, which moves the most sediment (i.e., has the greatest influence on channel form) over time?

The 1950s and 1960s saw the development of classical concepts in fluvial geomorphology, based on observations in humid Atlantic-climate landscapes and snowmelt dominated rivers of the Rocky Mountains, whose channel dimensions correspond to more frequent floods, often taken to be the Q1.5, which is the flood that occurs (as an annual maximum) 2 years out of three (Leopold et al., 1964), rather than larger floods. For these channels, the Q1.5 was also found to be the "effective discharge," the flow that moves the most sediment over time. Wolman and Miller (1960) used the analogy of a wood-cutting contest among a giant, a man, and a dwarf, with the man—representing the frequent, moderate flood—cutting the most wood over time because he spends more time cutting than does the giant so the cumulative effect of his moderate efforts exceeds the cumulative effect of the giant's stronger but shorter efforts. Over time, the Q1.5 was widely assumed to be equivalent to the "bankfull" flow.

Episodic channels

The notion that the active channel is shaped by the 1.5-year flow is an easily comprehended idea, and one that has clearly fixed itself in the mindset of natural scientists in allied fields and among restoration practitioners (NRC, 1992). However, in climates with more variable hydrology, such as Mediterranean and semi-arid climates, less frequent floods have a greater role in shaping the channel, as discussed by Kondolf et al. (2013). As noted by Wolman and Miller (1960, p.60), "The evidence also suggests that the more variable the regimen of flow of the stream, the larger the percentage of total sediment load which is likely to be carried by infrequent flows." Thus, it is the large, infrequent flood—the "giant"—that will accomplish the most geomorphic work in Mediterranean and semi-arid climates. These have been termed *episodic* channels because they can go for years will little geomorphic work going on, but suddenly in a year with a large flood, large changes result. For example, on the Santa Clara River, California, of the roughly 57.6 million tons of sediment load measured at Montalvo from 1968 to 1975, 55% was moved in only 2 days in the years from 1928 to 2000, and 25% was transported in just 4 days (Warrick, 2002). In this episodic channel, the effective discharge is not the Q1.5. Rather, the channel is formed primarily by larger, infrequent floods (Downs et al., 2013), consistent with the observations of Wolman and Gerson (1978). While smaller features adjacent to a perennial baseflow channel (termed the *lit mineur* in French) can be shaped by smaller, frequent high flows, the overall form of the active channel (the *lit majeur*, Bravard and Petit, 1997) in Mediterranean-climate rivers is shaped by larger floods. Despite Wolman and Gerson's (1978) admonition that in drier climates, it is the larger, less frequent floods that shape the channel, and despite research demonstrating that bankfull channels very frequently did not correspond to Q1.5 (Williams, 1978), the notion that river channels are shaped by the 1.5-year flood became widely accepted, and has been a common basis for stream restoration designs (NRC, 1992).

The ecological implications of episodic channel processes are profound. Unlike the bottomland of a stable, humid-climate river, where a clearly defined channel is flanked by stable stands of mature riparian vegetation, the channel substrate in an episodic river channel is "renewed or rejuvenated abruptly, at intervals shorter than that typically needed for a mature woodland to develop" so that the banks and islands are dominated by early successional-stage vegetation (Hecht, 1994). These channels are typically disturbed at intervals of one to several decades, when they experience sudden influxes of sediment (as from landslides and debris flows) during floods, and especially after wildfires. The valley floor may be reworked beyond the limits of the current riparian vegetation, with erosion commonly eating into the depositional aprons at the toe of slopes. For months or years after such a sediment influx, pools can be filled and riffles buried, but in subsequent years, flows scour out the deposits, and pools reemerge or reform within the rearranged channel (Hecht, 1994). From a flood-risk management perspective, episodic channels present challenges, because floods are so infrequent that inhabitants may not have experienced a flood and do not understand the risks of living in a flood zone, and certainly not the ultra-hazardous flooding that occurs in semi-arid regions (Sanders and Grant, 2020). In many cases, land developers, elected officials, and government agency staff responsible for land-use decisions may not even recognize dry washes as active river channels (Stein, et al., 2011).

River forms and processes

When viewed from above, one of the most apparent differences among alluvial channels is the contrast between single-thread meandering and braided channel patterns (see Fig. 1 for examples). The latter refers to alluvial channels where multiple low flow water channels (i.e., the area where water flows most of the time) exist and one channel is not predominant, in terms of size, over the others. Braided rivers are characterized by relatively high rates of coarse sediment transport, and the islands in between the channels are ephemeral features that change and disappear as the channels shift. Single-thread channels include iconic meandering rivers, which have well-developed bends, with the deepest water, highest velocities (and highest rates of erosion) on the outside of

the bends. The inside of the bend is a site of deposition, with development of a sandy (or gravelly) point bar. The typical meander bend provides a wide range of habitats for aquatic and riparian organisms: at the outside of meander bends are deep pools for large fish and vertical silt banks in which bank swallows make their nests, on the point bar are secondary channels with shallow waters providing habitat to small fish and fresh surfaces on which riparian vegetation can establish.

For decades geomorphologists have asked what drives the fundamental difference in river functioning between single-thread meandering channel and multi-thread systems? The variety of existing river channel patterns and their functioning are nicely summarized in the classification scheme by Church (2006), summarized in the diagram of Fig. 1. This synthesis draws upon prior work by many authors (e.g., Brierley and Fryirs, 2005; Buffington and Montgomery, 2013; Gurnell et al., 2016; Kondolf et al., 2003; Schumm, 1977, 1985). The main logic beyond this scheme is that river forms and patterns are generated by specific drivers, namely: channel gradient, amount of sediment supply, and grain size (caliber) of the sediment supply.

At the top of Fig. 1 we can observe river-beds composed predominantly by cobbles (64–256 mm) and gravels (2–64 mm). In case of limited sediment supplied and greater channel stability, the river will have low sinuosity, single water channel, and alternated exposed sediment bars. Increasing its sediment supply (moving to the right in the diagram in Fig. 1) will develop larger and more frequent central sediment bars, which will divert water in multiple water channels. When one water channel remains larger than the others the river pattern is often referred as wandering. If sediment supply will still increase and channel stability will allow a widening of the active channel, it will develop a fully braided morphology. Similar reasoning applies also for river-bed composed mostly by sediment calibers such as sand (62.5—2 mm) or finer fraction. In this range of sediment fraction sinuosity is more accentuated, and increasing the sediment supply will develop more and more stable exposed sediment bars that will be colonized by stable vegetation. These morphological vegetated units within the channel are termed islands (see Fig. 2 for an example), and if islands are common, the channel pattern is considered anastomosed (see bottom right of Fig. 1).

Sediment supply, the amount of sediment contributed to a river reach from the upstream river network, is influenced by the topography and geology of the river basin, its land uses, presence of dams (which block sediment from moving downstream) and any sediment management measures implemented. Sediment caliber refers to the size of sediment particles (clay, silt, sand, gravel), which in turn affects the mode of transport. For example, gravel moves mostly as bed load (rolling, sliding or bouncing on the river bed), whereas sand or finer sediments move mostly in suspension in the water column. Type of transport and sediment sizes define the fluvial forms that can be generated: gravel-bed rivers develop periodically sequences of pools, areas of deep water and greater erosion (energy build-up due to less friction), and riffles, areas of shallow water created by deposition of coarse sediment during high flows. Whereas in sandy rivers sediment moves downstream through the development of sequences of dunes in the river bed. Channel stability is determined by the sediment caliber, the compactness of the river bed and bank material, and its lithology (rock type). These properties determine the erodibility of the river channel and then how easily it can widen.

Large wood also plays an important role in determining river channel form and nodes of sediment deposition (Wohl et al., 2015). Limbs or entire trees are transported by the flow until they come to rest, often in a debris jam with other such pieces, where they can then induce deposition of sediment upstream and downstream, create deep scour holes, and divert flows laterally. The result is complexity of channel forms and resultant habitats. Conventional river management practices have usually involved

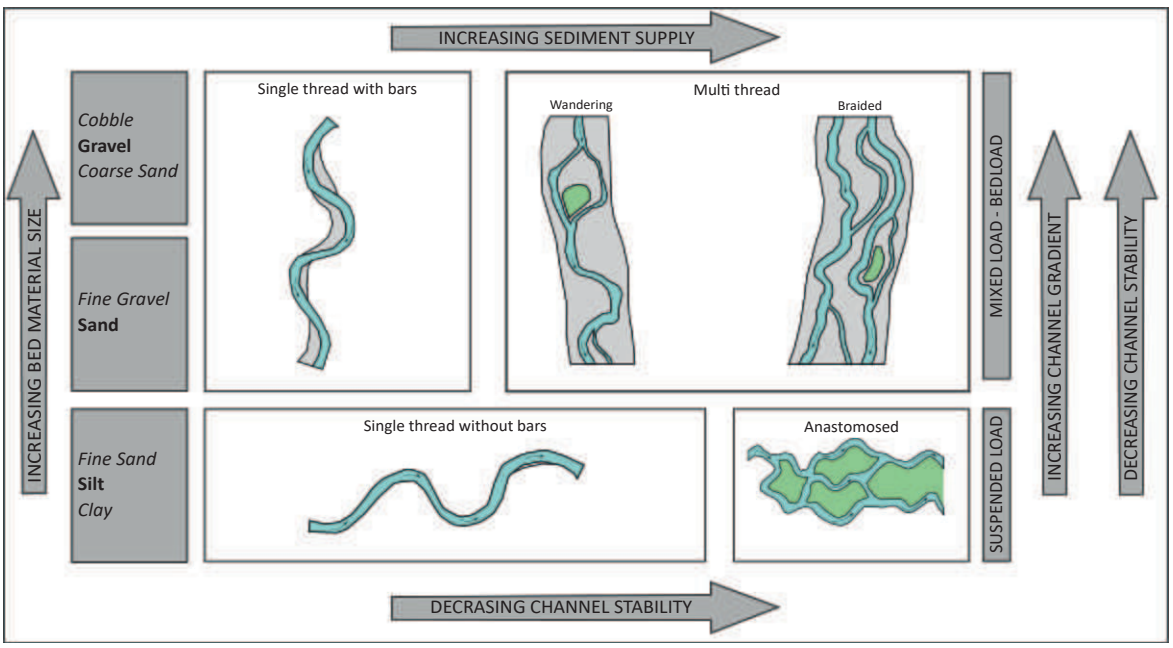

Fig. 1 Diagram showing the association of alluvial river channel form and the principal governing factors. Classically named channel types are located at appropriate positions within the diagram. Grey patches refer to exposed sediment bars within the active channel, whereas green areas to vegetated islands.

Fig. 2 The Tagliamento river in Italy, in a braided reach: water channels, floodplain, active channel, island and hillslope are labeled on the image. The white dashed line represents the area of transition between the two units. View looking upstream. Photo by Simone Bizzi (December 2020).

removal of large wood to reduce the chance of debris jams on bridges and other infrastructure, but with increasing recognition of the importance of large wood for the ecology of many rivers, management is evolving to leave wood in channels to the extent possible.

From a perspective of fluvial geomorphology, a river corridor can range from a narrow bedrock canyon to a wide valley bottom with a floodplain, in which the active channel can migrate up to the confining hillslopes along the valley margins (see Fig. 2). Floodplains are morphological units built of sediment transported and deposited by alluvial rivers. Within the active channel are channels carrying water and unvegetated or sparsely vegetated sediment bars. In other words, the active channel includes all those morphological units which are reworked regularly by frequent floods and for this reason stable and mature vegetation cannot grow because seedlings are regularly scoured by seasonal floods. The floodplain topographic level is typically slightly higher than the top of sediment bars in the active channel. In the area of transition between the active channel and the floodplain (see Fig. 2, the white dashed line between the two units) fine sediments are deposited by regressing floods, which allows younger vegetation to grow and to start creating riparian woods. Some exceptions could be represented by severely aggrading river reaches where for some period the active channel is on average higher than the surrounding floodplain. Over time the river moves laterally building its floodplain. These processes are also specific to every channel pattern and floodplains classification have been proposed as well in literature (Nanson and Croke, 1992). For instance, in case of a single-thread sinuous river, the floodplain is built by migration of a meander bend, which results from erosion of the cutbank and concomitant growth of the opposite point bar and associated overbank deposits. Whereas, in a braided river the floodplain is formed largely by the abandonment and infilling of braid channels.

Quantifying river processes

From an energy-balance point of view, river patterns are the results of a natural necessity to compromise between the available energy to transport sediment, the available material to be transported, the mode by which this material is transported, and the available space to do it (channel stability). Channel gradient determines together with the amount of water flow the energy that a river possesses to transport sediment. It can be expressed very simply as stream power (Bagnold, 1977; Bizzi and Lerner, 2015):

$$\Omega = \gamma\, QS \tag{1}$$

where Ω is the total stream power, γ is the specific weight of water, Q is the water discharge and S is the channel slope. Traditionally, the functioning of an alluvial river channel can be modeled by this simple qualitative statement:

$$\Omega \sim QsD/d \tag{2}$$

in which Qs is the bed material flux, D is sediment caliber and d is the flow depth (Lane, 1955). The relation states that, for given flow energy (Ω), so much sediment of some specified size can be transported. It also recognizes the importance of channel geometry and how that scales with the flow (d). This links to the reasoning about bankfull and effective discharge concepts previously discussed. We could rearrange Eq. (2) to obtain (Church, 2006):

$$Qs/Q = f\,[\rho g d\, S/g(\rho s - \rho)D] \tag{3}$$

with g being the acceleration of gravity, and ρs and ρ are the density of sediment and water, respectively. The term in brackets is an important variable in river hydraulics, the Shields number (Shields, 1936). It is conventionally notated by τ^* and it provides the shear stress imposed by the water flow on the river sediment. Eq. (3) is a sediment transport function, with which we can calculate transported sediment given the hydraulic conditions. It has been proven that when $Q_s/Q \rightarrow 0$, for unconstrained sediment mixture, then $\tau^* \rightarrow 0.045$ (Wilcock and Southard, 1988). This condition defines the hydraulic condition in a river channel which determines the beginning of the sediment transport respect to a given grain size.

The introduced equations state our ability to quantify in physical terms the functioning of river geomorphology as qualitatively described in Fig. 1 and previously discussed. In summary, water discharge determines mostly the channel dimensions (width and depth), slope the rate of energy expenditure, and river morphology is eventually shaped by amount of sediment supply and its caliber. The balance of Eq. (2) governs also the stability of the channel: if river energy is greater than the sediment available to transport there will be a propensity to erosion, whereas if river energy is not enough to transport incoming sediment there will be a propensity toward aggradation. Fluvial forms and river patterns reflect such equilibrium. Step-pools cascades, pool and riffles, and dunes are different modes used by rivers to transfer sediment downstream and dissipate energy in excess based on different sediment calibers and gradient conditions. Indeed, step-pool cascades provide high frictional resistance compared to planar bed channels. Similarly, meanders in lower gradient rivers create greater frictional resistance compared to straight channels. In a context of high sediment supply, increasing the number of incised water channels, toward braided or anastomosed patterns, changes how the flow scales with channel geometry (see Eq. 2) increasing the channel competence, i.e., the ability of the channels to transfer sediment downstream (Nanson and Huang, 2008).

Since alluvial rivers are the result of such sensitive equilibria, changes in flow or sediment regime can induce large changes in alluvial channel form or dimensions. Such changes can result from climatic changes and/or anthropic factors such as land-use changes or dam development. We next provide concrete examples of anthropic disturbances that caused shifts in river patterns. These types of alterations are of critical importance for the environmental quality and ecosystem services a river can provide (Palmer and Filoso, 2009). Channel patterns and their formative processes determine habitats and the availability of specific ecological niches. This means that different river patterns will sustain different types of biodiversity. For instance, dynamic and sediment-rich rivers, such as braided and wandering rivers, support significantly higher biodiversity than less dynamic single-thread rivers that are starved of sediment. It is then of primary importance to study historical patterns of river trajectories (Brierley et al., 2013; Kondolf et al., 2007) and be able to foresee future ones based on expected climatic conditions, anthropic pressures and management measured undertaken. Understanding these fundamental relations also suggest why it is futile to impose a designed channel pattern that is not sustained by current and future water and sediment conditions (Kondolf, 2006).

Anthropic impacts

Changes to the independent variables flow and sediment load

To understand changes in river systems from human impacts, it is often useful to study the system from the perspective of a *sediment budget*, which is a compilation and accounting for the magnitude and spatio-temporal distribution of sediment sources, sediment transport processes and deposition in a river network (Reid and Dunne, 2016). Many human alterations affect the sediment load of rivers. Land use change and poor agricultural practices, road construction, mining, and other land disturbances, especially in steep mountainous and upland areas (Fig. 3) drive increased sediment loads in headwater, sediment producing zones of river basins. Sediment loads from the downstream parts of the basin can also be increased by changes, such as increased erosion from agriculture, or by urbanization and the resulting increased runoff and channel incision, which in turn result in increased sediment loads from channel erosion. Despite widespread increases in land disturbance and consequent increased sediment yields from upland areas, the sediment loads of most major rivers have *decreased* in recent decades. While this might seem counterintuitive given the greatly increased impact of land disturbance in river basins worldwide, it reflects two principal anthropic effects that have reduced sediment loads in river basins world-wide. These are the extent of sediment trapping by dams (Walling, 2006) and the effects of sand and gravel extraction from river channels (Simon and Rinaldi, 2006; Surian and Rinaldi, 2003). The reduced sediment delivery to downstream reaches and coastal areas is increasingly manifest in accelerated coastal erosion and loss of delta lands (Syvitski et al., 2009).

Erosion from the construction of roads has become a significant cause of increased sediment yields, especially in the Global South, where roads have commonly been funded as components of international development projects without fully accounting for their environmental impacts (Sidle and Ziegler, 2012). These impacts are undoubtedly widespread, with impacts on the ecology of receiving waters that are rarely documented (Rios Touma et al., 2020). In the Upper Mekong River basin in China (known as the Lancang), new road construction has been extensive, and has resulted in a roughly 10-fold increase in sediment yields to the river

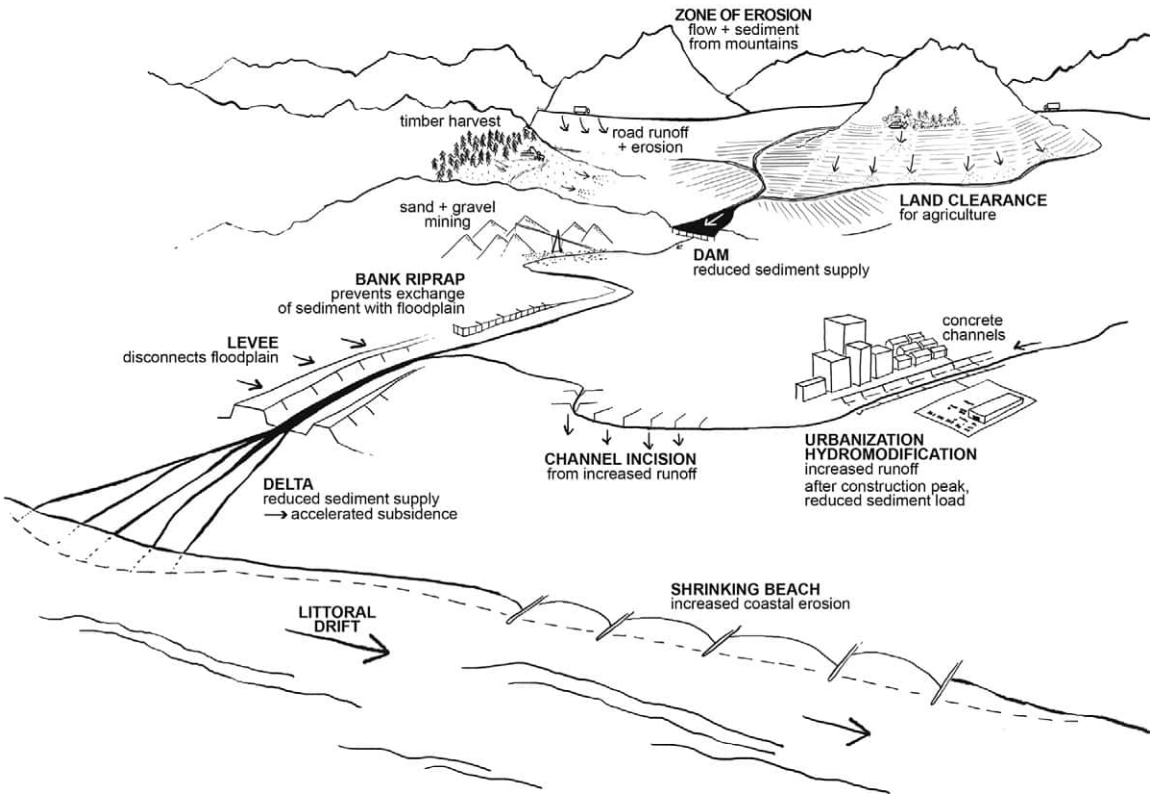

Fig. 3 Human alterations to runoff and sediment load: increasing sediment yields from the upland landscape, sediment trapping above dams, and consequences of sediment starvation downstream. From Kondolf GM and Podolak K (2013) Space and time scales in human-landscape systems. Environmental Management Springer Nature. used by permission of Springer Verlag.

network (Sidle and Ziegler, 2012). Consistent with the sediment trapping by dams described below, however, most of this newly eroded sediment will not move downstream to the Lower Mekong River and Delta in the future but will be trapped in multiple reservoirs downstream.

Urbanization alters runoff from river basins, typically increasing runoff for a given rainfall event, increasing the energy of runoff. The increased runoff means increased erosive potential of streamflow, which results in channel incision, widening, and simplification. In response to erosion, stream banks are commonly armored with rock, concrete, or other protective material. The simplification of channel form resulting from incision, bank erosion, and hardening of banks, results in loss of habitats for aquatic organisms.

Dams typically store water by design and store sediment as an unintended consequence, although some dams have been built as debris basins or sediment-control (*sabo*) dams (Wang and Kondolf, 2014). Dam-induced changes in flow regime are typically accompanied by reductions in the river's sediment load, as reservoirs trap sediment, creating conditions of sediment starvation in the reach directly below the dam. Reservoirs trap 100% of the river's *bedload* (the coarse sediment that moves along the channel bed by rolling, sliding, and bouncing, consisting of gravel and sand), and a varying percentage of the *suspended load* (sand, silt, and mud held aloft in the water column by turbulence), depending on the residence time of water in the dam, and thus on dam design and operation. The storing of water and sediment in the reservoir results in changes in the river flow regime and sediment load and regime downstream of dams, which almost always produce downstream changes in the form of alluvial channels.

Many reservoirs trap sediment but still release flows high enough to transport sediment, thereby creating sediment-starved, or *hungry water* downstream, so-called because these flows still have energy to transport sediment but little or no sediment load, and thus they possess excess stream power (Kondolf, 1997). This excess energy erodes the bed, a process known as channel *incision* or downcutting, which can undermine bridges and other built infrastructure, and scour away sand and gravel bars and riffles, resulting in loss of ecologically important habitats, as documented on the Colorado River downstream of Glen Canyon Dam (Schmidt et al., 1998).

Whether hungry water occurs downstream of dams depends on the balance of water discharge and sediment supply (see Eq. 2). Some river reaches below dams are in sediment deficit, others in surplus (Schmidt and Wilcock, 2008). Reservoirs with large storage to redistribute water between seasons and from one year to the next, commonly reduce high flows, and thus reduce the dynamism of the river channel downstream (Kondolf and Batalla, 2005). Gravel beds formerly mobilized every year or two may go for years without being moved, allowing fine sediments to accumulate within the gravel (clogging) and riparian vegetation to establish within the active channel, restricting flows to a narrower conveyance path, and scouring the low-flow channel (Kondolf and Wilcock, 1996).

By controlling a wide range of floods, large reservoirs can reduce the magnitude, duration and frequency of floods experienced by the downstream channel—with consequences for fluvial processes downstream. Dam-reduced flood flows may be incapable of transporting sediment delivered to the river by tributaries, inducing channel aggradation and potentially increasing flooding risk.

The ecological consequences can be profound. The complexity of alluvial channel forms depends upon the availability of coarse sediment (sand and gravel) that compose bars and riffles. In reaches starved of sediment by upstream dams, sand and gravel are transported downstream without being replaced, resulting in loss of gravel and sand bars, riffles, and beds, and with them, loss of channel complexity, resulting in a simplified "bowling-alley" channel form lacking in habitats needed for fish and invertebrates.

To mitigate dam-induced impacts on sediment transport and channel geomorphic processes, controlled high-flow releases designed to mimic the action of natural floods are increasingly required in hydroelectric licenses for dams and as part of programs to restore river functions (Williams, et al., 2019). These deliberate, high-flow releases constitute one component of environmental flow requirements for the maintenance of aquatic and riparian habitat. They reflect an evolution of environmental flow requirements from simple minimum flows to include periodic high flows to mimic flood effects on channels or on ecological processes (Kondolf and Wilcock, 1996; Poff et al., 2017). While terminology varies (e.g., "flushing flows," "channel maintenance flows," and "morphogenic flows," see Loire et al., 2021), the need for periodic high flows to accomplish geomorphic goals and to maintain the functionality of the sediments as physical habitat for stream organisms has been widely recognized (Yarnell et al., 2015).

However, even if a post-dam flow regime were to mimic precisely the pre-dam flow regime, the river system would be severely altered by the loss of its sediment load (Kondolf and Wilcock, 1996; Wohl et al., 2015). Thus, to prescribe most beneficial morphogenic flows for a given river, it is critically important to take into account the sediment load available to the reach downstream of the dam, such as sediment supplied from downstream tributaries (e.g., Grams et al., 2013). Increasingly, partial restoration of sediment load is prescribed along with morphogenic flows (Kantoush and Sumi, 2011; Kondolf, 1997; Tena et al., 2012).

Direct channel modifications

Among human activities resulting in direct modifications to river channels, dredging and channel straightening for navigation or flood control are among the most pervasive and severe. For navigation, a relatively straight, deep channel is ideal, and many rivers have been turned into such canals to allow navigation. To straighten the river's course, meander bends may be mechanically cut off and the river rerouted through a straight channel. Similarly, to improve flood control, many river channels have been straightened and dredged. Such simplified channel forms can be disastrous ecologically, as they do not provide habitat for fish and other organisms (Brooker, 1985). For flood control, many rivers have been lined with dikes to prevent floodwaters from flowing out onto floodplains, disconnecting river channels from their floodplains (Tockner and Stanford, 2002) and causing severe reductions in river-floodplain productivity (Bayley, 1995).

In addition to bank hardening undertaken in response to erosion induced by urbanization (discussed above), banks are hardened even when the erosion is perfectly natural, such as on the outside of migrating meander bends, to protect poorly-sited infrastructure, dwellings, and even undeveloped rural land whose owners do not want to see their pastures eroded. This has resulted in bank hardening ranging from engineered riprap, masonry, or concrete structures to informal dumping of rubble, debris, and even abandoned vehicles down banks to slow erosion. Bank hardening measures also include some that are mislabeled as "green" because they involve boulders and large wood (especially root wads), which are claimed as "natural materials" but whose use in these contexts is typically far from natural in that they prevent natural channel migration, and in many cases the boulders would not naturally be found in these channels. All these measures to harden banks take a toll on river ecology, by preventing the erosion, deposition, and channel migration processes that lie at the foundation of healthy river systems, and by directly replacing natural banks with artificial structures. For example, along the Sacramento River, vertical banks found along the outsides of meander bends (maintained in vertical profile by frequent toe erosion) provide habitat for bank swallows, but at many sites, banks have been riprapped, eliminating this habitat (Wright et al., 2011).

Rivers are also dredged to mine sand and gravel for construction aggregate, resulting in direct modifications to channel form, not only in the reach directly affected by the dredging, but also in reaches up and downstream. Channel incision propagates upstream from instream mines via regressive erosion (headcut migration) and downstream via sediment starvation (as coarse sediment is trapped in the mining pit) (Kondolf, 1994). Both navigational dredging and mining can trigger instability in river systems. For example, on the Apalachicola River, Florida, attempts to excavate and maintain a 3-m deep navigational channel in a loose sand bed resulted in collapse of the banks of the dredged channel, which triggered instabilities throughout the river system (Light et al., 2006). Mining of sand and gravel from the bed of the Douro River in Portugal resulted in the collapse of the Entre-Os-Rios Bridge during a subsequent high flow, killing 59 people (Antunes do Carmo, 2021).

Implication for management

Fluvial geomorphology expresses river forms and processes as the results of specific drivers: the geological, hydrological and ecological conditions of the river corridor but also how this is managed. Rivers are influenced not only by what occurs within the river corridor but also at the scale of the catchment, such as changes in land uses and climate change (Darby et al., 2016). We have discussed how river functioning depends upon the balance between water and sediment fluxes and how these determine different

channel patterns. The legacy of such factors, i.e., the historical trajectories of climate, geology, ecology and human disturbances co-exist and determine what is termed the river's trajectory: the geomorphological river changes that occur over time. Most rivers are dynamic by nature, and it is only through human intervention that we attempt to create more stable conditions, which in the long run very often do not work. From a river management point of view, it is meaningful to look at changes that have occurred in the recent history (10–100 years) because these define the starting conditions affecting future river trajectories. For instance, at the beginning of the 20th century many north Italian rivers showed braided patterns which shifted to single-thread meandering morphology due to reduced sediment load caused by sand and gravel mining and by land use changes following the second world war (Surian and Rinaldi, 2003). With controls on instream mining, some of these rivers have started to show signs of recovery toward multi threads system (Bollati et al., 2014; Surian et al., 2009). In the French Alps for similar reasons during the second half of 1900s, many braided rivers have transformed its pattern toward more single thread morphology (Piégay et al., 2009). In the latter half of the 19th century, some rivers in northern California became braided due to dramatically increased sediment loads caused by hydraulic mining for gold (Gilbert, 1917). In the Bega River catchment, NSW, Australia, significant geomorphic changes to rivers have occurred post European colonization (after 1850s), including widespread channel erosion and sediment mobilization (Brierley et al., 1999). River management must not only understand current conditions but also to investigate recent historical processes, and based on that, foresee future river geomorphological trajectories in terms of channel pattern dynamics and their sensitivity to changes by future climate and human disturbances (Bizzi et al., 2021; Downs et al., 2013; Fryirs, 2017). Over the last decades a number of river geomorphic analysis frameworks have been proposed to implement such visions in Europe (Gurnell et al., 2016; Rinaldi et al., 2013), Australia (Brierley and Fryirs, 2005), and Asia (Blue et al., 2013). These frameworks support river managers in reading river systems to interpret current fluvial processes and foresee future ones based on alternative management scenarios proposed.

Geomorphic analysis of river system must be tuned with ecological management targets and objectives: indeed, geomorphic processes shape habitats and ecological niches (de Jalón et al., 2016). Nonetheless, very often ecological targets defined for river management purposes fail to properly incorporate the concept of river geomorphic trajectories in their definitions and may adopt a static vision of river morphology and habitats (Belletti et al., 2015; Friberg, 2014). To develop a dynamic vision of river systems and translate that into implementable management schemes and measures, where ecological and geomorphic processes are investigated and interpreted on common basis, is a challenge for river management of the future. It is also a requirement to pursue a sustainable and healthy environment where human needs are wisely weighed with a scientific and appropriate understanding of river functioning.

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Hydrology and Classification of Rivers for Management

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Bankfull flow The maximum discharge a channel carries. On average, these flows generally occur every 1–2 years, although this varies by region and climate.

Baseflow Flow within river channels sustained by groundwater contributions from infiltrated precipitation.

Clustering Process of grouping objects of similar properties into categories. Clustering may involve the use of multivariate statistical procedures.

Deductive hydrologic classification Grouping rivers or watersheds based on generalizing landscape or climate features into regions, where the variation in physical properties of the landscape or climate are hypothesized to approximate hydrologic variation. Deductive reasoning generally follows a stepwise rationalization process where generalizations (e.g., landscape and climate influences hydrology) are used to infer a logical conclusion (e.g., landscape regionalization approximates hydrologic types).

Discharge A volumetric flux of water in river channels. Typically measured as $ft^3\ s^{-1}$, $m^3\ s^{-1}$, or ls^{-1}.

ELOHA (ecological limits of hydrologic alteration) A framework and methodological process for defining environmental flow standards for groups of rivers within regions. The central premise for identifying standards is using flow alteration-ecological response relationships to determine socially acceptable "limits" to hydrologic alteration (see Poff et al., 2010).

Environmental flows The quantity, timing, and quality of flows required to sustain freshwater and estuarine systems, and the humans that rely on those systems (Annear et al., 2004).

Flood frequency The number of occurrences of a flood event of a given magnitude within a specified time period.

Floodplain Portions of river valleys extending laterally and at higher elevations from river channels (bankfull areas) inundated periodically by flood events.

Flow duration curve (FDC) A non-linear relationship depicting the percentage of time a flow of a given magnitude is equaled or exceeded.

Hydrologic classification The process of grouping rivers into categories based on similarities in hydrologic behavior or hydrologic variability.

Hydrologic statistics Metrics used to summarize temporally variant measures of discharge into consolidated forms.

Hydrologic variability The spatially and temporally dynamic changes in discharge in rivers over multiple spatial and temporal scales.

Hydrology (of rivers) Study of the dynamic volumes of water within fluvial channels. Hydrology, more broadly, is the study of the movement of water across landscapes.

Inductive hydrologic classification Grouping rivers or watersheds into categories based on generalizing direct measures of discharge and hydrologic variability. Inductive reasoning used emergent properties of direct observations (e.g., discharge from gages) to make generalizations (e.g., hydrologic classes).

Natural flow regime The natural variation in the magnitude, timing, duration, frequency, and rate of change in discharge in rivers and streams, where natural refers to absence of human influences (e.g., dam regulation, withdrawals). See Poff et al. (2007).

Return interval Analogous to flood frequency, the period of time a flow a given magnitude is expected to re-occur.

Runoff Volume of water draining a given area of land or catchment over a specified time period.

Storm hydrograph A visual depiction of discharge changes over time immediately preceeding, during, and following a precipitation event.

Stream order A stream classification approach using a discrete numerical depiction of stream size. Integers (0,1,2) represent incrementally increasing sizes of streams where 0 is a headwater, 1 is 1st order, etc.

Surface flow (also stormflow) The portion of discharge or runoff resulting from precipitation flowing overland to river channels.

 https://doi.org/10.1016/B978-0-12-819166-8.00080-3

Introduction

Rivers are dynamic ecosystems. From the vantage point of a riverbank, one can see continuous physical movement of water as turbulent riffles, undercurrents in pools, and eddies. The downstream transport of water and other materials along an elevational gradient is the primary function of river systems and the key factor that distinguishes rivers from other ecosystems. While a seemingly simple concept, water molecules flowing downstream may have originated as rain or snow days or months ago and traversed hundreds of kilometers above and below ground. The rate at which those molecules arrived in the river depend upon climate, geology, soils, groundwater, vegetation, and, of course, humans. Rivers not only connect longitudinally disparate landscapes, but they also vertically interact with subsurface areas underlying channels, as well as creating lateral connections to the adjacent landscape during floods. These connections change from minutes to decades, depending on the dynamics of flowing water in rivers, generally termed *river hydrology*.

Hydrology is the master variable of river systems (Power et al., 1995), organizing the morphology of river channels, mobilizing sediments, scouring floodplains, influencing the physiochemical properties of water, and shaping the fluid and riparian environment in which aquatic organisms' life histories have adapted (Poff and Ward, 1990). Each river has a unique hydrologic regime that varies interannually, seasonally, and daily (Fig. 1). Organisms inhabiting these systems are sustained by the natural variability in hydrology across different temporal scales (Poff et al., 1997; Bunn and Arthington, 2002). Despite these unique hydrologic signatures, rivers draining landscapes with similar climate, geology, and topography tend to display reoccurring patterns in hydrology; these repeatable patterns have supported the development of hydrologic classifications, where streams are grouped according to similarities in hydrologic behavior. Hydrologic classifications have provided insights into regionally distinct hydrologic regimes important in organizing ecological communities (Poff and Ward, 1989; Olden et al., 2012; McManamay et al., 2015a).

Aside from improving the fundamental understanding of the importance of naturally variant hydrologic regimes on sustaining ecological communities and ecosystem functions, hydrologic classifications have also proven useful for managing flows in river systems altered by human disturbances. In the last 25 years, considerable research has been devoted to understanding relationships between river hydrology and ecological patterns, including the development of hundreds of indicators or statistics aimed to reduce the dimensionality of hydrologic patterns and the creation of hydrologic classifications to generalize patterns in hydrologic behavior. In this chapter, I will provide a broad background of the principles of river hydrology. These principles are carefully selected to provide the reader with a broad, yet relevant, background in order to appreciate the justification behind the growth of research in hydrologic statistics and hydrologic classifications in advancing the fundamental understanding of river behavior as well as their use in environmental management.

The water cycle and river discharge

Rivers, in their simplest form, are channels that carry water downhill. However, the volume of water flowing at any point in a river is the accumulation of a multitude of processes occurring just meters to hundreds of kilometers upstream. Indeed, how the water arrived within the river channel can be complex and determines the river's morphological organization and its hydrologic behavior. River systems, i.e., entire networks of rivers and their tributaries, follow a nested organization where small headwater systems join to form larger systems, and so on. To systematically characterize these patterns, Strahler (1964) developed a stream ordering system, known as Strahler orders, where two headwaters (0-order) join to form a 1st order streams, and where two 1st order streams join, a 2nd order stream emerges, and so on; however, the junction of a 0 order and 1st order does not result in a 2nd order, nor does the junction of a 1st and 2nd order result in a 3rd order system. Although the Strahler order is limited to a discrete numerical depiction of stream size, stream orders and spatial dendritic patterns of tributary branching can be useful in regional comparisons of stream densities, which provide an indication of the role of climate and geology have organized basins and how much water channels carry water downhill (Strahler, 1964; Selby, 1985).

A fundamental law of river organization is that as stream order increases, so does watershed area (or catchment area), i.e., the area of the landscape that drains towards a channel. Larger areas of the landscape receive more cumulative precipitation, which generally yields more water (although rare exceptions to this rule depend on the underlying structure of bedrock lithology). However, not all that precipitation will reach the river system, and the resulting water that does eventually arrive in channels, termed runoff, does not arrive all at the same time. At any point in time, the volumetric rate of water draining the landscape and resulting in surface water in a river, or discharge (Q), is a function of a balanced water budget (Fig. 2):

$$\Delta S = P - Q_s - E - I_v - Q_b \tag{1}$$

where ΔS represents the positive or negative change in storage in the watershed over a time period. In natural watersheds lacking human disturbances, ΔS at any instant is comprised of changes in water in soils and groundwater. Precipitation (P) that exceeds the infiltration capacity of soils results in surface runoff (Q_s). The remaining portion of precipitation that infiltrates the soil ($P - Q_s$) is available to vegetation and evaporated (E) or infiltrates to deeper soil horizons beyond the roots of vegetation (I_v), termed the vadose zone. This water eventually enters groundwater, termed groundwater recharge, which eventually enters streams as surface flow or base flow (Q_b). Total discharge in river (Q_R) is the sum of Q_s and Q_b. By replacing and rearranging terms in the above equation, Q_R can be calculated as:

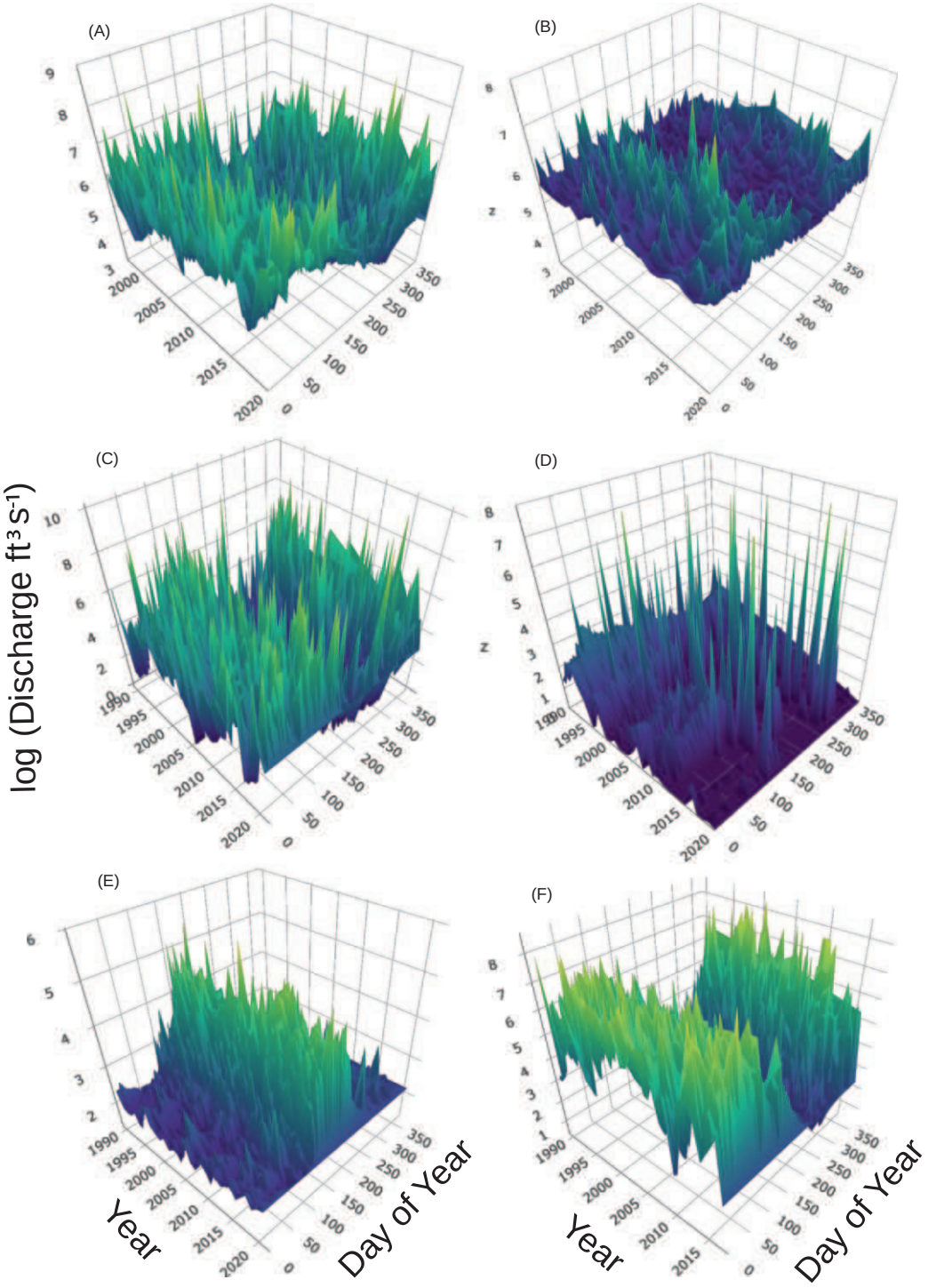

Fig. 1 Interannual, seasonal, and daily variation of different hydrologic regimes across the United States. (A) Valley River at Tomotla, North Carolina (USGS gage 03550000), (B) Pine River near Hoxeyville, Michigan (USGS 04125460), (C) Dutch Creek at Waltreak, Arkansas (USGS 07260000), (D) North Concho River near Carlsbad, Texas (USGS 08134000), (E) South Crow Creek near Ronan, Montana (USGS 12375900), (F) Redwood Creek near Blue Lake, California (USGS 11481500).

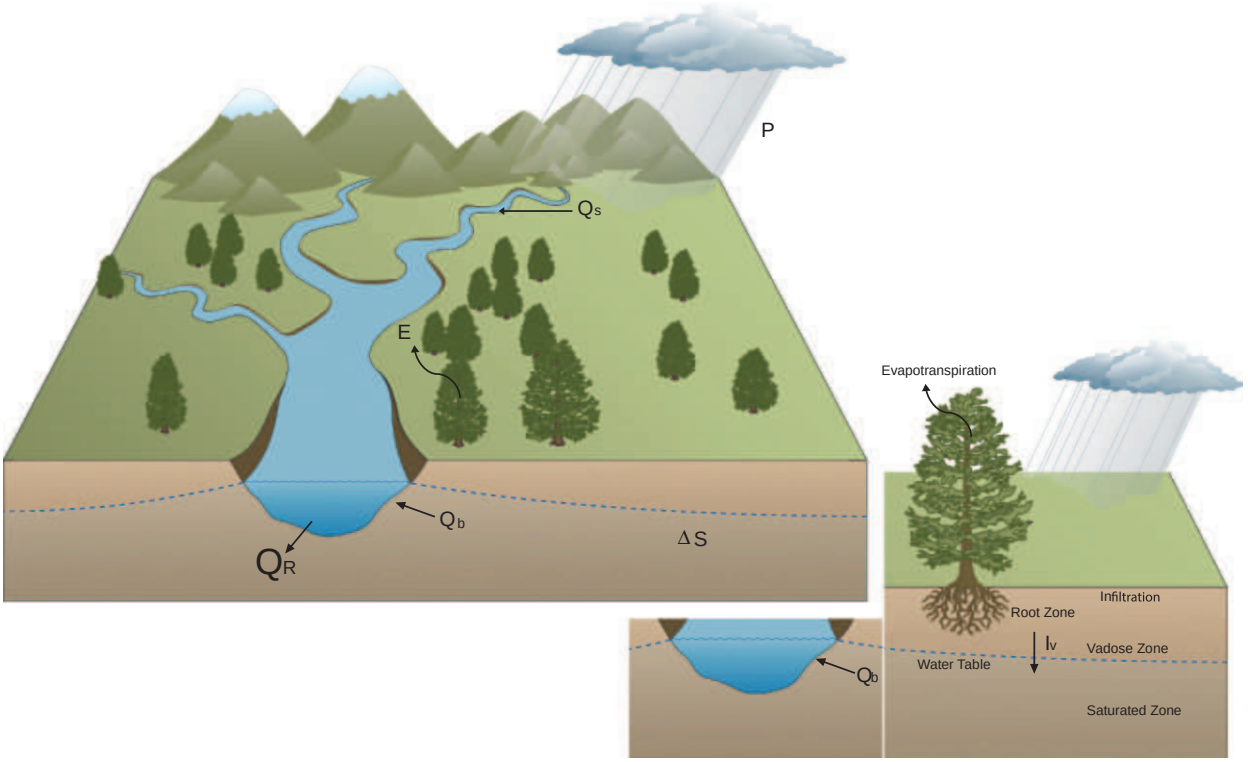

Fig. 2 Water budget and contribution to river hydrology. See text for definition of terms. Base conceptual diagrams were modified from original versions, which were courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

$$Q_R = P - E - I_v - \Delta S \tag{2}$$

The above equation can tell us a great deal about temporal variation in discharge for individual rivers, but also regional-to-global hydrologic variation. Regions vary extensively in the magnitude and seasonality of precipitation, which generally governs annual and interannual patterns in discharge. In humid regions with sustained rainfall throughout the year or significant portions of the year, rivers continually have surface flow—these are termed perennial rivers. In contrast, intermittent streams drain landscapes in arid regions and may have no discharge for portions of the year. A third major type of river or stream is called ephemeral channels, which are channels smaller than headwater systems that convey water only during rainfall. Whether precipitation is rain or snow defines the periodicity in high-flow conditions following snowmelt. In some high-elevation mountainous regions, such as the Rocky Mountain region of the United States, the majority of annual precipitation occurs as snow during a portion of the year and accumulates as snowpack, eventually melting and forming large spring freshets (peak floods). Snowmelt infiltrating soils then sustains baseflow during periods of the year with little precipitation.

Aside from major climatic differences among regions, hydrology varies with geology, soil characteristics, and vegetation. The amount of precipitation infiltrating soils and eventually entering groundwater depends upon soil texture, which generally refers to soil porosity and water-holding capacity, whereas the amount of precipitation reaching the vadose zone and the time it resides there (i.e., ΔS) depends on evaporation, soil depth, and lithology of underlying bedrock. Bedrock that is impenetrable to water (e.g., granite) forms distinct saturated zones and water tables, whereas porous bedrock (e.g., limestone) yields complex subsurface hydrology with less predictable behavior following precipitation. In some regions with deep aquifers, the exchange between surface and deep groundwater is not well known and may be measured on the order of centuries rather than days. Evaporation is portioned into precipitation that evaporates from the surface of the soil or vegetation and the part of infiltrated precipitation transpired by vegetation. The type and density of above-ground vegetation not only influences evaporation but also infiltration. Vegetation intercepts precipitation, termed throughfall, slowing the rate at which precipitation falls to the land surface. Vegetation cover lessens the velocity and impact of precipitation with soils, increasing the soil and water contact time, and increasing infiltration.

The same drivers of regional differences in discharge patterns also influence how an individual river responds to variation in annual (Fig. 3A) or seasonal (Fig. 3B) precipitation or a single precipitation event—termed a storm hydrograph (Fig. 3C). During a rainstorm, surface runoff (Q_s), also called overland flow, drains the landscape quickly, corresponding to rapid increases in discharge. Once rainfall subsides, river discharge decreases, but at a much slower rate. The leading and trailing edges are referred to as rising and falling or receding limbs, respectively, of a storm hydrograph. The rainfall entering groundwater takes on the order of days to months following precipitation, to emerge as surface flow (Q_b). Hence, a storm hydrograph can be separated into surface (Q_s) and

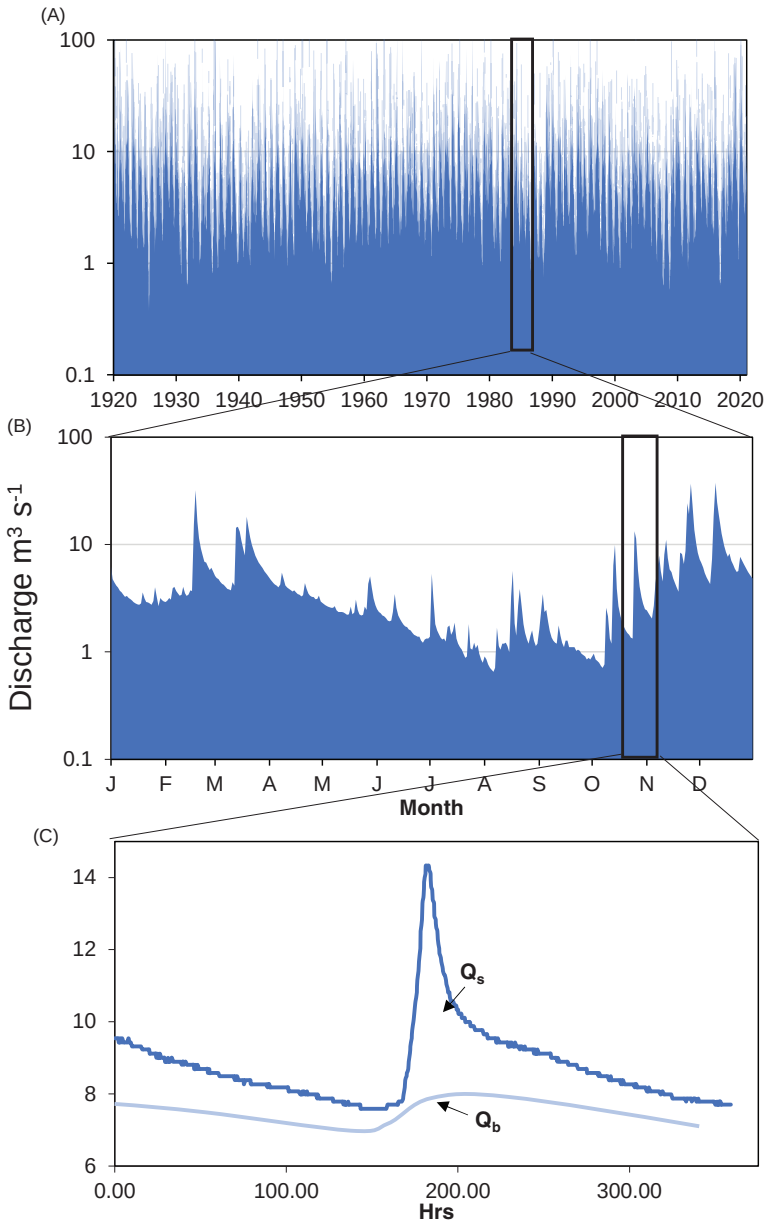

Fig. 3 Hydrologic variation over multiple temporal scales in the Valley River, North Carolina, USA (USGS 03550000). Variation is captured over (A) inter-annual, (B) seasonal, and (C) daily time scales.

baseflow (Q_b) components (Fig. 3C). Hence, most of time, flow within river channels is sustained solely by baseflow. The shape of storm hydrographs, the peak magnitude and rise and fall rates, indicate a great deal about a river's watershed characteristics, particularly geology and soils, and the overall response to precipitation. Additionally, individual storm hydrographs are closely related to seasonal and annual hydrographs for a river system (Fig. 3A–C).

River hydrographs, on daily to annual time scales, are predictable for many regions, although that predictability is shifting with climatic change. This predictability forms the basis of the discussion of river classification and its importance in later sections. Indeed, human societies have grown to depend upon this seasonal predictability for important services, such as dam operations, irrigation, and cooling for electric power generation. Extremities in climate, however, including excess rainfall or extended dry periods, induces unpredictable extremities in hydrologic patterns. For instance, 8 days of heavy rainfall during Hurricane Harvey in Texas exceeded 152 cm (60 in.) in some locations, inducing record breaking peak floods in at least 40 rivers and costing a cumulative of $125 billion in flood damages (Watson et al., 2018). In contrast, California's 5-year drought (2012–16) resulted in $10 billion worth of losses arising from water shortages to six major sectors of the state's economy and placed vulnerable aquatic species at increased risk of extinction (Lund et al., 2018).

Measuring river discharge

Understanding river channel geometry is critical to measuring discharge. River discharge and other materials in transport are conveyed through channels. The dimensions and stability of river channels are partially governed by the geological and topographic setting but otherwise are related to the magnitudes and frequency of water volumes carried downhill. Flowing water constantly carves the river channel, eroding and carrying sediment and materials; however, the channel shape remains relatively constant as materials from upstream replenish sediments as others are eroded. Hence, the river is said to be in dynamic equilibrium (Leopold, 1994). The maximum discharge a channel carries is termed the bankfull flow (Fig. 4). Bankfull flow frequency varies among regions but, on average, these flows generally occur every 1–2 years (Foster, 2012), although this varies by region and climate (Fig. 4). The frequency and magnitude of bankfull discharge is critical for maintaining channel dimensions and shape. Floods, then, are flows that exceed the bankfull capacity of a river channel and enter the floodplain. Floodplains may have multiple tiers, where lower floodplains are inundated annually or semi-annually and upper floodplains are inundated during less-frequent but larger events (Fig. 4).

Discharge is related to the cross-sectional area of water within a channel or, in situations where overbank discharge exceeds the channel's carrying capacity, within a floodplain. Discharge is a measurement of flux, or volume per unit time; therefore, to calculate discharge for a given cross-sectional area, an *estimate* of water velocity is required. Indeed, most methods that measure velocity are estimates, as river hydraulics are complicated by channel roughness, a term describing irregularities in channel geometry arising from variation in substrate size or obstructions to flow, such as boulders or logs. Roughness induces friction and turbulence, which creates highly variant velocities across a stream channel. If river channels consisted of perfect trapezoids or half-circular pipes, estimates of velocity and discharge would be far more reliable. In fact, some approaches to measuring discharge use weirs or other structures to constrain flow a known area to accurately characterize geometry and velocity.

Measuring river discharge can be generally classified into two approaches: instantaneous field measurement and automated or continuous measurements. Although continuous measurements are ideal, this approach requires more equipment, maintenance, and expense. Additionally, continuous measurements are reliant upon many initial and recurring instantaneous field measurements for equipment calibration and continued operation. Instantaneous field measurements represent a single discrete measurement of discharge in time. The wetted width of a channel is measured using a field tape and split into equidistant subsections (generally 10 to 20 sections) (Fig. 4). For each subsection, depth and velocity are measured and their product (width X depth X velocity) is discharge for that section. Discharges for all subsections are then summed to yield total river discharge. Velocity is measured using a velocity or current meter mounted to a wading rod (e.g., Fig. 5A), and there are generally two main types of instruments: a mechanical current meter or electromagnetic sensor. Mechanical current meters consist of metal cups that rotate around an axis, where the revolutions directly translate to current speed, whereas electromagnetic sensors measure voltage arising from conductive

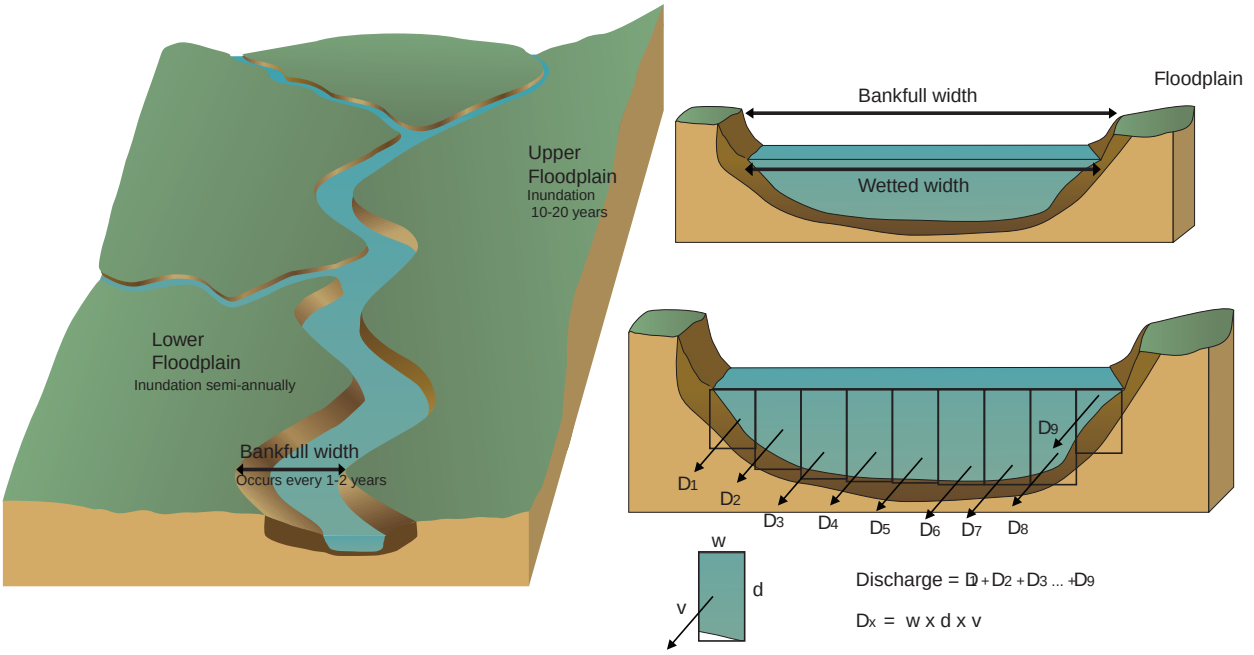

Fig. 4 Channel and floodplain morphology of a river and relations with discharge. Bankfull width is the maximum carrying capacity of a river channel before flows enter the floodplain. Bankfull flows occur, on average, every 1–2 years, whereas lower and upper floodplains may be inundated every 1–20 years. Discharge measurements rely on discretizing the channel cross section into equal subsections where width, depth, and velocity are measured. The sum of these products is discharge for a river at a given point in time. Base conceptual diagrams were modified from original versions, which were courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

Fig. 5 Approaches for discrete (instantaneous) and continuous discharge measurements. (A) Students assist the author in measuring discharge in Bullhide Creek near Lorena, Texas using a measuring tape (width), a wading rod (depth), and electromagnetic sensor (velocity). (B) United States Geological Survey (USGS) staff measuring depth and velocity in the Boise River, Idaho using an Acoustic Doppler Current Profiler (ADCP). (C) Stage rod and well containing a pressure transducer for estimating stage height in Bullhide Creek, near Lorena, Texas. (D) V notch weir at Coweeta Hydrologic Laboratory, North Carolina. (E) USGS gaging station on the Colorado River below Glenwood Springs, Colorado. (F) USGS Station stream gage 15,905,100 at the Atigun River, Alaska. (A) Photo credit: Rachel Alford, Baylor University, (B) photo credit: Tim Merrick, USGS, public domain, (C) photo credit, author, (D) photo credit: USDA Forest Service, (E) photo credit: USGS, public domain, (F) photo credit: Jeff Conaway, USGS, Alaska Science Center. Public domain.

fluids moving through a magnetic field to calculate current velocity. Current velocity varies considerably vertically within the water column, where surface velocity is higher compared to velocity near the streambed, where friction with the streambed slows the velocity. Hence, velocity is commonly measured at 60% of the depth (from the surface) for each subsection, as this generally represents the average current velocity of the entire water column (assuming a logarithmic velocity profile). Due to advances in technologies, the most modern approaches to measuring discharge in the field make use of an Acoustic Doppler Current Profiler (ADCP) mounted to a small watercraft and pulled across the entire channel (Fig. 5B). ADCP instruments use a doppler effect to measure the speed of particles in the entire water column and the cross-sectional depth, voiding the need for manual measurements. Because ADCP instruments measure the current speed across the entire water column and provide continuous depth profiles, these techniques are more accurate in measuring discharge, particularly in larger and deeper streams and rivers.

Translating field-based measures of discharge into continuous readings by automated equipment requires another important field measure, river stage, which is the height of the surface water from a selected location within a river's cross-section. Therefore, stage is completely relative to an individual reach within a specific river. Assuming the cross-section of the stream reach remains constant (which is not always a reasonable assumption), then the stage of the water column can be used to infer discharge based on a stage-discharge curve. Stage-discharge curves represent a relationship between stage and discharge developed from repeated instantaneous field measurements for a given cross-section. As you can see from the stage-discharge relationship (Fig. 6), discharge increases on a log-scale as stage increases; hence, peak floods that inundate floodplains have far more uncertainty (larger log values), as they are inherently difficult to measure accurately in the field. Automated equipment typically measures stage, or pressure, at high temporal intervals and uses the stage-discharge relationship to infer discharge. However, river channels are dynamic and shift regularly, which requires repeated field measurements to adjust cross-sectional profiles and take new stage-discharge readings. Examples of automated equipment to measure water height include floats or pressure transducers housed within small buildings or structures (Fig. 5C–F). The United States Geologic Survey (USGS) has operated over 25,000 stream gaging stations in rivers across the US and Puerto Rico; however, slightly more than 10,000 are currently operating (Fig. 7). Most of these structures are equipped with satellite communication instruments to transmit data to and from satellites and receivers (Fig. 5E and F), and eventually display real-time data on the internet (waterdata.usgs.gov/nwis/rt). In small watersheds, weirs or flumes of precise cross-sectional areas (e.g., v-notch weir) use a small dam to control and measure stage and discharge (Fig. 5D).

Deluge of discharge data—Characterizing river hydrology with statistics

Instantaneous field measurements take considerable time and effort to produce one discharge measurement for a point in space and time. Despite all the effort, those measurements only apply to a single reach within a river and may not coincide with important events, such as peak flood magnitudes, especially if conditions were unsafe to sample or if the event occurred outside of routine sampling. In comparison, consider the 10,000 USGS stream gaging stations in current operation (Fig. 7), most of which provide real-time data at 15-min to 1-h intervals. The continuous measurements from all those gages results in 3,650,000 daily averages or 87,600,000 hourly measurements for 1 year, all provided in real-time. Now, if you consider that many of these gages have been in operation for >15 years, that results in >1 billion observations! This volume of data present new opportunities but also create challenges, such as how to summarize the data to characterize hydrologic patterns in meaningful ways.

Variation in river discharge is generally represented by five components that organize riverine ecological processes: the magnitude, frequency, timing, duration, and rate of change of flow (Poff et al., 1997). Considering all these facets of a river's hydrologic regime, however, can be overwhelming, especially in managing river flows to support natural ecosystem function and human demands. To simplify this complexity and utilize information-rich discharge data, much work has been devoted to summarizing discharge into hydrologic statistics or indices. Summarizing discharge patterns into statistics is important for advancing our fundamental understanding of how river ecosystems are organized, by simplifying hydrologic patterns or making ecohydrological processes easier to discern. Hydrologic statistics also provide practical information for society. For instance, several

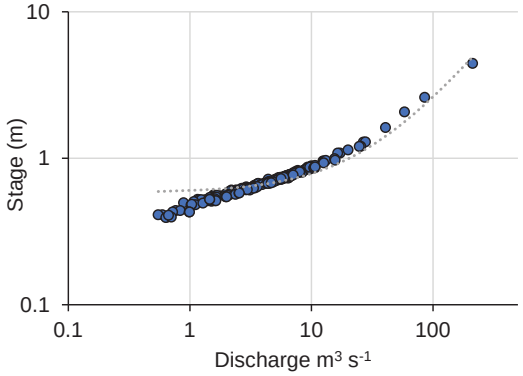

Fig. 6 Stage-discharge relationship for the Valley River at Tomotla, North Carolina (USGS gage 03550000).

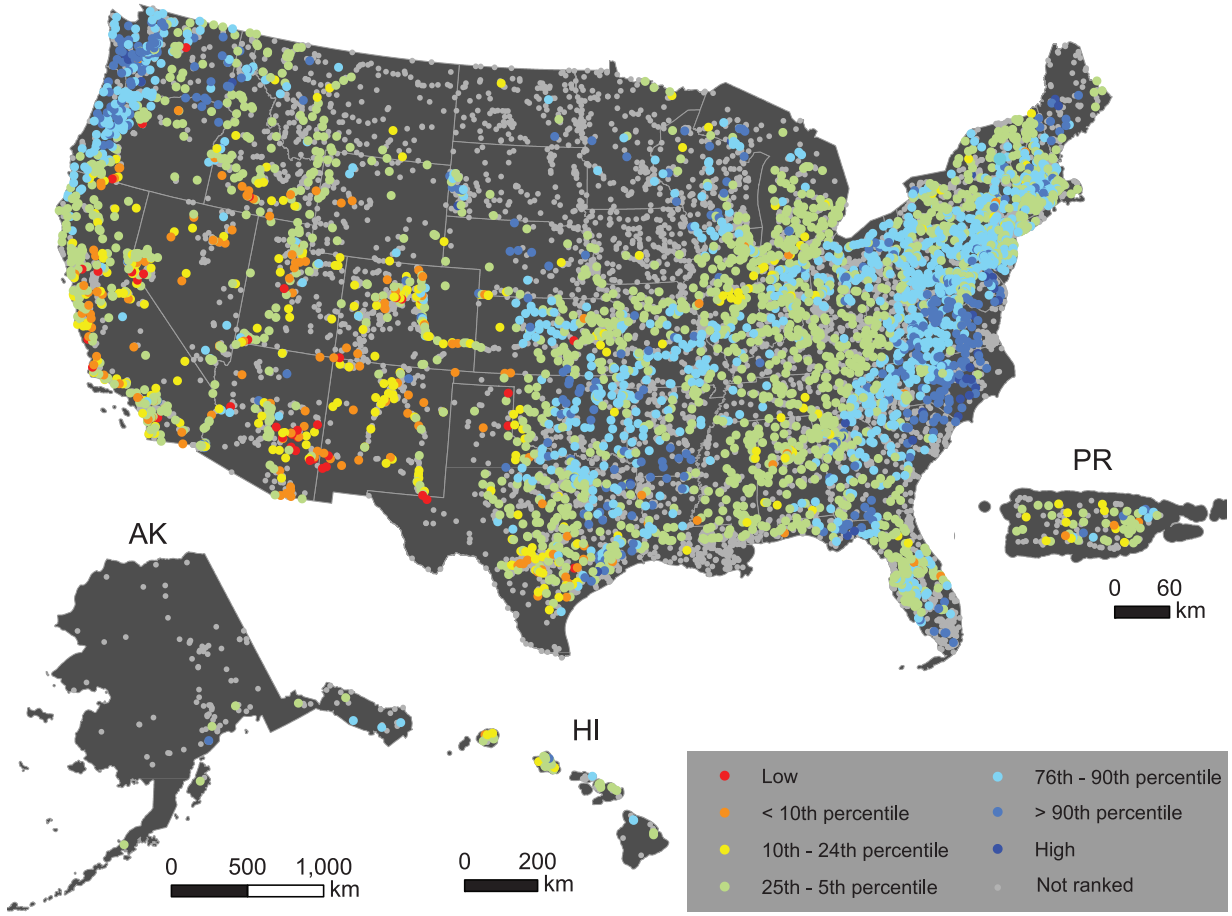

Fig. 7 United States Geological Survey (USGS) stream gaging stations currently in operation and ranked (via percentiles) according to their most-recent discharge value relative to their own 30-year discharge record.

hydrologic statistics have been used as guiding principles or generic thresholds to set water policies or standards for rivers to prevent excessive use of water or protect sensitive ecological components. Hydrologic statistics have also been used for designing infrastructure resilience in light of the variability of flows in rivers. Suppose a state department of transportation desires to build a new road requiring a bridge over a stream, or a developer desires to build a new water supply reservoir to meet growing population demands. In either case, the infrastructure design and materials need to withstand the disturbance of potential peak floods or prevent the occurrence of a dry reservoir. Although one strategy might be to "over-engineer" the infrastructures for the worst possible scenario, seemingly small increases in the size and volume of materials can exponentially increase the cost. Hence, accurate statistics of discharge are important for balancing financial expense with risks to human safety or risk of financial losses from infrastructure failure. One such statistic is peak flood frequency, which represents the return-interval (RI) of a flood of a given magnitude. Suppose the stream has a nearby gaging station with 105 years of discharge data (which is not uncommon) and engineers wanted to design the infrastructure to withstand a 500-year flood event. To calculate peak flood frequency, the peak discharge would be calculated for each year of data and the 105 observations would be ranked from smallest to largest. For each peak flood observation, RI is calculated using the following:

$$RI = \frac{n+1}{m} \tag{3}$$

where n is the total number of observations ($n = 105$) and m is the rank of a given observation (Leopold, 1994; Lundgren, 1986). A flood frequency curve can be generated by plotting peak flood magnitude versus the return interval in years (Fig. 8A), and the predictive relationship can be used to estimate the maximum magnitude of a flood event likely to occur within 500 years. The reciprocal of RI ($\frac{m}{n+1}$) is the probability that a given flood event will occur. For instance, in our observation dataset, the 100-year flood event has a rank $m \sim 1$, which corresponds to 0.01, or a 1% probability of exceedance. The problem with estimating a 100-year flood event with our dataset is that we only have 105 years of observations and hence, only one 100-year event. Using the

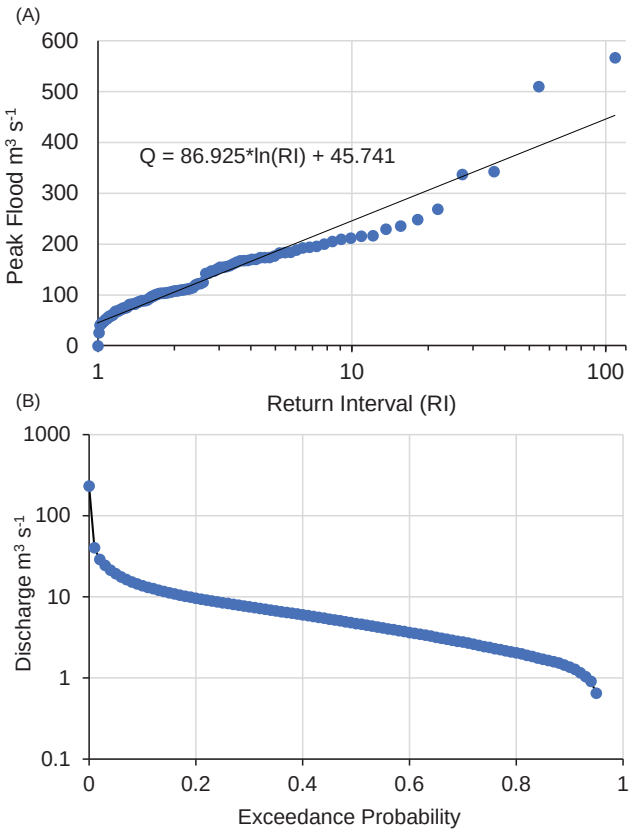

Fig. 8 Examples of hydrologic statistics including (A) peak flood return interval, and (B) a flow duration curve.

same dataset to estimate a 500-year flood events becomes even more uncertain, and in some situations, the uncertainty dramatically increases if the stream of interest does not have a gaging station. In these cases, discharge from the nearest neighboring gage is used and adjusted based for differences in drainage area.

Similar to flood-frequency curves, a flow-duration curve is typically generated from daily discharge values over the entire period of record for a stream gage (Fig. 8B). Percent exceedance values (1–100%) are calculated from daily average flow observations where the 1st percentile discharge value indicates that only 1% of daily flows exceed that value (e.g., daily maximum), whereas the 99th percentile value indicates that discharge exceeds such a value 99% of the time (e.g., the daily minimum). Flow duration curves represent daily discharge magnitudes plotted against percentiles (Fig. 8B). The distribution of values within flow-duration curves provides important information about hydrologic behavior, such as the stability of flows through the year or disparity between high- and low-flow magnitudes. Flow-duration curves also provide important information for water use planning, such as whether a stream can sustain certain human services, such as water withdrawals or hydropower generation. Flood-frequency and flow-duration curves are just two examples of the hundreds of statistics used to summarize discharge patterns.

The large number of hydrologic statistics emerged with the aim of being "ecologically-relevant," i.e., those flow events having relevance to ecological processes. To protect river ecosystems from excessive withdrawals for human use, especially during naturally occurring low-flow periods, statistics were designed to characterize minimum-flow conditions within rivers, such as average August or September flow, which commonly coincides with dry periods in North America. Another commonly used low-flow statistic is 7Q10, the lowest 7-day average flow that occurs (on average) once every 10 years or has a recurrence interval of 10 years. The minimum flow paradigm became a widely accepted and instream flow management approach for mitigating or preventing situations of withdrawals and dam regulation or setting flow regulations and policies (Tennant, 1976; Annear et al., 2004). Unfortunately, river managers became overly reliant upon the minimum flow paradigm, which was neither generally not protective of a river's dynamic flow regime nor useful for characterizing hydrology in ways meaningful to general ecological condition or to species the regulations were aimed to protect.

During the late 1980s through mid-1990s, a growing appreciation of the multi-dimensional nature of river hydrologic regimes (e.g., Poff and Ward, 1989; Poff, 1996; Richter et al., 1996) eventually gave rise to the natural flow regime paradigm, which was a framework to approach river management through holistic consideration of all five flow regime components (Poff et al., 1997). During this paradigm shift, a multitude of new and informative hydrologic statistics emerged to characterize discharge in ecologically meaningful ways (Poff and Ward, 1989; Poff, 1996; Richter et al., 1996, 1997; Olden and Poff, 2003). Among these

included the Indicators of Hydrologic Alteration (IHA), a series of 32 indices that summarized biologically relevant aspects of hydrology at daily to intra-annual scales (Richter et al., 1996). Measures of variation or dispersion in each IHA statistic resulted in 64 total indices (Richter et al., 1997). The IHA statistics were eventually incorporated into open-access software and designed for comparing human-altered hydrologic regimes with pre-altered or ideal natural conditions to inform flow management (Richter et al., 1996). To date, almost 2000 hydrologists, ecologists, researchers and water resource managers worldwide have used the IHA software to evaluate hydrologic alteration due to anthropogenic disturbance (TNC, 2018). More studies of various river systems and contexts demanded new hydrologic statistics specifically designed for associating discharge with ecological dynamics of interest or measuring unique situations of hydrologic alteration. Some of the various studies documenting these hydrologic statistics are provided in Table 1. Recognizing the challenges associated with the growing number of indices and selecting appropriate statistics for ecohydrology studies, Olden and Poff (2003) conducted a review documenting 171 hydrologic indices summarized from daily discharge records. They found that many of the indices were redundant or displayed multi-collinearity and that the 64 IHA indices explained the majority of multivariate space represented by all 171 indices. Even still, the number of hydrologic indices continue to grow, including those that characterize hydrology on sub-daily time scales (e.g., Bevelhimer et al., 2015). Most recently, Eng et al. (2017) calculated 612 daily hydrologic statistics for hydrologic classification and supporting future studies in hydroecology. Carlisle et al. (2019) later used these statistics to relate with measures of biological integrity to understand how anthropogenic modifications of stream flow have affected stream health.

Hydrologic signatures and classification

The previous section gave a high-level background of hydrologic statistics and their utility in decomposing thousands of discharge observations into a series of statistics meaningful for many applications, such as infrastructural engineering, setting water policies, or explaining complex ecological patterns. However, as Olden and Poff (2003) suggest, the pursuit of ecologically meaningful statistics has resulted in an over-abundance of indices, which has created new challenges of selecting the most appropriate and informative measures to guide river flow management. Considering the contextual specificity of river ecosystems in different climatic and physiographic settings with divergent riverine ecological communities, the over-abundance of indices adapted for each unique application should not come as a surprise. As Poff et al. (2007) describes, each river is characterized by a natural flow regime, a hydrologic signature unique to that river system (Fig. 1). Looking back at Eqs. (1) and (2), we notice that there are several variables that influence discharge, and there are many factors that influence each variable: climate, geology, topography, soils, and vegetation. Suppose for simplicity's sake that each factor is represented by several major categorical types, and there are a myriad of combinations of factor types that generate hydrologic variability in rivers. For instance, there are 6 generally recognized global climate regions (Mason et al., 2016), ranging from polar to tropical areas, and 12 textural types of soils (USDA, 2017), ranging by combinations of clay, silt, sand, and loam. The world is generally comprised of 5 major vegetation communities or biomes (forest, grassland, tundra, desert, and ice) (Bowman and Hacker, 2021) and 5 topographically variant landforms: plains, plateaus, mountains, valleys, and canyons (Page, 2015; Mason et al., 2016). Additionally, there are over 7000 lithostratigraphic units representing different geological bedrock and surficial deposits of the world (Kirkham et al., 1995; King and Beikman, 1974a,b), although these can be coarsened into 8 very simplified types (Kirkham et al., 1995). Assuming each type equally contributes to

Table 1 Studies reporting hydrologic statistics, their applicable flow components, and the temporal resolution of hydrologic information underlying the calculation of each statistic.

Study	*Hydrologic metrics*	*Flow components*	*Temp resolution*
Baker et al. (2004)	1	F, D, O	D
Bevelhimer et al. (2015)	13	M, R, D, V, O	H
Clausen and Biggs (1997)	34	M, F, D, T, V	D, A
Clausen and Biggs (2000)	35	M, F, D, T, V	D, A
Eng et al. (2017)	612	M, F, D, T, R, V, O	D, M, A
Hughes and James (1989)	16	M, F, D, V, O	M, A
Indicators of hydrologic alteration (Richter et al., 1996, 1997, 1998)	64	M, F, D, T, R, V	D
Olden and Poff (2003)	171	M, F, D, T, R, V, O	D, M, A
Poff (1996)	10	M, F, D, T, V	D, M, A
Poff and Ward (1989)	11	M, F, D, T, V	D, M, A
Puckridge et al. (1998)	11	D, V, O	M, A
Richards (1989, 1990)	7	M, V	D
USGS Stream Stats (USGS, 2021)	451	M, D, V	D
Wood et al. (2000)	36	M	M, A

Flow components refer to M = magnitude, F = frequency, D = duration, T = timing, R = rate of change, V = variability, O = other such as descriptions of distribution. Temporal resolution refers to H = hourly, D = daily, M = monthly, A = annual.

hydrologic variation, then a product of all these types results in 18,000 possible combinations, or unique, hydrologic types. As other examples, there are roughly 178,000 sub-basins across the world, where sub-basins are analogous to medium-sized river basins (Lehner and Grill, 2013), and there are at least 8.5 million river reaches globally with an average length of 4.2 km (Linke et al., 2019). If we assume each sub-basin or reach has its own unique hydrologic regime, then this suggests that the world has hundreds of thousands to millions of hydrologic signatures.

This immense variation, however, poses clear challenges to managing environmental flows in rivers. Particularly, there is a great need to generalize hydrologic behaviors and relationships with ecological processes in order to set water standards or general rules of thumb that protect the hydrologic components most critical to sustaining ecosystems. Classification systems help to consolidate variation in hydrologic regimes by generalizing rivers that behave similarly hydrologically. In doing so, hydrologic classifications provide management units, where types of rivers can be managed as a group rather than the individual hydrologic uniqueness of every river (Arthington et al., 2006). An overly simplistic classification might be grouping streams that have perennial, intermittent, or ephemeral flow, described in the "Water Cycle" section. However, this would provide little protection of variant seasonal or even interannual hydrologic patterns. In contrast, setting water policies for even 1000 different hydrologic types would be too complex for effective river management. Despite millions of hydrologic signatures unique to each river, river systems display reoccurring patterns in hydrologic regimes that predispose them to classification. The multi-collinearity and redundancy among hydrologic indices (Olden and Poff, 2003) further suggest that the dimensionality of multivariate measures of discharge can be dramatically reduced, specifically through clustering of hydrologic indices into groups or classes of hydrologic variation.

In the past 30 years, many hydrologic classifications have been developed to provide a fundamental understanding of hydrologic regime diversity (e.g., Poff, 1996) or to support environmental flow management (e.g., McManamay et al., 2012a) (Table 2). In a review of hydrologic classification efforts, Olden et al. (2012) distinguished two general approaches: deductive and inductive techniques. Deductive techniques use regional boundaries or grouping of environmental variations to infer regions of

Table 2 Examples of deductive and inductive approaches to hydrologic classification and a hybrid approach between the two.

Study	*Region*	*Spatial Resolution*	*Method*
Deductive			
Auerbach et al. (2016)	Ecuador	Small to large basins (100–600 km^2)	Used topographic, climate, soils, and land cover variables summarized in basins using Ward's hierarchical agglomerative clustering procedure and gap statistic for selecting optimal groups
Wolock et al. (2004)	United States	Small watersheds (200 km^2)	Ordination (principal component analysis) and clustering using a minimum variance criterion and the nearest neighbor chain algorithm
Snelder et al. (2005)	New Zealand	Stream Reaches	Hierarchical method where river segments were classified into groups for a number of different layers, each with different criteria
Inductive			
Archfield et al. (2014)	United States	Stream Gage	Used seven "fundamental daily streamflow statistics" characterizing the distribution of hydrology in a Ward's hierarchical agglomerative clustering procedure
Baker et al. (2004)	Midwestern United States	Stream Gage	Maps of four hydrologic groups were produced by partitioning gages by quartiles of values in Richard-Baker Flashiness Index
Haines et al. (1988)	Global	Stream Gage	Hierarchical clustering with average linkage procedure
Hughes and James (1989)	Victoria Australia	Stream Gage	Ordination via principal component analysis followed by hierarchical clustering using the average linkage procedure
Kennard et al. (2010)	Australia	Stream Gage	Used 120 hydrologic metrics in a non-hierarchical clustering using fuzzy partitioning Bayesian mixture algorithm
McManamay et al. (2012a,b)	Southeastern United States	Stream Gage	Used 66 hydrologic metrics in a k-means clustering procedure
McManamay et al. (2014)	United States	Stream Gage	Used 110 hydrologic metrics in ordination via principal components analysis followed by Gaussian mixture modeling with Bayesian parameter estimation
Monk et al. (2006)	United Kingdom	Stream Gage	Wards agglomerative hierarchical clustering procedure
McManamay and DeRolph (2019)	United States	Stream Reach	Clustering results for gages from McManamay et al. (2014) were used in a random forest model to map hydrologic classes to stream reaches
Poff (1996)	United States	Stream Gage	Using 10 metrics in a hierarchical clustering (density linkage) procedure
Puckridge et al. (1998)	Global	Stream Gage	Ordination via hybrid multidimensional scaling followed by hierarchical clustering using average linkage
Liermann et al. (2012)	Washington, United States	Stream Reach	Non-hierarchical clustering using fuzzy partitioning Bayesian mixture algorithm to classify gages to hydrologic groups. Predictive model was then used to assign gages to stream reaches
Hybrid approach			
Ouellet Dallaire et al. (2019)	Global	Stream Reaches	Average discharge, discharge seasonality, and hydrologic variability were simulated in WaterGap model (Döll et al., 2003) and then both supervised and unsupervised classification approaches were used to cluster streams

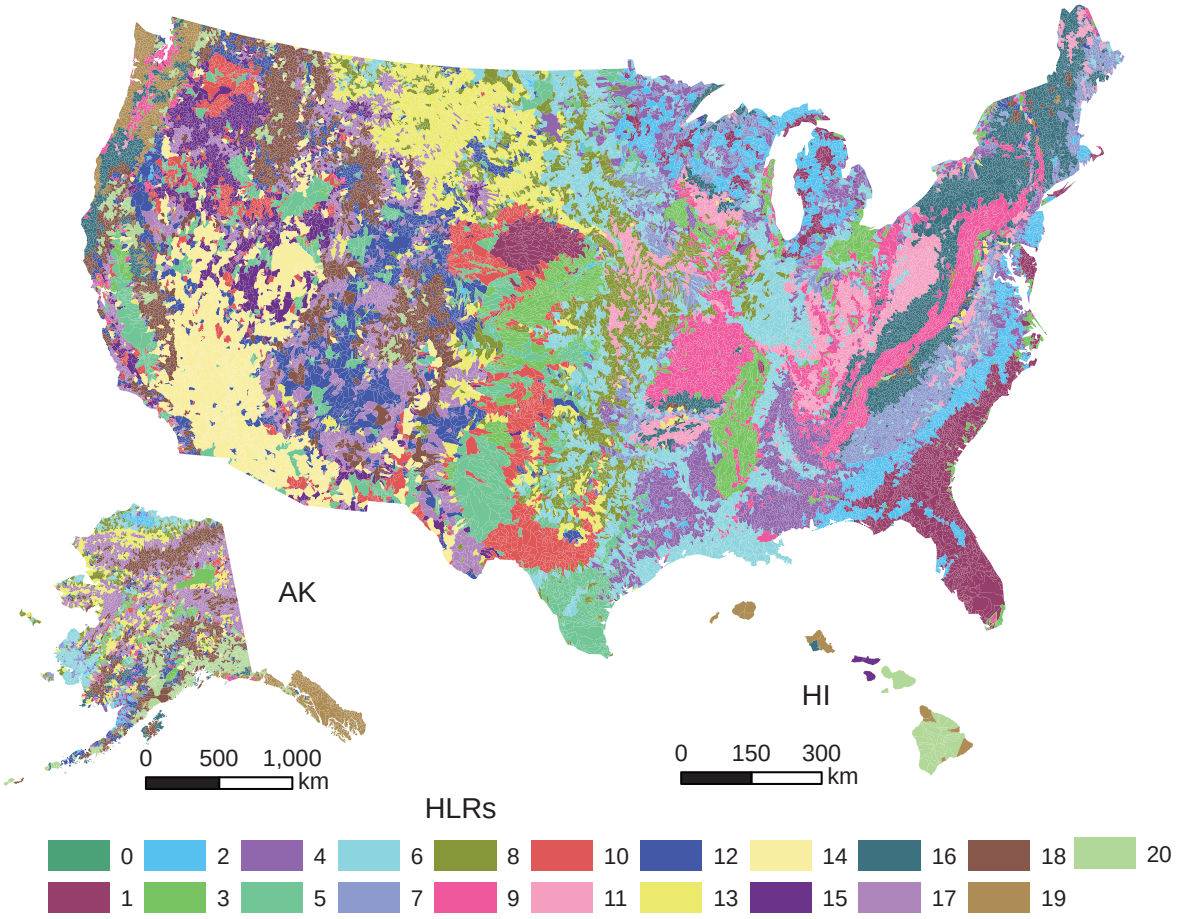

Fig. 9 Hydrologic landscape regions from Wolock et al. (2004) as an example of a deductive hydrologic classification technique.

similar hydrologic regimes, whereas inductive techniques directly use empirical hydrologic data to develop classifications (Olden et al., 2012). Deductive approaches rely on the logic of regionalization and best professional judgment, either assuming hydrology is similar within regional boundaries (Omernik, 2004) or that the variation of hydrologically relevant environmental variables (e.g., climate, soils, etc.) serve as reliable surrogates of hydrologic variation (e.g., Wolock et al., 2004; Snelder et al., 2005, 2011). Deductive approaches may be advantageous where crisp regional boundaries are preferred (Wolock et al., 2004), or in situations where hydrologic information is limited or unavailable (Auerbach et al., 2016). As an example, Wolock et al. (2004) assembled seven hydrologically relevant landscape attributes for over 40,000 small catchments in the US and then used principal components analysis and hierarchical clustering to yield 20 Hydrologic Landscape Regions (HLR) (Fig. 9). HLRs were used to stratify nationwide water quality study site locations by areas of similar hydrologic settings (Wolock et al., 2004). River systems are longitudinally organized into nested watersheds and tend to display hydrologic "inertia" despite flowing through different hydroclimatic regions (McManamay et al., 2012a). Because rivers may transect multiple regions, deductive regionalization may not accurately represent streamflow patterns, unless environmental attributes are structured according to relative importance of governing hydrology and developed a river reach-scale (McManamay et al., 2012b). Snelder et al. (2011) assembled climatic variables within nested watersheds of individual stream reaches to produce a deductive classification of rivers in New Zealand; this approach is presumed to more accurately represent differences in hydrologic regimes than regionalization approaches, as it was generated at the river-reach scale.

In comparison, inductive approaches rely on direct observations of discharge, and generally follow a stepwise procedure of summarizing streamflow records into statistics and then clustering streams based on correlative structure of hydrologic metrics (Olden et al., 2012). Inductive hydrologic classifications have been developed for individual states of the US (Kennen et al., 2007, 2009; Turton et al., 2008; Liermann et al., 2012), regions (Sanborn and Bledsoe, 2006; Chinnayakanahalli et al., 2011; McManamay et al., 2012a,b), continents (Kennard et al., 2010; McManamay and DeRolph, 2019), and the world (Haines et al., 1988; Ouellet Dallaire et al., 2019). Because inductive classifications are based on empirical observations of streamflow, they more accurately distinguish hydrologic regimes than regionalization or environmental surrogate approaches (McManamay et al., 2012b); however, until recently, inductive approaches were limited to locations with streamflow observations, leaving many ungauged rivers without

hydrologic class membership. Advances in geospatial datasets and statistical modeling (e.g., machine learning) have provided new opportunities to extrapolate class membership to ungauged river systems (e.g., Liermann et al., 2012; McManamay and Derolph, 2019), which is discussed below. Inductive classifications vary in the composition of hydrologic indices used to represent hydrologic variation, the statistical decomposition approach to reduce multicollinearity and dimensionality, and the clustering procedure to develop groups, all of which influence the classification outcome and interpretation of hydrologic regimes. Clustering procedures have varied from hierarchical or agglomerative statistical approaches (e.g., Poff, 1996; Monk et al., 2008; Archfield et al., 2014), to k-means procedures (Poff and Ward, 1989; Snelder et al., 2009; McManamay et al., 2012a,b), to "fuzzy" partitioning methods using Bayesian mixture modeling algorithms (Kennard et al., 2010; Liermann et al., 2012; McManamay et al., 2014) (Table 2). Ward's agglomerative procedure has been the most used statistical approach and is commonly preferred, as it yields interpretable results, clean cluster membership (not fuzzy membership), and cluster membership robust to the order of observations (compared to non-hierarchical approaches) (Olden et al., 2012). Aside from the choice of clustering algorithm, another important, yet rarely discussed, decision that noticeably influences clustering outcomes is whether to standardize magnitude-related hydrologic metrics according to river size. Standardizing metrics typically consists of dividing all magnitude-related variables by mean or median annual flow or drainage area prior to clustering (e.g., Poff, 1996; Kennard et al., 2010; McManamay et al., 2014). In the case of unstandardized approaches, raw values of metrics are used in clustering procedures (e.g., Archfield et al., 2014). Leaving magnitude-related metrics unstandardized results in classes influenced by drainage area, whereas metric standardization ensures class distinction is based on relative variation in hydrologic regimes. In the latter case, rivers of varying size may share similar cluster membership based on similarities in hydrologic behavior or signatures, regardless of the differences in flow volumes. Once standardized hydrologic classifications are developed, highly predictable relationships between drainage area and flow magnitudes can be developed (e.g., McManamay, 2014; McManamay et al., 2013).

Numerous examples of both deductive and inductive approaches are provided in Table 2. As mentioned previously, one of the past limitations of inductive approaches was that they were limited to only locations of empirical observations of streamflow, leaving many rivers without class membership; however, multiple recent approaches have used predictive models to extrapolate hydrologic classes from stream gages to ungauged reaches (e.g., Kennard et al., 2010; McManamay et al., 2014; McManamay and DeRolph, 2019) (e.g., Fig. 10). These approaches take advantage of compilations of geospatial climate and landscape variables summarized for the entire stream network draining to each river reach. For example, there are over 2.6 million stream reaches within the NHDPlus V2 dataset for the conterminous United States (CONUS) (EPA, 2020). For every NHDPlus stream reach, large suites of variables (climate, topography, geology, soils, and land cover) have been summarized for the entire drainage area upstream of each reach (e.g., StreamCat dataset, Hill et al., 2016). This provides a tremendous resource for extrapolating hydrologic class membership to all streams within a region. Recently, McManamay and DeRolph (2019) leveraged the StreamCat dataset within a predictive model to extend hydrologic class membership to all 2.6 million stream reaches in the CONUS (Fig. 10). Ouellet Dallaire et al. (2019) used a novel hybrid deductive-inductive approach to yield a global stream classification product at a river reach scale (Fig. 11). Rather than generate empirical hydrologic classes to extrapolate to ungauged reaches, the authors used synthetic estimates of mean monthly flow and flow variability from hydrologic models (Döll et al., 2003; Lehner et al., 2008) to cluster river reaches into hydrologic types (Fig. 11).

Applying hydrologic classifications to river management

Significant effort has been devoted to the science of developing hydrologic classifications, including the selection of reference-quality stream observations, hydrologic metrics, and clustering procedures (see examples in Tables 1 and 2). Despite this tremendous volume of research, far less effort has been devoted to the application of hydrologic classifications to advance the science of environmental flows; however, those efforts have increased considerably in recent years. Poff and Zimmerman (2010) suggest that the successful development of environmental flow standards requires regional specificity and context, perhaps partially addressed through hydrologic classifications.

Arthington et al. (2006) originally conceptualized hydrologic classifications as the basic management unit for developing environmental flow standards, specifically by providing a stratified approach to examine how river hydrology and ecological communities respond to human-induced hydrologic alteration. As a consensus among many international scientists, the Ecological Limits of Hydrologic Alteration (ELOHA) framework was proposed as a synthesis of science and techniques for determining environmental flow needs for rivers at regional scales (Poff et al., 2010). ELOHA constituted a paradigm shift in the approach to environmental flow management by focusing on defining environmental flow standards for groups of rivers rather than recommendations for individual systems. The central premise of ELOHA is developing flow alteration-ecological response relationships for each hydrologic class within a region; this information base is then used to by stakeholders to determine socially acceptable "limits" to hydrologic alteration and establish environmental flow standards for each hydrologic type. Since its conception, the ELOHA framework has been formally applied in at least 20 US states and several other countries, including the United Kingdom, Tanzania, South Africa, Australia, China, Colombia, and Mexico (TNC, 2020; Kendy et al., 2012; Liermann et al., 2012; McManamay et al., 2013; Mackay et al., 2014; Tavassoli et al., 2014; Martin et al., 2015).

Applications of the classification-based ELOHA process vary depending on the environmental flow management needs for different regions. Examples of studies include the following: examining whether dam regulation alters streamflow differently depending on hydrologic class membership (McManamay et al., 2012c; Mackay et al., 2014); evaluating associations between

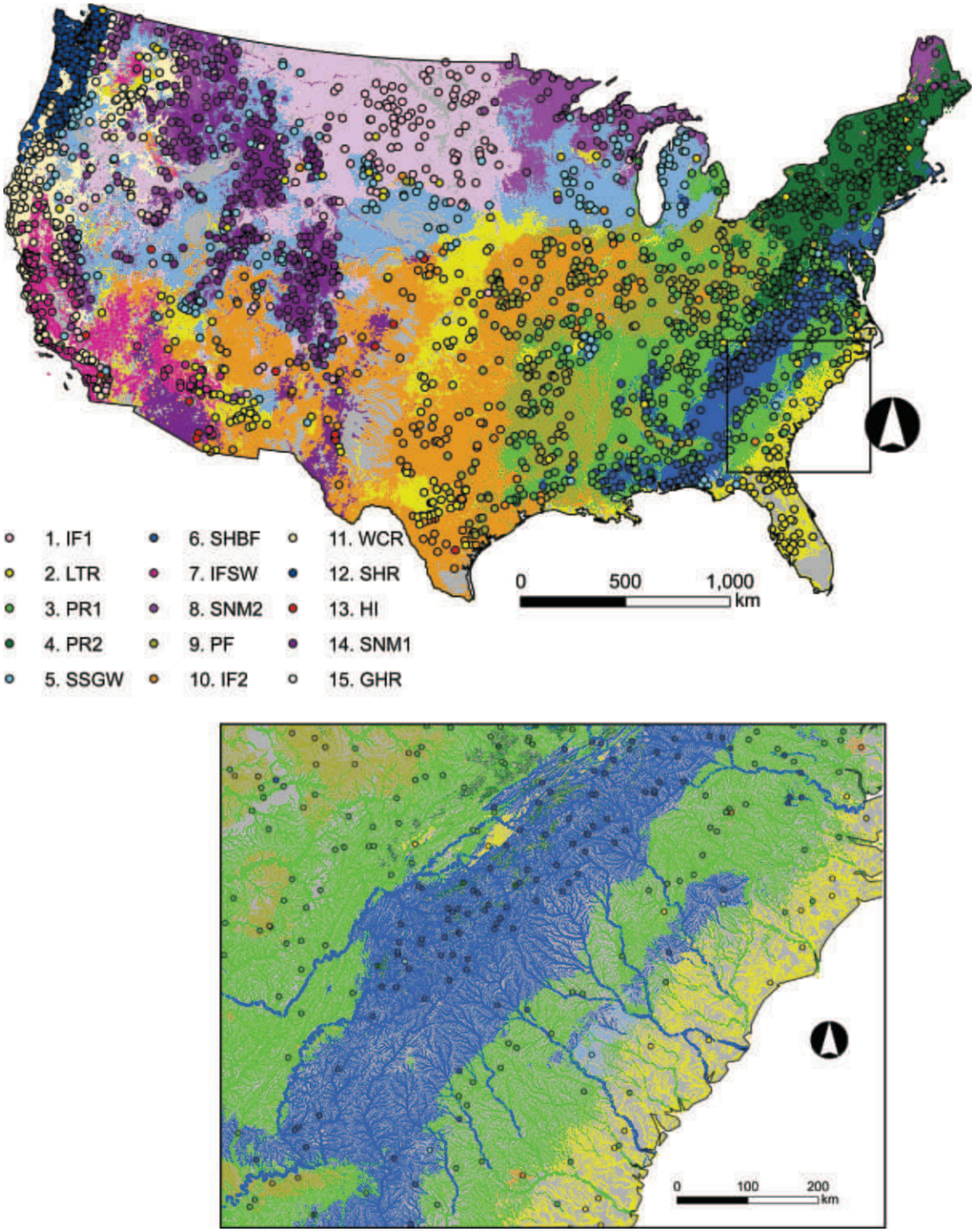

Fig. 10 Hydrologic classification at the stream reach level for the United States developed by McManamay and DeRolph (2019). An inductive approach was used to classify discharge statistics from stream gages into different groups. Predictive models were then used to extrapolate group membership to all streams based on climate and landscape characteristics.

hydrologic classes and community ecology patterns (McManamay et al., 2015a); determining how hydrologic regimes and variation may shift in light of climate change (Liermann et al., 2012); quantifying "ecological limit functions" specific to ecoregions (as opposed to hydrologic classes) (Knight et al., 2014); and testing ELOHA in prescribing flow restoration measures in dam regulated rivers (McManamay et al., 2013, 2015b). The science of environmental flow development continues to rapidly advance and ELOHA applications are still ongoing. More research is needed to understand how generalities in hydrologic behavior can be used to inform regional environmental flow standards.

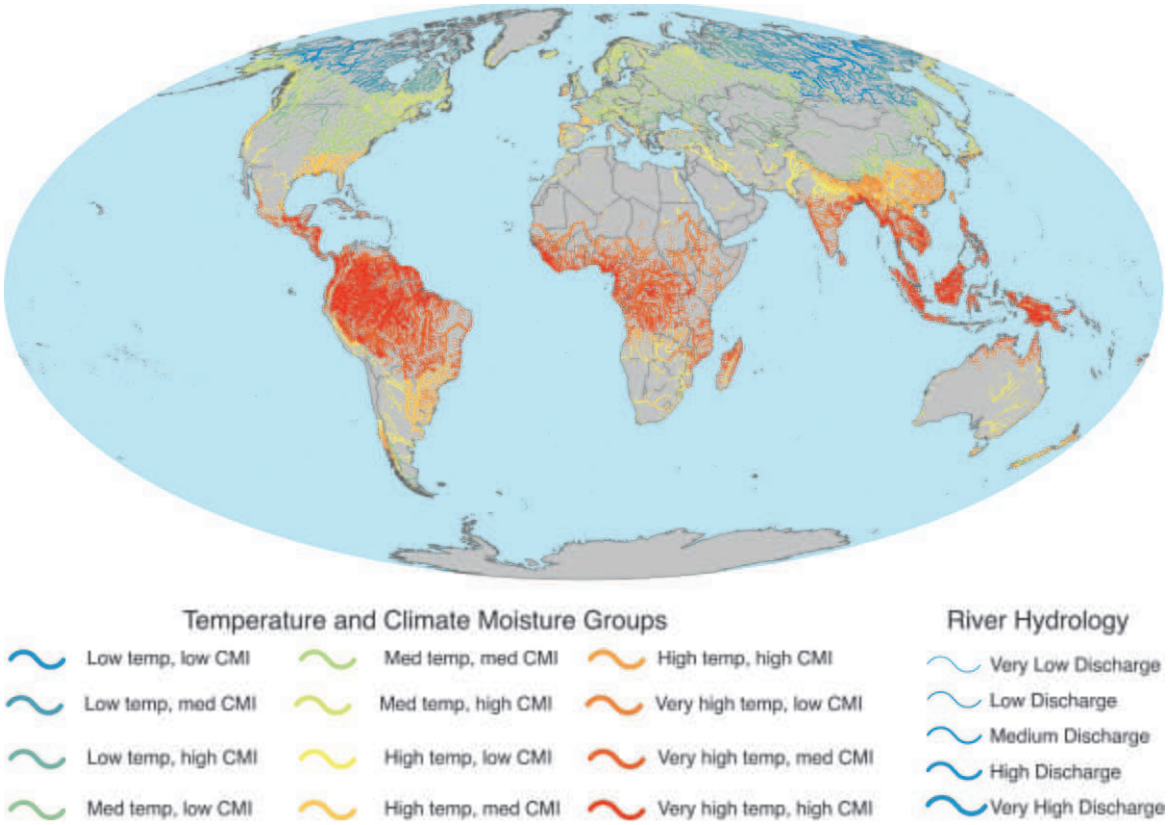

Fig. 11 A hybrid inductive-deductive hydrologic classification approach for streams of the world taken by Ouellet Dallaire et al. (2019). Streams were classified according to climate and hydrologic properties. Climate included temperature and climate moisture index (CMI). The WaterGap model (Döll et al., 2003) was used to model discharge in order to develop the river hydrology classification.

See Also: Structures and functions of Inland Waters - Rivers: Intermittent Rivers and Ephemeral Streams

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Riparian Zones

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Allochthonous External organic carbon contributed to an aquatic ecosystem (often from riparian areas).
Alluvial Material deposited as a result of fluvial processes.
Anoxic Soils with low levels of oxygen due to submergence and microbial oxidation-reduction processes.
Colluvial Deposits of rock, sediment and debris from side slopes resulting from gravitational delivery.
Endorheic basins Drainage basins that terminate in the interiors of continents into wetlands, lakes or mudflats rather than oceans or larger rivers. Endorheic basins are also called closed, terminal and internal basins.
Environmental flows The timing and quantity of stream flow required to sustain freshwater and estuarine ecosystems and the human livelihoods and well being that depend on these ecosystems.
Fluvial Of, relating to, or produced by flowing water.
Hydrophytic A plant that is adapted to living either in waterlogged soil or partly or wholly submerged in water.
Hyporheic Subsurface alluvial, saturated zone driven by groundwater that is connected to surface flows.
Process domain Spatially identifiable areas characterized by distinct suites of geomorphic processes in which ecological community structure and dynamics respond to distinctly different disturbance regimes.
Riparian Areas along/adjacent to stream channels and influenced by streamflow and fluvial processes associated with river flow and sediment regimes, surface and groundwater interactions, and region-specific disturbance regimes, species pools, and climates and geologies.
Riverine Aquatic and riparian ecosystems occurring along streams and rivers and influenced by streamflow volumes, stream processes, and human influences.

Introduction

The intent of this chapter is to define riparian ecosystems and to describe their range, distribution, extent and diversity of forms and functions worldwide. This section will briefly describe the processes governing aquatic and riparian (together "riverine") forms and functions, highlight natural and human-caused threats to them, their conservation, as well as discuss scientific opportunities in the field of riparian ecology. Riparian is derived from Latin word *riparius* (feminine *rīpāria*, neuter *rīpārium*) meaning "of or belonging to the bank of a river." Riparian areas are features of the landscape that are adjacent to rivers and streams and governed by river hydrology and associated fluvial processes. For the purpose of this overview, the banks and floodplains of flowing water (lotic) systems such as rivers, streams and spring outflows that are influenced by processes associated with open channel flow (fluvial) are considered riparian. Marshes, wet meadows, pond and lake margins not associated with flowing water may share many of the patterns, processes and functions of riparian ecosystems but are not considered riparian.

In addition to forming networks of various forms (e.g., dendritic, trellised, parallel, pinnate, etc.) that drain water, mineral sediment, wood and other organic material and dissolved compounds (and propagules) from watersheds, streams, rivers and their riparian zones perform many valued ecological and societal functions and services. Riparian ecosystems are among the most complex and diverse ecosystems on Earth, yet occupy only roughly 3% of the Earth's land surface, though this varies significantly from region to region (Lehner and Doll, 2004) (Fig. 1). Riparian habitat, which is typically distinct from and more productive and

Fig. 1 (A) High Cascade montane, step-pool, herbaceous vegetation-dominated stream, Oregon, USA (D. Cooper). (B) High Andes, herbaceous-dominated, Pastoruri River, Peru (D. Cooper). (C) Mogollon rim, pool-riffle, tree-dominated West Clear Creek, Arizona, USA (J. Monroe). (D) Mediterranean montane, pool-riffle, tussock-forest Sordo River, northeastern Portugal (F. Aguiar). (E) Wet-tropical, pool-riffle, liana forest stream, Little Mulgrave River, north Queensland, Australia (B. Pusey). (F) Temperate rainforest, cascade, conifer-dominated Mackenzie River, Oregon, USA (D. Herasimtschuk). (G) Boreal, pool-rapid Vindel River, northern Sweden (D. Merritt). (H) Colorado Plateau, canyon, pool-rapid Yampa River, Utah, USA (D. Merritt).

(Continued)

Fig. 1—Cont'd (I) High Himalayan plateau, pool-riffle, herbaceous vegetation-dominated, Baihi River, Hongyuan County, Tibet (D. Cooper). (J) Colorado Plateau, meandering, gallery forest, Green River, Utah, USA (D. Merritt). (K) Boreal, pool-rapid river, coniferous dominated, Vindel River, northern Sweden (Jonas Svedmark). (L) Sonoran desert, shrub-dominated, ephemeral wash, Yuma River, Arizona, USA (D. Merritt). (M) Large leveed floodplain, human-influenced, Danube River, Austria (D. Merritt). (N) Bedrock stream, Quebrada Sonodora River, Puerto Rico (D. Herasimtschuk).

physically and biologically diverse than adjacent upland habitats on all continents, represents a transitional zone, or ecotone, bridging uplands and aquatic habitats, and performs functions and supports ecosystems that are uniquely riparian compared to adjacent uplands (Naiman and Décamps, 1997; Sabo et al., 2005; Ward and Tockner, 2001).

Many riverine functions valued by humans are performed by riparian areas, which provide sites for detention, storage, uptake and biochemical transformation of a range of minerals, chemical compounds and organic material—performing water purifying processes (Wohl, 2021). Most often flowing through the lowest position in any landscape, river channels collect water, sediment, seeds and vegetation propagules, wood and other materials from surrounding landscapes. Riparian areas provide habitat for wildlife, carbon, nutrients, and channel maintenance functions, such as stabilizing banks and influencing hydraulics and sediment mechanics (Merritt, 2020). Riparian vegetation governs vertical and horizontal habitat structure, generates and delivers organic material which, along with autochthonous production, provides the basis for aquatic food webs. Further, the rich diversity of vegetation in riparian areas provides pollen, nectar, shelter, cavities, nest sites, wood inputs to streams, nutrient uptake, sediment detention, bank stabilization, thermal regulation, and microclimatic drivers that collectively contribute to the functions, values, and

biotic diversity of these areas (Baruch et al., 2021; Merritt and Bateman, 2012). Whereas larger flowing rivers serve as valuable transportation corridors for humans, and for many aquatic and amphibious species, adjacent riparian zones also serve as corridors for movement, resting sites for migratory species, and permanent or seasonal habitat for myriad organisms. Riparian areas and their health may be assessed through quantifying bird, arthropod (e.g., spider and butterfly), plant species richness, and overall diversity and community composition.

Riparian areas exhibit functional connectivity: (1) longitudinally, in an upstream to downstream dimension, connecting otherwise disconnected landscape elements and two way exchanges between the interiors of continents and oceans; (2) laterally through seasonal and/or permanent interaction with floodplains and valley bottoms outside of the river channel itself through exchanges of water, sediment, carbon and other chemical compounds and biotic components; and (3) vertically, extending from deep confining bedrock into the hyporheic zone (groundwater interacting with the river) and fluvial sediments, and up through the vegetation canopy into the atmosphere. As with all other ecosystem types, the fourth dimension considered important for riparian areas is change through time, which may be accelerated and dramatic along rivers, particularly in alluvial river systems, which may have high turnover of substrate, channel forms, and vegetation and other biotic patterns compared to other non-fluvial ecosystems.

Because riparian areas are typically transitional areas that span an aquatic to terrestrial gradient, components of many terrestrial ecosystems occur in riparian areas and this transition between riparian and adjacent uplands may advance and recede through time. Riparian areas vary as a function of climate, structural and Quaternary geology, evolutionary history, position within in channel networks, and direct and indirect human influences, and it is difficult to make broad generalizations or singularly describe riparian areas globally. Further, descriptions of patterns and processes in riparian areas must be placed within the context of the appropriate spatial scale. Riverine ecosystems are hierarchically organized from whole networks within large watersheds exceeding 7 million km^2 to sub-watersheds smaller than 1 km^2 representing a range of stream and river sizes. Within sub-watersheds, segment-scale valley and channel forms occur, and are comprised of reaches, sub reaches, geomorphic units, and at the smallest scale, microhabitats (<1 m^2) (Frissell et al., 1986). Each level in the continuum of scales in this nested organization is to some degree, governed by processes acting at the higher spatial scale. Riparian areas are a function of all processes occurring at each of these scales throughout a watershed and stream network. Therefore, understanding and interpretation of processes or patterns occurring at a microhabitat or reach scale must be considered with an understanding of processes occurring throughout the network, adjacent uplands within the watershed, and with an awareness of historical legacies, both natural and anthropogenic (Fig. 2).

It is with this definition of riparian ecosystems, and in the context of their diversity of form and function, that we consider the processes and patterns that all riparian ecosystems in the world share and what makes riparian areas distinct from other freshwater and terrestrial ecosystems.

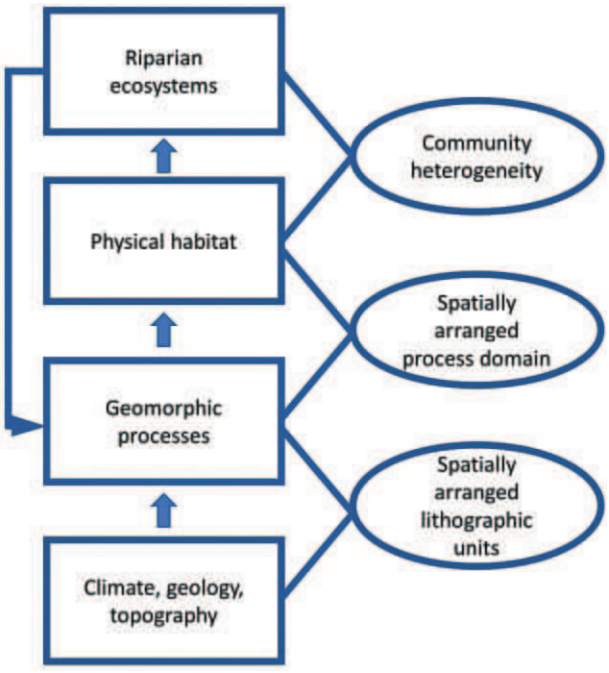

Fig. 2 Relations among geomorphic processes, habitat structure, and riparian ecosystems (left) and spatial hierarchy for examining geological controls on ecological systems (right). Redrawn and modified from Montgomery DM (1999) Process domains and the river continuum. *Journal of the American Water Resources Association* 35: 397–410.

Riparian ecosystems

Physical attributes of riparian ecosystems

The primary drivers of and constraints upon river processes include climate and geology. Climate determines the amount, timing, form (glacial melt, snow, rain, groundwater, etc.), and seasonal variability of water availability, governing hydrologic regime and geology and recent geologic history sets the template upon which water and sediment is routed. For example, rivers that flow through broad low gradient landscapes have distinct physical forms, riverine ecosystems, and functions compared to those that flow through (and perhaps carve) canyons or glacial valleys. Rates of chemical and physical weathering, solar radiation, temperature and atmospheric demand for moisture and are also governed directly or indirectly by climate. However, the routing of this water, the drainage network of watersheds, and channel geometry and geomorphic processes are conditioned by geology, both ancient and recent (i.e., <90 K years ago).

Globally, there are over 11.8 million kilometers of streams and rivers, a vast majority of these watercourses are ephemeral (flowing for part of the year) or intermittent (flowing for only part of their length) (Grill et al., 2019). Riparian areas and the river floodplains they occupy range from a few meters wide in headwater reaches to 250–330 km wide on deltas of very large rivers such as the Nile and Amazon, respectively. Estimates of the extent of river floodplains on Earth are on the order of 4 million km^2 (Lehner and Doll, 2004). In flowing from mountains and higher elevations on continents to the sea, streams increase in streamflow and volume of mineral sediment, dissolved compounds and organic material, whereas channel particle size and river channel gradient decrease. Headwater and mountain streams are typically higher gradient and erode and transport sediment (as transport capacity typically exceeds supply of sediment), transitional reaches largely transport sediment; and depositional reaches along larger (higher order) streams have lower gradients and may terminate in larger order streams, estuarine deltas, or endorheic basins in the interiors of continents. Timing and volume of flow and sediment and the hydraulic complexity of streamside and floodplain habitats are intimately tied to the structure, form and function of riparian areas.

The combination of climate and geology (and dominant geomorphic processes occurring) along a particular river reach or within a hydroclimatic regime are referred to as process domains (Montgomery, 1999)—suites of characteristic disturbance and recovery cycles governed by the dominant geomorphic processes. Different process domains have characteristic magnitude, frequency and duration of the physical ecological disturbances and periods of recovery, which influence riparian areas. Process domains vary in ecologically important ways along the course of a river and throughout a catchment. For example, in mountainous areas, colluvial inputs along confined canyons may dominate, whereas alluvial processes dominate along higher order, lower gradient reaches further downstream in a watershed (Friedman et al., 2006). Study of process domains reveals that along rivers, the main geomorphic units relevant to riparian ecosystems are hillslopes, channels and floodplains. The influences of geomorphic processes acting at these scales define the process domain and influence riparian functions and patterns (Fig. 2).

Valley morphology (gradient, lateral confinement, and form) and subsurface sediment stratigraphy and physical properties of valley fill also control surface water and groundwater patterns and their interactions (Fig. 3). Geologic controls on down valley and vertical groundwater movement have been shown to drive changes in the presence and productivity of key riparian trees (Harner and Stanford, 2003; Stanford and Ward, 1993; Wohl, 2021). Transitions from wide valleys with deep alluvial fill to narrow bedrock-constrained reaches result in upwelling of alluvial groundwater and nutrients, creating conditions that support productive riparian forests that may be absent or sparse in wider valley sections with deeper groundwater (Fig. 4).

Worldwide, many distinct forms of rivers have been recognized, each varying from ecoregion to ecoregion and position in the watershed from headwaters to terminus. The range of forms of high gradient streams include straight, cascade, plane bed, pool-riffle, and step-pool (Montgomery and Buffington, 1997) whereas lower gradient channels may take on braided, anastomosing, anabranching, and meandering pool-riffle forms (in order of decreasing channel gradient) (Leopold and Wolman, 1957; Tooth et al., 2008) (Fig. 1). Riparian vegetation establishment, survival, physiognomy, community composition, age-class structure and diversity all vary as a function of channel form, surface and groundwater hydrology, the frequency, intensity, form, and frequency of

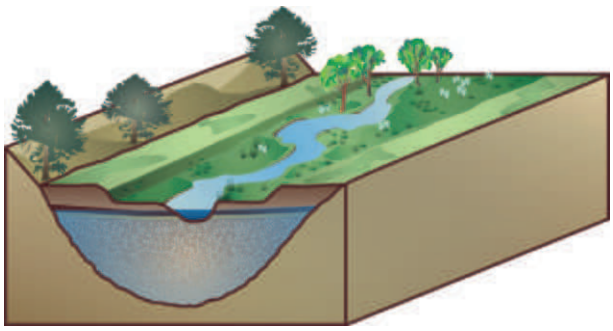

Fig. 3 Block diagram showing the three-dimensional nature of riparian areas. The diagram highlights the interconnectivity between the surface flow in the stream channel, the groundwater system, and the interface between floodplain sediments (and their stratigraphy) and the deeper alluvium (hyporheic zone). Zonation of vegetation from hydrophytic disturbance-tolerant plants near the channel to upland conifers along the valley perimeter is illustrated. A fourth dimension is change through time, which may be event-driven (flood and fluvial disturbance) or gradual (channel migration) and is accelerated in riparian areas.

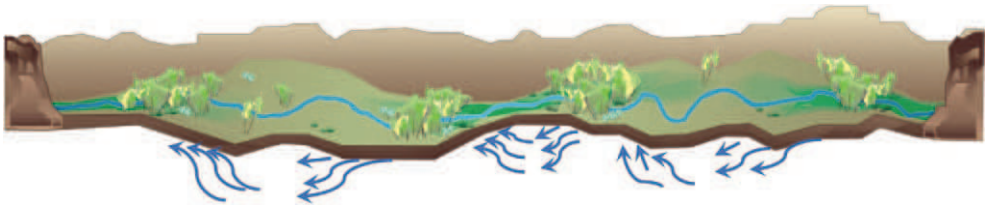

Fig. 4 Oblique view of a reach of river with alternative narrow and wide valley walls. Blue arrows indicate upwelling of groundwater along gaining reaches where groundwater is forced toward the rhizosphere of plants and downwelling along losing reaches. Studies show that primary productivity (growth rate) and nitrogen content of riparian trees are higher in areas of upwelling when compared to areas of downwelling. This higher growth rate is attributed to higher water availability along upwelling reaches and an order of magnitude greater concentrations of nitrate and soluble reactive phosphorus in these areas compared to losing reaches. Hyporheic flow enhances tree growth and leaf quality, thereby influencing soil and aquatic food webs of alluvial floodplains. From Harner MJ and Stanford JA (2003) Differences in cottonwood growth between a losing and a gaining reach of an alluvial floodplain. *Ecology* 84: 1453–1458.

disturbance. Meandering rivers may migrate back and forth across river valleys through time through the process of cutbank erosion and point bar extension. As point bars are often bare and seasonally inundated, these areas serve as sites where pioneer plant species may colonize. The presence of plant stems facilitates accelerated rates of sediment deposition and bar extension. As channels migrate and bars aggrade, arcuate bands of even aged vegetation may form in a successional sequence away from the channel as former bars aggrade to become floodplains—far from and at higher elevations above bars in the active channel.

The formation, maintenance, abandonment and destruction of channels and floodplains resulting from deposition and scour, result in floodplains, braidplains, and fluvial features that may be expressed on the surface as meander scrolls, chutes, oxbow lakes, abandoned floodplains as well as various subsurface stratigraphic features that are ecologically important. Deposits reflect past fluvial processes and may result in layering or lenses of sediment which influence the movement of groundwater, capillary rise, aeration and anoxia, soil chemistry, and the availability of moisture and nutrients to plants. Former low energy, slackwater areas such as those upstream from beaver dams or other obstructions to flow, backwaters and oxbow lakes resulting from the meandering process and abandonment of former channels, and overbank flood deposits may result in lenses or veneers (of various depths and volumes) of fine sediment with high water holding capacity. When buried by subsequent deposits, stratigraphic series are formed, imparting a diverse three-dimensional subsurface microhabitat into which plants may root and vegetation and habitat mosaics form.

River hydrology is influenced by a combination of surface and groundwater interactions. Seasonal and interannual patterns of hydrology along rivers are driven by the sources of moisture driving flow and flow regime. Sources of moisture include snowmelt, convective, frontal or monsoon rainstorms, groundwater discharge and any combination of these as influenced by localized and upstream climate and topography. The major streamflow components that are essential to riparian ecosystem functioning include low flows or base flows, intermediate and extreme peak flows, spates and small flow pulses, rates of change, number of peaks, and interannual variability in these components. Variations in climate, geology and landscape patterns result in regionally distinct natural flow (McManamay and DeRolph, 2019; Poff et al., 1997) and sediment regimes (Wohl et al., 2015) resulting in characteristically-timed flow components, rates of change, annual averages and extremes in streamflow and sediment entrainment, transport and deposition. Sediment regime is also key and is driven by geology, vegetation cover of uplands, and driving variables (such as overland flow) that connect uplands to valley bottoms and riparian and aquatic systems. Classifications of flow regimes of rivers highlights the regional heterogeneity that contributes to beta diversity of channel forms and processes, disturbance regimes, and aquatic and riparian ecosystems across continents (Mcmanamay and DeRolph, 2019).

Three of the most important functions of riparian forests and floodplain vegetation include: (1) supporting high species diversity through providing complex and productive micro and macro habitats, (2) influencing fluvial processes through providing substrate stability (roots), serving as roughness elements (stems, canopy, large wood) which affect fluvial processes and sedimentation in riverscapes, and (3) influencing primary productivity, biogeochemical processes, nutrient and carbon dynamics on floodplains and in aquatic habitat.

Biological attributes of riparian ecosystems

The tremendous variety of species utilizing and dependent upon riparian areas among rivers worldwide include combinations of upland, transient (annual, opportunistic, and colonizing/pioneer species) along with uniquely riparian, wetland and upland species. Species unique to riparian areas include those possessing adaptations enabling them to tolerate transient periods of flooding, drought and fluvial disturbance (Merritt et al., 2010). Water availability is generally higher in riparian zones, but it fluctuates seasonally as a function of surface flow, local and basin-wide weather patterns and groundwater regimes. The selective pressures associated with life in riparian areas have resulted in plants, insects, and animals with unique sets of physical and physiological adaptations (Lytle and Poff, 2004). The seasonal variability in hydrologically dynamic riparian systems can result in anoxia and drought along river margins over the course of a season, requiring sessile organisms such as plants to either tolerate such diverse stresses, develop adaptations (through natural selection) to survive them, or to avoid them all together (Grime, 1979). These suites of adaptations reoccur in riparian habitats worldwide, generating characteristic vegetation with similar physiognomies on depositional sandbars, in side channels and floodplain depressions, and in transitional areas near the riparian-upland transition (Lytle and Poff, 2004; Merritt et al., 2010) (Fig. 1).

Functional groupings (also known as guilds) of riparian species provide insight into the selective pressures associated with life in riverine habitats, often resulting through convergent evolution in unrelated species with similar sets of physical and physiological traits in different regions and continents (Merritt et al., 2010). Such traits may include the synchrony of phenology (e.g., timing of emergence, flowering, dispersing seeds) with components of the flow regime (Mahoney and Rood, 1998), the ability to tolerate fluvial disturbance (resprout ability/vegetative reproduction, adventitious rooting following burial, furrowed bark to resist abrasion) (Karrenberg et al., 2002), and the ability to disperse propagules along waterways (hydrochory) to enhance both dispersal distance and delivery of propagules to suitable habitats (Nilsson et al., 2010) and other riverine-specific adaptations.

Whereas ecologists have noted a trade-off between productivity and species diversity in terrestrial plant communities, riparian areas often exhibit both high diversity and high productivity due to a variety of interrelated factors associated with water availability, fluvial disturbance and rapid rates of decomposition and nutrient cycling (Araujo Calçada et al., 2015). Vegetation, habitat, species distributions and diversity vary in predictable ways longitudinally along a river's course and laterally from channel to uplands, as will be discussed below. Some fundamentals of these relationships will be discussed with examples from different riparian ecosystems from around the world.

Longitudinal connectivity and patterns of riparian diversity

There is no universal pattern of change in riparian biodiversity along longitudinal gradients traversing headwaters to terminus along river corridors. Some studies have shown that plant diversity peaks in intermediate reaches of large boreal rivers draining from the Scandic Mountains to the Baltic coast in Sweden (Nilsson et al., 1994). This pattern is attributed to the accumulation of propagules as a function of downstream distance (and the coalescence of water-transported seeds from tributary inflows to the mainstem) and to habitat heterogeneity that provides a combined boost in concentrations of microhabitats and potential species richness (Jansson et al., 2000). Higher plant species biodiversity in middle reaches of rivers flowing into the Baltic Sea in Sweden was shown to result from complex microhabitats associated with the transition from formerly glaciated landscapes to those that had once been submerged by a previously higher sea-level that resulted in deposited beach sediments and paraglacial substrates (Renofalt et al., 2005). Transition zones tend to have higher diversity due to the high concentration of habitats (habitat heterogeneity) in these areas (Tockner and Ward, 1999). In China, riparian plant species richness was shown to increase in a downstream direction along the Beijiang River (Zhao et al., 2018), whereas the San Pedro River in Arizona, United States exhibited highest richness at intermediately disturbed sites (Lite et al., 2005). In other river systems, diversity may be highest in headwaters or at the terminus and diversity can be elevated at tributary junctions (Osawa et al., 2010) and areas with shallow or upwelling groundwater (Fig. 4) (Jansson et al., 2007).

The lack of a globally consistent pattern of diversity varying along longitudinal gradients within river basins is in part due to the importance of local (reach and segment-scale) controls on species richness and to the variety of climates and geologies that river systems traverse (Kuglerova et al., 2015). Diversity throughout a river network is fundamentally limited by the regional species pool and a function of the magnitude, frequency and duration of disturbances (intermediate levels of disturbance have been associated with high species richness across taxa), the distributions of resources (water and nutrients), and the heterogeneity of habitats. Insect, bird and mammal diversity has been shown to track habitat heterogeneity, which stems from diversity of form and function of riparian vegetation. As a consequence, longitudinal patterns of diversity of insects and animals along riparian corridors are concordant with species and structural diversity patterns of riparian vegetation. Riparian trees serve as an important link between subsurface and surface hydrology and nutrient dynamics on floodplains, "affecting multiple trophic levels across aquatic and terrestrial food webs" (Tibbets and Molles, 2005).

Riparian areas have been shown to be relatively invasible by non-native species, and non-native species play a significant role in riparian plant communities from tropical to temperate zones. Among the factors identified to explain invasibility of plant communities include richness of incoming propagules (species pool), the presence of recruitment sites, and sites in which "harsh" environmental stressors are uncommon (Zefferman et al., 2015). Harsh habitats include sites with one or more abiotic stressors, including low levels of limiting resources, temperature extremes, and mechanical disturbance. For plants, limiting resources include nitrogen, phosphorous, oxygen and water and other factors that can contribute to harsh habitats include the presence of toxins in the soil. Indeed, the frequency of invasive plant species tends to be lower at colder temperature extremes such as high elevations and latitudes for plant communities (Zefferman et al., 2015). Mechanical disturbances that remove biomass and cause mortality may also be considered a stressor for individuals occupying such sites, but the bare, moist, sunny sites that are created from such disturbances along rivers serve as important areas for colonization by native and non-native species alike. Because disturbance and propagule delivery increase as a function of downstream distance, higher order streams are generally more susceptible to invasion than smaller, higher elevation streams.

In many parts of the world, rivers and riparian zones have been shown to be corridors of plant invasion. Examples of invasives that have become dominant in areas once introduced include northern hemisphere *Salix* spp. in Australia, Eurasian *Tamarix* spp. in western North America, south-eastern Australian *Acacia mearnsii* in South Africa, Himalayan *Impatiens glandulifera* in Europe, and Mexican-Central American *Leucaena leucocephala* throughout Indonesia. Invasive mammals in riparian areas may also have significant impacts on rivers and their riparian ecosystems. For example, nutria (*Myopotamus coypus*) introduced from South America into the southeast United States, North American beaver (*Castor canadensis*) introduced to southern Chile, and North American mink (*Neogale vison*) in northern Europe have had impacts on river channels and habitats and compete with native species for resources and space. Many successful non-native colonists are pre-adapted to the conditions along river margins where they are introduced, whereas others tend to succeed (or become dominant) in response to alteration of natural processes that support native

riparian vegetation (e.g., human development, flow alteration, climate change) (Merritt and Poff, 2010). In some cases, invasive species influence biodiversity through becoming dominant (even forming monocultures), whereas in other areas they may enhance local diversity by coexisting with native species.

Because riparian corridors traverse an elevational gradient and many larger rivers cross multiple ecoregions (climates and geologies), riparian areas contribute to regional and continental-scale beta diversity. In the Pacific Northwest of the United States, nearly two thirds of all plant species within one catchment were found in the riparian corridor, which occupies less than 10% of the catchment area (Naiman et al., 2005). According to other reports, all seasonally flooded floodplain forests in the Amazon basin may harbor about 53% of the 6727 estimated Amazonian tree species (Luize et al., 2018), and about 30% of the 1400 vascular plant species in the flora of France occurs along the Adour River riparian corridor in France (Décamps et al., 1995). It has been suggested that riparian zones increase regional diversity 50% or more by harboring distinct and unique species assemblages, rather than simply adding more species, when compared with surrounding uplands (Sabo et al., 2005).

Riparian areas also serve as important corridors, stopover sites and breeding areas for migratory species. Tropical birds travel hundreds of kilometers to breed in temperate riparian zones. Many species of birds migrate from tropical Africa across the Sahara to riparian areas in Europe to nest. Hundreds of species of neotropical birds from Central and South America migrate north to North America to forage and breed during summer months. One south to north trending river, the San Pedro, is among the most bird-diverse rivers in North America serving as a migratory, foraging, and nesting sites for over 400 species of birds (more than 45% of the total number of birds in North America) over the course of a season. Nearly 400 species of birds migrate along the East Asian Flyway to utilize temperate and arctic riparian areas as stopover and nesting sites. In addition to the habitat structure provided by riparian forests, the adjacency to open water and the diversity of food resources make riparian areas important stopover and nesting sites for birds. Recently, the exceptional nutritional value of emergent aquatic arthropods (rich in omega-3 fatty acids) has been recognized for its role in avian nutrition, nourishing birds during migration and enhancing breeding success (Twining et al., 2016).

High diversity in riparian areas stems from the dynamic fluvial environment that may result in mosaics of habitat, gradients of disturbance and resource availability, the presence of multiple age classes of vegetation and a variety of landforms across valley bottoms, provisions and habitat that attracts resident and migratory fauna, and the cycles of disturbance and recovery in river bottomlands (Fig. 1).

Lateral connectivity and patterns of riparian diversity

Another characteristic of riparian areas is distinct zonation of species and growth forms occurring in bands radiating out from aquatic to terrestrial areas. Transverse (cross valley) patterns of plant zonation are a common feature of riparian vegetation. Depending on climate and surrounding uplands, hydrophytic (water-loving, anoxia tolerant) and disturbance-tolerant vegetation typically occupy the zone nearest the channel, sub-shrubs and shrubs occur at intermediate distances, shrubs and trees at further distances and upland vegetation at the furthest extremes from the channel (Fig. 5). The process of meandering may also result in zonation of vegetation that corresponds to successive stages of riparian colonizers of bars, as they age and facilitate aggradation, floodplain formation and abandonment.

Distance away from and elevation above river channels are associated with a number of interrelated abiotic processes that may account for variation in vegetation. Vegetation zonation may be striking because of observable differences in plant physiognomy (height, leaf size, color, morphology, etc.), life-stage or age-class patterns. Species-specific flooding requirements explain patterns of zonation in vegetation along river margins. Moving from a river channel to upland generally reflects a moist-to-xeric gradient in soils, with decreasing anoxia and increasing depth to groundwater, decreasing intensity, frequency and duration of flooding and flow-related mechanical disturbance, with decreasing ice and debris scour and wave action, changes in nutrient and light availability, humidity, accumulation of litter, organic material and plant propagules, and with fining of substrate grain size from high to low energy fluvial habitats. Interspecific competition is more intense and facilitation less common as a function of distance from and elevation above a river channel towards the uplands. These biotic processes have been proposed as a major influence contributing to vegetation zonation and the associated lateral pattern of habitat variation along rivers.

Along active channels that have periodically disturbed sites, certain plant species have adaptations to disperse widely and colonize bare, moist, recently disturbed habitats. Many of these disturbance-adapted species release seeds in synchrony with the descending limb of the hydrograph so that the availability of sites suitable for germination and recruitment is maximized (Mahoney and Rood, 1998). The reproductive phenology of pioneer riparian tree species relative to the timing of seasonal floods around the world, root morphologies for water acquisition, and sexual versus vegetative reproductive strategies provide some examples of trait convergence relative to flow attributes/components. Riparian poplars (*Populus* spp.) and riparian willow species (*Salix* spp.) in western North America and river red gum (*Eucalyptus camaldulensis*) and swamp paperbark (*Melaleuca rhaphiophylla*) in Australia have phenological adaptations and release short-lived seeds for a short period of time in synchrony with the recession of floods and the availability of new sites to colonize. The capacity to produce roots that exploit the phreatic zone (aerated soils above the water table) exemplifies the convergence of root morphologic traits in phreatophytes in the northern (many species of Salicaceae and the mesquites *Prosopis* spp.) and southern hemispheres (e.g., *Eucalyptus sideroxylon*). Another example of trait convergence due to similar selective pressures across rivers of the world is selection for rapid life cycle and annual growth form in plants associated with areas experiencing frequent, channel forming fluvial disturbances. Sandbar and other sites with frequent turnover of substrates have distinctive colonizers and similar growth forms and habits worldwide (e.g., low drag, prostrate or flexible stems, water-dispersed seeds, short life cycle). These areas are often colonized by opportunistic annuals and species with rapid life cycles, and are thus often

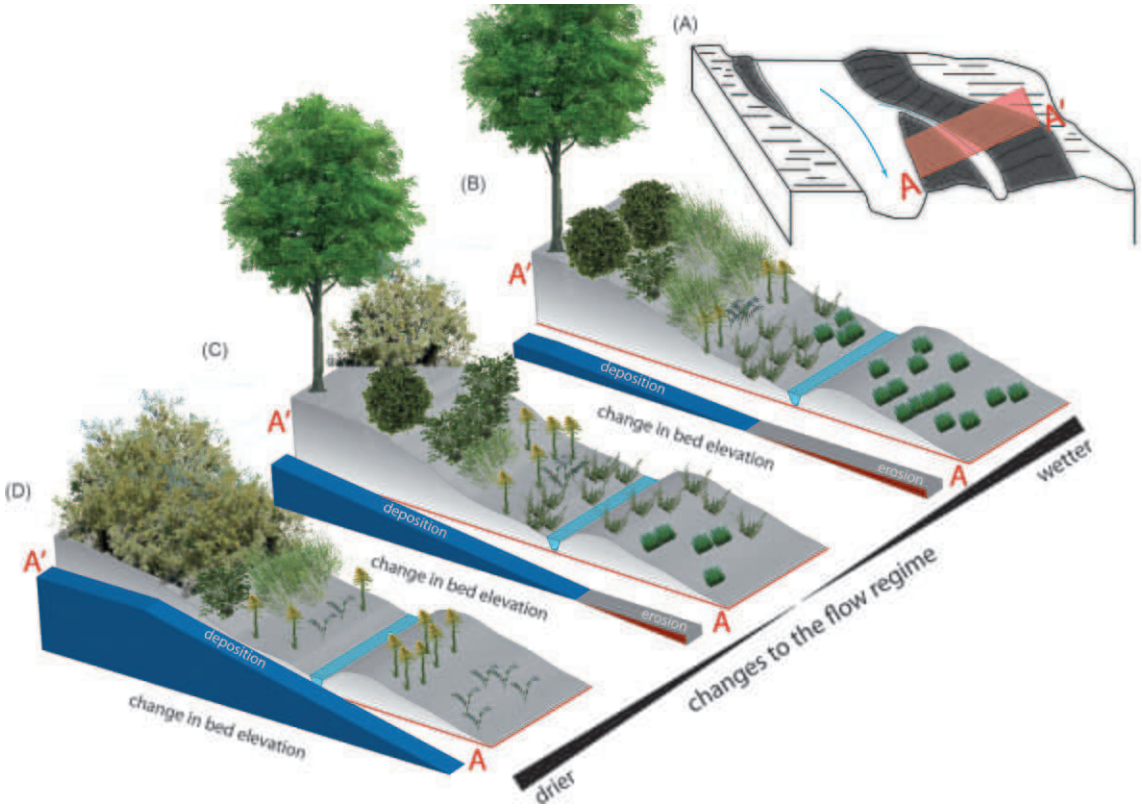

Fig. 5 For ecological plant guilds that respond to water availability and fluvial disturbance gradients, analyses indicate that the distribution of morphological traits—and therefore the plot-scale biotically controlled topographic response—can be predicted on the basis of these abiotic gradients. For a hypothetical section (A), where a steep gradient in water availability (high to low, A to A′) exists, ecological plant guilds trend from hydric to mesic to xeric (C). The flexural rigidity of the ecological guilds increases from A to A′. Observations from three flood events showed that deposition increased with increasing stem flexural rigidity. With a shift in flow attributes, the distribution of ecological guilds, morphological plant traits, and the topographic response change; (B) changes that may result from a drier flow regime and (D) changes that may result from a wetter flow regime. In (B)–(D), changes in bed elevation are indicative of an increased likelihood of either aggradation (plant-induced sediment deposition) or degradation (plant-induced sediment erosion). From Diehl RM, Merritt DM, Wilcox AC, and Scott ML (2017) Applying functional traits to ecogeomorphic processes in riparian ecosystems. *BioScience* 67: 729–743.

sites where non-native, generalist species may become established. In contrast, vegetative and perennial reproductive strategies are commonly found along relatively stable channels with less seasonal flow variability.

Species adapted to specific hydrograph attributes are particularly vulnerable to changes in streamflow regime. Flow alteration may decouple certain life stages (e.g., flowering, seed dispersal, colonization, growth) through de-synchronizing flow events from life histories that have evolved to them. In the tropical floodplain rivers around the world, fish and floodplain vegetation have coadapted a mutualistic relationship to seasonal flooding and floodplain inundation. Approximately 182 species belonging to 32 families of freshwater fishes consume and disperse the fruits and seeds of over 600 neotropical plant species in tropical floodplain rivers worldwide (Correa et al., 2007). In many floodplain rivers, fruiting phenology of tree species is synchronized with the annual flood cycle, fish swimming onto the floodplain when inundated and eating fruit and seeds fallen on the floodplain (Kubitzki and Ziburski, 1994). Over fishing in tropical rivers may lead to functional extinctions of frugivorous fish mutualists and cascade to extinctions of plants, resulting in ecosystem-level change in floodplain forests (Araujo et al., 2021). Other plants disperse seed in synchrony with hydrograph components to enhance water dispersal (hydrochory) and deposition along river margins (Nilsson et al., 2010). Conceptual models have been developed that can inform flow managers to accommodate key life history traits, such as seed deposition in suitable sites on receding waterlines along river margins, that may rely upon historic patterns of seasonal hydrographs. One such model that has been used to design hydrographs downstream from dams is the "recruitment box model" (Mahoney and Rood, 1998), which integrates suitable recruitment sites with river stage (level) decline to identify streamflow regimes that enhance the likelihood of survival. It is well understood that flows that may benefit one species, may be harmful to others, highlighting the role of interannual variability in accommodating a wide range of species over time, enhancing "temporal diversity" of riparian floodplains (Tonkin et al., 2021). The ability of highly specialized riparian species to adapt to changes in flow and sediment regimes in rivers resulting from slow-paced climate change will vary by species, their phenotypic plasticity, range of variation in populations, and other genetic factors.

Threats to riparian ecosystems

Riparian areas are subjected to all of the natural stressors that other ecosystems are faced with including wildfire, grazing and herbivory, animal activities, pathogens, insect herbivores and parasites, introductions of non-native species, and changes in weather conditions. Further, long-term changes imposed by climate change, such as shifts in the timing and volume of runoff, groundwater patterns, air and soil temperature, and the concentration of atmospheric carbon, also influence riparian ecosystems and their inhabitants. Though rivers and riparian ecosystems may adjust slowly to changes imposed by changing climate through gradual directional shifts in species distributions and adjustments of channel form, direct human effects on rivers are global in scale and may be extensive, severe and abrupt.

Threats to the functioning, diversity and characteristics of riparian areas include several direct human-caused stressors, the most pervasive one being water development: water diversion, dam construction and water storage, and surface and groundwater pumping. Dams fragment formerly connected rivers longitudinally as well as altering the flow and sediment regime, indirectly affecting lateral connectivity (Nilsson et al., 2005). The effects of dams on flow, sediment, carbon and propagule regimes can extend downstream for hundreds of kilometers and result in changes in channel morphology, floodplain formation and connectivity, and interrupting the life history requirements of riparian species adapted to natural flow regimes.

Worldwide, there are currently more than 45,000 dams above 15 m high, mostly in the northern hemisphere, capable of collectively storing greater than 6500 km^3 of water—about 15% of the total annual river runoff globally (Nilsson et al., 2005). Today, only 37% of rivers longer than 1000 km remain free-flowing along their entire length and only 23% of rivers draining to the sea remain uninterrupted to the ocean (Grill et al., 2019). In addition to the known effects that storing water and sediment behind impoundments has in altering downstream timing and volume of water and sediment delivery, dams affect geomorphic and biological processes which have direct effects on the functioning, physiognomy and species composition of riparian ecosystems. Changes in streamflow can decouple important life cycle stages of flow-adapted species from suitably timed flow attributes. In dam-regulated systems, small changes in the management of daily and seasonal flow release operations can result in recoupling of important life stages and flow regime, restoring key elements of riparian ecosystems that were compromised by dam operations (Rood et al., 2003).

Water storage reservoirs also submerge riparian zones and floodplain inhabitants upstream from impoundments, completely eliminating them from such systems. For example, the World's largest hydroelectric dam (Three Gorges) was recently constructed in China and displaced 10 million human inhabitants of the floodplain along with extensive riparian and floodplain habitats and the arthropods, birds, amphibians, reptiles and other mammals that once occupied these now-submerged riparian habitats. The shift from formerly lotic systems to lentic ones upstream from dams, often with sterile shorelines (or "bathtub rings") most often results in reduced biological diversity. Dams fragment rivers affecting riparian vegetation and associated riparian arthropods and animals through fragmenting the downstream dispersal of seeds and propagules and altering sediment, nutrient, organic material and water movement through watersheds.

Other stressors to riparian areas include those that directly affect soils and vegetation within the floodplain, channel and corresponding riparian zones, such as livestock, native ungulate and insect grazing, forestry and fuels reduction, fire, human encroachment (development, roads, levees, channelization, draining floodplain soils, agriculture, harvesting), in-channel mining operations for precious metals, gravels and aggregates, and fossil fuels, dredging and management of channel form for timber floating and transportation routes, large wood removal and the effects of off-channel land, vegetation, water management and development within watersheds. Most large European rivers have been disconnected from their floodplains, straightened, and simplified from their natural form. Most rivers are constrained to a narrowed floodplain between rigid dikes, with former floodplains landward of the dikes converted to agricultural land. This has resulted in floodplain forests being designated one of the most endangered ecosystems in Europe.

Though new dam construction has become less frequent in many developed countries of the world, dam construction remains high in developing countries such as China, India, and countries throughout Africa and South America. Developed countries of the world are currently in a renaissance of advancing the science of river management and river and riparian restoration having been through eras of extensive dam building and river channelization in the past and better appreciating the negative ecological effects of such development on rivers and their floodplains and riparian forests.

Conservation of rivers and riparian areas

Recognition of the widespread negative effects human development has had on riparian ecosystems worldwide over the past few centuries, and the continued threats to them has led to policy and legislation to protect remaining free-flowing rivers and functioning riparian ecosystems, and to better manage and to restore rivers and their riparian ecosystems in developed and developing countries. Legislative protections for rivers include the Wild and Scenic River system (Wild and Scenic Rivers Act 1968) and protections under the Clean Water Act (1972) in the United States, the inclusion of inherent rights of rivers to flow incorporated into the constitution of South Africa, the European Union Water Framework Directive to manage freshwater resources, and case-by-case protections funded from local or international sources often to protect sensitive species or biological diversity.

A small percentage of the linear distance of the World's rivers falls under protection on most continents. In the United States, only 0.25% (20,453 km) of rivers (and 0.4 km on either side of the river) are designated Wild and Scenic and some of them lie along dam-regulated river reaches. In Europe, the Water Directive Framework provides non-binding recommendations for protection of rivers and riparian areas, but there is no equivalent of Wild and Scenic Rivers protection throughout Europe, though individual countries including Slovenia, Finland, Sweden, and Spain have legal protection for rivers and their riparian areas that specifically aim at protecting their free-flowing character (Schäfer, 2019). One of the longest rivers in South America, the Orinoco River, supports vast riparian forests and charismatic species such as parrots, giant anaconda, crocodiles and river dolphins and is under heavy threat of human development. In such cases where there is no federal protection, global non-profit groups such as World Wildlife Fund may support local efforts to raise community awareness and protect such systems.

Riparian restoration efforts range from small, reach-scale efforts to larger, watershed and segment-scale efforts including pollution remediation, environmental flow management, riparian and floodplain rehabilitation, protected buffers—widths of riparian vegetation, targeted fish recovery and the removal of dams, diversion structures, culverts and other barriers to passage (Bernhardt et al., 2007). Riparian restoration can broadly be classified as active or passive, and most projects include a combination of approaches (Wohl et al., 2005). Active restoration methods include de-channelizing stream channels, recontouring channels and floodplains, mechanical soil disturbance and active planting of riparian vegetation, removing levees and laying banks back to allow for stream-floodplain interaction, deconstruction of development within active floodplains, removal or reduction in invasive species and reintroducing desired plant species.

Passive restoration approaches include changes to land and water use in a basin that may result in restored water, sediment and carbon regimes. A rapidly developing form of passive restoration is managed restoration of streamflow components that restore some defined geomorphic and ecological purpose downstream from dams. "Environmental flow" management has gained popularity and sophistication in the past couple of decades and has resulted in the restoration of native riparian vegetation and floodplain forests, in many cases without compromising water storage, power generating capacity and other intended utilities of dam operations (Tonkin et al., 2021). Guidelines for determining environmental flow needs range from those targeting single organisms such as riparian poplars (*Populus* spp.) (Lytle and Merritt, 2004; Rood et al., 2005) to multi-taxonomic approaches (Shafroth et al., 2010; Tonkin et al., 2018) and from the reach to segment and watershed scales (Poff et al., 2010; Webb et al., 2015).

Restoring streamflow components downstream from dams can be very effective for reestablishing desired processes in dam-impacted riparian ecosystems and re-synchronizing tightly coupled biotic and streamflow interactions. However, dams inhibit the passage of mineral sediment, and carbon (including leaves, wood and propagules), so restoring many processes cannot be accomplished through environmental flow prescription alone. In the rare situation in which there is a natural source of significant sediment inputs downstream from a dam, timing prescribed flows to coincide with sediment inputs such tributaries can be effective at restoring sediment deposits such as bars and river margin beaches (Melis, 2011), which serve as sites for vegetation colonization and establishment.

A combined form of passive and active restoration involves implementing environmental flows after conducting active restoration to floodplains to restore pre-development channel forms. Another hybrid approach to riparian restoration that is gaining popularity primarily in the United States, Europe and Australia is dam removal. Dam removal requires decommissioning and deconstructing dams, recontouring of river channels and possible eradication of invasive species and reintroduction of desirable ones, resulting in a restoration of natural flow, sediment and carbon regimes. Over 2300 dams have been removed in the United States since 2016. Over the past 20–25 years, at least 5000 small dams, weirs and culverts have been removed from rivers in France, Sweden, Finland, Spain and the United Kingdom.

As most of the world's major rivers have been affected in some way by direct and often deliberate human activities and by indirect and unintended factors (such as climate change and invasive species introductions), there are great opportunities to recognize the value of and to protect those last remaining free-flowing rivers on earth. The communities, floodplain forests and meadows, complex fluvial settings and mosaic of micro-habitats along free-flowing rivers represent a natural heritage that can be used to set goals for restoration of impacted streams. Free-flowing rivers can serve as sentinel rivers, natural laboratories where an understanding of the complex interactions between flow and the evolutionary history of the biota of sites can be better understood and applied to river management elsewhere.

Opportunities for future research in riparian and riverine ecology

The field of riparian ecology has advanced rapidly in the past several decades. Early advances include an expanded view from river reaches existing in isolation to an understanding of the river as a continuum of energy, carbon, and discharge cascading along the river network (Vannote et al., 1980). In the 1990s, the four dimensional nature of river systems, lateral floodplain connectivity and the ecological importance of the dynamic nature of riverine ecosystems emerged with concepts such as the three-dimensional nature of riverine connectivity (Gregory et al., 1991), the flood pulse (Junk et al., 1989), and the natural flow regime paradigm (Poff et al. 1997). These concepts distinguished rivers from other freshwater systems and provided a foundation in the importance of process and connectivity in the functioning of riverine ecosystems.

River and floodplain connectivity includes surface-water interactions with hyporheic zone (connected groundwater systems) (Stanford and Ward, 1993), the exchange of nutrients, water, and materials between aquatic and riparian systems (Baruch et al., 2021), and the movement of organisms (including non-native species) along dendritic networks of stream channels. In recent

decades, the role of floodplain inundation for soil microbial processes, decomposition, mycorrhizae and nutrient dynamics has been recognized (Beauchamp et al., 2006; Molles et al., 1998). The importance of reciprocal relations between sediment, vegetation and floodplain processes has been recognized (Corenblit et al., 2007; Merritt, 2020) and deterministic models developed to better predict the consequences of varying water and sediment regimes to channel evolution and form (Diehl et al., 2018). Intellectual developments such as the probabilistic river concept (Graf, 1984) and the concept of the normative river (Stanford, 1997) have also contributed to an advanced understanding of river function and process and our approaches to restoration, decision-making, modeling and management.

Despite this progress, a recent meta-analysis of the scientific trajectory of riparian vegetation studies (Dufour, S et al., 2019) revealed a lack of a well-identified scientific community in the peer reviewed published literature that focuses on riparian ecology, specifically on riparian vegetation. The authors suggest that by its very nature, riparian ecology is a diverse, interdisciplinary science that includes varied fields of knowledge. Indeed, the study of any riparian ecosystem requires an understanding of geology, groundwater-surface water hydrology, geochemistry, hydraulics, sediment mechanics, fluvial geomorphology, and the range of disciplines involved in understanding the biology of the system from microbial to evolutionary. Further, the reciprocal relations between vegetation, wildlife (e.g., beavers, hippopotamus, Crocodilia (alligators, caiman and crocodiles), fish, etc.) and channel form and process must also be considered. Climate change and non-stationarity must also be at the forefront when interpreting process-pattern relations, establishing realistic reference conditions, and transferring understanding of one system to the next in riparian studies.

Though many challenges remain in our understanding of riverine systems and the interdependency between riparian and aquatic ecosystems, advances in remote sensing, geographic information systems (GIS) technology, and light detection and ranging (LIDAR), laser surveying instruments, and structure from motion have rapidly advanced mapping of valley bottoms, floodplains, fluvial features, and riparian areas worldwide. Satellite imagery and thermal sensors, aerial and ground-based LIDAR technology, small aircraft and unmanned aerial vehicles (or drones), and advances in other remote sensing tools have enhanced the mapping and characterizing of riparian ecosystems, aquatic habitat, and vegetation patterns.

The application the stable isotopes of nitrogen, hydrogen, carbon and other elements has now been widely used to determine the sources of water utilized by riparian plants over time (Busch et al., 1992; Schook et al., 2020) and to determine how carbon cascades from organism to organism throughout riparian and aquatic ecosystems (Baruch et al., 2021). One such study found that the carbon from riparian trees comprised about 25% of the carbon in large predatory fish through the transfer from allochthonous inputs from leaf fall, into aquatic invertebrates and ultimately into the biomass of fish (Baruch et al., 2021). Other isotope studies have identified higher growth rates of riparian trees due to the influence of marine-derived nitrogen fertilization by grizzly bears (*Ursus arctos horribilis*) that consume anadromous salmon (*Oncorhynchus* spp.) which have migrated hundreds of miles from the sea to spawn in inland streams (Naiman et al., 2000).

New and emerging modeling techniques and tools will enable us to better understand cause and effect in riparian ecosystems, make better, science-based management decisions, and to forestall extinctions and further losses of some of the most biologically diverse and functionally rich terrestrial ecosystems on earth.

Conclusions

Riparian zones stand out as striking ribbons of green traversing arid landscapes and serve as more subtle centers of diversity and productivity through temperate, humid and more lushly forested upland systems. Public appreciation of rivers, and policies and laws that inform management, sustainability and protection of them has never been more important than it is now. Climate change and human population growth are exerting increasing pressure on freshwater resources and leaving systems vulnerable to unprecedented extremes in hydrologic events (droughts and flooding). With most of the world's rivers impaired to some degree directly or indirectly by humans, and an onslaught of new development proposals such as micro-hydropower, pump storage facilities, and water diversion on lower order streams and massive mainstem dams on some of the largest river systems in the world, diversity of the world's riparian areas could see a continued decline in coming decades.

Preservation of extant free-flowing rivers requires deliberate action. Science-informed management of rivers, an engaged and energetic public and politicians, and a social river ethic aimed at preserving water in streams is necessary to protect these diverse ecosystems. Myriad organisms rely on rivers to complete their life cycles and maintain their existence at local, regional, and intercontinental scales. Managing rivers with a recognition of the importance of key components of historic seasonal flow regimes as well as historic sediment, carbon and nutrient regimes is key to supporting dynamic floodplain processes, riparian mosaics, structurally and compositionally complex floodplain forests, groundwater systems and the diverse interdependent systems that they support.

Knowledge gaps

- Deterministic models that predict geomorphic change in rivers in response to changes in water and sediment regimes would facilitate more reliable models of riparian vegetation change. Integrated models that incorporate the reciprocal relations between vegetation and river channel change would further refine our predictive abilities.

- How the distribution of the range of riparian ecosystem forms and functions will change as a function of direct and indirect effects of changing climate patterns. For example, direct effects include changing atmospheric temperature, CO_2 levels and cascading changes to the hydrologic cycle. Indirect effects of global change include landscape-scale changes in upland vegetation composition and cover, rates of decomposition and biochemical processes, rates of chemical and physical weathering, extreme events (e.g., temperature and precipitation), landscape sediment yield, and shifts in the state (frozen or liquid) and temporal delivery of water and its effects on surface and groundwater patterns.
- The role of water storage reservoirs and regulated flow releases as a tool that could be strategically used for mitigating (and providing resilience to) the effects of climate change on river and riparian ecosystems.
- The role of rivers and riparian zones in resistance and resilience to climate change relative to upland ecosystems. The role of riparian ecosystems to serve as corridors (providing thermal refugia) facilitating the range shifts of organisms in response to global change.
- The relationships between species diversity and trait functional diversity and the functioning and resilience of riparian ecosystems. The rate of evolutionary change in different taxonomic groups of riparian organisms relative to the rate of climate change.
- Methods for engaging the public and policy makers in understanding how important functioning and connected rivers and riparian areas are in providing ecosystem services and supporting biodiversity.
- The ability to coordinate complex social and legal systems with our understanding of the requirements of riparian ecosystems to balance climate change, continued human water development and uncertainty and prevent further degradation, loss of natural heritage and extinction of riparian species. Through dam management, conservation, water right transfers, and other creative means, developing techniques to most efficiently distribute water to human water users while ensuring biologically important flows in key stream reaches.

See Also: Structures and functions of Inland Waters - Rivers: Dam Removal and River Restoration; Effects of Dams on Rivers; Environmental Flows: Ecological Effects of Hydrologic Alterations, Assessment Methods for Rivers, Challenges and Global Uptake; Hydrology and Classification of Rivers for Management

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Flood Plains of Large Rivers☆

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This is an update of S.K. Hamilton, Flood Plains, in *Encyclopedia of Inland Waters*, Elsevier Inc., Edited by: Gene E. Likens, 2009, https://doi.org/10.1016/B978-012370626-3.00052-1

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Abandoned floodplain A floodplain that has become isolated from the main river and is no longer subject to inundation by that river. Abandoned floodplains may still be flooded by water from local rainfall and stream inputs. They typically lie on fluvial terraces that are sufficiently elevated to be out of reach of flooding from the main river, although they often drain to the river via streams.
Active floodplain A floodplain that is subject to inundation by the main river at least occasionally and often every year.
Alluvial fill Sediment deposited by flowing water, generally over a long period of time. Floodplains tend to lie on alluvial fill.
Anastomosed channel A river reach where flow is divided into two or more interconnected channels with floodplain between the channels. Usually more stable that a braided channel.
Blocked-valley lake Lakes that have formed in tributary valleys now back-flooded by the main river, often resulting in a dendritic form. In the central Amazon floodplain, such valleys were carved out at lower relative river levels, possibly in the late Pleistocene when sea levels were lower, then have not filled in with sediment as the main river channel subsequently accumulated alluvial fill (Latrubesse, 2012). Their water levels are controlled by the main river but through-flow of sediment-laden river water is restricted by the lake morphology and/or inputs of local streams.
Braided channel A river reach with multiple interconnected channels separated by small islands. Usually characterized by dynamic geomorphology due to erosion and deposition.
Flood pulse Periodic inundation and drainage of floodplains, particularly along large rivers where inundation may last for weeks to months. The Flood Pulse Concept articulates the importance of the natural flood regime to the ecology of floodplains along large rivers.
Oxbow lake (Billabong) A U-shaped floodplain lake formed when a meander of a river channel is cut off from the main channel flow. Oxbow lakes may be connected to the river all year, usually only on one end, or can be completely isolated from the river except when intervening floodplain is inundated. In Australia the term "billabong" is commonly used.
Point bar An alluvial deposit that has accumulated on the inner side of curve in the river.
Run-of-river reservoir A reservoir in which dam operations do not result in large variation in water level and volume, such that river inflows are approximately equal to outflows except on short time scales.

Introduction

Floodplains are often defined as land that is seasonally or episodically inundated by overflow from river channels, and people in urbanized areas often think of floodplains in terms of potential flooding hazard to life and property. Farmers around the world recognize that floodplains can provide particularly fertile croplands or pastures. In contrast, ecologists view floodplains as a

☆*Change History*: October 2020. SK Hamilton. Revised text in general, plus addition of new sections as prescribed in the instructions. Title changed from that suggested in letter of invitation. References now cited throughout text. Replaced Figure 8. Revised text in response to the review by the Subject Editor, LeRoy Poff. Glossary and Further Reading section have been added.

distinctive, often highly productive wetland ecosystem that harbors unique combinations of biodiversity and contributes to ecosystem services by virtue of the hydrological connectivity with rivers. Floodplains can exist anywhere in a river network, but they are often particularly well developed—and have longer and more predictable periods of inundation—in the lower reaches of larger rivers (Scott et al., 2019). Larger rivers tend to flow across more level terrain, facilitating the accumulation of sediment deposits to form floodplains, and in many cases their valleys and deltas have filled with sediment in reaction to the global rise in sea level since the last glaciation (e.g., Day et al., 2008; Syvitski et al., 2009). This chapter focuses on floodplains associated with large rivers.

The aforementioned definition of floodplains belies their spatial complexity. Many floodplains along large rivers are mosaics of distinct wetland systems that include areas flooded by local precipitation and stream inflows, often in distinct locations or times compared to inundation by riverine overflow. Topographic variation across floodplains, even over scales of <1 m, produces a continuum of flood regimes, akin to the flow regime concept widely applied to stream and river research (Poff et al., 1997; Bunn and Arthington, 2002). The resultant spatial and temporal gradients in hydrological dynamics and water sources can strongly affect the structure and function of the floodplain ecosystems (e.g., Battaglia and Sharitz, 2006; Ferreira-Ferreira et al., 2015). Floodplains along larger rivers also commonly contain water bodies that are permanent or semipermanent, including floodplain lakes and channels, as well as shallow wetlands (sometimes called backswamps) in the lowest lying parts of the floodplain that may retain water all year (e.g., Sippel et al., 1992; Hamilton et al., 2007; Emmerton et al., 2007; Day et al., 2008).

The occurrence and patterns of seasonal or episodic inundation strongly affect the ecology of large river floodplains, including both the aquatic and terrestrial biota, and explains their high biodiversity (Junk et al., 1989; Lewis Jr. et al., 2000). The Flood Pulse Concept articulates the myriad ways in which inundation regimes of large river floodplains determine their ecological structure and function, and how the biota are adapted to cope with and often depend on long-lasting flood pulses common to the largest river systems.

Examples of floodplain environments

Remotely sensed images of contrasting types of flood-plain environments are depicted in Figs. 1–7. Images of four large South American floodplains (Amazon, Madre de Dios, Pantanal, and the Llanos de Moxos), as well as the Cooper Creek system in Australia (Figs. 1–5) depict the diversity of landforms, water bodies, and vegetation in large floodplains with minimal human disturbance. Examples where floodplain hydrology has been strongly altered are shown for the Kalamazoo River (Fig. 6) and the Mississippi River (Fig. 7). The ensuing discussion will refer to these images. In addition, photos of many of these sites appear in the online Floodplain Photo Gallery see (Supplementary Material in the online version at https://doi.org/10.1016/B978-0-12-819166-8.00091-8).

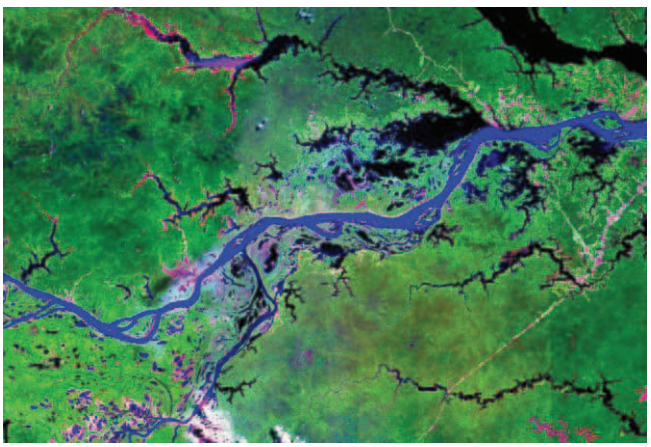

Fig. 1 Amazon River (locally known as the Rio Solimões in this reach) and its fringing floodplain up river of the city of Manaus and the confluence with the Negro River. This image covers land extending about 240 km in width. The Negro River is visible in the upper right. The main river channel contains high inorganic turbidity (blue) and clearer waters on the floodplain as well as in the Negro River are dark (due to lack of turbidity). The floodplain here shows diverse geomorphic features, including numerous lakes, most conspicuous of which are the dendritic blocked-valley lakes (defined in Glossary). Blocked-valley lakes along the main Amazon River normally maintain a hydrological connection with main river all year. Image coordinates are 61.20 W, 3.61 S. Image shows Landsat 7 ETM+ data (bands 7, 4, 2) from the Geocover 2000 data set, obtained from NASA World Wind version 1.3.

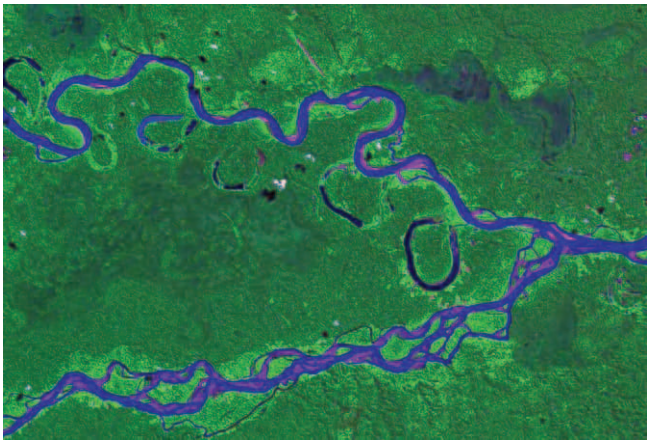

Fig. 2 Madre de Dios River (upper) and its tributary the Inambari River (lower) in the Peruvian Amazon basin. This image covers land extending about 29 km in width. The river channels contain high inorganic turbidity while some oxbows contain clearer water and hence appear darker. Lighter green areas are vegetation in early successional stages following fluvial disturbance. The floodplain along the Madre de Dios contains oxbow lakes in various stages of separation and infilling. Much of the Inambari floodplain occurs as islands and bars along the highly braided channel. Between the two rivers is an extensive interfluvial backswamp, and in the upper right the darker blue areas are palm swamps lying on fluvial terraces. Image coordinates are 69.83 W, 12.70 S. Image shows Landsat 7 ETM+ data (bands 7, 4, 2) from the Geocover 2000 data set, obtained from NASA World Wind version 1.3.

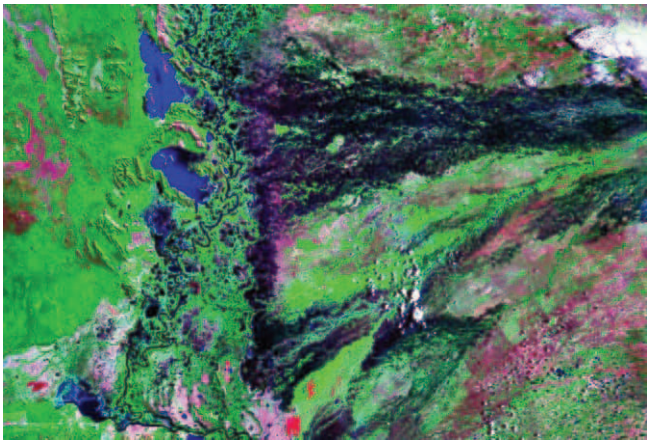

Fig. 3 Floodplains of the upper Paraguay River and tributaries in the central Pantanal (Brazil and Bolivia). This image covers land extending about 200 km in width. The floodplains here include the fringing floodplain of the sinuous Paraguay River (running from north to south), large turbid lakes with permanent connectivity to the river, and seasonally flooded savannas of the Taquari River alluvial fan, which covers the right side of the image. Lower lying areas of the fan are subject to backwater effects from the Paraguay River, making them appear dark in this image. Image coordinates are 57.14 W, 18.51 S. Image shows Landsat 7 ETM+ data (bands 7, 4, 2) from the Geocover 2000 data set, obtained from NASA World Wind version 1.3.

Geomorphological processes on floodplains

Much attention has been paid to the study of fluvial geomorphology, including the ways in which the action of moving water interacts with sediment deposition and erosion and vegetation to produce a variety of floodplain landforms (reviewed by Dunne and Aalto, 2013). Floodplains are built of alluvial fill that normally originates as sediments carried by the main river and deposited as point bars along the migrating channel, and/or during overbank flooding (Meade, 2007; Trimble, 2010). Hydrologists refer to bankfull discharge as the river discharge above which the floodplain becomes inundated (Leopold, 1994). In large river floodplains the concept of bankfull can be difficult to apply, however, because much water enters and exits the floodplain via low areas or discrete openings in the levees, as described later. Many rivers reach bankfull at least annually, but inundate their floodplains less frequently, whereas others inundate their floodplains every year, sometimes in multiple events.

River valleys commonly have one or more abandoned floodplains lying on elevated terraces that are normally above the present-day reach of riverine flooding. Such terraces may still contain wetlands and permanent water bodies that reflect their fluvial origin (e.g., Hamilton et al., 2007). Wetlands on such terraces may be sustained by groundwater and surface runoff emanating from adjacent uplands in addition to direct precipitation inputs. For example, terraces containing palm swamps that retain surface water all year are visible to the north of the Madre de Dios River just above its confluence with the Inambari River in Peru (Fig. 2).

Larger flood events can be particularly important in sculpting the surface geomorphology of floodplains. Fluvial deposits can be highly heterogeneous and subject to constant change in active floodplains along rivers with high sediment loads (Constantine et al., 2014), as for example, in the floodplains close to the Madre de Dios River and on islands in the Inambari River in Fig. 2. Fluvial landforms tend to become smoothed out over time, as may be reflected by increased distance from or, in the case of terraces, elevation above the main river. Erosion of elevated features and infilling of depressions contribute to the long-term homogenization of floodplain surfaces. Yet even in humid tropical climates, traces of the geomorphic features produced by fluvial action may remain visible for tens of thousands of years (e.g., Llanos de Moxos of Bolivia in Fig. 4).

Elevated strips of land known as levees often border the river channel and reflect the higher rates of sediment deposition where the river water first decreases in velocity as it exits the channel. Successively formed, concentric levees and swales may form meander scrolls. In some floodplains, these are created by the meandering of smaller channels within the floodplain rather than by the lateral migration of the main channel (Mertes, 2000).

Floodplains can be readily classified based on their hydrology and geomorphology, and several schemes have been proposed that apply to particular regions (e.g., Brinson, 1993; Junk et al., 2014). Floodplains can be broadly classified as fringing floodplains (i.e., found along the banks of rivers), coastal deltaic floodplains (formed where rivers meet lakes or the ocean), and internal deltaic floodplains (formed internally where a tributary meets a larger river and is subject to backwater effects). Some river channels, particularly those with braided morphology such as the Inambari River of Peru in Fig. 2, have much of their floodplain on

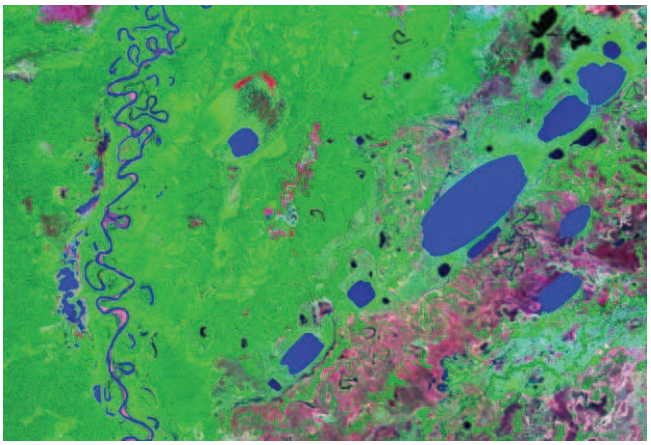

Fig. 4 Savanna floodplains of the Llanos de Moxos (also spelled Mojos) in the upper Amazon Basin in Bolivia. This image covers land extending about 108 km in width. The meandering Beni River with numerous oxbow lakes flows from south to north. The floodplain here reveals topographic features created by past fluvial activity. Superimposed on this landscape are strikingly regular depressions filled with shallow turbid water; these lakes have been attributed to subsidence patterns reflecting lineaments in the basement rock far below the alluvium. Image coordinates are 67.20 W, 13.99 S. Image shows Landsat 7 ETM+ data (bands 7, 4, 2) from the Geocover 2000 data set, obtained from NASA World Wind version 1.3.

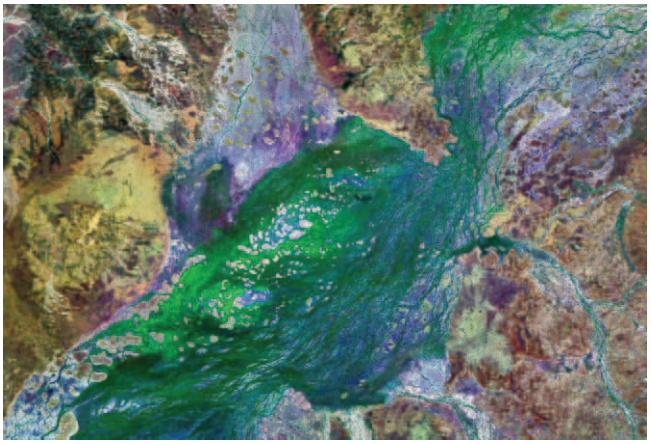

Fig. 5 Floodplains and river channels of Cooper Creek near Windorah (Queensland, Australia). This image covers land extending about 136 km in width. The floodplains were relatively vegetated lands in this image because they recently had been inundated, providing soil moisture for growth of herbaceous plant cover. Surrounding uplands are semiarid, sparsely vegetated shrublands and grasslands. The floodplain here receives river water through a complex system of anastomosed channels that are mostly dry in between the occasional flows. A few deeper channel reaches hold water between flows and are known as waterholes; these are too small to resolve here. Image coordinates are 142.47 E, 25.56 S. Image shows Landsat 7 ETM+ data (bands 7, 4, 2) from the Geocover 2000 data set, obtained from NASA World Wind version 1.3.

Fig. 6 Hydrological alterations to the floodplain along the Kalamazoo River (Michigan, United States). This image covers land extending about 11 km in width. The reservoir in the lower part of this view was created by impoundment of the main channel for hydroelectric generation. Downstream is a diked area where water levels are managed for wildlife. The remaining floodplain is covered by deciduous forest and retains an approximately natural flood regime because this and other, upstream reservoirs are managed as run-of-river (i.e., they do not vary much in water levels over the year). Image coordinates are 85.94 W, 42.57 N. Image source: U.S. Geological Survey digital aerial photography (DOQQ) taken in March 1999, obtained from NASA World Wind version 1.3.

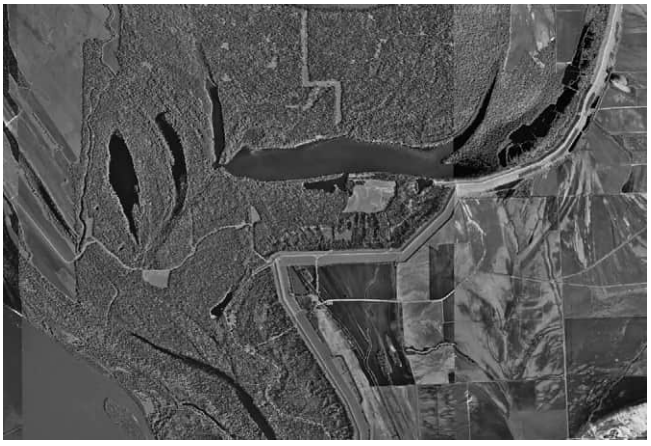

Fig. 7 Hydrological alterations to the floodplain along the Mississippi River (northeastern Mississippi east of Helena, Arkansas, United States). This image covers land extending about 9 km in width. Much of the floodplain here has been disconnected from the river by dikes and is used for agriculture; other parts are deforested but not diked. Oxbow lakes are visible in the forested parts; topographic floodplain features can also be seen in cleared and diked areas. Image coordinates are 90.51 W, 34.59 N. Image source is U.S. Geological Survey digital aerial photography (DOQQ) taken in April 2001, obtained from NASA World Wind version 1.3.

mid-channel bars and islands, and smaller channels can become isolated from the flow and exhibit lake-like conditions at lower discharge. Wetlands that resemble riverine floodplains but may not be subject to direct inundation by river water include floodplains on fluvial terraces, and poorly drained plains adjacent to rivers that tend to become flooded with local runoff during the wet season. Examples of the latter include much of the land in images of the Pantanal (Fig. 3) and Llanos de Moxos (Fig. 4).

Hydrology of floodplains

By definition, floodplains share the characteristic of being subject to inundation, but key hydrological features of inundation are highly variable. The timing, frequency, and duration of inundation can be collectively considered as the hydroperiod or flood regime. In many kinds of floodplains, there is a range of flood regimes depending on the land surface elevation with respect to the river. Subtle differences in topography can result in considerable differences in hydroperiod with corresponding variation in soil moisture and ecological characteristics, particularly when the range of inundation depth is relatively small.

Where riverine overflow and/or river-level backwater effects control water levels on the floodplain, river discharge often dictates timing and predictability of inundation, while depth and routing of flow within the floodplain reflect its geomorphology and vegetation. Larger river systems tend to have broader and more predictable flood peaks because their large drainage basins integrate the smaller-scale spatial variability of individual precipitation events. The presence of extensive floodplains or water bodies along larger rivers attenuates the flood pulse downstream.

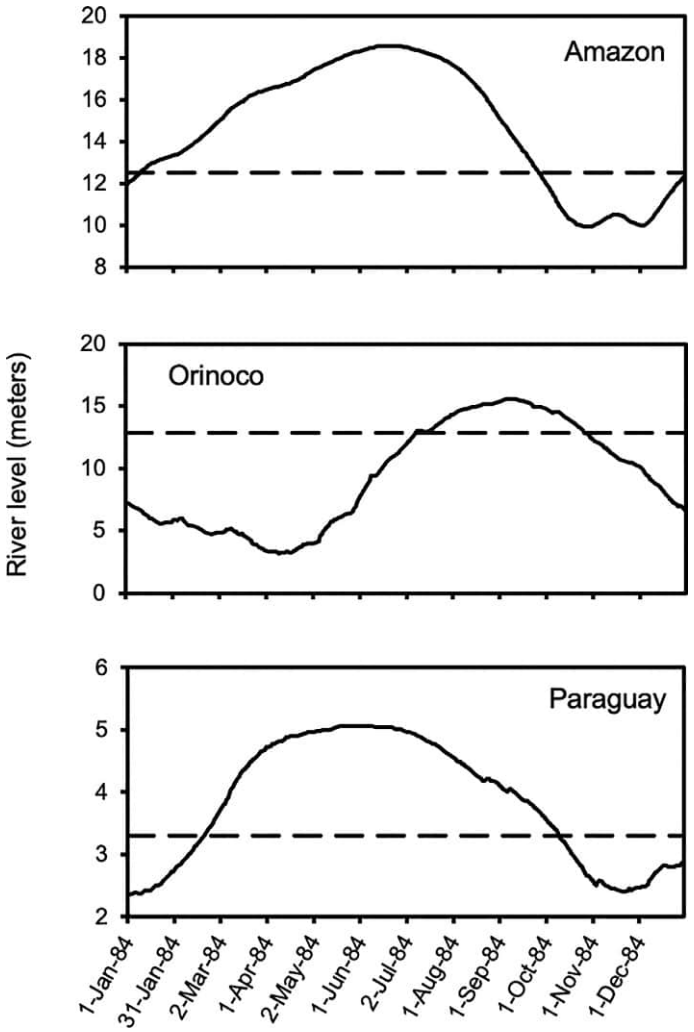

Fig. 8 Daily river level measurements for the year 1984 from the Amazon River (Rio Solimões at Manacapuru, Brazil), the Orinoco River (Ciudad Bolívar, Venezuela), and the Paraguay River in the southern Pantanal (Corumbá, Brazil). Dashed lines show approximate bankfull stages, above which the adjacent floodplains become inundated with river water. These flood regimes are essentially natural with no significant upstream regulation. Data collected by the Brazilian Agência Nacional de Energia Elêtrica (Amazon River), the Venezuelan Ministerio del Ambiente y de los Recursos Naturales Renovables (Orinoco River), and the Brazilian Navy (Paraguay River).

Particularly attenuated and prolonged flood pulses are observed in large, mostly unregulated river systems of South America, where the floodplain typically is inundated once per year, lasting for months and covering much of the floodplain with water to depths up to several meters (Hamilton et al., 2002). Fig. 8 shows examples of daily river water level measurements from three large rivers with extensive floodplains—the Orinoco, Amazon, and Paraguay rivers of South America. In the vicinity of these measurement sites, the Orinoco has the least extensive floodplain relative to its discharge, while the Paraguay River has the most extensive floodplain (these data come from the southern Pantanal in Brazil: Fig. 3). In each case, the inundation lasts for months, with the most protracted inundation in the savanna floodplains of the Pantanal where standing water often persists for more than 6 months of the year, but in some years of markedly lower rainfall (e.g., 2020) most of that land can become dry. These river systems and their floodplains are so large that the passage of the flood wave through the system takes months, resulting in a time lag between the wet season runoff and the inundation of the floodplain. This time lag reaches 4–6 months in the case of the southern Pantanal (Hamilton et al., 1996).

At the other extreme are floodplains that typically are inundated for only a few days or weeks per year. Examples shown here include the Madre de Dios River (Figs. 2 and 9), which drains mountain and lowland landscapes in Peru, and the Kalamazoo River (Figs. 6 and 10), which drains a lowland glacial landscape in southern Michigan, United States. In both of these river systems, the timing and duration of floodplain inundation are highly variable. In a particular year, inundation can occur several times or not at all. The tropical Madre de Dios responds to rain events in the Andes as well as the lowland plains. The temperate Kalamazoo River responds to rain events but also to snowmelt and rain on snow, which produce a higher proportion of overland runoff in a landscape where rainfall infiltrates the soils during most of the year (Hamilton, 2015). Most floods in the Kalamazoo River occur

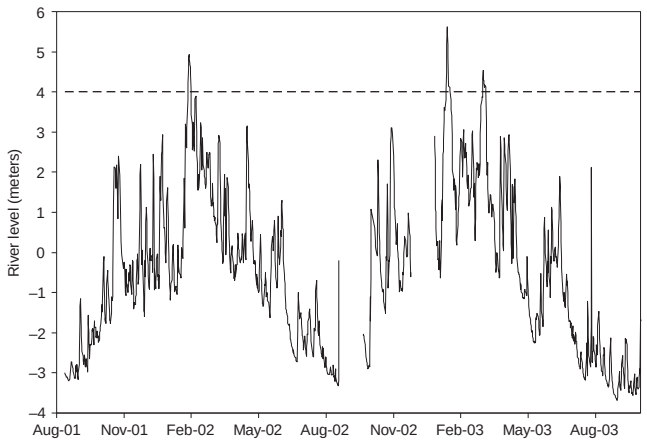

Fig. 9 Daily river level measurements over two annual cycles from the Madre de Dios River above the confluence with the Los Amigos River in Peru. This river drains Andean mountain and lowland environments, and has a natural flow regime. Dashed line shows approximate bankfull stage, above which most areas on the adjacent floodplains become inundated with river water. Data collected by the Centro de Investigación y Capacitación Río de los Amigos (CICRA), operated by the Amazon Conservation Association.

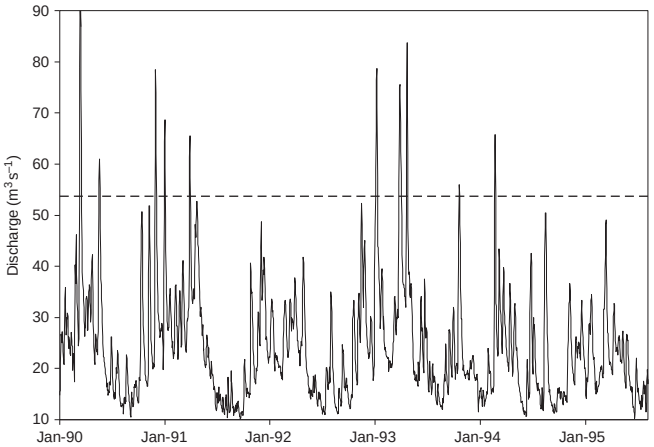

Fig. 10 Daily river level measurements over six annual cycles from the Kalamazoo River (Battle Creek, Michigan, United States). Reservoirs and urbanization have a small effect on the flow regime of this river. Dashed line shows approximate bankfull stage, above which most areas on the adjacent floodplains become inundated with river water. Data collected by the U.S. Geological Survey.

during cooler months (especially March and April) when biological activity is relatively low, and the mean number of days flooded. per year is only eight, with substantial inter-annual variability. Summer flooding has recently increased in the Kalamazoo River floodplain in response to intensification of rain events.

Even brief flooding can be important as a geomorphological force, but from an ecological perspective, brief and unpredictable floods may act more as a disturbance that limits the plant and animal life rather than benefits it. In cooler climates, the timing of the inundation is critical as well. Some large boreal/arctic rivers that flow in a northerly direction, such as the Mackenzie River in northwestern Canada and the Ob and Yenisei rivers in Siberia, exhibit spectacular flood pulses as the river breaks through ice in the spring (Pavelsky and Smith, 2004).

The most variable river discharge regimes, and hence the most unpredictable flood pulses, occur in certain dryland rivers such as Cooper Creek and the Diamantina River in the endorheic Lake Eyre basin of interior Australia (Fig. 5), which tend to flow only when monsoons bring heavy rainfall far into the continent (Puckridge et al., 1998). In these semiarid environments water limits biological activity most of the time, and hence inundation of extensive floodplains and anastomosed channel systems can be important in stimulating aquatic and terrestrial primary production despite its erratic and ephemeral nature (Bunn et al., 2006). Permanent waters in these systems are known as 'waterholes', which are particularly deep channel reaches of restricted length that hold water long after the river has ceased to flow and most of the channels have dried, thereby serving as important refugia for the aquatic biota, including invertebrates and fishes.

The routing of flood waters across floodplains is complex and often changes over the course of the flood event. Commonly, water first enters the floodplain through low breaks in the levees known as crevasse splays, and this water may follow floodplain

channels for some distance before spreading out into backswamps or lake basins. Water also commonly backs up through downstream openings, for example, through the lower end of tributaries or oxbow lakes that are connected with the channel. Thus, floodplain inundation commences before the levees become submerged. At the highest river stages, most or all levees may be underwater, and bulk water flow across the floodplain proceeds generally in the downriver direction.

Although the water that inundates floodplains does not necessarily originate from overbank flow of the main (also called mainstem) river, the river may control water levels by backwater effects. Locally derived water entering from lateral tributaries can be impounded temporarily by river flood waters, or travel down the floodplain as deferred flow before mixing with the main river. In extensive floodplains such as the Pantanal, the flood waters can be derived entirely from delayed drainage of precipitation falling directly on the floodplain. Groundwater inputs from adjacent uplands also can be important, especially in smaller floodplains or in floodplain wetlands lying close to the upland boundary. Such inputs may maintain a high water table, and thus create wetland conditions for most or all of the year. These distinct sources of flood waters often differ in chemistry and suspended matter, enhancing the biogeochemical and ecological heterogeneity across floodplains (McClain and Naiman, 2008).

Freshwater rivers near their confluences with the sea can have floodplains subject to tidal control of water levels, superimposing a short-term cycle of variability on longer-term, discharge-driven flood pulses. Examples include the Amazon and Orinoco deltas, where freshwater discharge is high enough to prevent seawater intrusion yet tidal fluctuation can be observed for considerable distances upriver (~200 km for the Orinoco and ~800 km in the Amazon). In contrast, rivers with little or no dry-season flow can experience substantial intrusion of seawater in their lower reaches (Berger et al., 2019). In such river systems, seemingly modest changes in relative sea level can alter the zone of seawater influence, producing dramatic implications for the river and floodplain ecosystems. Sea level rise associated with climate change increasingly will pose a threat to many low-lying floodplain (and other kinds of coastal wetland) ecosystems that contain freshwater in close proximity to the coastal zone (White and Kaplan, 2017). Conspicuous stands of dead trees resulting from the dual stresses of higher water levels and saltwater intrusion, often called "ghost forests," are increasingly common along the Atlantic and Gulf coasts of North America (Kirwan and Gedan, 2019).

Floodplain Lakes

More or less permanently flooded depressions on the floodplain that are deep enough to have open water at least seasonally often are called floodplain lakes, although floodplain water bodies typically exist as a continuum in area and depth from what would normally be called wetlands to lakes (Downing et al., 2006). There is no universal definition that distinguishes a lake from a wetland and usage of 'lake' or comparable terms varies regionally. Commonly water bodies that are called lakes have an open-water area for most or all of the year, which distinguishes them from entirely vegetated wetlands. Their open-water areas may not fill with aquatic vegetation even though they can be quite shallow at low water, which can be a result of the changing water levels and low light penetration. Interannual variation in the flood regime can produce striking changes in the proportions of open water and emergent or floating vegetation. Although they are often small in area, floodplain lakes are one of the most abundant types of lakes in the world, particularly in the tropics where large, unregulated floodplain rivers remain (Lehner and Döll, 2004). Very large lakes are associated with some floodplains, such as the Grand Lac on the Mekong River, though these may have a distinct geomorphological origin.

Floodplain lakes are formed by a variety of processes, including the isolation of main channel meanders (oxbows), formation of swales between successive levees, subsidence of alluvial fill, and permanent flooding of incised tributary valleys. Examples of each of these are visible in Figs. 1–7. Floodplain lakes may be permanently or seasonally connected to the *main* river, and the connections can be broad or very restricted. Lakes that become seasonally isolated from the *main* river may become perched at higher elevations than the river level as the river falls, and they may accumulate water of local origin during the phase of isolation from the river, often maintaining a stream that drains to the river.

Lakes typically occupy a minority of floodplain area but this depends on the geological history of the floodplain. Sometimes subsidence or back-flooding exceed rates of new alluvial deposition (accretion), producing lakes that cover much of the backswamp areas. Tectonic processes that cause subsidence, tilting, or uplift of basement rock can create areas of permanent flooding on floodplains (Dunne and Aalto, 2013).

Most kinds of floodplain lakes are no deeper than the *main* river, and they can become very shallow during low water. During periods of isolation or at least minimal through-flow of river water, they can be rich in phytoplankton, although in many cases they become shallow enough that sediments are resuspended by wind-induced turbulence and inorganic turbidity greatly restricts underwater light availability (e.g., the large oval lakes in the Llanos de Moxos: Fig. 4). During inundation they receive through-flowing river water and this may drastically reduce the water residence time to the point where plankton growth is suppressed by flushing and the water chemistry of the lake increasingly resembles that of the river (e.g., Hamilton and Lewis Jr., 1990; Melack and Forsberg, 2001).

Functions of floodplains

The permanent and temporary aquatic environments of floodplains along large rivers are locations for a number of important ecosystem processes, or functions, which provide values and services to people.

Floodplains tend to be highly productive ecosystems and have long been utilized for production of food and fiber and harvest of wild plants and animals. Perhaps the greatest contrast in productivity between uplands and floodplains occurs in dryland regions, but even in humid climates the floodplain is often desirable for farming and livestock production.

The temporary residence of water on floodplains can be an important hydrological function because it delays the passage of flood waters through the fluvial system. This delay tends to attenuate the flood peak downriver, reducing peak water levels (Lininger and Latrubesse, 2016), which often is advantageous to riverside communities and floodplain agricultural activities. Passage of river water through floodplains can significantly enhance evapotranspirative losses, which in dry regions may be viewed as negative, but this also may increase groundwater recharge, a positive service for water-limited regions. Some floodplains overlie extensive alluvial aquifers and these can provide a readily accessible water supply that is recharged by seasonal flood pulses.

Passage of river water through floodplain environments changes its content of dissolved and suspended matter, which can affect the composition of riverine exports. Suspended sediments tend to show net loss by deposition, whereas nutrients may show net retention or transformations. Concentrations of certain pollutants, particularly those associated with particulate material (e.g., trace metals) as well as labile nutrients (e.g., nitrate), are often greatly reduced in water passing through floodplains. High rates of primary production can result in net export of organic matter back to the river, although floodplains can evidently act as either a net source or sink for riverine organic carbon, based on the few available comprehensive carbon budgets for floodplains (Sjögersten et al., 2014).

Under certain circumstances, water quality can be diminished by passage through floodplains. Strong oxygen depletion upon initial inundation of some tropical floodplains is known to result in fish kills (e.g., the Pantanal in Brazil: Hamilton et al., 1997). In coastal plains of tropical Australia, initial contact of flood waters with acid sulfate soils can cause marked decreases in pH and result in aluminum toxicity for fishes (Townsend, 1994). Such leaching effects usually diminish as the floodplain is increasingly flushed by flood waters.

Extensive floodplains can be important as sources of greenhouse gases to the atmosphere. It remains uncertain whether floodplains tend to be net sources of sinks of atmospheric carbon dioxide, but like other wetlands they certainly tend to be net sources of methane while they are wet, and they may be important sources of nitrous oxide as well, particularly in regions with nitrogen pollution. Tropical floodplains are a globally significant source of methane emission to the atmosphere because of their extensive area and high biological activity (Sjögersten et al., 2014).

In rivers with extensive floodplains that are inundated for relatively long periods, much of the primary and secondary production in the overall river-floodplain system can occur in the floodplains. The Flood Pulse Concept articulates how large river floodplains serve as the locus of biological production in the river system, supporting rich aquatic and terrestrial biodiversity including economically and culturally valuable fisheries (Junk et al., 1989; Tockner et al., 2000).

Human modification of floodplain hydrology

The age-old proclivity of humans to control river systems, combined with our ever-increasing technological ability to do so, has made floodplains one of the most altered aquatic ecosystems. River regulation, mainly through construction of dams, has strongly impacted flood regimes of rivers across all spatial scales, and even many of the largest rivers of the world have been regulated to some degree (Ward and Stanford, 1995; Vörösmarty et al., 2010; Grill et al., 2015, 2019). Construction of new dams on large rivers, particularly in the Tropics, is ongoing and expected to increase in the future (Zarfl et al., 2014; Winemiller et al., 2016).

Impoundments tend to create permanently flooded reservoirs in place of seasonally flooded lands (Fig. 6), and in many cases, they alter the discharge regime and often the water quality and temperature well downstream. Dams and reservoirs block longitudinal migration of riverine fishes and other aquatic animals, and fish passage structures are often inadequate. Reservoirs often trap a large fraction of the riverine sediment load, leading to geomorphological destabilization of the river-floodplain system downriver of the dam (e.g., Kondolf et al., 2014) and potential nutrient impoverishment of downstream water bodies and floodplains (Forsberg et al., 2017). Dams operated for hydroelectric generation may impose highly unnatural, short-term fluctuations in water levels (known as hydropeaking: Moreira et al., 2019), while those operated primarily for agricultural irrigation tend to change the seasonality of river flow in addition to removing water from the system for consumptive use.

Modification of river channels to facilitate navigation usually impacts floodplains by altering the relation between water levels and discharge. Removal of natural barriers to navigation can entail dredging, channel straightening, and excavation of rock outcrops. All of these measures tend to enhance flow conveyance and diminish the backwater effect that produces overbank flooding (Hamilton, 1999). Construction of navigation locks may have similar effects as dams. Low-head navigation dams that allow passage of flood waters, such as those on the upper Mississippi River (United States), are less damaging but still create extensive permanently impounded areas at low water levels (Sparks et al., 1998; Schramm et al., 2015).

Floodplains have often been isolated from their *main* rivers by construction of dikes, commonly for the purpose of farming the land (see Mississippi River example in Fig. 7). Such land can be highly productive but may require costly measures to remove or control water, and over time land subsidence, loss of fertility, and occasional incursion of flood waters can detract from its sustainability. Nonetheless, agriculture on converted floodplains has played an important role in many societies and continues to be significant throughout the world. In some regions, floodplains have been extensively mined for clay, sand or gravel, gold, or diamonds, a provisioning service that is sustainable only if subsequent floods replenish the material that is removed.

Aquatic ecosystems on floodplains are also impacted by urban and agricultural development in the upland watershed, which results in alterations to the flow regime and water quality of the main rivers (Bayley, 1995; Vörösmarty et al., 2010). Runoff is

intensified by impervious surfaces and stormwater runoff drainage in built areas, and by land clearing and wetland drainage for agriculture. Nutrient loading to rivers and their floodplains increases with development, although the floodplain biota can have a large capacity for nutrient uptake and retention, and the nutrient removal as water flows across intact floodplains can be viewed as a valuable ecosystem service.

Conclusions

Floodplains of large rivers are a unique and valuable class of wetlands that are important for biodiversity and ecosystem services. These ecosystems are often complex mosaics that reflect spatial and temporal variability in flood regimes, which in turn are due to topography, water sources, and vegetation. Many of the world's large floodplain systems have been altered by human activity, particularly river regulation by dams and isolation of floodplain lands from river connectivity to permit agricultural use. Yet examples of unregulated rivers with extensive floodplains remain, particularly in less developed parts of the world.

Knowledge gaps

- How will climate change and the consequent altered precipitation and river flow regimes affect floodplains and the ecosystem services they provide?
- How will new dam construction affect the remaining unregulated large rivers, and what can be done to mitigate the impacts?
- Can we restore floodplains that have been historically disconnected from rivers by dams and levees?

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Hyporheic Zone and Processes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Biogeochemistry Processes and conditions that can be described by biological, geological, and chemical processes and conditions all together.
Breakthrough curve Plot of the concentration of a substance (natural or artificial) against time; important parameter of tracer tests.
Ecosystem services The benefits an ecosystem offers to humans.
Hydraulic gradient Difference between the hydraulic head at two points, divided by the distance between these two points.
Hydraulic head Pressure head of the water at a given elevation.
Hyporheic exchange flux (HEF) A parameter for the amount of water that enters and leaves the hyporheic zone per time unit.
Hyporheic zone (HZ) The upper streambed where surface water and groundwater meet (different definitions exist, Introduction).
Hyporheos Fauna of the hyporheic zone.
Interface The area where different compartments are connected and interact with each other.
Residence time Time a water parcel or substance spends in a defined volumetric space.

Introduction

Historically, research on groundwater and surface water was separated in different disciplines; their connectivity and water exchange are still current research topics. In streams, the groundwater-surface water interface is known as hyporheic zone (HZ). The term "hyporheic" was first mentioned by Orghidan (1955) as a "new habitat" at this interface. Nevertheless, a re-thinking considering groundwater and surface water as a "single resource" began much later (Winter et al., 1998). The term "hyporheos" is derived from the Greek words hypo (beneath) and rheos (flow/stream) and summarizes the organism community inhabiting this zone. However, different disciplines use different definitions for the HZ, and sometimes they even differ within the same discipline (Lewandowski et al., 2019). Biologists, for instance, identify the HZ based on its characteristic community of organisms. Hydrologists often define the HZ based on flow paths beginning and ending at the sediment-water interface. Biogeochemists delineate the

HZ based on a minimum percentage of surface water (e.g., 10%, Triska et al., 1989) present in the subsurface. Groundwater-surface water interfaces exist in other aquatic systems as well. They can, for example, be found at the groundwater-lake water as well as groundwater-seawater interfaces.

The aim of this chapter is to introduce the reader to the current knowledge about HZs and the most important hydrological and biogeochemical processes taking place within the HZ. Moreover, this chapter introduces measurement and modeling techniques used in lab, mesocosm, field, and modeling studies to investigate hydrological and biogeochemical processes in the HZ. The HZ's extraordinary importance and vulnerability to human disturbance is highlighted. Furthermore, we present up-to-date research fields and major, current knowledge gaps.

Characteristics and processes of hyporheic zones

Hydrological processes

The HZ is formed at the interface of surface water and groundwater. Due to substantial differences in physical parameters between these two compartments, the HZ is characterized by strong biogeochemical gradients. Usually, fast-flowing, air-temperature-influenced surface water mixes with slowly flowing, thermally-stable groundwater.

Differences in hydraulic heads between two locations in relation to their distance are called hydraulic gradients (Fig. 1A). The hydraulic gradient between surface water and groundwater determines the main flow direction. If the hydraulic head of the surface water is below the hydraulic head of an adjacent groundwater body, groundwater exfiltrates into the surface water ("gaining river" or "upwelling") (Fig. 1B). If the hydraulic head of surface water is higher than the hydraulic head of groundwater, surface water infiltrates into the aquifer ("losing river" or "downwelling"). In arid regions, low groundwater tables cause the rivers to completely disconnect from the aquifer (Fig. 1B).

Darcy's law can be used to determine flow velocities and volume fluxes in the HZ based on hydraulic gradients. The volume flux, or discharge Q ($m^3\ s^{-1}$), which passes the cross-sectional area A (m^2) in a porous medium, is proportional to the hydraulic gradient, termed i, which is calculated by the hydraulic head difference Δh (m) of two locations with distance L (m):

$$v_f = Q/A = v_a/n_e = k_f * i = k_f * \Delta h/L$$

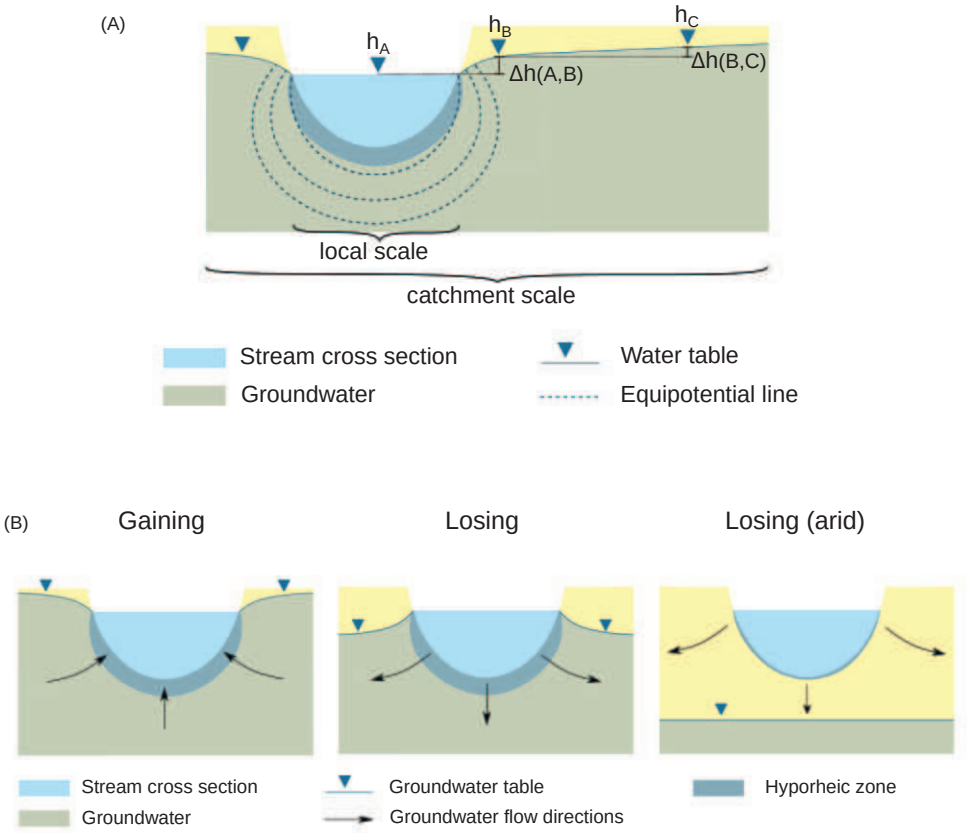

Fig. 1 Schematic representation of (A) hydraulic heads (h) and difference in hydraulic heads (Δh) on a local and catchment scale, and (B) gaining and losing rivers, and losing rivers in arid regions with flow directions in the hyporheic zone and the adjacent aquifer.

The quotient of Q and A is the so-called Darcy velocity v_f (m s^{-1}) which can be transformed into the distance velocity v_a (in m s^{-1}) by division through the flow effective pore space n_e (m^3 m^{-3}). The saturated hydraulic conductivity k_f (m s^{-1}) (also known as permeability coefficient) quantifies the water permeability of the aquifer material. The hydraulic conductivity depends predominantly on the particle sizes of the aquifer material and can be determined either directly by Darcy experiments (manually or with a KSAT device, company: Meter Group, Germany) using undisturbed sediment samples collected in cylinders, by pumping tests, by slug tests or indirectly by means of a grain size analysis. Depending on grain size, hydraulic conductivities vary over several orders of magnitude and are divided into classes ranging from "highly permeable" ($>10^{-2}$ m s^{-1}) over "permeable" (10^{-4}–10^{-6} m s^{-1}) to "impermeable" ($<10^{-8}$ m s^{-1}).

Following Darcy's law, hydraulic gradients at the streambed's sediment surface cause hyporheic exchange flux (HEF), i.e., flux of surface water into the hyporheic zone and back into the overlying water body (Fig. 2). HEFs control transport, residence time, and distribution of dissolved oxygen, nutrients, and contaminants in the hyporheic zone. They are spatially and temporally dynamic and are related to local pressure differences, large scale head differences, hydrological conductivity and porosity of the sediment (Krause et al., 2011).

Varying surface water discharge or groundwater table fluctuations can result in a shift between downwelling, neutral or upwelling conditions. Consequently, the percentage of surface water or groundwater in the HZ changes and even the extent of the HZ is altered. Intense hyporheic exchange occurs at sediment ripples. These streambed features can be highly dynamic and can migrate downstream with alternating celerity (i.e., the speed of motion of that feature) depending on the surface water velocities (Wolke et al., 2019).

Biogeochemical processes

The HZ is a bioreactor with microbes controlling the biogeochemical processes and main ecological functions (Krause et al., 2011). Naegeli and Uehlinger (1997) determined the contribution of hyporheic respiration to up to 96% of the overall ecosystem respiration, underlining the importance of the biogeochemical processes in the HZ as part of river ecosystems. In the HZ, biogeochemical processes are closely coupled to hydrological processes. Groundwater and surface water may differ greatly in their chemical composition including nutrients, organic matter, pollutants, dissolved oxygen concentration, and other redox indicators such as iron, manganese, sulfate or nitrate. Therefore, distinct biogeochemical gradients develop in the zone where groundwater and surface water mix. Microbes play a key role in the formation of these gradients. Close to the sediment surface, oxic conditions and aerobic biogeochemical processes dominate. Along a flow path, aerobic microbes consume oxygen, nutrients, and dissolved organic carbon supplied by the surface water. This eventually leads to anoxic and nutrient-depleted conditions as well as anaerobic processes and related microbial communities further down along the pore water flow path (Fig. 3).

In addition to a changing chemical milieu, biomass and productivity of the streambed community decrease with increasing depth (Peralta-Maraver et al., 2018). The HZ and its biogeochemical gradients provide diverse ecological niches for a variety of organisms and make the HZ a biological hotspot in a river. HEFs through ripples or dunes are often spatially heterogeneous and temporally variable, resulting in different residence times and turnover of solutes in the hyporheic zone (Krause et al., 2011).

Due to temporally varying environmental conditions, the biogeochemical zonation of the HZ is dynamic. Temperature is a major driver of biogeochemical processes and varies both seasonally and in the course of a day. Diel temperature fluctuations might alter oxygen saturation of surface water and diel light cycles alter oxygen production and consumption at the sediment surface and within the HZ.

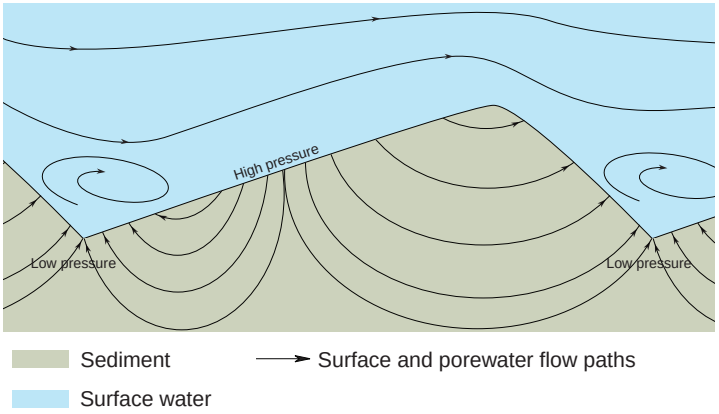

Fig. 2 Hyporheic flow paths in dune-shaped bedforms that can occur in sandy streambeds. The flow paths result from pressure differences at the sediment surface. The flow direction is from high pressure to low pressure zones.

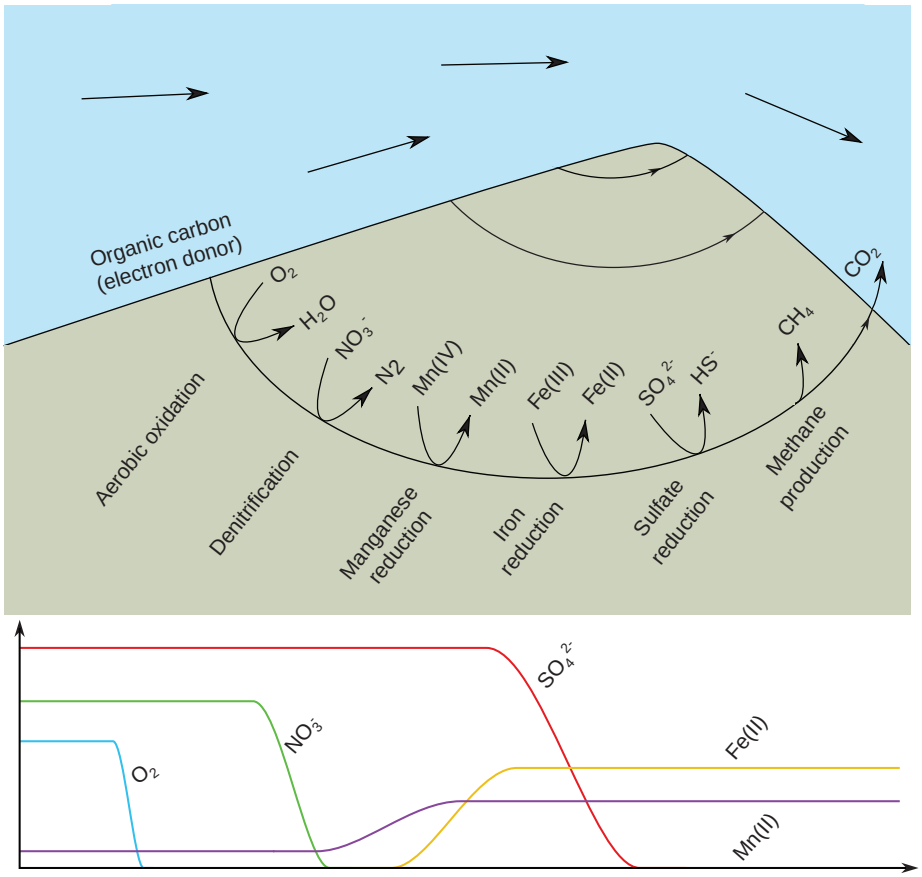

Fig. 3 Schematic figure visualizing the redox sequence along a flow path through a ripple or dune. The lower panel shows schematically the resulting concentration patterns along the flow path.

Importance and vulnerability of the hyporheic zone

Ecosystem services provided by hyporheic zones

HZs provide a diverse number of ecosystem services. Diverse microbial communities promote cycling of carbon (C) and high attenuation rates of the nutrients nitrogen (N) and phosphorus (P). Ammonium and phosphate might be released due to the mineralization of organic matter in the HZ. In addition, the weathering of bedrock and the reductive dissolution of iron-bound P under anoxic conditions might release phosphate. However, HZs might also be sinks for nutrients. P might be bound to iron(oxy) hydroxides under oxic conditions or removed by other compounds. Uptake of P by biomass might also be a relevant removal process. In anoxic hyporheic sediments, denitrification might remove nitrate by conversion to N_2 but sorption and assimilation are additional removal processes of inorganic nitrogen. However, oxidation of ammonium in the oxic part of the HZ causes formation of nitrate (nitrification) (Lewandowski et al., 2019).

Elevated concentrations of iron, manganese, zinc, copper and lead in rivers, lakes and groundwater are usually due to mining-related contamination. In general, the HZ can contribute to the attenuation of metals under conditions with high oxygen concentrations and a high pH but can also release sorbed or precipitated metals if conditions change to anoxic and a low pH (Gandy et al., 2007).

The HZ is also a hotspot for the attenuation of contaminants in rivers. This attenuation is promoted by bedforms on the sediment surface (Boutron et al., 2011), as they increase the hyporheic flux and therefore the water volume flowing through the HZ increases. Trace organic compounds such as pharmaceuticals, industrial compounds, personal care products or pesticides have several degradation pathways, among which microbial degradation and sorption are the most important ones in the hyporheic zone. For many polar trace organics, microbial degradation is the major attenuation process while sorption can also play a significant role for non-polar substances. For many polar trace organics, the upper centimeters of a riverbed are the zone where attenuation is most efficient. This is due to the presence of easily degradable organic matter and oxic to suboxic redox conditions close to the sediment surface (Schaper et al., 2018).

Moreover, the HZ has a filtering capacity for natural and anthropogenic suspended particles (e.g., microplastics), despite the low density of some of those particles (Drummond et al., 2020). Even though filtration is positive from the perspective of surface water

quality, filtration can have severe negative impacts on other ecosystem services: e.g., colmation reduces HEFs and results in alteration of the hyporheos community (Descloux et al., 2013). Furthermore, particulate matter might be toxic itself or might carry sorbed contaminants that might harm the biota inhabiting the HZ.

The HZ is considered a refuge for aquatic organisms, such as juvenile fish (Benjankar et al., 2016), amphibians, or invertebrates. It offers a habitat protected from strong currents in the surface water, temperature extremes, droughts and predators. Surface water entering the HZ provides organisms with oxygen and nutrients while water returning from the sediment back to the surface water removes biological waste products from the HZ. Salmon, for example, dig nests in gravel sediments of HZs for spawning. The resulting structure of the nest and increased hydraulic conductivity around the eggs enhances hyporheic exchange and the oxygen supply to the eggs (Tonina and Buffington, 2009).

Vulnerability

In the HZ, diverse hydrological and biogeochemical processes are in a vulnerable balance. One of the biggest threats to a functioning HZ is the decrease of its permeability combined with a decline in hyporheic exchange. Clogging of the top layer can occur due to inputs of fine sediment into streams by anthropogenic activities such as mining, agriculture, urbanization or dam construction (Hancock, 2002). Clogging can also result from the absence of higher discharge, e.g., natural flow regimes, that would regularly break up the river bed and flush fine sediment downstream (Schälchli, 1992). Moreover, clogging and a decrease in hydraulic conductivity can result from an increase in nutrients stimulating algal blooms and biofilm growth at the sediment-water interface (Boulton, 2000; Hancock, 2002).

A straightened river loses many of its diverse structures that promote hyporheic exchange. These structures include meanders, pools, or obstacles such as large rocks or woody debris. Especially in urban areas, river construction leads to obstructed river banks and sealed riverbeds that, in extreme cases, may completely eliminate the HZ. Nevertheless, river construction can also create obstacles which force water flow into the sediment and increase hyporheic exchange (Crispell and Enreny, 2009).

The input of anthropogenic substances has consequences for all types of organisms throughout the food web. Increased concentrations of heavy metals or other contaminants result in toxic conditions for many organisms (Courtney and Clements, 2002). Hyporheic microbial communities, for example, react to a change in the chemical milieu through altering their composition and performance (Danczak et al., 2016; Febria et al., 2010; Nelson et al., 2019). If the contaminant is toxic for invertebrates which dig in the sediment or graze on microbial biofilms, the extinction of those organisms could also lead to a decrease of hyporheic flow (Hancock, 2002).

Artificial discharge and resulting water temperature fluctuations might impact the HZ. They can be caused by infrastructures, including hydropower and waste water treatment plants, irrigation practices, etc. Those fluctuations may alter the physiochemical conditions of the HZ and, hence, impact the habitat of organisms living in and on the sediment (e.g., for hydropower plants: Bruno et al., 2013).

Methods

Choosing the right research approach

The available techniques to study the processes in the HZ are manifold. When planning an experiment, the research question or hypothesis is the basis for selecting the appropriate methods, temporal and spatial scales. One of the main challenges in hyporheic research is the overlap of spatial heterogeneity and temporal variability (Fig. 4, "Characteristics and processes of hyporheic zones" section). For instance, groundwater is usually characterized by temporally rather constant chemical compositions while spatially chemical compositions can be very heterogeneous due to slow mixing rates. In contrast, surface water bodies are characterized by spatially rather homogeneous water composition as mixing rates in streams are fast but the temporal variability is high. In the HZ, as the transition zone between groundwater and surface water, the water composition is both temporally variable and spatially heterogeneous even though the temporal variability of the surface water body might be damped. Consequently, HZ research must account for both spatial heterogeneity and temporal variability.

Given this complexity, another important aspect of experimental planning is determining the level of simplification acceptable to answer the research question. Generally, experimental studies can be divided into field, mesocosm, and laboratory studies (Fig. 5). Field studies are conducted in real and complex river systems, including all involved and non-separable processes with their spatial heterogeneities and temporal variabilities. In contrast, in batch or column experiments in the laboratory, many parameters can be controlled well. Although simplification helps to focus on single processes and differentiate their individual impacts, important links to other processes or parameters present in reality might be missed. Artificial river channels (i.e., flumes) and other mesocosm experiments are in between the complexity of field sites and the simplicity of batch and column experiments as some parameters can be controlled but others cannot. Laboratory studies and mesocosm studies have the advantage to allow for statistical replication, which is hardly or not at all possible in field studies.

Besides experimental studies, another possibility to study hyporheic processes are models. Models can either be used for pure modeling based studies or they can complement experimental investigations. Modeling studies allow for controlling parameters and can cover a large range of complexity and realism. While models always simplify reality, they make it possible to narrow down value ranges of parameters which are either hard to measure or cannot be measured at all.

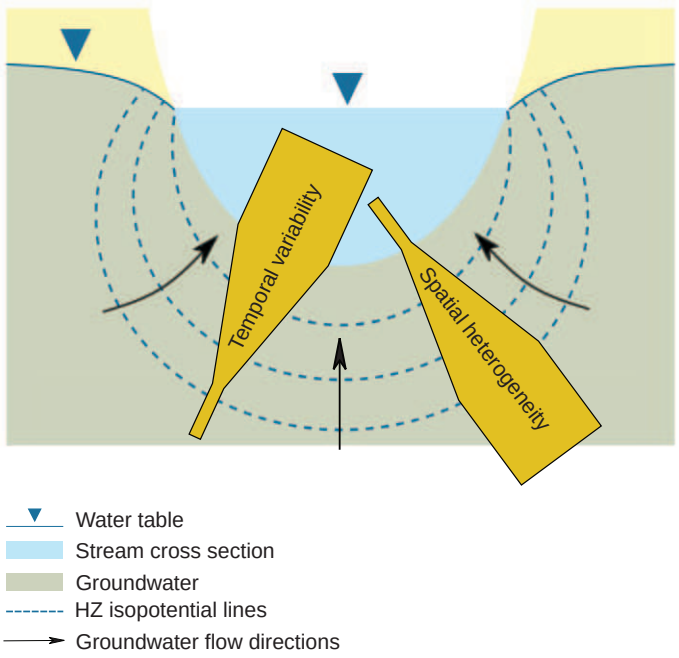

Fig. 4 Schematic overview over temporal variability and spatial heterogeneity at the groundwater-surface water interface. Width of yellow polygons represents degree of heterogeneity/variability.

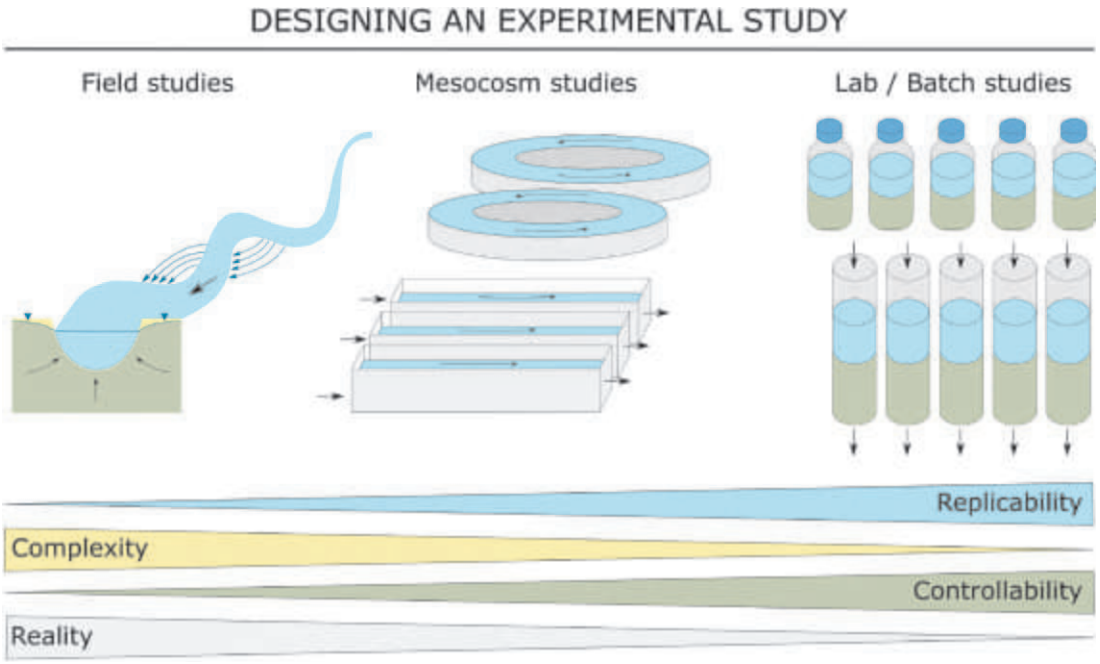

Fig. 5 Schematic overview of different forms of experimental studies, i.e., field, mesocosm, and lab/batch studies, and their variability in replicability, complexity, controllability, and closeness to reality.

Methods to study hydrological processes in the HZ

In the following, we present frequently used lab, mesocosm and field methods to investigate hydrological processes in the HZ. Understanding of these processes is an important prerequisite for assessing biogeochemical processes and contaminant degradation.

Methods used in laboratory and mesocosm studies

Laboratory methods for investigating hydrological processes include batch tests and column experiments. Column experiments are conducted to study flow in sediments collected in the field or in artificial sediments with known grain size distribution and grain shape. Hydrological column experiments are often combined with conservative tracer tests (Section "Methods used in field studies" below). Hydrological processes investigated in mesocosm flume studies include the characterization of hyporheic flow paths and HZ extension, turbulent water flow and the water-sediment interface including erosion and deposition of sediments.

Methods used in field studies

Field methods to study hydrological processes in the HZ examine pore water flow direction, quantity and velocity. Methods based on Darcy's law use observation wells, so called *piezometers*, i.e., tubes with a filter screen at the lower end. They are installed in the streambed or aquifer to measure hydraulic heads either manually with dip meters or as time series by pressure loggers. Hydraulic head differences between wells or/and the water table of the river can indicate vertical or horizontal flows. *Seepage meters* are large cylinders with one open side that is pressed into the sediment. Groundwater exfiltrating within the seepage meter is collected and its volume used to calculate the exfiltration rate (Lee, 1977). *Heat-Pulse-Sensors* determine the 3D flow direction and velocity in the HZ using temperature breakthrough curves. A heating element introduces a short heat pulse into the sediment which travels then through the sediment and is detected by temperature sensors placed around the source (Angermann et al., 2012).

Natural temperature differences between groundwater and surface water can also be used to quantify exchange rates and record spatial flow patterns in the HZ. While groundwater temperatures fluctuate only slightly over the course of the year, surface water shows daily temperature fluctuations and is often significantly colder than groundwater in winter and significantly warmer in summer. *Temperature lances* with multiple temperature sensors record temperature profiles in the water column and in different depths of the sediment. Mathematical models, e.g., VFLUX (Gordon et al., 2012), are then applied to calculate vertical fluxes in the HZ. *Fiber-optic distributed temperature sensing (FO-DTS)* uses long fiber optic cables located at the sediment-water interface that determine temperature changes along the fiber. Deviations from the stream water temperature indicate that cooler or warmer groundwater (depending on the season) is entering the stream (Gaona et al., 2019). In *thermal infrared imaging (TIR)*, a camera records an image of surface water temperatures. The exfiltration of warm or cold groundwater in winter or summer, respectively, might cause visible signals in the TIR image and thus allows for a fast and easy localization of exfiltration zones (Hare et al., 2015).

Electric resistivity tomography (ERT) is a non-contact method that provides information on the subsurface sediment matrix or subsurface flow if combined with an electrically conductive tracer (Ward et al., 2010). With one pair of electrodes, electric current is injected into the ground and the electric potential difference is measured with another pair of electrodes. The resulting data allows conclusions about hydraulic conductivities. *Hydrograph analysis* (Bayou et al., 2021) of surface water flow is based on the proportion of base flow, often groundwater, and event flow from precipitation or snow melt, in a river. A *water mass balance* between two gauging stations at a river can determine groundwater ex- or infiltration by detecting higher or lower discharge at the downstream station, respectively.

Tracers are another useful tool to study surface water-groundwater interactions. They are divided in *natural and artificial tracers*. *Stable water isotopes* naturally occur in certain ratios of heavy to light isotopes. This ratio is altered by different processes such as evaporation or precipitation. As these two processes mainly influence surface water but not groundwater, the isotopic signal of those two water bodies differs and can be used by mixing models to determine the contribution of them both (Sklash and Farvolden, 1979). If the *electrical conductivity* of groundwater and surface water differs, this parameter can also be used to examine interactions of the two water bodies in the hyporheic zone. For a period of several days, *radon* gas can be used to calculate the age of water (Bourke et al., 2014). Radon is produced by the decay of radium, which naturally occurs in rocks, and has a half-life of 3.8 days. It occurs in groundwater but rapidly degasses from surface water. Therefore, elevated radon concentrations in surface water indicate nearby exfiltration of groundwater into the surface water body. In contrast to natural tracers, *artificial tracers* are injected into the system to study hydrological processes by looking at breakthrough curves at certain locations of the system. Conservative tracers such as salt (NaCl), bromide, lithium, and artificial dye tracers, such as rhodamine WT; fluorescein and uranine, are applied to investigate flow paths and times, discharge or mixing of different water bodies. Salt requires larger amounts, because of higher background concentrations, but can be easily measured as electrical conductivity. The other tracers require only small amounts, but are more elaborate to be detected.

Methods used in modeling studies

Models are nowadays generating a large part of HZ research. Boano et al. (2014) extensively reviews modeling studies conducted over the history of HZ research and divides mathematical models into two groups: physical and phenomenological models. Physical models use the "physical principles of mass and momentum balance" as a basis. These physical models are used to predict transport and residence times of water and dissolved compounds in streambeds and are suitable to examine the relative importance of factors and processes regulating flows at the groundwater-surface water interface (Boano et al., 2014). Phenomenological models are models based on the phenomenological description of the surface water-groundwater system (Boano et al., 2014), e.g., transient storage models by e.g., Bencala and Walters (1983) and Runkel (1998). Phenomenological models are often applied to reach scales and calibrated by field tracer tests, e.g., OTIS by Runkel (1998) and Boano et al. (2014).

The determination of groundwater upwelling and downwelling can be determined by modeling hydraulic heads (Cardenas and Wilson, 2007) or by assessing phase shift and amplitude damping of diel temperature signals along a profile in the sediment by Dynamic Harmonic Regression using the VFLUX method (Gordon et al., 2012).

Methods to study biogeochemical processes in the HZ

Biogeochemical processes in the hyporheic zone are a crucial part of the functionality of this interface. Based on sediment and hydrological characteristics, different redox zones develop. These zones can be either stable or dynamic and regulate all other biogeochemical processes. These processes can be nutrient cycling or attenuation of contaminants, among others.

Methods used in laboratory and mesocosm studies

Batch tests are used to determine specific biogeochemical features of hyporheic sediments or pore water. Examples are sorption and desorption processes or the impact of e.g., organic matter on the attenuation of contaminants or microbial metabolism. Compared to batch tests, *column experiments* are more realistic as they can feature pore water flow through the columns. Adjusting flow velocities and resulting redox conditions in the sediment allows for analyzing the influence of these parameters on the biogeochemical processes. Biogeochemical processes can be examined by comparing input and output concentrations, by measuring concentration gradients over depth, or by using reactive tracers (e.g., resazurin) as surrogates for the compound or microbial biota of interest. To capture more reality, *mesocosm* studies are used. Examples are many, but include flumes with either circular or straight channels to study for instance how surface water flow velocities affect dissolved O_2 in the sediment (Wolke et al., 2019) or how trace organic compounds (TrOCs) are degraded in the riverbed (Jaeger et al., 2021).

These setups can be equipped with a wide range of measurement devices. Sensors combined with data loggers can automatically record, for example, temperature, pH, O_2, electrical conductivity, and some solutes. *Microsensors*, for instance used by De Falco et al. (2018), are used to measure depth profiles of O_2, redox potential, pH, etc. in the hyporheic zone. Due to their small size in the μm range, depth profiles can be recorded with minimum disturbance of the sediment. 2D measurements of O_2, CO_2 or pH are possible with *planar optodes (solute imaging)* installed at a transparent wall of the studied system and associated excitation light sources combined with a camera (Wolke et al., 2019).

As microbes are a major factor determining biogeochemical processes, microbial communities in the hyporheic zone can be of interest. While *genetic analysis* like sequencing disentangles the composition of microbial communities by their genome, tests such as *community-level physiological profiling* (Weber and Legge, 2010) separate microbes into functional groups based on metabolic similarities on microplates. Microbial activity can be measured using *smart tracers* e.g., resazurin (Knapp et al., 2018).

Methods used in field studies

Field studies investigating biogeochemical processes in the hyporheic zone often focus on nutrient cycling, contaminant attenuation or transport processes of compounds. Many techniques introduced in Section "Methods used in laboratory and mesocosm studies" can also be used in the field. In addition, taking samples to be able to analyze the water composition in the laboratory is often required. A number of such sampling methods are explained below.

Mini piezometers (Martinez, 2009) are miniatures of groundwater observation wells with a small diameter down to 2 mm. Due to their small diameter, peristaltic or syringe pumps are used for sampling. The pumping rate must be very low to avoid pumping induced surface water intrusion to the sampling port. *Multilevel piezometers* consist of a bundle of tubes with sampling ports located at different depths in the sediment. This allows for simultaneous pore water sampling from several depths within the sediment. *Pore water samplers* (also called peepers, dialysis samplers or diffusion samplers) consist of a plate with chambers at regular intervals. The chambers are filled with deionized water and covered with a semi-permeable dialysis membrane (Hesslein, 1976). Peepers are installed vertically in the river bed, usually with an exposure time of 14 days. Solutes diffuse through the membrane until concentration equilibrium is reached between chamber and surrounding pore water. *Seepage meters* can not only be used to quantify the volume flux but also to determine the quality of exfiltrating groundwater. The water collected can be used for analytics but precaution needs to be taken against oxygen contamination of anoxic sample water (Lee, 1977; Downing and Peterka, 1978).

Methods used in modeling studies

HEFs cause high spatial heterogeneity of hydrological and biogeochemical conditions in river sediments (Boano et al., 2014). They strongly control biogeochemical processes in the HZ (Krause et al., 2011) by, for example, supplying nutrients, organic carbon, and oxygen. As mentioned earlier, complexity occurs by spatial heterogeneity in groundwater-surface water interaction. This complexity

forms a great challenge for modelers. According to Boano et al. (2014, p. 644), "no current model considers this full range of coupled physical and biogeochemical complexity" and up to date most models focus on single processes, scales or connections of interest. Models that integrate hydrological and biogeochemical processes focus on single streambed formations and are strongly simplified if applied to reach or stream network scales (Boano et al., 2014). Existing models include models on hyporheic transport of solutes (such as metals, Boano et al., 2014), models of HEF and the deposition of fine particles (e.g., Preziosi-Ribero et al., 2020), models on microbial metabolism (Boano et al., 2014), metabolic models combined with HEFs (e.g., Caruso et al., 2017), generally reactive transport models (e.g., Runkel, 2010), and transient storage models (e.g., Salehin et al., 2003).

Knowledge gaps

- Coping with the challenge of spatial heterogeneity of sediment composition and temporal fluctuations of porewater composition
- Flow path determination in HZs as basis for understanding of biogeochemical processes
- Dynamic flow paths changes and changing residence time distributions
- Influence of discharge dynamics (natural, e.g., rainfall or artificial, e.g., hydropower plant) on hyporheic exchange fluxes, biogeochemical and microbial processes in HZs
- Effects of moving bed forms on hydrological and biogeochemical processes and microbial respiration in the HZ
- Improvement of micro sensors for minimum disturbance of sediments needed
- Further development of sensors and measurement techniques
- Reactive transport in streams and their HZs, i.e., linking hydrology with biogeochemistry, especially for analysis of contaminant attenuation and transport
- Hyporheic microbial community composition and its impact on biogeochemical processes and contaminant degradation
- Further development of smart tracers to investigate microbial activity
- Contribution of the HZ to total greenhouse gas (GHG) emissions of a river

Conclusions

The HZ is nowadays a widely studied river compartment involving many different disciplines. Recent HZ research explored a huge diversity of hydrological and biogeochemical processes occurring in the HZ. The advancing knowledge of the HZ unravels the extraordinary importance of this interface and of the ecosystem services it provides. It offers filtration of surface water and habitat for juvenile fish, invertebrates and microorganisms. Microorganisms building up as biofilms are crucial for the nutrient turnover in a river. They offer great potential for organic contaminant attenuation through microbial degradation. The HZ is a vulnerable system which is threatened by river engineering, clogging and consolidation of the sediment, artificially altered discharge regimes, modified temperatures, and increased pollutant or nutrient loads. The latter two are leading to an increased oxygen consumption and subsequent oxygen depletion in the HZ. This might result in a reduction of the self-purification capacity of streams.

Hyporheic studies apply a variety of methods depending on the aspect or question examined. Unfortunately, previous studies revealed that several parameters, e.g., hyporheic exchange fluxes (HEF) or hydraulic conductivities, differ significantly depending on the method applied. Therefore, it is recommended to apply multiple methods giving information about the same target compound in each study to be able to compare their results. Furthermore, a detailed documentation of the applied methods is important for later use of data and comparison between studies. Future work on method standardization is recommended to improve comparability. As hyporheic processes (e.g., flow, transport, transformation) are closely linked to each other, it is furthermore recommended that future studies use a combination of different methods (field, lab, models) and scales (spatial and temporal). One of the main findings of HZ research is the close coupling of biogeochemical processes to hydrological processes. In other words, the knowledge of flow paths is essential for understanding biogeochemical processes.

This chapter showed the extraordinary importance of the hyporheic zone as part of the surface water-groundwater continuum. Further research is necessary to enhance our knowledge about the HZ to acknowledge and promote its ecological importance. Future research should increasingly involve water resource managers, authorities, the public, and other stakeholders to better protect and use this resource.

Important case studies

Site/Research Group	*Country*	*Location*	*Topic/Concept*	*Key references*
Environmental Change Outdoor Laboratory	United Kingdom	University of Birmingham	A high-capacity research platform to understand environmental change; a very large number of flumes	https://www.birmingham.ac.uk/research/activity/ecolaboratory/index.aspx e.g., Jaeger et al. (2019a)
Worldwide Hydrobiogeochemistry Observation Network for Dynamic River Systems (WHONDRS)	United States of America	worldwide network	A consortium of researchers and other interested parties that aims to understand coupled hydrologic, biogeochemical, and microbial function within river corridors; data sets of measurements following a standardized sampling scheme at several world-wide sites	https://whondrs.pnnl.gov/
Flume laboratory	Israel	Zuckerberg Institute for Water Research, Ben-Gurion University of the Negev	Hydrological and biogeochemical process understanding in rivers systems, especially hyporheic zone by flumes capable of simulating gaining/losing conditions and moving sediment beds	e.g., Fox et al. (2014) and Wolke et al. (2019)
River Erpe	Germany	Berlin/Brandenburg	Understanding of closely coupled hydrological and biogeochemical processes in rivers and their hyporheic zones including degradation of micropollutants; well-studied lowland sandbed stream receiving high loads of treated wastewater	Jaeger et al. (2019b) and Schaper et al. (2018)
Watershed Science, Engineering and Management Group at Indiana University	United States	Bloomington	River Corridor Science	https://www.wardhydrolab.com/research.html
Water Research at Technical University of Munich	Germany	Munich	Soil columns to study the attenuation of trace organic compounds during managed aquifer recharge	https://www.wasser.tum.de/forschung/

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Algae and Primary Production of Streams and Rivers Ecosystems☆

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This is an update of R.J. Stevenson, Algae of River Ecosystems, in *Encyclopedia of Inland Waters*, edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00142-3.

This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editor LeRoy Poff.

Glossary

Allelopathic Types of interactions among organisms generated by one organism that secretes chemicals that affects another organism with potentially positive or negative effects.
Allochthonous Matter originating from outside the ecosystem.
Autochthonous Matter origination from within the ecosystem.
Autogenic Means self-produced or self-generated, rather than determined by other organisms or habitat scale drivers of physical and chemical conditions.
Benthic algae Algae that in association with surfaces in aquatic ecosystems (the benthos). Some are microscopic (microphytobenthos, or biofilm) and some are large enough to see strands of cells without a microscope (microphytobenthos).
Epiphytic Refers to living on plants.
Functional redundancy Refers to the ability of different species to perform the same function in an ecosystem, such as primary production or nutrient cycling. If there is sufficient functional redundancy of species in a regional species pool, then ecosystem functions can be maintained with modest changes in environmental conditions if rates of changes in those conditions allow sufficient time for immigration and reproduction.
Metaphyton Algae that are occupy the water column that can determine their distribution and are therefore relative stationary in location by entangling with substrata on the bottom of the habitat or potentially attaching to substrata.
Photoinhibition Low levels of light have positive effects on photosynthesis, but high light intensities can cause negative effects organisms that increase with higher and higher light intensities.
Phytoplankton Algae that are suspended in the water column that cannot determine their distribution and float wherever currents take them, which is typically downstream.

Introduction

Algae in rivers occupy two distinct habitats, the benthos and water column. Benthic algae are algae attached to or associated with substrates in streams and rivers. Thus, periphyton and biofilms (microphytobenthos), macroalgae (macrophytobenthos), and metaphyton are benthic algae. Phytoplankton are suspended in the water column. The amount of these algae and their function and biodiversity varies greatly among different types of streams and rivers and with time. River ecosystems, broadly defined, include all flowing water sections within a watershed, streams, and rivers, and may be bordered or interrupted by lakes, reservoirs and wetlands. Groundwater connections are also important parts of river ecosystems that affect algae.

☆*Change History*: October 2021. R Jan Stevenson updated text, added two new figures, deleted one figure, deleted one table, and added new references.

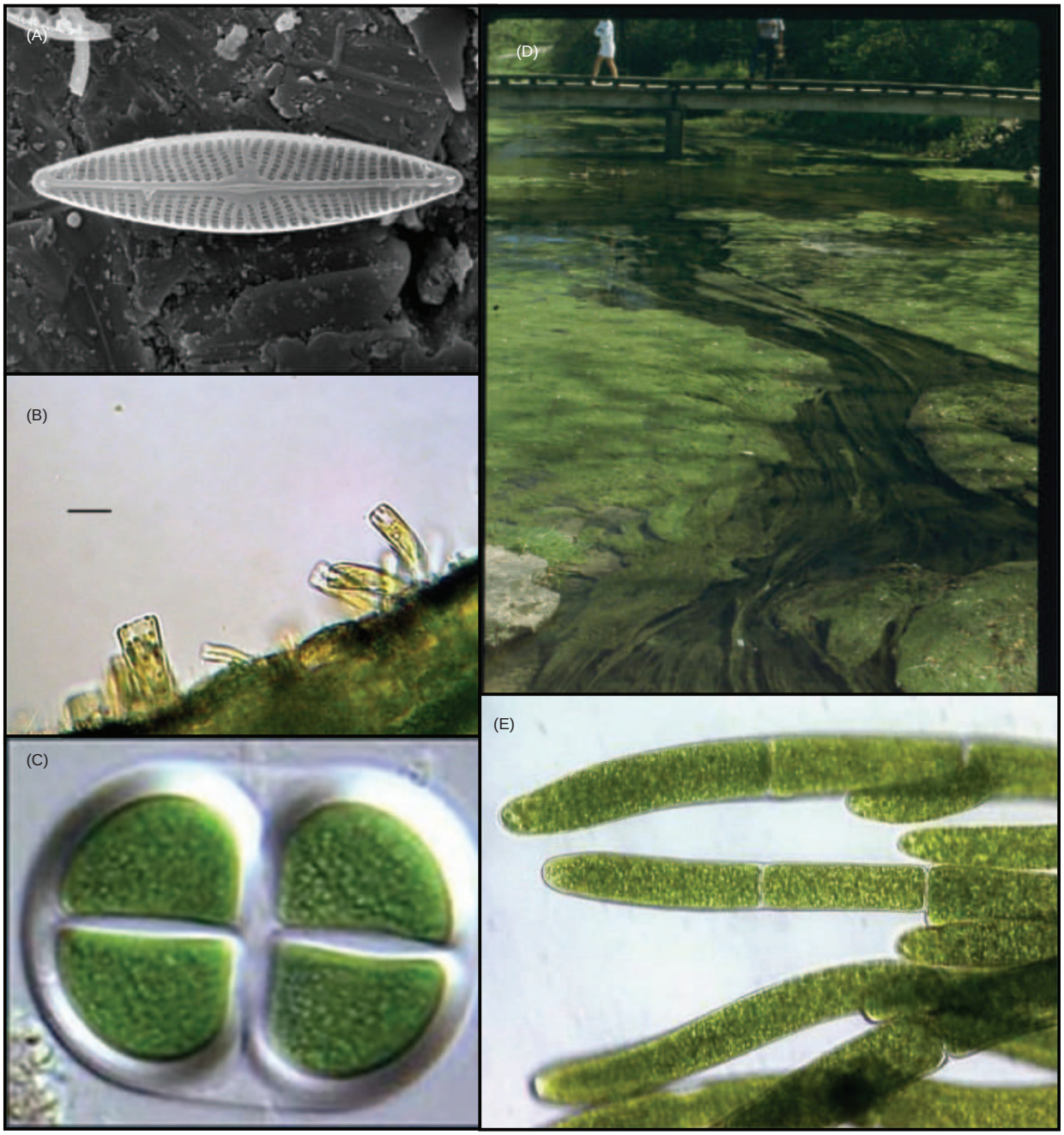

Fig. 1 Three common types of algae in rivers and streams: (A) glass cell wall of a diatom viewed by scanning electron microscope; (B) photomicrograph of diatoms with golden brown pigments attached to the cell wall of a green alga; (C) photomicrograph of a cyanobacterium; (D) photograph of filamentous green algae in a stream; (E) photomicrograph of a filamentous green alga, Cladophora that is in the stream (D).

Taxonomic and morphological diversity of algae varies among habitats and seasonally within rivers as well as among rivers with different environmental conditions. Species composition varies in most river ecosystems from diatom-dominated benthos and phytoplankton during winter and spring to a varying diversity of green algae and cyanobacteria during warmer seasons (Fig. 1). However, a wider diversity of almost all kinds of algae—euglenoids, reds (Rhodophyta), crytomonads, chrysophytes, xanthophytes, dinoflagellates, and even browns (Phaeophyta)—can be found in rivers. Size of these organisms varies from less than 5 μm for small diatoms and chrysophytes in the plankton to meters in length for some filamentous green benthic macroalgae. Morphologically, algae occur as unicellular, colonial, and filamentous forms in both benthic and planktonic habitats. Both unicellular and colonial flagellates use flagella to move vertically in the plankton. Unicellular diatoms may use their raphe and filamentous cyanobacteria move through sheaths in benthic habitats. Many planktonic species rely simply on water currents or periodic resuspensions to maintain sufficient exposure to light to survive.

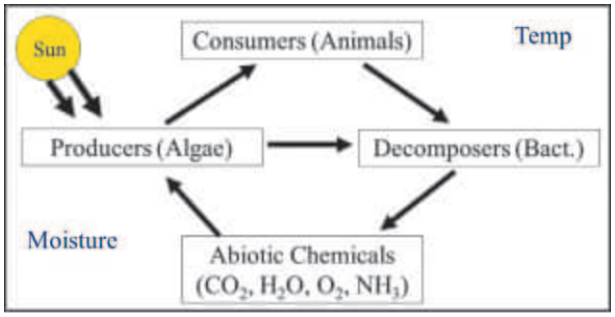

Fig. 2 Basic food web illustrating role of algae as primary producers in relation to consumers (herbivores and predators) and decomposers (bacteria and fungi).

Despite the great variation in algae of rivers and the complexity of factors that affect them, we have learned much about the environmental factors that regulate the processes that control algal biomass, diversity, and function. For example, floods and grazing invertebrates can reduce algal biomass, reduce primary production, and shift species composition to flood- or grazer-tolerant organisms (Power and Stewart, 1987; Steinman et al., 1987; Biggs, 1988; Grimm and Fisher, 1989; McCormick and Stevenson, 1989). Whether or not floods and grazing invertebrates are important in river ecosystems is determined by the climate, geology, and resulting hydrology of the ecosystem (Frissell et al., 1986; Biggs, 1995b; Riseng et al., 2004). In this chapter, I will use a hierarchical conceptual framework for the factors that affect algae in rivers and streams. This framework will help organize the interrelationships among factors that regulate the complex patterns of algal biomass, function, and biodiversity and thereby, will help predict or generate hypotheses to explain patterns of spatial and temporal variation of algal attributes within and among ecosystems. Ultimately, this broader conceptual model will help us predict longer term changes in algae of river ecosystems and how human activities can be managed to solve and prevent environmental problems.

Algae are important elements of river ecosystems and important determinants of the goods and services provided by rivers. Algae are important in the food web in terms of primary production, biogeochemical cycling, and habitat formation and alteration (Fig. 2; see review in Stevenson et al., 1996; Allan and Castillo, 2007). Algae transform sunlight and CO_2 via photosynthesis (i.e. primary production) into sugars. Algal photosynthesis is responsible for the oxygen in every other breath a human takes, although admittedly most of that comes from oceans and not rivers and streams (Field et al., 1998). Algae consume large amounts of nutrients from rivers and streams to combine with the sugars made in photosynthesis to produce amino acids, proteins, lipids, and nucleic acids that are needed for algal reproduction. In food webs, algae can be consumed by herbivores or decomposed by bacteria. In general, microalgae are consumed by aquatic herbivores, mostly insects. In contrast, most macroalgae and plants, which are also important primary producers in some rivers and streams, are more directly decomposed by bacteria and fungi because few aquatic herbivores are adapted to eat it. In addition, algae secrete great amounts of polysaccharides that are used by bacteria and even help bacteria decompose other more recalcitrant organic matter (Wyatt et al., 2012; Danger et al., 2013). Remineralization of nutrients from organic matter occurs by many processes which enable completion of the nutrient cycle as algae again take up nutrients, bind them with sugars from photosynthesis and make cell components for reproduction.

Algae support human wellbeing by producing food and cleaning water for drinking. Excess algae in rivers cause many problems by altering physical habitat and depleting dissolved oxygen supplies. This affects biodiversity and productivity of rivers. Algae can also cause taste, odor, and toxicity problems in drinking water supplies and foul the pipes and filters of water users. So understanding algal ecology is important for managing river ecosystems to protect the goods and services that rivers provide.

Factors affecting algae in rivers and streams

Both benthic algae and phytoplankton in rivers live in highly variable habitats. To help understand how algae are regulated by their environment, we should focus our attention on algae at a specific location. There we find five fundamental processes affecting how much and which algae occur in that location: immigration, reproduction, grazing, emigration, and death (Fig. 3; Stevenson, 1997). Immigration of cells or groups of cells into the space provides the initial colonists as well as ongoing replacement for cells that are continuously leaving the habitat via loss factors, such as grazing, emigration (drifting and sinking), and death. Reproduction by cells within that location, as well as immigration, affects accrual positively. Algal metabolic processes, such as photosynthesis, respiration, and nutrient uptake, directly affect reproduction. These fundamental processes determine the structure of algal communities in rivers: the biomass of individual species as well as all algae at a location, and therefore species composition.

Both abiotic and biotic factors either directly or indirectly regulate the five fundamental processes of cell accrual. These include: (1) light intensity and duration, (2) nutrient concentration, and density of grazers, bacteria, and viruses that have direct effects, as well as (3) flood frequency, (4) climate and (5) geology that have more indirect effects. Many patterns are possible because they depend on the relative magnitude of each of the biological processes and their many direct and indirect environmental determinants. Relating patterns in algal biomass and species composition to the biological processes and environmental factors in rivers requires, in most cases, application of non-equilibrium models in algal ecology.

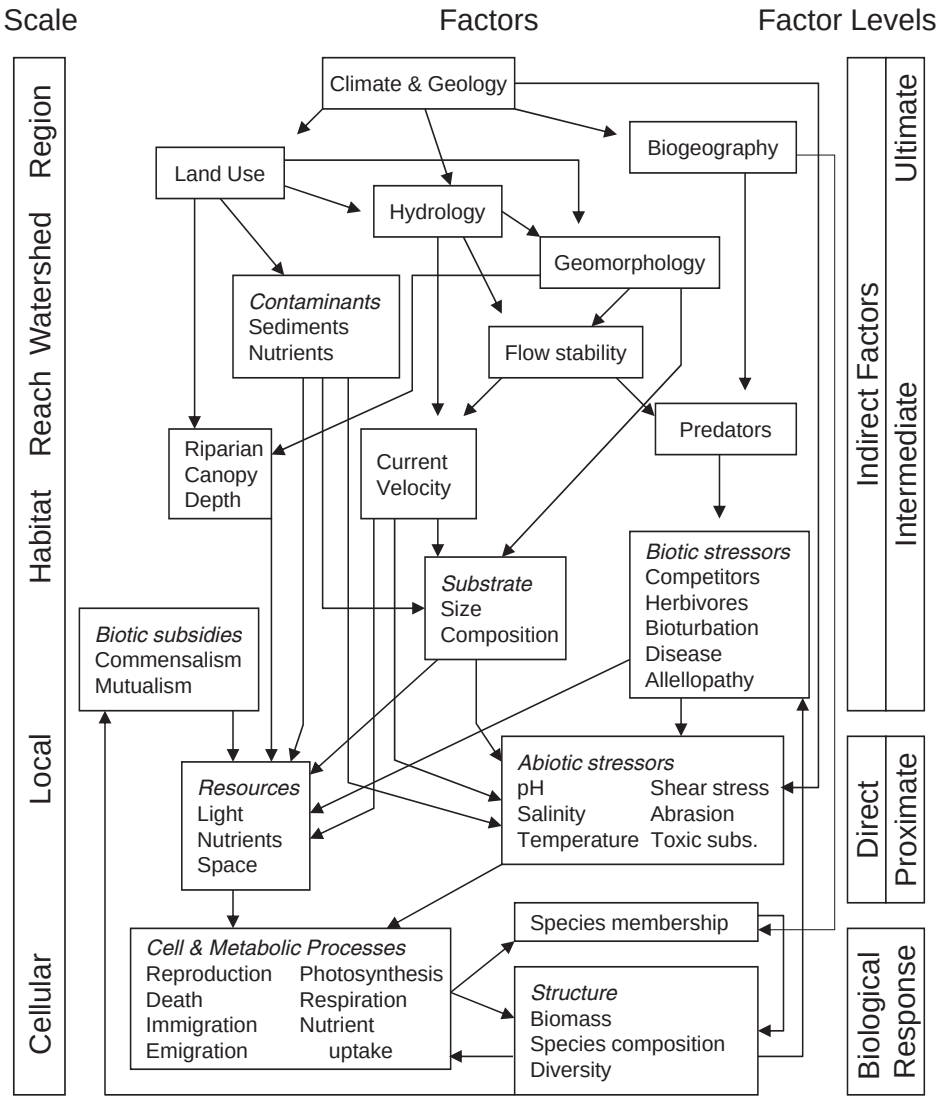

Fig. 3 Hierarchical interrelationships among proximate, intermediate and ultimate determinants of benthic algal structure and function. The relative spatial scale is shown at the left. Modified from Stevenson, 1997.

Factors that regulate algae in rivers operate at different spatial and temporal scales (Fig. 3). The processes of accrual and losses of cells at a specific location operate at the cellular or local spatial scale and reflect the biological responses to other ecosystem factors that are regulated at larger spatial and temporal scales. Abiotic factors that directly affect algae include both resources and stressors, such a nutrients and light versus pH, salinity, shear stress, and heavy metals. Biotic factors can also be classified as positive or negative, and they include commensalistic and mutualistic interactions, as well as competition, predation, disease, and allelopathic interactions. At the habitat scale, riparian canopy, current velocity, and substrate presence and size affect algae, but primarily by mediating the direct biotic interactions, resources, and stressors. At watershed and regional scales, climate and geology ultimately regulate land use, hydrology, and geomorphology of rivers. They also regulate species biogeography and their availability to colonize rivers. The spatial and temporal hierarchy of these factors will regulate the complexity of possible interactions and facilitate understanding and prediction of local conditions and resulting algal structure and function in rivers and streams.

Local abiotic factors

Resources

Algal reproduction can be regulated by light, nutrients, and space. A variety of metabolic processes have similar functional responses to light intensity and nutrient concentration. Metabolic rates increase relatively rapidly in response to light and nutrient increases at low levels of resource availability, but eventually saturate at high levels of resources and respond little to further increases (Fig. 4A). Light has the possibility of having an additional negative effect at very high intensities due to photoinhibition processes (Boston and Hill, 1991). Light intensity strongly regulates photosynthetic rates and carbohydrate synthesis. Nutrient concentrations regulate their uptake rates, use in protein and lipid synthesis, and cell reproduction (Bothwell, 1989; Rier and Stevenson, 2006).

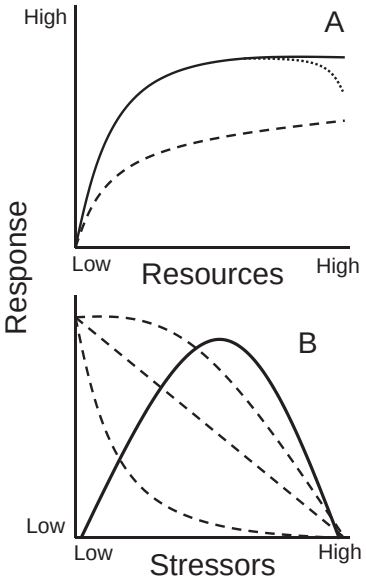

Fig. 4 Responses of algae to abiotic factors. (A) Resources have asymptotic responses with rapid increases to saturating levels (solid line). Light can have a negative effect at very high levels (dotted line). Density of algae reduces supply rates and response of algae to given resource levels (dashed line). (B) Stressors negatively affect algal processes either non-monotonically like temperature (solid line) or monotonically (family of dashed lines), when there is no positive effect at low levels of stressors.

Variation in light and nutrients does affect algal biomass, metabolism, and species composition in streams and rivers (Biggs and Close, 1989; Guasch et al., 1995; Rosemond et al., 2000). High light intensity and nutrient concentrations are required for accrual of high algal biomass on substrata or in the water column. Although reproduction or algal growth saturates at low light and nutrient levels, self-shading and reduced nutrient transport (when eddy mixing and diffusion are less than nutrient uptake rates) limit resource supply at the local scale as algae accumulate on substrates (Stevenson and Glover, 1993). For example, phosphorus limitation of thin biofilms of diatoms requires concentrations lower than 5 $\mu g\ L^{-1}$ PO^4-P, whereas 30 $\mu g\ L^{-1}$ is required to saturate growth of thicker mats (Bothwell, 1989). As algal biomass increases, more light as well as nutrients are required to produce the metabolism, growth, and accrual of high biomasses in relatively short periods of times (Hill and Boston, 1991; Dodds et al., 1999). However, high algal biomasses can accumulate over longer periods of times at lower light and nutrient concentrations in hydrologically stable habitats, such as some springs, where disturbance does not interrupt accumulation processes. Thus, this process-based approach helps us understand how we can have high algal biomass at intermediate as well as high nutrient concentrations.

Experiments using nutrient diffusing substrates and dosing in experimental streams show that both nitrogen and phosphorus can limit algal growth in streams (Fairchild et al., 1985; Bothwell, 1989; Pringle, 1990; Rier and Stevenson, 2006). There is also some evidence that micronutrients can limit growth of some algae that need large amounts of an element for enzymes in critical processes, such as Fe availability for nitrogen fixation by cyanobacteria. In published meta-analyses of this research with benthic algae, the trend is for about half of all streams being nutrient limited, and of those streams that are nutrient limited, a quarter are limited by P, a quarter are limited by N, and about half are co-limited by both N and P (Francoeur, 2001). In streams with high accumulations of diatoms, Si may become limiting for both benthic and planktonic algae. Nutrient ratios have been used successfully to predict which lakes are limited by N or P, but this approach has not been as successful in streams where nutrient concentrations in the water column are highly variable, supply rates may differ with time, groundwater supplies are not often accounted for, and differential cell leakage of N versus P over time may increase relative N demand.

Much less is known about space limitation than nutrients and light. Space limitation has not been evaluated well because it is difficult to isolate space versus density-dependent interactions. Space limitation applies most directly in the case of algae that must attach directly to substrates, such as the diatom *Cocconeis*. Space becomes an indirect factor or resource when algal biomass accumulates on substrata and reduces light and nutrient supply rates to cells in benthic algal mats. Space limitation can be relieved for algae in general when epiphytic microalgae can grow on macroalgae, such as *Cladophora*, but some species may be excluded from this extra space because they cannot attach well to *Cladophora* even though they can attach to benthic mineral substrates.

Species composition as well as biomass and function vary among rivers, corresponding to differences in light and nutrient concentrations (Kelly, 1998; Pan et al., 1999). Species require different amounts of nutrients and light to survive. Thus, low levels of nutrients and light constrain species membership to those species that can survive in these resource-stressed habitats. High nutrients or light enables species with requirements for high resource levels to colonize a habitat with high nutrient or light. Some experiments, theory, and now some field evidence suggest that tradeoffs for species do exist between being able to grow fastest in low and high nutrient concentrations, which would help explain the dramatic changes in species composition along nutrient gradients.

Diversity is complexly related to resource availability. As resources increase, more algal species can invade and successfully reproduce in the river based on physiological requirements (Passy, 2008). Evenness of species abundances change non-monotonically with increasing nutrients, from low to high to low evenness as nutrient concentrations increase. Evenness is low in low nutrient conditions because only a few species are adapted to grow well in low nutrient concentrations. As nutrients increase, more species can invade the habitat and their growth rates increase faster than species adapted to low nutrients; therefore, evenness of species abundances is highest when evenness of reproduction rates of species are highest. At high nutrient concentrations, growth rates and species abundances become uneven again as some species can grow faster than others in high nutrient concentrations. Many models predict that numbers of species (richness) would follow the same pattern as evenness along resource gradients. These models predict richness would increase as the habitat became more available to more species, i.e. the species that require higher nutrient concentrations to reproduce sufficiently fast to persist in the habitat. Species richness could decrease in high nutrients conditions because one or more resources became depleted, competitive relationships shift, and some species are competitively excluded. Observations of this pattern have not been satisfactory because estimating species richness of organisms is difficult in habitats where they are so abundant and difficult to observe.

Stressors

Stressors are environmental factors that can have negative effects on metabolism and other attributes of species' performance. Stressors affect reproduction according to one of two groups of response functions (Fig. 4B). One group consists of negative linear and non-linear responses in which there is no or very little positive effect of a stressor on species performance. Fine sediments that bury cells and toxic inorganic and organic substances are examples of factors with monotonic negative effects. Suspended sediment has strong indirect effects on phytoplankton, by reducing light transparency. Temperature and the ionic factors (salinity, pH, and alkalinity) produce non-monotonic effects on species performance. Algal performance is optimal at some intermediate level of these factors because high and low levels of temperature, salinity, pH, and alkalinity limit species performance for one reason or another. Temperature, for example, stimulates metabolism as temperature increases from relatively low to intermediate levels as kinetic energy and metabolic rates increases. However, high temperatures denature enzymes and reduce metabolic function. Salinity, pH, and alkalinity probably affect enzymes and enzyme-mediated processes most, for which an intermediate condition is optimal for species.

Because almost all algal species are negatively affected by sediments and toxic substances, biomass of algae can be negatively affected by these stressors. Similarly, the negative effect of high temperatures is "toxic" for most algae above 30 °C, except for some cyanobacteria that tolerate temperatures as high as 55 °C in hot springs. So high temperatures may reduce algal biomass, as low temperatures may. However, algal species are adapted to an unusually wide range of pH, alkalinity, and salinity, so that biomass is only affected by the ionic factors in extreme conditions. Throughout much of the range of the ionic factors, species composition differs with varying ionic factors, but functional redundancy is able to maintain community-level reproduction and biomass.

Local biotic factors

Biotic factors can have positive or negative effects on algae in rivers (Fig. 3). We know relatively little about commensalistic and mutualistic interactions, but some examples do exist. One example of commensalisms would be the attachment of some benthic diatoms on stalks of other diatoms, which provides an advantage to species that can attach to stalks and has little negative effect on the stalked diatoms. Diatoms with endosymbiotic cyanobacteria provide an example of mutualistic interactions (DeYoe et al., 1992; Peterson and Grimm, 1992). Of the negative interactions, much more is known about herbivory and competition versus allelopathic interactions and disease-like effects of fungi, bacteria, and viruses. Many have hypothesized that the latter two biotic stressors should have great effects in dense microbial assemblages like benthic algae. They are known to be important in lake and ocean phytoplankton. Unusual white circles in periphyton with high numbers of bacteria and fungi indicate "disease," but little investigation has pursued this line of research.

Competition is probably a more important determinant of algal biomass, function, and species composition for benthic algae than for phytoplankton. Phytoplankton seldom accumulate to sufficiently high densities to deplete nutrient concentrations in rivers because of the relatively short hydrologic residence times of these organisms in their habitat. However, competition may be important in very slow flowing, lake-like rivers where residence time is sufficiently high to deplete nutrients or light by biological uptake or shading. These are the processes that are thought to be important in benthic algal communities (McCormick and Stevenson, 1991). If species membership is constrained to diatom dominated communities, peak biomass of communities may be constrained by light and nutrient depletion. We know that light and nutrient availability within benthic algal mats decreases with increasing density; less light penetration and decreasing nutrient transport rates and cell nutrient content have been documented as diatom biomass increases on substrata. Per capita rates of metabolism and reproduction decrease with increasing benthic algal biomass. Species composition changes with increasing biomass of diatoms on substrata. All indicate autogenic changes in environment that are consistent with strong competitive regulation of benthic algal communities (Peterson et al., 1994).

Herbivory is also an important determinant of algae in rivers (McCormick, 1994; Lamberti, 1996). It is more frequently important for benthic algae than phytoplankton because of the lack of time for zooplankton to accumulate in the water column of rivers. Low disturbance frequency by floods and drought is important for determining whether herbivory is important for benthic algae, too. When river conditions allow herbivores to accumulate to high densities, they can regulate biomass, function, and species composition of benthic algae in rivers. The importance of zebra mussels in some rivers is a good example of herbivores affecting

river phytoplankton, but examples of zooplankton regulation are not common (Smith et al., 1998). Filter feeding invertebrates like blackflies and net-spinning caddisflies may also be important regulators of suspended algal abundance in streams, but this is not well understood.

Aquatic insects, snails, and some fish consume benthic algae, but aquatic insects and snails are the most important in most situations. Protozoa have also been shown to consume benthic algae (McCormick, 1991), but their importance does not seem to be as great as the much larger cased caddisflies, mayflies, and snails that graze algae from substrata. These invertebrates can constrain diatom biomass to very low levels. Many of them can consume filamentous green algae during early stages of growth, but not after filaments have exceeded the size that can be controlled, largely because of the small size of herbivores and their mouthparts. Herbivores seem to avoid consumption of filamentous cyanobacteria, pushing it back from actively grazed areas or knocking it off the substrate. In addition, they selectively graze overstory versus understory diatoms (stalked and filamentous forms versus tightly adnate and prostrate forms). Although grazers consume algae, not all are killed. Estimates of algae passed alive and viable through guts of aquatic invertebrates often exceed 50% (Peterson, 1987; Peterson et al., 1998). In a sense, grazing of cells removes cells from the substratum and either causes death or emigration of the cells downstream when they are egested alive. Because of the importance of grazing as a process of removing algae from a location and conceptually within food webs, it merits inclusion as one of the five fundamental processes.

Bioturbation is another process that affects benthic algal biomass accumulation. Invertebrates, fish, and terrestrial animals are common sources of disturbance of benthic algae as they move through streams. Diel patterns in algal drift are observed in some streams that correspond to the dawn and dusk activity patterns of aquatic invertebrates (Stevenson and Peterson, 1991). Paths of disturbed benthic algae in shallow riffles can be observed in deeper upstream-downstream channels where fish have moved from pool to pool. Movement of fish in pools disturbs the development of periphyton and clouds the water. Raccoons and larger animals, such as manatees, crocodiles, hippopotamus, and humans probably have great effects on benthic algae when moving; but these effects have not been quantified.

Habitat scale factors

Riparian canopy, depth, substrate, and current velocity vary among habitats within a reach and have indirect effects on the five fundamental algal processes (Fig. 3). Covariation among depth, substrate, and current velocity are regulated by the riffle-pool structure carved in most rivers. Coarser substrates are found in the shallow, high velocity riffles. Finer substrates are found settling in the deeper, slow velocity pools. Riparian canopy and depth regulate light availability, whereas current velocity and substrate have relatively complex effects that warrant further discussion.

Substrate is very important for algae as a stable surface for attachment and growth and potentially as a source of nutrition. Some algae have special morphological adaptations for attaching to substrata, such as the raphe and mucilaginous stalks and tubes of diatoms. Many filamentous green algae produce specialized cells that attach to a substrate and then form filaments when they divide. The species composition of true river phytoplankton, i.e. not just benthic algae dislodged from substrata and suspended in the water, is very different than the benthic algae. Surprisingly, the adaptations that so clearly separate species occurring in the phytoplankton and benthos are poorly understood, except for benthic algae and not phytoplankton having morphological adaptations that enable their attachment to substrata. Given the great differences in habitat conditions when suspended in the water versus attached to substrata, such as greater ranges in current velocity and denser packing of cells for benthic algae, great physiological differences must accompany these morphological adaptations.

For benthic algae, size, roughness, and nutritional value of substrata may have great effects (Stevenson and Hashim, 1989; Schneck et al., 2011). The smallest substrates, silt and organic sediments, are smaller than the smallest algal cells. So, organisms that live in this habitat tend to be large and motile, such as the diatoms *Nitzschia* and *Surirella* or the flagellated euglenoids. Sands, slightly larger and inert, are large enough for attachment by small diatoms in streams. During hydrologically stable periods, other algae can colonize sands, but only small diatoms can survive in the crevices of individual sand grains when the sands tumble across the bottom of streams. As rock substrates become larger, they tend to become more resistant to hydrologic disturbance. Almost all pebble and larger substrates can support diverse diatom assemblages. As substrates become larger and more stable, they can support luxurious growths of filamentous green algae that require longer stable periods for colonization by spores and growth of filaments. Woody debris and plants are other common substrates in rivers, and both may have nutritional properties that affect algae. Wood provides nutrition to bacteria, which may actually have a negative effect on benthic algal colonization because of competition with bacteria for nutrients (Tank and Dodds, 2003). Plants leak nutrients that become available to epiphytic algae attached to them (Burkholder et al., 1990).

Current velocity has watershed- and habitat-scale effects on algae. For phytoplankton, current velocity determines residence time of water and algae in the river and the time for cells to accumulate (Reynolds and Descy, 1996; Yang et al., 1997). For benthic algae, increases in current velocity during rain events may be sufficient to scour algae from stable substrates. Higher velocities can disturb the substrate in riffles and cause severe scouring of algae from substrates (Biggs and Thomsen, 1995). The time between scouring events provides the time for recovery of benthic algal communities (Biggs, 2000). Thus, variations in current velocity at the watershed scale determine the frequency and intensity of disturbance and are important, ultimate determinants of non-equilibrium ecological dynamics of algae in rivers.

The habitat-scale effects of current velocity on benthic algae are relatively well understood, compared to effects on river phytoplankton. Eddy mixing of the water column surely slows sinking of phytoplankton and shear in the water column may

reduce nutrient depletion in waters surrounding cells. One of the important premises of current effects on algae is that, in still waters, algae develop nutrient-poor shells of waters around cells. This shell develops because nutrient uptake rates from waters around cells exceed diffusion rates of nutrients into the shell. Water near surfaces, whether cell or substrate surfaces, has different physical properties than water away from these surfaces. Although measurements of nutrient concentrations in these 1–2 um thick layers around cells has not been practical, many observations between current velocity, metabolic rates, and transport of nutrients through periphyton mats indicate that these shells do exist. Thus, as current velocity around cells increases, the shearing of layers of water around cells increases and disrupts this layer of nutrient-poor (and potential waste-rich) water from around cells, thus increasing nutrient delivery.

Habitat-scale effects of current velocity on benthic algae have both positive and negative effects. While the shear stress of current velocity decreases immigration rates and likely increases emigration rates from habitats with moderate and fast current velocities, the increased physical mixing of water through attached masses of microalgae or macroalgae stimulates metabolic rates (McIntire and Phinney, 1965; Stevenson, 1984). Concentration gradients in micro- and macroalgal communities can cause severe nutrient depletion within this microhabitat. Assuming a common 10–30 cm s^{-1} range in velocities from slow (pool) to fast (riffle) current habitats, profound differences in current effects on immigration and reproduction help relate the patterns of benthic algal colonization after flood disturbance to these processes. Initially, algal biomass and accrual rates will be slower in riffles than pools because immigration is the dominant process affecting colonization when algal biomass on substrates is low, for example $5–10 \times 10^3$ cells cm^{-2}. As more cells accumulate, reproduction becomes more important than daily immigration of cells and the positive effects of current outweigh the negative effects (Stevenson, 1996). So, we eventually observe higher algal biomasses in riffles than pools, even though that pattern may not be evident immediately after flood-related disturbances.

Reach to regional scale factors

Whereas reach or segment scale factors (such as hydrology, channel geomorphology, flow stability, and stream size) interact to shape habitat structure and local abiotic conditions, regional processes associated with climate, geology, and biogeography regulate the more general spatial and temporal patterns of algae in rivers (Fig. 3). Climate and geology also affect human activities in watersheds, which have profound effects on contaminants in streams, channel geomorphology, and hydrology. Extensive discussion of human effects on algae in rivers is beyond the scope of this chapter. Here, I want to synthesize the review of algal ecology in rivers by describing three common large-scale patterns: seasonal and longitudinal patterns of phytoplankton in rivers, algae and the river continuum hypothesis, and the effects of disturbance on benthic algal-grazer interactions.

Phytoplankton in rivers has a distinct longitudinal pattern that varies in magnitude with seasonal variations in discharge (Stevenson and White, 1995; Reynolds and Descy, 1996). Suspended algal densities are usually low in headwater sections of rivers and largely composed of algae that have emigrated from benthic substrates and are entrained in the water column. As water flows downstream, species better adapted to life in the water column immigrate into a mass of water and stay in it as it moves downstream. Gradually, as the river becomes larger, fewer benthic species are suspended in the water than planktonic species. The longer that mass of water resides in the river before reaching a lake, estuary, or ocean, the higher the biomass of algae in the water column will become. More phytoplankton accumulates in rivers of geologic regions where rivers have low gradients versus those with high gradients. Climate determines the time of year and the extent of hydrologically stable periods when algae can accumulate in streams. In climates with periodic storms during the dry season, high discharge events may disrupt the development of phytoplankton communities. During long dry and hot periods, high and often problematic biomasses of algae can develop with sufficient quantities that deoxygenation occurs and toxic algae accumulate.

The river continuum hypothesis (RCC, Vannote et al., 1980; see Dodds and Maasri this volume) proposes the ecology of rivers is regulated by upstream-downstream patterns in the hydrogeomorphology and connectivity within rivers. Although originally defined for free-flowing rivers in temperate climates with forested landscapes, the model has been adapted for dammed rivers and many ecological regions. The original model described how narrow streams in forests would be covered by a riparian canopy that would limit light, and therefore, algal production. As streams became wider downstream, light would become more available and benthic algae would be able to accumulate. Correspondingly, the base of the food web was predicted to shift from allochthonous detritus in the headwaters to autochthonous primary production in the mid-reaches of the river. Farther downstream as algae became entrained in the water column and depth increased, autochthonous productivity in rivers would shift from benthic to planktonic algae. Although this upstream-downstream pattern in hydrogeomorphology and connectivity may vary greatly among regions, it tends to vary with climate and geologic conditions of a region, and to some extent with local landscape conditions. Most differences occur in headwater regions where the river may not have accumulated sufficient erosional power or geology constrains their ability to carve channels and broad floodplains. Headwaters vary from springs arising in deserts to high gradient channels in mountains or low gradient channels emerging out of wetlands. Each of these provides a different starting point in downstream regulation of the ecology of rivers and very different environments for algae.

One of the challenges for understanding the ecology of algae in streams has been understanding the relationship between resource availability and disturbance intensity. This challenge underpins: (1) the prediction of top-down or bottom-up regulation of river food-webs, (2) relationships between nutrients and algal biomass for management of these important contaminants of streams, and (3) biodiversity of algae in streams. Increases in nutrient concentrations should result in an increase in algal biomass of streams. Increases in hydrologic stability also should result in increases in algal biomass of streams because algae have, on average, longer periods of time to accumulate between disturbances. Thus, in streams that are relatively hydrologically stable, we

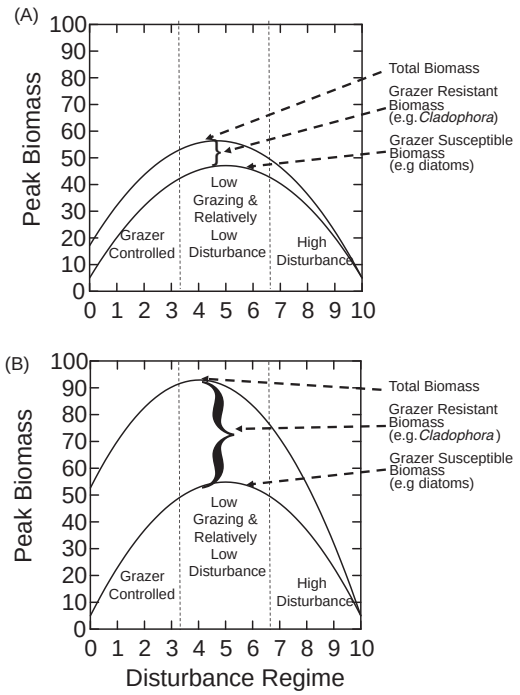

Fig. 5 Conceptual model of effects of physical disturbance regime on peak biomass of grazer susceptible algae, grazer resistant algae (such as *Cladophora*), and all benthic algae in relatively low (A) and high (B) nutrient conditions. Grazer density is hypothesized to be high in low disturbance regimes, where grazers regulate accumulation of grazer-susceptible algae (such as diatoms). In high nutrients and low disturbance, grazers cannot regulate density of grazer resistant forms, such as *Cladophora*. Grazer density decreases with disturbance (Riseng et al., 2004) and enables accrual of both grazer-susceptible and resistant forms in habitats with intermediate levels of disturbance. In high disturbance, accrual of both grazer-susceptible and grazer-resistant forms are constrained by physical disturbance. From (Stevenson et al., 2006).

should have greater responses of algae to nutrients than in frequently disturbed streams. This is what we see in New Zealand streams where hydrologic stability ranges from great to average on the global scale (Biggs, 1995a,b). However, in the middle of North America, we see the opposite end of the disturbance continuum. Algae in low disturbance streams respond relatively little to increases in nutrient concentrations compared to relatively high disturbance streams in this region. Here, accrual of algae is constrained by high grazing pressure in hydrologically stable streams (Riseng et al., 2004, 2010). Flood and drought disturbances in relatively hydrologically variable streams of this region constrain grazer abundances, so grazers no longer regulate algal biomass in the most hydrologically disturbed regions of central North America—which compared to the global range of possibilities, is only intermediate on the hydrologic disturbance scale (Stevenson et al., 2006). Globally, we find complexity arising from the non-linear and multi-trophic level effects of disturbance on algal-resource interactions. Herbivores and disturbance constrain algal response to nutrients in the most highly hydrologically stable habitats and the most hydrologically variable habitats, respectively; and algae respond most to nutrients at intermediate levels of disturbance when they have sufficient time to recover from disturbance, but not so much time that invertebrates can also recover and consume the algae (Fig. 5).

Summary

Interactions between algae and their environment are complex, yet predictable based on accurate linkage of processes, scale of determining factors, and algal attributes. Although much is yet to be understood about algae in rivers, we have learned much by a marriage of three basic scientific approaches: large-scale field observations from environmental monitoring projects, experiments, and process-based models. Study of algae in rivers provides a model for how to understand complex systems that are tightly coupled to human effects on the environment.

Knowledge gaps

1. Future work in rivers should address:
   a. the importance of the biodiversity of river algae and ecosystem function,
   b. how ecological systems respond to environmental change,
   c. the role of dispersal in ecological resilience and stream restoration and
   d. the importance of algae in ecosystem goods and services

2. The lessons that we have learned in the study of algae in rivers should be applied to studies of algae in other habitats as well, such as:
   a. wetlands,
   b. terrestrial habitats in rainforests, and
   c. the arctic tundra.

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Secondary Production in Streams

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Allen Curve A plot of numbers in a cohort vs. individual growth; the area under the curve is proportional to secondary production.
Allen's Paradox An imbalance between estimated predator consumption of prey and prey production whereby estimated prey production does not appear sufficient to support local predator production.
Annual P/B Annual production to biomass ratio, which is related to individual growth rate.
Cohort A group of individuals that begin life (hatch or are born) at about the same time.
CPI Cohort Production Interval correction, which is used to standardize a secondary production estimate to 1 year; used for animal species with life cycles that are less than or greater than 1 year.
Production efficiency *Net production efficiency* is the efficiency of an animal at converting assimilated materials into tissue production; *gross production efficiency* is the efficiency at converting ingested materials into production.
Secondary production Tissue elaboration by heterotrophs regardless of fate (e.g., whether it is eaten, dies, is molted, etc.)
Voltinism Life cycle length relative to a year; a *univoltine* taxon has a 1 year life cycle.

Introduction

Secondary production is the generation of tissues by heterotrophs, regardless of the fate of the generated materials; death, consumption by predators, molting, etc. do not matter, as the tissue was produced at some point before any of those occurred. Secondary production is ultimately the result of a series of ecological efficiencies, starting with the assimilation efficiency (AE) of consumed food, and then the efficiency at which assimilated materials are converted to production, or net production efficiency (NPE). The overall efficiency of conversion of ingested materials to production is the gross production efficiency, or GPE. These efficiencies, and thus secondary production, are influenced by a wide range of intrinsic and extrinsic factors spanning scales from individuals and populations, to communities and habitats, to regional climate differences. Secondary production has been referred to as the "ultimate dynamic variable" because it integrates all elements of fitness, including abundance, biomass, growth, survival, and other important population metrics in to one value (Benke, 1993). Secondary production studies draw upon elements of both population biology and ecosystem ecology (Benke and Whiles, 2011).

The two main components of secondary production are biomass and individual growth rate. As such, biomass can be considered a predictor of secondary production in some cases, but not in cases where there is great disparity between biomass and individual growth rate. For example, high biomass of adult unionid mussels in a mussel bed in a river would not necessarily translate into high production because of slow individual growth rates of the long-lived adult mussels. Conversely, moderate levels of biomass of dipteran (true flies) Chironomidae larvae in sediments of a stream pool can result in relatively high production because of rapid individual growth rates. Thus, the occasional use of biomass as a proxy for production can be inaccurate; however, empirical estimates of production, rather than application of statistical models based on biomass, temperature, and literature values of P/B, are better. Obviously, the highest production estimates are associated with animals with both high biomass and high individual growth rates.

The annual production to biomass ratio (mean annual production divided by mean annual biomass), a measurement of turnover, is a proxy for individual growth rate. Annual P/B values vary tremendously across stream-dwelling taxa as a function of individual growth rates and life histories. Small, rapidly growing taxa often have annual P/B values that exceed 10, and in some extreme cases exceed 100. In contrast, slower growing species may have values around 1–2, and even <1. Many univoltine stream invertebrate taxa with moderate growth rates have annual P/B values ~5–6. Annual P/B values can be used to estimate actual tissue turnover times by dividing the number of days in a year by the P/B. For example, a stream invertebrate with an annual P/B of 5 will have a tissue turnover rate of 365/5 = 73 days for complete turnover of the tissues as the individual grows.

Methods for estimating secondary production

Despite some of the challenges of generating secondary production estimates, stream ecologists have recognized the importance of these estimates for decades. Overall, there is a strong bias toward aquatic habitats in the secondary production literature (Benke and Whiles, 2011), and this is likely related to interests in fish production for food and sport, and the associated production of fish food. Accordingly, development of many of the methods for estimating secondary production were based in aquatic habitats and focused on fishes and their prey (Ricker, 1946, 1975; Waters, 1977). In fisheries, secondary production methods often focus on mass-balance bioenergetic approaches based on metabolic and ecological efficiency estimates for organisms. Here, we focus on more general, ecosystem energy flow approaches that are commonly used for studies of invertebrates and that dominate the literature on secondary production in streams. Along with invertebrates, these approaches have also been applied to fishes (Huryn, 1996) and amphibians (Colón-Gaud et al., 2009) in streams.

While many relatively simple methods for estimating primary production exist, and thus primary production estimates for streams are relatively common, estimates of secondary production, particularly for whole communities, are limited. Estimates of secondary production require estimates of abundance and biomass through time, size-specific individual mass, and depending on the method, growth rates or population age or body size structure estimates through time. As such, secondary production estimates for systems that are difficult to sample (e.g., large rivers) and for taxa with rapid generation times (e.g., many small invertebrates) or complex life cycles that include metamorphosis and/or resting stages (e.g., many insects and amphibians) are limited in the stream ecology literature. However, if the proper information is available, reasonably accurate estimates of secondary production for many systems and taxa can be easily generated.

The common methods for secondary production studies in streams track changes in density and individual mass in a cohort (Benke and Huryn, 2017). The relationship between cohort density and individual mass over time can be depicted with an Allen curve (Allen, 1951) (Fig. 1). This curve shows production of a cohort for a given time interval (the trapezoid underneath the *Allen curve* defined by rectangle A + triangle B in Fig. 1), which is the biomass produced by those that survived (A) and those that died (B) over the sampling interval. Total production by the cohort is the total area under the Allen curve. The Allen curve is useful for visualizing secondary production. For example, if there were no mortality over time, secondary production would be the entire area of the plot underneath the dotted line in fig. 1.

The area representing biomass production under an Allen curve during a time interval can be estimated from densities and individual mass by multiplying the average number of individuals during the time interval by the change in individual mass:

$$\frac{N_t + N_{t+1}}{2}(W_{t+1} - W_t)$$

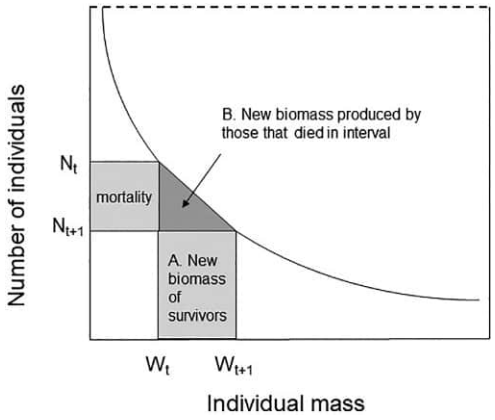

Fig. 1 An Allen curve showing relationships between abundance of individuals in a cohort and individual size over time. N is number and W is individual weight or mass; subscript t and t + 1 indicate points in time. Rectangle A and triangle B together represent production for the time interval depicted. If there was no mortality over time, secondary production would be the entire area of the plot underneath the dotted line.

Table 1 Production calculations for the stream dwelling caddisfly, *Brachycentrus spinae*, using the increment summation method.

Date	*# Days in interval*	*Density (no. m^{-2}) N*	*Avg. indiv. Weight (mg) W*	*Biomass (mg m^{-2}) N * W*	*Weight change (N_{t+1}—N_t) Δ weight*	*Avg. N*	*Production Avg. N * Δ weight Mg m^{-2} P*
18-May	14	283	0.021	5.94	0.036	255.0	9.2
1-Jun	12	227	0.057	12.94	0.031	204.5	6.3
13-Jun	16	182	0.088	16.02	0.085	160.5	13.6
29-Jun	14	139	0.173	24.05	0.179	124.0	22.2
13-Jul	13	109	0.352	38.37	0.588	98.5	57.9
26-Jul	22	88	0.940	82.72	0.266	74.0	19.7
17-Aug	13	60	1.206	72.36	0.590	54.0	31.9
30-Aug	16	48	1.796	86.21	0.025	42.5	1.1
15-Sep	18	37	1.821	67.38	1.378	32.0	44.1
3-Oct	42	27	3.199	86.37	0.358	20.0	7.2
14-Nov	23	13	3.557	46.24	1.074	11.0	11.8
7-Dec	51	9	4.631	41.68	2.222	6.5	14.4
27-Jan	21	4	6.853	27.41	1.624	3.5	5.7
17-Feb	24	3	8.477	25.43	3.071	2.5	7.7
13-Mar	45	2	11.548	23.10	3.252	1.0	3.3
27-Apr		0	14.800	0.00			
Total Mg m^{-2} $year^{-1}$							256.0

This species has a 1-year life cycle. Dates are days when samples were collected; May is the start date because this is when recently hatched larvae first appeared. Maximum larval size was estimated at 14.8 mg on April 27, but densities at this time were ~0.

Data are from Ross DH and Wallace JB (1981) Production of brachycentrus-spinae ross (trichoptera, brachycentridae) and its role in seston dynamics of a southern appalachian stream (USA). *Environmental Entomology* 10: 240–246.

Where N_t is the number of individuals at the beginning of the time interval and N_{t+1} is the number at the end of the interval; likewise, W_t is average individual weight at the beginning of the interval and W_{t+1} is average individual weight at the end. This yields production for a given time interval; total production is the sum of the interval values (Table 1). This method for estimating production is called the *increment summation method* (Waters, 1977; Benke and Huryn, 2017). It is one of the so-called cohort methods and is considered relatively accurate but can only be used when a cohort can be followed through time; this is often not possible because of sampling design and/or life history characteristics (e.g., rapid, asynchronous development of cohorts in a population).

The instantaneous growth method can often be used when cohorts cannot be followed. Only estimates of interval average biomass and individual growth rate are needed for this method. Biomass estimates are easily obtained from field measurements but overlapping generations and/or rapid generation times can make estimation of growth rates difficult. Approaches include laboratory rearing studies, caging individuals in the field, or marking and recapturing individuals, all of which can generate reliable individual growth rate estimates. Changes in individual weight over time are then used to estimate instantaneous growth as follows:

$$G = \frac{\ln(w_{t+1}) - \ln(w_t)}{t}$$

where G is the instantaneous growth rate, W_t the individual weight at the beginning of the interval, and W_{t+1} the individual weight at the end of the interval. The instantaneous growth rate has the units of $time^{-1}$, with time usually in $days^{-1}$.

Once G and average biomass for the interval is obtained, interval production is estimated as:

$$P = G * \overline{B} * t$$

Where P is interval production, $\overline{B}$ is average biomass during the interval, and t is time.

As an example, for the first interval of May 18—June 1 from Table 1:

$$G = \frac{ln(0.057) - ln(0.021)}{14} = 0.0714/\mathrm{d}$$

Using biomass estimates for the same interval (9.44 mg m^{-2}), production for the interval was $P = .0714 * 9.44 * 14 = 9.43$ mg m^{-2}. This method requires less detailed information and is easier to calculate, but production estimates using the instantaneous growth method are generally considered less precise than those obtained using cohort approaches such as the increment summation method. In this case, the estimates for the first sampling interval obtained with the instantaneous growth and increment summation methods are close, but this is not always the case.

The size-frequency method has become increasingly common for estimating secondary production because it can be used in situations when cohorts can or cannot be followed. This method involves constructing an "average" cohort from sampled size

classes, much like population ecologists use in constructing life tables (Benke, 1979). Subsequent calculations are similar to those of the increment summation method, except that interval production estimates, which in this case are size class intervals, are multiplied by the total number of size classes because they are not actually being followed through time. The production estimates for each size class interval are then summed to estimate total annual production for taxa with 1 year life cycles. Those with shorter or longer life cycles can be expressed as production over the length of the life cycle, or they can be standardized to 1 year using a cohort production interval (CPI) correction (Benke, 1979). The CPI is obtained by simply dividing 1 year by the length of the life cycle, generally in months. For example, a taxon with a 10 month life cycle would have a CPI correction of $12/10 = 1.2$, so the production estimate for this taxon would be multiplied by 1.2 to estimate annual production. Details on the size frequency method and other production methods are presented by Benke and Huryn (2017).

Estimates of the CPI should be as accurate as possible given that the CPI can greatly influence annual production estimates. The most accurate CPI estimates come from detailed studies of life histories in the habitats sampled or similar habitats.

Statistical considerations

Replication and statistical analyses are inherently limited in secondary production studies, particularly in lotic systems that vary over time and are difficult to replicate. While in some cases, such as experimental manipulations in artificial streams, replication can be achieved and parametric statistical approaches applied. An unsatisfying end result of many secondary production studies is a single value with no associated error estimate. As such, alternative methods to estimate error in secondary production estimates have been developed, and these generally involve bootstrapping, which is a non-parametric re-sampling procedure. For this procedure, all data are randomly resampled with replacement until multiple (often 1000 or greater) data sets are produced. These are then used to produce vectors of estimates for each parameter (e.g., abundance, biomass, production), and then a mean and confidence interval are calculated. Huryn (1996) provides some details on these procedures.

Spreadsheet based methods are commonly used for estimating secondary production and performing bootstrap analyses, but some investigators have developed R code for both. Venarsky et al. (2018) provide descriptions of R code they used for both secondary production estimates and bootstrapping procedures to examine stream invertebrate production along a stream disturbance gradient in the US Rocky Mountains.

Production and energy flow food webs

Secondary production estimates, along with the ecological efficiencies discussed earlier in this chapter, can be used to examine energy flow paths and the trophic basis of production. Using these estimates, the amount of food consumption required to sustain the observed level of production estimated. For example, a population of detritivorous stream insects with 5 g m^{-2} y^{-1} production, and an assimilation efficiency of 20% and net production efficiency of 50%, consumes $5/(0.2^{*}0.50) = 125$ g m^{-2} y^{-1} of detritus. This information is obviously valuable for examining how invertebrates and other animals contribute to important ecosystem processes such as decomposition and energy flow.

Fecal particles are important components of stream food webs, and these same efficiencies can be used to estimate egestion by a population. For the detritivorous insect population example used above, egestion would be $125 * 0.8 = 100$ g m^{-2} y^{-1} of fecal material, which could contribute greatly to the pool of fine particulate organic material in the stream food web. The 0.8 used in this equation is simply the inverse of the assimilation efficiency (100%—20% = 80%, or 0.8 egested). The low assimilation efficiencies and high consumption and egestion rates of detritivores such as these make them strong contributors to energy flow in streams.

Trophic basis of production values can be used to construct quantitative food webs and analyze energy flow through ecosystems. Such analyses have been used to examine energy flow patterns in systems ranging from tropical headwater streams (Frauendorf et al., 2013; Mello et al., 2020), temperate forested and grassland streams (Benke and Wallace, 1980; Huryn, 1996; Stagliano and Whiles, 2002), and mid to large sized rivers (Cross et al., 2013).

Reported variation in population and whole community secondary production

Compared to other ecosystem functions, such as primary production, which are routinely measured in running waters, secondary production has received relatively little attention. The most recent meta-analyses of published values that explicitly evaluated variation among stream invertebrate populations was published almost three decades ago (Benke, 1993). However, whole community estimates of secondary production have received more recent treatment in the literature (Huryn and Wallace, 2000; Patrick et al., 2019). Using these references as guides, supplemented with some additional sources, here we summarize what is known about variation in estimates of biomass, production, and P/B ratios at the population and community levels. Summarizations of population level estimates are derived from the database assembled by Benke (1993), with additional relevant observations added to provide context regarding developments since then. Summarizations of community level estimates are derived from Huryn and Wallace (2000) and Patrick et al. (2019).

At the population level, estimates of production, biomass, and P/B ratios vary widely within and among taxonomic groups and functional feeding groups (Table 2). For example, among phyla, the mollusks have highest reported mean production (12,553 mg ash-free dry mass (AFDM) m^{-2} $year^{-1}$) and biomass (7073 mg AFDM m^{-2}), but values within this phylum vary widely, ranging from 0.39–659,499 mg AFDM m^{-2} $year^{-1}$ for production and 0.15–160,651 mg AFDM m^{-2} for biomass (Table 2). When population estimates are viewed as simple averages, biomass rankings from highest to lowest are Mollusca > Annelida > Arthropoda > Platyhelminthes, mean production estimates are Annelida > Mollusca > Arthropoda > Platyhelminthes, and P/B ratios are Arthropoda > Annelida > Platyhelminthes > Mollusca. This gives the impression that mollusks and annelids make up the majority of biomass and production in running waters. However, anyone who has conducted work in these systems would rightly view this conclusion as suspect. Biases in the types of studies that are included in the dataset skew the results. Non-arthropod groups are often ignored in studies of invertebrate secondary production, and estimates are usually undertaken only when they obviously make up a large and important part of biomass and production. For example, some of the highest reported invertebrate production estimates come from studies quantifying the effects of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) on streams in Wyoming (Hall et al., 2006).

Comparative estimates among taxa within Arthropoda may be more meaningful because these are more frequently undertaken by investigators. Across studies, crustaceans have the highest mean reported annual production (Isopoda ~3257, Amphipoda ~8703 mg AFDM m^{-2} $year^{-1}$), followed by Diptera (2605 mg AFDM m^{-2} $year^{-1}$) and Trichoptera (1773 mg AFDM m^{-2} $year^{-1}$). A similar pattern is apparent for annual biomass estimates with the highest mean values again coming from crustacea (Decapoda ~684, Isopoda ~623, Amphipoda ~1879 mg AFDM m^{-2}) followed by Diptera (363 mg AFDM m^{-2}) and Trichoptera (386 mg AFDM m^{-2}). However, patterns of P/B ratios, which reflect individual growth rates, diverge significantly from biomass and production patterns, with highest mean values for Diptera (~29) and Ephemeroptera (~15), and the next highest mean value dropping to ~6 (Megaloptera). These mean values only represent what is typical, not what is possible. For example P/B ratios as high as 222 have been reported for Diptera in the Chironomidae tribe Chironomini in the Ogeechee River (Hauer and Benke, 1991).

Reported values for functional feeding groups (Cummins, 1973) from all reported population data skew heavily toward highest biomass and production estimates for the collector-filterer group, reflecting high reported values from filter feeding bivalves in the Mollusca (Table 2). When summarization is restricted to Arthropoda, collector filterers still comprise the largest share of production (~2995 mg AFDM m^{-2} $year^{-1}$) and mean biomass (410 mg AFDM m^{-2}). Collector-gatherers, predators, scrapers and shredders comprised notably smaller amounts of biomass and production, on an order of 0.125 × – 0.25 ×. Again, these general patterns must be viewed in context of the dataset and are not fixed rules. For example, groups such as shredders, which in many systems represent a minority of biomass and production, may comprise significant proportions of biomass and production in forested headwater streams (Benke, 1993).

Similar to the reported variation in biomass and production estimates at the population level, there is a wide range of variation in reported values of biomass and production at the whole community level. Reported annual production ranges from 3.6–13.3 g AFDM m^{-2} $year^{-1}$, biomass ranges from 3.1–10.0 g AFDM m^{-2}, and whole community P/B values range from 1.0 to 1.9. It is worth noting the highest whole community production values reported in Patrick et al. (2019) are a good deal lower than the highest population level estimates reported in the literature. Whole community estimates are less frequently undertaken than population level estimates, and thus these estimates fail to capture the possible extremes. Additionally, estimates from unusual habitats such as artificial lake outflow streams (e.g., Voshell, 1985) were excluded from the analysis. However, the dataset is useful for making meaningful comparisons among streams and rivers to better understand the dominant drivers of variation in secondary production.

Drivers of variation in secondary production

Secondary production is dependent on the factors that limit individual and population growth rates, including food availability and quality, habitat features, environmental conditions, biotic interactions, and the frequency and intensity of disturbance. At the whole community level, Patrick et al. (2019) found that the frequency of low flow events and water temperature were the key factors influencing global variation in secondary production in running waters (Fig. 2). Production rates generally increased with water temperature, likely due to positive relationships between temperature and growth rates. In contrast, production decreased with the duration of low flow events each year in streams, likely due to such disturbances causing organism mortality and reducing resource and habitat availability. A number of other factors in the analyses appeared important but could not be effectively evaluated given the limitations of the dataset.

For example, food availability was not reported for the majority of studies reviewed in Patrick et al. (2019), but this is likely an important factor (Wallace et al., 1997; see "Case studies" section below). The most commonly reported resource, coarse particular organic matter (CPOM), was reported in only ~1/3 of studies, but for that subset of studies it explained 32% of the variation in whole community production and 47% of the variation in whole community biomass. It is likely that CPOM was reported in cases where the investigators thought it important to measure and that similar general relationships could be expected for predictors like algal biomass or seston quality and volume. Indeed, some of the highest reported values of production come from filter-feeding communities associated with lake outflow streams that are fed by a constant stream of high-quality phytoplankton and zooplankton produced in the epilimnion of the source lake (Voshell, 1985). High production estimates also come from open-canopy, arid land streams in Arizona that have high algal production when the water is flowing (Fisher and Gray, 1983). Similarly, Finlay (2011) reported the impact of human activities in a watershed was associated with significant increases in GPP and by extension

Table 2 Biomass, production, and P/B estimates by Order, Phylum, and functional feeding groups (FFG) calculated from the meta-analysis dataset used by Benke (1993).

			Biomass (mg AFDM/m^2)		*Production (mg AFDM/m^2/year)*		*P/B*	
Phylum	*Class*	*Order*	*Mean ± SE*	*Range (Min-Max)*	*Mean ± SE*	*Range (Min-Max)*	*Mean ± SE*	*Range (Min-Max)*
Arthropoda	Insecta	Diptera	363.202 ± 219.913	0.001–87,097.5	2605.554 ± 1296.44	0.026–600,000	28.83 ± 1.861	1–355.667
Arthropoda	Insecta	Trichoptera	385.959 ± 67.269	0.032–18,168.086	1773.737 ± 289.49	0.183–76,305.96	5.788 ± 0.3	0.1–115.786
Arthropoda	Insecta	Ephemeroptera	121.058 ± 21.795	0.041–3570.005	1141.139 ± 183.147	0.077–27,457.2	14.793 ± 1.588	0.696–240.26
Arthropoda	Insecta	Plecoptera	77.911 ± 19.199	0.522–1461.6	345.455 ± 87.594	0.386–8821.8	5.879 ± 0.373	0.903–26.792
Arthropoda	Insecta	Coleoptera	29.466 ± 10.879	0.017–606.7	110.069 ± 40.045	0.004–2160	3.693 ± 0.122	1–7
Arthropoda	Insecta	Odonata	55.999 ± 11.349	0.031–385.758	214.725 ± 58.722	0.141–2975.4	3.303 ± 0.178	1.694–6.719
Arthropoda	Insecta	Megaloptera	166.97 ± 54.108	0.435–1460	1648.925 ± 541.684	1.044–13,190	6.361 ± 0.526	2–11.916
Arthropoda	Malacostraca	Amphipoda	1879.097 ± 312.632	1.044–5659.206	8703.199 ± 1660.452	3.861–32,519.987	5.101 ± 0.266	2.272–8
Arthropoda	Malacostraca	Isopoda	622.983 ± 272.759	0.015–7089.32	3257.025 ± 1564.81	0.073–42,059.116	5.003 ± 0.115	3.728–6.3
Arthropoda	Malacostraca	Decapoda	683.369 ± 138.774	8.639–3070	739.453 ± 238.338	11–4468.32	1.059 ± 0.232	0.173–4.688
Annelida	Clitellata	Oligochaeta	6320.945 ± 4376.45	0.261–78,387.75	23,391.719 ± 16,902.784	2.61–373,167	7.958 ± 0.612	2.25–10
Platyhelminthes	Trepaxonemata	Neoophora	4.39 ± 2.435	0.209–30	18.037 ± 9.003	1.044–100	4.872 ± 0.128	3.333–5
Mollusca	Bivalvia	Veneroida	12.674 ± 3.699	0.149–42.804	43.455 ± 11.706	0.522–130.5	3.462 ± 0.038	3.049–3.5
Mollusca	Bivalvia	Heterodonta	19639.856 ± 17667.224	25.757–160,651	78750.789 ± 72687.701	94.998–659499	3.208 ± 0.306	1.494–4.326
Mollusca	Gastropoda	Basommatophora	563.588 ± 255.925	38.712–1939.529	1897.553 ± 869.275	168.009–6375	3.454 ± 0.53	2.041–5.949
Annelida	Clitellata	Hirudinea	741.648 ± 202.747	39.974–1210.009	1740.532 ± 513.386	120.697–3509.37	3.043 ± 0.117	2.646–3.451
Mollusca	Bivalvia	Palaeoheterodonta	27,269.169 ± 8435.225	11703.814–64819.802	4955.935 ± 1716.749	2000–13219.802	0.184 ± 0.022	0.128–0.255
Annelida	–	–	5081.102 ± 3415.836	0.261–78,387.75	17804.316 ± 12651.125	2.61–373167	6.73 ± 0.596	2.25–10
Arthropoda	–	–	326.562 ± 81.547	0.001–87097.5	1922.464 ± 466.355	0.004–600000	15.405 ± 0.777	0.1–355.667
Mollusca	–	–	7073.421 ± 3268.093	0.149–160,651	12553.206 ± 10454.874	0.386–659499	3.054 ± 0.181	0.128–5.949
Platyhelminthes	–	–	4.39 ± 2.435	0.209–30	18.037 ± 9.003	1.044–100	4.872 ± 0.128	3.333–5
		Whole Community	7246.233 ± 102.073	3144–10008	9118.677 ± 112.618	3560–13325	1.27 ± 0.011	1.032–1.875
		FFG	Mean ± SE	Range (Min-Max)	Mean ± SE	Range (Min-Max)	Mean ± SE	Range (Min-Max)
All taxa		CF	3148.349 ± 726.986	0.1–136328.22	3446.267 ± 710.921	0.09–183800	12.507 ± 0.999	0.1–230
All taxa		CG	287.309 ± 98.105	0.09–41400	1033.377 ± 253.017	0.015–125100	15.9 ± 1.159	0.366–337
All taxa		P	93.856 ± 10.781	0.1–5258	445.217 ± 73.943	0.09–49275	9.311 ± 0.666	0.52–277
All taxa		SCR	79.633 ± 20.464	0.1–6400	705.756 ± 129.872	0–24300	11.513 ± 1.13	0–240.26
All taxa		SHR	79.008 ± 12.645	0.009–2300	348.315 ± 52.971	0.002–8480.7	5.888 ± 0.244	0.52–33.1
Arthropods		CF	409.95 ± 85.915	0.1–18232	2995.027 ± 749.582	0.1–183800	12.507 ± 0.999	0.1–184
Arthropods		CG	93.619 ± 8.734	0.09–1467	710.895 ± 135.519	0.015–52,470	15.9 ± 1.159	0.366–337
Arthropods		P	93.891 ± 26.871	0.1–1570.5	388.589 ± 92.2	0.09–5772.6	7.067 ± 1.033	0.573–18.063
Arthropods		SCR	82.705 ± 10.958	0.1–5258	448.73 ± 80.839	0.09–49275	9.311 ± 0.666	0.52–277
Arthropods		SHR	43.417 ± 7.678	0.1–1901	621.62 ± 123.192	0–19710	11.513 ± 1.13	0–240.26

CF, collector filterer; CG, collector gatherer; P, predator; SCR, scraper/grazer; SHR, shredder.

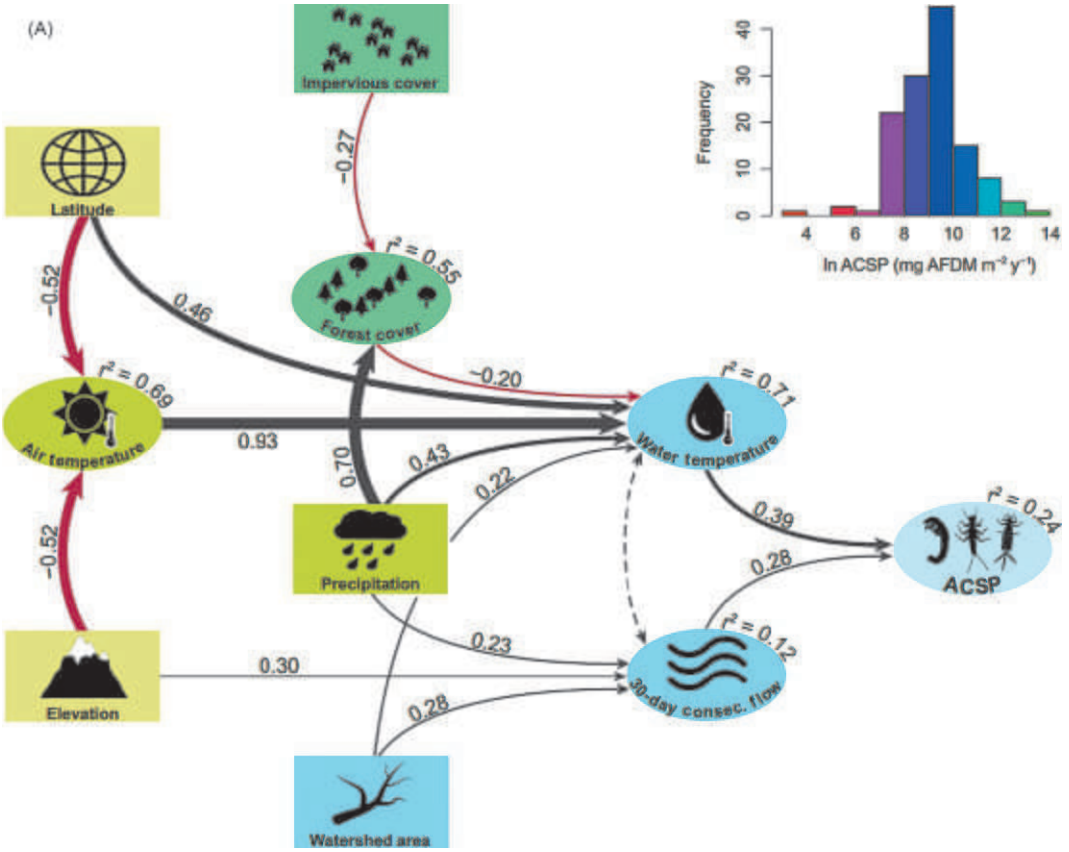

Fig. 2 Structural Equation Model of annual community secondary production (ACSP) in streams and rivers in the United States. Exogenous variables are indicated by rectangles, and endogenous variables are represented by ovals. Coefficients of determination (r^2) are shown for all endogenous variables, and standardized path coefficients are shown for all modeled relationships. Positive and negative effects among variables are depicted by black and red arrows, respectively, with arrow widths proportional to effect sizes (i.e., path coefficients). Significant covariance between mean annual water temperature ("Water temperature") and the minimum average discharge that persists for 30 consecutive days ("30-day consec. flow") is depicted by a dashed double-headed arrow. All relationships are significant at $P = .05$. Inset histograms show the distribution of natural log (ln)-transformed ACSP at U.S. and global scales. Reproduced with permission from AAAS.

invertebrate secondary production due to increased nutrients and light driving bottom-up processes. Further evidence for the importance of food resources comes from Benke's (1993) reported relationships between discharge and the proportion of production attributable to each functional feeding group (Fig. 3). As stream size increases, shredder production decreases, scraper and collector gather production follows a hump shaped pattern, and filter feeder and predator production increases. These patterns largely conform to expectations of the River Continuum Concept and are driven by longitudinal shifts in resource availability for these functional groups (Vannote et al., 1980).

Habitat stability is another general category that is only partially explored in Patrick et al. (2019). The overwhelming importance of low flow events as a universally important predictor of secondary production makes logical sense and the mechanism can be extended to consider other factors that were not available. For example, substrate stability is a very good predictor of secondary production when it has been explicitly considered. Benke et al. (1984) found that secondary production of communities associated with stable large woody debris (snags) was 5–6× times higher than that in the nearby unstable sand substrate in low gradient, Coastal Plain streams in Alabama (Benke et al., 1984). The negative impacts of occasional anthropogenic disturbances may also be considered in this conceptual framework. For example, punctuated or press disturbances in the form of contaminants from mine drainage reduced secondary production in comparison to reference streams (Carlisle and Clements, 2003).

Biotic interactions such as predation and competition may also limit secondary production. The best evidence for this comes from case studies of secondary production of invasive species that have no natural predators, diseases, or parasites in the introduced range. Extremely high rates of secondary production of New Zealand mud snails in Wyoming streams exemplify this (Hall et al., 2006). Left unchecked, mud snails can reach levels of biomass and annual production that rival the highest estimates in the literature. If we assume that reported explosions in abundance are correlated with biomass, the wealth of literature examples of population explosions of invasive species in streams and rivers may serve as additional examples of secondary production unchecked by predation, competition, and/or pathogens in native ranges.

Beyond empirically tested hypotheses of variation in secondary production, there are some patterns that have been observed across types and sizes of streams that speak to mechanism. Benke (1993), Finlay (2011), and Patrick et al. (2019) all observed a

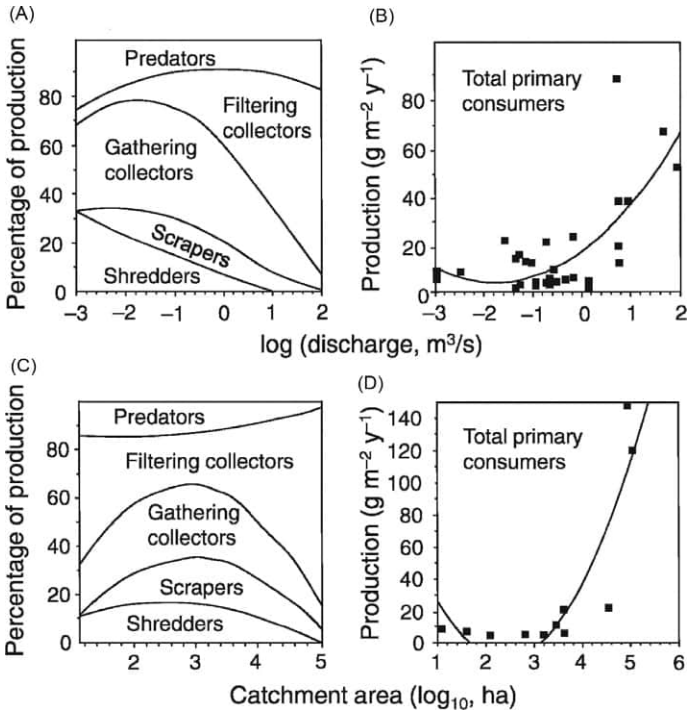

Fig. 3 Relative production (percentage of P) (panels A and C) and total production fitted to 2nd degree polynomials (B and D) of functional feeding groups along a river continuum (Benke and Huryn, 2010). Total primary consumers include all functional feeding groups except for predators. Data are from a meta-analysis by Benke (1993) (A and B) and (Grubaugh et al., 1997) (C and D). Figure used with permission from the University of Chicago Press. From Benke AC and Huryn AD (2010) Benthic invertebrate production-facilitating answers to ecological riddles in freshwater ecosystems. *Journal of the North American Benthological Society* **29**: 264–285.

Table 3 Biomass, Production, and P/B estimates from whole communities by Strahler stream order.

Strahler Stream Order	*n*	*Biomass (g AFDM/m^2)* *Mean ± SE (n)*	*Production (g AFDM/m^2/year)* *Mean ± SE (n)*	*P/B* *Mean ± SE (n)*
1	70	6.968 ± 0.108 (70)	8.884 ± 0.129 (67)	1.247 ± 0.012 (51)
2	28	6.77 ± 0.21 (28)	8.656 ± 0.252 (26)	1.268 ± 0.022 (22)
3	17	6.855 ± 0.276 (17)	8.946 ± 0.298 (16)	1.302 ± 0.028 (14)
4	16	7.684 ± 0.438 (16)	9.118 ± 0.576 (15)	1.337 ± 0.075 (11)
5	8	8.049 ± 0.685 (8)	10.768 ± 0.541 (6)	1.378 ± 0.093 (6)
6	9	8.923 ± 0.388 (9)	10.778 ± 0.398 (9)	1.216 ± 0.04 (9)
8	2	8.266 ± 0.677 (2)	9.743 ± 0.509 (2)	1.182 ± 0.035 (2)
9	2	5.233 ± 0.207 (2)	7.324 ± 0.054 (2)	1.402 ± 0.066 (2)

Dataset from Patrick CJ, McGarvey DJ, Larson JH, Cross WF, Allen DC, Benke AC, Brey T, Huryn AD, Jones J, Murphy CA, Ruffing C, Saffarinia P, Whiles MR, Wallace JB and Woodward G (2019) Precipitation and temperature drive continental-scale patterns in stream invertebrate production. *Science Advances* **5**: eaav2348.

general pattern of increasing secondary production with increasing stream size (Table 3). Finlay (2011) attributed this pattern to increased probability of anthropogenic impacts, such as nutrient loading that increases production. However, Patrick et al. (2019) observed that as streams increase in size, water temperature increases, while the intensity of low flow events decreases. The actual mechanism is likely a combination of these factors, with larger rivers tending toward both greater nutrient loading but also more stable flow regimes and more moderate temperatures that enhance production. At larger scales, secondary production estimates also vary among ecoregions of the world (Benke, 1993; Patrick et al., 2019). Dry and humid temperate ecoregions have been observed to have higher whole community production and biomass than humid tropical and polar regions. However, P/B ratios reported from humid tropical regions are higher than the other biomes, a pattern likely linked to higher individual growth rates in warm tropical stream waters.

Case studies

Detritus availability in headwater streams; bottom-up controls on secondary production

Some of the most important studies regarding the secondary production of invertebrates in streams took place at the Coweeta Long Term Ecological Research Site in the Blue Ridge Mountains of North Carolina, United States. Among these, a unique, reach-scale litter exclusion study performed by Wallace et al. (1997) serves as an important case study for understanding bottom-up effects on secondary production. Investigators began monitoring the abundance, biomass, and production of stream invertebrates in two comparable fishless headwater streams in 1992. After 12 months, the investigators set up exclusion nets over the top and sides of 180 m reaches of one of these streams (hereafter the treatment stream) to prevent fall leaf litter from entering the stream directly or through lateral movement (Fig. 4). For the next 3 years, they observed the effects of the litter exclusion on the abundance, biomass, and production of the animals by monitoring both the treatment and the reference streams. In mixed substrata (the dominant cobble, pebble, gravel, and sand/silt substrates of the streams), they observed a continual decline in total secondary production in the treatment stream while production actually increased each year in the reference stream (Fig. 4). The declines were most strongly reflected in detritivores that eat large particles (shredders, collector-gatherers) and the predators that consume these groups. In contrast, communities on moss-covered bedrock that mostly feed on fine particles showed no discernable difference between the treatment and reference streams. This classic experiment clearly demonstrates that resource availability can limit production of primary consumers, and that this limitation can cascade up to secondary consumers that depend on them as prey.

Examining the Allen paradox; top-down and bottom-up processes and production

During the mid-20th century, research on the secondary production of streams that supported trout came to the puzzling conclusion that observed invertebrate production was insufficient to support the production of the trout populations that lived in those streams (Allen, 1951). This phenomenon came to be known as the Allen Paradox (Hynes, 1970). Huryn (1996) examined these same streams to re-evaluate the paradox and today we now recognize that the solution to the Allen Paradox can be found in the combination of several factors: (1) Secondary production estimates are prone to error, (2) trout populations are supported not only by secondary production of surface dwelling benthic invertebrates but also allochthonous inputs of terrestrial insects as well as secondary production occurring in the hyporheic zone, (3) only a relatively small portion of secondary production needs to escape predation and reproduce to maintain invertebrate populations in streams. Huryn (1996) conducted a detailed study of New Zealand trout streams and calculated production estimates for surficial invertebrates, hyporheic invertebrates, and terrestrial insects falling into the stream. He also estimated the energy needs of the resident trout populations. He concluded that the mean estimates yielded a surplus of zero (Fig. 5), but that it was likely that his production estimates underestimated surplus production by as much as 20%. Notably, terrestrial inputs made up roughly 20% of available food resources, with a 95% confidence range of 10–37% of available food resources. This study both resolved the Allen Paradox and demonstrated the importance of terrestrial prey inputs into streams, which are linked to riparian habitat quality, for supporting the production of higher trophic levels (Huryn, 1996).

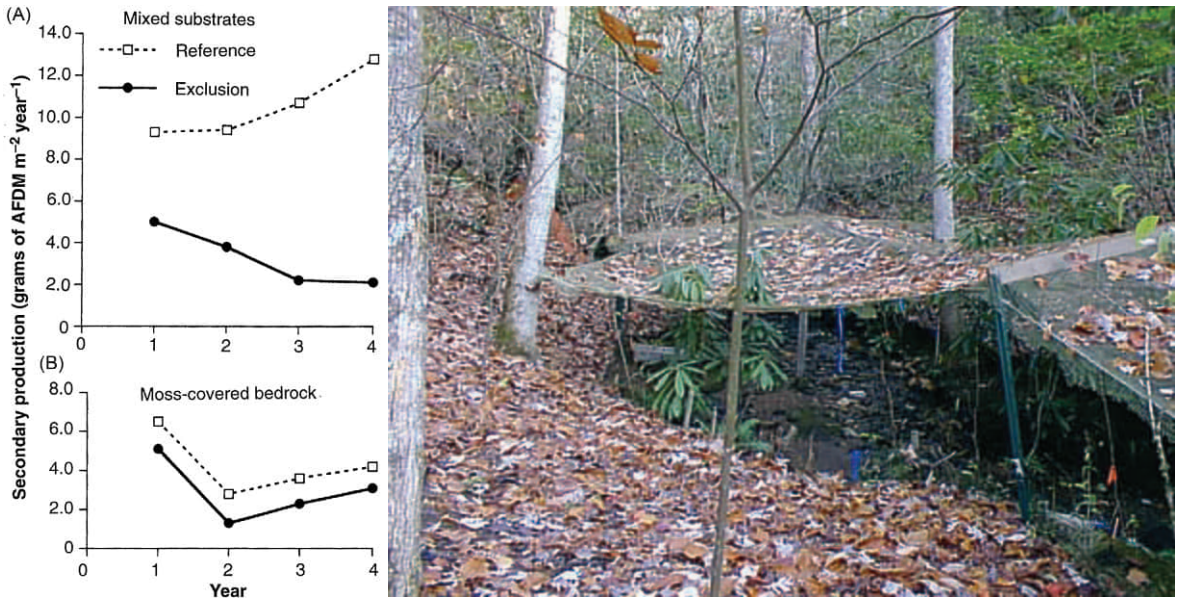

Fig. 4 Experimental set-up and annual secondary production estimates from Wallace et al. (1997) (left). Benthic invertebrate production estimates. Year 1 was the pre-treatment year followed by 3 years of litter exclusion. Data are shown for (A) mixed substrate habitats in the reference and litter exclusion streams and (B) moss covered bedrock outcrop habitats in the same streams (right). Depiction of the canopy erected to prevent litter from entering the stream. Reproduced with permission from AAAS. Wallace JB, Eggert SL, Meyer JL and Webster JR (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* **277**: 102–104.

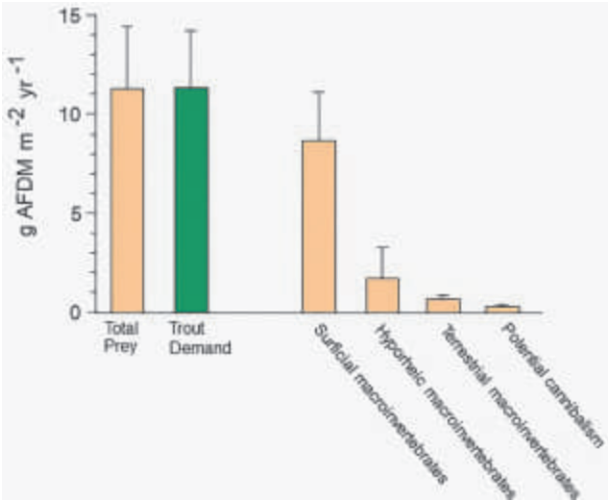

Fig. 5 Comparison of total prey available for consumption by trout and breakdown of prey available from different sources in g ash-free dry mass. Error bars are bootstrapped 95% confidence intervals. Figure provided by A. D. Huryn; redrawn from Huryn AD (1996) An appraisal of the Allen paradox in a New Zealand trout stream. *Limnology and Oceanography* **41**: 243–252.

Ecological responses to loss of a dominant consumer group: Biotic interactions and secondary production

As catastrophic, disease-driven amphibian declines moved through the mountains of Central America in the early 2000s, a group of biologists began looking at ecological responses to the losses of amphibians at multiple scales, from plots and chambers to reach-scale production and metabolism (Whiles et al., 2006). Following the loss of tadpoles, including taxa that were abundant grazers and detritivores in these systems, Colón-Gaud et al. (2009) found that overall patterns of secondary production did not change as dramatically as expected, with no large compensatory increases in grazing or detritivorous groups that hypothetically competed with tadpoles for food. While large-bodied grazing insects did show some increases, production of small-bodied grazers such as mayflies declined with amphibians, as did shredders. Small-scale manipulations demonstrated that these patterns in production were linked to positive effects of tadpoles on some insect groups; tadpoles facilitated small-bodied grazing mayflies by removing sediments overlying the periphyton the mayflies feed on (Ranvestel et al., 2004). It was later discovered that tadpoles also facilitated leaf shredding insects by enhancing microbial activity and abrading and penetrating the tough tropical leaves with their rasping mouthparts (Rugenski et al., 2012). While many secondary production studies focus on top-down and bottom-up controls, or responses to physicochemical gradients, this study showed that biotic interactions, in this case facilitation, can also influence patterns of community production. This series of studies also illustrates the power of using small-scale manipulations in conjunction with reach-scale production estimates to identify mechanisms underlying patterns of production.

Future directions

One of the greatest issues standing in the way of further synthesis and enhancing our theoretical understanding of secondary production in flowing waters is simply lack of data. Benke (1993) was based on 159 studies, 40 of which were whole community estimates from different rivers and streams. Patrick et al. (2019) was based on whole community estimates from 164 different rivers and streams. This indicates that conservatively there have been 4.5 new studies on whole community secondary production coming out each year. Furthermore, Benke (1993) pointed out several specific areas where more data were needed, such as larger rivers (>10 m^3 s^{-1} discharge) and low latitudes ($<30^o$); unfortunately these data limitations persist, with only five estimates from Patrick et al. (2019) from tropical regions and only four estimates from 8th order or higher rivers (Tables 3 and 4). The literature bias is even greater when biogeographic location is considered. There are almost no estimates from Africa and Asia and relatively few estimates from South America. The literature bias remains centered on wadeable streams, primarily in North American and Europe, the majority of which are temperate and forested.

The challenge is not an easy one to address using existing methods. While Benke and Huryn (2010) report that estimating secondary production is easier today than in decades past, it remains a tedious, laborious, and often expensive process. As long as high-quality estimates require monthly sampling visits to field sites and long hours of tedious laboratory work identifying, enumerating, and measuring all collected individuals, the rate of advancement in this area will remain slow and geospatially limited to areas that are close to research groups with easy access to field sites. Considering this, methodological advances in measuring secondary production to reduce the cost and time required are a laudable research goal that could potentially advance the field in the long run. Refinement and application of approaches being developed in other disciplines such as using machine learning

Table 4 Biomass, Production, and P/B estimates from whole communities for ecoregions and ecoregion divisions.

EcoReg_Domain	*EcoReg_Division*	*n*	*Biomass (g AFDM/m^2)* *Mean ± SE (n)*	*Production (g AFDM/m^2/year)* *Mean ± SE (n)*	*P/B* *Mean ± SE (n)*
DRY		43	7.385 ± 0.235 (43)	9.377 ± 0.252 (41)	1.291 ± 0.022 (37)
	TEMPERATE_DESERT	6	6.326 ± 0.642 (6)	8.138 ± 0.533 (6)	1.309 ± 0.051 (6)
	TEMPERATE_STEPPE	13	6.985 ± 0.16 (13)	9.477 ± 0.116 (12)	1.362 ± 0.026 (12)
	TEMPERATE_STEPPE_REGIME_MOUNTAINS	22	8.034 ± 0.375 (22)	9.559 ± 0.414 (22)	1.215 ± 0.02 (18)
	TROPICAL/SUBTROPICAL_STEPPE	2	6.843 (2)	11.608 (1)	1.696 (1)
HUMID_TEMPERATE		92	7.436 ± 0.111 (92)	9.244 ± 0.141 (85)	1.252 ± 0.014 (64)
	HOT_CONTINENTAL	7	NA	9.415 ± 0.167 (7)	NA
	HOT_CONTINENTAL_REGIME_MOUNTAINS	23	7.703 ± 0.236 (23)	9.457 ± 0.341 (18)	1.168 ± 0.039 (8)
	MARINE	6	7.973 ± 0.464 (6)	9.484 ± 0.417 (6)	1.196 ± 0.029 (6)
	MEDITERRANEAN_REGIME_MOUNTAINS	1	6.263 (1)	8.31 (1)	1.327 (1)
	PRAIRIE	3	7.763 ± 0.081 (3)	9.8 ± 0.151 (3)	1.262 ± 0.016 (3)
	SUBTROPICAL	18	7.263 ± 0.326 (18)	9.065 ± 0.483 (17)	1.354 ± 0.042 (14)
	SUBTROPICAL_REGIME_MOUNTAINS	26	7.537 ± 0.146 (26)	9.284 ± 0.176 (25)	1.233 ± 0.007 (25)
	WARM_CONTINENTAL	8	6.685 ± 0.419 (8)	8.605 ± 0.454 (8)	1.248 ± 0.036 (7)
HUMID_TROPICAL		5	5.168 ± 0.514 (5)	7.755 ± 0.468 (5)	1.535 ± 0.087 (5)
	RAINFOREST_REGIME_MOUNTAINS	4	5.674 ± 0.114 (4)	8.22 ± 0.072 (4)	1.45 ± 0.022 (4)
	SAVANNA_REGIME	1	3.144 (1)	5.896 (1)	1.875 (1)
POLAR		16	6.638 ± 0.228 (16)	8.065 ± 0.221 (16)	1.219 ± 0.008 (16)
	SUBARCTIC	10	6.134 ± 0.052 (10)	7.604 ± 0.059 (10)	1.24 ± 0.003 (10)
	TUNDRA	6	7.478 ± 0.426 (6)	8.832 ± 0.439 (6)	1.184 ± 0.011 (6)

Dataset from Patrick CJ, McGarvey DJ, Larson JH, Cross WF, Allen DC, Benke AC, Brey T, Huryn AD, Jones J, Murphy CA, Ruffing C, Saffarinia P, Whiles MR, Wallace JB and Woodward G (2019) Precipitation and temperature drive continental-scale patterns in stream invertebrate production. *Science Advances* **5**: eaav2348.

and image analyses of samples to rapidly classify and measure invertebrates may make these methods more cost effective and efficient in the future. Development of statistical approaches that reduce frequency of sampling required to develop defensible estimates would also cut down on time and labor in the field and laboratory.

Our understanding of the drivers of secondary production has come a long way in recent years, but much remains to be done. Unlike primary production, which is easily measured in the field and laboratory and lends itself to experimental manipulation, secondary production has proven to be a much more challenging response variable to study. All areas of general theory concerning ecosystem functioning could stand to be more thoroughly tested with secondary production. For example, one topic that has received very little attention is the importance of biodiversity to secondary production. Theory predicts that as biodiversity increases, secondary production should also increase. This relationship can be related to factors such as complementarity and facilitation among co-occurring species, and sampling effects whereby the odds of having highly productive taxa in a community increase with richness. However, little support exists for this in streams (but see Statzner and Resh, 1993, Pollock, 2008), and some of the highest secondary production estimates come from relatively low diversity systems (e.g., Voshell, 1985; Hall et al., 2006). Furthermore, Finlay (2011) reports covarying patterns of biodiversity declining and secondary production increasing as rivers get larger. It seems likely that this pattern can be reconciled by the covarying pattern of anthropogenic impacts both reducing diversity while increasing nutrients and food availability, but it speaks to a larger issue regarding a need for independent assessment of the relative importance of, and interaction between, the various drivers of secondary production. While additional studies are needed to fill current gaps, there remains an open opportunity for synthesis of the work that has been done that goes beyond recent publications. An exhaustive review of published population level estimates of secondary production, coupled with geospatial data and causal network analysis, would greatly enhance our understanding of the drivers of secondary production and provide a useful resource for advancing theory and statistical tools for understanding secondary production and energy flow in running waters.

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Ecological Stoichiometry in Streams

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Assimilation efficiency (AE) The efficiency at which a consumer digests or incorporates consumed elements into its metabolic pool. Defined as assimilation rate divided by consumption rate of a particular element.

Consumer-driven nutrient dynamics (CND) Direct and indirect effects of consumers on nutrient cycling within their environment.

Egestion The release of materials or elements as fecal matter. These elements have been ingested, but not assimilated.

Elemental imbalance The degree of elemental mismatch (ratio of C:nutrient, e.g., C:N or C:P) between consumer elemental demands and the elemental contents of their food resources.

Excretion The release of dissolved materials or elements. These elements have been ingested and assimilated but are not used for growth or storage.

Functional feeding group (FFG) A behavioral classification scheme that categorizes organisms based on feeding acquisition strategy.

Gross growth efficiency (GGE) The efficiency at which a consumer converts consumed elements into new biomass, defined as growth rate divided by ingestion rate for a particular element.
Growth rate hypothesis The hypothesis that organisms with higher growth rates have an increased demand for ribosomal RNA production to sustain rapid growth, and thus have higher phosphorus (P) concentration in their tissues.
Luxury consumption An organism's ability to assimilate and store excess available elements within tissues.
Nutrient spiral The cycling of nutrients in streams as they are assimilated from the water column into benthic biomass, temporarily retained, and mineralized back into the water column in a downstream trajectory that resembles a spiral.
Stoichiometric homeostasis The ability of an organism to maintain relatively constant internal tissue stoichiometry despite variation in the stoichiometry of its resources.
Threshold elemental ratio (TER) Resource ratio at which consumer growth switches limitation between two different elements.

Introduction

The role organisms play in biogeochemical processes has become central to our understanding of ecosystem function. All organisms are made of elements in varying proportions. The relative rate of supply of these elements in the environment and the degree to which the ratio of these elements is constrained or flexible within organisms have fundamental consequences ranging from cellular-level processes to the ecosystem. Ecological stoichiometry (ES) is a general framework that follows the law of conservation of mass and has been used to understand the balance of multiple key elements (traditionally carbon (C), nitrogen (N) and phosphorus (P)) in ecological interactions and processes (Sterner and Elser, 2002). ES has been used to model the coupled flow of multiple elements between organisms and their environments and has enhanced our understanding of two main areas in aquatic ecology: resource quality effects on consumer growth and consumer-driven nutrient dynamics (CND). Using mass balance principles to track pools and fluxes of elements from the cellular to ecosystem level, ES enables predictions of relationships among the elemental composition of consumers, their food resources, their waste products (i.e., excretion and egestion), and how other organisms (i.e., microbes and autotrophs) use these waste products to support growth (Frost et al., 2006; Schiettekatte et al., 2020).

Many core concepts of ES were originally derived from pelagic systems (open waters of lakes and oceans), focusing on interactions between zooplankton and their phytoplankton resources (Sterner, 1990; Sterner and Elser, 2002). However, recent work has applied ES concepts to advance understanding of stream organisms and ecosystems (Maranger et al., 2018; Cross et al., 2005; Atkinson et al., 2017). Compared to pelagic systems, streams are characterized by unidirectional water flow and stronger interactions between the water column and the benthos, both of which strongly influence the transfer of elements between biota and their environments. For example, streamflow converts nutrient cycles into "spirals" between biota and the environment, and nutrient spiraling is controlled by stoichiometric constraints on organisms (Newbold et al., 1981; Schade et al., 2011). Because of their close proximity to terrestrial systems, basal food resources in streams also encompass a wide range in quality, from low-quality allochthonous detritus (e.g., tree leaves and woody tissues) to high-quality autochthonous benthic algae and macrophytes (e.g., higher quality resources have a lower C:nutrient; e.g., lower C:N or C:P). Below, we review principles of ES as they relate to organism-nutrient relationships in streams, emphasizing principles of organism homeostasis and physiology (Fig. 1), patterns in stream food web stoichiometry (Fig. 2), and scaling from organisms, to communities, to ecosystem-level processes like nutrient cycling (Fig. 3). We close by summarizing knowledge to date (Fig. 4) while highlighting knowledge gaps on this topic.

Nutrient uptake and homeostasis in autotrophs versus heterotrophs

Within the context of ES, homeostasis refers to an organism's ability to maintain a relatively constant nutrient content or ratio in its tissues over short time scales (e.g., hours or days) (Sterner and Elser, 2002). Broad groups of organisms have distinct elemental compositions in their body tissues, with autotrophs having higher intraspecific variability (i.e., lack of homeostasis) than heterotrophs (Persson et al., 2010). Autotrophs obtain energy (mostly sunlight) and nutrients from different, uncoupled sources within their environment. As a result, autotrophs have distinct strategies to store these resources, as the availability of one resource does not guarantee availability of another one (Frost et al., 2005). These resource uptake strategies are often linked to storage capacity and therefore to plasticity in cellular, and hence organismal, stoichiometry. Due to their ability to store nutrients, C:N:P ratios in tissues of autotrophs vary greatly with available nutrient ratios, indicating a high flexibility in chemical composition and a lack of homeostasis (Stelzer and Lamberti, 2001; Hill et al., 2011). This adaptation allows autotrophs to store cellular nutrients when in excess, a process called luxury consumption. However, the response of benthic periphyton elemental composition to the availability and ratios of dissolved nutrients in stream water is complicated by concomitant shifts in algal species composition (Stelzer and Lamberti, 2001). Further, while aquatic macrophyte stoichiometry is partially driven by background nutrient concentrations, taxonomic identity is a stronger driver (Cedergreen and Madsen, 2003; Demars and Edwards, 2007), highlighting the role of homeostasis in generating interspecific variation among autotrophs (Nifong et al., 2014).

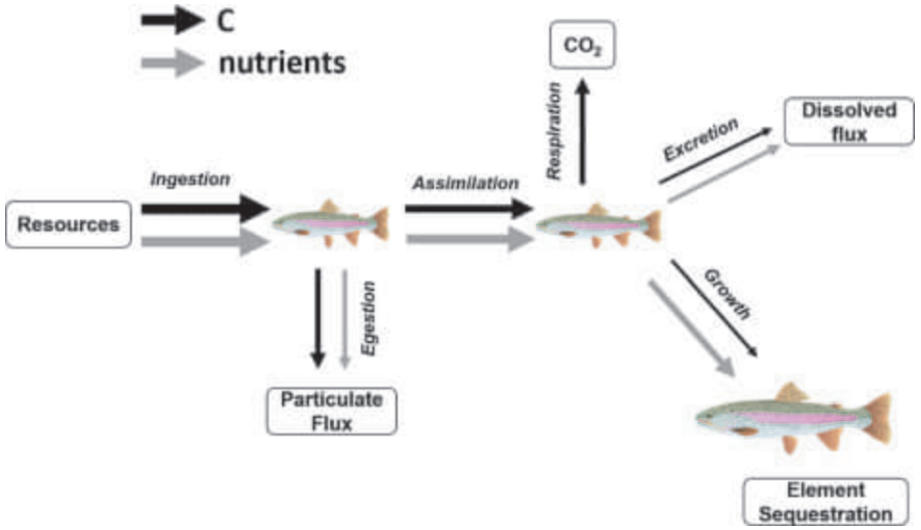

Fig. 1 Heterotrophic animal consumers ingest resources that vary in elemental composition (C:nutrient). The body elemental composition and nutrient storage capacity govern the amounts of C and nutrients heterotrophic animals assimilate. Post-assimilation, heterotrophs regulate internal body composition by preferential mineralization and excretion of the element in excess to maintain growth. As the degree of limitation varies among consumers due to feeding status and structural demand, there is interspecific variation in sequestration and nutrient recycling.

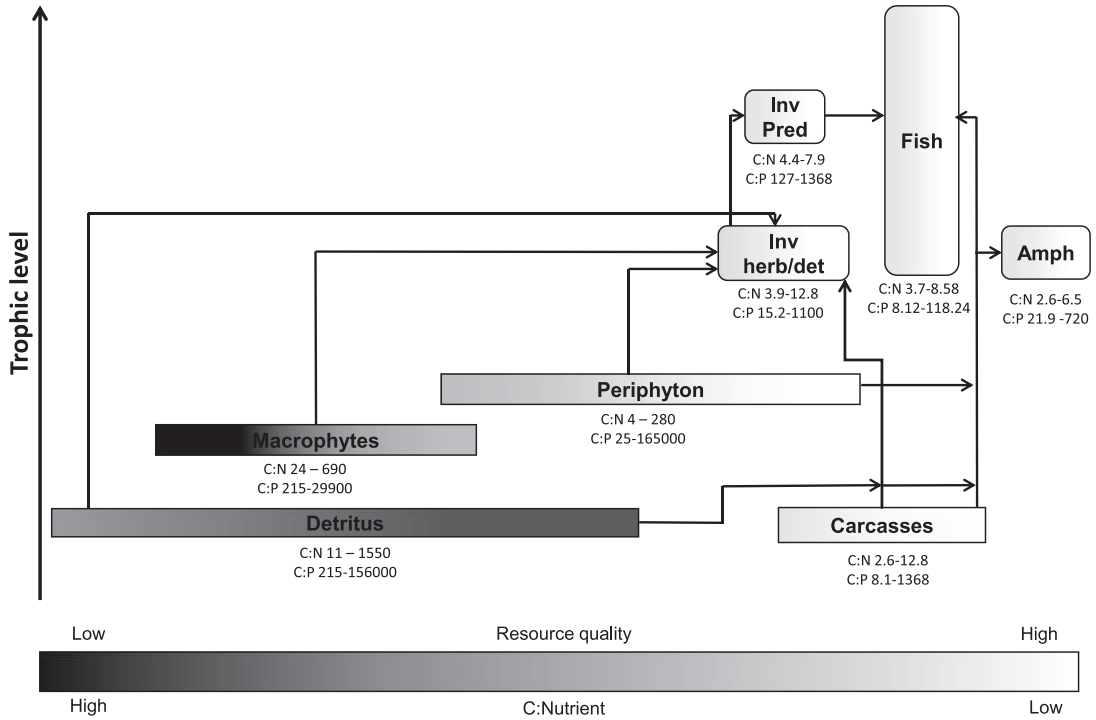

Fig. 2 Conceptual food web illustrated in the context of stoichiometric mismatches such that animals (rounded boxes), basal resources (sharp boxes) and their degree of shading reflects the C:nutrient (C:N or C:P) of each food web compartment. Solid arrows represent consumptive interactions and the flow of energy and elements up trophic levels. Detritus combines wood and leaves from Cross et al. (2005), and the width of each box represents the relative stoichiometric variation within each compartment. Mismatch between consumer and food source is reflected by the horizontal distance (left to right) between consumer and food sources. Resource stoichiometry values are based on ranges reported in Cross et al. (2005) and animal stoichiometry values are from Vanni and McIntyre (2016). "Inv pred" indicates invertebrate predators. "Inv herb/det" combines stoichiometry values for herbivores and detritivores insects. "Amph" indicates amphibians. "Detritus" combines wood and dead leaves.

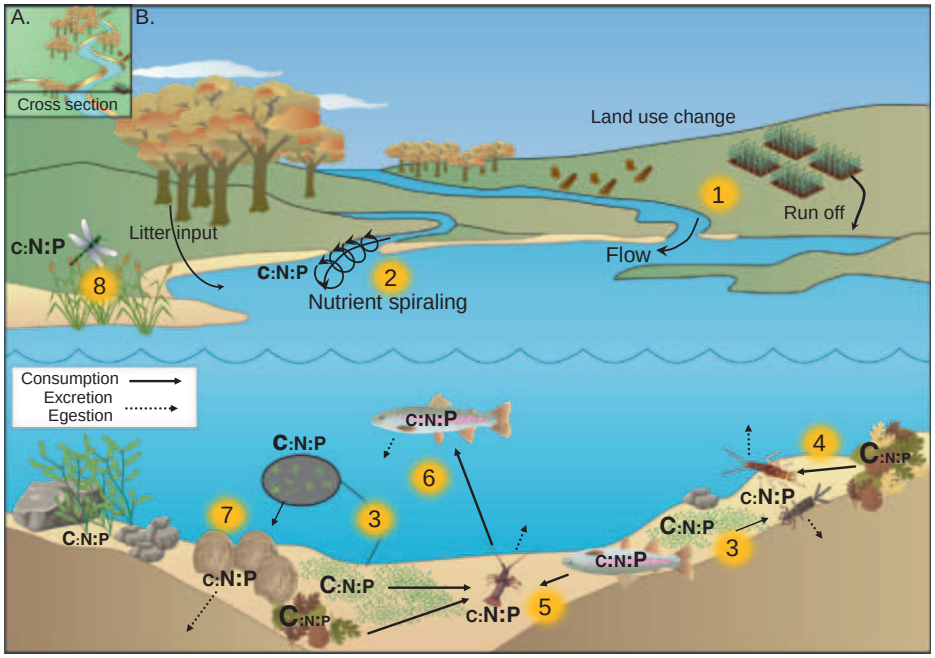

Fig. 3 (A) Aerial view of a stream. (B) Cross section view of inset illustrating a simplified diagram of a stream food web showing stoichiometry of compartments. Relative elemental size reflects differences in composition. (1) Streams integrate nutrients from their watershed. Land use changes impact nutrient loading that can shift food resource stoichiometry. (2) Unidirectional downstream flow converts nutrient cycles into spiraling that flow between biomass and the abiotic environment. (3) Biofilm and seston stoichiometry are generally plastic and determined by ambient conditions and biofilm is generally higher quality (lower C:nutrient ratio); grazer-biofilm mismatch is lower than shredder-leaf litter stoichiometric mismatch. (4) Leaf litter is typically recalcitrant (high C:nutrient ratio)—shredders have a greater elemental imbalance. (5) Omnivores can exhibit compensatory feeding (e.g., feeding on nutrient-rich decomposing animals) to reduce mismatch. (6) Predators have a lower stoichiometric mismatch. Mobile predators can translocate nutrients. (7) Filter-feeders are mismatched with food source and translocate materials from the water column to the benthos. (8) Aquatic insect emergence links aquatic and terrestrial ecosystems as nutrient and energy subsidies. (9) Unidirectional downstream flow converts nutrient cycles into spiraling that transitions between benthic biomass and the abiotic environment.

Heterotrophs, including bacteria, fungi, and animals, are generally more homeostatic than autotrophs in their elemental ratios, resulting in more constrained elemental body composition and nutrient storage capacity (Persson et al., 2010). As heterotrophs take up, transform, and store nutrients through consumption, metabolism and growth, the elemental composition of their resources dictate the efficiency of uptake and resultant release of elements in waste products (Fig. 1; Mooshammer et al., 2014; Manzoni et al., 2017; Schiettekatte et al., 2020). Heterotrophs typically rely on C-rich resources in comparison to their body composition, with important implications for performance and subsequent trophic dynamics; for example, herbivores may be limited by the amounts of N or P they can assimilate from C-rich autotroph tissues (Hessen and Anderson, 2008). Heterotrophs deal with these imbalances with a wide range of pre- and post-assimilation strategies. Pre-assimilation strategies include selective ingestion such as preferentially feeding on nutrient-rich resources (Hood et al., 2014) and regulating their body elemental composition via selective assimilation, the process by which organisms digest and acquire nutrients into their metabolic pool (Clissold et al., 2010). Post-assimilation, organisms regulate internal body composition by preferential mineralization and excretion of the element in excess (Fig. 1; Dalton et al., 2017). The degree of homeostasis, and the roles of these regulatory processes in maintaining homeostasis, vary across taxonomic groups and trophic levels.

Although evidence suggests that animals are relatively homeostatic in terms of body elemental composition, microbial heterotrophs (bacteria and fungi) have a more variable degree of homeostasis. While historically thought to be inflexible in their internal nutrient content, recent research has highlighted that both bacteria and fungi are flexible in their P content (Scott et al., 2012; Gulis et al., 2017). Aquatic fungi can be relatively homeostatic with respect to their C:N ratio (~11:1), but non-homeostatic with respect to C:P and N:P (Gulis et al., 2017). Dissolved N greatly enhances fungal growth rate and production, but has little effect on C:nutrient stoichiometry. In contrast, dissolved P does not seem to affect fungal growth and production, yet it controls fungal biomass C:P and N:P. The proposed mechanism dictating alteration of C:P and N:P ratios in fungi is luxury P uptake and storage (as polyphosphate-P) during periods of high P availability. Bacteria also exhibit substantial plasticity in cellular P contents, with the capacity to grow with extremely P-deplete tissues, as well as store excess P via luxury consumption (Scott et al., 2012; Godwin and Cotner, 2015). The ability of bacteria and fungi to flexibly immobilize and store excess P may alter nutrient flow through aquatic food webs and affect ecosystem functioning.

Animal body nutrient composition, an indicator of an organism's relative demand for nutrients, is relatively homeostatic and is a product of multiple ecological, evolutionary, and environmental factors (Fig. 1; Persson et al., 2010, Sterner and Elser, 2002). Structural characteristics, such as P-rich bones or N-rich carapaces, are often phylogenetically conserved and can contribute

substantially to the nutritional makeup and demands of an animal (Leal et al., 2017a,b). Ecological (e.g., diet) and environmental (e.g., temperature) factors influence physiological processes and also affects body nutrient composition. For example, rapid growth rates during early stages of development or among species with fast turnover rates (i.e., r-selected species) have been correlated with high levels of P-rich ribosomal RNA and consequently high body P demand (i.e., growth rate hypothesis; Sterner and Hessen, 1994; Meunier et al., 2017). The premise that animal nutrient contents vary across species, but remain relatively static within species, led to the concept of the threshold elemental ratio (TER; Urabe and Watanabe, 1992; Frost et al., 2006). The TER predicts the elemental ratio at which growth limitation switches from one element to another (generally C:nutrient), signifying the C:nutrient ratio for optimal consumer growth. TER models for animals have been modified over time to include variable assimilation efficiencies of limiting elements and metabolic loss terms. (i.e., animals need C not only to build tissues, but also for respiration; Fig. 1) which has improved estimates of animal element demand (Doi et al., 2010; Halvorson et al., 2015; Moody et al., 2019; Schiettekatte et al., 2020). As a result of variable TERs, the degree of limitation varies among consumers, generating interspecific differences in nutrient recycling rates and overall ecosystem-level effects.

Stream food webs: Patterns and mismatches across trophic levels

Basal resources

The energy base of ecosystems affects both stream food web structure and biodiversity (Wallace et al., 1997; Cross et al., 2007). Stream ecosystems are generally supported by two major resource types: (1) "green" or autochthonous resources, such as benthic algae and macrophytes, and (2) "brown," generally allochthonous (terrestrial) detrital resources in the form of coarse particular organic matter (CPOM; e.g., leaves and wood) and fine particulate organic matter (FPOM; e.g., feces, soil, leaf litter fragments) and their associated fungal and bacterial communities. Basal resource availability can vary temporally (e.g., autumn leaf fall), and spatially as a result of stream size (i.e., River Continuum Concept, Vannote et al., 1980) and interactions with the adjacent floodplain (i.e., Floodpulse Concept, Junk et al., 1989). Here we highlight the controls on "green" and "brown" resource stoichiometry for stream consumers (Fig. 2).

Autochthonous/green resources

Generally, autochthonous resources such as benthic algae are a higher quality food resource than allochthonous detritus because the N and P content of living plant material tends to be higher than that of detrital leaves and wood (Evans-White et al., 2005; McManamay et al., 2011). Previous work has indicated that light, nutrient availability, and flow interactively affect both water column and benthic algal stoichiometry (Dickman et al., 2006; Kohler et al., 2012). Specifically, enhanced nutrient availability decreases C:nutrient ratios while light increases C:nutrient ratios (Dickman et al., 2006; Sanches et al., 2011), and variation in flow impacts stoichiometry of primary producers by shaping algal community structure and influencing nutrient flux (Dodds and Biggs, 2002; Francoeur and Biggs, 2006). In terms of nutritional quality, macrophytes tend to be intermediate between algae and allochthonous detritus, as indicated by higher C:nutrient ratios in macrophytes (Fig. 2), large quantities of cellulose and lignin, and decreased digestibility of proteins compared to algae (Demars and Edwards, 2007; Cebrian, 1999). Macrophytes, however, can also provide substrates for periphyton and bacterial colonization (Dodds and Biggs, 2002; Vadeboncoeur et al., 2006) and make significant contributions to the detrital pool (Wallace and O'Hop, 1985; Minshall, 1978).

Allochthonous/brown resources

While terrestrial plant litter is of poorer quality than autochthonous algal-based resources, the former is often the dominant energy input to many stream communities supporting "brown" food webs. This is especially true among low-order streams in temperate forested ecosystems (Webster and Meyer, 1997; Rosi-Marshall and Wallace, 2002; Vannote et al., 1980) where a suite of detritivores and microbial decomposers process this allochthonous material (Marks, 2019; Cummins and Klug, 1979). Allochthonous detrital matter differs greatly in chemical composition from autochthonous resources, having greater amounts of refractory compounds and higher C:nutrient ratios, making it a lower-quality food source for consumers (Rosi-Marshall and Wallace, 2002; Allan and Castillo, 2007). Detrital stoichiometry changes as this material is processed, through animal feeding (e.g., shredding) and colonization of detritus by nutrient-rich bacteria and fungi increasing CPOM nutritional quality for subsequent consumers (Grattan and Suberkropp, 2001). Shredding of large particles into smaller particles (FPOM) by physical abrasion and animal feeding also increases surface area (Anderson and Sedell, 1979), facilitating further microbial colonization by bacteria and fungi, increasing N and P contents (Ferreira et al., 2006; Manning et al., 2015), and thus lowering C:nutrient ratios (Cross et al., 2003; Atkinson et al., 2009). As a result, CPOM tends to be of poorer quality (highest C:nutrient ratios) compared to FPOM (Cross et al., 2005). However, this may be partly driven by low C content of FPOM, as CPOM can actually exhibit higher N content than FPOM (Farrell et al., 2018).

Consumers

Since primary consumers have lower C:nutrient contents than the basal food resources upon which they feed, there can be differential imbalances in green- versus brown-based food webs (Cross et al., 2003; Evans-White and Halvorson, 2017), with implications for consumer performance and subsequent trophic dynamics. Primary consumers in streams span a large breadth of feeding strategies categorized into functional feeding groups (FFGs) and since basal resources vary in quality, FFGs vary in their

nutritional imbalances (Fig. 2). Below we highlight what is known regarding feeding strategies and dietary mismatches in four broad trophic groups: herbivores, detritivores, omnivores, and predators.

Herbivores

Herbivores in streams comprise several FFGs including scrapers, which graze on benthic algal biofilms, and collector gatherers and collector-filterers, which feed on both autotrophic and detrital resources. Herbivores can have strong top-down controls on autotrophic production by constraining total autotroph biomass (Lamberti et al., 1995; Hillebrand et al., 2004) and altering community composition through selectively feeding on more palatable species or removing overstory taxa (Rosemond et al., 1993; Feminella and Hawkins, 1995). The degree of stoichiometric mismatch between herbivores and their resources determines assimilation efficiencies and growth, with multiple studies indicating that herbivores that ingest algae or macrophytes with high C:nutrient ratios have lower assimilation efficiencies and growth rates (Stelzer and Lamberti, 2002; Fink and von Elert, 2006; Hillebrand et al., 2004). Elevated concentrations of available (dissolved) nutrients can both increase autotroph growth (Rosemond et al., 1993) and nutrient content (Hessen et al., 2002), which can reduce nutritional imbalances for herbivores. In addition, beyond active selection of high-quality resources (e.g., Rosemond et al., 1993), herbivores may employ compensatory feeding to respond to nutrient-deficient basal resources (Plath and Boersma, 2001; Liess, 2014).

Detritivores

Several FFGs, such as shredders and collector-gatherers, use predominantly terrestrial-derived detrital resources and have greater stoichiometric constraints relative to herbivores (Fig. 2; Tant et al., 2013; Farrell et al., 2018). The overall lower nutrient content and high recalcitrance (e.g., lignin) of detritus (Cross et al., 2003; Chapin et al., 2002) relative to algae may result in lower detritivore assimilation efficiencies (AE) and lower gross growth efficiencies (GGEs, i.e., growth rate divided by ingestion rate) relative to herbivores (Halvorson et al., 2015; DeMott et al., 1998). Several mechanisms can explain how detritivores deal with the high degree of mismatch in diet versus tissue stoichiometry such as compensatory feeding rates, selective feeding, or element-specific AEs (Flores et al., 2014; Frainer et al., 2016; Eggert and Wallace, 2007). For example, the detritivorous shrimp, *Xiphocaris elongata*, ingests a significant amount of CPOM, yet most of its energy is derived from autochthonous C sources (March and Pringle, 2003). As a result of feeding on more recalcitrant resources than herbivores, detritivores are anticipated to excrete nutrients at lower rates and egest at higher rates in comparison to herbivores (McManamay et al., 2011), with important implications for consumer-resource dynamics (Atkinson et al., 2017).

Omnivores

Omnivory is prevalent among both stream invertebrates and vertebrates. Although the FFG classification scheme highlights the overall feeding strategy, there can be a high degree of resource mixing (e.g., Hood and Sterner, 2010). The reasons underlying omnivory are numerous and include mechanisms such as seasonally varying food availability, life cycle patterns, and key life history and growth strategies (Hood et al., 2014; Hellmann et al., 2013; Evans-White et al., 2003) that likely enhance AE. For example, omnivory can be driven by seasonal prey availability in *Hydropsyche* caddisflies and life-cycle patterns in amphipods (Hellmann et al., 2013). Additionally, some detritivorous insects primarily consume detritus in early instars, but then switch to cannibalism and intraguild predation during later instars (Wissinger et al., 1996). This suggests highly dynamic consumer-resource mismatches among omnivores, a varying role for omnivores in CND over their lifetime and within and across seasons.

Predators

Predators are more balanced with their food resources than are primary consumers, as they feed on resources that have a similar stoichiometry to their own body tissues (Fig. 2). As a result, predator AEs tend to be higher (Wallace et al., 1987; Benke and Wallace, 1997). Among predators, egestion rates may be lower than excretion rates due to greater assimilation efficiency of nutrient-rich animal tissues in comparison to primary consumers (Atkinson et al., 2017). Not only do predators have consumptive top-down effects (Woodward and Warren, 2007), but they can also induce indirect top-down effects on prey behaviors and stoichiometry (Rinehart and Hawlena, 2020; Hawlena and Schmitz, 2010). Predators can reduce biomass or alter the movements of primary consumers, potentially modulating the intensity and spatial pattern of primary consumer feeding (Power, 1990; Lundvall et al., 1999). For example, predator chemical cues can influence patterns of algal heterogeneity (McIntosh et al., 2004) and predator-avoidance behaviors may reduce consumer foraging time (Cowan and Peckarsky, 1994; McIntosh et al., 2004). Predation risk can also affect prey nutrient cycling by increasing prey respiration (Bell et al., 2019), therefore increasing C uptake and N and P excretion (Leroux et al., 2012), while other studies have shown predators enhance prey N and P sequestration (Costello and Michel, 2013). These effects have cascading effects on how consumers impact the abundance, species composition, and location of basal resources and how consumers recycle nutrients via their excretion and egestion.

Scaling to the community and ecosystem level

In most streams, ecosystem production is limited by N and/or P, thus the rates and ratios at which organisms store these nutrients and release them in their wastes can alter nutrient dynamics (Fig. 3; Atkinson et al., 2017). For example, animals can directly regulate stream nutrient spiraling by sequestering elements in their body tissues (nutrient storage), releasing them via excretion and

egestion, and translocating them through their movements having direct and indirect impacts to stream ecosystems. ES mass-balance principles allow researchers to scale organismal processes that mediate elemental flux and storage within and among ecosystems—below, we focus on how ES connects animals to community and ecosystem-level processes.

Nutrient storage

Within streams, animals are often a dominant pool of biomass (McIntyre et al., 2008, Atkinson and Vaughn, 2015) and can represent an important ecosystem reservoir of nutrients. ES predicts that animals with a high N (i.e., high body N:P, low body C:N) or P demand (i.e., low body N:P and C:P) for growth and production can retain the high-demand element more efficiently in their tissues. This storage can even result in a shift of nutrient limitation of primary production to the element stored in animal biomass (Knoll et al., 2009). For example, grazing snails can store more N and excrete more P than grazing crayfish (Evans-White et al., 2005), and periphyton in experimental streams stocked with crayfish had greater periphyton C:P and alkaline phosphatase activity, suggesting greater P-limitation than periphyton in streams stocked with snails (Evans-White and Lamberti, 2006). Elements stored in animal biomass can be sequestered until death, when scavengers or microbial decomposition mineralize the stored nutrients. However, high animal biomass does not necessarily mean that animals are a sink for nutrients; rather, whether they are sources or sinks for autotrophs depends on where animals feed vs. release wastes, how their biomass changes over time, and the fate of their stored nutrients after death (Vanni et al., 2013).

Nutrient release

Animal excretion can represent a major source of labile nutrients that alleviates nutrient limitation, but this is context dependent. Several factors influence the supply of nutrients by individual animals, including biomass, temperature, diet, and body stoichiometry (McIntyre et al., 2008; Hopper et al., 2018). At the ecosystem level, animals will be most important when they supply a substantial mass of nutrients relative to other sources, or relative to ecosystem nutrient demand. In particular, aggregated animal biomass is often important at the ecosystem level by generating "hotspots" of nutrient cycling. Many factors also regulate ecosystem-wide nutrient demand such as external supply (e.g., surface or groundwater inputs) and internal recycling pathways (e.g., nutrient remineralization by microbes). Biomass, metabolic rates and the nutrient limitation status of organisms (e.g., primary producers and microbes) can influence ecosystem nutrient demand. Studies relating animal nutrient supply to ecosystem demand allow for broad comparisons of animal-mediated nutrient cycling across ecosystems. Among studies, animals meet a variable proportion of ecosystem nutrient demand; for example, excretion by fish supports anywhere from 5% to over 90% of nutrient demand (McIntyre et al., 2008; Small et al., 2011; Wilson and Xenopoulos, 2011). Mortality also results in nutrient releases (Fig. 3, Flow 5). Nutrient release from carcasses occurs in stages defined by high rates of elemental release from soft tissues occurring within days to weeks (DuBose et al., 2019; Novais et al., 2017; Childress et al., 2014), followed by mechanical breakdown and chemical dissolution of bones and shells (Strayer, 2014; Strayer and Malcom, 2007) that may persist for decades to millennia. Historical accounting of previously abundant animals showed that Alligator Snapping Turtle (*Macrochelys temminckii*) carcasses and spent mussel shells could act as continuous slow-release P sources that contributed nearly 1% to total P in rivers annually from typical mortality (Wenger et al., 2019).

Nutrient subsidies

Animals can move nutrients against potential energy gradients (e.g., upstream, uphill) resulting in subsidies from one aquatic ecosystem type to another (suckers that move nutrients from lakes to streams; Childress et al., 2014). Stream animals move nutrients from aquatic to terrestrial ecosystems during ontogenetic changes, such as insect emergence (Fig. 3, Flow 8; Small et al., 2013) and amphibian metamorphosis (Tiegs et al., 2016; Capps et al., 2015b), and excretion by stream invertebrates such as mussels, which can support riparian macrophyte production (Fig. 4; Lopez et al., 2020). Terrestrial animals also contribute nutrient subsidies through movement into and defecation in streams and carcass decomposition (Subalusky et al., 2015, 2018). Subsidy importance is determined by its quality, quantity, timing, and duration, and the characteristics of the recipient ecosystem (Subalusky and Post, 2019).

Indirect effects of animals

In addition to their direct effects, animals can indirectly affect microbially-mediated nutrient transformations such as primary production, decomposition, and redox conditions (Rugenski et al., 2012; Trentman et al., 2019; Nickerson et al., 2019). For example, herbivores can reduce periphyton C:nutrient and increase nutrient turnover rates by reducing periphyton mat thickness and nutrient diffusion limitation (Evans-White et al., 2005; Hillebrand and Kahlert, 2001). Animals can also indirectly facilitate microbially-controlled nutrient transformations through the release of nutrients and by physically modifying the environment (Moore, 2006; Atkinson et al., 2018). For example, freshwater mussels supply limiting nutrients through their excretion and bioturbation of sediments, resulting in enhanced denitrification rates (Trentman et al., 2019; Hoellein et al., 2017; Nickerson et al., 2019). The indirect roles of organisms on ES in streams merit more attention.

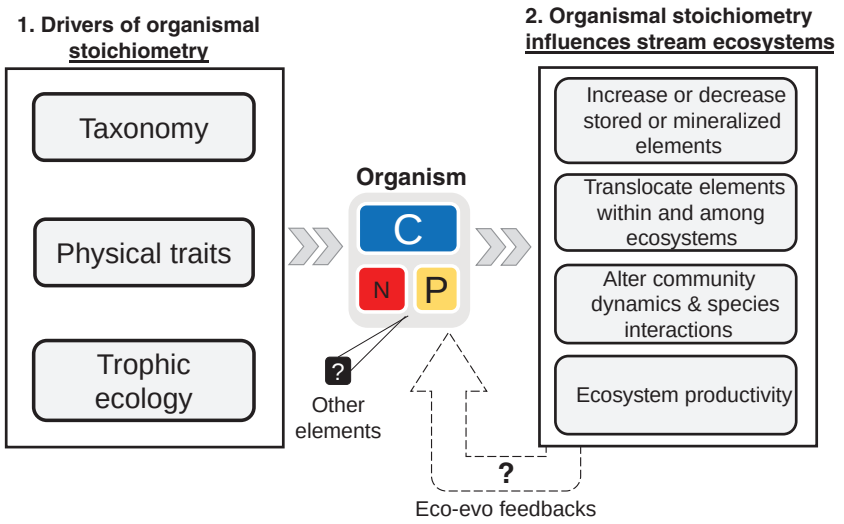

Fig. 4 Conceptual figure illustrating drivers of organismal stoichiometry and the influence of organismal stoichiometry in stream ecosystems. (1) Taxonomy, physical traits, and trophic ecology of an organism interact to govern its stoichiometric composition. (2) Variable stoichiometry of stream organism can increase or decrease local elemental availability, subsidize ecosystems via elemental translocation, alter species interactions that affect community dynamics, and ecosystem productivity through control of elemental availability, and ecosystem productivity. Whether elements beyond C, N, and P in organisms are under the same controls or influence ecosystems and eco-evolution studies in the context of organismal stoichiometry are research areas warranting attention.

Conclusions and moving forward

While we have learned much about ES in streams as reviewed here, there are still many unknowns. Here we conclude by highlighting multiple avenues for future research directions within this topic.

Trait- and organismal-based stoichiometry

Phylogenetic patterns

Broadly, phylogeny explains variance in elemental composition among animals, often indicating important variation at the family level (Allgeier et al., 2020; Vanni et al., 2002; Hendrixson et al., 2007; González et al., 2018). A recent meta-analysis by Andrieux et al. (2020) found a significant phylogenetic signal among taxa across three nested taxonomic levels (classes, orders, and families). This is consistent with the idea that structural and life-history (e.g., development and growth) characteristics are evolutionarily constrained (Fig. 4). However, within-family level analyzes have also found that phylogenetic distance dictates patterns in stoichiometric ratios which may be related to differences in life history strategy (Atkinson et al., 2020). Considering how phylogenetic signal relates to stoichiometry across a broad spatial extent and taxonomic groups warrants future study, as it may help to predict ecosystem-level importance based on taxonomic composition.

Eco-evolutionary dynamics

Stoichiometric traits have been useful for linking organisms to ecosystem processes (Atkinson et al., 2017), but more work is needed to identify consequences of stoichiometric trait variation in eco-evolutionary dynamics (Yamamichi et al., 2015; Leal et al., 2017b). For example, differential nutrient supply may influence gene-expression and life-history trait evolution by altering allocation trade-offs (Elser et al., 2000, 2003). Directional selection on stoichiometric traits may reduce elemental imbalances between a population and its resources or fluctuating selection may maintain stoichiometric trait variation within populations when there is variation in resource quality (Tsoi et al., 2011; Prater et al., 2017). Relating stoichiometric traits to fitness variation (Kay et al., 2005; Frost et al., 2006), organismal adaptation to diet elemental imbalances (El-Sabaawi et al., 2012), and selection pressures to direct or indirect effects in ecosystems (Leitch et al., 2014; Rudman et al., 2019) will be important to understanding the origins of biodiversity and eco-evolutionary consequences of global change, as stoichiometric traits may be useful for studying feedbacks between phenotypic evolution and ecosystem processes (Fig. 4).

Ontogenetic changes

Some organisms undergo substantial changes during development, potentially affecting nutrient fluxes through ontogenetic elemental allocation (Fig. 4). Ontogenetic changes in body content are most evident in vertebrates, where the development of P-rich skeletons results in a substantial increase in whole-body P content (e.g., fishes, reptiles, and amphibians; Tiegs et al., 2016, Sterrett et al., 2015, Pilati and Vanni, 2007). Other elements also can vary ontogenetically. In some species, eggs are rich in lipids and hence C, so whole-body C declines during early stages of development as lipids are metabolized. However, body C may then

increase during subsequent development as individuals store fat (Pilati and Vanni, 2007; Boros et al., 2015). In fishes, body N often declines with age (Boros et al., 2015; Pilati and Vanni, 2007), whereas trends in body N seem more variable across other taxa (e.g., invertebrates: Back and King, 2013; amphibians: Capps et al., 2015b). Ontogenetic changes must be viewed within the context of other drivers affecting body stoichiometry because genotype and environmental factors (especially diet) can interact with ontogeny to drive variation in body stoichiometry (Leal et al., 2017a). Few studies have isolated ontogenetic effects from other factors using controlled experiments.

Elements beyond C, N, and P

While ES has revealed substantial diversity among taxonomic groups and within populations by characterizing C, N and P, ES should encompass other elements (Merchant and Helmann, 2012). Ionomics is a relatively new field that has been used widely to study the complete elemental composition (i.e., ionome) of plants (Lahner et al., 2003; Huang and Salt, 2016) and microbial communities (Merchant and Helmann, 2012), but its utility in aquatic systems has only recently been demonstrated. Recent research highlights both intra-and interspecific ionomic responses of invertebrates and vertebrates to life-history (Goos et al., 2017; Hopper et al., 2021a) and resource stoichiometry gradients (Prater et al., 2020). A recent study of salmon carcass subsidies demonstrated that seasonal spawning runs are sources of micronutrients that may be essential to some freshwater streams (Currier et al., 2020). Because ionomics recognizes the coupling of multiple elements in biological systems, a nutrient balance concept that extends traditional stoichiometric ratios can be useful in generating hierarchical sets of relationships between elements based on prior knowledge (Parent et al., 2013).

Linking diet to nutrient cycling

Because consumer diet stoichiometry can affect consumer nutrient acquisition and growth rates, diet also affects the rates and ratios at which organisms release nutrient wastes into their environment (Elser and Urabe, 1999). Although models predict causal relationships between diet stoichiometry and waste stoichiometry, these models are based on assumptions including strict consumer homeostasis and fixed resource stoichiometry (e.g., no selective feeding). A recent model combines the nutrient requirements and energetic needs of fishes and provides predictions of their ingestion, respiration, excretion and egestion rates (Schiettekatte et al., 2020), and could serve as a means to make predictions for different animal taxa. Controlled feeding studies have generally supported predictions of theoretical models, empirically showing that higher-nutrient diets result in greater nutrient excretion and egestion rates across invertebrate taxa (Evans-White and Halvorson, 2017), and higher N:P diets are associated with higher N:P excretion rates across many fish taxa (Moody et al., 2015). Still, the link between diet and nutrient recycling is less clear from field data, which show mixed relationships between diet and consumer waste stoichiometry (McManamay et al., 2011; Vanni and McIntyre, 2016). To provide more realistic links between diet stoichiometry and nutrient cycling, particularly in the field, future studies must address the role of selective feeding, consumption rates, predation stress, and deviation from strict homeostasis to link diet to consumer waste stoichiometry (Halvorson et al., 2019).

Community and ecosystem level effects

CND relative to demand

The importance of animal-mediated nutrient cycling varies tremendously across systems, and we currently lack the ability to predict when and where animals will be important contributors to nutrient availability. For example, increased external nutrient loading should increase ecosystem nutrient demand and decrease the importance of animals in the short-term. However, depending on if and when animal biomass increases, their increase may render their role more important than in systems with low nutrient inputs. Studies in streams (Wilson and Xenopoulos, 2011) and lakes (Vanni et al., 2006) showed that fish were more important in systems impacted by agriculture than in less impacted systems. This may seem surprising given that agriculturally impacted systems receive more nutrients, but this was driven by higher fish biomass in the watersheds with more agriculture. In contrast, Spooner et al. (2013) found that the importance of excretion by freshwater mussels decreased in watersheds with high agriculture. These conflicting findings could be driven by differences in the population dynamics of the animals being considered. Freshwater unionid mussels are long-lived and their biomass may not increase with nutrient loading as rapidly as fish with much shorter generation times, suggesting that mussel biomass may not yet be in equilibrium with landscape nutrient inputs. In contrast, where animal species with short generation times and/or high reproductive rates dominate, animal biomass may respond more strongly to short-term variation in external nutrient supply. For example, Sharitt et al. (2021) found that excretion by gizzard shad, a dominant fish, supported anywhere from 9% to 53% (mean 31%) of summer phytoplankton P demand over a 15-year period, and most of that variation was driven by fluctuations in young-of-year biomass. Given the difficulties associated with understanding animal population dynamics and the many potential feedbacks (operating on different temporal scales), understanding where and when animals are important in ecosystem-wide nutrient cycling remains a challenging endeavor.

Importance of egestion

Many of the classic studies of CND focused on excretion of dissolved nutrient wastes in terms of the balance of C, N, and P in consumers (Vanni, 2002; McIntyre et al., 2008). Yet, consumers can also produce particulate nutrient wastes (i.e., egestion; Wotton and Malmqvist, 2001). The magnitude and fate of egestion as a nutrient flux remains understudied among many taxa, especially under in situ conditions and within whole-stream nutrient budgets (Halvorson and Atkinson, 2019), because study is still limited

by a lack of standard methods and the extended timeframe required to understand long-term fates compared to excretion (Halvorson et al., 2017). Compared to dissolved wastes, particulate wastes are transported and processed differently, and also vary widely in flux rates and C:N:P ratios (Halvorson et al., 2017; Masese et al., 2020). Further work must address the role of egestion as a cross-ecosystem nutrient flux, such as between terrestrial and aquatic systems (Subalusky et al., 2015; Dutton et al., 2018) and consider the role of animal traits, including phylogeny and feeding mode, in driving variation of the magnitude and fate of egestion (Ramamonjisoa and Natuhara, 2018).

DOM excretion and composition

Much research has highlighted the importance of animals in mediating inorganic N and P cycling; however, limited work has sought to understand animals as sources of dissolved organic matter (DOM) that can support microbial production in the brown food web (Meyer and O'Hop, 1983; Parr et al., 2020). Stream consumers span a continuum of feeding traits (i.e., FFGs) and body elemental compositions, which together dictate the composition of DOM released. For example, DOM fluorescent signatures highlighted differences among FFG in organic matter transformations, showing that predatory insects had distinct labile DOM fluorescent signatures compared with insects feeding at lower trophic positions, which excreted more recalcitrant DOM (Parr et al., 2019). Other work has indicated that DOM release within a single FFG can also vary as shown with filter-feeding bivalves (Hopper et al., 2021b). Further work is needed to fully understand how animal biomass distribution, taxonomic identity, and functional trait composition influence DOM cycling that may link green and brown food webs.

Role of CND in mediating other ecosystem processes

Consumer wastes can likely affect all ecosystem processes which are limited by nutrient availability. However, many processes associated with microbial heterotrophy, such as organic matter decomposition and community respiration, are still poorly understood particularly at the ecosystem level (Atkinson et al., 2017). Consumer wastes stimulate microbial heterotrophs such as bacteria and fungi, facilitating greater microbial respiration and breakdown rates during leaf litter decomposition (Atkinson et al., 2021; Ramamonjisoa and Natuhara, 2018; Rugenski et al., 2012). However, it is still poorly understood whether consumers can shift heterotrophic microbial communities by altering bacterial versus fungal dominance or microbial community structure, both of which are sensitive to background N and P availability (Juvigny-Khenafou et al., 2020; Gulis and Suberkropp, 2003). The stimulatory roles of CND on heterotrophic microbes are also likely counter-balanced by consumer selective feeding on nutrient-rich heterotrophic biomass, particularly consumers feeding on high C:N and C:P detritus such as wood and leaf litter (Chung and Suberkropp, 2008). These CND effects on heterotrophy may scale up to whole-ecosystem heterotrophy, affecting C storage versus mineralization at reach scales, a topic which remains open for further inquiry.

Responses to environmental stressors

Species introductions and species loss

Species introductions and losses can have profound effects on ecosystem structure and function (e.g., Strayer, 2010; Hooper et al., 2012). Declines in native biodiversity in freshwater ecosystems far exceed those in most terrestrial ecosystems, and projections indicate the rate of species decline will increase due to a variety of threats (Strayer and Dudgeon, 2010; Vaughn, 2010). The loss of formerly abundant taxa or a shift in species dominance can alter elemental balances and fluxes (Atkinson et al., 2014; Hopper et al., 2020). For example, a disease-mediated decline of 98% of tadpole biomass in a Neotropical stream resulted in higher algal and detrital biomass and a 50% reduction in N turnover rates (Whiles et al., 2013). Freshwater systems also are plagued by increasing introductions of invasive species that often possess unique structural traits (Capps and Flecker, 2013) or have high processing rates (Strayer, 2009) that can strongly modify the storage and flux of elements (Capps and Flecker, 2013). Collectively, major changes in biomass of stoichiometrically distinct organisms can lead to subsequent changes in the flux and storage of elements in ecosystems (Capps et al., 2015a).

Land use and land cover change

Humans have dramatically altered ecosystems through urbanization and agricultural land uses, which have dramatically impacted loading into streams by enhancing nutrient runoff through the application of fertilizers to lands and by reducing infiltration into soils (Galloway et al., 2003; Steffen et al., 2015; Dodds and Smith, 2016). Stream autotroph biomass generally increases with nutrient enrichment, but detrital resource quantity often decreases due to stimulated decomposition resulting in greater export of fine particles out of the ecosystem (Rosemond et al., 2015; Manning et al., 2016). Algal and detrital C:nutrient ratios tend to decrease with rising nutrient concentrations (Stelzer and Lamberti, 2001; Cross et al., 2005), improving their quality as a food resource. Nutrient enrichment of basal food resources can drive increases in consumption and growth (Evans-White and Halvorson, 2017; Halvorson et al., 2018), body size (Davis et al., 2010), biomass and secondary production (Cross et al., 2006; Demi et al., 2020), and a shift in community stoichiometry to species with lower body C:P, which likely increases nutrient demands (Evans-White et al., 2009; Tsoi et al., 2011; Prater et al., 2015).

Climate change

The reverberations of climate change are resulting in altered ecosystem structure and functioning in freshwaters worldwide (Woodward et al., 2010; Grimm et al., 2013). Aquatic organisms are especially vulnerable to climate-mediated changes because they are ectothermic and confined to aquatic habitats. Current projections suggest changes in species distributions (Heino, 2010;

Markovic et al., 2014) and enhanced metabolic demands (Seebacher et al., 2015) due to rising temperatures. Additionally, rising temperatures in aquatic ecosystems have not only led to general physiological stress (Spooner and Vaughn, 2008; Frenette et al., 2019), but also changes in resource consumption patterns. A recent literature survey found that increased temperatures increased herbivory by multiple freshwater taxa (Zhang et al., 2020). Additionally, enhanced atmospheric CO_2 is predicted to alter C:N:P ratios of basal resources, which could lead to profound shifts in the stoichiometry of elemental fluxes between consumers and resources at the base of the food web (Woodward et al., 2010). For example, leaf litter from trees grown under elevated CO_2 concentrations are of lower quality and support lower production of decomposing bacteria and fungi (Ferreira and Chauvet, 2011) and growth of a detritivorous cranefly in streams (Tuchman et al., 2002). Understanding how stoichiometric relationships in streams may change as a result of these interacting factors resulting from climate change remains a challenge.

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Relevant website

https://ratiosmatter.wordpress.com/contact-2/—Ratios Matter (RM).

Aquatic Food Webs In Rivers

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Attributes Numerical properties of food webs that describe aspects of structure. Examples include food web size (number of species or nodes), connectance (proportion of possible links that occur) and average and maximum food chain lengths.
Environmental flows Managed flows within a river or wetland targeted to producing ecological benefits (Watts et al., 2020).
Food chain A series of trophic linkages which connect consumers and resources.
Food web A representation of trophic linkages between organisms as a compilation of food chains. These may be represented as presence/absence (binary food web) or weighted links (flux food web). Food webs can also be described as trophic networks. Some food web studies also incorporate non-trophic interactions such as competition.
Network A group of points or nodes connected by links or edges. In food web ecology the nodes are generally species or groups of species and the links are trophic connections. Networks can include a diversity of different types of interactions.
Topology The structure of a food web as described using a range of attributes.

Part one: An introduction to riverine food webs

A food web is a representation of interactions between organisms. Elton (1927) (reprinted 2001) coined the term food chain, and termed all the food chains in a community as a food cycle, which we now call a food web. Lindeman (1942) described the food web structure of Cedar Bog Lake in central Minnesota as a representation of flows of energy and nutrients. In so doing he defined the underpinnings of much of modern food web ecology, particularly within the tradition of ecosystem ecology. Originally specifically describing trophic interactions and fluxes of energy, modern food webs can encapsulate a wide range of trophic and non-trophic interactions (Dunne, 2006; Ings et al., 2009; Thompson et al., 2012). More correctly, this new generation of food webs, called 'interaction networks, often include non-trophic interactions including competition, plant-pollinator interactions behavioral interactions among others (see Ings et al., 2009 and references therein).

Food webs allow the visualization of interactions between groups of organisms in order to describe direct and indirect effects and how they may propagate through ecosystems (Fig. 1). Individual species, aggregations of species, or life-stages of species form the

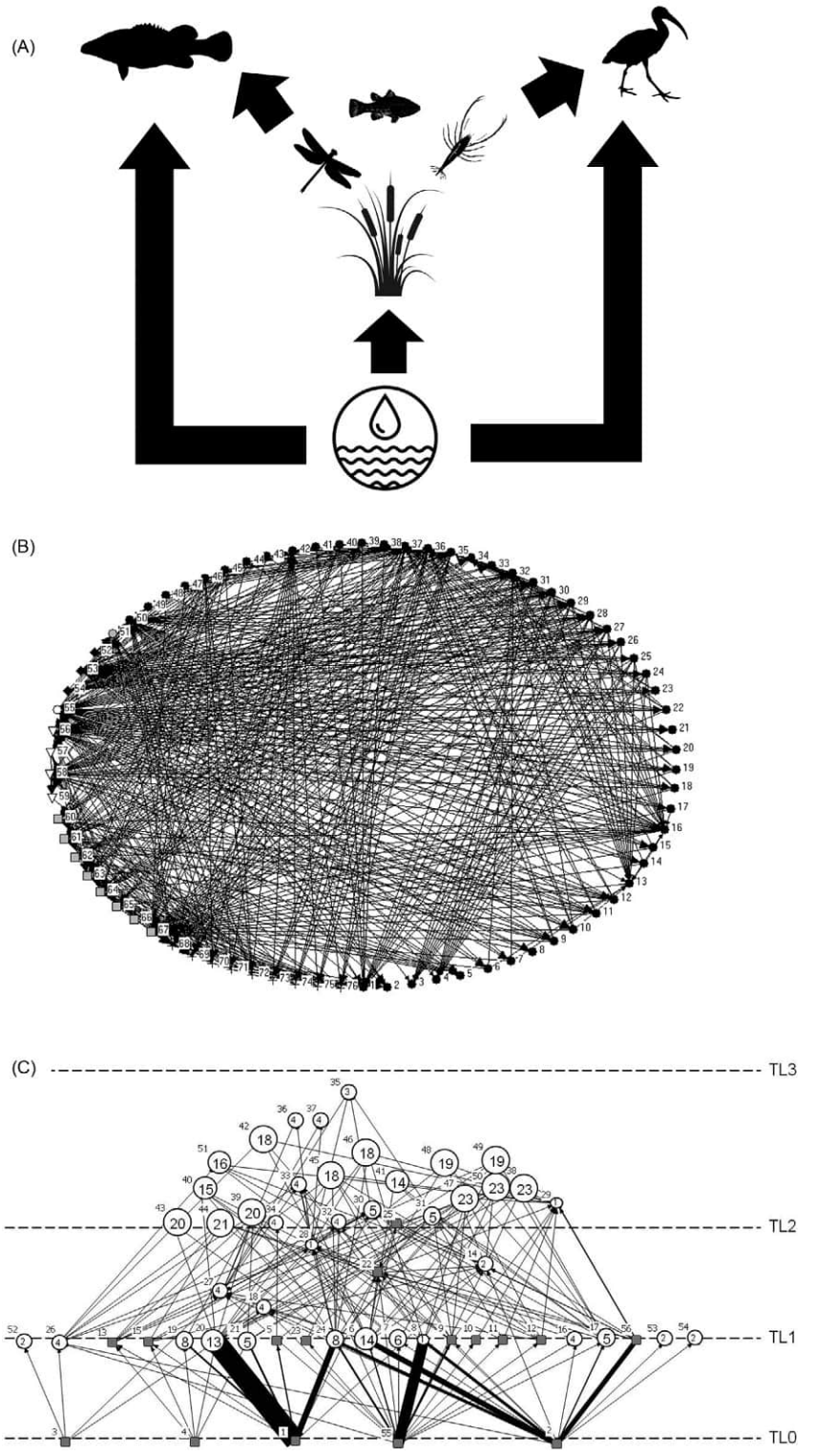

Fig. 1 Different approaches to describing food webs. (A) Simple conceptualization of links between major groups (Pollino et al., 2020). Representations of trophic interactions as (B) binary links and (C) weighted networks of energy flows (Thompson et al., 2005). From (A) Pollino C, Thompson R and Flett D (2020) *Flow-MER Basin-scale Evaluation and Research Plan. Flow-MER Program.* Commonwealth Environmental Water Office (CEWO): Monitoring, Evaluation and Research Program, Department of Agriculture, Water and the Environment, Australia. (B and C) Thompson RM, KN, Mouritsen and Poulin R (2005) Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *Journal of Animal Ecology* 74(1): 77–85.

components (nodes) within the food web and the flows of energy via transfers of live or dead biomass between nodes form the trophic links (edges). At their simplest, food webs allow a conceptualization of the complexity of a real ecosystem and allow development of hypotheses concerning direct and indirect effects of changes on ecosystems (Fig. 1A). Conversion of food webs into binary matrices allows calculation of a range of numeric attributes and application of a range of modelling approaches without the need for exhaustive information on biomass and energy flow (Fig. 1B; see Thompson et al., 2012 for a review). Non-binary energetic food webs include information on the biomass of each node and the magnitude of energy fluxes along trophic links, but they require detailed information and often grouping species into functional groups to make their description tractable (Fig. 1C). Weighted networks can be powerfully applied to generate estimates of biomass yields using simple mass-balance models (see Ings et al., 2009 for a review). These type of energetic food webs can incorporate the data that emerge from stable isotope analyses of diet (e.g., Peterson, 1999) and stoichiometric studies (e.g., Evans-White and Halvorson, 2017).

The analysis and interpretation of the attributes of food webs has been carried out for several decades. The nature and application of food web attributes is beyond the scope of this chapter, but it has been reviewed in detail in recent years (Dunne, 2006; Ings et al., 2009; Thompson et al., 2012). Over time the focus has shifted from seeking generalities in food web structure towards using food web attributes as indicators of ecological condition, as results of evolutionary processes and as predictors of ecosystem dynamics. Development of empirical models has allowed the exploration of a range of predictors of ecosystem dynamics, including niche segregation (Williams et al., 2010), effects of changes in consumer behavior (Kondoh, 2003) and the role of body-size distributions (Brose et al., 2006a,b). Most recently food web approaches have been directed towards understanding applied management issues such as the effects of land-use change (e.g., Thompson and Townsend, 2003), the impacts of invasion (see David et al., 2017 for a review) and management of flows (see Robson et al., 2017).

In rivers, food web studies have taken the full spectrum of approaches. Some of the earliest work on food web energetics was carried out by Allen (1951) who sought the basis for salmonid productivity in streams. Benke and Wallace (1997) played a critical role in revitalizing the energetic perspective on riverine food webs through their secondary productivity work. Long term investigations of food webs in single catchments have provided profound insights into community ecology, particularly with respect to the impacts of disturbance, seasonal variability and consumer impacts (e.g., Power et al., 2008; Cross et al., 2013). Ecosystem ecology has also benefited from the understanding generated by long-term studies of single river systems, particularly work at Hubbard Brook (e.g., Likens and Bormann, 1974) and other US Long Term Ecology Research sites (Kratz et al., 2003). Comparative studies across river systems have been applied to achieve a general understanding of the effects of ecological drivers such as disturbance (e.g., Townsend et al., 1998), changes in top predators (e.g., Romanuk et al., 2006), habitat size (e.g., Sabo et al., 2010; McHugh et al., 2015), and water quality (e.g., Layer et al., 2010). Experimental studies including whole-stream manipulations have been a critical part of understanding the role of cross-ecosystem fluxes of energy and materials (e.g., Wallace et al., 1997). The purpose of this review is to consider the key concepts which form the basis of riverine food web ecology and to extract some of the main insights that have emerged from the field in both a fundamental and an applied sense.

Part two: The conceptual basis for riverine food web research

Freshwater ecology has been characterized as focusing on testing general ecological theory rather than developing novel theory (Thompson and Lake, 2010). Certainly, the way in which the study of riverine food webs has been approached has drawn heavily on existing ecological theory. In part this is because rivers lend themselves to testing some areas of theory due to the nature of the ecosystem. Riverine food web ecology developed in parallel with ecological theory being developed in inter-tidal ecosystems, which share many characteristics including a focus on benthic processes, broadly similar food chain structure (algae-invertebrates-vertebrate consumers), an over-arching effect of physical disturbance and relative openness to fluxes of materials. Early marine community ecology research on keystone species, trophic cascades and disturbance (e.g., Paine, 1966) was particularly influential in guiding food web investigations in freshwater ecology.

Through the 1960s and 1970s studies of riverine food webs occurred in two loose groupings. Studies focusing on fish and fisheries tended to draw heavily on concepts from population biology and ecosystem ecology. This included the development of population models and the later extension of those into bioenergetic and population genetic models (e.g., Frank et al., 2011). Habitat work tended to focus on the requirements for a single species or small groups of species. This line of inquiry developed sets of physical habitat models aimed at optimizing management for fish habitat which ultimately linked to work on bioenergetic costs of habitat occupancy (and to environmental management (e.g., Dunbar et al., 2012; Naiman et al., 2019). Key concepts that have underpinned fisheries-oriented riverine food web studies have been based on bottom-up processes and habitat control of biomass, principles of meta-populations and connectivity, and managing for relative habitat stability.

The second major grouping of riverine food web studies have focused primarily on the invertebrate components. This work has been more heavily based in community ecology, with an initial focus on community composition and functional feeding groups evolving into a more dynamic view of trophic interactions including trophic cascades (Minshall et al., 1985). Habitat work had as a major driver the area of bioassessment, which sought to use primarily invertebrate communities to assess environmental condition and responses to a diverse range of stressors including water quality and channel modification (see Clarke et al., 2003 and references therein). The recognition of disturbance as a key driver in river ecosystems drove a focus on disturbance and succession processes, later extended to larger spatial scales (e.g., Feminella and Resh, 1990). Much less prominent, in part because of the logistic

challenges of such work, were ground-breaking studies of energy flows within river food webs (e.g., Benke and Wallace, 1997). Integrating studies of energetics and community structure became more tractable through the use of stable isotope analysis (e.g., Finlay, 2001; Jepsen and Winemiller, 2002).

Concepts from population biology

Size structure

The analysis of individual traits and population trait-distributions has been a significant part of ecology for decades. The inclusion of species traits as attributes in food webs has emerged as an important advance over the last 20 years, with studies incorporating behavioral traits (e.g., Moran et al., 2017) and trait diversity (Gravel et al., 2016). Among traits, body size has a pivotal position as a fundamental ecological characteristic with implications for trophic role, competitive ability, fitness and habitat occupancy (see Woodward et al., 2005a,b,c; Ings et al., 2009; Brose, 2010 for reviews). In aquatic communities size structure is influenced by a range of ecological drivers including physical and chemical disturbance regimes (e.g., Townsend et al., 1997a,b) and predation regimes (e.g., Layman and Winemiller, 2004). Incorporating body size into descriptions of riverine food webs has provided an increased understanding of the processes that operate to maintain diversity by preventing competitive exclusion and predator-prey interactions leading to the local extinction of prey (e.g., Layman et al., 2005; Woodward et al., 2005a,b,c). There is now clear evidence from river food webs that body size distributions are sensitive to effects of disturbance. For example, resilient species are characterized by short life cycles, rapid growth and high reproductive rates, and are also usually small. Thus altered disturbance regimes can directly influence size distributions (e.g., urbanization; Walsh et al., 2005).

Beyond considerations of body size distributions within populations, ratios between predator size and the average size of their prey (hereafter: body-mass ratios) have been the focus of considerable attention in general ecological theory (e.g., Warren, 2005; Brose et al., 2006a,b). These relationships have been suggested as being important predictors of food web structure, dynamics and stability (Otto et al., 2007). In riverine food webs, allometric scaling relationships have been shown to be altered by the over-arching effects of physical flow, which constrains the form of large consumers (Riede et al., 2011).

Meta-populations and dispersal

Perspectives from population biology provide opportunities to achieve better understanding of food webs. Predator-prey population dynamics can be extended into a food web framework and have been shown to affect food web structure and dynamics (Brose et al., 2006a; Otto et al., 2007). Within populations, differences in the trophic role of reproductive and non-reproductive individuals and differently sized individuals can influence food web structure (e.g., Woodward et al., 2005a,b,c). Population models are widely applied to the management of fish in river ecosystems, particularly for endangered large-bodied, and commercially significant, fish species (e.g., Gouraud et al., 2001). Although fisheries biology began as a science based on relatively simple population models with little consideration of movement between populations, the study of fish movement across riverscapes emerged as a core line of enquiry in riverine food webs through the 1980s and 1990s (e.g., Winemiller and Jepsen, 1998; Humphries et al., 2020). The critical role of connectivity across river networks became integrated into studies of fish population biology and community structure (e.g., Romanuk et al., 2006; Yeakel et al., 2014). Exploring these questions was enabled by the application of tools from remote sensing, population genetics and isotope science (see Lucas and Baras, 2000 for a review). What these studies have revealed is the critical importance of maintaining connectivity across river networks to support populations and riverine food webs (Winemiller and Jepsen, 2004; Liao et al., 2017). A key part of applying this insight to river management has been the development of meta-population models for riverine fisheries that include quantitative assessments of dispersal (e.g., Bellard and Hugueny, 2020). The application of population genetic tools has allowed not only a greater understanding of the role of dispersal in determining food web structure in rivers but also the importance of managing rivers as networks of interacting populations linked by dispersal (e.g., Morán-Ordóñez et al., 2015).

Concepts from community ecology

The habitat templet

Perhaps because of clear sub-habitat divisions (pools, riffles, runs, differences in substrate and flow velocity), riverine ecology through the 1960s and 70s drew heavily on ideas which linked physical habitat to community and food web structure. Southwood (1977) described the concept of the habitat templet, which acts on taxa over evolutionary time to select for traits closely matched to habitat axes. This was formalized for river systems by Townsend and Hildrew (1994). From an initial focus on physical habitat, habitat templets in river systems were expanded to incorporate differences in resources and functional feeding traits (e.g., Compin and Céréghino, 2007) and the effects of disturbance regime and associated traits (e.g., Huryn et al., 2005).

The focus of early riverine ecology on smaller 'wadeable' systems has a legacy which is evident in riverine ecology to this day. There tends to be a focus on patches of habitat and matching between local conditions and local communities. Numerous studies have related community composition and trait distributions to substrate characteristics and hydraulic variables (e.g., Gayraud and Philippe, 2001). Fewer studies have investigated the impacts of these patch-scale differences on food web structure. Power (1992a) showed that patch scale habitat heterogeneity affected food web structure by reducing the feeding efficiency of fish. Power and Dietrich (2002) emphasized the likely importance of connections between patch scale food webs within river systems. Thompson and Townsend (2005) illustrated this with a study of riverine food webs that showed a diversity of patch-scale food webs were

linked by the movements of predators at larger spatial scales. The recognition that movement between patches is a critical process influencing riverine food webs has reduced the emphasis on local habitat associations and led to studies which incorporate much larger scales within a nested and hierarchical understanding of the drivers of local food web structure (Woodward and Hildrew, 2002; Woodward et al., 2005a,b,c).

Trophic cascades and top-down vs bottom-up dynamics

The potential importance of predators in driving patch-scale food web structure brings together concepts of patch dynamics and trophic dynamics in river food webs. Debate over the relative importance of top-down (consumer-controlled) and bottom-up (resource-controlled) processes raged in ecology from the 1970s onward (see Power, 1992b; Matson and Hunter, 1992 for reviews). The most extreme examples of top-down influences, where consumer effects result in alternating positive and negative impacts along food chains have been observed in river food webs as a consequence of fish predation and appear particularly strong and prevalent in freshwater ecosystems (e.g., Brett and Goldman, 1996; Woodward et al., 2008). This may be because riverine food webs are dominated by invertebrate herbivores (Borer et al., 2005) and tend to have a lower proportion of omnivores (Thompson et al., 2007) than other ecosystems.

Studies of top-down and bottom-up influences in river food webs have revealed genuine complexity in these processes through space and time. Fish exclusion experiments in the South Fork Eel River in California, United States showed that the strength and direction of trophic influences varied with substrate type, time since disturbance and inter-annual variability in discharge (Power et al., 2008). Other studies have suggested that nutrient status, water temperature (Su et al., 2021), local hydrology (Strayer et al., 2008) and body size distributions of predators and prey (Detmer and Wahl, 2019) may also affect the strength and duration of trophic cascades in rivers. The modern synthesis suggests that strong top-down and bottom-up influences may be particularly common in rivers, but that those effects are transient in space and time and strongly influenced by a wide range of interacting drivers (Su et al., 2021).

Disturbance

A fundamental feature of riverine ecosystems is flow, flow variability and flow-elated disturbance regimes. Highly variable and/or unpredictable patterns of discharge in rivers act as disturbances with various frequencies and intensities (Poff and Ward, 1989). These disturbances can modify population and community processes and through evolutionary time have selected for traits hat confer resilience (adult mobility, habitat generalism, rapid population rowth) or resistance (clinging behavior, streamlined/ flattened morphology, several terrestrial life stages) (Townsend et al., 1997a). In recent years it has become clear that the effect of river flow on body form has implications for riverine food webs. Riverine ecosystems deviate from general scaling models for body mass and trophic levels, seemingly because flow selects for elongate rather than globular body forms (Riede et al., 2011; Brose et al., 2019). This morphological constraint may contribute to shorter food chains in rivers than in other ecosystems (Brose et al., 2019).

Disturbance is also an important driver of community dynamics in rivers. Studies of river food webs have shown that disturbance may have a role in affecting the outcomes of competitive interactions between species (Wootton et al., 1996; Townsend et al., 1997a,b). Moderate levels of disturbance appear to result in more diverse food webs with longer food chains (Townsend et al., 1997a,b; McHugh et al., 2015; Sabo et al., 2010), consistent with Connell's (1978) Intermediate Disturbance Hypothesis. However, this relationship appears to have complex relationships with other drivers including productivity (Townsend et al., 1998), trophic structure (Wootton, 1998) and the presence of refugia in the landscape (Harvey et al., 2018). Refugia from disturbance can occur at multiple spatial scales ranging from stable patches of substratum to adjacent undisturbed reaches (Sedell et al., 1990; Rempel et al., 1999). Improved understanding of the complex interplay of disturbance with food web dynamics in rivers has led to the concept of the 'Natural Flow Paradigm' (Poff et al., 1997) as a focus of restoration. This has the objective of restoring not only volumes of flow but also the timing and relative magnitude of flow events.

Increasingly it has become clear that local habitat, disturbance and energy supply influence food web structure in streams, with complex interactions in space and time driving the primacy of physical or biological processes (Townsend et al., 1998; Van Looy et al., 2019). The dynamic nature of these processes in space and time creates challenges in understanding how best to restore river food webs and how to detect trend changes because of press disturbances such as land-use alteration and climate change.

Concepts from ecosystem ecology

Bioenergetics

Food webs are fundamentally maps of energy and material flows, and as such might be expected to have close associations with disciplines such as ecophysiology. Intellectually food web ecology has tended to align more with community ecology than individual or population biology, particularly in rivers. There have in recent years been attempts to bring individual and population perspectives into food web ecology. It has been suggested that individual behavior can have profound impacts on food webs via effects on factors including prey selectivity, body size and fitness (e.g., Brose, 2010; Moran et al., 2017). This provides a clear link between evolutionary processes and food web structure, although these relationships remain relatively little explored (but see Valdovinos et al., 2010; Moya-Laraño et al., 2014). Individual variation in behavior and physiology can cascade up to ecosystem processes and can be incorporated into food web models (Stouffer, 2010). There have been relatively few studies at the junction of ecophysiology and food web ecology (but see Gaye-Siessegger et al., 2004 and Chikaraishi et al., 2007 for riverine examples). The fact that both disciplines share the use of energy as a fundamental currency provides rich opportunities for integrating individual level physiological studies into a food web context (Olff et al., 2009).

In marine systems, bioenergetic food web models have been used widely to advise fisheries management (e.g., Pauly et al., 2000). Adoption of these approaches in rivers has been slower, although the EcoPath (Pauly et al., 2000) modelling tool has been applied to investigating fisheries impacts of major impoundments (e.g., Deng et al., 2015). There remains considerable opportunity to use models of this type to bring together population processes and energetics within quantitative food web models (Robson et al., 2017).

Subsidies across ecotones

Across both fisheries-focused and other riverine food web studies, awareness of the importance of connectivity laterally and longitudinally emerged beginning in the 1970s (Likens and Bormann, 1974). This concept was formalized in a number of ways including in the River Continuum Concept (Vannote et al., 1980) and the Flood Pulse Concept (Junk et al., 1989). In rivers floods are important for allowing movement of materials and biota between the channel and the floodplain (Junk et al., 1989; Høberg et al., 2002). These movements can have profound impacts on in-channel food webs in terms of subsidizing productivity, connecting refugial aquatic habitats and providing access to breeding habitat (e.g., Winemiller, 2004). Movement of large mobile predators into the floodplain acts to connect food webs spatially and can provide the stimuli and resources necessary to support fish spawning (e.g., Jiménez-Segura et al., 2010; Humphries et al., 2020). Loss of floodplain connectivity as a consequence of impoundments, water abstraction and flood management has had a significant impact on river food webs globally, including loss of top predators, simplification of local food webs and increased heterogeneity of food web structure across the landscape (e.g., Ward et al., 1999; Jiang et al., 2021).

Work on river subsidies has included quantification of fluxes of carbon from marine systems into rivers and between floodplains and rivers (e.g., Wipfli et al., 2003). Influential experimental studies in the 1990s illustrated the importance of energy flows across the ecotone between rivers and terrestrial ecosystems (e.g., Wallace et al., 1997; Fausch et al., 2002). These showed that subsidies from adjacent ecosystems could profoundly alter food webs; for example, Nakano et al. (1999) was able to show that riparian insect inputs into rivers affected the strength of trophic cascades by providing alternate resources for trout. Other studies have shown the importance of aquatic subsidies in driving the dynamics of terrestrial food webs (e.g., Baxter et al., 2005; Wipfli and Baxter, 2010). The modern perspective of food webs in rivers recognizes that movements of energy and materials laterally and longitudinally are critical drivers of local food web structure and dynamics (Marcarelli et al., 2011).

Meta-communities and landscape processes

The recognition of the importance of the flow of energy within river ecosystems coincided with the emergence of landscape ecology as a discipline. Over recent decades food web ecology and landscape ecology have increasingly merged, as it has become clear that landscape processes (movements of individuals, energy and materials) are critical to local food web structure (Polis et al., 1997; McCann et al., 2005). This perspective has brought together studies of patch dynamics, disturbance ecology, meta-populations and energy subsidies in a spatial framework that recognizes the importance of nested spatial and temporal drivers (Thorp et al., 2006).

Building on concepts from community ecology, meta-community perspectives recognize the role of movement across landscapes in determining community composition and food web structure (Polis et al., 1997). This recognizes the critical role of dispersal in linking food webs spatially. The study of dispersal traits and landscape genetics have emerged as important areas of research endeavors to understand aquatic food web dynamics (e.g., Heino et al., 2015). Connectivity has also become integrated into studies of fish population biology (e.g., Yeakel et al., 2014). Large scale analyses of freshwater communities and food webs have revealed complex interactions with different spatial scales, dispersal traits, habitat variables and landscape position (Thompson and Townsend, 2006; Heino et al., 2015). The complex, nested and hierarchical nature of the relationships between drivers of community structure and food webs in riverine systems requires the adoption of sophisticated statistical approaches to disentangle the effects of different ecological factors (e.g., Thomson et al., 2012).

Novel features of river food webs emerge from the meta-community approach. Firstly, connectivity is a critical feature linking local-scale food web dynamics but is highly directional due to the effects of flow. This creates strong dependencies in lowland rivers on processes occurring upstream (Vannote et al., 1980; Power et al., 2013). Secondly, high frequency of food webs structured by top-down effects means that movement of vertebrate predators (mainly fish, but also birds; Steinmetz et al., 2003) at large spatial scales has important effects on food web dynamics. Movements of fish have been shown to have significant effects on food web structure (e.g., Winemiller and Jepsen, 1998, 2004; Cross et al., 2013). Consequently, river food webs are particularly vulnerable to the effects of dams and dewatering of channels which disrupt both movements of energy and organisms through the river network (e.g., Power et al., 1996; Naiman et al., 2012).

Part three: Three key insights from riverine food web ecology

The importance of a landscape perspective

The artificial silos of scientific disciplines have tended to segregate food web ecologists working on terrestrial and aquatic ecosystems. However cross-ecosystem perspectives have provided important conceptualizations that have driven river science. The River Continuum Concept, developed for North American streams flowing through deciduous forest, was important in recognizing that longitudinal variation in conditions and resource available can be expected to be reflected in food web structure (Vannote et al., 1980). The Flood Pulse Concept (Junk et al., 1989) provided a similar framing for the lateral movement of materials

between floodplains and rivers. Developments of these concepts have described temporal and spatial variability in subsidies of energy from upstream and lateral sources, creating a biogeochemical landscape of 'hot spots and hot moments' (McClain et al., 2003). There is an emerging understanding of the importance of connectivity at a wide range of scales for a wide range of biota and processes in terms of supporting food web structure and function (Vinagre et al., 2011; Liao et al., 2017).

Because of these linkages between rivers and their catchments, river food webs are profoundly influenced by the effects of land use change. The effects of land use change on rivers are both multi-facetted and highly complex, incorporating changes in hydrology, geomorphology, resource supply, impacts of contaminants and impacts of invasive species (e.g., Stets et al., 2020). The proximal effects of riparian land use change on food webs have been described in numerous studies ranging from the impacts of clear-cut forestry (see Wootton, 2012 for a review) to the effects of urbanization (e.g., Calizza et al., 2012). The nature of the effects on food web structure from land use change is strongly driven by the type of physicochemical impacts. Impacts appear to be particularly profound where land use change affects disturbance regimes, sources of productivity and physical habitat. Because rivers integrate the impacts of landscape level changes in landcover, impacts on the lower reaches of large rivers are particularly significant (e.g., Stets et al., 2020).

Food web studies in the 20th Century largely focused on small spatial and temporal scales (McCann et al., 2005) but that has dramatically changed in the last decades, enabled by a range of tools from population genetics, stable isotope chemistry and the geospatial sciences. Spatial coupling of habitats at different scales due to different sizes and dispersal traits of top predators is an important process in food webs generally, but particularly in rivers (e.g., McCann et al., 2005). Species dispersal between patches affects the local and global dynamics of populations with strong effects on food web persistence (Gravel et al., 2011). These results suggest strong feedbacks between local and landscape-scale dynamics that may interactively determine food web topology, species extinctions and ecosystem functioning.

Although many general principles of landscape ecology apply in river systems, connectivity within rivers is distinguished by the effects of directional flow. Accordingly, any point in a river is more likely to be influenced by conditions x distance upstream of that point than it is by conditions the same distance downstream. Although upstream movement of organisms acts to connect food webs in the lower reaches of rivers with those upstream, *net* movement of materials is from upstream to downstream (Wubs et al., 2016) in concert with substantial lateral fluxes (Junk et al., 1989; Nakano et al., 1999). Capture of organic matter from upstream and retention of organic matter are important drivers of local food web structure in rivers (Thorp et al., 2006; Roach, 2013). Features that trap and store organic matter, for example snags and depositional areas, are often hotspots of productivity and diversity (e.g., Benke and Wallace, 1997, 2015; Sheldon and Thoms, 2006). Similarly, adaptations to capture and retain organic matter are a feature of a wide range of riverine biota (e.g., freshwater mussels, filter-feeding caddis flies and crustaceans). Dams and impoundments that disrupt these flows of energy have substantive effects on food web structure in rivers and in some cases adjacent coastal ecosystems (e.g., Sabo et al., 2018; Vinagre et al., 2019).

Disturbance is the norm

Flowing water ecosystems illustrate the critical role of disturbance in shaping food web structure and dynamics. Every part of a river system is either experiencing disturbance or recovering from disturbance all the time. The combined effects of multiple disturbances, and lag and legacy responses to previous disturbances create a spatial and temporal mosaic of successional processes in rivers that is at odds with the traditional equilibrium view of ecosystems (Leitner et al., 2021). Food webs have been proposed as the over-arching framework that generates stability as an emergent property, through generating feedback loops, providing alternate energy pathways to consumers and supporting functional redundancy. Increased food web complexity appears to buffer species from the effects of species loss (Brose et al., 2005) and invasion (Romanuk et al., 2009). Elements of empirical network structure such as niche contiguity (Martinez et al., 2006) and compartmentalization (Stouffer and Bascompte, 2011) do increase dynamic stability beyond that observed in more randomly-structured networks. Adaptive behavior within food webs is likely to be important for stability and persistence by preventing consumers driving resources extinct (Valdovinos et al., 2010). The broadly consistent patterns in body sizes distributions and ratios may also generate stabilizing forces in food web structure (Otto et al., 2007). Allometric scaling relationships are less consistent in river food webs than in other ecosystem types (Riede et al., 2011) and it might be expected that this would mean less dynamic stability.

The persistence of complex, diverse river food webs despite effects of disturbance can be explained by the combined effects of individual species' resistance and resilience traits, consequences of network structure within food webs at a location, and landscape-scale processes of dispersal (Thompson and Williams, 2017; Liao et al., 2017). Of particular concern in an applied context is that a number of stressors have been able to be shown to disrupt these mechanisms. Brose et al. (2005) have shown that nutrient enrichment can result in the loss of keystone species. Fragmentation of habitats can disrupt the landscape processes that would act to 'rescue' species undergoing local extinction events and maintain river-scale biodiversity (e.g., Ru et al., 2020; Wang et al., 2020). In degraded rivers the importance of restoring physical habitat *and* the 'natural' disturbance regimes that maintain physical and ecological processes is now well understood (Poff et al., 1997). However, there are substantive management challenges in recreating these processes in rivers which are dammed, affected by water extraction and subject to regional scale impacts of invasive species, land use change and climate change (Poff, 2018).

The importance of energy as a unifying currency

Food webs provide a framework for combining perspectives from community ecology that largely focus on biodiversity, with those from ecosystem ecology that generally focus on energy flow (Thompson et al., 2012). The literature on biodiversity/ecosystem function relationships has predominantly focused on single trophic levels rather than full food webs (Qiu and Cardinale, 2020). The majority of these studies have occurred in terrestrial ecosystems, although freshwater studies have also contributed insights (Lecerf and Richardson, 2010). More recent studies have explicitly tested relationships between food web structure and ecosystem functioning (O'Connor et al., 2009). Food web approaches emphasize that the relationship between biodiversity and ecosystem function is one of co-dependence, and that the mechanisms underpinning these relationships are crucial to maintaining functioning ecosystems (Thompson et al., 2012).

The new synthesis emerging in riverine food webs uses energy as a common currency that links the river to its catchment, headwaters to lowland reaches and species to one another. The basis for this integration emerges from the early work of Lindeman (1942) and Fisher and Likens (1973) but is now enabled by a suite of new analytical tools. These allow organic matter sources to be identified using stable isotope analysis (e.g., Pingram et al., 2012; Fig. 2) and productivity to be measured in situ using open-channel metabolism (Demars et al., 2015). These measurements can be integrated with high resolution remote sensing data (Piégay et al., 2020) and powerful modelling approaches (e.g., Robson et al., 2017). The emerging ability to tractably track the movement of carbon in all its forms (dissolved, particulate, in organisms) through rivers, across ecotones with terrestrial and marine ecosystems and into and out of the atmosphere presents the immediate potential for virtual models of river systems that allow testing of management scenarios in silico within the next decade.

Part four: Applications of food web ecology to managing rivers

For decades most food web studies were fundamental in focus, with debate as to when, and even if, food web analysis could be applied to real-world problems (e.g., Memmott, 2009). However, the advances conceptually and empirically described in this chapter illustrate that food webs are now a powerful tool to understand, predict, and manage ecosystems experiencing multiple competing demands and environmental perturbations. Conceptually, food webs provide a simple framing of ecological systems that recognizes interdependencies between ecosystem compartments and the potential for indirect effects and feedbacks (Fig. 1A). This need not require an exhaustive description of trophic links or quantification of energy flows to provide a useful tool for integrating multiple sources of data from across river ecosystems into a single framework. When used in an empirical way, food webs can be applied to trace and predict the distribution of contaminants within ecosystems, allowing a better understanding of

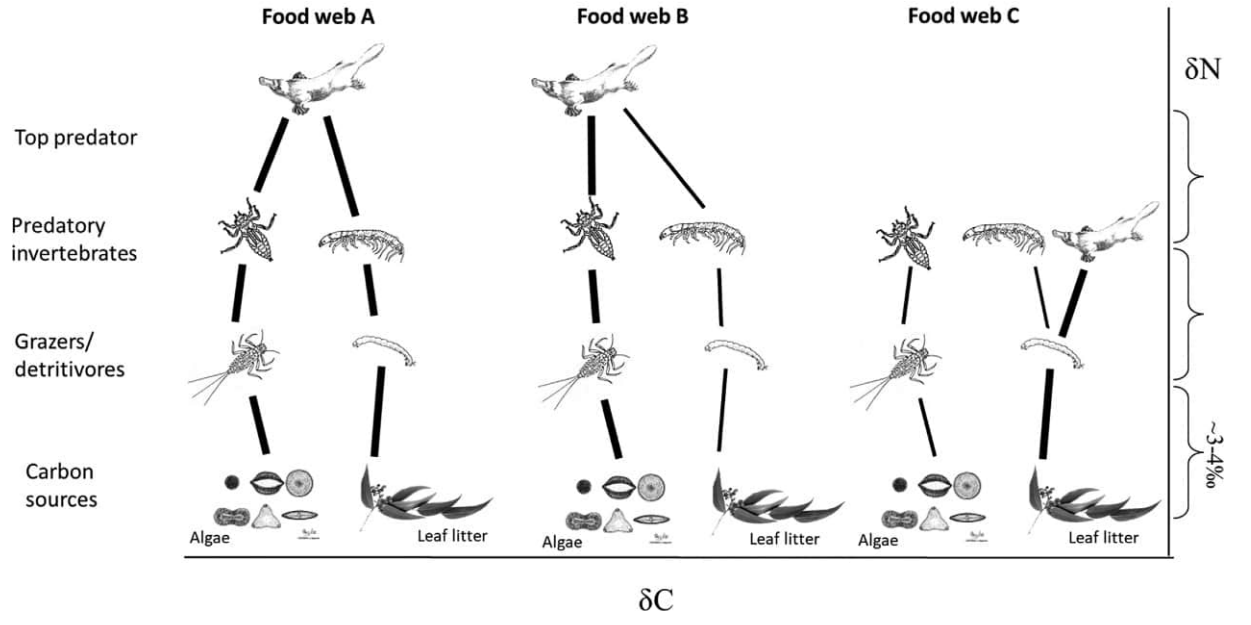

Fig. 2 Simplified representation of the use of stable isotopes to determine the trophic relationships of aquatic organisms. The x-axis shows the ratio between the two stable isotopes of carbon (δC), which differs between carbon sources. The y-axis is the ratio between two stable isotopes of nitrogen (δN). Each time a compound is consumed and excreted this ratio increases by 3–4 parts per thousand. In Food web A the top predator (platypus) has the highest δN value and therefore will be consuming predatory invertebrates. Because the platypus has a δ_C value intermediate between algae and leaf litter, energy is likely to be flowing from both carbon sources along food chains to the platypus. In Food web B the platypus has a δ_C value similar to the value for algae, so most energy is likely to be flowing along the food chain originating with algae. In Food web C the platypus has a δN value similar to that of the predatory invertebrates and a δ_C value similar to leaf litter. The platypus is likely to be directly competing with the predatory invertebrate which is sourcing its energy from the leaf litter-based food chain.

patterns of exposure across species within food webs and public health risk from consumption of fish and other taxa. Advances in dynamic modelling of food webs allow exploration of management scenarios for a range of environmental issues where species invade, go extinct or are harvested. Finally, where systems are being managed for both biodiversity and ecosystem functions, food webs provide a way to bring these perspectives together to guide whole-of-ecosystem management.

Framing a systems approach to river management

Managing small-to-large river basins incorporates a range of complex, interacting networks, including social, economic and ecological. Adopting systems thinking in natural resource management provides a suite of advantages including a refined ability to visualize interdependencies, predict indirect effects and manage for multiple outcomes (Thompson et al., 2019; Jacob et al., 2020). This not only involves treating the biological components of rivers as networks, but also linking food web networks with networks of other drivers. Food web frameworks for combining trophic networks with hydrologic metrics have been developed and applied in rivers already (e.g., Cross et al., 2013; Robson et al., 2017). However, the broader challenge is to link trophic networks into social-ecological systems treating river basins as a bio-geo-physical unit with associated social actors and institutions. Recent reviews have illustrated the ways in which this can be approached, ranging from simple conceptualizations of connections to communicate complexity through to networks of models that can be used in dynamic optimization (e.g., Dee et al., 2016). There is considerable opportunity to learn from marine fisheries management in adopting systems approaches to large river basin development (Jacob et al., 2020).

Multiple stressors and emerging contaminants

The vast majority of the world's river ecosystems are subject to anthropogenic stressors including hydro-electric development, abstraction for irrigation, urban development, water pollution and the multiple interacting impacts of climate change (e.g., Johnson and Penaluna, 2019). Understanding the effects of multiple stressors on rivers and their interactions across spatial and temporal scales is a significant challenge made more complex when those effects occur in food webs (Birk et al., 2020). However, food webs are already showing their utility in terms of predicting which taxa will be affected to what degree by a range of river pollutants (e.g., Liu et al., 2020). The need for an integration of food web ecology and ecotoxicology has been discussed before but an emerging understanding of interactions between networks of stressors and trophic networks is only now emerging (e.g., Gessner and Tlili, 2016; Nilsen et al., 2019).

Invasion and conservation management

The study of riverine food webs also provides a useful framing for understanding the effects of species' invasions and extinctions (Tylianakis et al., 2008). Unpredicted ecosystem-wide consequences of species invasions have been described from numerous systems (e.g., Rezende et al., 2007). The addition or deletion of species alters energy flows in ecosystems, and the degree to which an ecosystem changes will depend upon the network structure and the strengths of these connections. Food web models can be used to predict ecosystem impacts of species additions or deletions, and the vulnerability of food webs to invasion (Romanuk et al., 2009). Understanding the trophic role of invaders allows an assessment of whether they will substitute roles for an equivalent native species or significantly disrupt energy flow to other parts of the food web with the risk of secondary extinctions or altered ecosystem processes (Van Riel et al., 2006). Food web studies of invasions of rivers and streams appear to suggest that impacts are most profound when invaders have novel foraging strategies not present in the receiving community or physiological advantages such as more effective energy acquisition (e.g., Charlebois and Lamberti, 1996; Singh et al., 2013). Similarly, consideration of food webs during restoration activities can provide useful guidance on the order of management interventions and potential unintended consequences (Vander Zanden et al., 2006).

Impacts of flow modification—dams and water abstraction

Most large river systems globally are now heavily impacted by human activities and these pressures will be exacerbated by the effects of climate change (Hanjra and Qureshi, 2010) and increasing river development (Poff and Olden, 2017). Most often, the pace of river basin development has outstripped the ability to impose limits and develop policy to manage these pressures. Because river management involves numerous drivers and often multiple targets, food webs can provide a useful integrating framework. Cross et al. (2013) studied flow restoration in the Colorado River, by describing the full food web including energy flows. Understanding the patterns of energy flow in a food web context allowed determination of the mechanisms that led to increases in trout biomass. In a major environmental flow monitoring program in Australia (www.flow-mer.org.au) links are being sought between flows, patterns of production and respiration and in-channel food webs (Fig. 3). This advances a conceptual framing of relationships (Fig. 1A) to a process-based model that relates flow management to energy flow to top consumers (Fig. 3). Food web approaches are particularly important in studying and mitigating effects of large river impoundments because of the profound impacts that these have on energy flow (Ru et al., 2020).

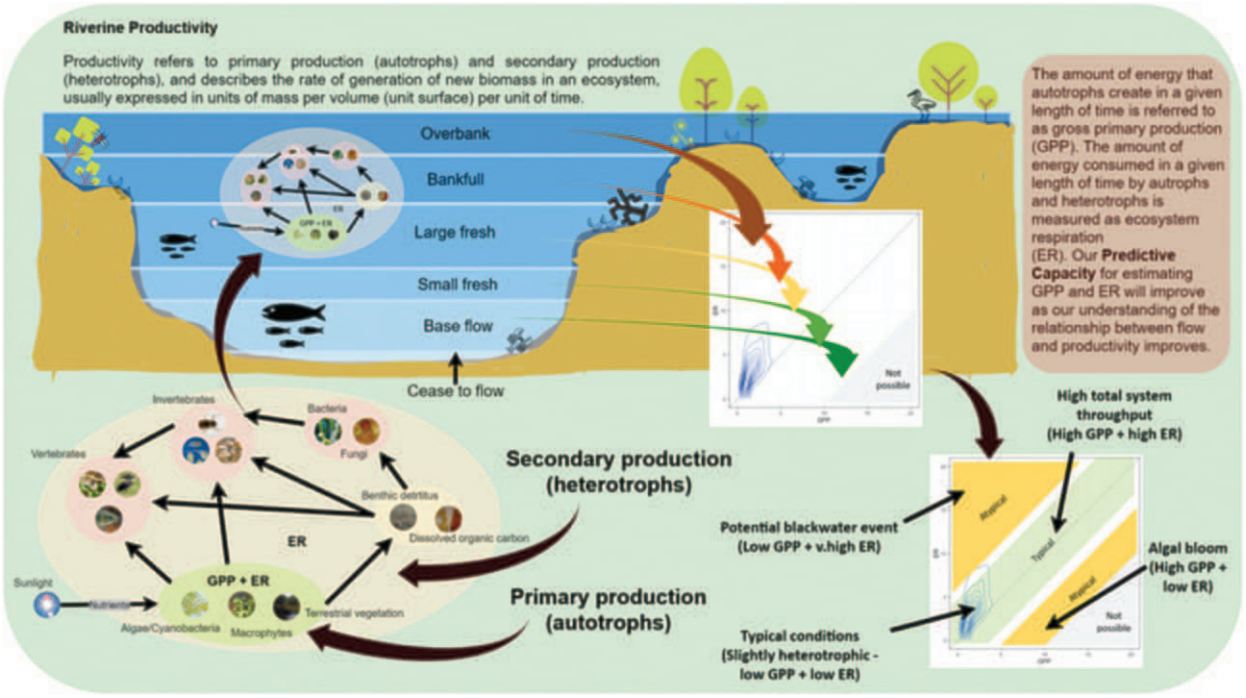

Fig. 3 Representing the effects of water level manipulation on production and respiration in a large floodplain river in southern Australia. A representation of the food web (lower left) links biodiversity to indices of ecosystem functions (bottom right). Figure: Paul McInerney, CSIRO.

Part five: Conclusion

River systems are defined by their connectivity. River food webs provide a framework for the integration of diverse sub-fields of ecology and quantification of links between biodiversity and ecosystem processes. Decades of research on river systems have elucidated drivers of food-web structure and dynamics at scales from the microscopic to the landscape. These clearly indicate the ways in which perturbations in food webs can have direct and indirect impacts that propagate throughout ecosystems. Adopting a food web approach does not necessitate exhaustive description of trophic links. At its simplest, adoption of food web thinking in rivers simply recognizes a set of inter-dependencies that allow predictions of potential knock-on effects of changes. This kind of systems thinking is important for avoiding unintended consequences of management interventions and predicting potential effects of perturbations. In a similar way, recognizing that river food webs are connected at whole-of-landscape scales provides a framework for understanding what stressors may be affecting a location in a river network. The development of food-web and network approaches is making it increasingly feasible to build systems models to test management scenarios via computer models. This scale and sophistication of food-web integration is the future of river management.

Acknowledgments

Particular thanks to the editors for their patience and to two anonymous reviewers for comments that improved the quality of the text. Colleagues in the Flow Monitoring Evaluation and Research, Environmental Watering Knowledge and Research and the Long Term Intervention Monitoring program, particularly Ben Gawne (Alluvium Consulting), Carmel Pollino and Paul McInerney (CSIRO), Fiona Dyer and Darren Giling (University of Canberra) and Darren Ryder (University of New England) greatly contributed through sharing concepts and data.

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Energetics and Food Webs in Large Rivers☆

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This is an update of J.H. Thorp, Models of Ecological Processes in Riverine Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00264-7.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Community ecology Research on the species diversity and functional relationships of multi-species populations within a specified area and time scale.

Endorheic Streams Rivers terminating in a desiccation basin or lake (freshwater or saline) and without ultimate flow to the sea; while these are the most downstream portions of some basins, assigning them a stream order number is misleading because the largest discharge component may be at the terminus or farther upstream, depending on whether the river flows into a lake or disappears by evaporation or into a sinkhole.

Floodscape That portion of a river lateral to the riverscape (main channel and slackwaters); it consists of normally dry floodplains, high elevation wetlands, and lakes/ponds that are inundated periodically by floodwaters.

Food Webs Feeding relationships within a community involving pathways for the transfer of energy and nutrients from primary producers to top carnivores.

Functional Process Zones (FPZs) Sections of all rivers characterized by one of many possible physical (hydrogeomorphic) structures, such as constricted, braided, meandering, and anastomosing channels; biotic diversity and functional processes typically vary in different FPZs.

Large River A vague term describing systems having a stream order greater than six; "great rivers" are large rivers often considered as having a stream order of 11 or greater.

Lotic Ecosystems Streams from small ephemeral headwater creeks to large or great rivers.

Riverscape The wetted portion of a river below the floodscape, including the main channel, side channels, and true backwaters (the latter with no flow-through during low to average river discharge).

Slackwaters Area where water flow rates are low in comparison to those in the middle of the main channel; includes wetted shorelines, embayments, and side channels of rivers.

Stable Isotope Analyses Analytic techniques for tracing elements passing from the abiotic to biotic environment and back; in food web studies the most common approach involves analyses of bulk tissues for the ratio of heavy-to-light carbon (13C vs 12C) and nitrogen (15 N vs 14 N) to determine food source and trophic position from producer to highest carnivore, but a more recent, precise, and expensive technique (e.g., Bowes et al., 2019) involves analyses of the presence or absence of essential amino acids in order to trace food sources (CSIA-AA).

Stream Order A hydrologic and geomorphic term providing vague information on the size of a stream based on the amount of branching occurring in a river basin; the lowest stream order equals "1" and is assigned to a relatively permanent stream that lacks upstream tributaries entering its main channel; the stream order increases by one when two equal sized stream orders join (e.g., two second-order streams produce a third-order stream but a second order plus a first order does not). Ecological process within two streams of the same stream order may vary significantly within the same or different basin.

The physical nature of large rivers and some ecological implications

This encyclopedia article is focused on "large rivers", but what does that term mean and how does the physical nature of a river influence its food web? A colloquial but surprisingly germane definition of such rivers for scientists and the public alike could be:

☆*Change History*: October 2021. James H. Thorp updated the chapter.

"One that is big enough to intimidate!" - perhaps reflecting the width, depth, physical complexity, high current velocity, and potential danger of these rivers. From a tributary junction perspective, a large river requires a stream order of at least 7 but may reach 12–14, depending on how you count the order of headwater streams (which altogether can constitute 80% of the river's total length). For example, the Mississippi has a stream order of 10–12 and the Amazon 12–14. Determining which rivers in the world are the largest depends on the metric you use and which reference you consult and for what time span, but for comparative sake the following is roughly correct: (a) the Nile (6695 km) and Amazon (6400 km) are the longest rivers (compared to the Missouri-Mississippi at 5971 km); (b) the Congo is the deepest river at its mouth (220 m); and (c) the Congo (41,000 cubic meters per second) and Amazon (209,000 cubic meters per second) and have the greatest annual discharge.

Large rivers are extremely powerful and typically deep, but their flow can be visually deceptive because of their relatively laminar flow nature when compared to the obvious turbulence of water flow in many low to mid-order streams. Their power becomes evident when something obstructs their path or you try to move upstream against the flow . . . and especially when the river breaks through a levee and sweeps away human-built structures. The proverb "still waters run deep" (apparently of Latin origin) succinctly describes the relationship between flow and depth in these massive rivers.

Generally speaking, all streams (headwaters up to the largest rivers) flood periodically. The ecological impacts of a flood are strongly related its spatial extent, duration, seasonality, and temporal predictability. Headwater streams are subject to rapid, more ephemeral, less predictable, and sometimes dangerous fluctuations in discharge, especially in confined canyons. In contrast, floods in large rivers can generally be predicted many days in advance and the rate of increase and decrease in discharge is far slower. Humans are often more cognizant of the effects of flooding in large rivers, however, because their flood waters spread farther laterally and typically cause more damage to human structures, especially those built close to levees if flood waters break through them. The seasonal timing of a river's flood, its temporal length, and the change in discharge vary greatly latitudinally (maximum in tropical latitudes) and with the primary source of flood waters (e.g., seasonal snow melt vs monsoons vs unpredictable rainfall).

The long-term temporal pattern and extent of flooding have significant influence on ecological patterns and biotic processes occurring in the riverscape and floodscape. If an annual flood occurs consistently by season and predictably lasts for long periods (e.g., in the Amazon River), then natural selection may favor species adapted in diet preferences, growth, and reproduction to an inundated floodscape. In contrast, an early spring flood in many temperate zone rivers (e.g., the Mississippi) that usually lasts for only a few weeks and occurs outside periods of maximum algal productivity and animal growth rates will likely have a minor selective effect on community composition and reproductive patterns compared to floods lasting for many months and regularly occurring during periods of maximum animal growth and reproduction.

Large rivers carry an enormous amount of sediment derived from tributaries, and thus are generally highly turbid, though exceptions occur such as the cobble-bottomed Yellowstone River in the northern USA and the Eg River in northern Mongolia. Consequently, the photic zone of these rivers is shallow; therefore, light typically does not reach the bottom of the river in the main channel of most large rivers except nearshore. As a consequence, primary production is often substantially depressed in most areas of the main channel. The downstream helical flow of the river also carries phytoplankton below the photic zone on a regular basis (see later discussion on river primary production). Another consequence of this sediment load is that the bottom substrate in the main channel of most large rivers tends to be sand or gravel (see later contrasts with side channels). From an ecological perspective, this low physical complexity results in a very limited diversity of niches for zoobenthos except near shore and in slackwaters. As a result, sediment-dwelling dipteran larvae (e.g., midges) and suspension-feeding bivalved mollusks often dominate the zoobenthos in much of the main channel (other than along the shores).

In contrast to the low habitat diversity in most of the main channel, the slow moving slackwaters of the main and side channels of the riverscape may contain a substrate diversity comparable in many ways to that present farther upstream. In particular, wood snags often dominate these areas in the form of whole tree trunks (especially after floods), branches, and roots from the riparian trees. Such areas provide vital hard substrates for invertebrates and hiding places for small through large fishes and other vertebrates. In addition to tree snags in these lateral areas, large rivers also may be characterized by extensive growths of macrophytes near shore, such as wild celery (*Vallisneria americana*), which provide protective habitat for small fish and invertebrates while also slowing the water currents. In navigable rivers of many countries in Europe and North America, these vital wood snags have been largely eliminated, at least from the main channel (initially for passage of paddlewheel steamboats in the mid-1800s), while at the same time access by fish to side channels and inundated floodplain habitat have been impeded by weirs and/or levees. The result of these government policies that were designed to support boat/barge navigation and flood control was a major reduction in habitat diversity of large river systems with subsequent severe ecological alteration. This can be seen from a century of changes in the Upper Mississippi River, as shown in Fig. 1.

From a more macro-perspective, the channels of rivers are not characterized by a simple increase in width from upstream to downstream, as often portrayed in classical theories from the last century and even today in many general ecology textbooks. Instead, they are often a mosaic formed by different hydrogeomorphic reaches that may vary throughout their length from a constrained or meandering channel all the way to multi-channel sections characterized by braiding, anastomosing, or even more permanent anabranching channels (Fig. 1). The different hydrogeomorphic areas ecologically form functional process zones (FPZs), which can support major differences in fauna and ecological processes. The most terminal point of a river that enters the often consists of multiple channels, but may instead be represented by other hydrogeomorphic forms, including by a constrained channel in more mountainous regions. Although floodplains may be more common downstream with a decline in a river's gradient, they can also be found in other low gradient sections of a river including within headwater regions.

Potential knowledge of large river ecology in the absence of anthropogenic disturbances is substantially limited by the extensive physical modifications of most large, temperate-zone rivers where the majority of river ecologists conduct their research (principally

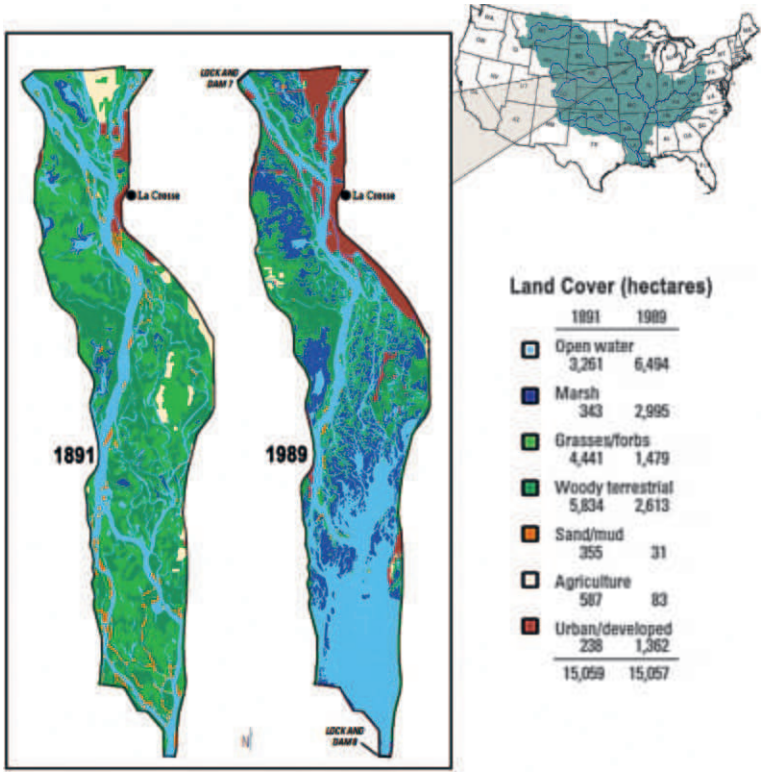

Fig. 1 Shown here are land cover and land use maps of the Mississippi River at Pool 8, located near La Crosse, Wisconsin, USA (GIS data from USGS.gov) showing the extensive decrease in slackwaters of this large river over time. The 1891 map provides a look at the river prior to the development of the lock and dam system in the 1930s. The 1989 map displays the significant changes impoundment of the river introduced into the system. This figure was copied verbatim from Bowes et al. (2019), and all data were obtained from: https://www2.usgs.gov/science/cite-view.php?cite=1587, and https://www.umesc.usgs.gov/data_library/land_cover_use/land_cover_use_data.html.

in Australia, Europe, and North America). Less modified rivers typically occur in tropical to sub-tropical regions of Africa, Asia, and South America. The presence of impoundments and levees has sometimes inadvertently led to misunderstanding about the importance of a river's hydrogeomorphic structure on ecological patterns and processes (see the next section). In particular, the relatively few studies of the importance of hydrologic connectivity and interactions laterally from the main channel to both slackwater areas of the riverscape and the floodscape have contributed most extensively to misunderstandings about large river ecology.

Energetics and food webs

To understand the nature of energetics and food webs in large rivers, at least five basic components of the system must be understood: (1) the physical structure of rivers as it may influence the metabolism, biomass, and growth rates of producers and consumers; (2) the types and proportions of functional feeding groups (consumer feeding guilds) in various habitats; (3) the composition and relative concentrations of organic materials derived from allochthonous (terrestrial in this case) and autochthonous (local and upstream aquatic) sources; (4) environmental and enzymatic limitations to the production, uptake, and transformation of these materials; and (5) seasonality of food web processes. For the sake of space in this article, the following discussion will partially focus on food webs located in one of the most physically complex, functional process zones, i.e., those with anastomosing channels.

Complex FPZs: An anastomosing FPZ (e.g., Williams et al., 2013) has a riverscape consisting of the main channel (the area with the highest flow rates, except for its low flow areas near shore) along with one or often more side channels, and sometimes one or more true backwaters (strictly speaking, those areas where through-flow occurs only during higher river stages). In comparison to main channel habitats, these lateral slackwater areas as a group are characterized by more substantial interactions of organisms with the riparian zone and significantly higher aquatic primary production as a result of slower current velocities, shallower depths, and generally low turbidity, thereby allowing a greater depth of sunlight penetration. All other FPZs - with the possible exception of

those with temporarily disconnected, anabranching channels - are likely to have lower densities and diversities of vertebrates and invertebrates as well as less complex food webs with a lower maximum trophic position (food chain length).

Aquatic Organisms: The freshwater faunas in slackwater areas of the riverscape (main channel border and side channels) - in contrast to high flow areas of the riverscape - are more likely to resemble those present in mid-sized rivers (orders 4–6) than they will to fauna in the higher flow areas of the main channel. This almost certainly reflects the combined effects of diversity in current velocities, turbidities, available benthic substrates, and food resource abundance and composition. This is true for bony fishes (and cartilaginous species in some parts of the world), other vertebrates (amphibians, reptiles, and a few mammals), aquatic insects, other benthic invertebrates, and zooplankton. While the dominant zoobenthos in higher flow areas of the main channel of large rivers primarily consists of animals that burrow into the soft substrate (e.g., Diptera such as chironomid midges along with patches of native unionid mussels and the invasive Asian clam *Corbicula* in some continents), one can find snails, small crustaceans, insects and other invertebrates along the shoreline of the main channel (especially in areas with abundant wood snags), though not in as great abundance or diversity as in lateral channels of the riverscape.

Among the most significant differences between fauna in main channel habitats (headwaters to large rivers) and lateral slackwaters (in mostly mid-order to large rivers) are the abundance and diversity of zooplankton. One common misconception among some aquatic ecologists is that freshwater zooplankton are not native to rivers and instead are merely recent and continuous immigrants from human-constructed reservoirs. From a conceptual perspective, this ignores the fact that rivers on many continents are typically more ancient than lakes (many natural lakes in Europe and North America are derived from relatively recent glacial scouring and lake formation). Moreover, one of the most ancient and signature species in large rivers of the Mississippi River Basin is the large paddlefish, *Polyodon spatula*, which as adults feeds primarily on river zooplankton (a related zooplanktivorous species, *Psephurus gladius*, may still survive in some areas of the Yangtze River of China)! The greatest diversity and abundance by far of lotic crustacean and rotifer zooplankton species occur in the lateral channels of anastomosing rivers where they primarily consume phytoplankton, some bacteria, and other zooplankton. Consequently, these zooplankton play important roles in secondary production of fishes, nutrient cycling, and funneling nutrients from the plankton to the benthos and transfer of some nutrients from slackwaters to the main channel.

Food Sources: Five potential sources of organic carbon contribute in varying degrees to food webs in lotic systems (as listed in random order): (1) mostly recalcitrant carbon derived from upstream organic processing; (2) allochthonous, terrestrially-derived carbon from the local riparian zone; (3) methane-derived carbon from the anaerobic riverscape bottom; (4) autochthonous carbon from benthic algae, phytoplankton, and some macrophyes in mostly slackwater and true backwater habitats of the riverscape; and (5) allochthonous carbon from the floodscape during flood events. These sources vary substantially in their seasonal abundance potential nutritive value, and how easily they can be obtained, chemically transformed - and most especially - assimilated into consumer tissues. Carbon derived from terrestrial habitats (floodscape and the upstream and local riparian zones) is usually far more structurally recalcitrant and thus more difficult to digest efficiently than are the chemically simple, labile organic compounds produced locally by eukaryotic algae. Consequently, in per unit carbon consumed, recalcitrant carbon does not lead to equivalent growth rates by consumers unless it has been colonized and transformed by prokaryotes into more labile and nutritious forms. Methane derived carbon must be transformed from a gas by specialized methanotrophs (e.g., methane-oxidizing bacteria) into a usable biochemical form before it enters metazoan food pathways. While the study of methane in lotic food webs is in its infancy, its overall contribution to eukaryotic food webs is probably minimal in most lotic habitats because it usually requires anoxic conditions. Its greatest importance is likely restricted to slow moving side channels and especially true backwaters where dissolved oxygen is depleted from bottom water and sediments for much of the year.

In contrast, stable isotope studies using either bulk-tissue analysis or compound specific stable isotope analysis with amino acids (CSIA-AA) (see description of both techniques in Arsenault et al., 2021a) have overwhelmingly demonstrated the primary importance of algae as the primary base of the food webs in most rivers with quasi-natural flow (i.e., without high dams or levees that eliminate access to slackwaters or other off-channel aquatic habitats). This has been recently demonstrated for both headwater (Fig. 2; Arsenault et al., 2021b) and large river food webs (e.g., Thorp and Bowes, 2017).

One caveat to this conclusion is related to potential contributions of allochthonous organic matter from the floodscape to the river metazoan foodweb. A prominent conceptual model (Junk et al., 1989) argued for the importance of terrestrially derived carbon from floodplains of the Amazon River as a subsidy to the main channel food web. Conclusions from that theoretical study, however, are questionable even for the Amazon because the role of floodplain algae (phytoplankton and attached algae) as a food source was not considered (nor were potentially crucial isotope data collected in that early study). In tropical floodplain rivers, the length of inundation of the floodscape is often long (months), the seasonal timing and flood length are relatively predictable, and the floods coincide with periods of high secondary productivity and reproduction of aquatic animals. In contrast, floods in temperate zone rivers, even if seasonally predictable (often during spring snow-melt), are typically short-lived (on the order of weeks rather than many months) and often not aligned with periods of maximum secondary production. Consequently, the contribution of floodscape carbon to metazoan production in temperate zone rivers is almost certainly significantly reduced in comparison to tropical floodplain rivers, although it may be important in sustaining populations through non-reproductive and largely growth-neutral periods. Note, however, that the largely recalcitrant carbon from the floodscape probably contributes substantially to carbon flow and system metabolism via the microbial-viral loop. This organic energy probably also enters the metazoan food web in both the inundated floodplains and the usually flooded riverscape via uptake first by heterotrophic microorganisms like protozoa and rotifers which are then consumed by crustacean zooplankton as part of a microbial-viral component of aquatic food webs.

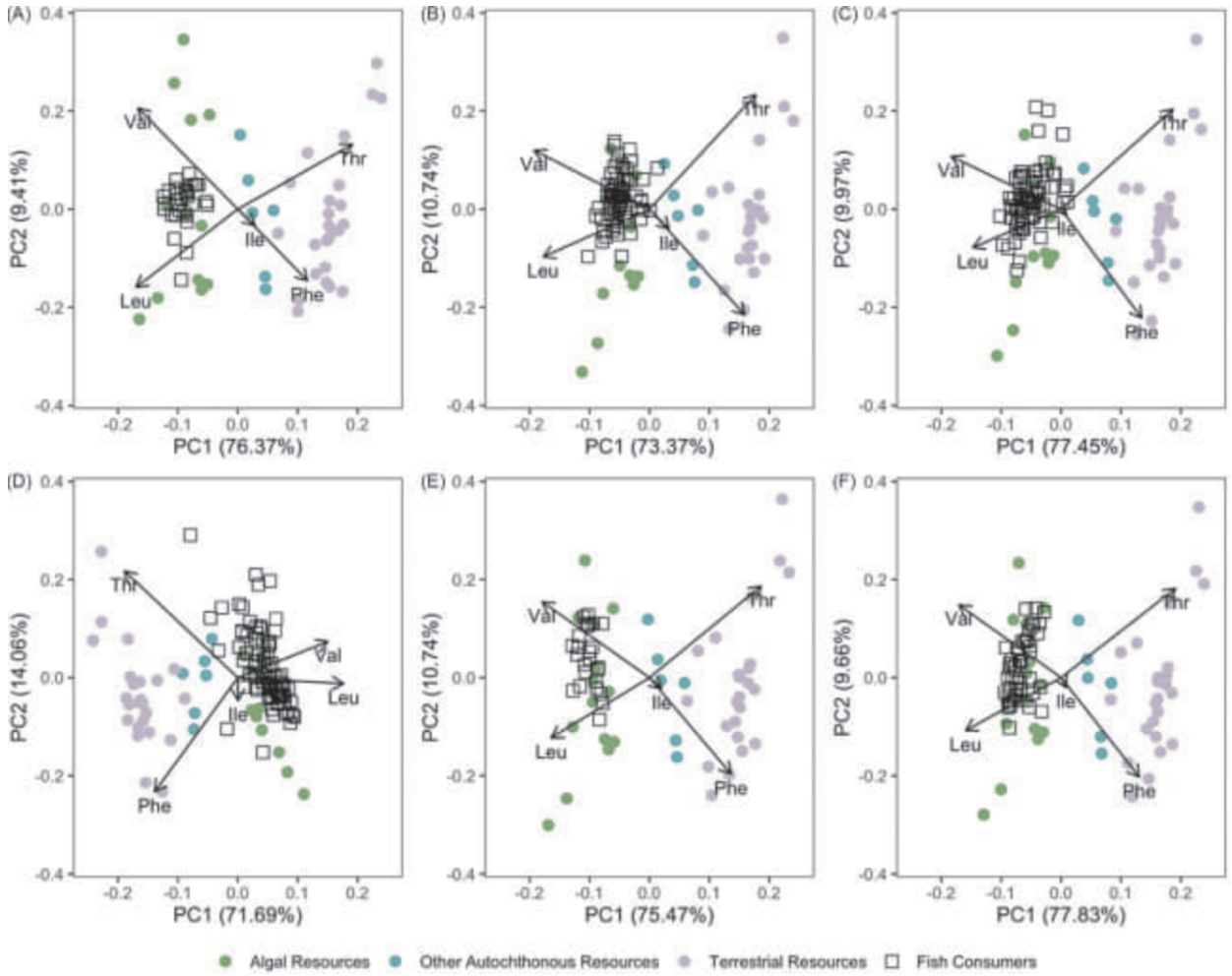

Fig. 2 Original graph from Arsenault et al., (in review): Principal component analysis showing normalized δ13CAA profiles of essential amino acids isoleucine (Ile), leucine (Leu), phenylalanine (Phe), threonine (Thr), and valine (Val) for six ecoregional types in two countries (A = United States grassland, B = United States mountain steppe, C = United States semi-arid terminal basin, D = Mongolia grassland, E = Mongolia mountain steppe, and F = Mongolia semi-arid terminal basin). Solid points represent potential basal carbon resources for freshwater systems, categorized as algal, other autochthonous, and terrestrial, and fish consumers collected in each ecoregion are represented by open boxes. Overlap between sources and consumers indicates likely basal dietary contribution.

Conclusion/synthesis

The physical structure of large rivers (stream orders seven and above) varies from single constricted channels to multiple anastomosing and anabranching channels, and these hydrogeomorphic structures have substantial effects on the abundance and diversity of metazoan organisms and food web processes in natural rivers (those where levees have not eliminated vital lateral channels). Rivers with abundant side channels typically have a higher overall species diversity and secondary productivity than other types of rivers present in similar ecoregions. The vertebrate, benthic invertebrate, and planktonic fauna present in slackwaters of anastomosing rivers are often more typical of mid-order rivers than they are of the main channel fauna of the contiguous large river.

A common misconception about large rivers is that zooplankton are naturally rare and perhaps even refugees from reservoirs, when in fact they are naturally abundant in side channels and backwaters where they provide food for both aquatic fauna and migrating waterfowl; and in some rivers, they energetically support large, ancient planktivorous vertebrates like riverine paddlefish.

The metazoan fauna of large rivers are principally supported energetically at the base of the food web by autochthonous sources (primarily algae), but overall carbon metabolism in rivers is heavily fueled by recalcitrant carbon processed in the microbial-viral loop. Terrestrially derived carbon from immersed floodplains can be important along with algae when the flood period is long, predictable in length, and coincident with periods of maximum secondary production and reproduction of resident aquatic animals.

Knowledge gaps

- What is the relationship between the timing (vis-a-vis growth and reproduction) and length of annual floods to the relative importance of autochthonous and allochthonous carbon sources for secondary production and species diversity in large rivers?
- How significant is the role of methane in carbon cycling and food webs in rivers and what factors influence its role?
- To what degree are latitudinal and ecoregional differences in the location of rivers critical for food web processes?
- How are energetics, food web structure, and community composition influenced by the hydrogeomorphic structure of rivers?
- What role does the hydrogeomorphic structure of rivers play in the transformation of recalcitrant to labile carbon and its subsequent incorporation into metazoan food webs?
- How important are energy subsidies from adjacent terrestrial zone to riverine food webs?
- What is the relative importance of autochthonous and allochthonous carbon to rivers through two metabolic food web pathways, one founded primarily on algae and a large metazoan component and the other based mostly on terrestrial carbon and a bacteria-dominated, microbial-viral loop?

Acknowledgments

The author appreciates insightful critiques of an earlier draft of this manuscript by Drs. F. Andrew Casper and Clifford A. Ochs. Production of this manuscript was aided by NSF research grants to study lotic and lentic systems in the USA and Mongolia (NSF 1442595 and 1926596).

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Ecological and Evolutionary Consequences of Disturbance in Freshwater Ecosystems

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Alpha and beta diversity Alpha diversity describes local richness (e.g., of macroinvertebrates) while beta diversity describes the turnover in species between locations.

Disturbance driver versus disturbance impact A *disturbance driver* is a 'force, either biotic or abiotic, that generates a deviation from the local, prevailing background conditions', whereas a *disturbance impact* 'represents the social-ecological consequences of a driver relative to a scale-dependent baseline state' (sensu Graham et al., 2021).

Life history Evolutionary adaptations relating to survival and reproduction that determine persistence in an environment, including traits associated with timing of reproduction, number of offspring, or lifespan.

Metacommunity Local communities linked at landscape scales by dispersal of potentially interacting species.

Pulse, ramp and press disturbances In *pulse* disturbances the driver is typically shorter and intense, whereas in a *press* disturbance, the driver may start suddenly but a consistent level is maintained over a longer period (Lake, 2000).

Refuges versus refugia Both terms are used to refer to habitats that convey spatial and temporal resistance and/or resilience to populations affected by disturbances, however 'refuges' operate on shorter timescales of minutes to decades, so reflect ecological processes, whereas 'refugium' (plural: 'refugia') are based on longer evolutionary timescales (i.e., millennia) (Davis et al., 2013).

Resilience The capacity to recover from the disturbance even though the biota and ecological processes have been diminished (sensu Lake, 2013).

Resistance The capacity of ecological entities to withstand the disturbance (sensu Lake, 2013).

 https://doi.org/10.1016/B978-0-12-819166-8.00144-4

Introduction

Disturbances have far-reaching and pervasive influences on rivers, where floods have been regarded as principal structuring forces on populations and communities (Death, 2010). However, more recently, the roles of drought and drying-related disturbances on rivers have been brought into focus, with very large amounts of stream length world-wide thought to be intermittent and with similarly far-reaching consequences for stream inhabitants (Leigh and Datry, 2017). Many human influences have also come to be regarded as disturbances, with similarly profound consequences for river ecosystems. In understanding the breadth of ecological and evolutionary consequences of the broad range of disturbances affecting freshwater ecosystems, appreciating the characteristics of the disturbance drivers helps explain their subsequent impacts on biota. Thus, we first describe and define disturbance in freshwater ecosystems, before outlining the types of ecological and evolutionary consequences.

Even though knowledge of disturbance underpins our fundamental understanding of freshwater ecosystems, ecologists have not always agreed about how to define it. To meet global-change challenges an interoperable understanding of disturbance in freshwaters is useful (Graham et al., 2021), so we introduce a generally-based framework for understanding both disturbance *drivers* and disturbance *impacts*, and highlight the dimensions they can take. We include human-driven as well as natural influences.

The impacts of disturbance are pervasive across levels of biological organization in freshwaters, so we organize our summary across those levels, from organismal traits, to population responses, to community-level effects, and finally to food webs. These consequences have high relevance for freshwater futures because disturbance drivers linked to global change processes are set to become more influential as climate warming takes hold. This is because the disturbance regimes freshwater systems experience now will likely not be what they experience in the future (Tonkin et al., 2019). Thus, we conclude by framing the challenges of predicting and managing the influences of disturbance in response to the large range of global changes affecting freshwaters, but especially those driven by climate change. All river taxa are impacted by disturbance (algae, insects, fish, plants), but we will focus mostly on insect examples here.

The dimensions of freshwater disturbance

A definition of disturbance

Even though disturbances are fundamentally important for understanding virtually any aspect of freshwater systems, our grasp of them has been hampered by inconsistent terminology. That 'disturbance' can refer to both the physical alterations that change ecosystems and the consequences of those events is particularly confusing (Graham et al., 2021). Thus, separating biological or other responses, from their drivers is critical for defining aspects of disturbance (Death, 2010).

Following emphasis on physical removal processes, early definitions sought to characterize disturbance in terms of the removal of organisms associated with specific physical events. For example, a disturbance in a stream could be 'any relatively discrete event in time that removes organisms and opens up space which can be colonized by individuals of the same or different species' (Townsend, 1989). Around this time, Resh et al. (1988) suggested that predictable events, like high discharges due to spring snowmelt runoff, might not be disturbances since organismal life histories were geared to cope, and communities showed relatively little change in response. On the other hand, Poff (1992) argued focus should be on when habitat was disrupted and any tautological linking of disturbance occurrence with impact should be avoided. These debates certainly fueled awareness of the multiple dimensions of freshwater disturbances, and the need to separate disturbance drivers from their impacts, but they did not regard human influences as disturbances.

More recently, human influences on freshwater systems have also been characterized as disturbances. For example, Collier and Quinn (2003) describe deforestation and conversion to pasture, which alters wood and leaf-litter inputs, channel shapes, temperatures, nutrient inputs and flow regimes, as a disturbance. Similarly, a synthesis of the urban stream syndrome describes urban streams as disturbed because their physical conditions are degraded relative to those not affected by urbanization (Booth et al., 2016). Managers have embraced this view as a way to frame and communicate human impacts on freshwater systems, even though it does not fit with Townsend's (1989) definition above. Many would see human influences as stressors and would prefer to label more discrete events as disturbances. Moreover, because disturbance is an integral part of maintaining freshwater biodiversity (Bunn and Arthington, 2002), it's important that we do not necessarily associate a disturbed system as being in any way generally unhealthy. Nevertheless, the many uses across freshwater science, and the clear human influence on most disturbances regarded as natural, mean a definition reflecting the diversity of use is essential.

Recognizing that many scientists, and those implementing disturbance ecology, hold a wide range of views, we prefer the Graham et al. (2021) framework that broadly defines disturbance while also clearly distinguishing the disturbance driver from the disturbance impact. Thus, a *disturbance driver* is a 'force, either biotic or abiotic, that generates a deviation from the local, prevailing background conditions', and a *disturbance impact* 'represents the social-ecological consequences of a driver relative to a scale-dependent baseline state'. Of course, impacts will be relative to the scale and context, but as long as we seek to clearly distinguish *drivers* and *impacts*, this definition can be used.

Types of disturbance drivers

A great array of disturbance drivers has been characterized from freshwater systems and measured using a variety of techniques (Table 1). In addition to the flooding and drying of aquatic habitats, these include physical alterations associated with forest fires that affect floodplains, channel characteristics and resource inputs (Malison and Baxter, 2010), and cause pulses of sediment know as 'sand slugs' (Lyon and O'Connor, 2008). In winter, stream channels can freeze and be enclosed in ice, with the entire channel freezing solid in some cases also creating a disturbance (Parker and Huryn, 2013). Natural processes are often involved in these disturbance drivers, but event magnitude is most important. For example, blackwater events, where large amounts of dark-colored deoxygenated (i.e., hypoxic) water are released downstream (e.g., ~2000 km of the Murray Darling in Australia; Whitworth et al., 2012), are associated with decomposing plant litter that releases dissolved organic carbon (DOC). It is the scale and extent of the DOC released in blackwater events that fuels aerobic bacteria, potentially depleting oxygen for kilometers downstream. The poisoning of aquatic animals through discharge of human-associated contaminants like heavy metals in urban stormwater is also unfortunately common (Booth et al., 2016).

Freshwater disturbance drivers can be characterized in terms of their magnitude, frequency, timing, predictability, duration, rate of change and extent, similar to flow regimes, but three general types of disturbance driver are generally recognized based on their temporal characteristics (Fig. 1). Firstly, in 'pulse' disturbances the driver is typically shorter and intense like a flood (Lake, 2000). Although the driver may have a sudden onset in a 'press' disturbance, a consistent level is maintained over a longer period (Lake, 2000). Many human-associated disturbance drivers, such as the presence of a dam or acidity associated with mining, are press disturbances, because they continue over long periods. Regular or 'seasonal' drying could also be a press disturbance (Lake, 2003). Finally, in 'ramp' disturbances the strength of the driver changes steadily over time. Ramp disturbances may include increasingly severe drought conditions, such as a multi-year (or supra-seasonal) drought (Lake, 2003), or decreasing disturbance such as stream restoration that slowly alleviates degradation.

Connections to ecological stability and the roles of resistance and resilience

Another important aspect of the temporal dimensions of disturbance is the connection to ecological stability, especially resistance and resilience. Ecological stability has multiple dimensions, but most simply, stable communities either maintain, or return to, their previous state after a disturbance, so disturbance impacts are closely related to the resistance and resilience of communities (Donohue et al., 2016). *Resistance* is 'the capacity of ecological entities to withstand the disturbance,' whereas *resilience* is 'the capacity to recover from the disturbance even though the biota and ecological processes have been diminished' (sensu Lake, 2013). Resistance and resilience can be assessed by measuring changes over time relative to a baseline. For example, applying a disturbance assay that involved water-blasting stream beds followed by comparison of community recovery relative to control reaches revealed that the communities of small streams were much less resistant to disturbance than those of large streams (Greig et al., 2021). A full evaluation of factors affecting the stability of river communities is beyond the scope of this chapter, but in general recovery is closely related to the availability of resources, recruits and refuges (Van Looy et al., 2019).

Influences on individuals, life histories and populations

Disturbance avoidance strategies

Since disturbances can cause widespread mortality among organisms, they have been a powerful force shaping the behavior of individuals, their life histories, population dynamics and ultimately distributions. Not surprisingly, river organisms try to avoid their consequences! Tactics vary according to waterway type, but these generally include life history, behavioral and morphological adaptations that provide benefits by enhancing survival or recolonization (Lytle and Poff, 2004).

Table 1 Examples of disturbance drivers and their measurement in freshwater systems.

Disturbance driver	*Measurement approach*	*References*
Flooding	Insertion of marked tracer particles in the stream bed	Townsend et al. (1997a,b)
Flooding	Multivariate disturbance index incorporating the Pfankuch bed stability score	Death and Winterbourn (1995)
Floods and stream drying	Spectral analysis and extreme event analysis	Sabo et al. (2010)
Freezing	Temperature loggers	Parker and Huryn (2013)
Stream drying	Range of flow-related statistics associated with magnitude, timing/predictability, frequency and duration of long-term and antecedent (immediately prior) flows.	Leigh and Datry (2017)
Flood-disturbed patches	'Scour chains' to measures patterns of bed filling and scouring	Matthaei et al. (1999)
Sedimentation (sand slugs)	Sediment depth transects over time	Lyon and O'Connor (2008)
Wildfire	Periphyton chlorophyll *a* or ash-free dry mass	Malison and Baxter (2010)

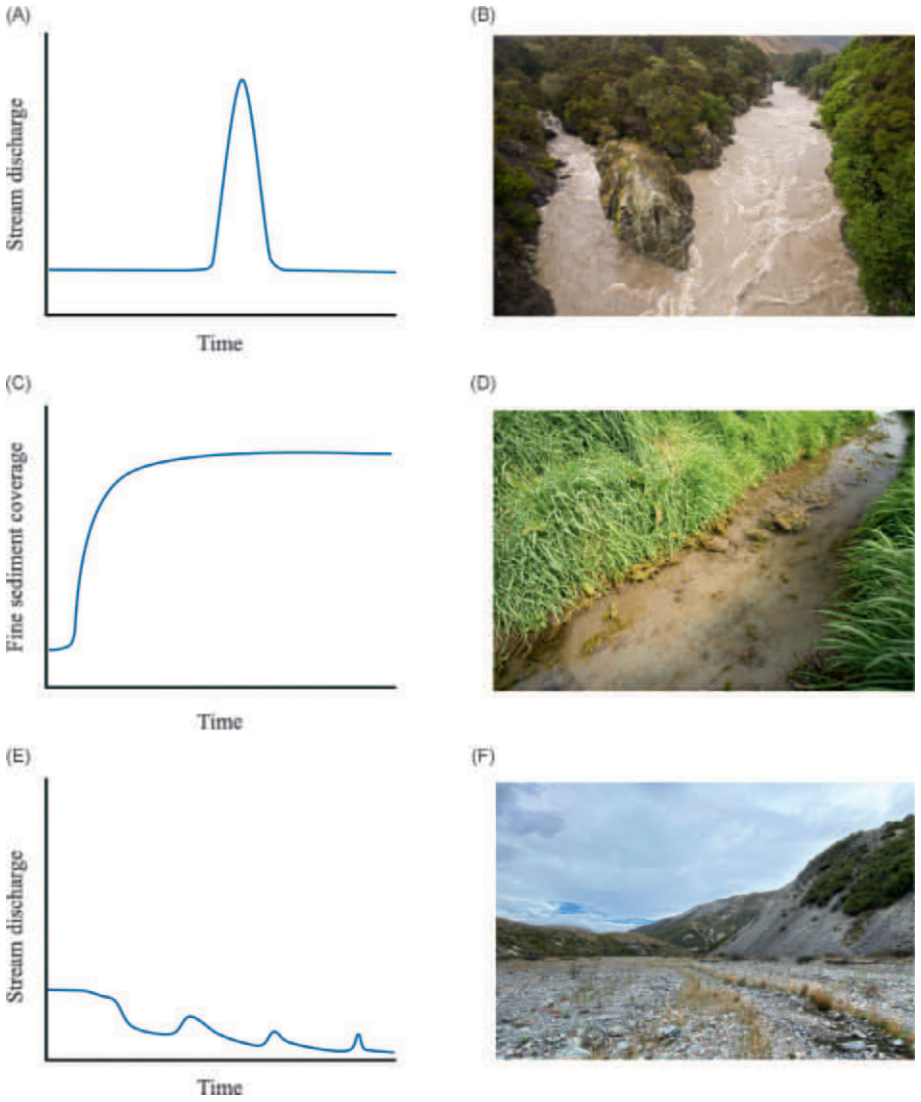

Fig. 1 Three general types of disturbance drivers in freshwater ecosystems indicated by change in important driver-related measures over time: pulse (A and B), press (C and D) and ramp (E and F). Pulse disturbances are usually short and intense like the flood in this New Zealand river (B), whereas press disturbances maintain a more constant level over time as in the case of fine sediment inputs to a stream following land use change from forest to pasture (D). Finally, during ramp disturbances the strength of the driver changes over time, such as the in the river shown (F) where a drought initially exposed part of the river bed, but then progressed to full drying downstream.

The trade-off between growth and development versus disturbance mortality risk

Although animals employ the strategies described above, they still have to balance growth and development with the risk of disturbance-driven mortality. For example, the disturbance avoidance strategies described above almost always come at some cost like the loss of biomass, smaller body size or reduced competitiveness (Lytle and Poff, 2004). This trade-off is especially important for those completing most of their growth in aquatic environments like many stream insects. Research in the arid Southwest of the United States, where flash flooding caused by localized thunderstorms can cause widespread mortality of stream faunas, has been particularly helpful in understanding these trade-offs. For example, 86% of *Phylloicus aeneus* caddisflies emerged from montane streams in the Chihuanhuan Desert before the long-term average arrival date of seasonal flooding (Lytle, 2002). The life history of these caddis also reflects the growth versus survivorship trade-off because they adjust their body size according to the likelihood of flooding, speeding up development and emerging smaller as the risk of flooding approaches (Lytle, 2002).

One of the most interesting examples of adaptation to flash floods is the behavior of a flightless giant waterbug, *Abedus herberti* (Order Hemiptera), in streams of the Madrean Sky Islands, again in the Southwest United States. The waterbugs' use persistent rainfall on the stream surface as a cue for an impending flash flood, and they walk out of streams to avoid the wall of water and almost certain death (Lytle et al., 2008). The behavior is even able to be triggered by simulating rainfall with a pump and firehose (see video in https://lytlelab.science.oregonstate.edu/floodescape).

Disturbance predictability and life history evolution

The effectiveness of the strategies for avoiding drying described above strongly depends on the characteristics of the disturbances. Theory explaining the evolution of life-history responses to freshwater disturbances suggests the strength of selection pressure for such strategies will only be strong when both disturbance magnitude and predictability are high (Lytle and Poff, 2004). This is because the consequences of lost foraging opportunities linked to false alarms are also important. Giant waterbug behaviors in the Madrean Sky Islands also illustrate this. The waterbugs are much less responsive to local rainfall cues in small catchments because floods seldom occur there, whereas local rainfall in medium-sized catchments is a reliable indicator of immanent flash flooding, and that is where the waterbugs are most responsive to the rainfall cues (Lytle et al., 2008).

If predictable disturbances are required for finely tuned disturbance responses, what do organisms do when presented with quite unpredictable or non-seasonal disturbances? In an analysis of the seasonality and predictability of 30-year rainfall records from around the world, Tonkin et al. (2017) showed this is exactly the sort of flooding regime that occurs in places affected by a strongly oceanic climate like New Zealand. Winterbourn et al. (1981) explained that, 'New Zealand stream invertebrates possess flexible, poorly synchronized life-histories with non-seasonal or weakly seasonal patterns of development, and extended flight and egg-hatching periods' and linked these characteristics to the unpredictability of New Zealand's floods. These life history traits contrast those from locations with predictable flooding like Colorado's Rocky Mountains, where development is synchronous and tightly linked to seasonal snow-melt (Peckarsky et al., 2000) (Fig. 2). Thus, unpredictable disturbance is associated with flexible life histories and generalist traits.

The flexible life histories and generalist traits involved in responses to unpredictable disturbance regimes are exactly what life history theory predicts (Lytle and Poff, 2004). Unpredictable disturbances are difficult for organisms to forecast and pose risks, but such habitats can also offer large benefits if organisms can exploit windows of opportunity in them.

Effects of disturbances on genomic diversity

Understanding how disturbance ultimately affects populations, including how the various strategies described above evolve, will be aided by genetic studies. Understanding at this level is still developing, but recently Poff et al. (2018) demonstrated extreme flooding across 14 streams had a variety of effects on genomic diversity (allelic richness). Among six stream invertebrate species studied, two declined in allelic richness and one increased following the flooding. The one increasing, the common mayfly *Baetis tricaudatus*, probably recolonized from upstream populations, presumably adding new alleles to local populations. The variety of genetic responses observed suggested that making generalizations about the evolutionary processes involved would be difficult, but this study did highlight the potentially important role for refuges (upstream reaches in this case).

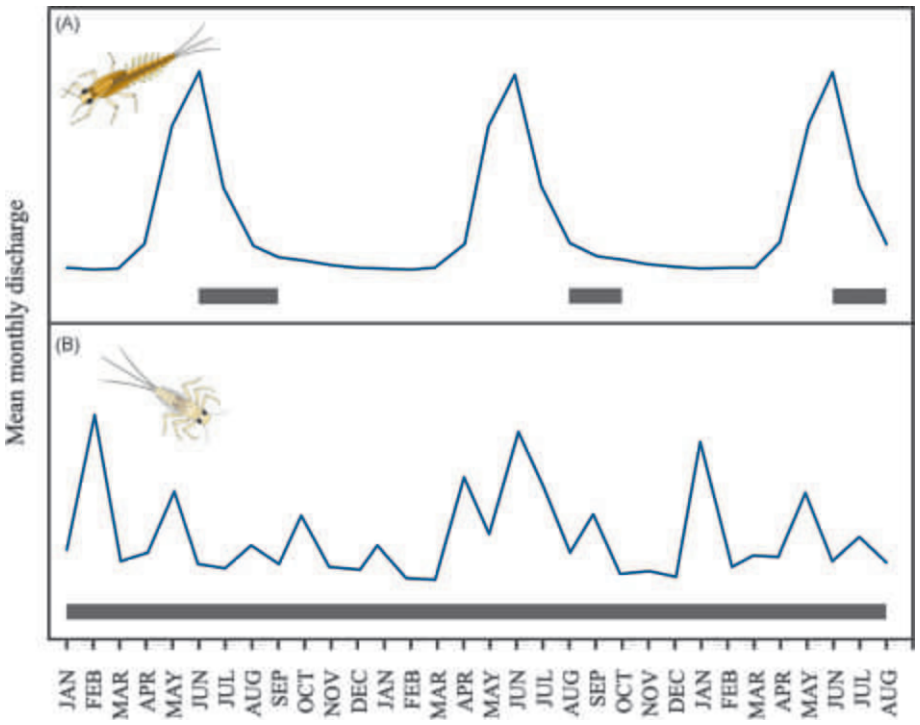

Fig. 2 Examples of synchrony and lack of synchrony in invertebrate life cycles associated with predictable and unpredictable disturbance drivers, respectively, indicated by emergence (gray bars) of *Baetis* mayflies in Colorado, United States, in line with seasonally predictable flooding (blue line; A), and asynchronous emergence of *Deleatidium* mayflies in New Zealand where the flooding regime is highly unpredictable (B).

Ecological 'refuges' versus evolutionary 'refugia'

As the genomic information implies, the resilience of populations in response to disturbances is closely related to the availability of individuals from elsewhere to repopulate disturbed areas. The terms 'refuges' and 'refugia' are both used to refer to habitats that convey temporal resilience to populations affected by disturbances, but the key difference is the timescale that these operate on (Davis et al., 2013). 'Refuges' operate on shorter timescales of minutes to decades, so reflect ecological processes, whereas 'refugium' (plural: 'refugia') are based on longer evolutionary timescales (i.e., millennia) (Davis et al., 2013). Distinguishing between refuges and refugia in aquatic systems is integral to understanding the processes that maintain them in aquatic landscapes (Davis et al., 2013).

Perennially-flowing reaches to which aquatic organisms can retreat to, and recolonize from are important refuges in drying rivers. For example, in rivers with seasonally-drying reaches associated with Mediterranean climates, the recovery of populations of stream invertebrates following dry periods depends on connectivity to perennially flowing reaches (Robson et al., 2013). For many flood-prone rivers, less impacted tributaries upstream can act as refuges, as the Colorado study above demonstrated (Poff et al., 2018). Similarly, stable portions of the stream bed (Matthaei et al., 1999) or even deep stream-bed sediments, an area known as the hyporheic zone, can act as refuges in flood-prone rivers (Stubbington, 2012). In all cases, dispersal, recolonization and recruitment facilitated by connectivity with the refuge are important for population recovery (Van Looy et al., 2019). The identification of refugia has been more difficult, because of the much longer time scales involved, but Davis et al. (2013) have identified evolutionary refugia in the arid zone aquatic habitats of Australia. These are groundwater-dependent habitats like subterranean aquifers and springs that supported relict or poor-dispersing fauna. Thus, both refuges and refugia are important in recovery from disturbance, but the refugia are much less well known and may be crucial given ongoing climate change.

Disturbance impacts on aquatic community composition and diversity

Many of the stream disturbance impacts described as profound in the literature are linked to substantial effects on the composition, richness, diversity and traits of organisms in affected communities.

Mostly, disturbance reduces taxonomic richness in communities

Both linear and non-linear relationships between local diversity components and river disturbance have been identified across disturbance gradients. The intermediate disturbance hypothesis, whereby a trade-off between competitive and disturbance-tolerance drives richness, has been invoked in stream disturbance studies, but empirical support for this hump-shaped relationship is low (Lepori and Hjerdt, 2006). A diversity peak in stream community richness at intermediate levels of flooding disturbance has been found (Townsend et al., 1997a), but most studies typically reveal that species are removed from communities as the harshness of the flooding regime increases so richness declines with flood disturbance (Death and Winterbourn, 1995). Gradients of human-driven stream disturbance usually show similar patterns whereby both richness and measures of diversity decline with disturbance drivers that increase the harshness of stream environments (Booth et al., 2016). Patterns conforming to the IDH may be uncommon in streams because competition is less likely in movement-dominated open systems (Death, 2010). However, comparisons could also be confounded because stable streams could also have more habitat heterogeneity (e.g., through more aquatic plants which add additional habitats), thereby making exclusion less likely. Overall, richness usually declines at the harsh end of disturbance gradients, but the drivers of richness at the stable end of disturbance gradients involve a range of different drivers and resulting patterns.

Relationships with time since disturbance and productivity

Relationships with time since disturbance and productivity shed further light on these patterns in richness. Time since disturbance tends to show strong relationships with diversity and abundance. For example, insect abundance in flood-prone streams of the Venezuelan Andes is closely related to days since the last storm reflecting the time taken for recolonization and recruitment from refuges (Flecker and Feifarek, 1994). More frequent, less intense disturbance events may also have a more severe impact on long-term community composition than fewer, more intense disturbances, because high disturbance frequency more severely disrupts those recolonization and succession processes (Hemphill and Cooper, 1983).

An important mechanism behind the effects of disturbance on community richness are influences on resource availability (Parker and Huryn, 2013). This is particularly important with flooding, where bed movement and scour remove attached algae from stone surfaces and washes away detrital accumulations. For example, the direct effects of flood-driven bed movement on fish whereby fish are washed away are of similar magnitude to the indirect effects via influences on their invertebrate food supplies (Jellyman et al., 2013). Overall, it is likely that both productivity and disturbance interact additively to strongly influence diversity, whereby productivity sets an upper limit to richness that can be achieved by colonization, and disturbance acts to remove taxa below that level (Death, 2010).

The importance of traits that confer resistance and resilience

Delving beyond species identities and investigating their traits (i.e., biological attributes such as body shape, feeding method, movement type, etc.) provides further insights into the influences of disturbances on communities. As described above, disturbances impact taxa differently depending on their capacity to withstand and recover from disturbance. Persistent species have disturbance-resistant traits. For example, mobile invertebrates can better survive floods than more sessile taxa (Wootton et al., 1996; Jellyman and McIntosh, 2020), and detritovores can better survive fine sediment deposition in gravel beds than scrapers which require clean gravels to feed (Burdon et al., 2020). Analyses of whole communities also show the frequency of traits which confer resistance and resilience to disturbance increase with disturbance magnitude (Townsend et al., 1997b). Thus, disturbance likely shapes communities by invoking an environmental filter that selects for species with characteristics that confer resistance and resilience.

A particularly important trait conferring resilience is dispersal. During recovery from disturbance, freshwater communities are often dominated by organisms with strong dispersal (Vieira et al., 2004). These species usually have a terrestrial adult stage, and therefore ability to recolonize after unfavorable conditions. For example, after the extreme Colorado flooding mentioned earlier, 84% of taxa present had mobile larvae or terrestrial adult stages (Poff et al., 2018). In the aftermath of a large flood in Ireland, it was species with shorter life cycles (i.e., more r-selected traits) that colonized fastest, whereas longer lived mayflies or stoneflies took much longer (Woodward et al., 2016). Overall, trait-based information can give important mechanistic insights into how disturbance affects community structure that diversity metrics alone do not resolve.

Disturbance-driven community assembly processes

Given that disturbances are widespread in freshwater ecosystems, it is not surprising that they have a strong influence on community assembly. Studying those communities at various stages during and after disturbance has provided insights into the processes involved.

Community disassembly and then re-assembly following disturbance

Streams undergoing wet-dry cycles illustrate community disassembly during drying and then re-assembly following re-wetting. Although drought is a ramp disturbance with conditions getting progressively worse over time, the magnitude of the effect on fauna is also connected to key thresholds being surpassed (Boulton, 2003). One of the best descriptions of this comes again from the Madrean Sky Island streams (Fig. 3). The drying process starts with loss of lateral flow connectivity, progresses to loss of longitudinal connectivity especially riffle habitat and formation of remnant pools, and then if drying is particularly harsh (e.g., during a drought lasting a long time), loss of all surface water followed by loss of the refuges in the hyporheic zone (Bogan et al., 2015). Most flowing water (i.e., lotic) species disappear with loss of longitudinal connectivity leaving only still water (i.e. lentic) species. This has been described as a stepped response, with the gradual change punctuated by swift transitions in community structure as particular types of habitat are lost (Boulton, 2003). Recovery then depends on the extent of water loss in the initial drying as well as the isolation from colonization sources (Boulton, 2003; Bogan et al., 2015). Upstream perennially-flowing reaches provide particularly important sources of colonists (as described in Section "Ecological 'refuges' versus evolutionary 'refugia' above), but if all local refuges including the hyporheic zone have dried and taxa lack desiccation-resistant stages, then recovery will depend on recolonization from distant sources and will be affected by taxon mobility.

After disturbance, community succession starts. A classic example of this is the changes in algal community composition and benthic macroinvertebrates described from Sycamore Creek, a desert stream in Arizona that experiences flash floods. Detailed sampling over 60 days after such a flood revealed substantial changes in algal communities over time with diatoms initially dominating and then being joined by cyanobacteria and the filamentous green alga, *Cladophora* (Fisher et al., 1982). Much of the work in streams indicates these sorts of successional processes are controlled by the environmental tolerance of the organisms. One of the most complete records of succession following the removal of disturbance illustrating this comes from the streams revealed after glacial retreat in Glacier Bay, Alaska. Milner et al. (this volume) sampling over 28 years revealed that most species colonizing, except cold-tolerant early successional midges, persisted over time, with more species being added as conditions became less harsh. The development of riparian vegetation and the addition of the associated leaf-litter resources were particularly important stages in the succession of these glacial stream, and by providing food resources, reduced environmental harshness.

Using a metacommunity framework to investigate community recovery following disturbance

Recently, investigations of controls on recovery from disturbance have broadened to include a range dispersal-related process as alluded to above. This involves increasing emphasis on processes driven at large spatial scales, including isolation from colonist sources and the role of chance (i.e., stochastic) events. The approach reflects that local stream communities are part of metacommunities linked at landscape scales by dispersal of potentially interacting species (Tonkin et al., 2018). At one extreme, limited dispersal ability and chance events could restrict recolonization regardless of environmental tolerances to local conditions, whereas at the other extreme high dispersal rates may override local habitat controls on assembly. The configuration of a river network will

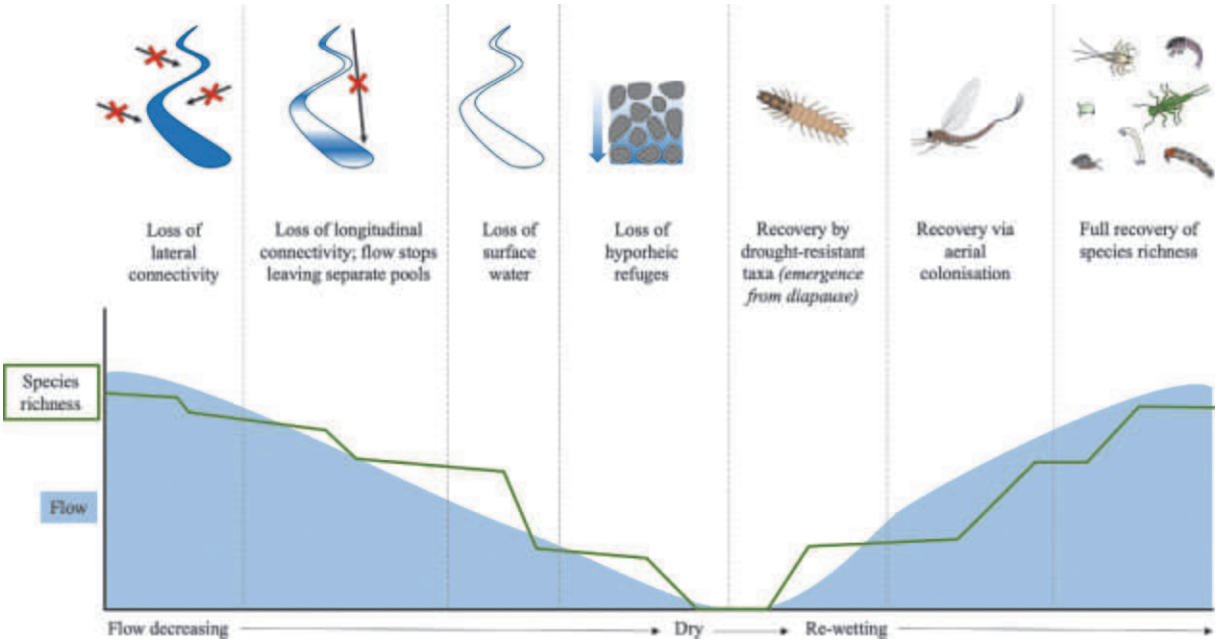

Fig. 3 Stages of community disassembly and re-assembly associated with stream drying and subsequent re-wetting. Adapted from Bogan MT, Boersma KS and Lytle DA (2015) Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land headwater streams. *Freshwater Biology* **60**: 2547–2558.

also be important here, having more influence on organisms restricted to aquatic habitats (like fish) compared to those with aerial dispersal stages like aquatic insects (Tonkin et al., 2018). Investigation of these effects has really just begun, but a study of 21 rivers undergoing restoration in Germany indicated that factors related to the regional pool of taxa and the proximity of colonist sources had an overriding effect on local recolonization outcomes (Tonkin et al., 2014). Similarly, a review of processes affecting reassembly in intermittent rivers suggests that dispersal and stochastic processes were important immediately after the drying disturbance, but local factors such as biotic interactions and species habitat requirements become more important as more speciose communities establish (Datry et al., 2016).

Disturbance effects on both alpha and beta diversity

Given that stochastic dispersal is likely to be particularly influential on recovery from disturbance, one would expect that to be reflected in between-site differences in measures of biological diversity. A broad-scale analysis of rivers ranging from intermittent to permanent in Australia and Europe revealed that flow loss acted as a strong environmental filter, eliminating species lacking traits to resist drying and thereby decreasing local macroinvertebrate richness (alpha diversity) (Leigh and Datry, 2017). This is consistent with other studies reporting disturbance effects on local richness described in Section "Disturbance impacts on aquatic community composition and diversity" above. However, the effects of disturbance on beta diversity, or the turnover in species between locations, suggested the full range of community assembly processes was involved. Firstly, drying disturbance appeared to both increase beta diversity by enhancing the sorting of taxa along an environmental gradient, thereby increasing differences in species identity between localities, and also decreased beta diversity by increasing selection for a common core of disturbance-tolerant taxa (Leigh and Datry, 2017). Secondly, strong flight-driven dispersal decreased beta-diversity effects (Leigh and Datry, 2017). This combination of positive and negative influences on the turnover of species between sites reflects the mix of local conditions affecting who can occupy a site, the differences in those conditions between sites and the influence of dispersal on the resulting diversity patterns.

Just as the predictability of the environment is associated with the evolution of responses to disturbance, it is also involved in these diversity patterns. For example, communities living in highly seasonal climates with predictable disturbance regimes tend to have complete turnover of species between seasons and thus high beta diversity (Tonkin et al., 2017). However, communities experiencing unpredictable and non-seasonal fluctuations in assembly show more random (i.e., stochastic) patterns of community assembly and hence lower temporal beta diversity (Tonkin et al., 2017). Overall, these studies of disturbance-driven community assembly point to strong roles for both species sorting based on local environmental conditions and dispersal-related stochastic processes influencing community assembly, with the combination depending on particular local disturbance regimes and the configuration of the stream network (Tonkin et al., 2018).

Disturbance influences on food webs

Disturbance has particularly important ramifications for energy flow through freshwater ecosystems, especially via effects on the strengths of interactions between organisms, including the relative importance of top-down and bottom-up influences.

Alterations to top-down and bottom-up effects in food webs driven by flood-influences on consumer traits

Because of the strong influences of floods on the composition of invertebrate consumers in river food webs, flood disturbance alters energy flow to higher trophic level consumers like fish in rivers. This is nicely demonstrated in northern Californian river. These rivers typically experience harsh winter flooding, with consumer assemblages consequently dominated by mobile invertebrates like midges and mayflies that are good at escaping floods (Wootton et al., 1996). However, when flood-disturbance is removed via dams (which moderate flows), or in benign years with few floods, invertebrates with protective cases like cased-caddisflies, especially *Dicosmoecus*, are able to dominate. These disturbance-driven changes in consumer composition strongly affect energy flow because mobile invertebrates, like the midges and mayflies, are easy for drift-feeding fish like trout to catch, whereas the cased-caddisflies, which are protected by their case, are much more difficult for trout to capture. As a result, either dams or benign years can lead to reductions in fish populations because the prevalent invertebrates, cased-caddis, are so well protected from predators, an effect called bottom-up limitation (Wootton et al., 1996). Overall, this switch in invertebrate consumer types is driven by a trade-off between vulnerability to disturbance and vulnerability to predatory fish that affects invertebrate traits. Mobile invertebrates lacking cases or shells can escape floods but are more easily consumed by fish, whereas those with cases or shells are relatively protected from predation but are much more vulnerable to being crushed in floods (Wootton et al., 1996). The disturbance-driven changes in consumer traits also affect interaction strengths; in flood-free conditions there is more competition meaning caddis dominate, but predatory interactions between mayflies and trout strengthen after flooding (i.e., top-down effects increase).

Similar flood-driven changes in invertebrate composition also control the energy flow and strength of interactions in streams of New Zealand's South Island high country, but the effects extend to altering the composition of fish assemblages. In these New Zealand streams, the top-down predatory effects of the fish on invertebrates are much weaker on consumers protected by a case or shell (e.g., cased caddisflies or snails) compared to those lacking such protection (e.g., mayflies) similar to the Northern California situation (Jellyman and McIntosh, 2020). However, since particular types of fish have feeding niches connected to different invertebrate traits, the most common type of predatory fish also changes along the disturbance gradient due to bottom-up effects (Jellyman and McIntosh, 2020). In this case, eels dominate spring-fed habitats lacking floods because their benthic-foraging habitats are better suited to eating cased invertebrates, whereas trout dominate intermediately disturbed habitats where mobile invertebrates like mayflies are common. Finally, and involving another influence of disturbance on organism traits, native galaxiids occupy the most flood-prone streams because they are more tolerant of the flooding influences than the non-native trout. Thus, in both California and New Zealand, through a combination of both top-down and bottom-up effects mediated by the differential effects of disturbance on invertebrate and fish traits, disturbance influences how and to who energy flows in river food webs.

These flood-driven effects on organism composition and energy flow also have one other major influence via limiting the development of long food chains in rivers. There are two major mechanisms involved here. Firstly, reductions in prey availability associated with periodic flooding mean that there is less energy available and availability fluctuates depending on the time since the last flood, leading to so called dynamic constraints on energy availability. Secondly, there are fewer taxa like predatory invertebrates and small fish at intermediate trophic levels in flood-prone streams, forcing bigger fish, which are usually the top predators, to gain a greater proportion of their energy from primary consumers thereby causing a change in their trophic omnivory. Together, both the dynamic constraints on energy flow to top predators and the changes in top-predator trophic omnivory, mean that food chains are shorter in flood-prone streams compared to more stable streams because top predators are generally gaining a greater proportion of their energy at lower trophic levels (McHugh et al., 2010).

Food-web collapse associated with predator loss in drought-affected streams

River drying disturbances also cause dramatic effects on energy flow in river food webs, but in this case the reduction in habitat size and stress associated with water loss generally leads to food-web collapse associated with species loss. This has been well studied using stream channels in southern England where water flow was controlled such that channel dewatering occurred for 6 days every 33 or 99 days (Ledger et al., 2013). In comparison to controls, basal species (e.g., algae) in dewatered channels weren't greatly affected, but dewatered channels experienced substantial loss of primary consumer species and biomass; 37% of invertebrate primary consumer taxa were eliminated and their biomass was reduced by 64%. The effects were greatest on large-bodied species (78% loss of taxa), and because most of those larger species were predatory, this led to partial food-web collapse associated with big reductions in the amount of energy flowing to predators. Thus, these food webs subjected to experimental drying were simplified and contained many fewer predatory taxa.

This loss of predatory taxa associated with stream drying also affects the length of river food chains. Gradual longitudinal water loss in rivers flowing across a bed of porous alluvial gravels revealed a corresponding loss of predatory taxa that was in turn associated with reductions in food chain lengths that eventually ended in food-web collapse (McHugh et al., 2014). In these real streams, the reduced number of trophic levels present was closely associated with reductions in the maximum body size of the top predators. Thus, as the drying disturbance strengthened and habitats became smaller downstream, the food-web collapse measured

by food chain lengths was driven by the inability of large predators to survive in the increasingly small and harsh conditions. Overall, the most dramatic reductions in food chains are caused by the loss of whole trophic groups in drying streams (e.g., predatory fish), compared to the dynamic constraints and alterations in trophic omnivory of predatory fish that typically shorten food chain length in flood-prone streams (Sabo et al., 2010).

Conclusions and synthesis

Disturbance drivers in rivers have far-reaching influences starting with organismal traits and population responses, that then lead to community-level effects, and finally to important changes in stream food-webs. These influences will only increase as climate change continues. Since most so-called natural disturbances are being altered by humans, having a widely applicable and general definition of disturbance that doesn't split human-driven and natural-driven disturbances will aid disturbance ecology assist river management. Moreover, the many dimensions of river disturbance described above, and the prospect that many future disturbances regimes are likely to be characterized by changing intensity and timing of extreme events suggest that disturbance ecology will be particularly important for future management. We conclude by highlighting these important connections.

Climate change will alter the predictability, magnitude and other disturbance dimensions, necessitating predictive approaches

Firstly, of the influences of climate change on freshwaters, alterations to the predictability, magnitude and other dimensions of hydrology-related disturbance regimes (i.e., floods, drought and habitat drying) will be some of the most important (Woodward et al., 2016). The non-stationarity (i.e., continual alteration) of hydrological influences means the future dimensions of disturbance drivers will be different to those experienced in the past, requiring more sophisticated predictive approaches to help prepare freshwater ecosystems for those impacts (Tonkin et al., 2019).

Places where disturbance drivers are changing the most will be worst affected, so maintaining evolutionary refugia will be critical

Rivers experiencing the largest changes in disturbance drivers will be disproportionately affected by climate change. Some of these include high latitude, high altitude or very dry areas where organisms and system dynamics are highly attuned to the current predictable disturbance regimes (Davis et al., 2013; Parker and Huryn, 2013; Peckarsky et al., 2000). In extreme cases, identifying evolutionary refugia critical for maintaining biodiversity will be particularly important (Davis et al., 2021).

Altered disturbance regimes will affect invasion

Another particularly important aspect of changing disturbance regimes will be the consequences for invasion and invaders. In some cases, natural disturbance regimes keep invaders at bay, effectively creating natural invader-free space (Boddy and McIntosh, 2021), whilst in others, disturbances, especially human driven ones, facilitate invasion (Marchetti et al., 2004). Thus, changes in the disturbance regimes experienced by freshwater systems are very likely to influence invasion and associated consequences, indicating that better understanding of these controls is needed. Here, it may not be just maintaining one disturbance regime in a river network that is important, but the variety of disturbance types in a location may also be critical for maintain biodiversity in the face of invasion (Boddy and McIntosh, 2021).

Insights from disturbance ecology will be important for improving restoration success

Given the widespread impacts of invaders, the influences of human-driven disturbances such as land-use change, and the pervasive effects of climate change, the importance of freshwater ecosystem restoration will only increase. Restoration effectively involves disrupting the current, degraded, state of an ecosystem to move it to a more desired state, so understanding the controls on the resistance and resilience of ecosystems to disturbance will be integral to restoration (Lake, 2013). Degraded freshwater ecosystems are often highly resistant and resilient, possibly due to the traits of the organisms that constitute those communities (Barrett et al., 2021), and failure to account for this in restoration may underlie a lack of restoration success in freshwater ecosystems (Lake, 2013). Better understanding of how disturbance drivers might affect restoration-resistant communities could help improve restoration success (Barrett et al., 2021).

Disturbance drivers have cross-ecosystem consequences

Finally, we have concentrated on the consequences of freshwater disturbance drivers for aquatic ecosystems, but those disturbance drivers often have important cross-ecosystem effects. Disruptions or alterations to cross-ecosystem energy subsidies from aquatic to terrestrial ecosystems associated with freshwater disturbances can alter riparian populations and communities (Greenwood and McIntosh, 2008). Likewise, terrestrial subsidies to aquatic ecosystems may also be important for the resistance of freshwater ecosystems to freshwater disturbances, so will be important in management. Thus, the relevance of freshwater disturbance-drivers is certainly not restricted to just aquatic ecosystems.

Knowledge gaps

- The non-stationarity (or continual alteration) of hydrological influences means the future dimensions of disturbance drivers will be different to those experienced in the past, requiring more sophisticated predictive approaches to help prepare freshwater ecosystems for those disturbance impacts.
- Future changes in disturbance regimes imply that evolutionary refugia will be critical for maintaining biodiversity, so identifying refugia in landscapes will be critically important.
- Understanding how climate change influences on the dimensions of disturbance, especially their predictability and magnitude, will affect a myriad of other processes such as invasion and the flow of energy through food webs, but we currently lack an adequate understanding to predict and manage those consequences.
- Disturbance is closely associated with restoration because it involves altering community resistance and resilience, but understanding of those process in aquatic restoration is still poorly developed.
- Disturbances in aquatic ecosystems have cross-ecosystem consequences for terrestrial ecosystems and vice-versa, but knowledge of controls on those influences is also poor.

See Also: Structures and functions of Inland Waters - Rivers: Climate Change and Extreme Events in Shaping River Ecosystems; Invasive Species in Streams and Rivers

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Succession in Streams

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Allogenic succession Succession is a result of abiotic or physical processes.
Autogenic succession Succession occurs as a result of biotic interactions.
Deterministic The successional trajectory occurs in a predictable way for a given region.
Facilitation Early colonizers make the habitat more suitable for later colonizers.
Inhibition Early colonizers prevent later colonizers from establishing, either by modifying the environment or through direct competition/predation until they are eliminated by a disturbance.
Press disturbance Abrupt and reaches a disturbance level that is then continual.
Primary succession Process of succession in which no remnants of the previous biotic community are present following a disturbance.
Pulse disturbance Short term and time delineated, i.e., transient.
Ramp disturbance Increases in severity over time.
Secondary succession Elements of the biotic community persist after a disturbance.
Stochastic The successional trajectory is influenced strongly by chance events, depending on the traits of the colonizers or extreme disturbances.
Tolerance Taxa that colonize co-exist.

Introduction

Succession is defined as change in community composition following a disturbance (Fisher, 1983, 1990). Succession may be primary (no remnants of previous biotic community exist) or secondary (species remain after disturbance). Potentially we could consider a tertiary succession where, linked to human modifications, species are able to colonize where they would not naturally establish. The process and pattern of succession depends upon traits and life histories of the individual species. Succession may be allogenic where changes in the community are modified by the abiotic environment, or autogenic where biotic processes influence community change. Conceptually, community changes during successional processes end in the climax community—the final community for that specific region and climate.

The concept of succession has been around since the early 20th century when it was developed initially for terrestrial plant communities. Clements (1916) proposed a deterministic model where the vegetation progresses through a series of successional stages towards a predetermined climax community for a given area, whereas Gleason (1926) suggested an individualistic, more

stochastic model depending upon the attributes of the colonizers. Connell and Slatyer (1977) proposed three models for considering succession in different ecosystems: (1) facilitation where early colonizers make the habitat more suitable for later colonizers, (2) inhibition where early colonizers inhibit later colonizers until they themselves are eliminated and (3) tolerance where all the taxa are present initially or colonize later but biotic interactions are negligible. Fisher (1990) considered that any theory of succession relevant to lotic ecosystems should potentially be developed directly from the study of streams, rather than use ideas developed for other ecosystems.

Nevertheless, the concept has elicited much discussion and debate. One aspect is whether changes in species composition are directional or whether they are non- directional, but in either case succession represents any change over time in species composition (Platt and Connell, 2003). Because succession has suffered from confusion over time, Fisher (1990) even suggested that the term should be abandoned for streams, in favor of the broader view provided by stability theory. However, these two concepts are linked. In this chapter, we view succession as the progressive change over time as the ecosystem progresses to a mature community, whereas stability relates to the extent to which disturbances or internal dynamics reset or shift the trajectory of that successional movement.

Biological traits related to feeding specialization, dispersal ability, and habitat specialization, along with taxonomic and phylogenetic identity, mediate organism responses to disturbance (Van Looy et al., 2019). A directional view of succession assumes that community assembly is deterministic whereas a non-directional view infers that assembly and associated succession is stochastic. This has created a great deal of debate in the literature and Fisher (1983) considered stream succession to be stochastic with deterministic evidence lacking. Although often considered opposing, stochastic and deterministic processes undoubtedly interact with their relative contributions to community assembly being determined by the strength of the disturbance. Potentially a successional sequence could be determined initially by deterministic controls depending on the severity of the disturbance and then by stochastic processes. In terrestrial ecosystem theory, the community potentially reaches a stable state (Olito and Fukami, 2009), but this is often not the case with streams.

In this chapter we will not consider seasonal succession as this relates to changes in abundance due to the seasonality of the organisms, particularly insects, and thus it is not true succession as defined above. In addition, this chapter does not examine longitudinal succession in any detail; which Fisher (1983) stated was unique to streams. This is more appropriately termed 'longitudinal zonation' according to distance from water source, and detailed synthesis articles are available elsewhere (Doretto et al., 2020). Initially this chapter considers the disturbance regime that may initiate stream succession (see McIntosh and Barrett this volume) and the ways in which successional process knowledge can be applied to enhance the potential success of river restoration. We then examine the temporal dynamics of different groups of organisms from microbes to fish and consider how stream succession may be influenced by links to other ecosystems, such as the terrestrial riparian zone, or the underlying hyporheic and groundwater systems. The chapter subsequently examines anthropogenic and climate change effects on stream succession and concludes by synthesizing key evidence for successional pathways that are evident in streams and and compares stream succession with terrestrial and nearshore marine ecosystem succession.

Disturbance regime and succession

Compared to other ecosystems, streams are subjected to frequent natural disturbances (mainly floods and droughts) that typically restructure the physical habitat and the distribution of resources, thereby causing extensive loss of biota. Thus, disturbance is the dominant organizing factor in stream ecosystems (Resh et al., 1988). Given the importance of disturbance many authors have strived to create a systematic framework for classification of disturbance e.g., (Poff et al., 2006). In any review of stream succession then, the characterization of the disturbance regime is important to facilitate interpretation of the subsequent successional processes. Lake (2000) suggested three levels of classification based on the temporal pattern and structure of a disturbance (Fig. 1). Pulses are short term and time delineated (e.g., intermittent drying or floods, sediment pulses), presses are abrupt and

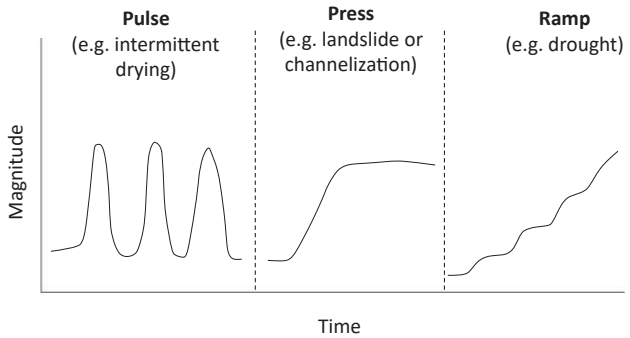

Fig. 1 Three disturbance types. After Lake PS (2000) Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* **19**: 573–592.

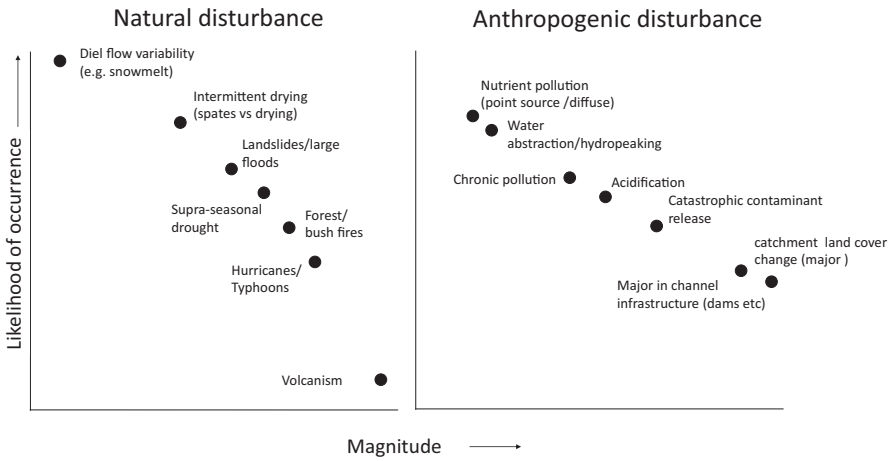

Fig. 2 The relationship between predictability and magnitude of disturbances in streams for natural streams and anthropogenically modified streams. Adapted from Jentsch A and White P (2019) A theory of pulse dynamics and disturbance in ecology. *Ecology* **100**: e02734.

reach a disturbance level that is then maintained (e.g., channelization, continual sediment pulses) and ramps increase in severity over time (e.g., drought). Typically anthropogenic modification such as pollutant inputs, flow modification or land use changes lead to press or ramp disturbances (Van Looy et al., 2019). Although some authors (Reice et al., 1990; Resh et al., 1988) do not consider predictable events (e.g., seasonal drying that occurs every year at the same time) as a disturbance, in this chapter such events are considered disturbances sensu Poff (1992), as successional sequences are initiated.

The magnitude of the disturbance is also a highly important variable in influencing successional trajectories for all biotic communities. For example, recovery trajectories of lotic diatom assemblages following a major landscape-scale disturbance due to wildfire were a function of disturbance magnitude resulting from differences in catchment characteristics (Robinson et al., 1994). In addition, the link between magnitude and likelihood of occurrence is noteworthy (Fig. 2; Jentsch and White, 2019). For natural disturbances there are highly predictable disturbances of low magnitude that occur very frequently (e.g., diel flow variability associated with snowmelt), whereas natural disturbances of very high magnitude (e.g., a volcano or violent hurricane) are extremely rare. The relationship between anthropogenic disturbance magnitude and likelihood of occurrence is less pronounced, with high magnitude disturbances such as land cover change or construction of in channel infrastructure (e.g., dam construction) being comparatively more frequent than volcanoes or hurricanes (Fig. 2). Potentially, anthropogenic disturbances are more likely to be press than pulse.

Linking successional theory to stream restoration

Stream restoration projects offer a unique opportunity to study successional processes. While restoration projects often define goals and endpoints, the successional pathways and mechanisms by which these may be achieved are rarely considered, despite the large of body of theory (Lake et al., 2007) as outlined in this chapter. Successional theory informs us that the distance to colonizer source pools and dispersal pathways (i.e., metacommunity processes) must be considered in any stream restoration planning and in this respect connectivity is a major issue (Westveer et al., 2018). Indeed, Li et al. (2016) developed a new metric reflecting temporal succession of benthic invertebrates in the restored reaches based on their dispersal abilities. Strong dispersers will colonize early in the sequence and weaker dispersers will appear later and the authors believe their approach could also be used for recovery from extreme events like floods, droughts and major pollutant episodes. In addition, seasonality is an important considerations for the timing of the stream restoration projects, particularly new channels, to ensure rapid colonization when colonizers are available and shorter successional sequences (Westveer et al., 2018).

With restoration there is often the Field of Dreams adage "build it and they will come" and in certain instances this works for stream communities (Bogan et al., 2020) where there is high connectivity to systems that are not degraded. However, sometimes resilient degraded communities inhibit the colonization by other taxa (e.g., NZ mudsnail https://bioheritage.nz/if-you-build-it-will-they-come/) or seeding is required to overcome dispersal limitations and initiate/modify the successional process.

Space-time considerations

The impact that a disturbance has on a community and successional trajectories that follow may differ depending on the spatial scale at which succession is assessed, for example on a boulder vs a stream reach vs a whole catchment as seen for temporary streams (Godoy et al., 2016). Townsend (1989) proposed the patch dynamics concept in streams, where disturbances create different size patches in stream reaches which can then be in different successional stages, thereby contributing to community heterogeneity.

The timing of disturbance is also important as exemplified by an atypical winter flood in Ireland where the successional recovery pattern was different when compared to a summer flood (Jackson, 1988). Similarly, Boulton et al. (1992) showed that when floods occurred in summer, succession occurred more rapidly, possibly due to higher water temperature when compared to spring floods. At the finer scale, use of refugia may differ as function of the life history stage of a given taxon, with implications for the pioneer species that can quickly re-colonize a habitat following a disturbance (Van Looy et al., 2019). Field experiments have highlighted the role that differing macroinvertebrate pioneer species can have on community succession (e.g., facilitative vs inhibitory—see autogenic effects below). Furthermore, disturbance timing can have important implications for structural abiotic legacies, such as micro-habitat availability, or resource legacies, such as nutrient or detritus availability (Johnstone et al., 2016). Newman et al. (2015) showed that the timing of leaf litter input influenced microbial succession. Even time of day can shape patterns of succession after flooding as diel emergence, mating and oviposition behavior varies among insect species (Woodward et al., 2015).

Biological community succession

Groups of organisms have different traits that facilitate colonization, use of refugia and resources—see Table 1. Hence, groups may display different responses and recovery to a particular disturbance as outlined below.

Microbial communities

Succession among stream microbial communities (fungi, bacteria) has received less attention than the macrofauna, although understanding of biofilm (a collection of microorganisms on the substrate surface) succession has developed in recent years with advances in molecular biology. Similar to other types of ecosystems and organismal groups, microbial communities shift over time from those that are predominantly influenced by physical properties of the environment to ones in which coupled biophysical controls become important (Besemer et al., 2007).

Bacteria and fungi rapidly colonize surfaces in running water, such as mineral particles, plants and other organisms and modify the habitat to facilitate later colonizers arriving via the water column with rapid increases in species richness (Jackson et al., 2001). Richness may then decline, as some species are out-competed; later colonizers become more dependent on autotrophic production within the biofilm matrix, leading to enhanced niche availability and further increases in richness (Besemer et al., 2007). These successional dynamics, however, have been monitored over very short timescales (week-months) compared to 'traditional' ecological studies of succession, which span years-decades or even centuries when using a chronosequence approach. In periods of stable environmental conditions in rivers, successional pathways within biofilms can proceed to a point at which a 'climax' community is established (Lyautey et al., 2005).

Table 1 Comparison of different biotic groups for some key elements of stream succession.

Group	*Successional Mechanisms*	*Deterministic v Stochastic*	*Time Frame*	*Traits/main drivers (Van Looy et al., 2019)*	*Role of refugia/ legacies*
Bacteria	Both facilitation and inhibition (Besemer et al., 2007)	Initially stochastic then deterministic (Jackson et al., 2001; Lyautey et al., 2005)	Rapid (Veach et al., 2016)	High fecundity, easily dispersed.	Less important
Algae	Potentially all three mechanisms at play.	Stochastic	Relatively rapid unless after major disturbance e.g., Mt. St Helens (Steinman and Lamberti, 1988)	Strong Dispersal, reproductive potential and nutrients (McCormick and Stevenson, 1991; Stevenson et al., 1991)	Less important except maybe phytoplankton in slow flowing areas
Invertebrates	Tolerance (Milner et al., 2011) although facilitation does occur (Cardinale et al., 2001; Tumolo et al., 2019; Hammock and Bogan, 2014)	Deterministic initially where water temp/ channel stability low but then stochastic	<1 year typically unless following press disturbances or new streams after glacial recession/channel relocation	High fecundity, drift. Differences in colonizing abilities drives community, particularly in primary succession (Miyake et al., 2003)	Major role in successional trajectories (Ledger et al., 2006; Dodds et al., 1996)
Fish	Mostly tolerance but some examples of facilitation (Schlosser and Kallemeyn, 2000)	Stochastic	Longer than the other groups	Strong disperser with migration ability and high fecundity.	Some habitat specialists can enter substrate but less important with anadromous fish

Besemer et al. (2007) showed experimentally that successional pathways could diverge due to flow variations, with filamentous bacteria and cyanobacteria developing more strongly in experiments where flows were laminar. However, over longer time scales the differences were lost and all biofilms developed similar compositions. During the early stages of succession, benthic microbial biofilms are influenced by stochastic processes linked to dispersal and colonization success from the water column (Jackson et al., 2001; Lyautey et al., 2005). As succession proceeds, control from biological interactions increase and can be attributed to algal community development (Besemer et al., 2007) implying facilitation was also a key process influencing the development of these communities. Fungi play a role in the major river ecosystem function of organic matter decomposition, and communities differ in streams as glaciers recede in alpine areas (Fell et al., 2021).

Algal communities

Benthic algal succession occurs in lotic environments following a disturbance. Within a primary successional framework of 6 years following the eruption of Mount St. Helens, increased richness of cyanobacteria (blue-green algae) and chlorophyte green algae taxa occurred (Steinman and Lamberti, 1988), dominated by *Achnanthidium minutissimum* (Rushforth et al., 1986). In a desert stream following flash flooding, diatoms were the first colonizers dominating the community followed by filamentous greens and blue-green algae in the successional pattern (Fisher et al., 1982). Colonization was rapid within about 2 weeks. This sequence was also observed following experimental flow releases from dams, with the first colonizers including the diatoms *Cocconeis*, *Synedra* and *Fragilaria*, followed by a proliferation of the filamentous green *Stigeoclonium* in the later successional community (Davie et al., 2012). Diatom succession was also evident in a tropical rainforest stream over a 60-day period involving a total of 127 taxa falling into four distinct groups (Rondon and Aragon, 2018). Early successional dominance of diatom taxa in streams is a result of colonizing abilities through their small size and large population sizes enabling rapid dispersal such as via downstream drift or by terrestrial vectors such as birds (Manning et al., 2021), and the high reproductive potential of the algal assemblages overall plays a major role in the outcome of the successional pathway. Patchy dewatering of habitat patches during periods of low flows influences the successional dynamics of algae, thereby creating distinct mosaics of algal species on the stream bed (Ledger et al., 2008). Riparian vegetation on small streams and afforestation practices can reduce successional patterns and community complexity by reducing light availability, thus favoring dominance by low-profile species tolerant of low light conditions (Cibils-Martina et al., 2017).

Acid mine drainage can seriously impair stream water quality reducing pH, and has been shown to affect diatom succession in streams and consequently may play a role in bioassessment where diatoms are used to assess water quality (Smucker and Vis, 2013). Diatom succession was more simplified with less turnover at sites severely impacted by acid mine drainage than at less impacted sites and control sites.

Invertebrate communities

It is a rare flood that initiates a primary successional sequence in invertebrate community recovery. However, new river channels created either through stream restoration or glacial retreat offer an opportunity to examine successional sequences under primary successional processes. Meiofauna (invertebrates <500 μm <45 μm) colonization of a newly constructed tributary of the Thames showed that the colonization and successional trajectory was rapid, potentially because of the close proximity of the colonizers, but the community that established was significantly different than the colonizing source (Robertson et al., 2014).

Malmqvist et al. (1991) examined invertebrate colonization of a new stream channel in Sweden and found blackflies (Diptera) were the pioneer colonizers in high densities but their abundance decreased after a year when hydropsychid caddisflies (Trichoptera) became numerically dominant. Coleoptera, Odonata, and some Trichoptera were generally slower to colonize than Ephemeroptera and Plecoptera. Invertebrate colonization of former sewage channels restored as streams (Winking et al., 2016) followed a primary successional sequence from pioneer assemblages to mature communities, which resembled that of proximal unpolluted sites. For restored channels that were connected to an upstream colonizing source, the successional timeframe was up to 19 years to reach a mature community but longer where no connection existed.

One rare and very high magnitude disturbance was the eruption of Mount St. Helens in Oregon in 1980, where community assembly in newly formed streams was under primary succession. Chironomids, baetid mayflies and capniid stoneflies were initial colonizers, and subsequently richness increased to between 38 and 58 taxa after 36 years. However, the combination of disturbance magnitude and hydrologic source variation of the Mount St. Helens streams has driven divergent successional trajectories in streams of similar age, geology and the macroinvertebrate colonizing pool (Claeson et al., 2021).

Glacial recession affords unique opportunities to examine community assembly in the new streams subsequently created under a primary successional framework. One such example is Glacier Bay National Park in southeast Alaska, where glaciers have retreated from a Neoglacial maximum in 1750, thereby creating a chronosequence time gradient of 270 years across a spatial gradient of 70 km. Typically these streams are initially fed by remnant ice with a pro-glacial lake creating a stable channel until the lake is no longer connected to the stream. In addition, Milner and co-workers (Milner et al., 2008, 2018) have assembled the longest single record of site-specific temporal primary successional sequence at one stream Wolf Point Creek (WPC) that extends to 40 years.

Initially, WPC was fed by ice and was cold (about 2 °C) and turbid (approximately 150 NTU) and the first macroinvertebrate colonizers were chironomids (*Diamesa* and *Paratrichocladius*) adapted to the inhospitable conditions. In particular *D. davisi* was found in large densities (>5000 m^{-2}) with no predators or competitors. At WPC these pioneer taxa were followed by mayflies

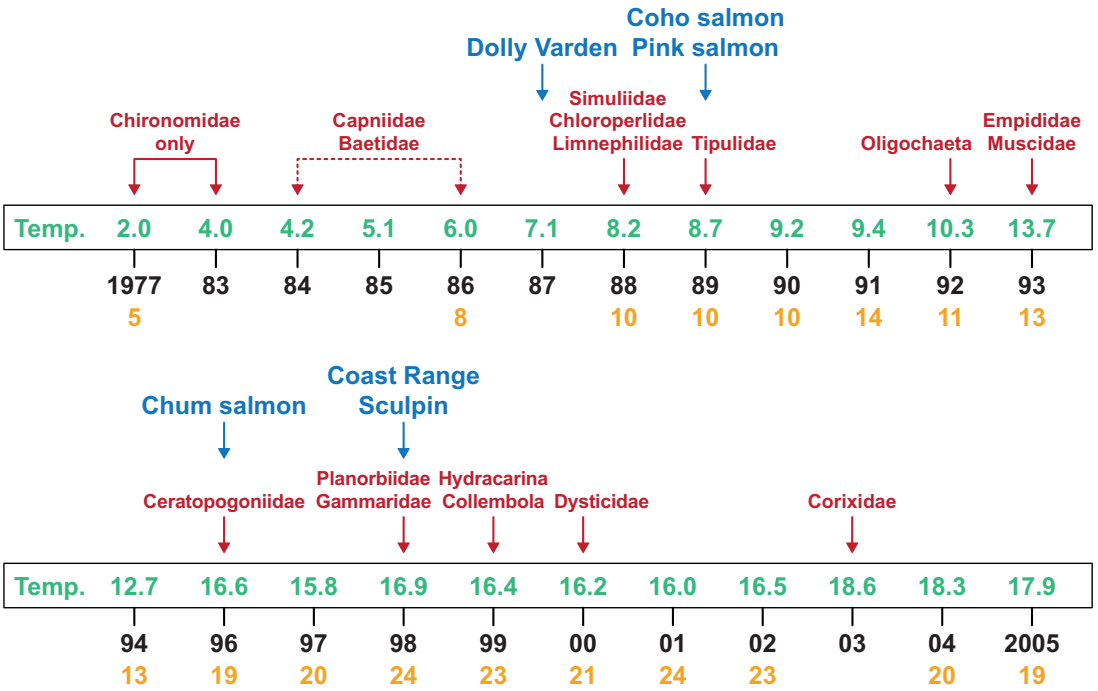

Fig. 3 Year of appearance from 1977 to 2005 of specific macroinvertebrate families and fish species in Wolf Point Creek, SE Alaska with the water temperature in green and the number of taxa orange below the year in black. After Milner AM, Robertson AL, McDermott MJ, Klaar MJ and Brown LE (2013) Major flood disturbance alters river ecosystem evolution. *Nature Climate Change* **3**: 137–141.

(Baetidae) and stoneflies (Capniidae) between 1984 and 1986, when maximum water temperature reached 6.0 °C. Blackflies (Simuliidae) and chloroperlid stoneflies were first collected in 1988. The first macroinvertebrate non-insects to colonize WPC were Oligochaeta in 1992, followed by snails (Planorbidae) and freshwater amphipods (Gammaridae) in 1998. Water beetles (Dytiscidae) colonized in 2000 and water boatmen (Corixidae) in 2003 as more pool habitat was formed in the stream (see Fig. 3). In alpine glacier-fed streams, new sites that open up as ice recedes are initially dominated by Diamesinae, but over time this group can decrease in abundance by up to 40% as stoneflies and mayflies colonize from downstream areas (Robinson et al., 2014).

Some of the early colonizing *Diamesa* species in WPC became extinct when water temperature increased, notably *D. davisi* which was not collected in August after 1992 when water temperature reached 10 °C. *Pagastia partica*, which first colonized WPC in 1986, was numerically dominant from 1990 through 1998. Initially it was considered that *D. davisi* became extinct due to being a cold stenothermal, but later experiments showed that this species was eliminated due to competition by *P. partica* and not water temperature (Flory and Milner, 1995). The chironomids *Orthocladius mallochi* and *Eukiefferiella gracei*, which colonized in 1988 and 1991, respectively, were both relatively abundant in the mid-1990s, but numbers subsequently declined. *Eukiefferiella claripennis*, first collected in 1986, was co-dominant in 2001 with *Cricotopus tremulus*, which first colonized in 1996. *Tanytarsus*, a genus that typically inhabits stable habitats, was dominant in 2004. *Paratrichocladius* was the only chironomid that has been collected throughout the entire record (1977–2018) (Milner et al., 2008).

Macroinvertebrate community assembly appears to have been initially strongly deterministic in the early successional sequence owing to low water temperature associated with remnant ice masses, in that similar patterns of macroinvertebrate succession were found in another new stream (Stonefly Creek) that emerged from ice recession later than WPC (Milner et al., 2011). However, as stream age and water temperature increased, macroinvertebrate colonization was also more stochastic, and taxonomic similarity between Stonefly Creek and Wolf Point Creek at the same stage of development was <50%. Dispersal constraints have also influenced the succession, as non-insect taxa required at least 20 years to colonize these new streams. Tolerance was suggested as the major mechanism of macroinvertebrate community assembly. Most taxa, with the exception of the cold-tolerant first colonizers, have persisted within the community following colonization, although relative abundance has changed markedly with time (Milner et al., 2011). Similar initial deterministic trends and the tolerance model were proposed for invertebrate community succession in streams affected by the Mount St Helens eruption in 1980 (Claeson et al., 2021).

Interestingly, WPC experienced two major floods in November of 2005 and during the summer of 2014 prior to sampling that year. These floods markedly reset the successional sequence causing the elimination of some of the later colonizing taxa. The November 2005 flood reset the community to approximately 15 years earlier based on taxa composition, and the summer 2014 floods reset an additional 5 years (see Fig. 4). Amazingly *D. davisi*, which became locally extinct in 1992, re-colonized after both flood events due to less competition and persisted for 2 years before becoming extinct from the community as numbers of other taxa increased (Milner et al., 2013, 2018). Slow flowing habitat did not recover after both flood events and pool-dwelling taxa (e.g., Gammaridae, Planorbidae, and Dytiscidae) have never recolonized to date.

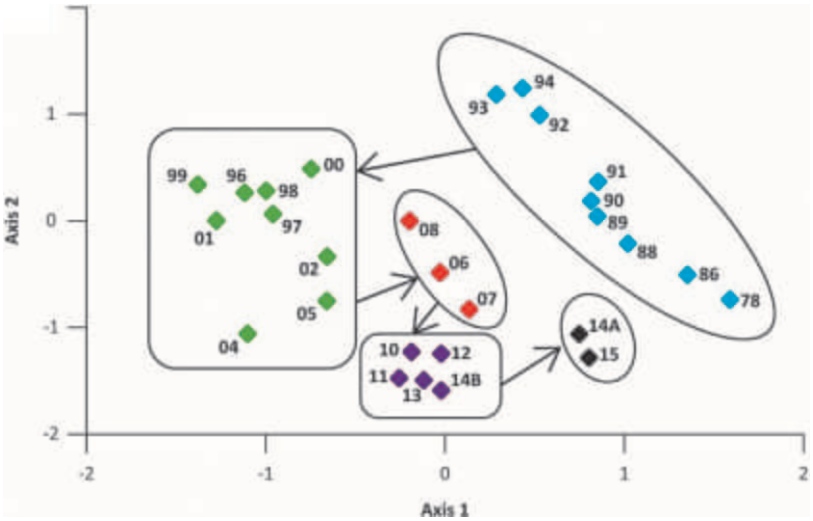

Fig. 4 Non Multi-Dimensional Scaling (NMDS) plot for macroinvertebrates from 1978 to 2015 using mean abundance data from 10 replicates collected in August/early September. 1978 to 1994 in blue represents early successional stages while 1996 to 2004 shows a later more mature successional stage in green. 2006 to 2008 in red shows a reset of successional trajectories after a major flood in November 2005 which shows some recovery 2010–2013 in purple. 2014 to 2015 in black shows a further reset after a second summer flood prior to sampling in 2014. Increased community diversity appears to the left of Axis 1. After Milner AM, Picken JL, Klaar MJ, Robertson AL, Clitherow LR, Eagle L and Brown LE (2018) River ecosystem resilience to extreme flood events. *Ecology and Evolution* **8**: 8354–8363.

Fish communities

Of the biotic communities, fish succession has been the least studied. One study of fish diversity of a restored large floodplain after connection to the upper Danube River showed that 46% of the species pool rapidly colonized after only 2 months (Pander et al., 2015). Colonization by fish of newly constructed habitats and channels is highly dependent on lateral and longitudinal connectivity and distance from colonizing source as evidenced in Glacier Bay (Milner et al., 2008, 2011). Anadromous fish have the advantage for colonization with glacial recession, but greater species richness was associated with older streams, with more habitat complexity and aquatic vegetation and algae, as observed in the Bering Glacier region of Alaska (Weigner and Von Hippel, 2010). Although the ever-changing aquatic landscape has been colonized by fish species typical of the region, some have evolved in atypical ways including populations of dwarf Dolly Varden (*Salvelinus malma*) and sympatric pairs of sticklebacks (*Gasterosteus aculeatus*) (Weigner and Von Hippel, 2010).

Autogenic effects on successional trajectories in streams

The role of autogenic (biotic or within community) effects on successional processes in streams have not been widely documented, particularly with relation to Connell and Slatyer (1977) models of facilitation and tolerance. A fascinating experimental study by Hammock and Bogan (2014) demonstrated that blackfly larvae facilitate diatom colonization through their production of silk as a substratum for diatoms that can then enhance later invertebrate colonizers. The authors compared this occurrence in streams to facilitation by nitrogen-fixing alder trees following glacial retreat enhancing later successional plant species. Additionally, experimental approaches showed that the net-spinning caddisfly, *Ceratopsyche bronta*, facilitated recruitment of later species by constructing their retreats and catch nets that increased microhabitat complexity (Cardinale et al., 2001). Similarly, Tumolo et al. (2019) showed that modification of the habitat by net-spinning Hydropsychidae caddis flies facilitated changes in the stream community.

Successional sequences in stream biofilms is driven primarily by algae, which modulate the microenvironment by reducing the physical effects of flow and by influencing community biofilm succession (Besemer et al., 2007). Colonization of river ecosystems by invertebrate grazers can be expected to lead to continual removal of biomass, thus limiting microbial biofilms and inducing continual turnover and successional sequences (Veach et al., 2016). Likewise invertebrate can graze on selected species and thereby influence algal communities and taxa abundance (Wellnitz and Rader, 2003).

Colonization by predators could initiate succession in streams. For example, climate change could facilitate predators being able to colonize further up-valley in alpine streams and thereby influence prey community composition and taxa abundance. Experiments have shown that when the predatory stonefly *Perla grandis* colonizes more upstream reaches in alpine streams, the abundance of *Baetis* spp. was depressed through direct consumption or predator avoidance and that their body size generally decreased (Khamis et al., 2015).

Legacies of the biota that survive a disturbance may influence the successional sequence that follows. Ledger et al. (2006) found in post-disturbance channels that the snail, *Radix peregra*, facilitated the settlement of filter feeders by removing algal growth and that the freshwater shrimp, *Gammarus pulex*, excluded or reduced abundance of subsequent invertebrate colonizers. There are also potential abiotic legacies like coarse woody debris that may influence successional recovery in streams after a disturbance.

The amphipod, *Dikerogammarus villosus* (known as 'the killer shrimp'), invaded western Europe via the Danube-Main-Rhine canal (van Riel et al., 2006). In some habitats, there is evidence that the beds of a previous invasive species (akin to a press disturbance), the zebra mussel, *Dreissena polymorpha*, facilitated the shrimp's invasion by providing habitat and food. The case of *D. villosus* provides a good example of how alterations to trophic interactions may lead to successional change in community structure and functioning and could be considered an example of "tertiary" succession. Stable isotope studies have shown that this small-bodied shrimp can actually occupy the same trophic level as predatory fish (van Riel et al., 2006). In addition, oligochaete worms, caenid mayflies, chironomids and tipulids are also particularly vulnerable to *D. villosus* predation (MacNeil et al., 2013), leading to successional changes in the benthic community.

Interactions with other ecosystems influencing stream succession

Stream systems do not exist in isolation from other ecosystems, particularly the terrestrial ecosystem, which can potentially influence succession in streams. Following glacial recession in Glacier Bay southeast Alaska, new watersheds are formed with vegetative succession occurring on the landscape. The development of riparian vegetation in a new stream in Glacier Bay with a stable channel due to an upstream lake markedly influenced colonization of the stream by certain invertebrate taxa, thereby playing an important role in the successional sequence of macroinvertebrates and overall assemblage development (Flory and Milner, 1999). Several features of riparian interaction were documented, including invertebrate use of willow catkins entering streams in summer and of submerged alder roots as a substrate for attachment and as a source of building material for caddisfly cases (Milner and Gloyne-Phillips, 2005). In a study of restored channels, woody riparian vegetation supported the development of the invertebrate assemblage by providing habitat (sites for oviposition and leaves for case building) and food sources (leaves for shredders; Winking et al., 2014). Riparian vegetation requires time for development before interacting strongly with the stream, so this can delay the successional pathway to the mature invertebrate community.

When Pacific salmon and other anadromous fish from the marine ecosystem enter freshwaters and construct redds on the streambed to lay their eggs during the summer/fall, substantial disturbance of the bed occurs that can alter invertebrate community structure and thus potentially initiate secondary succession in the disturbed patches (Moore and Schindler, 2008). Monaghan and Miner (2009) found that pink salmon (*Oncorhynchus gorbuscha*) redd construction caused $\sim 10\times$ reduction in overall invertebrate abundance and reduced invertebrate taxa richness from 18 to 10 in a 10 m reach. However, certain taxa, like simuliids, increased in abundance, suggesting that redd construction potentially facilitates the persistence of these fugitive taxa in the community. This biotic effect on succession is not true facilitation, because it does not improve the habitat for a later colonizer, but it is evidence of biotic effects on succession processes.

Refugia in streams influencing succession after recovery from disturbance

Rapid recovery from disturbances, like floods, may be enhanced by the close proximity of colonizers in refugia, from which taxa may re-colonize disturbed patches and influence the successional sequence of recovery. Most refugia in streams are characterized by extensive coupling of the main channel at a variety of spatial scales with streamside forests, floodplain features and groundwater like the hyporheic zone (Sedell et al., 1990). The hyporheic zone also affords invertebrates a refugia from floods and droughts allowing taxa to recolonize rapidly after subsidence of the event.

Anthropogenic allogenic (abiotic) effects on successional pathways

Humans can directly influence succession in streams via direct engineering activities in or adjacent to the stream channel (e.g., dam construction, culverting or channelization), major alteration of the land cover in the catchment (e.g., logging or urbanization) or diffuse/point source release of contaminants (Wallace, 1990). The impacts of such activities vary from months/several years for discrete events to decades for chronic contamination or physical habitat change. However, clear examples in the literature highlight the impact humans have on successional pathways in streams.

Cibils Martina et al. (2013) found that downstream of a dam, the successional sequence of epilithic algal communities was advanced by reduced current velocity and flow variation. However, upstream of the dam, frequent flow fluctuations caused sloughing of the biofilm thereby resetting the algal community to an early successional stage. By acting as barriers to dispersal, dams can alter successional trajectories following low and high flow disturbances (Liu et al., 2013). This is unsurprising, as differences in colonizing ability among taxa are major factors governing succession in stream invertebrate communities.

Clear cutting of forests can have immediate and long-term effects on macroinvertebrate succession in stream by changes in the energy base of the stream food web with increased autochthonous production enhancing scraper species with loss of shredders

(Haefner and Wallace, 1981). Conversely, afforestation of riparian zones can influence succession of periphyton communities with lower biomass, and diversity and increased small, low-profile, unicellular and stalked algal species when compared to streams flowing through regions with limited riparian tree cover.

Pesticide contamination can have significant implications for riverine macroinvertebrate communities with loss of sensitive species from impacted sites (Thompson et al., 2016). Pesticide impacted streams with forested headwaters can display enhanced recovery of invertebrate communities compared to streams in uniform agricultural landscapes that are more prone to local extinction and long-term shifts in climax community diversity and structure (Orlinskiy et al., 2015).

Summary

In this overview we have reviewed and synthesized publications since Fisher's classic chapter on stream succession (Fisher, 1983). Successional processes in streams have been compared with terrestrial and nearshore marine ecosystems (Table 2), highlighting that stream systems have some unique attributes. Specifically, successional process for most biotic groups in streams are more rapid than in other ecosystems, and in addition the role of refugia, legacy effects and linkage to other ecosystems is more important in stream ecosystems.

A matter of great debate in the literature is whether successional pathways in streams are deterministic or stochastic. Fisher (1983) thought that the dominant mechanism for macroinvertebrate succession was stochastic. However, from a review of colonization by lotic invertebrates, Mackay (1992) concluded that recovery from disturbance was not stochastic, as recurring ecological patterns among early colonizers occurred. For macroinvertebrate primary successional sequences with long temporal records, it is probable that both mechanisms occur. Initially deterministic control will occur when channels have low water temperature and unstable habitats that are suitable for a limited number of taxa. But as conditions become more generally favorable, there is a switch to stochastic control, as seen a few years after glacial recession or volcanic eruptions. Microbes exhibit successional dynamics highly influenced by deterministic processes such as physical conditions, but may also be controlled by stochasticity i.e., random speciation or extinction events, dispersal or drift during certain stages of succession.

Traits of the different biotic groups are important in terms of successional strategies. For example, macroInvertebrate succession of new stream habitat is shaped by a number of factors including distance from the regional species pool, dispersal capacity and life history traits (e.g., number of generations per year) of colonizing taxa, suitable habitat for colonization, and timing of dispersal. Differences in colonizing ability among taxa is one of the major factors that creates succession in stream invertebrate communities.

An appreciation of successional patterns in streams is critical, as this understanding will lead to greater understanding of the management of biodiversity and thus ecosystem processes in these dynamic and changing ecosystems. Understanding successional processes also has important management implications in terms of planning and implementing appropriate restoration approaches in the face of both natural and anthropogenic disturbances.

Table 2 Comparison of the main elements successional processes for stream, terrestrial and nearshore marine ecosystems.

Process	*Streams*	*Terrestrial*	*Nearshore Marine*
Dominant Mechanism of succession	Tolerance dominant. Many cases of inhibition (Hammock and Bogan, 2014; Cardinale et al., 2001)	Facilitation and Inhibition	Mostly inhibition (Sousa, 1979)
Autogenic/ Allogenic	Mostly Allogenic	Autogenic	Both autogenic/allogenic
Relative Time Frame	Rapid for microbes, algae and invertebrates, longer for fish (<3 years)	Long term (often >50 years)	Medium term
Deterministic v Stochastic	Both - often deterministic where abiotic variables dominate early in successional sequence	Invertebrates mostly deterministic (Kaufmann, 2001) Plants deterministic/stochastic	Mostly stochastic
Climax Community?	Possible, but highly disturbed relatively to other ecosystems so resets to earlier stage	Yes, except where disturbances occur	Relates to disturbance sheltered shores more likely to have a climax community
Disturbance regimes over time	Highly disturbed over large areas occurring frequently, except for groundwater streams.	Only small percentage disturbed large areas not disturbed relatively over time.	Relates to shore exposure—exposed high disturbance frequently, sheltered shores less so
Use of refugia	For certain disturbances like floods and droughts extensive particularly the hyporheic zone	Potentially for invertebrates	Not widespread
Legacy Effects	Evident—both biotic and abiotic	Low	Low
Links to other ecosystems	Succession affected by the riparian zone and spawning salmon from the marine ecosystem.	Riparian zone succession linked to stream flooding.	Negligible link

See Also: Structures and functions of Inland Waters - Rivers: Ecological and Evolutionary Consequences of Disturbance in Freshwater Ecosystems

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Dispersal in Stream Networks: Meta-populations and Meta-communities

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Dendritic network The landscape of stream networks are dendritic, mimicking the dendrites of animal nervous systems. In a dendritic network, there are no discrete nodes or patches; habitat is contiguous throughout the network. The branching nature of dendritic networks affects how materials and information move along the network between sites. In a similar fashion, the dendritic nature of stream networks affects how organisms move between locations within the network.

Dispersal Dispersal is the movement of organisms between populations and communities. Dispersal may be an active behavior or a passive process.

Drift dispersal The active or passive dispersal by aquatic organisms as they become entrained in the water column and carried downstream.

Drift Paradox Due to the downstream drift of aquatic insects and the lack of upstream sources of recolonization, logic suggests that upstream reaches could be left devoid of individuals. Experimental work has demonstrated that aerial upstream flight by adult life stages allows for recolonization of upstream areas.

Graph-based dispersal proxy A proxy based on the distance between populations and communities within the stream network. There are numerous ways to measure this distance, including overland dispersal between sites as well as stream network distance between sites.

In-network dispersal (IND) This dispersal is limited to the confines of the aquatic habitat of the stream network. The dispersal of obligate aquatic taxa, such as fish and some macroinvertebrates, is restricted to the aquatic habitat of streams.

Meta-community An extension of meta-populations, a meta-community is a network of communities connected by the dispersal of organisms between communities.

Meta-population A network of populations on a landscape connected by dispersal.

Network Position Hypothesis Suggests that the position within a stream network affects patterns of biodiversity and community assembly. As you move across a stream network, levels of dispersal, habitat conditions, and species interactions may vary, and this variation may produce predictable patterns based on network location.

Organismal-based dispersal proxy A proxy based on an organismal attribute or trait. These traits may be directly measured, such as body size, or categorical, such as dispersal ability (weak versus strong).

Out-of-network dispersal (OND) Dispersal that occurs outside the aquatic habitat of the stream network. For instance, salamanders and crayfish may disperse overland between headwater streams and adult aquatic insects may fly between adjacent streams and networks.

Radio telemetry A technique to monitor dispersal that relies on the generation and detection of radio waves to identify the location of aquatic organisms. Common methods utilize PIT tags (passive integrated transponder tags).

Introduction

Meta-approaches in ecology

The substantial variation in dispersal that exists between organisms contributes to the structuring of ecological populations and communities in space and time. Most organisms find a way to get around on a landscape, including sessile organisms like plants and corals that use their reproductive stages as a major vehicle for dispersal. The influences of dispersal were included in a number of approaches aimed at understanding the distributions and diversity of species, including the Island Theory of Biogeography (MacArthur and Wilson, 1967), and Supply Side Ecology (Sale, 1977), but these approaches addressed the influence of dispersal at very large and very small scales, respectively. However, the influence of dispersal at a landscape or meso-scale has historically been one of the underappreciated aspects of the ecology of organisms, populations, and communities.

Two bodies of theory, meta-population ecology and meta-community ecology, emphasized the incorporation of meso-scale dispersal of organisms into the study of the distributions and abundances of species. A meta-population is a spatially separated group of populations connected on a landscape by the dispersal of individuals (Hanski and Gilpin, 1997). The multi-species extension of this idea, a meta-community, is a group of multi-species communities connected on a landscape by the dispersal of one or more species (Leibold et al., 2004). These ideas are conceptually linked in that they (1) emphasize the importance of dispersal in structuring populations and communities and (2) necessitate a multi-scale approach in their investigation. Local scales are defined by the structure and dynamics of a single population or a single community on a landscape, while regional scales are the aggregate properties of all local populations or local communities on a landscape.

Both meta-population and meta-community theory have had profound impacts on the field of ecology, by presenting testable predictions for empiricists and catalyzing research that includes mathematical theory, simulation studies, survey approaches, and experimental manipulations. Virtually every subfield of ecology has benefitted from the insight of meta-approaches, including the study of diversity in stream and river networks. However, the study of meta-patterns in riverine ecosystems presents challenges and opportunities that are quite unique.

Meta-approaches in stream networks

By their very nature, stream networks present challenges to meta-scale approaches. Prototype meta-populations and meta-communities were defined as distinct populations or communities on a landscape that are connected by dispersal (Fig. 1). The populations and communities within these networks exist in habitat patches with discrete boundaries, such as a forest patch in a grassland. In contrast, riverine systems are constructed dendritically (Fagan, 2002; Grant et al., 2007). Dendritic systems—so named because of their structural similarity to the dendrites of animal nervous systems—are linear, hierarchically-branching continuous habitat (Fig. 1); thus there are no discrete patches in dendritic systems (Fagan, 2002; Grant et al., 2007). The lack of distinct patches also leads to the lack of distinct boundaries by which to define the populations and communities that are members of a meta-population or meta-community. A second challenge is that, while much of the theory constructed from meta-approaches assumes that organisms disperse randomly, dispersal in river networks is often strongly directionally oriented. Fish, amphibians, and both the larval and adult stages of aquatic insects have been found to move in fairly specific and repeatable directions relative to the downstream flow of water (Mackay, 1992; Hershey et al., 1993; Skalski and Gilliam, 2000; Lowe, 2003; Petersen et al., 2004;

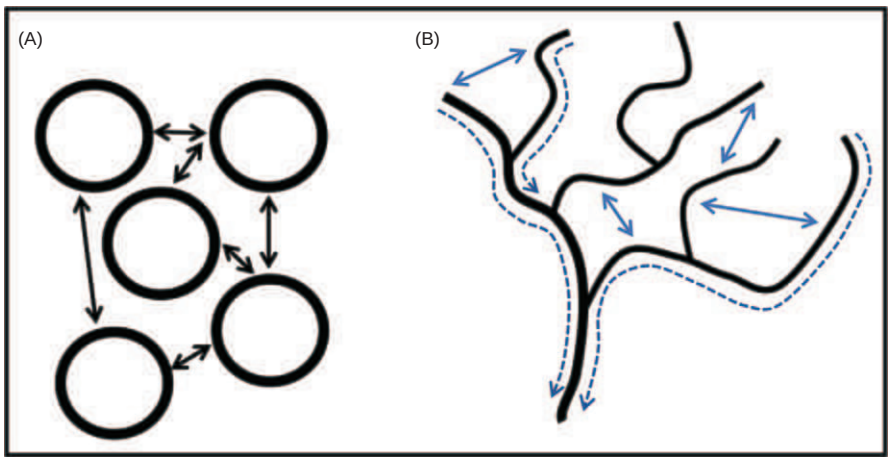

Fig. 1 Schematic examples of aquatic networks. (A) A "classic" aquatic meta-community in which habitat patches are fairly discrete entities like ponds, and dispersal of species occurs among those patches. (B) A stream dendritic network in which there are two modes of dispersal: In Network Dispersal (IND), represented by dotted arrows, is dispersal via waterway within the network and that often has a distinct downstream bias, and Out of Network Dispersal (OND) represented by solid arrows occurs when organisms walk, crawl, or fly overland to other points in the aquatic network.

Finn et al., 2006). However, while these two properties of river networks initially challenged the utility of meta-population and meta-community approaches in riverine systems, both sets of theory have proven to be adaptable and broadly applicable for understanding the diversity, distribution, and abundances of species in river networks.

Even though meta-populations and meta-communities are often conceived and visualized as sets of discrete patches (Fig. 1), this particular depiction does not reflect an actual requirement of meta-approaches. Delineating "patches," even in continuous habitat, allows the application of the same theory and approaches that are applied in landscapes with spatially distinct patches. This tactic is particularly effective in networks where habitat characteristics are expected to differ depending on location in the network. Although stream networks are continuous dendritic habitat, that habitat is not uniform throughout. This foundational principle was codified by the River Continuum Concept which details how a large number of environmental parameters predictably change from the smallest headwater streams to progressively larger streams and rivers (Vannote et al., 1980). Along this gradient, stream size and discharge increase, while stream gradient and average substrate particle size decrease. The base of the stream food web also shifts progressively from leaf-litter decomposition to increasing amounts of algal primary production (Vannote et al., 1980). While these changes in stream environmental characteristics occur gradually down the length of a stream network, delineating spatially separated "patches" within this network allows an investigator to not only apply meta-approaches to river networks, but is also likely capture the environmental heterogeneity that creates unique conditions in different parts of river networks. Additionally, environmental conditions are not the only predictable differences between sections of stream networks; dispersal abilities and propensities vary predictably with network location.

Dispersal in stream networks

The dispersal of stream organisms is highly variable among taxa, and one major difference among taxa is whether or not their dispersal is restricted to inundated sections of the stream network. Fish and snails, for example, are strictly limited to in-stream dispersal, while a number of aquatic taxa including crayfish, amphibians, and some aquatic insect larvae have the ability to make limited journeys across land. Thus, in stream networks, there are two major dispersal modes: in-network dispersal (IND), and out-of-network dispersal (OND) (Fig. 1). Aquatic insects, the most commonly studied organisms in streams, actually use both IND and OND during their life cycles. In their larval forms, most aquatic insects are limited to IND by either crawling or allowing themselves to be swept along in stream current, a process termed "drift." Initially, drifting by macroinvertebrates was thought to be accidental or passive and that entry into the drift was the product of organisms losing purchase on benthic substrate and being swept away by current. While such passive drift entry certainly occurs, especially in high flow conditions, subsequent investigations have revealed that drift entry is most often an active process used to change foraging locations or escape predation (e.g., Kohler and McPeek, 1989). However, as stream insects meta-morphose into reproductive adults, most aquatic insects possess wings that allow them considerable freedom for OND. The typical life cycle of an aquatic insect is a prolonged larval stage, followed by a short-lived winged adult stage that quickly reproduces and then deposits eggs in or near a stream. These winged flying stages not only allow OND, but may be a primary mechanism for recolonizing upstream sites, especially headwaters, whose populations have been denuded by constant downstream drift (Hershey et al., 1993, but see Anholt (1995) for alternative resolution to the so-called Drift Paradox).

As with environmental conditions, dispersal dynamics of organisms may change with network position. With highly mobile organisms like fish, dispersal is rarely limited by the physical ability of a species to move between stream networks and river basins. However, a number of abiotic factors limit the ranges of fish in stream systems. For example, fish are often excluded from upstream sections of stream networks because of perennial drying or lack of adequate depth, or they may be excluded from some sections of stream networks because the stream thermal regime lies outside of a species' tolerance range. The effect of network location on benthic invertebrates may be even more profound. The major IND mode of benthic macroinvertebrates is drifting, which has been measured to occur over two kilometers (Hershey et al., 1993), and drift dispersal is unidirectional because water flows downhill. Additionally, drift propensity and distance are related to discharge, stream substrate, and local densities of similar species (James et al., 2009). Taken together, these factors suggest that dispersal has a considerably stronger influence on macroinvertebrate diversity and distributions in larger streams when compared to smaller, headwater streams (Brown and Swan, 2010). This conclusion has profound implications for the factors that dictate diversity and distributions of species in river networks.

The Network Position Hypothesis (NPH; from Schmera et al., 2018, based on hypotheses presented in Brown and Swan, 2010) suggests that the factors that control diversity and distributions of organisms in stream networks depend on the position of a population or community within a river network. Based on the NPH, the influence of IND is expected to increase from smaller to larger streams within a river network, thus the structuring forces on a population or community are predicted to shift from more local factors like environment and species interactions, to more regional controls driven by the movement of organisms. The NPH has been evaluated in a large number of studies primarily focusing on benthic invertebrates and fish. The results of these investigations have been mixed, with some studies strongly supporting the NPH (e.g., Wilson and McTammany, 2014; Tornwall et al., 2017; Brown et al., 2018), some studies producing results counter the NPH (e.g., He et al., 2020), and some studies showing mixed or equivocal results (e.g., Schmera et al., 2018; Henriques-Silva et al., 2019). Taken together, these studies suggest that the NPH does capture a fundamental pattern in river network systems, but that the overall model may be strongly modified by context. Those contexts include the life histories and dispersal abilities of organisms involved, the spatial heterogeneity captured in a river network, and human modifications to stream networks.

Meta-approaches have had a strong influence on the study of stream biodiversity. Not only have they provided new theoretical foundations for understanding the biodiversity of organisms in running waters (e.g., Brown and Swan, 2010; Holt and Chesson, 2018), but they have also provided empirical tests of these theories (e.g., Swan and Brown, 2017; Tornwall et al., 2017) and described new patterns of biodiversity in river networks. Additionally, they have informed management of threatened native species (e.g. White and Wagner, 2021). Foundational to applying meta-approaches is the study of organismal dispersal in river networks.

Studying organism dispersal in streams

Challenges to studying dispersal in streams

Studying dispersal in a meaningful way is difficult for many organisms (Heino et al., 2017). Some organisms like fish and amphibians can be marked, tagged, or tracked using various individual marking techniques, radio transponders, or passive integrated transponder (PIT) tags, and there are numerous examples of studies that use such techniques to infer dispersal behavior (e.g., Bubb et al., 2002; Hedden and Gido, 2020). However, invertebrates are the most commonly studied organisms in stream and river networks (Tornwall et al., 2015), and to date, no practical method has been developed to directly monitor the movement of benthic invertebrates with the possible exception of PIT tagging in large macroinvertebrates like crayfish (Bubb et al., 2002). For smaller benthic invertebrates like aquatic insects that make up the vast majority of benthic biomass and diversity, such marking or tagging is either methodologically impossible or impractical for three reasons. The first is the limitation imposed by the small size of most benthic macroinvertebrates, many of which are <1 mm in length and which rarely exceed 2 cm in length, a size that prohibits the use of radio or PIT tagging. Secondly, there is a low probability of recapture of marked organisms. Smaller invertebrates could conceivably be marked using a surficial marking like latex paint. However, due to the small size and high densities of these organisms, the probability of recapturing organisms marked in such a manner would be quite low. Additionally, great care would be necessary when marking these small organisms to prevent the marking compound from hindering organism function by coating gills or sensory structures. Third, insects molt, and some taxa molt frequently. Each molt would shed the exoskeleton and thus any superficial marks on the organism.

Given these limitations, there has been a considerable amount of creative science devoted to inferring the dispersal behavior of stream organisms. For larger organisms, the methods are often more direct. However, for smaller organisms like stream insects, investigators rely on inferential methods that include estimating species dispersal pattern by their abundances in drift samples, isotopic tracing of labeled populations, scaling-up based on the results of small-scale controlled studies, and modeling studies that predict dispersal based on known organism traits. Below we categorize and describe the major ways that the dispersal of aquatic organisms is either directly studied or indirectly inferred.

Approaches for studying the influence of dispersal in river networks

Movement monitored

Capture-mark-recapture work in stream meta-populations has mainly relied on radio telemetry. These approaches have been used to study the dispersal of larger stream organisms, predominantly fish, but also crayfish and salamanders, and even river otters. After stream organisms are captured and radiotagged, radio transponders may be placed along the stream bank to detect organisms as they move, or organisms may be detected within the stream itself by more active recapture or tracking techniques. For example, Hedden and Gido (2020) used mark-recapture methods to investigate the effects of stream drying on fish communities in stream networks. Deploying PIT antennas upstream and downstream of a perennial stream, the researchers found that stream fishes recolonized rewetted reaches. White and Wagner (2021) also used radio telemetry to monitor the dispersal of wild brook trout (*Salvelinus fontinalis*) in a small network in Pennsylvania (United States). They tracked the movement of the trout by actively monitoring them through the stream network to find that half of the tagged fish were sedentary. The mobile fish that dispersed moved over a short duration of time, and this behavior may be important for maintaining connectivity within the stream network.

For smaller organisms, tagging with radiotags is not currently possible. For stream insects, researchers have marked aquatic larvae by enriching the stream benthos with stable isotopes. As aquatic insect larvae feed on stream periphyton (i.e., algae and attached organic detritus), they too are marked with the stable isotope. The insect larvae can then be caught in stream drift nets. To understand the drift dynamics of stream insects, Hershey et al. (1993) captured drifting *Baetis* may fly larvae along the Kuparuk River in Alaska, determining that the larvae drifted at least 2.1 km downstream over the course of the Arctic summer.

Stable isotope enrichment has also been used to understand the aerial flight dynamics of adult stream insects. After enriching the stream benthos, researchers have set up nets at locations within and across stream networks to capture the marked insects. Briers et al. (2003) used this approach to understand the dispersal dynamics of stonefly populations (*Leuctra inermis*) in Wales, becoming the first to show insect dispersal between streams. Macneale et al. (2005) used a similar approach at Hubbard Brook Experimental Forest, New Hampshire (United States), where they added enriched nitrogen to streams before capturing adult stoneflies (*Leuctra ferruginea*) to identify their dispersal patterns. Their work demonstrated that stonefly populations can be connected across catchments within one generation via aerial dispersal.

To detect trends in species movement, there are a variety of traps and nets that may be used to capture stream organisms as they move within and across networks. Researchers often use Malaise traps to capture adult insects, drift nets for larval stream insects, and various traps, such as minnow traps, for fishes (Baxter et al., 2017). Malaise traps are set up along stream corridors and various distances from streams to capture flying adults as they move around stream networks. Petersen et al. (2004) trapped adult insects in malaise traps within a stream network and identified the crucial role that the stream corridor can play in the dispersal of adult aquatic insects. Likewise, traps have also been used to extensively estimate the movement of flying adult insects in urban stream corridors (Smith et al., 2015a, 2015b). Drift nets are deployed to catch the larval stages of aquatic insects as they drift in the current downstream, and they have been used in a large number of studies to produce estimates of dispersing aquatic insects and to infer how this dispersal behavior influences meta-population and meta-community patterns (e.g., Lancaster and Downes, 2017a, 2017b). Similar techniques can also be used for fish, including weir traps. For example, Schlosser (1998) used weir traps to demonstrate that the creation of beaver ponds was the primary factor driving the dispersal of fish to upstream reaches.

However, the measures of organism movement derived from the use of nets and traps have to be interpreted with extreme caution for two reasons. First, temporal variability in movement patterns can be profound. For example, aquatic insect drift density changes on a diel cycle, with the majority of drift occurring at night (Waters, 1965), so studies need to integrate both diel and diurnal movements. The second concern is that some organisms may actively avoid traps, so trapping may be an underestimate of actual dispersal behavior.

Organismal-based proxies

Due to the limitations of directly monitoring the dispersal of stream organisms within and between stream networks, researchers often turn to organismal-based proxies to infer dispersal. These proxies may include traits-based approaches that utilize organismal attributes relating to size, dispersal ability, and dispersal mode, as well as approaches that examine the population genetic structure and the natural isotope abundance of stream organisms. For symbiotic stream organisms, the dispersal of the host may also be used to understand symbiont dispersal.

Traits relating to size, such as body size, wing size, or fin size, are commonly used as proxies for dispersal ability. Wing morphology is also used as a proxy to understand dispersal dynamics in stream networks. Over the course of 3 years, Lancaster and Downes (2017a, 2017b) measured the size and shape of the wings of *Ecnomus* caddisflies. Pairing this information with data from benthic samples that allowed them to categorize individuals as residents or immigrants, they were able to determine that wing morphology may serve as a proxy for dispersal ability.

For aquatic insects, researchers often rely on the dispersal traits available in published trait databases to examine the role of dispersal in community assembly. Brown and Swan (2010) used a traits-based approach to examine how the dispersal ability and mode of stream macroinvertebrates affected patterns of community assembly across three Maryland (United States) stream meta-communities. Using traits for both adult and larval dispersal, they determined that dispersal-driven dynamics were more important in well-connected mainstem sites within the river network, while more isolated headwater sites were driven by local conditions.

Grönroos et al. (2013) applied a similar approach to investigate how the dispersal mode of aquatic insects affected community assembly of stream macroinvertebrates. They grouped the macroinvertebrates based on whether the larval stages of the organisms were active or passive dispersers and whether the adult stage was aquatic or terrestrial. They found that macroinvertebrates with an active larval dispersal stage and a terrestrial flying adult stage were more likely to be affected by the environmental conditions of the stream network (such as sediment size and flow conditions), suggesting that those organisms may be better able to track environmental conditions.

Examining the population genetic structure of stream organisms can be used as a proxy for dispersal as it may provide insight into gene flow between stream populations. Alp et al. (2012) examined the population genetics of two aquatic species with different dispersal strategies, a baetid mayfly (*Baetis rhodani*) and an amphipod (*Gammarus fossarum*). This work revealed that the mayfly, with its overland dispersal capabilities and its generalist niche, had little genetic structure across the river network. The population genetic structure of the amphipod, on the other hand, was impacted by its dispersal limitation within the stream network.

Historically, population genetics work has examined processes that occur over larger spatiotemporal scales. Recently, including within the freshwater ecology literature, researchers have been using population genetics studies to understand community assembly and processes at finer spatial scales. Yaegashi et al. (2014) used a population genetics approach to investigate the population genetic structure of the caddisfly *Stenopsyche marmorata* across four stream networks. Through this approach, the researchers found that the dispersal distances inferred from genetic work were similar to those distances measured for one generation in the field. Kelson et al. (2015) also used a fine-scale genetics approach to examine the genetic structure of brook trout (*S. fontinalis*) within a New Hampshire stream network. This study revealed the effects of isolation due to waterfalls on the genetic structure of the meta-population as well as the dispersal of highly migratory individuals across the network. As demonstrated by Kelson et al., population genetics studies at fine scales within river networks can reveal insights that may improve conservation and management strategies.

The stable isotopic signatures of species may provide clues to their dispersal in stream networks. Cook et al. (2007) analyzed isotopic data alongside the population genetics of the southern pygmy perch (*Nannoperca australis*) to examine dispersal across a stream network. This approach allowed them to determine that at least half of the fish sampled were residents of the stream where they were captured, suggesting little population connectivity within the network.

For freshwater species that participate in symbioses, one way to understand the dispersal of the symbiont is to determine the dispersal of its host. Terui and Miyazaki (2015) studied the dispersal of the freshwater mussel *Margaritifera laevis* based on the dispersal of its host fish, *Oncorhynchus masou masou*. After identifying the location of mussel beds within the river network, the researchers conducted fish sampling during the seasons of symbiont larval attachment and detachment periods. With this approach, they found that fish that were "tagged" with mussel larvae dispersed over four kilometers, demonstrating the importance of the host for symbiont dispersal across the river network.

Graph-based proxies

To understand the role of dispersal in stream networks, researchers often use graph-based proxies to infer dispersal based on the distance between populations and communities (Heino et al., 2017). These proxies differ based on which metric is used to quantify distances between sites in the network (Fig. 2). Often, ecologists will utilize more than one graph-based proxy in their study and compare how the various distance methods better describe dispersal within and between networks. In addition, certain proxies may be better suited for certain taxa or life stages. For instance, Euclidean distance, or the overland, straight-line distance between sites, may be a more appropriate proxy for taxa with both aquatic and terrestrial life stages or for the adult life stages of aquatic insects. On the other hand, for taxa that passively disperse with the current, dispersal distance may be better described with network distance, a graph-based proxy that relies on the contours of the stream network and/or flow distance, which accounts for the direction of dispersal based on streamflow (upstream versus downstream). To study community assembly dynamics in a Swedish stream meta-community, Göthe et al. (2013) employed all three of these graph-based proxies: overland (Euclidean) dispersal, network (along-stream) dispersal, and flow (directional downstream) dispersal. This approach, coupled with their traits-based analysis, allowed them to identify the role of these different dispersal strategies in structuring stream communities and how this role changed with taxa, season, and spatial scale.

In addition to relying on linear distances for graph-based proxies, stream ecologists have developed proxies that utilize circuit theory to study dispersal (Cañedo-Argüelles et al., 2015). For instance, the topographical distance between study sites can be used to account for the effect of landscape features on dispersal, with species traveling downhill facing lower resistance to movement between sites. Stream organisms also have to contend with the intermittency of aquatic habitats in stream networks. This circuit theory-based approach can also be extended to intermittent networks. Here, species traveling between sites that are separated by perennial flows face lower resistance to dispersal.

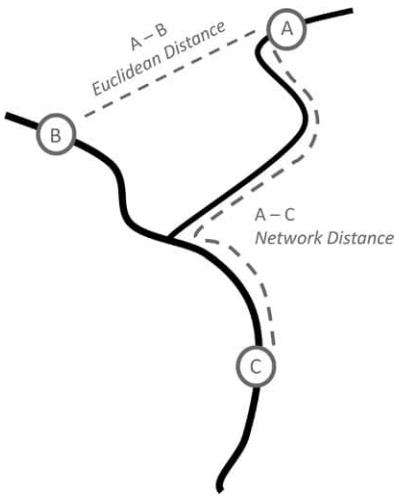

Fig. 2 Illustration of measures of distance in river networks using three hypothetical sampling points, A, B, and C. Euclidean distance is the shortest distance between two points, illustrated by the distance between sites A and B. Network distance is the distance between points, following the contours of the river network, illustrated by the distance between sites A and C.

Experimental approaches

Experimental approaches can be used to disentangle the role of dispersal in driving patterns of biodiversity and community assembly in river networks (Fig. 3). Microcosm experiments have been effectively used to test meta-population and meta-community theory in dendritic systems. Using protozoan and rotifer communities, Carrara et al. (2012) created meta-community networks with different levels of connectivity and examined how network configuration affected patterns of diversity. With this approach, they were able to experimentally demonstrate that the dendritic connectivity of stream networks can produce different patterns of biodiversity than in networks with higher levels of connectivity. Altermatt and Fronhofer (2018) also used a microcosm approach to test how population densities varied within a dendritic network based on network configuration and position within the network. This work confirmed previous theory that communities connected to both headwaters and central nodes emerged as those with the highest population densities.

Investigating the dispersal dynamics of stream organisms is not only important for understanding biodiversity patterns and community assembly, but also for developing a knowledge base for how stream communities will respond to certain management strategies, such as stream restoration. A growing body of recent literature has set out to understand how communities at different locations within stream networks respond to disturbance and habitat manipulation and what role dispersal plays in the resulting community assembly dynamics. Tornwall et al. (2017) manipulated stream habitat complexity within headwater streams and at mainstem sites within stream networks. Only the communities of the headwater streams were affected by the manipulation, providing evidence in favor of the NPH. Similarly, Lancaster and Downes (2017b) manipulated the retention of detritus in a stream to disentangle the roles of environmental condition and dispersal in structuring macroinvertebrate communities. The manipulation revealed an interaction between resource levels and dispersal in which areas with augmented resources were quickly colonized by species not present before the manipulation.

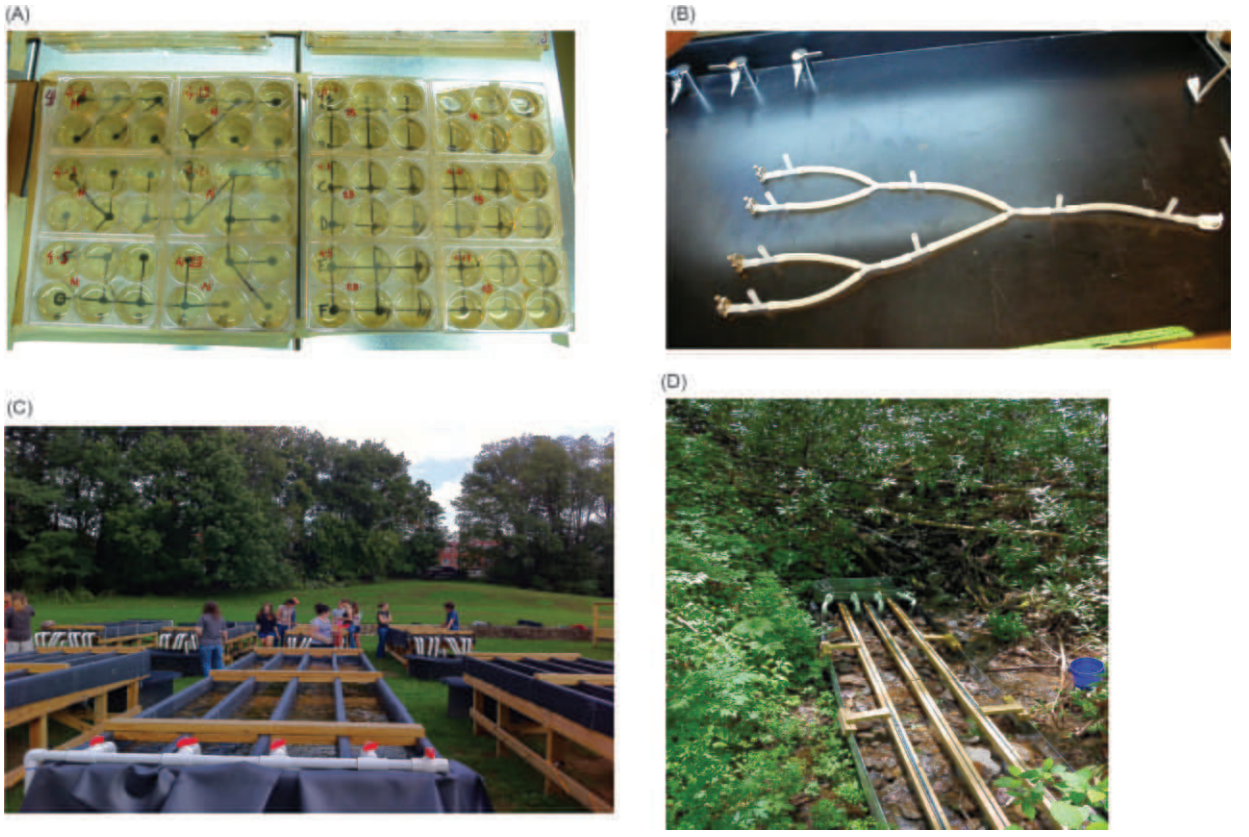

Fig. 3 Representative experimental methods for investigating dispersal in stream meta-communities. (A) Microcosms consisting of eight protist species. Network architecture was controlled by the transfer of medium between "connected" local communities. From Carrara et al. (2012), photo by Florian Altermatt; (B) Microcosms consisting of 14 protist species and 1 rotifer species in physical networks of tubing. From Seymour et al., 2016; photo by Florian Altermatt; (C) Replicated flume systems. Each flume set consisted of four recirculating flumes colonized by macroinvertebrates from local streams. Brown et al., 2018 used eight sets of these flumes to test the influence of dispersal and community source pool. Photo by Chris Swan; (D) In-stream flume system. Flumes are actually located in stream beds but the flumes can be manipulated. In this case, nets over the outflow valves (not shown in this picture) reduced in-network dispersal, while screens over some of the channels (not shown in this picture) prevented aerial dispersal. This research is currently in-progress. Photo by Bryan L. Brown.

Stream ecologists are also experimentally investigating how dispersal mode influences community dynamics and stability. Baumgartner and Robinson (2017) used a field experiment to investigate how upstream active dispersal modes (swimming and crawling) and aerial dispersal dynamics influenced the recovery of agricultural streams following disturbance. After disturbing the uppermost reaches of the streams, the researchers blocked aerial dispersal from half of the stream to differentiate the role of aquatic and aerial dispersal in the colonization dynamics of stream macroinvertebrates. While they didn't find an influence from aerial dispersal, they did find that aquatic, upstream dispersal allowed for the stream benthos to recover rapidly following disturbance.

Theoretical modeling

Modeling based on theoretical principles is a longstanding tradition in ecology. The primary utility of theoretical modeling is that it allows for "tests" of hypotheses that cannot be performed practically, often because of methodological or temporal limitations. Accordingly, theoretical models have strongly influenced thinking on the consequences of dispersal in stream meta-populations and communities.

Early contributions of theoretical modeling in stream networks addressed the so-called "Drift Paradox." The Drift Paradox recognized that, despite empirical measures of large numbers of organisms drifting in a downstream direction, the small headwaters of streams did not become depopulated through time. Initial resolutions to the paradox theorized that adult insect flight was upstream-biased and promoted recolonization of headwaters, and these theories were supported by numerous observations of upstream-biased flight (Hershey et al., 1993; Williams and Williams, 1993). However, such bias was not observed for all stream insects, and the hypothesis did not explain the persistence of non-flying headwater species like amphipods. Modeling studies of the Drift Paradox suggested that an upstream bias in adult flight was an unnecessary condition for promoting persistence in headwaters. Rather, a combination of random or unbiased dispersal and density dependence of populations could theoretically account for persistence (Anholt, 1995; Kopp and Allen, 2021).

Theoretical modeling has also been largely responsible for the appreciation of the effects of dendritic structure on organism dispersal in stream networks. Meta-population modeling of organisms in dendritic networks suggested that the size and architecture of stream dendritic networks strongly affected meta-population persistence and gene flow, and that fragmentation in dendritic networks could have highly variable effects that depended on the specifics of network architecture (Fagan, 2002; Chaput-Bardy et al., 2009; Grant, 2011). Other work extended similar concepts to multi-species communities in dendritic networks. Insights from this work include elucidating the role network architecture and dispersal tradeoffs between species create patterns of community composition in river networks (Auerbach and Poff, 2011). In addition, modeling work has shown that that network structure affects the spread of Proliferative Kidney Disease in salmon (Carrara et al., 2012) and that the stability of communities in river networks is promoted by asynchronous fluctuations in populations at different parts of a network (Anderson and Hayes, 2018). Species coexistence in river networks largely depends on the spatial heterogeneity of environmental conditions in a network and how that heterogeneity interacts with effects of the network on species' dispersal (Holt and Chesson, 2018).

Conclusion

Meta-approaches have permeated much of the theory and practice of ecology in the last few decades, first through the introduction of meta-population theory (Hanski and Gilpin, 1997) and later through meta-community theory (Leibold et al., 2004). Both of these concepts link local-scale patterns, like those occurring in a single stream reach, to larger-scale patterns that occur at the scale of multiple stream reaches, whole watersheds, or even entire river drainages (Schindler et al., 2010). The link between those scales is the dispersal of organisms. The growing influence of meta-frameworks highlights the importance of being able to accurately measure or estimate the dispersal of aquatic organisms.

Case studies of scientific investigations of dispersal in stream networks.

Investigative Method	*Technique*	*Method III*	*Taxa*	*Biological scale*	*Name of site*	*Country*	*Source*
Movement monitored	Capture-mark-recapture	Radio telemetry	Crayfish	NA	Rivers Wharfe and Urfe	England	Bubb et al. (2002)
			Fish	NA	Johns Creek network	Virginia, United States	Albanese et al. (2003)
			Fish	Metacommunity	Kings Creek	Kansas, United States	Hedden and Gido (2020)
			Fish	Metapopulation	Loyalsock Creek	Pennsylvania, United States	White and Wagner (2021)
		Red latex dye	Fish	Metapopulation	Mill River	Massachusetts, United States	McLain and Ross (2005)
		Elastomer tags	Fish	Metapopulation	Leslie Tributary and Berczy Creek	Ontario, Canada	Poos and Jackson (2012)
		NA	Salamanders	Metapopulation	Shenandoah National Park	Virginia, United States	Campball Grant (2011)
	Mark-recapture	Stable isotope enrichment	Aquatic insects	NA	Kuparuk River	Alaska, United States	Hershey et al. (1993)
			Aquatic insects	Metapopulation	The headwater streams of the Rivers Severn and Wye	Wales, United Kingdom	Briers et al. (2003)
			Aquatic insects	Metapopulation	Hubbard Brook Experimental Forest	New Hampshire, United States	Macneale et al. (2005)
	Traps	Malaise traps	Aquatic insects	NA	Detroit River and Lake St. Clair	Ontario, Canada	Kovats et al. (1996)
			Aquatic insects	NA	Llyn Brianne reservoir	Wales, United Kingdom	Petersen et al. (2004)
		Weir traps	Fish	Metapopulation	Gould Creek	Minnesota, United States	Schlosser (1998)
Proxy	Organismal-based proxy	Body size	Fish	Metapopulation	West Brook	Massachusetts, United States	Letcher et al. (2007)
		Wing size	Aquatic insects	NA	Hughes Creek	Victoria, Australia	Lancaster and Downes (2017a, 2017b)
		Dispersal ability	Aquatic insects	Metacommunity	Youghiogheny, Savage, and Casselman River basins	Maryland, United States	Brown and Swan (2010)
			Aquatic insects	Metacommunity	Chiricahua Mountains	Arizona, United States	Bogan and Boersma (2012)
			Aquatic insects	Metacommunity	Lower West Branch of the Susquehanna River	Pennsylvania, United States	Wilson and McTammany (2016)
		Dispersal mode	Aquatic insects	Metacommunity	Streams within Iijoki, Koutajoki, and Tenojoki basins	Finland	Grönroos et al. (2013)
			Aquatic insects	Metacommunity	NA	Germany	Li et al. (2016)
			Benthic macroinvertebrates	Metacommunity	NA	Germany	Li et al. (2018)
		Host dispersal	Bivalves	Metapopulation	Mill River	Massachusetts, United States	McLain and Ross (2005)
			Bivalves	Metacommunity	Ontario	Canada	Schwalb et al. (2011)
			Bivalves	NA	Shubuto River	Japan	Terui and Miyazaki (2015)
		Natural abundance of stable isotopes	Fish	NA	Connecticut River	Massachusetts, United States	Kennedy et al. (2002)
			Fish	Metapopulation	Granite Creeks	Australia	Cook et al. (2007)
		Population genetic structure	Aquatic insects	Metacommunity	Rocky Mountain National Park	Colorado, United States	Finn and Poff (2011)
			Aquatic insects	NA	River Sense	Switzerland	Alp et al. (2012)

(*Continued*)

(Continued)

Investigative Method	*Technique*	*Method III*	*Taxa*	*Biological scale*	*Name of site*	*Country*	*Source*
			Aquatic insects	NA	Ou Mountains	Japan	Yaegashi et al. (2014)
			Aquatic insects	NA	Victoria Range, Grampians National Park	Australia	Chester et al. (2015)
			Crayfish	Metapopulation	Bear Creek and Cahaba River drainages	Alabama, United States	Barnett et al. (2020)
			Fish	Metapopulation	Lahontan Basin	Nevada, United States	Neville et al. (2006)
			Fish	Metapopulation	Granite Creeks	Australia	Cook et al. (2007)
			Fish	NA	Fridley Gap	Virginia, United States	Hudy et al. (2010)
			Fish	NA	Kent Falls Brook, Jefferson Hill Brook, and Spruce Brook	Connecticut, United States	Kanno et al. (2011)
			Fish	Metapopulation	Arkansas River watershed	Colorado, United States	Fitzpatrick et al. (2014)
			Fish	Metapopulation	Diamond River watershed	New Hampshire, United States	Kelson et al. (2014)
			Frogs	NA	Mount Kilimanjaro	Tanzania	Zancolli et al. (2014)
			River otter	NA	Alentejo Region	Portugal	Quaglietta et al. (2013)
			Salamander	NA	Hubbard Brook Watershed	New Hampshire, United States	Lowe et al. (2006)
			Salamander	NA	St. Regis, St. Joe, and Locha river basins	Idaho and Montana, United States	Mullen et al. (2010)
	Graph-based proxy	Dendritic network distance	Bacteria	Metacommunity	Lookout Creek watershed, H.J. Andrews Experimental Forest	Oregon, United States	Wisnoski and Lennon (2020)
		Flow distance	Bivalves	Metapopulation	Shubuto River basin	Japan	Terui et al. (2014)
		Network distance	Aquatic insects	Metacommunity	lower West Branch of the Susquehanna River	Pennsylvania, United States	Wilson and McTammany (2014)
			Benthic macroinvertebrates	Metacommunity	South Island (Six stream networks)	New Zealand	Campbell et al. (2015)
			Bivalves	Metapopulation	Neosho River basin	Kansas, United States	Smith et al. (2015a, 2015b)
			Fish	Metapopulation	Boise River basin	Idaho, United States	Dunham and Rieman (1999)
			Fish	Metapopulation	Sorachi River basin	Hokkaido, Japan	Koizumi and Maekawa (2004)
			Fish	NA	Kent Falls Brook, Jefferson Hill Brook, and Spruce Brook	Connecticut, United States	Kanno et al. (2011b)
			Fish	Metacommunity	Lake Balaton catchment	Hungary	EROS et al. (2012)
		Overland (Euclidean) distance	Aquatic insects	Metacommunity	Central Amazonia	Brazil	Landeiro et al. (2012)
		Overland (Euclidean) distance and network distance	Aquatic insects	Metacommunity	Youghiogheny, Savage, and Casselman River basins	Maryland, United States	Brown and Swan (2010)
			Plant	Metacommunity	Krycklan watershed	Sweden	Kuglerová et al. (2019)
		Overland (Euclidean) distance, network distance, and flow distance	Benthic macroinvertebrates and periphyton diatoms	NA	River Don watershed	United Kingdom	Rouquette et al. (2013)
			Diatoms	Metacommunity	Dalalven River catchment	Sweden	Göthe et al. (2013)

		Overland (Euclidean) distance, network distance, and fragmentation-based distance	Benthic macroinvertebrates	Metacommunity	10 stream networks	France	Gauthier et al. (2020)
		Overland (Euclidean) distance, network distance, topographical distance, and perennial distance	Aquatic insects	Metacommunity	Upper San Pedro River basin	Arizona, United States	Cañedo-Arguelles et al. (2015)
		Overland (Euclidean) distance, watercourse distance, and flow distance	Benthic macroinvertebrates	Metacommunity	Ecological Reserve of Antisana	Ecuador	Cauvy-Fraunié et al. (2015)
	Experimental approach	Dispersal manipulation	Aquatic insects	NA	Eygues River	France	Vander Vorste et al. (2016)
			Aquatic insects	Metacommunity	Maryland	United States	Brown et al. (2018)
			Aquatic insects	Metacommunity	Río Fardes	Spain	López-Rodríguez et al. (2021)
			Benthic macroinvertebrates	NA	Hombrechtikon and Volketswil streams	Switzerland	Baumgartner and Robinson (2017)
		Habitat manipulation	Benthic macroinvertebrates	Metacommunity	Jefferson National Forest	Virginia, United States	Tornwall et al. (2017)
		Microcosm experiment	Protists and rotifers	Metacommunity	–		Carrara et al. (2012)
			Protist	Metacommunity			Altermatt and Fronhofer (2018)
Theoretical modelling	Metapopulation model	–		Metapopulation	–		Anholt (1995) Kopp et al. (2001) Fagan (2002) Lowe (2002) Chaput-Bardy et al. (2009) Morrissey and de Kerckhove (2009) Campbell Grant (2011) Mari et al. (2014) Streib et al. (2020)
	Metacommunity model	–		Metacommunity	–		Auerbach and Poff (2011) Anderson and Hayes (2018) Carraro et al. (2018) Holt and Chesson (2018)

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Macrosystem Ecology of Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Community ecology Research on the organization and simultaneous ecological functioning of multi-species populations within a specified area.
Ecosystem metabolism Chemical reactions associated with the breakdown and synthesis of organic and inorganic molecules and compounds needed by living organisms.
Ecosystems ecology Study of living and both permanently or currently non-living components of multiple communities within an ecosystem, including research on system metabolism, elemental cycling, and other ecological processes.
Endorheic streams Rivers terminating in a desiccation basin or lake (freshwater or saline) and without ultimate flow to the sea.
Food webs Feeding relationships within a community involving pathways for the transfer of energy and nutrients from primary producers to top carnivores.
Landscape ecology Study of effects of spatial heterogeneity on ecological processes at the community and ecosystem level, with a predominant emphasis on terrestrial systems.
Lentic ecosystems Ephemeral pools, semi-permanent wetlands, ponds, lakes, and reservoirs.
Lotic ecosystems Rivers from small ephemeral headwater creeks to large or great rivers.
Macroecology Study of population through community ecology of terrestrial and aquatic systems at large spatial scales (up to continental).
Macrosystems ecology Study of community through ecosystems ecology of terrestrial and aquatic systems at large spatial scales (up to continental).
Metacoupling Interactions between separated macrosystems over either short (pericoupling) or long distances (telecoupling) that involve the movement of material or organisms and can be natural or human-induced.
Nutrient cycling Movement of organic and inorganic matter through the living and non-living components of the ecosystem.

Introduction to macrosystem ecology

Since the middle of the 20th century, ecological research in aquatic systems has gradually increased in functional and spatial scales from an emphasis on species interactions within communities of small spatial extents (typically a few hundred meters or less in rivers) to functional processes occurring within whole, individual ecosystems (often one to hundreds of kilometers), and now in a few cases to studies of structural and functional properties of multiple ecosystems occurring among ecoregions, biomes, and even continents. Simultaneously, the impacts of climate change and invasive species have gained prominence in ecological studies. This newer emphasis on very large spatial scale research is increasingly classified under the overlapping terms "macrosystems ecology" and "macroecology" (Thorp et al., 2021). The former primarily employs techniques of community or ecosystem ecology in studying very large spatial extents (Table 1), while the latter typically focuses on methods in population or community ecology and may encompass comparably large geographic areas. To some readers, the terms ecosystem studies and macrosystem research may seem equivalent. However, past "ecosystem studies" (e.g., analyzes of nutrient cycling) in rivers have occurred at spatial extents as small as one or more stream reaches and have been predominately undertaken in one or multiple headwater sites within a single river, especially when chemical tracers are used.

Ecological research at the macrosystem scale, in particular, may involve many collaborating scientists working in either lotic or lentic ecosystems and having diverse expertise in areas such as hydrology, geology, ecosystem metabolism (including analysis of

Table 1 Perspectives on defining spatial extents and research approaches in ecosystem vs. macrosystem research for lotic and lentic systems, with possible system examples.

Lotic systems	*Ecosystem research projects*		*Macrosystem research projects across multiple ecosystems project*	
	Single river basin	*Small stream sections in many rivers of multiple ecoregions or biomes*	*One very large river basin passing through multiple ecoregions or biomes*	*Many whole river basins in different ecoregions or biomes*
Spatial research category	Single river basin with sampling in one or more stream orders	One to few stream orders but in multiple streams and watersheds	Sampling many stream orders within a large basin consisting of many rivers in different ecoregions	Multiple independent (unconnected) watersheds in similar types of eco-regions or biomes
Example lotic rivers on various continents	AU: Cooper Creek; EU: River Tweed; NA: Kanawha River SA: Rio Traful	Similar stream order in rivers of different basins in different ecoregions or biomes	EU: Rhine River; NA: Mississippi River; AS: Mekong River or large sub-basins	Rivers from different basins in different biomes or ecoregions, such as those on US West Coast
Breadth of dependent variables	Usually system metabolism and elemental cycling in multiple stream orders	A few biotic traits or processes in one or more orders of multiple rivers	One to many of the same dependent variables in one or more stream orders throughout basin	One to many dependent variables present in multiple stream orders of each river

Lentic systems	*Single lake or wetlands*	*One aquatic zone in multiple lakes or wetlands*	*Hydrologically connected lakes from higher to lower elevations*	*Whole lake or wetland studies in multiple ecoregions or biomes*
Spatial research category	Multiple ecosystems with sampling in one or more zones (or throughout wetlands) in multiple ecoregions or biomes	Epilimnion or other zones in multiple lakes distributed across a broad geographic area	Sampling one or more dependent variables from higher to lower elevations in connected lake systems	Multiple ecosystems with sampling in one or more zones (or throughout horizontal zones broad geographic area elevations in connected wetlands) in multiple ecoregions or biomes
Example lentic systems	AF: iSimangaliso Wetland EU: Vättern Lake AS: Lake Baikal	AS: Xinjiang Lakes (CH) EU: Lake District (EN) NA: Lake District (CA)	AF: Lakes of White Nile EU: Plitvice Lakes NA: Paternoster lakes	Multiple lakes across EU and NA in particular; NA: Playa wetlands
Example dependent variables	Multiple dependent variables	Usually one or a few dependent variables	Few to many dependent variables	Few to many dependent variables

Continental abbreviations for potential research sites: A, Africa; AS, Asia; AU, Australia; EU, Europe (including Great Britain and Ireland); NA, North America; SA, South America. Based in part on Thorp et al. (2021).

primary production), nutrient cycling, food web ecology, and trait-based analyzes of invertebrates and fish. In most macrosystem projects, however, only a subset of disciplines is employed when the geographic area is especially large.

Lotic macrosystem research is occurring on multiple continents even though the specific terms "macrosystem ecology" and "macroecology" have not always been applied. Some examples of this research have been undertaken in Asia (e.g., Mekong River), Australia (Murray-Darling River system and rivers of tropical northern Australia), Europe (e.g., Danube River system), and North America (e.g., Mississippi River system and the St. Lawrence River basin). This research has included studies of many ecological attributes in a single, very large basin (e.g., the Danube) spanning multiple ecoregions as well as in many temperate steppe rivers in countries on two continents (e.g., Mongolia and the United States). Other macrosystem studies have emphasized one ecological attribute (e.g., stream metabolism) in many small stream reaches (usually headwaters) in a large number of separate watersheds distributed across a continent or even throughout a single, moderate-sized river basin (e.g., the Connecticut River Basin).

Macrosystem-type research in lentic systems has a long history of studying both hydrologically linked and isolated lakes within and among continents. The former includes, for example, paternoster lakes in Switzerland (the 16 lakes connected by limestone waterfalls in UNESCO's World Heritage Plitvice National Park of Croatia) and the linked Laurentian Great Lakes of the United States and Canada. Macrosystem comparisons among more isolated lakes are even more common among and within continents, including studies in the Windermere Lake District of Great Britain, the Experimental Lakes Area of Canada, and recently the widely distributed ephemeral wetlands (playas and prairie pothole systems) of the North American Great Plains.

Why macrosystem approaches are needed

A reader unfamiliar with macrosystem ecology might ask: "Why do we need to expand the spatial extent from: (a) stream reaches to whole rivers; and (b) single rivers to multiple rivers in different ecoregions, biomes, or even continents?"

The answer to the first part of this question is that biodiversity and ecological processes vary substantially from upstream to downstream in different ecoregions and at different spatial and temporal scales. These differences reflect some combination of predictable to highly variable variations in river width and depth, riparian cover (e.g., organic inputs and stream shading), autochthonous primary production, turbidity (affecting photosynthesis), water velocity and turbulence, and hydrogeomorphic complexity. The last component includes, for example, the presence of side channels in the riverscape and periodically connected floodscapes with their temporally isolated lakes and normally terrestrial floodplains.

The response to the second part of this question is that community characteristics (species diversity and functional attributes) and ecological processes in different locations typically become more disparate with increased latitudinal, longitudinal, and continental separation. A macrosystem approach employed across large geographic areas could reveal hidden ecological drivers not normally apparent in geographically constrained areas, while also better enabling investigators to predict effects of future trends in the environment. These reflect changes in climate, the biotic and abiotic nature of the stream and surrounding basin, and differences in the degree and type of human impacts. Two rivers in the same latitude or longitude might vary tremendously from upstream to downstream if one flows eventually to the sea and the other does not. One example of the latter is the endorheic Carson River that flows from forested mountains in California and Nevada (United States) to an evaporation basin in the scrub desert of Nevada. On the other side of the world, the Khovd River of Mongolia flows from the forested Altai Mountains into the saline Khar-Us Lake in arid western Mongolia and never reaches the sea. Moreover, rivers that flow to the sea in temperate steppe biomes of the North American Great Plains and the mountain steppe and grassland rivers of Mongolia can be located at nearly the same latitude and yet differ substantially in fauna and ecological processes for both natural and anthropogenic reasons. For instance, the Eg River in northern Mongolia and the Yellowstone River in the northern United States overlap in latitudes (though the Eg flows north into the Selenge and eventually into the Arctic Ocean while the Yellowstone eventually flows via the Missouri and Mississippi Rivers into the Gulf of Mexico). Large expanses of both rivers feature relatively clear waters, forested shorelines (except where modified by grazing in both cases), and rocky bottoms. However, the fish diversity in the Yellowstone consists of both native and many introduced species, while all fish species in the Eg are native at present. Downstream in the Yellowstone where it joins the Missouri River, the system has been impounded by multiple large dams, while the Eg presently lacks dams (this is likely to change by the late-2020s). Finally, the average annual temperatures for northern Mongolia are rising three times the north temperate zone average. Combining all these observations provides insights to ecologists which may allow them to predict future trends in both rivers from knowledge of conditions in other rivers.

Ecological conditions within a river or lake macrosystem can be influenced by conditions in distant aquatic macrosystems present within or even among continents in a process called "metacoupling" (LaRue et al., 2021; Tromboni et al., 2021). This process can be subdivided into interactions occurring over relatively short distances ("pericoupling") and those transpiring over long distances ("telecoupling"). Examples of the latter were much less common in the past, but human-influenced metacoupling (=intra-coupling) has greatly expanded these interactions. Aquatic metacoupling can occur through natural colonization, such as the transmission of fertilized eggs, young, or adults via by wind, waterfowl, floods, or adult migration. Two examples of pericoupling include short-distance migration among aquatic systems by flying adult dragonflies (which also may migrate long distances) and overland migration on moist nights by crayfish and "walking" catfish (*Clarias batrachus*). Natural telecoupling is primarily related to transmission of propagules by wind (e.g., freshwater rotifers) and waterfowl (e.g., fairy shrimp eggs on feathers and in a bird's alimentary track) because of the distances involved, but tropical floods can also lead to species migration among previously isolated water bodies. Anthropogenic changes in ambient temperatures and precipitation may be increasing the tendencies of some species to migrate by diminishing the quality of the previous home river, wetland, or lake.

Despite some attempts to control intra-coupling, the diversity and total amount of human-nature interactions are probably rising because of the joint effects of climate change, habitat destruction, and intentional and unintentional species introductions. While intentional and accidental intra-coupling have both been occurring for centuries if not millennia, the increasingly global economy and frequent destruction of tropical forests for crop production (with resulting effects on freshwaters) have substantially caused both local extinctions within the watershed and rarer movement of species among countries and even continents. While current macrosystem research emphasizes fundamental studies, ecosystem management would benefit from integrating macrosystem techniques at regional, national, and global scales. In addition to requiring a greater degree of communication and collaboration among scientists, politicians, and multi-national corporations across the globe through an existing or new international organization, this widespread integration will demand a better understanding and control of potential telecoupled pathways and a recognition of which species have both a greater potential transmission rate and more likely negative environmental impacts in a new geographic location.

Conclusion/Synthesis

Meeting future challenges of a changing environment while enhancing our ecological knowledge of aquatic systems will require an improved understanding of how large, whole aquatic systems (=macrosystems) function. A necessary component of this process will be for groups of scientists with disparate but complementary disciplines to work together in teams. Such projects will require enhanced financial and political support from governments, especially because most projects are likely to cross political boundaries within and among countries.

Knowledge gaps

1. What are the general principles of "macrosystem ecology" that would allow us to predict ecological responses from one geographic location to another?
2. How significant are basin morphometry and geological composition for aquatic macrosystem ecology in lotic and lentic systems?
3. Which factors that are primarily responsible for the functioning of individual macrosystems vary predictably among macrosystems in different ecoregions, biomes, and continents?
4. Do factors primarily controlling the ecology of endorheic river macrosystems differ significantly from those of rivers flowing to the sea?
5. Can the management of rivers benefit from a focus on macrosystem approaches by government agencies and environmental foundations?
6. What characteristics of macrosystems make individual systems more susceptible to the effects of climate change and invasive species?
7. What approach might we develop that would better enable us to predict the ecological effects of impending climate change on the structure and function of macrosystems and constituent communities, and would an international macrosystem rivers organization be useful in achieving these goals?
8. Would better knowledge of macrosystem ecology improve our ability to predict invasion from exotic species and possibly prevent or ameliorate their ecological impacts on macrosystems.

Representative case studies

The number of lotic and lentic macrosystem-type studies are slowly expanding worldwide but are primarily limited by research funds and sometimes by cooperation among governments. As examples, recent stream and river macrosystem research projects funded by the National Science Foundation have focused on: (1) applied and basic ecology of a large river that passes through multiple countries with different natural conditions and human impacts; (2) macroinvertebrate communities in permanent and perennial headwaters located in 10 forested ecoregions; (3) organic matter fluxes within headwaters streams of a single, large river basin; (4) data base development of annual metabolism in streams across a continent; and (5) analysis of the effects of downstream position, hydrogeomorphology, and riparian cover on metabolism, species diversity and traits, and food webs in temperate steppe biomes of two continents. Some representative studies of lake and wetland, macrosystem research include: (a–b) metabolism and nutrient conditions in lakes across a continent; (c) country-wide assessments of climate and land-use on populations of amphibians and waterfowl in wetlands; and (d) latitudinal analyzes of genetic links and transport mechanisms (teleconnections) by wind and waterfowl of fairy shrimp among ephemeral wetlands in a temperate steppe biome.

Acknowledgments

The author appreciates insightful critiques of an earlier draft of this manuscript by Drs. Alain Maasri, Kevin McCluney, and Caleb Robbins. Production of this manuscript and funding for the macrosystem research projects upon which it is partially based were aided by NSF research grants to study rivers in the United States and Mongolia (NSF 1442595) and ephemeral wetlands in five states of the U.S. Great Plains (NSF 1926596).

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River Resilience

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Functional redundancy A single ecological function is provided by more than one species (functional equivalence of species) in a community. If one of the species is lost, the function is maintained for the ecosystem.

Geomorphic unit A discrete patch within a riverine landscape defined by morphology, sediment texture and/or flow pattern.

Metacommunity dynamics Metacommunities are interacting metapopulations determined by exchanges through dispersal. Exchange can be affected by disturbances; recruitment recovery determines the rate of return to preceding exchanges.

Recruitment The processes of regeneration and recolonization that follow disturbance enabling the recovery of the biotic community.

Refugia Used here in a wider sense, that is, sites offering (a) refuge to changing environments and (b) continuity in environmental conditions together with habitat heterogeneity offering opportunities for speciation and specialization.

Regime or state In ecological studies, the regime or state can be defined by the set of abiotic and biotic conditions observed for a focal ecosystem or component. A regime or state of an ecosystem can be characterized as the set of structures, functions and interactions. These structures, functions and interactions are scale dependant.

Regime shift A regime shift refers to large, persistent change in the structure, function and set of relationships of an ecosystem or Social-Ecological Systems associated with the crossing of a tipping point. Regime shifts have major impacts on ecosystem services and human well-being as they are costly, difficult to manage and impossible, to reverse. Regime shifts are similar to social-ecological transformations, but tend to focus on unintended, negative shifts rather than more intentional, positive shifts in SES.

Resilience The classical definition of resilience (cf. Holling, 1973) refers to the amount of change an ecosystem can undergo and still retain its essential structures, functions and feedbacks, i.e., its capacity to return to its pre-disturbance state. In this definition, both the resistance to and recovery after disturbance are accounted for. More recently, resilience has been defined as the capacity of a social-ecological system to persist in the face of disturbance and change, while continuing to adapt and develop along a pathway or transform and navigate new pathways to sustain human well-being. This form of resilience takes into account and integrates notions of governance systems, ecosystem services and human well-being, adaptive capacity and transformation.

Resource facilitation Facilitation is a significant ecological process that produces community-level effects through individual positive interactions. Such interactions are considered "mutualisms" when both species derive benefit from the interaction.

Resource pulses Strong fluctuations in availability of resources occur under pulsed disturbances of floods and droughts in river ecosystems, with consequences to biotic communities.

 https://doi.org/10.1016/B978-0-12-819166-8.00088-8

Resource The use of this term is not restricted to food but it also encompasses elements such as light (especially for primary producers), oxygen, substrate, and temperature.
Shifting habitat mosaic An array of geomorphic units or ecological patches that change over time in response to disturbances and provide areas for pioneer species to invade through to areas of well-established organisms.
Social-ecological systems Social-ecological systems (SES) are complex adaptive systems whereby social and ecological agents and processes are closely linked.
Thresholds Threshold is a boundary separating different behaviors, such as sediment movement and deposition or different river channel planforms like meandering or braider river channels. In ecology, e.g., light thresholds allow photosynthesis of plants, temperature thresholds initiate fish spawning etc.
Tipping points Tipping points are a particular type of threshold. Crossing a tipping point results in a regime shift and once crossed the system cannot revert back to the previous state.

Introduction

The aim of the chapter is to highlight the main elements of the resilience of riverine landscapes. These include factors that contribute to the resistance and recovery of rivers to environmental stress and the determinants of disturbance(s). These will reflect some combination of physical (based in geomorphological features), ecological (based in the biotic community traits), and social-ecological (originating in management of societal policies) conditions. The interplay between resistance, recovery and disturbance can result in a state change of river systems.

There are many perspectives of resilience. Definitions of engineering and ecological resilience emphasize the role of physical and biotic characteristics of river systems. For the physical characteristics, the resilience concept has many parallels in the study of geomorphology (Thoms et al., 2018). A consideration is how geomorphological resilience interfaces with other dimensions of resilience, especially ecological resilience and socioeconomic resilience, the latter commonly being defined in terms of ecosystem service delivery (Stallins and Corenblit, 2017). The geomorphological view on equilibrium conditions is similar to an engineering definition of resilience, which emphasizes efficiency, constancy, and predictability, and focuses on stability and steady state equilibrium conditions; where resistance to disturbance and the speed of return to a steady state equilibrium are used to measure resilience (Tilman and Downing, 1994). By comparison, ecological resilience (Holling, 1973) considers the amount of disturbance an ecosystem (or community) can tolerate before it loses its original structure, internal functions and set of feedbacks. This definition emphasizes persistence, change, and unpredictability, and looks for instabilities that can flip a system into another regime, i.e., another domain or basin of attraction (Holling, 1973). The measurement, from an ecological perspective, is the magnitude of disturbance that can be absorbed before the system changes its structure, functions, and sets of feedback (Walker et al., 1969). In ecological resilience, studies have considered how food webs absorb, recover from and adapt to environmental change (DeBoer et al., 2020), thus emphasizing the importance of biological mechanisms and responses to disturbance. Socioeconomic perspectives of resilience start from viewing river systems as social-ecological systems and responses to disturbance are influenced by societal perceptions and risk evaluation, resulting in management for resilience.

Mechanisms of river resilience are, however, being challenged by human-induced alterations to the characteristic properties of river systems, including hydrologic disturbance regimes, network connectivity, and the coupled longitudinal and lateral resource pulses. The interplay between climate change, land-use intensification and human population growth is likely to bring new challenges to the management and conservation of freshwater ecosystems globally, highlighting the need for a better understanding of and adaptive management approaches for river resilience.

Engineering resilience; the geomorphological perspective

Concepts

Engineering resilience, defined as resistance to disturbance, or the ability of a system to remain close to an equilibrium or steady state, views systems in terms of stability and predictability. This brings us to the physical impact of externally-driven disturbance on the state of a system, with recovery as the operation of intrinsic processes to restore the system towards, or back to, an equilibrium state. The concept of equilibrium in geomorphic systems is based on the notion of balance between process and form. Thus, when a geomorphic system is disturbed, there is a period of time—relaxation time—during which the system returns to a relative state of balance (Phillips and Jerolmack, 2016). In river systems, which are prone to disturbance from a range of variable drivers (e.g., floods and sediment overload), a true steady state is unlikely because disturbance intervals tend to be shorter than relaxation time. Thus, systems may not trend towards a steady state but rather a state of pseudo-equilibrium, which is normative in most river systems (Phillips, 2009).

The geomorphological perspective of river resilience relates to some engineering resilience elements. Here the focus is on the ability of morphological attributes and landforms to absorb, respond or recover from disturbance, within specific degrees of freedom. In riverine landscapes, degrees of freedom are properties such as river channel width, depth, slope, planform and channel

roughness. For example, if river channel banks have the least resistance to change they would adjust over other degrees of freedom. Thus, the concept of resilience is implicit in the study of geomorphology (Thoms et al., 2018). Principles of resistance, recovery and change underpin our understanding of the way geomorphic systems function via equilibrium theories (Stallins and Corenblit, 2017) and of the role that extrinsic and intrinsic thresholds (Schumm, 1979) play in governing the form and behavior of geomorphic landforms. Resistance is an important term in geomorphology, as it controls the likelihood of erosion and sediment transport during floods and, therefore, landforms gaining or losing sediments that are required to change morphological character. In systems with low resistance there is likely to be more geomorphic adjustment and often a longer period of recovery (termed recovery or relaxation time) or a greater likelihood of the river system moving to a new state (e.g., a regime shift from a single-thread actively meandering gravel bed river to a multi-thread wandering gravel bed river).

Definitions of resilience variables relating to a geomorphic process-response system are shown in Fig. 1. The concept of equilibrium in geomorphic systems is based on the notion of balance between process and form. Thus, when a geomorphic system is disturbed, there is a period of time—the relaxation or recovery time—during which the system returns to a relative state of balance or equilibrium (Phillips, 2014). In river systems, which are prone to a range of disturbances (e.g., floods, sediment pulses, wood inputs), a truly steady state is unlikely because disturbance intervals tend to be shorter than recovery time. Thus, riversystems more normatively trend towards a state of pseudo-equilibrium (Phillips 2009). Fig. 1 shows that resilience concepts and ideas can be visualized in relation to geomorphic equilibrium concepts and the associated terminologies of thresholds, relaxation times and meta-stability, magnitude and frequency (cf. Phillips, 2014; Fuller et al., 2019).

To understand implications of changing the magnitude and frequency of hydrogeomorphic processes one has to consider the nature of geomorphic equilibrium—a long-established and normative concept in geomorphology. There are many definitions and classifications of geomorphic equilibrium. Here we classify four types of geomorphic equilibrium (Fig. 2) and equate them directly to types of resilience trajectories. Using the classic ball and cup model of resilience (Scheffer, 1990), the cup can be represented as a geomorphic river type (e.g., meandering, braided etc.) and the ball reflects changes in channel properties of an individual river type, e.g., width.

- *Static* equilibrium is where the disturbance regime does not exceed the system's morphological resistance—a state of no change or where the ball sits unaltered and static in the bottom of the cup i.e., there is no morphological adjustment in the river channel.
- *Steady state or stable* equilibrium: the tendency for a system to move back towards a previous equilibrium condition, i.e., to recover after a disturbance as the ball moves up the sides of the cup but eventually returns to its original position i.e., river morphology (e.g., width) may adjust (widen) following a flood but will return to its original morphology or dimension.
- *Dynamic* or unstable equilibrium: balanced fluctuations about a constantly changing system condition may have a trajectory of unrepeated states that change over time (e.g., meander form changes)—the ball stays in the cup but the nature of the ball (e.g., size) gradually changes over time, or the cup is tilted and the balls sits in another position at the bottom of the cup.
- *Metastable* equilibrium: when a disturbance carries the system state over a geomorphic threshold into a new equilibrium regime (e.g., meandering to braiding) and the ball exits the previous cup and enters a new cup. A new river channel morphology or river type is established following a disturbance—this is also referred to as transformation or regime shift.

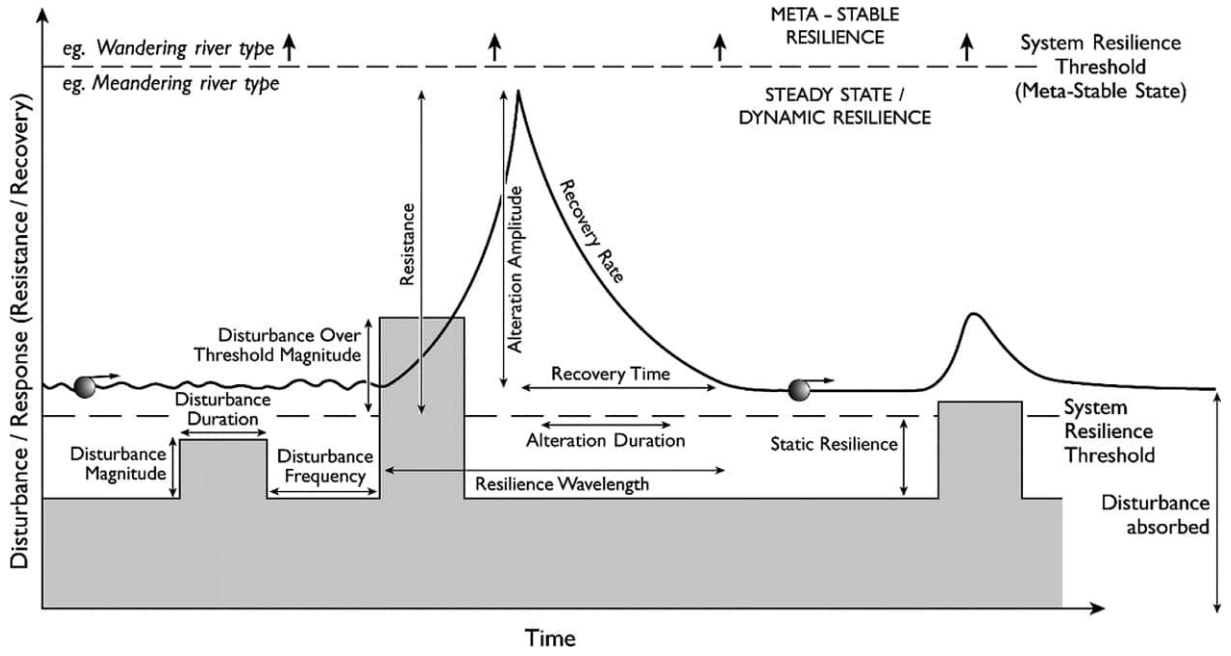

Fig. 1 Resilience concepts and terminology related to river channel equilibrium. Adjustment properties related to the magnitude of change from an equilibrium state and the temporal property of recovery time are depicted. In this example the disturbance would be a flood and the river adjustment (the solid line) represents the changing character of the river channel planform. Adapted from Fuller IC, Gilvear DJ, Thoms MC, and Death RG (2019) Framing resilience for river geomorphology: Reinventing the wheel? *River Research and Applications* 35: 91–106. doi: 10.1002/rra.3384.

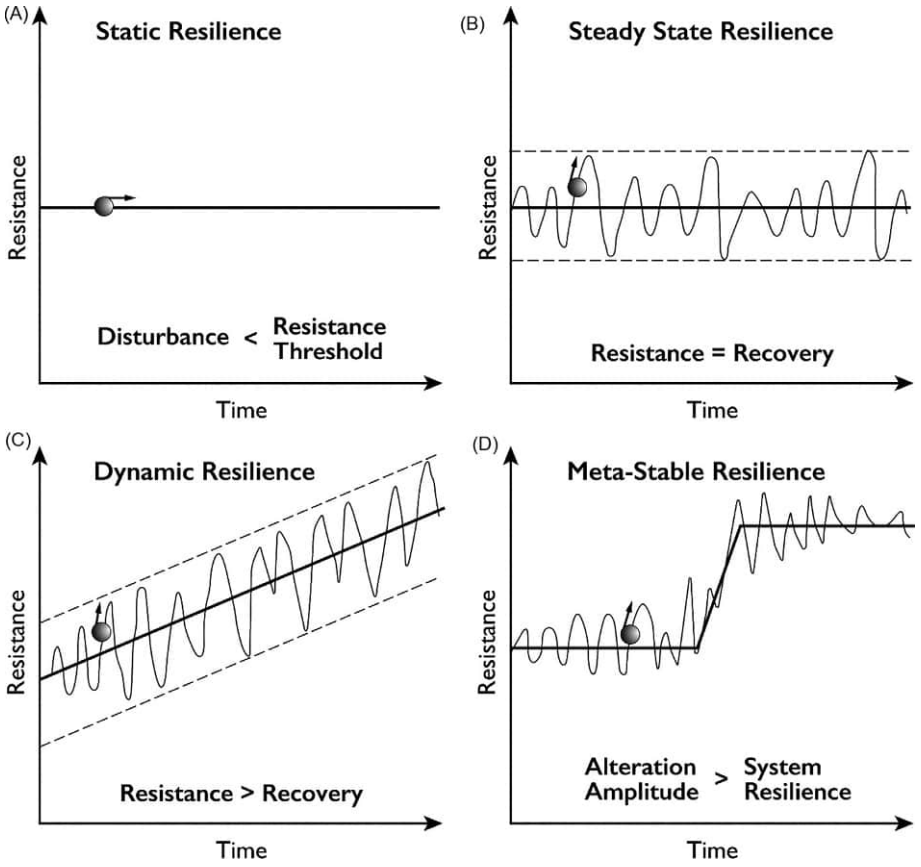

Fig. 2 Geomorphic-resilience trajectories (A) static, (B) steady-state, (C) dynamic, (D) meta-stable (regime shift). The resilience ball would follow the trajectory shown and in the case of (D) flip between resilience domains. Adapted from Fuller IC, Gilvear DJ, Thoms MC, and Death RG (2019) Framing resilience for river geomorphology: Reinventing the wheel? *River Research and Applications* 35: 91–106. doi: 10.1002/rra.3384.

Central to the process of resilience and recovery following disturbance is the concept of feedbacks, which can be negative or positive. Negative feedback is any process that neutralizes the recovery of geomorphic systems following a disturbance. A river widened by a high magnitude flood for example, will result in lower flow velocities for a given size of flood event leading to an increase in sediment deposition in subsequent (smaller) floods. As such, the morphology will have a trajectory back to the pre-disturbance channel morphological state. This is negative feedback and exemplifies a resilience response to disturbance by a high-magnitude, low-frequency event. It also shows the futility of engineering wider channels in that negative feedback processes will occur resulting in the need for channel maintenance to restore the engineered channel design. Such a negative feedback response is enhanced by vegetation colonization and stabilization of deposited sediments, leading to further deposition of fines within the vegetation and accelerated bank construction and channel narrowing. Indeed, vegetation colonization and related feedbacks are a fundamental part of the recovery process on many rivers, increasing resilience by accelerating a negative feedback process. An example of positive feedback is where straightening and reinforcing of a channelised reach leads to enhanced bank erosion in the downstream reach where the banks are unprotected. A typical response would be to install more bank protection, so moving the problem even further downstream and reducing resilience of the system.

Assessing engineering resilience in geomorphic thresholds & state changes

The capacity of a river at the reach scale to absorb (resist or recover) disturbance is conditioned by its proximity to a threshold (Brunsden and Thornes, 1979). Changes in river channel type (meta-stable/regime shift), such as a change from a meandering to a wandering or braided river planform, occur when thresholds relating to stream power, or flow regime and sediment regime are exceeded (Schumm, 1979). A disturbance that fails to exceed the resistance of the channel and its geomorphic units results in no change in river size, morphology or physical habitat composition. In this situation, channel resilience is "static" (Fig. 2A) and may describe the behavior of river geomorphology to frequent floods (>1–2 per year). Such small (within-channel) floods are critical for maintaining the ecological quality of in-channel habitats, e.g., by preventing clogging of gravel spawning habitat with fine sediment.

Where alteration amplitude or recovery following disturbance is rapid, resilience can be considered as "steady state" (Fig. 2B). This is because the system has absorbed the disturbance and returned to its pre-flood condition (i.e., channel form and assemblage of morphological units). Vegetation re-colonization is important for the rapid recovery of fluvial surfaces to the pre-disturbance

state following perturbation (Gurnell, 2014). In this respect, healthy, resilient riverine landscapes are those with well-developed riparian margins. Without rapid vegetation colonization and related sediment retention and stabilization of river margins, the likelihood of changes from meandering to wandering river morphologies greatly increases. In turn, such planform changes pose challenges for river management, as the lateral extent of the active river corridor has to increase.

Phillips (2009) argues that if the pre-disturbance state of a system is not restored, a system can be construed as non-resilient, or having low resilience. Nevertheless, resilience is itself dynamic (Fig. 2C) when progressive change occurs in a system adjusting to new boundary conditions. For example, a progressive increase in discharge and bed load with an increasingly wet climate through time may increase channel width, width:depth ratio, meander wavelength and channel gradient, while reducing sinuosity, but a meandering channel is maintained. In New Zealand, where land-use change has rendered catchments prone to erosion, some rivers have been more dramatically transformed, changing from narrow, single-thread systems to rapidly aggrading multi-thread rivers (Fuller and Rutherfurd, 2021). While in many cases, change can proceed over several decades, centuries, or even millennia. The Raparapariiki River, New Zealand, which transformed within a decade, is an excellent example of this (Tunnicliffe et al., 2018). The adjustment across a threshold by this channel was associated with a major storm event in 1988, a classic example of metastable resilience (Fig. 2D).

The interplay of disturbance frequency, rate of recovery and amplitude of response is important to the resilience of river systems (Fig. 3). Highly dynamic rivers, sensitive to small floods, which absorb disturbance and do not experience changes in the morphologies exhibit robust behavior, are resilient as moderately dynamic or steady state rivers. In this case, each adjusts to the frequency of disturbance, amplitude of response and rate of recovery that are inherited from the catchment boundary conditions. The range of natural capacity for adjustment will be dependent upon the character of each river system (cf. Fryirs and Brierley, 2013). As such, both dynamic and non-dynamic river types in their natural state are resilient to the natural range of disturbance (i.e., floods) in their catchment. In its unaltered condition, a river responds with resilience to even the largest floods, because its natural form and character will adjust and recover over time.

The problem for river management is that many rivers are now no longer in a natural catchment setting. Anthropogenic disturbances have resulted in river systems moving to a new cup—a new regime from which they cannot return. As such there is often mismatch between process and form even where no direct channel modifications have taken place. Resilience defined as the magnitude of the disturbance a system needs to shift to an alternative stable state, is a critical trait in the Anthropocene era. Therefore, we need to orient to specific measures and measurement of the tipping points and especially of the early warning signals to these tipping points. Furthermore, we need to develop guidelines for managing for resilience. However, we are far from having baseline resilience data to guide decision makers towards more resilient river systems. Resilience indicators have to test for the quantitative impact that changes might cause, with indications based on both intensity and relevance. We develop these ideas and discuss the challenges of river management in the Anthropocene below, following discussion of ecological resilience, because river management for resilience must be informed by both geomorphology and ecology.

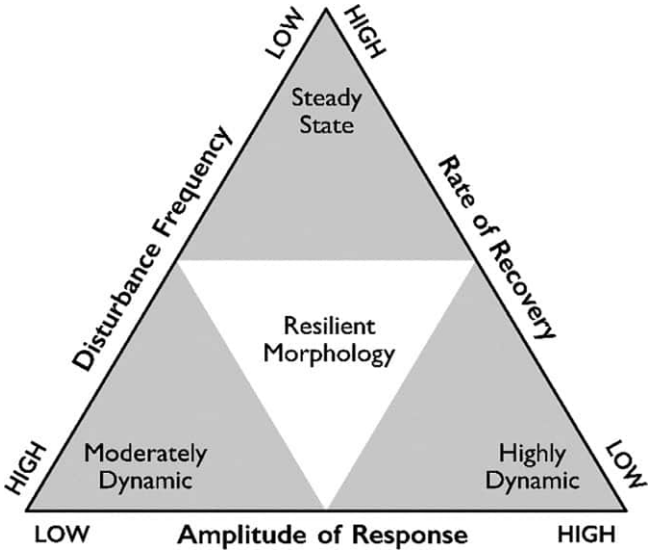

Fig. 3 Resilience in amplitude, frequency and recovery space. Adapted from Fuller IC, Gilvear DJ, Thoms MC, and Death RG (2019) Framing resilience for river geomorphology: Reinventing the wheel? *River Research and Applications* 35: 91–106. doi: 10.1002/rra.3384.

Ecological resilience

Concepts

The Resilience Alliance (https://www.resalliance.org/) defines resilience in terms of system change. It is the amount of change a system can undergo (its capacity to absorb disturbance) and essentially retain the same function, structure and set of feedbacks (Walker and Salt, 2006). This ecological view of resilience focuses on change and unpredictability and is linked to ecological principles of adaptation and evolution. Resilience in ecology has been simply viewed as the recovery phase from disturbance to its original condition.

Resilience in river ecosystems requires that organisms must persist in the face of highly dynamic hydrological and geomorphological variations. Disturbance events such as floods and droughts are postulated to shape life history traits that support resilience, but river management and conservation would benefit from greater understanding of the emergent effects in communities of river organisms. Species in disturbance driven systems like rivers pulsed by floods and droughts (Parasiewicz et al., 2019) have evolved strong fitness and specific life history traits to resist or recover from the disturbance. Relevant traits are, for example, maximum size and longevity, which foster resistance. Young age at maturity and fecundity also enable quick recovery (van Treeck et al., 2020). Organism response to disturbance is further mediated by biological traits related to feeding specialization, dispersal ability and habitat specialization, along with taxonomic and phylogenetic identity. Measures of these factors might also enable assessment of the relative contributions of different mechanisms to community resilience. Community-wide, there are three mechanisms that underlie resilience: (1) partitioning (competition/facilitation) of dynamically varying resources; (2) dispersal, re-colonization and recruitment promoted by lateral and longitudinal connectivity; and (3) functional redundancy in communities promoted by resource heterogeneity and refugia.

The ensemble of individual species' responses to disturbance through competition/facilitation for resources, dispersal that avoids mortality, or persistence through adapted traits in specific niches, result in resilience at the community level through one or more of the three resilience mechanisms (Van Looy et al., 2019).

In contrast to natural pulse disturbances, human-induced alterations, such as flow regime alteration, pollutant inputs, climate change or habitat degradation, are press or ramp disturbances (increasing gradually or incrementally in intensity) (Lake, 2000). Human activities such as land cover modification result in shifts in seasonality, frequency and duration of pulse disturbances, and thus challenge river resilience mechanisms. Further, the timing of disturbances may be more important than pulse magnitude in terms of effects on resilience capacity (Woodward et al., 2016; Poff et al., 2018). Floods and droughts in river systems show specific effects on resources, connectivity and habitat heterogeneity. As a result, organisms respond specifically to events, either in benefiting from resource pulses or avoiding flood disturbance by moving away, or to seek refuge in a specific niche, rather than some combination of response mechanisms (McMullen et al., 2017).

Resource competition/facilitation

Resource competition/facilitation is the mechanism for species that can take advantage of changed (either pulsed or depleted) resource conditions during disturbance. Strong fluctuations in availability of resources such as light (especially for primary producers), oxygen (anoxic conditions occur in river sediments), substrate (such as bare sediment for riparian plants and ground beetles or gravel and branches for benthic organisms), temperature (for thermophilic organisms) and food or habitat (inundated floodplain) occur under pulsed disturbances of floods and droughts in river ecosystems, with consequences to biotic communities.

Resource competition and facilitation are opposite interspecies response mechanisms to temporal resource variation. In response to resource pulses, the resilience mechanism at the community level involves internal re-organization, i.e., reassembly, based on biotic interactions including competition and facilitation. Facilitation is a significant ecological process that produces community-level effects through individual positive interactions. By increasing access to resources, facilitation can impact community structure and diversity. Such interactions are considered "mutualisms" when both species derive benefit from it.

Rivers and adjacent terrestrial ecosystems have permeable boundaries that are frequently crossed by two-way resource subsidies, e.g., from flooding, insect emergence, and vice versa, e.g., floodplain feeding by fish, leaf litter input in autumn (Larsen et al., 2016). Adaptations to both resource pulses and subsidies exist and are reflected in flexible timing in resource use (Holt, 2008).

Recruitment

Recruitment recovery depends on species' abilities to move through space and time (Heino et al., 2015) in combination with reproductive traits (van Treeck et al., 2020). Metacommunity dynamics are determined by exchanges through dispersal and mortality in interacting metapopulations. The strength of these regeneration and recolonization dynamics can be affected by disturbances; recruitment recovery determines the rate of return to preceding conditions. The recruitment mechanism of resilience relies on metacommunity dynamics based on habitat connectivity, species' dispersal abilities and size of the regional species pool.

Studies have elucidated the role of dispersal, landscape connectivity and exchange processes in the resilience of communities and ecosystems (Hughes et al., 2005). This can occur either by active dispersal, by quick regeneration or by resting stages, and serves to avoid disturbance and/or rapidly recolonize afterwards. So, recruitment is supported by life history traits such as high mobility, fecundity and early maturity.

Recovery of riverine biotic communities is presumed to be largely based on dispersal capacity in metacommunities as source-sink dispersal and drift rates are particularly high in river networks (Heino et al., 2015; McCluney et al., 2014). We may expect that dispersal capacities affect recovery rates, with strong dispersers recovering rapidly depending on proximity to source areas. In addition to dispersal, some species may also form seedbanks or resting stages that survive unsuitable periods (e.g., floods or drought-induced drying) inside the sediments. This can be understood as "temporal dispersal" or "traveling in time," observed for both riparian plants (Honnay et al., 2009), aquatic invertebrates (Stubbington and Datry, 2013), and even fish species (Furness et al., 2015) in intermittent rivers.

Through their greater connectivity, downstream locations may be more influenced by mass effects (i.e., high dispersal rates from favorable "source" to unfavorable "sink" localities; Pulliam, 1988) than more isolated headwaters (Brown and Swan, 2010), and thus be more resilient through stronger recruitment recovery. In contrast, species sorting should be stronger in headwaters, because high dispersal rates typical of mainstems do not influence local dynamics in the headwaters (Grönroos et al., 2013; Brown and Swan, 2010). This is especially true for benthic invertebrate communities that appear highly influenced by connectivity to upstream habitats (i.e., sources for drift dispersal) (Göthe et al., 2013). By contrast, fish community response to disconnection is mostly determined by local conditions in combination with barriers to dispersal in downstream sections (Van Looy et al., 2014).

In addition to dispersal capabilities, reproduction traits foster recruitment and recovery after disturbances. Life history traits promoting regeneration comprise high fecundity with the production of many eggs or seeds and seed banks. For fish, multiple spawning (iteroparity) or batch-spawning in combination with a protracted spawning season insure successful reproduction at broad ranges of environmental fluctuations (Wolter et al., 2016).

Refugia

Functional redundancy is the third mechanism of river ecological resilience. A single function can be supported by more than one species (functional equivalence of species) in a community. If one of the species is lost, the function is maintained for the ecosystem. Associated to the notion of response diversity, i.e., the variation in responses to environmental change by species within a functional group (Elmqvist et al., 2003), functional redundancy immediately leads to a resilience mechanism in refugial environments. Refugia are environments characterized by heterogeneity and continuity in habitat conditions favoring increased species survival and hence functional redundancy, as more species of the same functional group will co-exist and show variation in response to disturbance. Species differ in their ability to find and use refugia, but the more heterogeneous the habitat, the more likely many species will survive (Keppel et al., 2012). Refugia is used here in a wider sense, that is, sites offering (a) refuge to changing environments and (b) continuity in environmental conditions together with habitat heterogeneity offering opportunities for speciation and specialization. Environments with strong gradients in moisture and temperature like fluvial ecosystems are rich in micro and macrorefugia, respectively, at site and landscape scales. The role of landscapes as refugia is ruled by local and riverscape scale environmental heterogeneity, together with the continuity of provision of a habitat mosaic under changing environmental conditions (Keppel et al., 2012). River ecosystems offer refugia from disturbance through a mosaic of habitat patches that confer habitat heterogeneity and promote specialization of organisms (Townsend and Hildrew, 1994).

Most resilience literature puts forward functional redundancy as the principal mechanism by which communities persist through disturbances (Angeler and Allen, 2016). In the high dynamics of river ecosystems, we believe the resource and recruitment-based mechanisms that benefit from the disturbance are more prevalent—at least for short-term effects—than the refugia mechanism that depends on the hiding from disturbance.

The redundancy response to disturbance is determined in species habitat-specific resistance and resilience mechanisms that are generally described with life history traits that promote survivorship, such as behavioral and morphological traits (e.g., Lytle and Poff, 2004). The mechanism behind functional redundancy is the functional similarity of species in one trait, but their speciation or conditional differentiation in others.

Assessing ecological resilience

The mode of response to a disturbance can evolve over time. The prevailing response mechanism is influenced by an ecosystem's historical disturbance characteristics, which vary substantially across climatic, geologic and land-cover gradients (Rinaldi et al., 2015). Thus, we assume that rivers with strong resource pulses will host communities that re-assemble more readily, while those in river networks with high connectivity can recover quickly through recolonization after disturbance, and rivers with high habitat heterogeneity at local and riverscape scales offer refugia that promote species persistence and functional redundancy. Trait-based representation of these relationships allows for a better understanding of these interactions and can potentially inform adaptive resilience management (Larsen et al., 2016). Current knowledge in this domain of species interactions and food webs already offers tools for assessing strength and resilience of food web interactions (Wootton and Emmerson, 2005).

Many functional trait metrics and indices of disturbance response exist. In fish, for instance, responses to fluctuations of resources have been observed in batch spawning and extended spawning seasons, while for recruitment recovery high fecundity

promotes resilience. By contrast, multiple spawnings per year increase the probability at least some of the offspring will encounter favorable environmental conditions (Wolter et al., 2016). For benthic invertebrates, mobility by larvae, high drift rates or a hard exoskeleton (or shell) can provide resistance to flow disturbances (Poff et al., 2018). Further, mobility of all stages is seen as a recovery mechanism to both droughts (Leigh and Datry, 2017) and floods (Woodward et al., 2016; Poff et al., 2018). Dispersal through drift, swimming and adult flight ability implies important functional traits in this regard. With disturbance, associated resource pulses/fluctuations should mean generalist species with high fecundity and short life-cycles (multivoltine) have more chances in re-colonization. The refugia and redundancy mechanism, on the other hand, should be promoted by the presence of specialists, like those species that have strategies of oviposition by aerial adults, or survive with buried eggs or under anoxic conditions. The nature of the disturbance regime (magnitude, frequency, timing) of individual streams will result in different expectations of which 'mechanism' dominates based on the local spatio-temporal dynamics (Poff et al., 1997).

The recognition of these three mechanisms and their quantitative assessment based on the trait indices can be used to measure the strength of resilience, in a framework applicable for river management. The arrows in Fig. 4 highlight the external drivers of specific community resilience mechanisms. Strong resource dynamics drive organisms to resource competition or facilitation; high connectivity allows dispersal and re-colonization; and increasing habitat heterogeneity promotes species survivorship and functional redundancy. Hence, community composition as reflected in the prevailing traits indicates the relative contribution of the three specific mechanisms, and thus can indicate a community's potential sensitivity and resilience to specific types of disturbance. A community with a majority of good dispersing species, for example, might be vulnerable to strong resource pulses, while a community with many trophic or habitat specialists might be vulnerable to changes in ecosystem connectivity, which might provide opportunities for generalists to dominate.

Responses to and the relative importance of mechanisms operating at the community level will vary with the severity and predictability of the disturbance (Tonkin et al., 2017). Accordingly, relative changes of trait composition at the community level might offer strong indications of the dominant mechanisms and the strength of community resilience to specific disturbances. We illustrate this framework's application with the longterm data on trophic position of fish guilds of the Upper Mississippi River. Measured in "trophic position diversity," the lock-and-dam construction around 1940 reduced floodplain access and thus diminished refugia leading to diminished functional diversity (Delong and Thoms, 2016) thus a retreat on the Refugia axis (Fig. 5). In the resulting resilience surface, Recruitment also diminished slightly through partial loss of connectivity (loss of diadromous fish species), and resources increased slightly through the increase in peaks of algal blooms due to flow regulation.

Resilience thinking can inform of possible management interventions for long term sustainability. For example, communities characterized by resource resilience traits indicative of specific resource dynamics can be managed around "constraining" or restoring resource pulses and fluctuations, while preserving heterogeneity and connectivity. For recruitment recovery, for communities dominated by species with high dispersal capacities, management should focus on preserving well-connected systems (removing barriers/obstacles for dispersal). Where poor dispersal abilities dominate at the community level, connections should focus primarily on lateral connectivity with floodplain habitats. Finally, for refugia, communities with many habitat specialists can be preserved by maintaining habitat heterogeneity and managing for environmental quality conditions (even for extreme conditions such as in alpine streams).

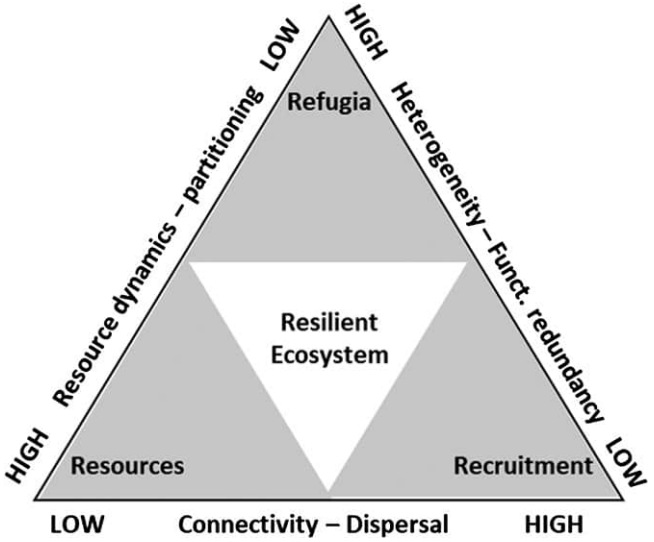

Fig. 4 Conceptual river resilience framework representing the three mechanisms driving ecological resilience: resource competition/facilitation, dispersal-based recruitment recovery and refuge-mediated functional redundancy. The extrinsic drivers at the ecosystem scale (arrows) that steer the prevalence of specific mechanisms are resource dynamics, landscape connectivity and environmental heterogeneity. After Van Looy K, Tonkin JD, Floury M, Leigh C, Soininen J, Larsen S, Heino J, LeRoy Poff N, Delong M, Jähnig S, Datry T, Bonada N, Rosebery J, Jamoneau A, Ormerod S, Collier K, and Wolter C (2019) The three Rs of river ecosystem resilience: Resources, recruitment, and refugia. *River Research and Applications* 35: 107–120. doi: 10.1002/rra.3396.

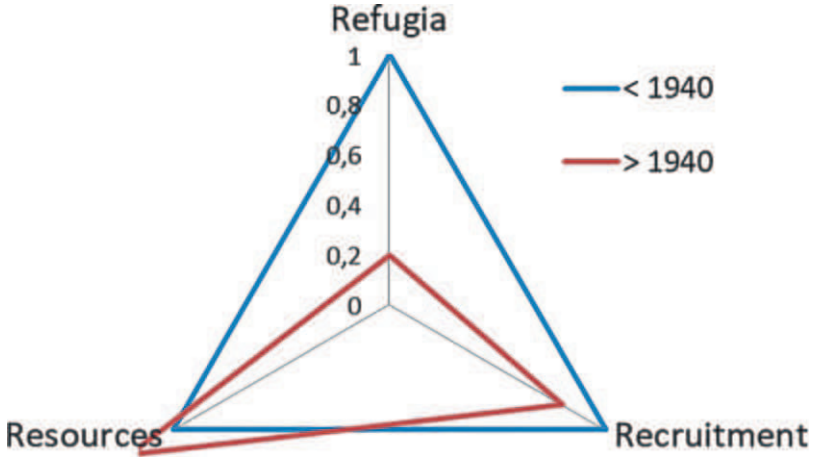

Fig. 5 Radar chart presentation of the resilience of the Upper Mississippi River communities of fish before and after the construction of the locks and dams (example in text). The post-1940 resilience surface is strongly reduced due to diminished functional diversity.

Social-ecological resilience; managing for river resilience

Concepts

Rivers are Social-Ecological Systems (Parsons and Thoms, 2018; Parsons et al., 2016), with interdependency for resources provided by ecosystems and by human activities (Berkes and Folke, 1998). The high degree of coupling between rivers, floodplains and society is a feature of riverine landscapes (Thoms et al., 2020) that requires insight into how ecological and social interactions influence the landscape.

Resilience provides a framework to understand, study and manage rivers as social-ecological systems. However, an important distinction must be made between resilience as a property of river systems and resilience as an approach to understanding social-ecological systems. As a property, resilience is the capacity of a river system to continuously self-organize and adapt to withstand a regime shift or to manage against transforming to another regime. As an approach, resilience thinking focuses on sustainability and stewardship, and seeks to understand social-ecological systems characterized by change and uncertainty. Both meanings are used interchangeably, although the latter tends to apply in policy settings while the former is the basis for empirical studies of resilience.

The concept of social-ecological resilience mirrors the development of the concept of Social-Ecological Systems (SESs), in which biophysical and social structures and processes are inextricably interlinked. There are three key concepts to social-ecological resilience (cf. Parsons and Thoms, 2018): (1) humans are integral component of landscapes in which they live; (2) social-ecological systems are complex adaptive systems; and (3) the key to sustainability is the ability of a system to absorb disturbance. Social-ecological resilience emphasizes the dynamics of SESs as complex and adaptive and their governance, which occur at multiple levels, can collectively increase or decrease system resilience. Environmental governance has the ability to not only influence the response of a SES to a disturbance, but also to mitigate or adapt a system so that it is forcibly transformed to new regimes of function (Chaffin et al., 2016) i.e., management actions can flip a river system into a new regime. A definition for river resilience in a social-ecological systems context is: "the capacity of communities to prepare for, absorb and recover from natural and societal events and to learn, adapt and transform in ways that enhance these capacities in the face of future events" (cf. Parsons et al., 2016).

The integration of resilience thinking into river assessment provides an approach for understanding social-ecological linkages in river systems. However, resilience does not currently have a strong operational and implementation procedure. Components pertinent for the development of a framework for assessing the resilience of rivers as social-ecological systems are provided by Thoms et al. (2020). This framework recognizes three logical levels or tiers representing, respectively, the "why," "what" and "how" of a best practice framework for assessing river resilience (Fig. 6). The first tier has resilience as the highest component of the framework (Fig. 6). Resilience forms the principle that guides the other tiers of the framework. In this case resilience is the context for assessing the socio-ecological linkages of rivers as a means maintaining the capacity of the system to absorb change or disturbance while remaining in essentially the same regime that retains the same function, structure and feedbacks (Walker and Salt, 2006). The second tier defines the components of the framework that represent the essential elements of understanding needed to assess resilience in rivers. The three components of this tier are an ecosystem understanding of rivers, their dynamics, and the influence of social systems. The first two components are directly related to concepts of geomorphic resilience (cf. Figs. 1 and 2). System dynamics can be viewed via adaptive cycles—the cycles of collapse and renewal. The position of the ecosystem within the adaptive cycle influences the characteristics of the system, vulnerability to change, and opportunity for change (Gunderson and Holling, 2002). Social systems represent the social components of assessing resilience in river ecosystems, and pertain to communities,

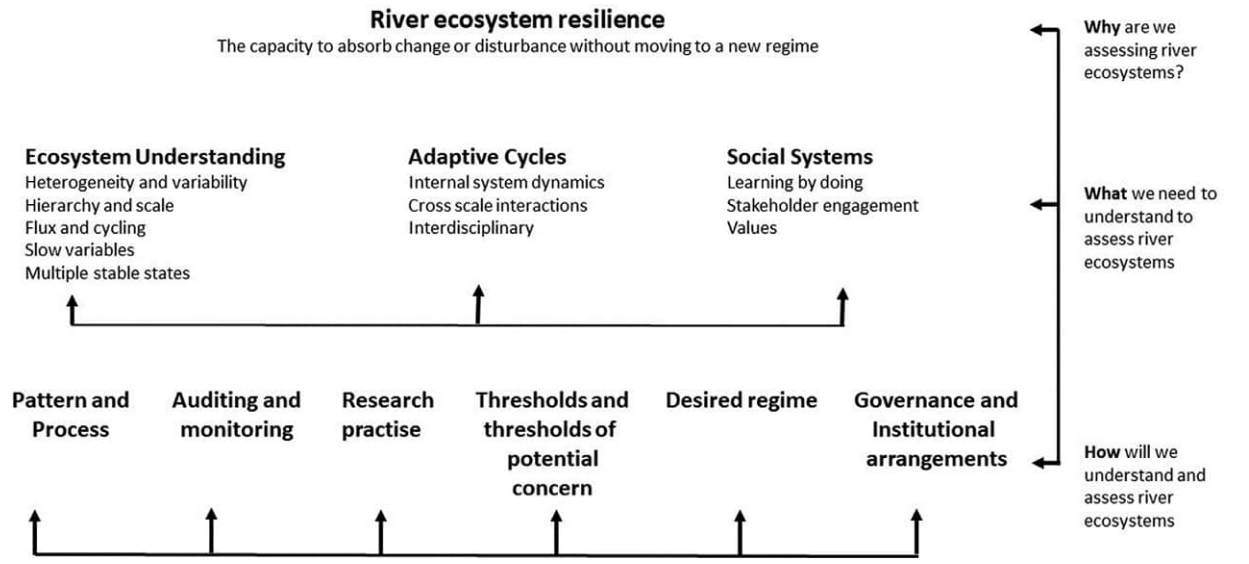

Fig. 6 A framework for assessing the resilience of rivers as social—ecological systems. Modified from Thoms MC, Rayburg S, Neave M, Parsons M and Chiew F (2020) The physical diversity and assessment of a large river system: The Murray-Darling Basin, Australia. In Gupta A (ed.) *Large Rivers*, pp. 587-608. Wiley, Chichester.

stakeholders, governance and institutions. The third tier of the framework describes how the components of understanding will be achieved. These components are essentially methods and tools that can be used to operationalize the understanding about resilience assessment and six components are suggested (Fig. 6). Successful implementation of a resilience paradigm into the assessment of rivers will require major shifts in thinking among all stakeholders, including scientists, citizens, and management agencies.

Resilience and the rivers of the anthropocene: Implications

Humans have modified riverine landscapes through land-use changes, urbanization and the construction of dams and weirs that regulate downstream flow and sediment regimes. These pronounced and sustained modifications result in regime shifts—a state change—of rivers. Viewed through a resilience lens, Anthropocene rivers have a different structure, function and set of feedbacks to their more "natural" cousins (DeBoer et al., 2020).

Establishing the "state" of Anthropocene riverine landscapes is essential for the study and management of these contemporary riverine landscapes. Recent research by DeBoer et al. (2020) showed the Illinois River ecosystem (Illinois, United States), once degraded by pollution from the Chicago metropolis did not recover to its Pre-Settlement state following major system wide restoration efforts. Rather the Illinois River showed "novel" unexpected responses, some of which suggest a reduction in its capacity to absorb future disturbances. Targets for the restoration of Anthropocene riverine landscapes need to be established because those based on our understanding of pristine systems are not applicable (Kopf et al., 2015). Anthropocene rivers are 'novel ecosystems' that do not conform to disciplinary paradigms, especially in terms of their response to drivers of change (cf. Hobbs et al., 2006). Drivers of change are not only disturbances events like floods but also river restoration activities. River scientists and managers must work across biophysical, social, economic and political domains to set objectives and manage for multiple, often competing, outcomes (cf. McLoughlin et al., 2020). This complex and unpredictable setting often paralyzes management actions, particularly those framed within traditional management paradigms. This requires developing our understanding of novel Anthropocene river systems through a far greater depth of interdisciplinary thinking. The dominance of biophysically-focused contemporary river assessment and monitoring approaches can be merged with those for assessing rivers as social-ecological systems. Frameworks describing how the social and ecological components of river ecosystems can be included in river assessment programs, based on principles of resilience thinking and strategic adaptive management, i.e., continuous success monitoring and adjustment of rehabilitation measures and management actions.

Assessing adaptive and resilient river management

Managing for river resilience must take into account the challenges posed by Anthropocene riverine landscapes. Because the fundamental state of these systems has been shifted, their dynamic trajectory has changed and management/restoration must accommodate this (Fuller et al., 2020). Fundamentally, rivers need "room to move" and the space required for this is a fundamental component of the resilience of any river type (Biron et al., 2014). Resilience based river management must incorporate "Freedom Space" to enhance geomorphic resilience and accommodate phase-shifted dynamic trajectories of Anthropocene rivers.

If consistently implemented such an approach not only provides space for current river dynamics and flooding but it could also accommodate river type and flood regime responses to climate change.

From an ecological resilience perspective, tipping points are often searched for in resilience indicators, to determine the critical change from one ecosystem state to another (Scheffer et al., 2015). The highly dynamic nature of natural river ecosystems and their pulsed hydrologic disturbances makes the presence of alternative stable states implausible (Lake, 2000), rather they exist on a continuum of states in response to antecedent flow conditions. On the other hand, anthropogenically altered flow regimes, patch and habitat dynamics, pollutant input or resource depletion can be expected to initiate tipping points. Indications for such tipping points have been observed at the scale of the river section in large rivers with artificial embankments causing significant declines in indicators of community diversity (Wolter and Vilcinskas, 1997; Van Looy et al., 2008). Human induced pulse disturbances might furthermore be better buffered in river systems than press disturbances. Correspondingly, increased frequency of extreme events associated with climate change might be better buffered due to the pulsed nature of such events than, for example, land use changes (=press or ramp disturbances) (e.g., Van Looy et al. 2016; Woodward et al. 2016).

Operating at the edge of instability generates immediate signals of changing opportunity. That surely is at the heart of sustainable development—the release of human opportunity. It requires flexible, diverse, and redundant regulation, early signals of error built into incentives for corrective action, and continuous experimental probing of the changes in the external world. Those are the features of adaptive environmental and resource management, and the societal transition needed to develop river management from a resilience perspective, instead of a curative and constricting "classic" approach.

Conclusion

The three resilience perspectives (Engineering, Ecological and Social-Ecological) can be merged in one framework to operationalize resilience research into management applications. The constraints that natural and anthropogenic disturbances place on river forms and biological communities' persistence have considerable implications for what actions are targeted when, and where to maintain and restore lotic systems. River management and restoration projects should thus focus on the catchment geomorphological context, the biological context of the species pool and underlying network connectivity, the habitat mosaic and resource dynamics, and the social-ecological system interactions. The better understanding of resilience mechanisms in river ecosystems must trigger and guide a sustainable management of rivers under future climates and societies.

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Ecosystem Services of River Systems – Irreplaceable, Undervalued, and at Risk

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This article was reviewed for the Encyclopedia of Inland Waters, Section Editor, LeRoy Poff.

Glossary

Biocultural diversity The diversity of life exhibited by interrelating natural systems and human cultures.
Cultural services All material and non-material (intangible) ecosystem services that have a cultural significance, or a symbolic or intellectual meaning.
Ecosystem integrity Characterizes the ability of an ecosystem to maintain its functions, processes, and biodiversity equivalent to that of a natural or healthy condition.
Ecosystem processes and functions Physical, chemical, and biological processes, and their roles and interactions, which underly ecosystem functioning and related ESS.
Ecosystem services (ESS) The benefits society receives from ecosystems. ESS are typically divided into provisioning, regulation and maintenance, and cultural services. River ESS (rESS) are water-related benefits society receives specifically from river systems.
Global critical natural capital The part of the global natural environment that fulfills important and irreplaceable ecosystem functions and is, therefore, of very high value for the services it provides.
Nature's contributions to people (NCP) A framework that builds on the concept of ESS by designating culture as central to all connections between humans and nature, and which recognizes broader values and knowledge systems, e.g. those of Indigenous peoples. Contributions from nature may be perceived as both positive and negative depending on the cultural, temporal, or spatial context.
Provisioning services All ecosystem outputs that can be traded, consumed, or directly used.
Regulating and maintenance services The benefits provided by ecosystems to society from the natural regulation and maintenance of ecosystem processes and functions.
River system All rivers in a hydrologically defined catchment, consisting of a main river and its network of tributaries, and the surrounding catchment or landscape.

 https://doi.org/10.1016/B978-0-12-819166-8.00129-8

Socio-ecological system A system in which different components, such as social, ecological, cultural, economic, and political components, are interconnected and considered as a whole. Interactions between humans and nature are particularly emphasized.
Total economic value A concept to classify different values of an ecosystem, based on the idea that the benefits of nature for society are composed of several elements including present use and non-use values with the latter possibly generating benefits in the future.

Introduction

Rivers, streams, and their floodplains and coastal areas provide an extensive and diverse range of river ecosystem services (rESS) (Fig. 1). They support the provision of drinking water and fish as food, create floodplain areas that retain floods, supply water for crop growing, provide cooling to urban areas during heat waves and spaces for spiritual and recreational activities, offer artistic inspiration and, in many places, are revered by local peoples (Fig. 2). River valleys have been preferential sites for human settlement for millennia, as they provide food, water, flat areas for housing, fertile farming grounds, and construction materials, as well as transport and migration routes. The earliest urbanized civilizations have developed as 'hydraulic empires' (Wittfogel, 1957); for example, the Egyptian civilization has benefitted for several millennia from the predictable annual floods of the Nile River that fertilized their crop fields. Other civilizations have attempted to optimize the use of natural capital available in floodplains for agriculture and settlements through the modification of river systems, e.g. by draining floodplains or building longitudinal and transverse dams, barrages, or water diversions along river channels. These modifications, however, often have been accompanied by major socio-economic trade-offs such as salinization of agricultural soils (e.g. Mesopotamia), increased risk of catastrophic floods when dykes of embanked river channels failed (e.g. Yangtze River in China), and ground subsidence of crop fields below river level resulting in the need for constant pumping of drain water (e.g. The Netherlands). In such highly modified rivers, the dramatic environmental trade-offs that have appeared have affected their ecosystem integrity, biodiversity and, hence, their ability to deliver key rESS. This has resulted in a strong narrowing of options for human uses of the rivers and their floodplains.

In these ways, human impacts have fundamentally transformed many river systems. The resultant state of river ecosystems worldwide is sobering: over the past centuries, 70–100% of floodplain areas have been lost in Europe alone (EEA, 2020a), the majority of the world's large rivers are no longer free flowing (Grill et al., 2019), and there has been an 84% decline in monitored freshwater vertebrate populations (WWF, 2020); for the future, a higher extinction risk has been projected, as compared with

Fig. 1 Rivers, streams, and their floodplain and coastal areas provide an amazingly diverse range of ESS; from left to right, top row: drinking water, food, irrigation; lower row: recreation, flood retention, culture. Photos: pixabay.com.

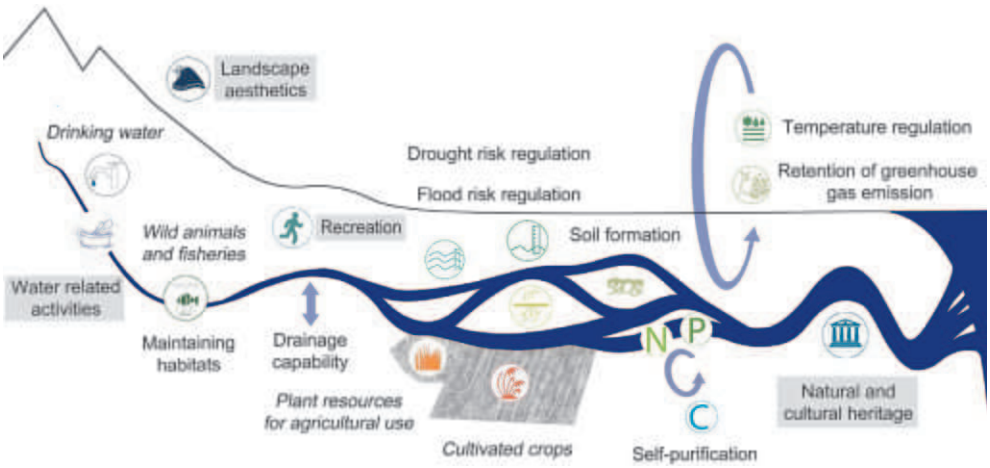

Fig. 2 Overview of major river ecosystem services in a riverscape context (compare Table 1 for further details). Regulating services appear in regular font, *provisioning services* appear in italic font, and cultural services are shaded in gray.

terrestrial and marine realms. On the other hand, there is an increasing awareness that river ecosystems should be protected, actively managed, or restored for multifunctionality, for instance concurrently targeting biodiversity conservation, flood retention, and recreational use (Schindler et al., 2016).

The ESS concept as it applies to rivers as socio-ecological systems

Brief history of the evolution of the ESS concept

The ESS concept can be traced back to the term natural capital (Daily, 1997), the global economic value of which is estimated at $125 trillion per year (Costanza et al., 2014). Lakes and rivers produce a natural capital of ~$12,500 ha^{-1} y^{-1} including contributions to water regulation, erosion control, waste treatment, food production, and cultural services. The Millennium Ecosystem Assessment (MEA, 2005) linked the delivery of ESS to human well-being in a socio-ecological system framework. From this point onwards, ESS received global recognition and gained a policy foothold.

The Economics of Ecosystems and Biodiversity initiative (TEEB, 2010) aimed at reflecting the value of nature's services by emphasizing the global economic benefits provided by biodiversity. Acknowledging the fundamental dependency of society on nature, the Intergovernmental Science-Policy Platform on Biodiversity and ESS (IPBES) was established in 2012 to foster the link between science and policy for matters related to biodiversity and ESS (IPBES, 2019).

Based on the MEA (2005), which originally defined four different types of ESS, the recently developed Common International Classification of ESS (CICES) distinguishes three ESS groups (Haines-Young and Potschin-Young, 2018): provisioning, regulation and maintenance, and cultural services. The CICES dropped MEA's 'supporting services' and considers them as a set of physical, biological, and environmental processes and functions that are fundamental to support and sustain ecological integrity - a change that was implemented to help identify the 'endpoint services' valued by people.

After the provision of ESS were included as a strategic goal in the Convention on Biological Diversity (CBD, 2010), as well as in the UN Sustainable Development Goals (SDGs), the concept gained further momentum in freshwater-related policies (EEA, 2020a). Currently, it is recognized internationally that the ongoing erosion of biodiversity and ESS, including that of rivers, is undermining efforts to achieve sustainable development, and that this pressure must be reduced (e.g., UNEP, 2021).

The concept of ESS has not, however, been without controversy or debate. It has been criticized for being anthropocentric and used to promote the exploitation of nature (e.g. for hydropower development) at the expense of ecosystem integrity and biodiversity conservation goals (Vigerstol and Aukema, 2011). It has also been criticized for being overly focused on economic valuation and the commodification of nature as well as for not moving beyond vague definitions and classifications (Schröter et al., 2014). An attempt has been made to address this critique in the recent 'nature's contributions to people' (NCP) concept, which acknowledges a broader appreciation of all benefits, including social, cultural, spiritual, and religious aspects as well as detrimental contributions such as disease transmission or predation (Díaz et al., 2018).

ESS provided by river ecosystems

The three groups of ESS are all pertinent for river ecosystems (Table 1. Fig. 2): First, provisioning services are defined as material things and bioenergetic products provided by ecosystems, with rivers and their floodplains and estuaries generating these as an interconnected unit. Second, regulation and maintenance services entail all processes that influence the environment (abiotic and

Table 1 ESS of rivers and floodplains as considered in the River Ecosystem Service index (RESI) based on the Common International Classification of ESS (CICES).

Main group	*Subgroup*	*Ecosystem service*
Provisioning	Nutrition	Cultivated crops
		Plant resources for agricultural use
		Wild animals and fish
		Surface water for drinking
		Groundwater for drinking
	Resources	Fibers and other materials from plants for direct use or processing
		Water for non-drinking purposes
	Biomass-based energy resources	Plant-based resources
Regulating	Retention (Self-purification)	Retention of organic carbon (C)
		Retention of nitrogen (N)
		Retention of phosphorus (P)
	Global climate regulation	Retention of greenhouse gas emission/carbon sequestration
	Extreme discharge mediation	Flood risk regulation
		Drought risk regulation
	Drainage	Drainage capability
	Sediments	Mass flow/sediment regulation
		Soil formation in floodplains
	Local climate regulation	Local temperature regulation/cooling
	Habitat	Maintaining habitats
Cultural	Cultural	Landscape esthetics
		Natural and cultural heritage
		Unspecific interactions with riverine ecosystem
		Education and science
		Water-related activities

Modified from Podschun SA, Albert C, Costea G, Damm C, Dehnhardt A, Fischer C, Fischer H, Foeckler F, Gelhaus M, Gerstner L, Hartje V, Hoffmann TG, Hornung L, Iwanowski J, Kasperidus H, Linnemann K, Mehl D, Rayanov M, Ritz S, Rumm A, Sander A, Schmidt M, Scholz M, Schulz-Zunkel C, Stammel B, Thiele J, Venohr M, von Haaren C, Wildner M, and Pusch M (2018) *RESI - Anwendungshandbuch: Ökosystemleistungen von Flüssen und Auen erfassen und bewerten, 31/2018*. IGB.

biotic) and refer to both the river and any interlinked features, e.g. the retention of nutrients within the instream water column as well as carbon storage in floodplain soils. Third, cultural rESS continue to evolve rapidly from an early definition as "the nonmaterial benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation, and esthetic experiences" (MEA, 2005). In the freshwater context, MEA's 'supporting services' related to a river's hydrology and maintenance of water flows and levels, i.e. discharge, flow regime dynamics, and connectivity with aquifers and floodplains, as well as to morphology, thus to the physical structure of the river channel and the floodplain.

In an in-depth review of the field, Milcu et al. (2013) discuss current typologies of ESS and different subcategories, such as cultural services: sense of place, cultural heritage values, cultural diversity, social relations, recreation and tourism, esthetic values, spiritual and religious values, educational values, bequest, intrinsic and existence, inspiration, and knowledge systems. They also cover the growing diversity of terms that pertain, such as cultural services, life-fulfilling functions, information functions, amenities and fulfillment, sociocultural fulfillment, and cultural and amenity services. Many of these cultural ESS are inextricably and/or indirectly linked to other types of ESS, as well as to the integrity of the socio-ecological system as a whole. A consistently agreed characteristic (of many, but not all) cultural ESS is their intangibility, which renders them particularly sensitive and complex to appraise, especially quantitatively, which is at least part of the reason why, so far, they have seldom been integrated into management plans.

The broad 'domains' in which cultural heritage is manifested – knowledge and practices concerning nature and the universe, traditional craftsmanship, social practices, rituals and festive events, oral traditions and expressions, including language, as a vehicle of the intangible cultural heritage, and performing arts – encompass various cultural services. The full range of relationships of different cultures and ethno-linguistic groups of people with rivers is vast, and intimately and dynamically linked to the various rESS (Anderson et al., 2019).

Access to rESS and their availability in time and space is often tied to the pulsing hydrology of rivers. As such, cultural, human-river-relationships and dependencies on natural capital can be considered in an analogous way to biotic strategies that aim at benefitting from temporarily available natural resources while trying to avoid risks, which fosters a high biocultural diversity in river-floodplain systems (Wantzen et al., 2016). All over the world, the rhythm of the waters has spurred the evolution of rich cultures, shared use of common goods, well-being and intercultural communication (Wantzen, 2022). The fertile Mekong River floodplains of southeast Asia, for instance, have been sustaining rich cultures since Paleolithic times, and today they support 60 million people with fish as their primary source of protein (Campbell, 2022).

The relationship among river health, ecological integrity and resilience, and rESS

Ecosystem services have long been linked to the health or integrity of ecosystems. Rapport et al. (1998) outline how ecosystem integrity is enabled when an ecosystem's vigor, organization, and resilience is intact. Not surprisingly, a higher delivery of regulating and cultural rESS has been shown to be correlated with a better condition of aquatic ecosystems, while the use of provisioning services more commonly has been associated with stresses and impacts on ecosystems. However, the link between biodiversity and ecosystem functioning, and between biodiversity and rESS, is not yet fully established, and knowledge gaps still exist, including, for example, the multitude of functions supported by aquatic ecosystems, functional distinctiveness of rare species, multitrophic interactions, and the relevance of spatial-temporal scales (Daam et al., 2019).

While the availability and quality of rESS largely depends on ecosystem status, the valuation of rESS will additionally depend on how local stakeholders value the rESS which are accessible to them (Fig. 3). Some rivers are heavily modified from their natural state by channelization, levees, nutrient loading, invasive species, and other stressors, but they still may provide important ESS valued by local communities. For example, the biological retention of nitrogen and phosphorus originating from wastewater runoff from agricultural areas occurs at higher rates in more polluted streams (Gücker et al., 2006). Such systems should still be valued, because they provide waste treatment and carbon storage services, even if they have deficits in terms of biodiversity and esthetics. Identifying and negotiating rESS trade-offs are important parts of the deliberation by stakeholders when envisioning management options.

Managing rESS in a catchment-based approach

Approaches that consider biodiversity conservation and rESS provision in a catchment-context represent a prerequisite for efficient and effective sustainable river management. However, the spatially explicit, sometimes disconnected, and temporally dynamic nature of rESS supply and demand across a river catchment can make it difficult to consider these services in management approaches (Malinga et al., 2015). For example, the use or extraction of freshwater resources is typically local, but often results in a reduction of or change in the resource downstream. Hence, downstream communities (people, organisms) pay the environmental costs caused by e.g. reducing river flows, which can result in conflicts between upstream and downstream water 'users'. Another example is the partial to complete loss of river deltas caused by the retention of river sediments by dams. In the Mekong River, for example, only approximately 1% of the original sediment yield is projected to arrive in the delta (Kondolf et al., 2018). Since rivers integrate the effects of all forms of land and water management (or mismanagement) in their catchments, all territorial policies, including for agriculture, forestry, industrial use, navigation, or urbanization, ideally should be elaborated on the basis of an Integrated River Basin Management (IRBM) plan, respecting political levels and co-created by local decision makers and communities. A complicating factor, especially for large rivers, is that rivers often delineate the borders of political territories, which makes the application of catchment-wide policies difficult. In the past, transboundary river management schemes were mostly based on agreements related to the exploitation of rESS (e.g. navigation treaties) without considering the long-term maintenance of essential ecosystem processes. The historic, first transboundary initiative aiming at protecting a large river from pollution was initiated in 1950 with the establishment of the International Commission for the Protection of the Rhine (ICPR) on the basis of all catchment countries agreeing to overcome national and/or administrative boundaries by sharing the costs and benefits of rESS use (Wantzen et al., 2021).

One of the persistent key management challenges relates to balancing water availability with water use while maintaining healthy, resilient water bodies. Comparisons of trade-offs among multiple rESS under natural flow conditions or with altered flows are increasingly performed (as Table 2 examples illustrate). While few environmental flow determinations explicitly adopt an ESS

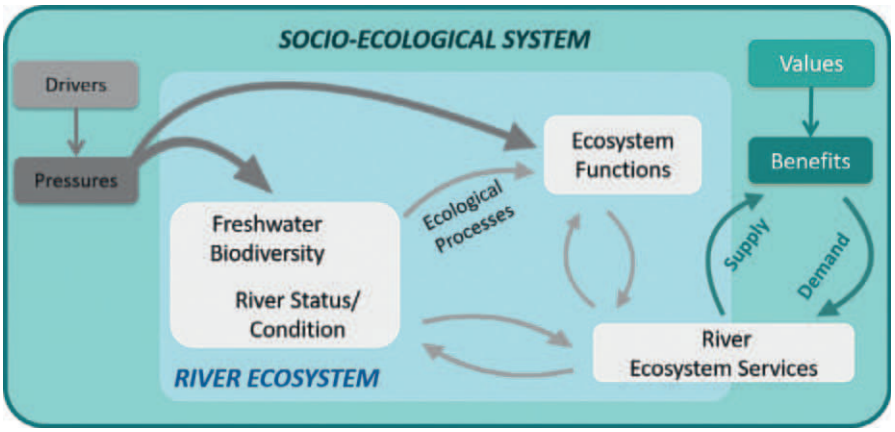

Fig. 3 Relationship between biodiversity, ecosystem functions and ecosystem services within the socio-ecological system. River Ecosystem Services (rESS) connect between the ecosystem and the socio-ecological system. Figured adapted from Nogueira A, Lillebø A, Teixeira H, Daam M, Robinson L, Culhane F, Delacámara G, Gómez CM, Arenas M, Langhans SD, Martínez-López J, Funk A, Reichert P, Schuwirth N, Vermeiren P and Mattheiß V (2016) Guidance on methods and tools for the assessment of causal flow indicators between biodiversity, ecosystemfunctions and ecosystem services in the aquatic environment. Deliverable 5.1, European Union's Horizon 2020 Framework Programme for Research and Innovation Grant Agreement No. 642317.

Table 2 Selected case studies to show diverse ways in which rESS are being addressed.

Location(s)	*Country/Region*	*Purpose/objectives/role/importance of considering ESS*	*Approach used incl. specific services covered, benefits of inclusion*	*References*
80 km of a Bavarian Danube stretch below the city of Ulm	Germany	Testing management options to increase flood retention capacity, balancing key uses and economic interests with floodplain restoration and nature conservation.	Non-monetary scores assigned for 1-km segments of floodplain, separated into river channel, the active and the non-active parts of the floodplain. Indicator value combined from several indices of rESS categories.	Stammel et al. (2021), Thiele et al. (2020), Fischer et al. (2019), Podschun et al. (2018)
Danube Catchment	Europe	Illustrating a model-coupling approach considering biodiversity and rESS supply and demand.	Hierarchical Bayesian models for fish biodiversity; four estimated ESS layers produced through ARIES platform; joint spatial prioritization of biodiversity and ESS using Marxan with Zones.	Domisch et al. (2019)
Intercontinental Biosphere Reserve of the Mediterranean (IBRM)	Spain, Morocco	Allocating restoration zones in a Green and Blue Infrastructure (GBI) network, considering cost-effectiveness, biodiversity, ecosystem services, and ecosystem condition.	Application of Marxan with Zones across freshwater, coastal, and marine ecosystems incl. stakeholder-defined scenarios of Green and Blue Intrastructure in the Intercontinental Biosphere Reserve of the Mediterranean.	Barbosa et al. (2019)
Continental Europe	Europe	Exploring links between ESS and good ecological status. Higher ecosystem service delivery is mostly correlated to improved ecological status. Results show relevance of protecting and restoring aquatic ecosystems.	Quantification of main ecosystem functions and services related to rivers, lakes, coastal waters across Europe (e.g. water purification, erosion prevention, flood protection, coastal protection, and recreation) by producing European performance maps of water ESS capacities, ESS flow and ESS sustainability.	Grizzetti et al. (2019)
Athens (Greece), Emscher River (Germany), Hoffselva (Norway), Llobregat River (Spain), Westland (Netherlands), Aarhus River (Denmark)	Multiple demonstration sites across Europe	Implementation guide for local-level evaluations of changes in water-related ESS related to specific water management measures.	Quantification and monetization of different water management measures showing benefits and impacts. Links between WFD state parameters and specific ESS classes are proposed. River related ecosystem service valuation related to restoration of several case studies.	Anzaldua et al. (2018), Gerner et al. (2018)
Ter River	Catalonia, Spain	Analyzing benefits and trade-offs linked to instream flows and related ESS. Accounting of stakeholders' views and interests, and multiple water withdrawals.	Stakeholder oriented ESS validation and five-step assessment of ESS production related to both diverted and instream flows in the basin.	Jordà-Capdevila et al. (2016)
Lower Mekong Basin (LMB)	Lao PDR, Cambodia, Vietnam	Tradeoff analysis between water use, food security supply and energy production related to proposed mainstream hydropower projects	Comparison of capture fisheries, sediment/nutrients, social mitigation costs, gains from electricity generation, improved irrigation and flood control.	Ziv et al. (2012), Intralawan et al. (2018)
Ganga River Basin	India	Determining the environmental water needs of the river ecosystem and communities, with flow regime alteration and water infrastructure development	Assessment of links between high and low flows and rESS, with focus on cultural services and traditional practices critical to cultural identities (e.g. rituals such as ceremonial bathing and meditation, flood recession farming), to calculate environmental water regimes for priority river reaches, Kumbh religious ceremony, and water management scenarios.	Lokgariwar et al. (2014), Anderson et al. (2019)
Mara River (Kenya and Tanzania), Kihansi and Great Ruaha rivers (Tanzania), and Zambezi River Basin	Sub-Saharan Africa	Balancing water resource use and ecosystem services within areas of nature conservation value. Assessing environmental water needs for priority areas of the river basin under different flow management scenarios	Multidisciplinary, holistic assessments of environmental water needs of river ecology, and associated ESS and other sociocultural dependencies of communities (e.g. tourism, rural subsistence livelihoods, wilderness value, endangered species), economic valuation of benefits and costs of trade-offs, improved flow management, and specific dam operation rules.	LVBC and WWF-ESARPO (2010), WWF-TCO (2010), Tilmant et al. (2010), McClain et al. (2013)
Tana River Basin	Kenya	Modelling the balance of ecosystem services with water, energy and food security	Search for (Pareto-) optimal allocation of benefits among sectors and scenarios. Analysis of trade-offs among achievable benefits from new rice, cotton and biofuel irrigation projects while maintaining ESS.	Hurford and Harou (2014)

framework, rESS are a regular focus of most holistic assessments, from fisheries and flood recession agriculture to sacred ceremonies linked to specific flow events (Horne et al., 2017). Similarly, the application of nature-based solutions in river management and decision-making draws extensively on ESS data to improve outcomes (Barbosa et al., 2019).

ESS in global and national policies, laws, and governance systems

In recent years, political awareness of the high relevance of ESS for human well-being has grown significantly (CBD, 2010; IPBES, 2019). Acknowledging their fundamental importance has already resulted in the development of various approaches for national assessments of ecosystems and their services in several countries such as the UK (UK NEA) and Germany (Albert et al., 2017; Grunewald and Bastian, 2015). However, these national assessments are often not directed toward water-ecosystem related issues, and legal frameworks still focus on individual sectoral objectives without explicitly mentioning ESS (Kistenkas and Bouwma, 2018). Nonetheless, significant scientific progress has been documented, e.g. for groundwater ecosystems (Griebler and Avramov, 2015), ESS quantification approaches (Hanna et al., 2018), or evaluation approaches in general (Anzaldua et al., 2018).

Positive examples are the German Federal Nature Conservation Act and the Water Management Act, which implicitly address rESS. The latter act refers to water services and introduces the principle of cost-recovery to compensate for financial, resource, and environmental costs caused by the user. It thereby stipulates incentive pricing, i.e. the polluter-pays-principle. The European Union Water Framework Directive (WFD) links its objectives to the ESS concept; for example, 'good ecological status' for rivers (and other waterbodies) will only be reached with good water quality, which in turn is a prerequisite for several provisioning and cultural rESS. In addition, at the practical level, most management measures that target WFD-objectives support the availability of different rESS (Hornung et al., 2019). Further, recent documents such as the EEA (2020a) freshwater report or the state of nature report (EEA, 2020b) underline the added value of the ESS concept in integrated management approaches.

Methods, tools and resources for mapping, assessing and reporting on status and trends of rESS

Despite the lag in practical applications of the ESS concept, a multitude of methods have been developed and tested that allow targeting objectives related to rESS in a management context. The methods address different aspects, such as assessing rESS, decision support, trade-off analysis, or stakeholder involvement. Often the data needed for these analyses are complex, since they are related to drivers, pressures, ecosystem states, as well as the capacity, flow and supply of respective rESS (sensu Grizzetti et al., 2016), and they need to be available at the appropriate temporal resolution and spatial grain.

Methods and tools for mapping and quantifying rESS

Ready-to-use software and sets of models that specifically target rESS have become freely available to use. A literature review of ESS mapping, with respect to geographic spatial scale and resolution, is provided by Malinga et al. (2015). One of the most widely known models is InVEST (Sharp et al., 2015). InVEST is a GIS spatially enabled model that allows the user to analyze the supply of various rESS, e.g. sediment retention, water purification, and fisheries (Vigerstol and Aukema, 2011). Recently, models based on machine learning have begun to emerge. For example, ARIES (Artificial Intelligence for Environment & Sustainability; https://aries.integratedmodelling.org/), uses semantics and machine reasoning methods to produce spatial maps of the supply and demand of ESS, from local to global scales (Villa et al., 2014). Currently, the ARIES platform provides several customizable global models, among them three that are contextually linked to rivers, addressing water supply, flood prevention, and recreation.

The 'River Ecosystem Service Index' (RESI) has been developed as an integrated approach quantifying multiple ESS in river corridors to establish a rationale for inter-sectoral decision making in complex management planning (Podschun et al., 2018; Stammel et al., 2021). The RESI provides a catalog of rESS (Table 1) that are spatially explicit and assessed in a non-monetary, uniform way using scores from 1 (very low) to 5 (very high). For example, the value for the provisioning services of agricultural land and pastures is calculated combining land use, soil quality, and flooding frequency data; cultural rESS are also assessed e.g. based on available surface waters, the parts of landscape experienced by different groups of people, and the number of protection categories present.

rESS market and non-market valuation

Many of the rESS provided for societal well-being are public goods, and because they are not traded in markets, do not have a market price. Examples are the esthetic value of river systems or the value of nutrient retention in floodplains. Since market prices remain the dominant expression of value, these services are often not considered in societal and political decisions, which, in an economic sense represents a market failure. Accordingly, the aim of an economic valuation of rESS is to give nature more weight in analyses based on monetary arguments and to be able to better and more transparently incorporate nature's value into decision-making. Different methods to assign value to ESS exist, such as market value, production-based, cost-based, revealed preference, stated preference, and benefit transfer. Provisioning services such as drinking water may be quite straightforward to assess using market-based methods, or regulating services such as carbon sequestration using cost-based methods (e.g. damage costs avoided). ESS not typically appreciated by society, sometimes known as 'hidden' or 'silent services', including cultural services such as

community cohesion, intergenerational knowledge transmission and sense of place, are difficult to address in monetary terms. A commonly used framework to represent such different values of an ecosystem in a more balanced way is that of Total Economic Value (TEV), which considers elements including use and non-use values (Turner and Pearce, 1990). Use values are associated with either a direct (such as food production or recreation) or indirect (such as regulating services) use of environmental goods. Non-use values are independent of a current or potential use, and are based on the assumption that the individuals may benefit only from knowing that an ecosystem exists.

Assigning a monetary value to ESS can be performed using a number of established valuation methods (Tinch et al., 2019). In environmental economics, values are generally measured in terms of preferences regarding the benefit(s) or utilities individuals derive from a change in environmental quality, such as an improvement in water quality. The monetary value of this benefit is measured in terms of the individual's maximum willingness-to-pay (WTP) for this improvement. The basic assumption is that there is a link between the traded goods (e.g. travel costs to a national park) and the benefit people derive from that ESS (e.g. recreational experience). Stated preference approaches directly ask people for their preferences, as a measure of the demand for an ESS. In contrast, market-based approaches use market prices to estimate the value of ESS. Provisioning services (e.g. food and fisheries) are usually estimated through market prices. Cost-based approaches use estimates of the costs that would arise if the services provided by ecosystems had to be provided by a technical substitute (e.g. replacement cost approach) or estimates of the costs caused by environmental damages (e.g. damage cost approach). Meanwhile, many studies demonstrate the substantial economic benefits of river restoration derived from different rESS, such as the improvement of fisheries and wildlife habitats, recreational benefits like angling and boating, or the appreciation of scenic landscapes (Dehnhardt et al., 2019).

Field-based measurements

Although many current rESS assessments are desktop, the foundational calculations to estimate the delivery of some rESS require field measurements. Notably, wastewater treatment and water purification, carbon storage and food production are underpinned by biogeochemical and ecological rates and quantities. These processes, and specifically their magnitude, are ultimately valued by stakeholders when they monetize or otherwise value rESS. For example, nitrate removal can be assessed by measuring denitrification rates in the communities of bottom-dwelling organisms of rivers. Mass balance approaches can reveal whether rivers and connected floodplain wetlands are net storers or releasers of carbon, by measuring the organic and inorganic carbon content of sediment cores (e.g., Shields et al., 2017). Fish yields per year or catch per unit effort of fisheries can act as a measure for provisioning services from rivers and reservoirs (Hoeinghaus et al., 2009). Together, these measurements that quantify the magnitude of a given rESS should inform the ranking or prioritization of the ESS delivered by waterbodies, despite being difficult to incorporate in a WTP-framework because their relative differences are unseen by the public eye. Solutions to this problem include spatial planning (discussed below) coupled with on-the-ground measurements.

ESS in planning and management of river systems

The contribution of the ESS concept to traditional spatial planning is that it explicitly addresses both the current supply of ESS and the present and future demand of ESS. The demand is related to two different perspectives: One is the actual use or consumption of a good or service, the other is the desire or preference for ESS; the latter also encompasses future uses or pure knowledge about the existence of certain ESS. A comprehensive understanding of the relationships between rESS supply and demand, their temporal and spatial patterns of distribution and quantity, and the flow of rESS to beneficiaries, plays a decisive role for the successful integration of the ESS concept into different stages of spatial planning and decision-making. However, integrating this information into planning processes remains conceptually and methodologically challenging, and depends heavily on the nature of the institutional setting, such as the availability of tools to integrate ESS into planning instruments or the sufficiency of knowledge of administrative actors.

Simons et al. (2017) provide a toolbox of state of the art technologies and remote sensing data which can be used to describe, quantify, and compare explicitly water-related ESS in space and time at the catchment scale and under different scenarios. The tools have been applied in relation to different land- and water management policies, and changing conditions of water availability under climate change, in the transboundary Da catchment (a sub-catchment of the Red River catchment in China, Viet Nam and Lao PDR). Concurrent conservation and management of rESS and freshwater biodiversity can be planned based on the concept of ecosystem-based management (Langhans et al., 2019) and operationalized using a variety of spatial optimizers, such as Marxan with Zones (Watts et al., 2009), Gurobi (Gurobi Optimization, Inc., 2021), Zonation (Moilanen et al., 2014), spatial multi-criteria decision analysis (Esmail and Geneletti, 2018) or ARIES accounting for multiple-criteria (Martinez-Lopez et al., 2019). All of these methods provide a robust framework to analyze large-extent, fine-grain spatial data in the light of user preferences and, thus, allow exploring management scenarios that are socio-ecologically relevant. Domisch et al. (2019), for example, used Marxan with Zones to spatially prioritize areas for fish biodiversity conservation and the supply and demand of carbon storage, flood regulation, recreation and water use in the Danube Catchment in Europe. Comino et al. (2014), by contrast, applied a spatial multi-criteria decision analysis model to produce thematic maps of naturalness and stressors to inform management and restoration planning within the Pellice River catchment, northern Italy. Martinez-Lopez et al. (2019) used a spatial multi-criteria analysis approach within ARIES (developed by Villa et al., 2014) to find the best management actions to compensate for the unintended loss of biodiversity and ESS in the Baixo Vouga Lagoon in Portugal.

Participatory assessments, citizen science, social media, and public awareness

Participatory approaches, including interviews, citizen science surveys, and exercises using GIS have in common that they foster the inclusion of local knowledge and preferences in rESS assessments. Recently, rapid technical advances provide the basis to apply these methods to large spatial areas, enabling the mapping of perceived ESS benefits and measures of the links to human well-being (Fagerholm et al., 2020). More than 30% of 89 rESS studies evaluated by Hanna et al. (2018) used data derived from participatory approaches. In contrast to data specifically generated for the purpose of a study, user data crowdsourced from social media (e.g. from Flickr or Twitter), citizen science portals (e.g. eBird, iNaturalist), or from outdoor activity-sharing platforms or applications (e.g. STRAVA, Geocaching) can provide fresh information on reporter location in addition to texts and pictures (Havinga et al., 2020). For instance, several studies have shown that the use of social media data enables a rapid, cost-effective and continuous prediction of visitor counts (Sinclair et al., 2020), which are important in assessing recreational use impacts on freshwater ecosystems and associated ecological and social carrying capacities (Venohr et al., 2018). Using geotagged photos in combination with a survey, Keeler et al. (2015) found a positive relationship between water clarity and visitor numbers.

Two novel research areas, Culturomics and iEcology, have recently gained attention for analyzing human-nature interactions and ecological patterns and processes. Information drawn from webpages, news and social media posts, photo and video documents, as well as from online engagement (i.e. searches, views, comments and shares), is used to study and demonstrate the public interest in nature and to frame conservation issues. Applications range from mapping cultural ESS to identifying potential aquatic flagship species (Jaric et al., 2020). Social media platforms also provide new opportunities for engaging scientists and stakeholders to contribute to raising awareness about the importance of ecosystems and biodiversity, enhance the acceptability of conservation measures to better balance rESS trade-offs or provide science–policy interfaces for interactively planning for nature-based solutions (Varumo et al., 2020).

Broader communication may include outreach by journalists, writers, artists, and other communicators. Documentaries like 'Planet Earth' and 'Planet Earth II' (BBC), 'Our Planet' (Netflix), 'NOVA' (PBS), or promoting certain species on journal covers (He et al., 2021) may bring the wonders of freshwater life into the public eye and call for action. Although social media may help to maintain public engagement, enhancing education about rESS through youth action in schools and educational institutions might be the best long-term investment. New formats, e.g. mixing teaching materials, videos, online content and targeted outdoor experiences are needed for knowledge mobilization that encourages participation, learning and creation.

Conclusion

Rivers and their floodplains provide a range of rESS such as water for drinking or irrigating crops, food, flood protection or spaces for recreational activities. Human use and activities have fundamentally transformed river systems, causing a reduction in the availability of many rESS. Political awareness of the implementation of the concept of ESS has grown significantly and has placed ESS central to multiple policy objectives (CBD, 2010) with the aim of advancing concepts and methods for recording and assessing ESS (Díaz et al., 2018; IPBES, 2019). Despite this promising advance, methods, tools and resources for mapping, analyzing, assessing, and reporting on status and trends in rESS are scattered and currently vary regionally, therefore rendering large scale evaluations of rESS approaches difficult. It is time to follow up with a more coherent, harmonized approach and set of methodologies for rESS assessment, and to develop and test guidelines of how to use these assessments in catchment restoration and management.

The climate crisis manifests in most regions of the world as a water availability crisis; therefore, key rESS that depend on water availability or are related to the presence of healthy, resilient water bodies have recently received increased attention. With increasing competition among various societal groups for water, the rESS concept provides a unique opportunity toward effectively negotiating the different interests in a sustainable way that also considers the need to combat the concomitant biodiversity crisis. The UN Decade of ecological restoration and the revision of the CBD with its 2050 biodiversity vision offer much-needed possibilities to position rESS as a central element of new policies and agendas for action toward sustainable development.

Knowledge gaps

1. Documentation and use of assessments of status and trends in the world's ESS for rivers and other freshwaters and the risks associated with future development, independent of assessments for terrestrial and marine systems.
2. Methodologies for scenario-based assessment of rESS comprehensively at the socio-ecological system and governance scales characteristic of large rivers.
3. Methodologies for examining trade-offs and synergies among rESS and biodiversity conservation.
4. Analyzing digital data or develop stakeholders' participation tools for the management, conservation, and restoration of rivers by culturomics and iEcology methods in the freshwater realm and beyond case studies.
5. Adaptation of technologies that use artificial intelligence (AI) to include big data and remote sensing data to quantify rESS at different spatial and temporal scales, and better aid decision making.

6. Develop common indicators for rESS to foster the uptake of rESS assessments in catchment conservation and management planning. As a prerequisite, the quantity and quality of input data need to be homogenized across countries at a level that allows the monitoring of the spatial patterns and temporal dynamics of rESS.
7. Define standards for data collection in cultural rESS research and methods that consider local and traditional ecological knowledge for catchment conservation and management.

Case studies

See Table 2.

Acknowledgments

We would like to thank Lisa-Lene Heinrich for help with the references and creating Fig. 2 and Gesa Wilhelmi for help with Fig. 3. SCJ acknowledges funding by the Leibniz Competition project 'Freshwater Megafauna Futures'. RET was supported by the LE STUDIUM Loire Valley Institute for Advanced Studies, Orléans and Tours, France, with funding from the European Union's Horizon 2020 research and innovation program under Marie Skłodowska-Curie grant agreement no. 665790. SDL was supported by the Spanish Government through María de Maeztu excellence accreditation 2018-2022 (Ref. MDM-2017-0714).

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https://dessin-project.eu/. —DESSIN project: Demonstrate Ecosystem Services Enabling Innovation in the Water Sector.
http://www.mars-project.eu/. —MARS project: Managing Aquatic ecosystems and water resources under multiple stress.
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http://teebweb.org/. —The Economics of Ecosystems and Biodiversity.

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Invasive Species in Streams and Rivers

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Biotic resistance The reduction in invasion success caused by the negative interactions with native (recipient) communities, most often through competition, predation, herbivory and/or pathogens.

Early detection and rapid response A coordinated set of actions to find and eradicate potential invasive species in a specific location before they spread and cause damage.

Establishment The process of a nonnative species in a new habitat successfully producing viable offspring with the likelihood of continued survival.

Hybridization The process by which interbreeding individuals from genetically distinct populations produce a hybrid.

Invasion meltdown The process by which a group of nonnative species facilitate one another's invasion by increasing the likelihood of establishment and/or of ecological impact.

Invasion A series of sequential stages (transport, introduction, establishment, spread and integration) through which individuals or populations need to pass to be considered invasive.

 https://doi.org/10.1016/B978-0-12-819166-8.00083-9

Invasive species Nonnative species whose introduction in a particular location causes or is likely to cause undesirable economic or environmental impacts, or negative impacts to human, animal, or plant health.
Nonnative species Populations that have become introduced and often established outside their native ranges but do not necessarily cause impacts so to be considered "invasive".
Pathway Any means, intentional or unintentional, that allows the entry or spread of a nonnative species.
Propagule pressure A composite measure of the number of individuals in each introduction event (propagule size) and the number of separate introductions (propagule number) for a given species in a particular recipient region.
Risk assessment The assessment of the consequences of the introduction and the likelihood of establishment and impact of an invasive species using scientific information.

Introduction

Aquatic invasive species (AIS) are a primary threat to streams and rivers across the world. Although not all introduced species successfully establish in their nonnative range, and a large fraction of those that do have little appreciable effects on their new ecosystems, some are associated with significant ecological, evolutionary, and economic consequences. Ecological effects of AIS have been shown to be severe and range from behavioral shifts of native species in the presence of invaders, to the complete restructuring of freshwater food webs and the extirpation of entire faunas (Gallardo et al., 2016). Economic impacts of invasive freshwater species are equally significant, with estimates of damage and management costs totaling at least $23 billion USD annually (Cuthbert et al., 2021). For researchers, managers, and policymakers seeking to ensure the integrity of riverine ecosystems (hereafter referring to flowing waters and their adjacent riparian zones), understanding the ecology of AIS is of utmost importance.

Freshwater invasion biology involves the study of diverse taxonomic groups from myriad geographies, ecosystems, and management contexts (Fig. 1). Here, we first provide an overview of invasion biology as it applies to riverine ecosystems. We summarize the invasion process depicting how species are introduced, attempt to establish, potentially spread, and potentially cause ecological and economic impacts. Each stage is supported with illustrative examples. Next, we discuss the management strategies and policy options available to prevent, contain, control and eradicate AIS in the future.

Fig. 1 Aquatic invasive species with demonstrated ecological, economic and societal impacts in riverine ecosystems. Photos depict (with photo credit): (A) Mozambique tilapia (Creative Commons); (B) rainbow trout (Creative Commons); (C) Eurasian milfoil (Tip of the Mitt Watershed Council); (D) Tamarisk (Gardenia); (E) northern snakehead (Associated Press); (F) red swamp crayfish (Julian Olden); (G) New Zealand mud snail (National Park Service); and (H) zebra mussel (USFWS).

Invasion process

The invasion process can be envisioned as a series of five stages—uptake and transport, introduction, establishment, spread, and integration—where barriers exist at each stage that must be overcome for a species or population to transition to the next stage. These stages reflect how individuals of a species are:

1. transported out of their native range via uptake into a vector and transit
2. introduced (disembark) into a new location
3. established in self-sustaining populations by surviving and reproducing
4. spread to new locations via dispersal into new environments
5. integrated into the recipient ecosystem resulting in effects that range from negative to positive.

In order to successfully progress as an invasive species, the barriers of the stage-based framework must be repeatedly overcome (Blackburn et al., 2011). Failure to overcome these barriers eliminates the invasiveness of a population. As such, a considerable amount of research within invasion biology focuses on understanding which traits facilitate species success across all invasion stages to ultimately define the final outcome of failure or success (Fig. 2).

Species introductions

The motives for, and mechanisms by which, AIS have been introduced to riverine ecosystems have been many and varied. There are three general mechanisms through which nonnative species may enter a new region (Hulme et al., 2008). First, importation as or with a commodity arises from direct human movement of goods. Species introduced as commodities occur when people identify a species as having desirable qualities and intentionally move it beyond its native range, resulting in intentional release (e.g., stocking fish for recreational angling, introduction of species as biological control agents) or unintentional escape (e.g., pet aquarium organisms released into the wild, ornamental plants and fish escape facilities). Species transport with a commodity occurs when traded organisms are contaminated with other nonnative species, including diseases and parasites. Second, arrival with a transport vector, refers to species that hitchhike on human modes of transport to regions beyond their native ranges. Modes of transport

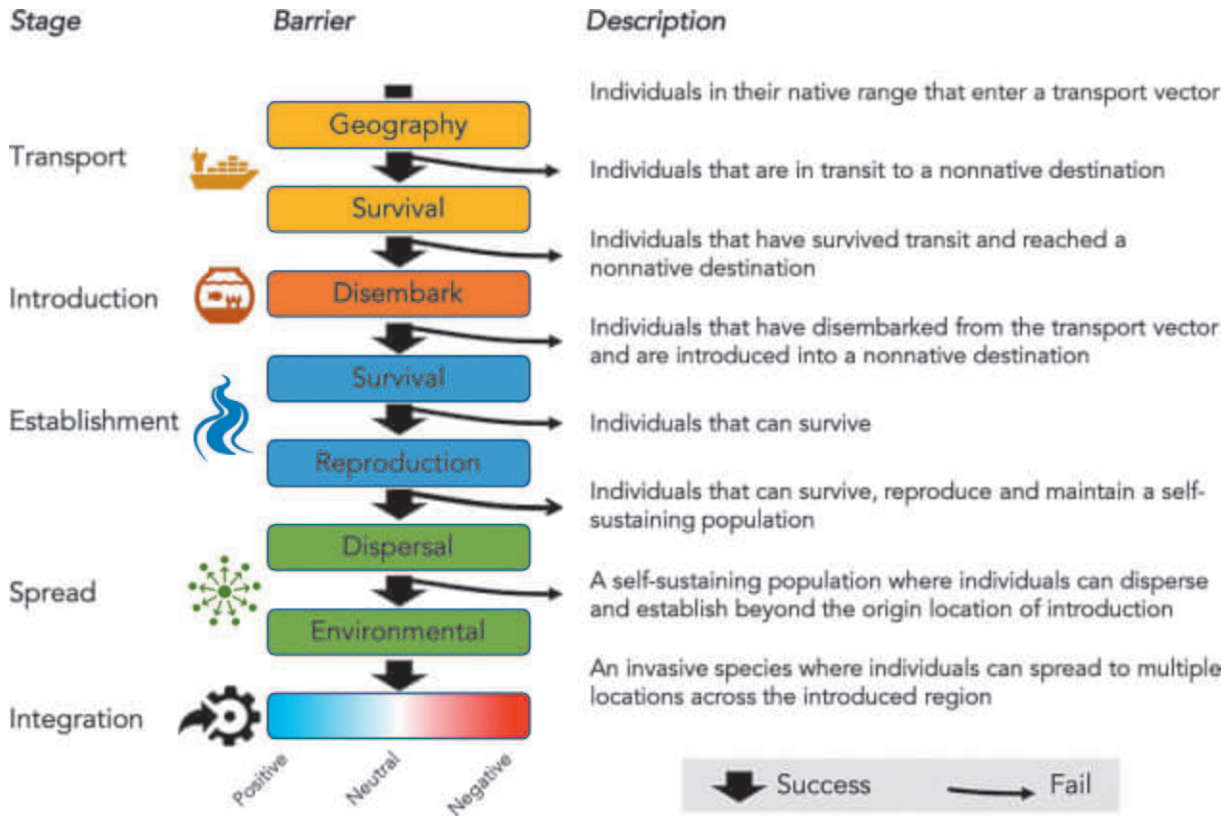

Fig. 2 The invasion process can be represented by a sequence of five stages (transport, introduction, establishment, spread, integration) through which individuals of nonnative species must transition to become successful invaders. Each stage has one or more barriers to overcome, whereby individuals are either successful (downward-pointing arrow) or fail (right-pointing arrow). Figure is inspired by Blackburn et al. (2011) and Chapple et al. (2012).

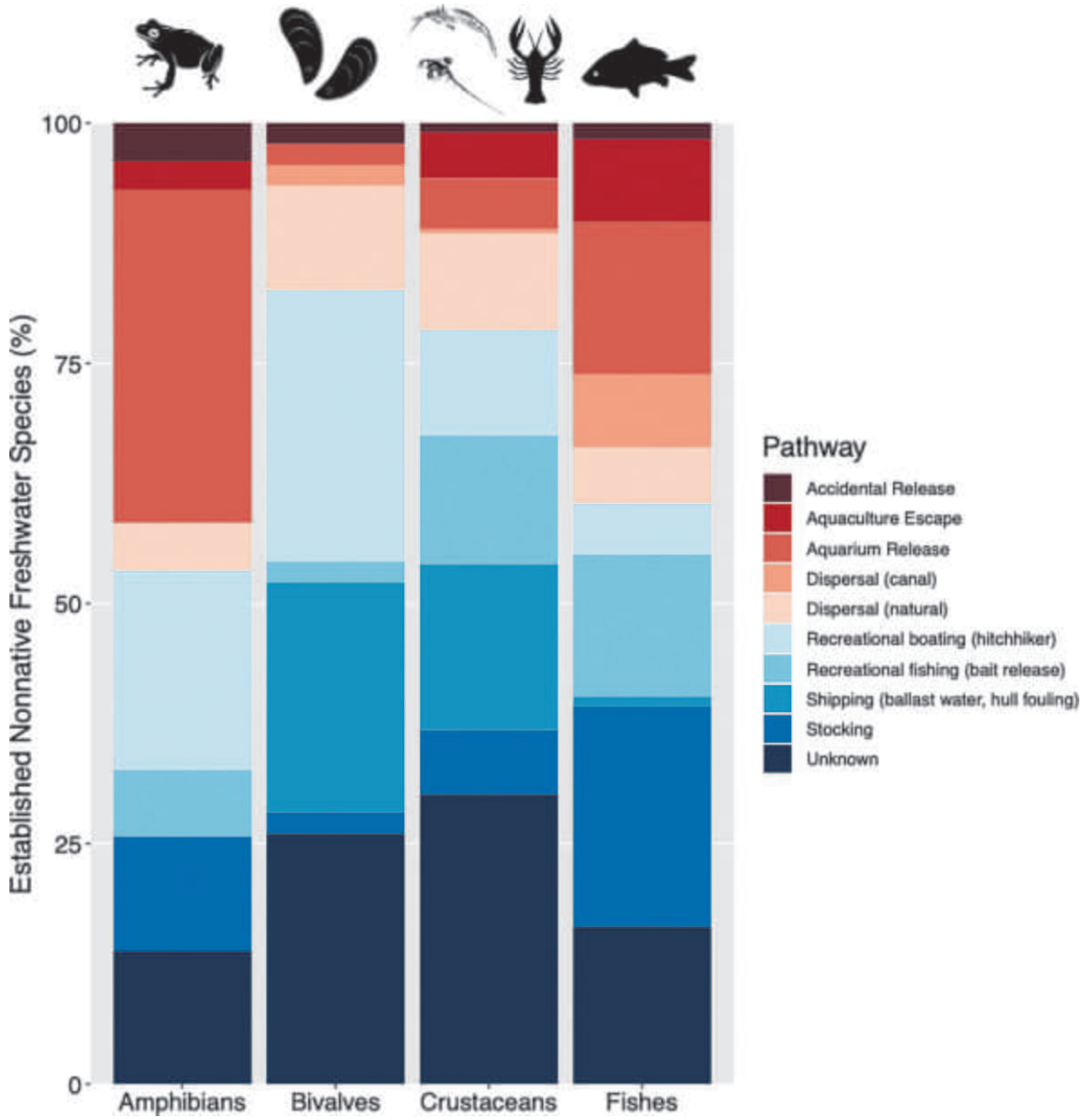

Fig. 3 Frequency (%) of established nonnative species introduced via major pathways for amphibians, bivalves, crustaceans, and fishes in the fresh waters of the United States. Total number of species are not reported because a single species can be introduced by more than one pathway and may therefore be counted more than once. Relatively more minor pathways (see text) are not included. Data source: USGS Nonindigenous Invasive Species Database; accessed June 24, 2021.

include ships (e.g., organisms in ballast water or attached to hulls) and angling equipment and recreational watercraft (e.g., boat motors, hulls and trailers). Third, self-dispersal, either along infrastructure corridors (e.g., irrigation or transportation canals) or unaided. Below we discuss a number of these major introduction pathways, noting that their importance varies taxonomically (Fig. 3) and that their strength and geographic routes have changed, and will continue to change, over time.

Stocking for sport and food

The primary motivation for early AIS introductions was for extensive fish culture and stocking of plants and animals for the "national good" (i.e., acclimatization societies). Introductions of common carp (*Cyprinus carpio*) to Western Europe occurred about 2000 years ago and were most likely facilitated by the Romans and later by Catholic monks who reared them in monastery ponds for food (Copp et al., 2005). Nowadays, fish are deliberately introduced for the enhancement of recreational fisheries and to establish new food resources. For example, rainbow trout (*Oncorhynchus mykiss*; Fig. 1) is perhaps the most introduced sportfish in the world, being primarily stocked by government agencies and private organizations in approximately 90 countries. Growing

awareness of the impacts of AIS has led to tighter regulations on sanctioned stocking in many countries; however, the unauthorized intentional release of aquatic animals to facilitate a local recreational fishery by so-called "bucket biologists" continues to be a significant problem.

Aquarium pet trade

The aquarium trade has been responsible for the introduction of many fish, plant, and invertebrate species worldwide. For example, studies report that the aquarium trade could be responsible for about 19% of fish introductions in Iberian Peninsula, 14% for the Laurentian Great Lakes (Canada and United States), 65% for Florida (United States), and 45% for England. Pet aquarium species are introduced when owners release unwanted organisms into the wild for various reasons, including large size, aggressiveness, no longer wanted or humane treatment (Padilla and Williams, 2004). The most popular fish sold in the aquarium trade are also the most likely to be introduced and established (Duggan et al., 2006). In addition to traditional "brick-and-mortar" stores, nonnative aquarium species are increasingly purchased from Internet marketplaces and online peer-to-peer platforms (Olden et al., 2020).

Aquaculture and the live food trade

Freshwater aquaculture, referring to the propagation of captive freshwater organisms, is undergoing a rapid worldwide expansion. Of significant concern is the increasing use of nonnative species, which may escape into the wild and cause direct ecological damage or indirect damage through spread of their associated pathogens and parasites (Cook et al., 2008). The aquaculture industry typically selects species that are fast growing, thrive in local conditions, and are tolerant of a wide range of environmental conditions. These qualities also predispose many aquaculture species to become invasive if they escape. Notable examples include silver carp (*Hypophthalmichthys molitrix)*, Mozambique tilapia (*Oreochromis mossambicus*), and signal crayfish (*Pacifastacus leniusculus*). AIS can also be unknowingly introduced when intentionally stocked fish are accidentally contaminated with other non-target species. An example is topmouth gudgeon (*Pseudorasbora parva*), which was accidentally introduced into Europe from China in the 1950s through the transfer of contaminated batches of large Asian carp being used in aquaculture. Topmouth gudgeon has since achieved a pan-European distribution through both further accidental introductions and natural dispersal (Copp et al., 2005). In another example, the crayfish plague disease (*Aphanomyces astaci*) was introduced to Europe on North American crayfish imported for aquaculture; this disease now widely endangers European native crayfish populations (Holdich et al., 2009).

Shipping activities

Ship-mediated vectors, including ballast water and hull biofouling, are a dominant global vector for unintentional translocation of freshwater, euryhaline and marine species. Ships fill their ballast with water at an origination port to control trim and draft, provide stability, and enhance voyage safety. Ballast water often contains a wide diversity of invertebrates (plankton and mussels) and vertebrates (fish). Discharge of ship ballast releases both water and the surviving organisms and pathogens into waters of destination ports when ships intend to unload and take on additional cargo. Similarly, organisms can become encrusted on ship hulls and transported between different regions. Transoceanic shipping activities continue to be an important vector for the transport of AIS, especially to North America. For example, since the 1970s, 75% of the flora and fauna introduced into the Great Lakes has been linked to ballast water releases by ships of Eurasian origin (Ricciardi and MacIsaac, 2000).

Recreational fishing and boating

Freshwater fishing generates significant economic benefits; however, anglers have repeatedly been implicated as vectors of AIS by entraining organisms on fishing lines and on boat motors, hulls and trailers, and releasing in live bait (Rothlisberger et al., 2010). Insufficient gear cleaning allows hitchhiking invaders to be moved short and long distances overland, promoting both their initial introduction into new catchments and secondary spread into adjacent waters. In North America, higher numbers of nonnative species have been found to coincide with areas of greater recreational fishing demand (Davis and Darling, 2017). Examples of ubiquitous nuisance species whose translocation has been partly attributed to angler activities include zebra mussel (*Dreissena polymorpha*) and quagga mussel (*D. rostriformis*), Eurasian milfoil (*Myriophyllum spicatum*) and rusty crayfish (*Faxonius rusticus*).

Dispersal through human infrastructure

Canals connecting different river basins have allowed for range extensions of many AIS, either by eliminating natural barriers to movement and/or by promoting shipping activity (Galil et al., 2007). For example, the complex European network of inland waterways built during the 20th century comprises >28,000 km of navigable rivers and canals that connect countries throughout Europe and facilitate the introduction of AIS. Similarly, the construction of the St. Lawrence Seaway, consisting of a system of locks, canals and channels in Canada and the United States, has permitted oceangoing vessels to travel from the Atlantic Ocean to the Great Lakes of North America, and has facilitated the unaided movement and establishment of AIS including the round goby *(Neogobius melanostomus)* and sea lamprey (*Petromyzon marinus*).

Other

A number of other pathways of introduction exist, albeit at lower frequency in relation to the pathways discussed above. These include: release of laboratory animals associated with scientific experiments, ceremonial wildlife release events, intentional release after school classroom use, and stocking for biological control (see "Management strategies" section), aesthetics and conservation purposes.

Species establishment

Species establishment refers to the stage of the invasion process where an AIS maintains self-sustaining populations (i.e., reproducing populations that do not depend on the immigration of new individuals). Establishment success of an AIS is linked directly to the number and condition of individuals introduced (propagule pressure), biological traits of introduced individuals, dispersal abilities and opportunities, and to the characteristics of the receiving environment.

Propagule pressure

Biological invasions can largely be considered a "numbers game," in that the probability that a population becomes established increases with both the number of individuals and the number of introduction events (defined as propagule pressure: Lockwood et al., 2005). Propagule pressure is considered a key determinant of establishment success as species are more likely to become established if many individuals are released simultaneously and if multiple introductions occur over long time periods. When propagule pressure is low, too few individuals may survive long enough to establish, and sexually reproducing individuals may not find mates. In addition to propagule pressure, the success of AIS establishment can also be dependent on the selection of favorable invasive traits in the original population (Chapple et al., 2012) and favorable conditions during the transport phase (Briski et al., 2015). Selection of favorable traits in the transported invading sub-population can facilitate local adaptation, potentially increasing the likelihood of invasion success (Briski et al., 2015).

Biological traits

Ecologists have analyzed common features that separate successful invaders from those that fail. Although each successful invasion has some unique properties, generalizations on biological traits allow better prediction of species that are most likely to invade. Invasion success largely depends upon four groups of characteristics that: (1) facilitate nonnative species to be entrained, transported and introduced to a new area ("Species introduction" section); (2) influence the ability of a colonizing species to succeed (described in this section); (3) affect the probability of dispersion beyond the point of introduction ("Species spread" section); and (4) influence the direction and magnitude of impacts in the recipient ecosystem ("Ecological implications" section).

Comparisons of biological traits between successful versus unsuccessful species invasions and native versus established introductions has revealed a suite of species attributes associated with the establishment of AIS populations. For example, greater establishment success has been linked to reproductive strategy, diet breadth and environmental tolerance in fishes (García-Berthou, 2007), large body size, fecundity, and aggression in crayfishes (van Kuijk et al., 2021), and traits related to resistance to hydraulic disturbance and greater dispersal (e.g., floating propagules, regrowth capacity, rapid growth from small segments even after desiccation) in riparian plants (Catford and Jansson, 2014). In one example, high fecundity and ovoviviparity (eggs and embryos carried inside the female's body) are fundamental reproductive traits to the establishment success of guppy (*Poecilia reticulata*) in riverine ecosystems of South America because offspring are less influenced by harsh external conditions such as temperature, turbidity, and predation (Oliveira et al., 2014). Beyond biological traits, attributes related to taxonomy and degree of human use/value (e.g., association with aquaculture, use as fishing bait or aquarium pet) have also proven to predict establishment success (Alcaraz et al., 2005). Biological traits have been found (or hypothesized) to be predictive of successfully overcoming barriers associated with each stage of species invasion; this is illustrated for crayfish in Table 1.

Environmental conditions

Nonnative species are expected to have greater likelihood of establishing new populations in those locations where their environmental requirements are met. Broad physiological tolerances to temperature, salinity, pH, and other environmental factors are often strong predictors of AIS establishment. For example, the ability to tolerate wide salinity variations can favor AIS arriving on cargo ships from other regions, and increase the probability of using estuaries as "saline bridges" to colonize adjacent rivers connected only by the ocean (Gutierre et al., 2014). One of the most accepted truisms in the field of invasion ecology is that disturbance - defined as any discrete event in time that disrupts population, community or ecosystem structure and changes resources or the physical environment—promotes biological invasions. In riverine ecosystems, land-use conversion (i.e., increase agriculture or urbanization), alteration of hydrology by dams, and climate change can all favor the establishment of AIS. For example, nonnative red swamp crayfish (*Procambarus clarkii*), American bullfrog (*Lithobates catesbeianus*), and nonnative fishes were all more abundant in more urbanized watersheds in southern California (Riley et al., 2005), and dam-regulated rivers have been

Table 1 Biological attributes of crayfish associated with successful transition of barriers across stages of invasion.

Stage	*Barrier*	*Associated biological traits*
Transport	Geography and Survival	Size of native range
		Bright body coloration (increase popularity in trade)
Introduction	Disembark	Preference or tolerance of lentic habitats
		Able to reproduce in aquarium conditions
		Absence of specialized hatching requirements
		Small or large body size
Establishment	Survival	Wide environmental and climatic tolerances
		Generalist diet
	Reproduction	Single parent reproduction
		High reproductive potential (fecundity)
		Short generation time
		High growth rate
Spread	Dispersal & Environment	Good dispersal
Integration		Ability to escape or survive natural enemies
		Long lived (resist mortality)
		Large body size
		High competitive ability

Modified from van Kuijk T, Biesmeijer JC, van der Hoorn BB and Verdonschot PFM (2021) Functional traits explain crayfish invasive success in the Netherlands. *Scientific Reports* **11**. doi: 10.1038/s41598-021-82302-4.

shown to promote greater establishment of nonnative Tamarisk (*Tamarix ramosissima*) (Stromberg et al., 2007). Substantial efforts have sought to forecast the potential geographic range of AIS by predicting areas of suitability establishment according to the invader's ecological requirements (defined by their biological traits) and environmental conditions in the foreign region.

Biotic resistance and facilitation

AIS establishment is less likely to occur where the recipient ecosystem is inhabited by closely-related native species, either with respect to phylogeny or function. So called 'biotic resistance' is often defined in terms of diversity-invasibility, where it is hypothesized that higher native species diversity (typically, the number of species) intensifies interactions with nonnative species (i.e., direct and indirect competition and predation), thus decreasing the probability of AIS establishment. Although long considered important, recent reviews show relatively low support for biotic resistance (29% of studies) and, further, that support was declining over time as more studies were published (Jeschke et al., 2012). Despite this, evidence does exist that biotic resistance may play a role in AIS establishment. For example, a quarter of all introduced fish species in the Parana River, Brazil, successfully established, and those that did demonstrated very different functional traits compared to native fishes (Skora et al., 2015). Studies have also revealed that native species may require time, leading to learned experience, to effectively control AIS populations. For example, predation by blue crab (*Callinectes sapidus*) caused high mortality and changed the population structure of invasive zebra mussels over time in the Hudson River (Carlsson et al., 2011).

Biotic facilitation (positive interactions) among AIS may lead to greater establishment success; this is termed the invasional meltdown hypothesis (Simberloff and Von Holle, 1999). Invasional meltdown describes the process by which a group of nonnative species facilitate one another's invasion by increasing the likelihood of establishment and/or of ecological impact. Evidence for invasional meltdowns in riverine ecosystems are inconclusive. For example, Jackson et al. (2014) examined interactions among two pairs of invasive crayfishes in the Thames River catchment, United Kingdom, and found amplified negative effects on benthic invertebrate communities, benthic algae and leaf litter decomposition rates. By contrast, in a series of experiments, Braga et al. (2020) showed that three AIS—Oscar fish (*Astronotus crassipinnis*), golden mussel (*Limnoperna fortunei*) and the aquatic macrophyte hydrilla (*Hydrilla verticillata*)—demonstrated only additive effects, thus providing no evidence for an invasional meltdown.

Species spread

Spread or dispersal is a defining feature of species invasions. This process, composed of multiple, sequential introduction and establishment events, describes the manner in which individuals move and populations expand in size beyond the initial point of introduction (Fig. 2). Rates of spread depend on the strength of the introduction pathway, propagule pressure, biological attributes of the AIS, and environmental characteristics of the landscape, including geographical barriers to movement.

Pathways implicated in the initial introduction of a species are similarly responsible for the secondary spread of AIS. For example, the overland movement of trailered boats has inadvertently spread AIS to new waters by carrying live organisms in bilge

water, live wells, and bait buckets, as well as being entrained on boat exteriors (Rothlisberger et al., 2010). Mobile organisms also disperse; this often occurs more in the downstream direction because upstream movement is limited by the physical forces of river flow and a variety of natural and artificial barriers. Invasive signal crayfish, for example, were found to move 1.5 km year^{-1} in a downstream direction according to radio-tagging study in northern England (Bubb et al., 2004). All downstream movements made by crayfish appeared to be active movements and related to water temperature and not the result of passive movement during periods of high discharge. Hydrology also plays a critical role in the spread of invasive riparian vegetation. For example, the successful spread of invasive plants are influenced by flooding events and the creation of colonization opportunities for seed propagules (Foxcroft et al., 2008). In many dryland rivers of the southwestern United States, seeds of invasive Tamarisk and Russian olive (*Elaeagnus angustifolia*) are viable for longer, and have longer dispersal time periods, than native species, resulting in rapid rates of downstream spread over time (Reynolds and Cooper, 2010).

A number of mathematical and statistical approaches have been used to model the spread of AIS at both large- and local-scale (Thompson et al., 2021). Reaction-diffusion models, for example, are spatially explicit spread models employing a continuous description of space which provide good descriptions of observed spread patterns for a variety of invasive species. Gravity and random-utility models can also be used to AIS spread, where nonrandom dispersal is primarily human-mediated (Thompson et al., 2021). For example, although detailed boater movement data is often not available, gravity models have been used to estimate the probability of boater movements among sites as a function of boat usage at individual sites and of the distance among sites. Such models become particularly useful for modeling potential invasive species spread when they incorporate invasive species life history and dispersal information, as well as the relative positioning of invaded and suitable sites on the landscape (Vander Zanden and Olden, 2008).

Agent-based models are another approach to modeling AIS spread. These models reproduce ecological events by simulating individuals that follow distinct rules by accounting for the effects of stochasticity and environmental factors on the biology and behavior of each individual organism in the population. Messager and Olden (2018) modeled the rapid spread of rusty crayfish in a tributary of the Columbia River from the putative time and location of initial introduction to present-day, and forecasted the spread into the future. This study reported that rusty crayfish had spread incredibly fast (c. 20 km year^{-1}) since their initial introduction to a single location (Fig. 4), and it predicted that the invasion may number on the order of 100 million individuals occupying over more than 1100 km of river by 2025.

Ecological implications

The environmental impact of a nonnative species can be defined as any measurable change that is caused to the properties of the recipient ecosystem (Blackburn et al., 2014). Generally, deleterious environmental or biological impacts are considered but they can be bidirectional in the sense that nonnative species can benefit ecosystems from a human perspective (e.g., increase regional species diversity, provide recreational angling opportunities). Negative ecological impacts are caused by numerous mechanisms (e.g.,

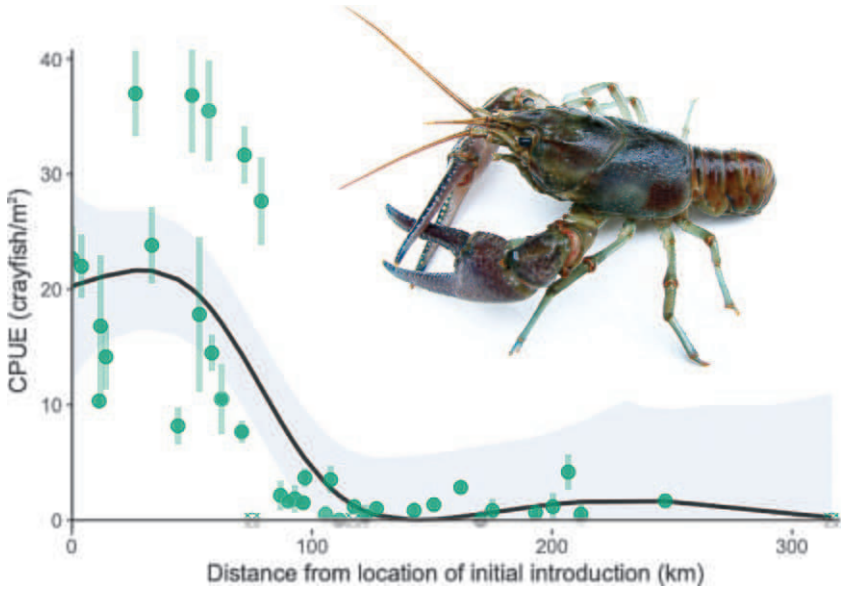

Fig. 4 Density of rusty crayfish as a function of distance from putative location of initial introduction in the mainstem John Day River, United States. Crayfish densities are expressed as the mean (points) and 95% confidence interval (bars) of the catch per unit effort (CPUE). The smooth solid line and shaded region represent the predicted mean CPUE and 95% credible interval. Data from Messager ML and Olden JD (2018) Individual-based models forecast the spread and inform the management of an emerging riverine invader. *Diversity and Distributions* **24**: 1816–1829. doi: 10.1111/ddi.12829. Photo credit: Julian Olden.

predation, competition, hybridization, disease) manifested across different levels of organization from genetic to the landscape and scales from local to global (Blackburn et al., 2014), as discussed in detail below.

Genetic

Genetic impacts of AIS include changes in gene expression and hybridization (Vitule et al., 2009). Hybridization affects native species through lost reproductive opportunity and introgression. For instance, many fishes within the cyprinid, centrarchid or salmonid families produce fertile hybrids, even between different genera, thus altering the genetic composition of the native population and sometimes resulting in the extinction of native genotypes. Examples of introgressive hybridization include alien rainbow trout (*Oncorhynchus mykiss*) with cutthroat trout (*Oncorhynchus clarki*) subspecies and other salmonids in North American streams, and nonnative mallard (*Anas platyrhynchos*) with native ducks in South Africa, Australia, and elsewhere.

Individual

Impacts at the individual level include changes in behavior, morphology or life history of native species (Cucherousset and Olden, 2011). Nonnative predators can change habitat use, diel activity and vital rates of native species. For instance, brown trout (*Salmo trutta*) and other salmonids introduced in rivers and streams worldwide often compete with native fishes altering their habitat use, activity and diet which indirectly reduces their growth, condition and survival. Many other invasive fishes are generalists and can similarly affect invertebrates, amphibians and other animals by direct predation and competition for resources (e.g., common carp). Introduced brown trout have also changed the behavior of stream invertebrates to be more nocturnal and less active during the day, thus reducing their grazing pressure on periphyton, and causing changes to entire food webs (Townsend, 2003). Comparative functional responses, whereby the relationship between resource availability and resource uptake rate is derived and compared among species (Dick et al., 2017), have consistently revealed that high ecological impact invaders have higher maximum feeding/consumption rates than trophically analogous natives. This was demonstrated, for example, for invasive channel catfish (*Ictalurus punctatus*) versus native *Rhamdia quelen* in a series of experiments in Brazil (Faria et al., 2019; Fig. 5).

Population

Population impacts include changes in the abundance and distribution of native species and the transmission of pathogens and parasites. For instance, the parasitic sea lamprey, which is native to the North Atlantic Ocean and spawns in rivers across Europe and eastern North America, invaded the Laurentian Great Lakes after opening canals for navigation. In the Great Lakes, this jawless fish caused dramatic population reductions of large fish such as lake trout (*Salvelinus namaycush*) and associated fisheries and extirpations of endemic whitefishes (Cucherousset and Olden, 2011). Similarly, nonnative crayfishes reduce the abundance of basal resources like aquatic macrophytes and aquatic invertebrates (e.g., snails, mayflies) through direct predation, and compete for habitat and prey with native amphibians and fish (Twardochleb et al., 2013). In Europe, native crayfishes have been extirpated in many streams, mostly because of the crayfish plague, a disease caused by the fungus-like oomycete *Aphanomyces astaci* that is carried by North American crayfishes (Holdich et al., 2009).

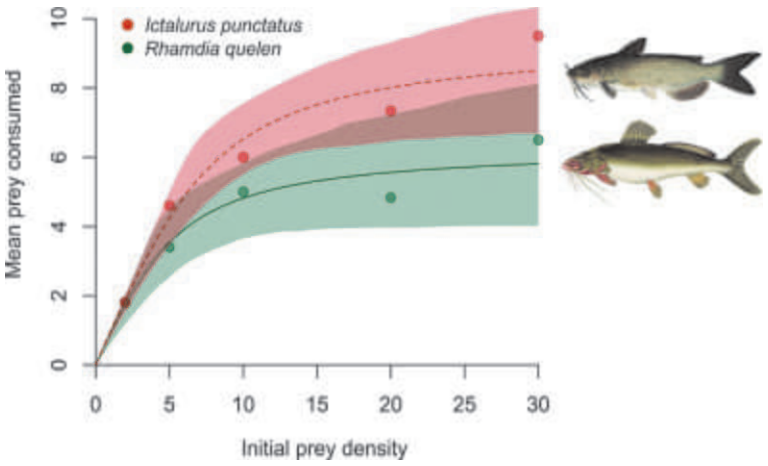

Fig. 5 Functional responses of ecologically damaging invaders have higher asymptotes compared to those of native analogues, as shown here for the consumption of a prey fish by invasive channel catfish (*Ictalurus punctatus*; top right) vs. native *Rhamdia quelen* (bottom right). Photo credit: Josh Leisen (*I. punctatus*) and Creative Commons (*R. quelen*). Modified from Faria L, Alexander ME and Vitule JRS (2019) Assessing the impacts of the introduced channel catfish Ictalurus punctatus using the comparative functional response approach. *Fisheries Management and Ecology* **26**: 570–577. doi: 10.1111/fme.12353.

Community

At the community level, AIS contribute to the local extinction of native species, and modify species composition and diversity. For example, the giant reed (*Arundo donax*), originally native from southwestern Asia, is one of the oldest plant invasions and has invaded many Mediterranean-climate and subtropical riparian areas of the world. This species promotes the loss of native diversity of riparian vegetation, leading to changes in the abundance and diversity of riparian invertebrates and birds (Maceda-Veiga et al., 2016). By dissolving physical barriers to movement and connecting formerly isolated regions of the world, human-mediated species introductions have also dramatically homogenized the present-day biogeography of riverine species. At the global scale, invasion by numerous species of cyprinid, salmonid, cichlid, and centrarchid fishes have fundamentally changed the composition of major river basins; elevating the number of fish species per river by 15% on average, and increasing the similarity of the world's fish faunas (Villéger et al., 2011). In the United States, pairs of states now have over 15 more species in common when compared to pre-European settlement times, representing a homogenization of 7.2% (Rahel, 2000). These changes in species composition have also been associated with modifications to functional trait diversity, which have clear implications for ecosystem functioning.

Ecosystem

Riverine ecosystems can experience significant change as a result of AIS, in particular those which are classed as "ecosystem engineers" (Gallardo et al., 2016). Invasive bivalves, such as the zebra and quagga mussel, the Asian clam (*Corbicula fluminea*), and the golden mussel (*Limnoperna fortunei*) act as ecosystem engineers through capture and consumption of suspended particles, production of feces and pseudofeces, functioning as an important resource subsidy, bioamplification of pollutants throughout the food chain and various biotic interactions (Sousa et al., 2014). At the ecosystem level, due to their high filtration rates, they typically reduce phytoplankton, increase water clarity, and thus change primary productivity and food webs to those more based on macrophytes and benthic algae. Other examples include the water hyacinth (*Pontederia crassipes*), hydrilla, giant salvinia (*Salvinia molesta*), and Eurasian milfoil, which alter nutrient cycling, reduce water quality (increasing water temperature and decreasing dissolved oxygen) and water quantity (high evapotranspiration rates), and have leaves of lower nutritional quality that have potential effects on food webs (Gallardo et al., 2016).

Economic costs

Aquatic invasive species have the potential to cause serious economic impact, either in the form of management- or damage-related costs (Cuthbert et al., 2021). Management costs relate to investment by legislative bodies with regards to prevention, control, containment, and eradication schemes (described more in the "Management strategies" section). For example, water companies in the United Kingdom spend approximately $18,000 GBP per year to control zebra mussel biofouling on infrastructure, while in the United States the daily cost of chemical control measures are estimated to be $1–$13 USD per million gallons (Chakraborti et al., 2016). Recently, the U.S. Army Corps of Engineers have proposed a new $778 million USD electric barrier to prevent Asian carp from entering the Great Lakes and threatening a $7 billion USD fishing industry (see below). Expenditures to manage invasive species generally vary according to the economic status of the region or funding body. The Australian government committed $15 million AUD to the National Carp Control Plan in 2016 to develop pathogen biocontrol methods. By contrast, the monetary investment needed to control and eradicate water hyacinth in South Africa was thought to exceed the perceived costs to ecosystem services. In North America, however, the cost of investment in biological control was shown to have a huge cost-benefit ratio in terms of ecosystem services gained as a result (Wainger et al., 2018).

Damage-related costs are a direct result of AIS impact on an economic commodity, supply chain, or ecosystem service. These costs are more commonly reported and are often of higher magnitude. The Eurasian ruffe (*Gymnocephalus cernua*), at one point the most abundant fish in the Saint Louis River Basin, United States, is estimated to be among the costliest freshwater invasive species worldwide. This species may have incurred damage costs, via predation, of up to $53 billion USD to native fisheries over a 40-year period (Cuthbert et al., 2021). In South America, biofouling of hydropower structures by nonnative golden mussels have resulted in damage to equipment and caused costs to escalate from servicing to massive energy losses when hydropower stations have to be shut down during repair. In the United States, financial losses due to tamarisk invasion (see "Ecological implications" section), estimated at $169–$362 million USD, are associated with water loss and resulting impacts on consumptive end uses by households and irrigators as well as non-consumptive uses like hydroelectric power generation and fishing (Zavaleta, 2000). Millions of dollars more are spent annually on management costs associated with mechanical removal, fire treatments, herbicide treatments and the introduction of biocontrol agents.

Nonnative species can simultaneously cause negative and positive economic impacts in different sectors. For example, nonnative species represent a significant proportion of inland fisheries both for subsistence and recreational purposes. In this respect they contribute to the income and livelihoods of tens of millions globally through direct fishing activities, as well as other financial opportunities along the value chain, e.g., gear provision and maintenance, processing, and distribution (Lynch et al., 2016). Interestingly, perceptions of costs and benefits from an invasion may also vary among people living with an invasive species and may change over time following an invasion. Examples include the marbled crayfish (*Procambarus virginalis*) in Madagascar, where

the species is now valued as a crucial source of food and income (Andriantsoa et al., 2020), and invasive salmonids in Argentina which are regarded as naturalized in legislation due to their socio-economic contributions (De Leaniz et al., 2010).

Management strategies

The management of AIS can involve four general strategies—prevention, containment, control, and eradication—each aiming to eliminate or reduce the ecological, economic, and human health impacts. The use of control options should actively consider the risks and benefits of implementing different strategies commensurate with its likelihood of success, costs, and socio-cultural considerations.

Prevention

Prevention is widely recognized as the cornerstone of invasive species management, as decades of experience have demonstrated that, following establishment by nonnative species, eradication or control is costly and difficult (Fig. 6). Preventing the transport and introduction of AIS can involve legislation to regulate or prohibit importation of unwanted species, for example associated with trade in ornamental pets and plants. Some nations and regions have created 'blacklists' of high risk of invasive species that are prohibited from use and trade (e.g., Australia *Environment Protection and Biodiversity Conservation Act*, European Union *Regulation 1143/2014 on Invasive Alien Species*, United States *Lacey Act*). Although firm preventive measures such as border controls may seem expensive, preventing the importation or illegal spread of an invasive species is considered an investment in eliminating or reducing future management and damage costs that they may cause (Vander Zanden and Olden, 2008; Box 1). Prevention strategies have also sought to limit the transport and introduction of AIS associated with particular pathways. For example, mandatory ballast water treatment and exchange in the ocean and anti-fouling hull treatments seek to prevent AIS associated with transoceanic shipping

Fig. 6 Management strategies for preventing, containing, controlling and eradicating aquatic invasive species. Photos depict (with photo credit): (A) ship ballast water exchange (International Maritime Organization); (B) small boat inspection (Monte Drape); (C) detection of AIS using environmental DNA (National Genomics Center for Wildlife and Fish Conservation); (D) physical carp barriers (Leigh Thwaites); (E) artificial crayfish barriers (Clyde River Foundation); (F) electrical carp barrier (Iowa DNR); (G) mechanical harvesting of aquatic plants (Don Seabrook); (H) biocontrol Tamarisk beetle (Doug Von Gausig); and (I) application of rotenone to eradicate invasive fish (William DeShazer).

Box 1 Risk Assessment for Aquatic Invasive Species.

Due to the significant socioeconomic and environmental impacts of AIS, many countries are increasingly regulating the introduction of nonnative species for commercial or personal use to reduce opportunities for invasions. This often takes the form of "black lists" (i.e., species forbidden because they were identified as potentially harmful AIS) or "white lists" (i.e., species that can be introduced because they were identified as safe) (Genovesi et al., 2015). The development of these lists generally entails a detailed risk assessment, referring to a process of evaluating biological and economic evidence to identify potential invasive species and determine the level of invasion risk associated with a species or pathway (Roy et al., 2018). Many useful scoring protocols for such risk assessments exist (González-Moreno et al., 2019). In the European Union for instance, a "List of Invasive Alien Species of Union concern" was implemented (Regulation (EU) 1143/2014) and is periodically revised to identify species with strong restrictions regarding possession, importing, and selling. As of May 2021, the list contains about 36 plants and 30 animals, including many AIS in rivers. Prevention remains the most efficient management tool to avoid invasions and their costs, and risk assessments play an important role in guiding management and policy in support of these efforts.

A U.S. Customs and Border Protection specialist inspects a parcel arriving in the United States at an international mail processing facility. Photo courtesy of Erich Glasgow, USDA.

(Briski et al., 2015), and road-side inspections and educational campaigns that promote cleaning of small boats and angling gear are implemented to help reduce the spread of AIS (Rothlisberger et al., 2010).

Even when legislative controls exist, intentional or accidental introductions of AIS do unfortunately occur. Early detection of invasive species before they spread is critical, as once an invasive species is established, it can be nearly impossible to eradicate. Early detection allows for rapid response control programs to be implemented that are more likely to be effective and affordable. Rapid detection can be extremely difficult however, as initial populations often exist at very low abundances, and they are often only detected inadvertently through chance citizen and angler reports or regular assessment programs. The effort required to detect a potential invasive species introduction can also be costly. Surveillance efforts may be more cost-effective if they target more likely invasion hotspots such as regions of high aquaculture or ornamental production, and high human population centers. The early detection and surveillance of invasive species has also been transformed recently with the use of environmental DNA (eDNA) and citizen science technologies (Larson et al., 2020; Baird et al., this volume). This allows for potentially more cost-effective programs to detect AIS both in pathways before introduction and in locations where populations have been recently established (Snyder et al., 2020).

Containment

Once an invasive species is established it is often challenging to eradicate it, and thus management efforts often turn to containment methods that focus on limiting the secondary spread of individuals and further range expansion (Fig. 6). Containment barriers have been used throughout the world, and can take many forms, including screens, weirs or nets, and velocity, electrical or chemical barriers (Jones et al., 2021).

Physical exclusion involving screens or weirs are the most prevalent form of barrier (Jones et al., 2021). Physical barriers reduce or prevent direct movements of animals such as fish and crayfish (Krieg and Zenker, 2020), but they are less effective barriers for smaller organisms such as plants propagules, invertebrates and the early life stages of fishes. For example, exclusion screens have been used to restrict adult common carp from entering wetlands to minimize their ecological impacts and spawning and recruitment potential, but they do not stop the movement of young carp (Hillyard et al., 2010). Constructed exclusion barriers can be used to isolate whole river catchments for the effective exclusion of AIS. For example, the construction of artificial barriers has been used to limit sea lamprey from accessing spawning tributaries of the Laurentian Great Lakes, and to stop upstream movement of invasive rainbow trout into native cutthroat trout habitats and subsequent genetic hybridization of populations. However, the restriction of movement potentially comes at a considerable risk and trade-off for the need to maintain river connectivity for native organisms and ecological processes (Rahel, 2013).

Electric fields have been used to deter or stun fish attempting to pass particular key points. For example, two large electric barriers in the Chicago Sanitary and Ship Canal were installed in 2002 to prevent invasive Asian carp from colonizing Lake Michigan. However, the need for constant power supply can prohibit electric barrier use in remote locations and also has increased risks of accidental transfer if the power supply fails. Other barrier types include the use of chemicals, bubble curtains, light and sound as behavioral deterrents for fish. Most containment barriers (of all types) tested seem to be very successful, deterring >70% of targeted individuals (Jones et al., 2021); however, long-term monitoring is extremely limited at present, and few studies investigate any negative impacts on native species. The use of multiple deterrents has also only rarely been attempted.

Control

Control methods aim to reduce the ecological impact of invasive species by reducing their abundance by acknowledging that their eradication is likely to be impossible (Britton et al., 2011; Hussner et al., 2017). Control options include mechanical/physical removal, chemical treatments to kill fish or plants (e.g., piscicides or herbicides), and biological control; these approaches vary in their suitability for different taxa, effectiveness, scale of application and costs (Fig. 6).

Mechanical harvesting approaches are commonly used to control invasive aquatic plants (Hussner et al., 2017). Although effective in reducing total plant biomass, the cutting of aquatic plants can produce large amounts of plant fragments that introduce new opportunities for spread. Physical capture and removal is also commonly used to control invasive fish and crayfish species, with techniques such as netting, trapping and electrofishing often highly effective in suppressing abundances, reducing recruitment and limiting dispersal, particularly at smaller scales (Rytwinski et al., 2019). The effectiveness of these techniques varies greatly depending on the targeted species and environmental conditions of the removal location. Water level drawdowns can also be used in highly regulated waters such as irrigation canals, to expose invasive plants to either summer drying or winter frosts to reduce vigor and increase mortality rates. Multiple temporary drawdowns, coupled with harvesting, have also been shown to be an effective control technique for signal crayfish in England (Chadwick et al., 2021). The effectiveness of chemical treatments varies considerably with environmental conditions (e.g., water quality, wind, depth, discharge), target species susceptibility, and application effectiveness. Typical chemical applications involve herbicides to control invasive plants (e.g., Eurasian milfoil), rotenone piscicides to control invasive fishes (e.g., northern snakehead, *Channa argus*) and biocides to control invasive crayfishes (e.g., red swamp crayfish); although unintended consequences on non-target species remains a concern.

Biological control options typically involve the intentional introduction of predators and herbivores to reduce the reproductive capacity or density of an AIS (Box 2). Biocontrol is commonly used for large-scale management of invasive plants, such as the release of grass carp (*Ctenopharyngodon idella*) for controlling submerged plants; or the Tamarisk beetle (*Diorhabda* spp.) introduced to

Box 2 Challenges to Controlling Invaders: A case study of common carp.

Common carp is one of the world's most invasive freshwater fish species. In Australia, carp can exceed 90% of total fish biomass in some regions, and the species has been implicated in the decline of native fishes, invertebrates, aquatic vegetation, and water quality. Management approaches to carp have included a diverse range of techniques to control abundance and dispersal, including screens on wetlands (to limit adult entry and spawning), traps on fishways, active harvesting, water management to discourage recruitment, commercial fishing and community 'carp buster' fishing events. In 2016, the Australian Government started the development of the National Carp Control Plan (NCCP), which included examining the feasibility of introducing a biocontrol agent (cyprinid herpes virus, CyHV-3) to control carp across Australia's waterways. Research on non-target species susceptibility and carp lethality suggested that the virus might be a potentially useful biocontrol agent (McColl et al., 2016). The NCCP also embarked on a large program of community consultations in regions affected by carp and of research on virus release and clean-up strategies, estimating carp biomass, water quality risks, risk and benefit assessments and the potential longer-term ecological outcomes of carp reduction (see https://carp.gov.au/). External studies also highlighted the ecological risks of removal, and questioned the effectiveness and benefits of the virus control (Kopf et al., 2017). At the time of writing, the Australian Government is considering the final outcomes of the NCCP.

Common carp. Photo courtesy of Biosecurity Queensland.

control the riparian tree tamarisk. Biocontrol agents are often nonnative as well (sourced from the native range of the targeted AIS), thus risking the introduction of another AIS. Genetic biocontrol is also increasingly being considered to disrupt the reproduction of invasive species; however, further research is needed to ensure that genetic biocontrol methods can be deployed in a way that minimizes potential environmental harm (Teem et al., 2020).

Eradication

Eradication as a management objective for invasive species usually has the best chance of success when applied early after detection, and where control techniques are applied heavily and in contained areas (Fig. 6). Piscicides, such as rotenone, are a reliable and cost-effective tool for controlling or eradicating invasive fishes particularly at smaller localized scales. For example, rainbow trout and smallmouth bass (*Micropterus dolomieu*) have been successfully eradicated in small streams in Australia and South Africa, respectively, using rotenone, with minimal ecosystem side-effects (e.g., Bellingan et al., 2019). There are few examples of successful large-scale eradication of established invasive species throughout the world. One such example, however, comes from large lakes in Tasmania, Australia, where after 14 years of intensive management using multiple control methods, common carp have been successfully eradicated in one large lake, and over 99% of the original population have been removed from another nearby lake (Yick et al., 2021). Similar examples from large river systems do not exist.

Conclusion

Aquatic invasive species are a primary threat to streams and rivers across the globe, impacting biodiversity, disrupting key ecological functions, and compromising ecosystem services. Threats posed by AIS often combine synergistically with other environmental challenges, including habitat loss and fragmentation, dams and river regulation, land-use conversion, water extraction, pollution, and climate change (Reid et al., 2019). River regulation by dams can promote invasion success by altering downstream hydrology, temperature, and substrate, to favor AIS and offering new opportunities for them to thrive in upstream reservoirs (Johnson et al., 2008). Global declines in wild freshwater fisheries have promoted the expansion of nonnative species aquaculture, leading to accidental escapees and longstanding ecological impacts (Cucherousset and Olden, 2011). Finally, climate change is expected to result in warmer water temperatures, shorter duration of ice cover, altered streamflow patterns, increased salinization, and increased demand for water storage and canals, which collectively bolster the pathways for and establishment of new freshwater invasions (Rahel and Olden, 2008). The future biodiversity, integrity and functioning of riverine ecosystems will depend on how societies manage current AIS and on whether the arrival of future AIS can be successfully prevented or minimized.

Knowledge gaps

- What are the ecological consequences of multiple invasive species to recipient ecosystems? Do synergistic or antagonistic interactions occur?
- How do ecological impacts of invasive species transverse multiple levels of ecological organization, from genes to ecosystems?
- What evidence is there for sleeper populations of invasive species, that is, established populations that persist at low abundance and have negligible impact for years until they are triggered by an environmental or anthropogenic change to become highly abundant and disruptive AIS?
- How will climate change promote or inhibit the introduction, establishment and spread of AIS in the future?
- How does the perception of costs and benefits of an invasive species change over time and vary among different sectors of human society?
- How might genetic biocontrol (genomic modification tools) offer novel risks or solutions to managing invasion?
- If large-scale biocontrol of AIS does occur, will ecosystem condition recover to its previous state?
- Is it possible for rapid evolutionary shifts to cause native and nonnative populations to become invasive?
- Can invasion syndromes—describing a combination of pathways, species traits, and characteristics of the recipient ecosystem—be used to develop more robust predictions of the dynamics and impacts of AIS?
- Can horizon scanning and scenario modeling be used to effectively prioritize decision-making and action against AIS?
- How can we better use and combine the tools of internet and mobiles and citizen science to help in studies of management and control of invasions in rivers and streams?
- How can we amplify and improve the importance of transversality between actors and the role of relationships between academia and decision makers and legislators?

See Also: Structures and functions of Inland Waters - Rivers: eDNA and Bioassessment of Rivers

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Inland Waters—Rivers: Land Use and Water Quality

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Biochemical Oxygen Demand (BOD) Measure of the oxygen consumed by the metabolism of aerobic bacteria.
Catchment/watershed Area of land, bounded by hill or mountain ridges, that directs and controls the flow of water downhill to a stream.
Combined Sewer Overflow (CSO) Discharge of raw sewage and stormwater into the environment due to the limited capacity of wastewater treatment plants, mostly occurs during precipitation events.
Contaminants Harmful biological, chemical, physical, or radiological substances in the environment, typically, but not always, due to anthropogenic activity.
Eutrophication Excessive levels of nutrients, commonly nitrogen and phosphorus, in waterbodies that often lead to elevated algal growth and death of aquatic organisms due to lack of oxygen.
Headwaters Small streams and wetlands in the upper parts of a catchment.
Land Use and Land Cover (LULC) Human purposes of land for economic and cultural activities (land use) along with the physical materials and vegetation that cover the land such as forests, wetlands, impervious surfaces, agriculture, and water (land cover).
Land Use and Land Cover Changes (LUCC) Patterns of land conversion over time due to the continued interaction between humans and the natural environment.
Non-point source (NPS) Pollution or environmental impacts that do not have a single, identifiable origin, but rather an integration of multiple sources over large spatial scales.
Point source (PS) Single, identifiable origin of pollution or environmental impact.
Sedimentation Processes by which sediment is eroded from land into waterbodies such as rivers, where it is suspended, transported, and deposited.
Water Quality Physical, chemical, and biological aspects of water and waterbodies.

Introduction

Among the most pervasive environmental effects of human activities are unprecedented rates and scales of changes in land use and land cover (LULC) (Crist et al., 2017). Land cover describes the physical land type such as forest or open water whereas land use indicates how people are using the land such as development or agriculture. Land-use and land-cover changes (LUCC) represent the interaction of multiple factors including socioeconomic, institutional, and environmental (Lesschen et al., 2005).

Inland waters, especially streams and rivers, are intimately linked to their surrounding environment through various pathways. In this sense, rivers are products of their landscapes whereby the "valley rules the stream": geology regulates the availability of ions and the supply of sediments, topography determines the slope and degree of containment, climate and soils determine vegetation type and coverage and therefore the availability of organic matter and extent of stream shading, and hydrologic processes including precipitation, runoff, and subsurface flows regulate water movement through the catchment (Hynes, 1975). The amount and condition of catchment and riparian vegetation are particularly critical variables influencing catchments (Naiman and Decamps, 1997).

LUCC have emerged as critical processes affecting many aspects of catchment structure and function as well as the quantity, distribution, and availability of clean, fresh water. Owing to the hierarchical structure of river systems (Fig. 1), patterns at one spatial

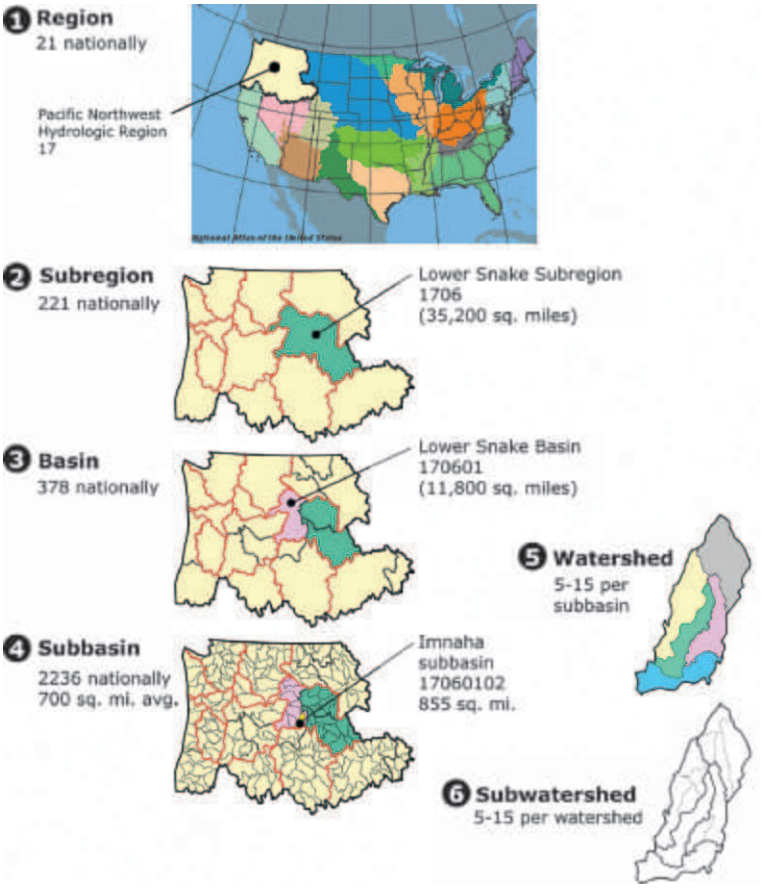

Fig. 1 Example of the hierarchical nature of catchments/watersheds across different spatial scales: the Lower Snake River basin in the Pacific Northwest of the United States, along with the Imnaha River subbasin and its tributaries (courtesy of Bruce McCammon, United States Forest Service, Portland, Oregon).

scale may be influenced or generated by processes operating at different scales or extents (Tagwireyi et al., 2017). Thus, the combined effects of both riparian and broad, catchment-scale LULC patterns on rivers are important to consider (Kautza and Sullivan, 2016).

This chapter explores how LUCC integrate many anthropogenic impacts (Fig. 2). Given their widespread global extent, we focus on agriculture, urbanization, and natural resource extraction as primary examples of the impacts LUCC can exert on water quality (Fig. 3). In particular, *we discuss the effects of these activities on the multiple dimensions of water quality—chemical* (e.g., *contaminants, nutrients)*, *biological* (e.g., *abundance, biodiversity, disease)*, *and physical* (e.g., *sedimentation, hydrology, fluvial geomorphic characteristics, light availability, habitat structure)*. The effects of land use on water quality are myriad and often context-dependent (Table 1), with specific catchments each having distinct responses to LUCC. However, general patterns can be observed that can inform us of risk factors and mitigation strategies.

Main topics

Agriculture

Global agriculture has ballooned from 7.3% of total land in 1700 to 29.4% in 1950 to 37.1% in 2015, with most change in the last century driven by increased pastureland for livestock (Goldewijk et al., 2017), a shift caused by an increasing global population and meat becoming a larger portion of the diet in developed countries (Sans and Combris, 2015). In the United States, the Lower Mississippi, Upper Mississippi, Ohio, Missouri, Colorado, Arkansas, and Red River catchments consist of over 40% agriculture (Allan, 2004). Some agricultural operations represent point sources of pollution (e.g., livestock and aquaculture), whereas row-crop, timber, and other agricultural activities that lead to excess fertilizers, pesticides, and sediment are non-point sources of pollution.

Within agricultural catchments, multiple factors might negatively affect river conditions. For instance, increased water turbidity and sediment deposition associated with increased sediment loads affect aquatic food webs (Power et al., 1996). In particular, agricultural practices including livestock grazing, tilling, and tile drainage can dramatically affect hydrology, channel morphology, and aquatic biota (Cuffney et al., 2000). Excessive fine sediment delivery to rivers—largely from agricultural practices—is the

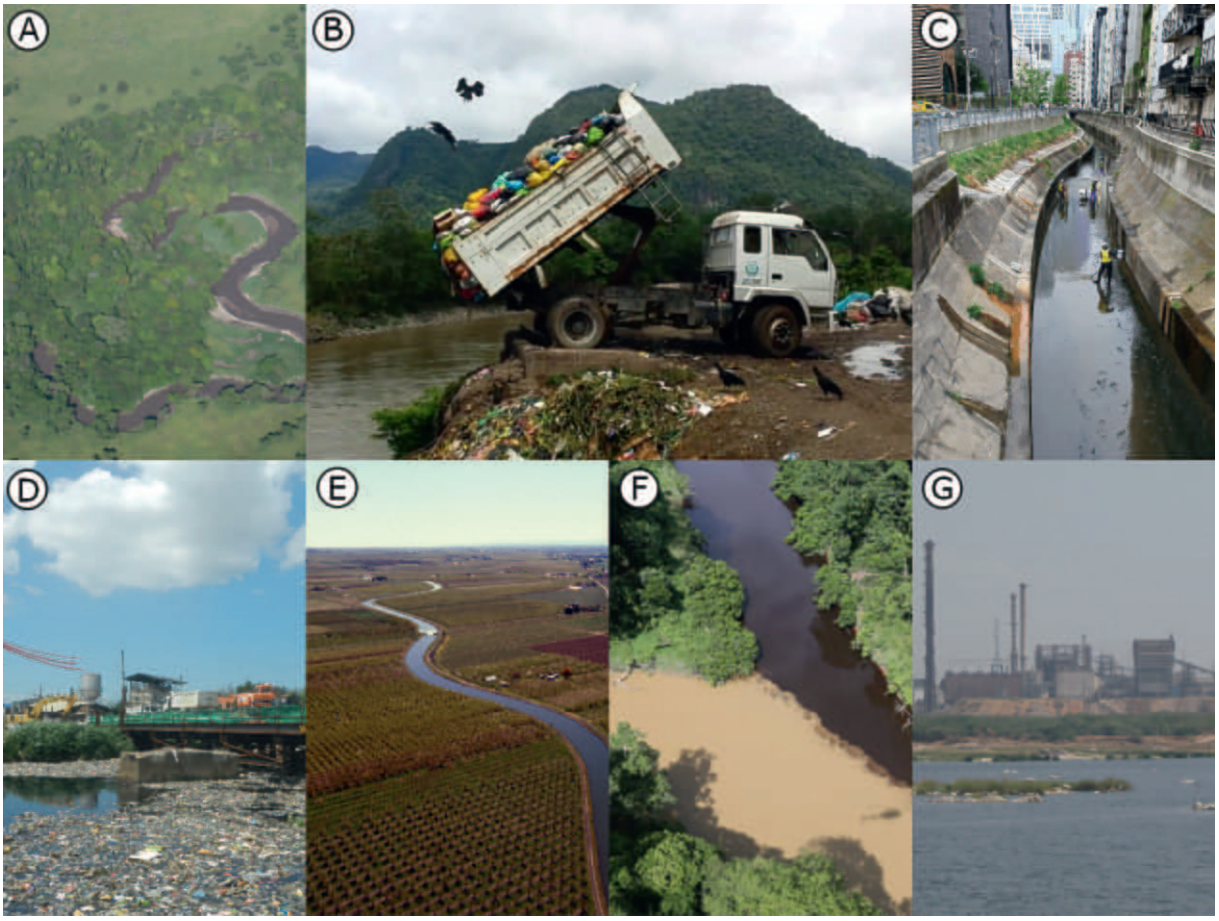

Fig. 2 (A) Natural riparian forests and grasslands surrounding Gremeti River in Serengeti National Park in Tanzania. (B) Toxic hospital waste dumped directly into the Huallaga River in the city of Tingo María, Perú (Hutchinson, 2016). (C) Concrete lined channel of the Shibuya River in Tokyo, Japan (Syced, 2021). (D) Trash pollution in the Marilao River in Marilao, Philippines (Velasquez Floro, 2021). (E) Agriculture surrounding a canal connected to the Yakima River in Washington, United States (Prechtel, 2006). (F) Sediment from an upriver logging operation mixes with unpolluted river channel near Sabah, Malaysia (Butler, 2019). (G) Paper mills on the banks of Tungabhadra River in Karnataka, India (Jangam, 2014).

leading river pollutant worldwide and can affect stream biota and ecosystem function through chemical (i.e., toxicity) or physical processes (i.e., impaired habitat, smothering) (Sullivan et al., 2019). For instance, sediment pollution can decrease primary productivity and macroinvertebrate biodiversity by decreasing light availability, substrate suitability, and filling interstitial spaces (Izagirre et al., 2009; Larsen et al., 2011). As agricultural land use expands to keep pace with a growing human population, more riparian systems are burdened with associated negative impacts.

Nitrogen (N) and phosphorus (P) are essential nutrients applied to crops as fertilizers to increase crop yields (Elser et al., 2007). Much of this fertilizer is not absorbed by target crops, and instead enters groundwater through leaching or flows into streams and rivers via surface runoff after precipitation or irrigation events (Domagalski et al., 2008). These nutrients commonly exist in aquatic ecosystems in various organic or inorganic forms. Inorganic nitrogen can be dissolved as biologically–unavailable gaseous nitrogen (N_2) or as biologically-available ammonia (NH_4^+), nitrite (NO_2^-), or nitrate (NO_3^-) ions, with nitrate being most common, mobile, and impactful. Inorganic phosphorus is dissolved as biologically-available orthophosphate (PO_4^{3-}). Both nutrients are also present as organic molecules, which contribute to total N and total P and can break down to more biologically-available inorganic forms. The addition of these fertilizers causes nutrient enrichment and excessive algae growth (Houser and Richardson, 2010), which can progressively worsen into a state of eutrophication in downstream waters such as reservoirs, lakes, and large rivers.

Eutrophication decreases macroinvertebrate (Gong and Xie, 2001), fish (Wang et al., 2007), and aquatic primary producer (Leibold, 1999) biodiversity by limiting or eliminating sensitive species and facilitating the success of pollution-tolerant organisms, many of which are typically non-native. Eutrophication also leads to harmful algal blooms (HABs) of green algae and cyanobacteria (Anderson et al., 2002) that cover water surfaces, substrate, and organisms (Landsberg, 2002). Harmful algal blooms in surface layers can prevent oxygen from effectively diffusing into the water column creating hypoxic zones. The death and decomposition of HABs increase aerobic bacteria and biochemical oxygen demand (BOD), which is largely a measure of the metabolic activity of microbes. High BOD can diminish dissolved oxygen concentrations below that which is necessary for fish and invertebrate life (Watson et al., 2016). Thus, HABs are a primary factor in mass die-off events, such as fish kills (Harrison et al., 2017).

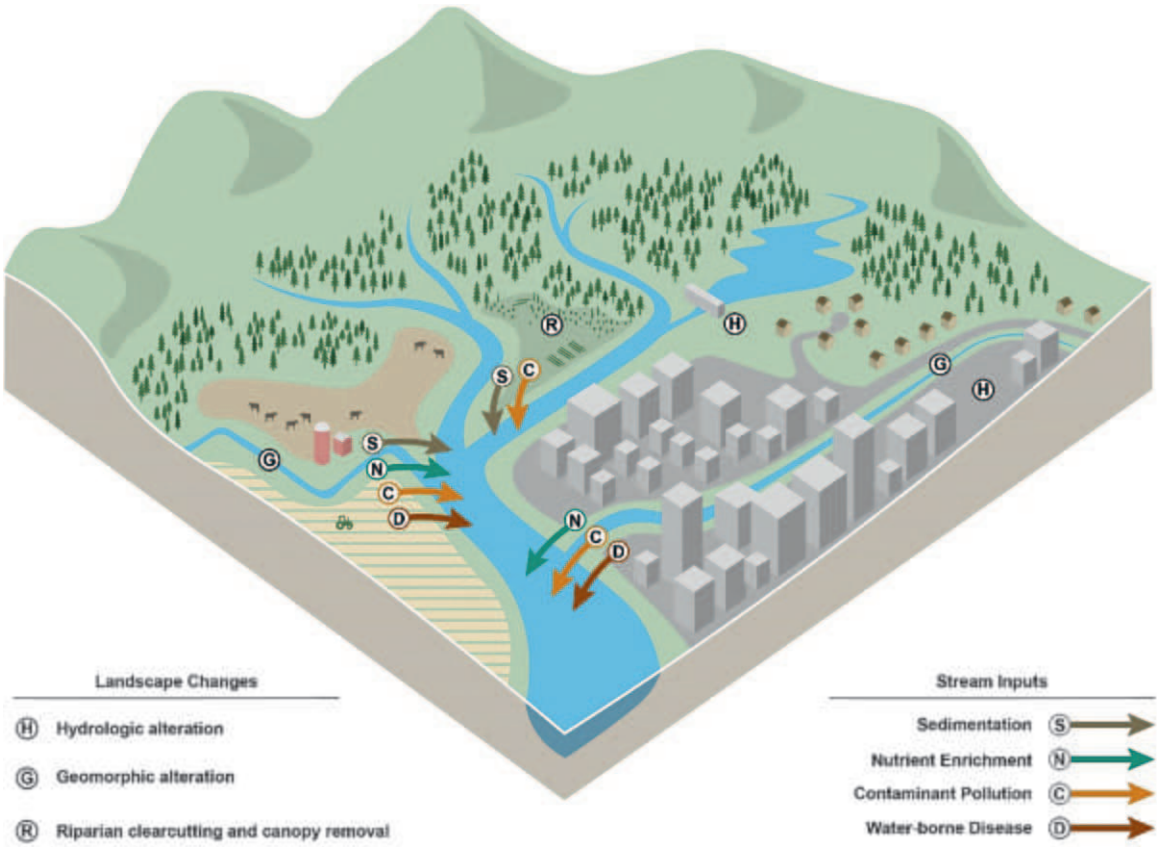

Fig. 3 Urbanization, agriculture, and resource extraction (i.e., mining, timber harvest, and dams/water withdrawal) represent globally common anthropogenic LULC types with significant consequences for water quality. Illustration: Robert Keast.

Cyanobacterial blooms can be particularly harmful because they also produce cyanotoxins, which affect the nervous system, liver, skin, or blood of aquatic organisms, and also humans (Christensen and Khan, 2020). Substrate can be particularly impacted by the prolific growth of nuisance filamentous algae that traps sediment (Berger et al., 2003), cements benthic substrata (Dodds, 1991), and leads to overall declines in macroinvertebrate diversity (Tonkin et al., 2014). The effects of HABs are only expected to get worse with climate change as warm temperatures exacerbate hypoxic conditions (Griffith and Gobler, 2020).

Pesticides (fungicides, herbicides, and insecticides) are contaminants commonly associated with agricultural land use (Fig. 4). Pesticides are applied to crops for pest control, but during precipitation events they enter streams and rivers where they can be toxic to aquatic life (Schäfer, 2019). There are over 2000 different pesticidal compounds used globally, along with hundreds of known metabolites deriving from their decomposition (Lewis et al., 2016). Tebuconazole and carbendazim, two commonly applied fungicides that are widely detected in surface waters (de Souza et al., 2020), negatively impact detrital pathways (Zubrod et al., 2011) and the health and survival of aquatic organisms (Singh et al., 2016). Three of the most widely used herbicides in the world are glyphosate, atrazine, and metolachlor, which are primarily used as weed-control agents in corn and soybean crops, but they are also commonly detected in surface waters (Medalie et al., 2020). Glyphosate has been shown to impact periphyton development and composition and cause acute toxicity in fish, amphibians, and crustaceans, among other developmental effects (reviewed in Annett et al., 2014). Atrazine and metolachlor are endocrine disruptors. Atrazine demasculinizes and increases hermaphroditism in frogs (Hayes et al., 2002), while metolachlor disrupts thyroid activity in fish (Jin et al., 2011). Furthermore, atrazine has transgenerational reproductive effects in fish (Cleary et al., 2019), and metolachlor has developmental effects in crayfish (Velisek et al., 2018). Although these pesticides can break down in the environment, even their degradation can be harmful, as the metabolites of glyphosate, atrazine, and metolachlor are also toxic (e.g., Maazouzi et al., 2016), sometimes even more toxic than the parent compound (Velisek et al., 2018).

Organophosphates have been the primary class of insecticides for decades, but their use has been declining in favor of pyrethroids, neonicotinoids, and other classes. That said, they are still widely used. Chlorpyrifos is one of the most widely used insecticides (Atwood and Paisley-Jones, 2017; de Souza et al., 2020) that has been shown to negatively impact aquatic macroinvertebrate assemblages (Ward et al., 1995). Pyrethroids like lambda-cyhalothrin, cypermethrin, and bifenthrin are seeing increased usage, but they are highly toxic to, and cause endocrine-disrupting effects in, aquatic organisms (Brander et al., 2016).

Table 1 Anthropogenic stressors of inland waters, examples of LULC type with which they are associated, whether they originate mostly from a point or non-point source, and common effects (see also Allan, 2004).

Anthropogenic environmental stressors	*Description*	*Examples of LULC Associations*	*Point or non-point source*	*Effects*	*References*
Sedimentation	Fine particulates sourced from runoff and erosion that are either suspended in river water or deposited onto the riverbed.	Agriculture Timber harvest	NPS	Fills interstitial refugial spaces, covers and homogenizes benthic habitat, increases turbidity, increases scouring, coats organisms and gill structures leading to loss of periphyton and sensitive taxa, bottom-up effects by decreasing primary productivity	Davies-Colley and Smith (2001), Sullivan and Watzin (2010), Burdon et al. (2013) and Blöcher et al. (2020)
Nutrient enrichment	Excess nutrients (primarily nitrogen and phosphorus) that enter rivers through agricultural runoff, erosion, or wastewater effluent.	Agriculture Urban	PS/NPS	Increases primary productivity with bottom-up effects; increases filamentous algae; increases tolerant, energy-inefficient taxa; may act as stressor in very high concentrations; leads to eutrophication and harmful algal blooms; increases bacterial abundance that decreases dissolved oxygen (e.g., BOD); facilitates species invasions; increases decomposition rates	Heiskary and Markus (2001), Ferreira et al. (2015), Ouyang et al. (2018) and Canning and Death (2021)
Hydrologic alteration	Deviations from natural annual flow patterns that result in brief, but extreme, peaks ("flashiness") caused by removal of natural vegetation, increased impervious surfaces, and decreased base flows from water extraction or damming.	Agriculture Urban Dams Water withdrawal	NPS	Increases peak flow magnitude and frequency, but also lowers base flows (more variability); increases erosion and channel instability; alters downstream transport of sediment, nutrients, and contaminants; decreases survival and growth of organisms; decreases metacommunity functional diversity	Roy et al. (2005), Dewson et al. (2007), Nilsson and Renöfält (2008) and Ruhi et al. (2018)
Fluvial geomorphic alteration	Channel modification that results in bank erosion, lateral or vertical channel adjustment; and loss of floodplain connectivity; related to alterations in hydrology and sediment load.	Agriculture Urban	NPS	Increases erosion and sedimentation; leads to channel widening, incision, aggradation, or change in channel planform; can cause entrenchment that can increase flows; alters habitat, community composition and abundance of aquatic biota, and food webs	Walters et al. (2003), Sullivan et al. (2004, 2006), Bey and Sullivan (2015) and Rieck and Sullivan (2020)
Contaminant pollution	Harmful chemicals (pharmaceuticals, synthetics, heavy metals, pesticides) from industry, agriculture, wastewater treatment plants, or non-point sources that are dissolved or suspended in river water or deposited in riverbeds.	Agriculture Urban Industrial Mining Oil & gas extraction Landfills	PS/NPS	Direct toxicity to organisms; decreases survival, fecundity, and growth rates; causes endocrine disruption, growth defects and developmental abnormalities	Schulz (2004), Golovanova (2008), Oehlmann et al. (2008), Pal et al. (2010) and Schäfer (2019)
Acidification	Anthropogenically lowered pH of streams and rivers due to acidic precipitation or acid mine drainage.	Urban Powerplants Mining	PS	Direct toxicity to organisms, mobilization of toxic metals from substrate, alteration of leaf litter breakdown rates, reduced species richness and abundances	Gerhardt (1993), Jardine et al. (2013) and Ferreira and Guérold (2017)
Deforestation Riparian clearing	Removal of vegetation from riparian areas, which reduces or eliminates canopy cover and allochthonous input.	Agriculture Urban Timber harvest	PS	Canopy removal increases temperature and filamentous algae growth, decreases allochthonous leaf litter and wood inputs that shifts invertebrate assemblages and functional traits, reduces refugia, decreases bank stability and increases erosion, increases tolerant taxa	Reid et al. (2008), Hubble et al. (2010) and Sturt et al. (2011) and Peres et al. (2017)
Water-borne disease	Prevalence and transport of water-borne diseases in rivers due to poor sanitation of human and/or animal wastes.	Agriculture Urban	PS	Transmit human and zoonotic diseases (e.g., diarrheal diseases, schistosomiasis, trachoma, ascariasis, trichuriasis, hookworm disease, malaria, avian influenza), transmit animal diseases (mastitis, foot and mouth diseases, parasitic and bacterial infections), reservoir of antibiotic resistant bacteria	Prüss et al. (2002b), Elahi et al. (2017) and Bailey et al. (2018)

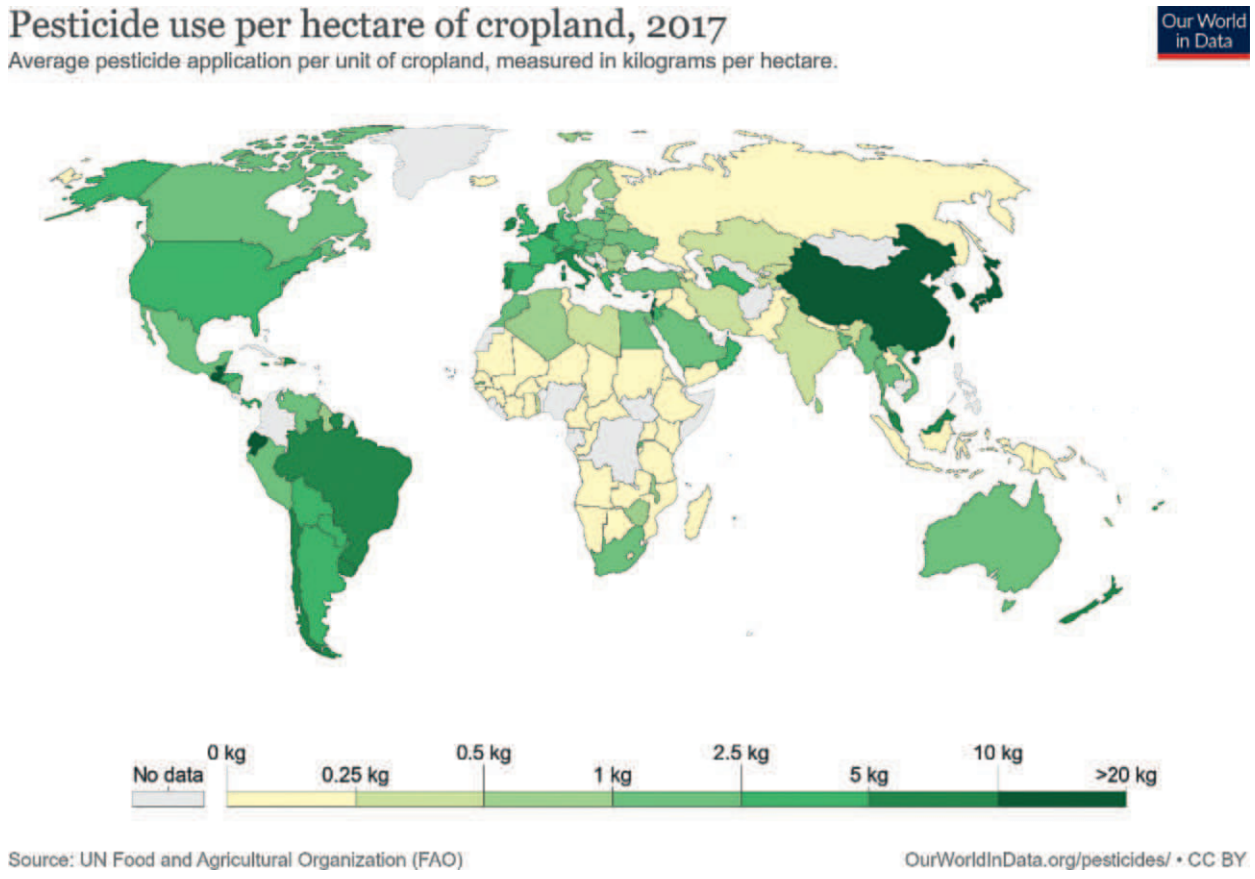

Fig. 4 Pesticide usage in kilograms per hectare by country (Roser, 2019).

Similarly, neonicotinoids have been show to negatively affect the abundances of macroinvertebrate and their avian predators (Van Dijk et al., 2013; Hallmann et al., 2014). In addition, pesticides run off into rivers where they form mixtures, which can be potentially up to 40 times more toxic than single compounds (Yang et al., 2018). Lastly, genetically modified crops such as glyphosate-resistant soybeans (e.g., Monsanto's "Roundup Ready" variety), facilitate overuse and overreliance of herbicides (Benbrook, 2012), whereas crops like Bt-corn contribute detritus to streams that harbor proteins toxic to stream insects (Rosi-Marshall et al., 2007).

Agriculture also directly uses water and accounts for 90% of all freshwater consumption (Shiklomanov, 2000) (Fig. 5). Irrigation of cropland by redirection of surface waters and pumping of hydrologically connected groundwaters directly decreases annual streamflow (Yin et al., 2021). Surface drainage, in particular, increases erosion and N, P, sediment, and pesticide inputs into rivers. Subsurface drainage mitigates P and pesticide inputs due to soil adsorption, but this is not commonly true for N because it is more mobile through soils. Likewise, sediment is physically trapped more readily by the soil matrix in subsurface flows compared to surface flows (Gramlich et al., 2018).

Livestock farming poses a significant threat to maintenance of water quality because it produces nutrient-rich animal wastes, leads to erosion-prone fields, and release of major ions, primarily Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, HCO_3^{-} (Cesoniene et al., 2019). Effluent from intensive livestock farming increases the overall organic pollution in rivers (measured by BOD; Wen et al., 2017). This type of organic pollution lowers oxygen levels, thereby suffocating aquatic organisms, and spreads pathogens, including those that cause diarrheal diseases, schistosomiasis, trachoma, ascariasis, trichuriasis, and hookworm disease in humans (Prüss et al., 2002a). This concern is especially prevalent in developing nations where BOD is only expected to increase (Wen et al., 2017). The cumulative effects of livestock grazing have also been shown to decrease aquatic macroinvertebrate species richness and increase the number of tolerant taxa (Herbst et al., 2012).

Estrogenic steroids (estrone, estradiol) and antibiotic pharmaceuticals in wastewater from intensive dairy farms and leachate from cattle burials (Matthiessen et al., 2006) enter surface and ground water. These hormones act as endocrine disruptors in aquatic organisms, where they have carcinogenic and mutagenic effects (Wang and Zhou, 2013). Antibiotics are used liberally in intensive livestock farming and many of these pharmaceuticals enter riparian systems through livestock waste. Research has shown that antibiotic contamination can induce antibiotic resistance in aquatic pathogens and impact the health of aquatic organisms (Bottoni et al., 2010).

Fig. 5 Water withdrawal from rivers for crop irrigation is a major stressor associated with agricultural land use as seen here in the Snake River valley, Idaho, United States. Photo: S.M.P. Sullivan.

Urbanization

The proportion of the human population living within urban areas is increasing rapidly, with projections that 68% of the total global population will live in urban centers by 2050 (United Nations, 2018). Urban land use within river catchments is estimated at 5–10% in catchments with the most urban development (Benke and Cushing, 2011). However, despite the small relative amount of total catchment land use, the effects of urbanization on water quality is disproportionately large due to many factors, including the integration of waste from a large, dense human population. Urban centers contain both point (wastewater treatment plants, industrial effluent) and non-point sources (impervious surface runoff) that contribute to water-quality impairment.

The "Urban Stream Syndrome" (USS) is a central concept used to describe a set of characteristics that commonly emerge in urban catchments once a stream is sufficiently impacted by urbanization. These characteristics include large fluctuations in hydrology, with high peak flows and low base flows, alteration of fluvial geomorphic patterns and processes, high relative concentrations of contaminants and nutrients, and deviations from natural mass and energy transfers (Booth et al., 2016). These effects can be largely traced to widespread impervious surfaces in urban areas that prevent precipitation from percolating through soils into groundwater. Impervious surfaces greatly increase the speed with which water moves from land into streams and rivers, leading to extreme flow variability (Fig. 6). Extreme flows not only contribute to erosion and contaminant input, but also can directly affect biota by increasing mortality and decreasing growth rates and functional diversity (Roy et al., 2005).

Stream geomorphic adjustment comes in concert with changes in hydrology and sedimentation resulting from LUCC, which represent major mechanisms regulating physical water quality. Channel adjustment can lead to alterations in sediment-size distribution, turbidity, streamflow variability, and habitat quality with impacts on aquatic insects (Sullivan et al., 2004) and fish (Sullivan et al., 2006; Rieck and Sullivan, 2020) (Fig. 7; also see Table 1). Highly incised streams limit the connectivity between the stream and its floodplain, having consequences for biodiversity (Sullivan and Watzin, 2009). Since channel instability can pose

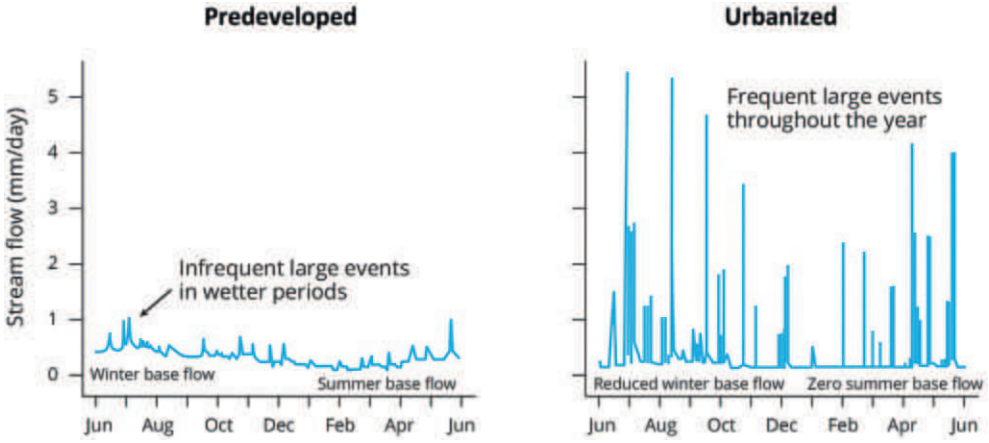

Fig. 6 After urbanization, streamflow becomes more variable with greater peak flows and lower base flows. From Stewardson MJ, Acreman M, Costelloe JF, Fletcher TD, Fowler KJA, Horne AC, Liu G, McClain ME, and Peel MS (2017) Understanding hydrological alteration. In: Horne AC, Webb JA, Stewardson MJ, Richter B and Acreman A (eds). *Water for the Environment.* pp. 37–64, Academic Press. ch. 3.

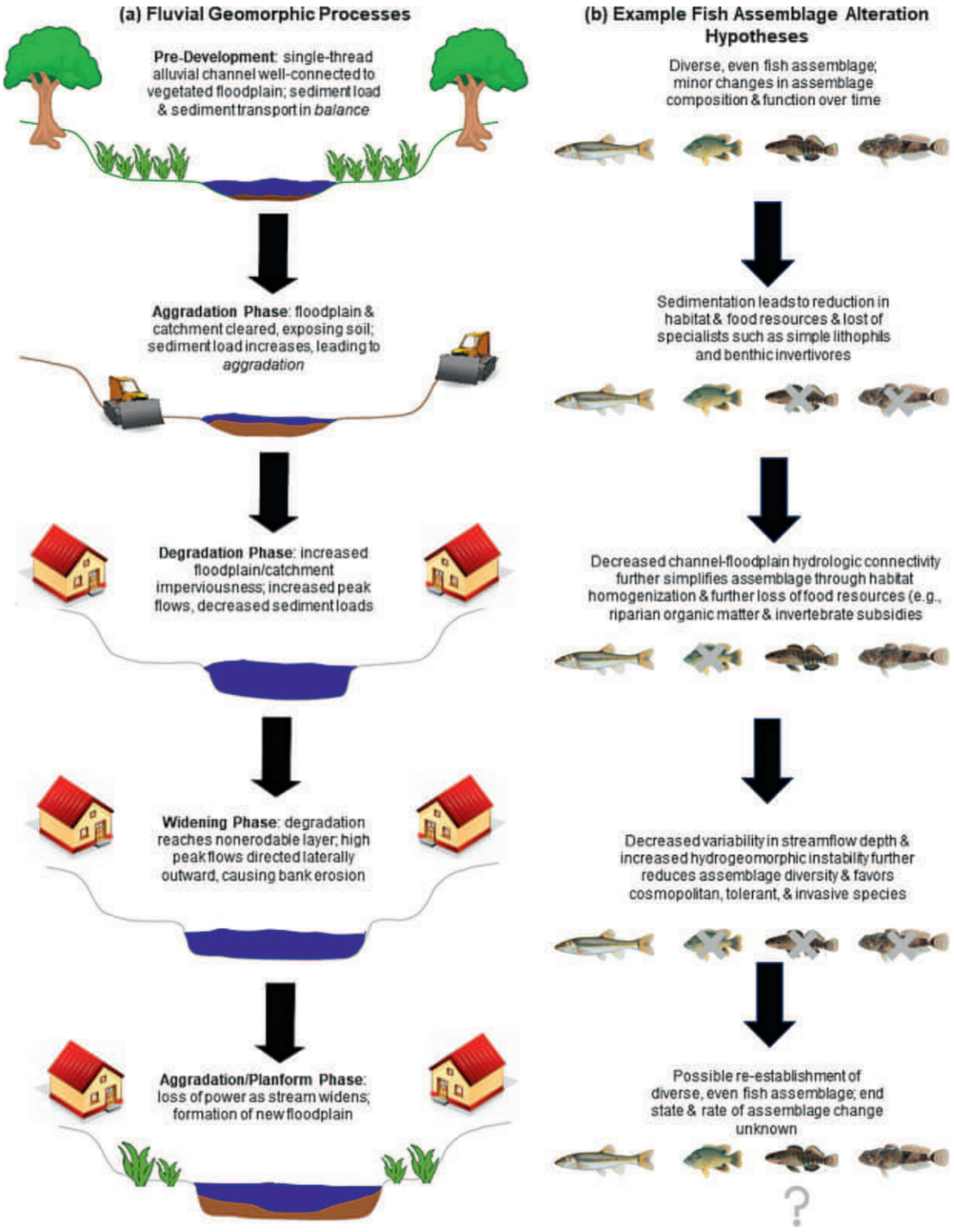

Fig. 7 Conceptual depiction of urban stream channel hydrogeomorphic evolution with example fish assemblage alterations. Hydrogeomorphic changes can lead to significant shifts in physical water quality. From Rieck LO and Sullivan SMP (2020) Coupled fish-hydrogeomorphic responses to urbanization in streams of Columbus, Ohio, USA. *PLoS One* **15**: e0234303.

risks to property owners, streams are often channelized with concrete or coarse riprap to improve channel stability, but these "solutions" homogenize structural habitat in morphologically-adjusted streams and further decrease the abundance and diversity of organisms (Cooke et al., 2020).

Urban areas support large human populations that produce substantial amounts of nutrient- and contaminant-rich waste. Combined sewer systems are common urban drainage systems that transport sewage to wastewater treatment plants (WWTPs), but they have limited capacities that are often exceeded during rainfall events resulting in raw combined sewer overflow (CSO) discharged directly into rivers (Yu et al., 2013). Untreated wastewater contributes significant contaminants, nutrients, and pathogens into rivers and represents a major challenge to water quality. For example, a diverse array of pharmaceuticals, but especially carbamazepine, sulfamethoxazole, and diclofenac, are discharged into the environment through WWTP effluent (de Voogt et al., 2007), along with other trace contaminants like polycyclic aromatic hydrocarbons, heavy metals, and hormones (Phillips et al., 2012). Fecal coliform bacteria, mostly *Escherichia coli* and fecal streptococci and enterococci are prevalent in combined sewer overflows, can cause a variety of diseases, and can exceed dry weather conditions by two orders of magnitude (Passerat et al., 2011). The combination of these pollutants create an environment that selects for and harbors antibiotic resistant bacteria (Honda et al., 2020), along with elevating BOD that can lead to oxygen depletion (Wen et al., 2017). These issues are especially problematic for people in regions that lack infrastructure to treat wastewater including, for example, areas of sub-Saharan Africa, Latin America, and southern Asia (Okoh et al., 2007; Wen et al., 2017). Lastly, though no transmissions have yet been detected via water or wastewater, SARS-CoV-2 has been detected in these sources (Godini et al., 2021).

Urban centers produce a wide range of contaminants that enter streams and rivers, but they are highly variable among cities and reflect local industry, technology, and cultural landscapes. Sources range from residential chemical usage to landfill runoff and leachate to WWTP and industrial effluent. Whereas pesticides are generally more closely associated with agriculture LULC, a number of pesticides are used in residential areas of urban centers to control weeds and household pests, such as the herbicide 2,4-D and the toxic pyrethroid insecticide bifenthrin (Weston et al., 2005; Atwood and Paisley-Jones, 2017). Heavy metals (e.g., Cd, Cu, Cr, Ni, Pb, Zn, and Hg) are contaminants found in urban-impacted rivers due to poorly managed landfills, industrial and domestic wastewater effluent, and atmospheric deposition from proximate industrial areas. These contaminants are toxic to aquatic invertebrates (Armitage et al., 2007) and are especially prevalent in rapidly urbanizing or underdeveloped regions that have little infrastructure (e.g., Islam et al., 2015). Lastly, salts (primarily Na^+, Cl^-, K^+, Ca^{2+}, CO_3^{2-}, HCO_3^-, SO_4^{2-}) contaminate urban rivers from de-icing applications, industrial effluents, and sewage leakage (Kaushal et al., 2005; Rose, 2007). Other emerging contaminants include microplastics (fragmented plastic particles <5 mm) and engineered nanoparticles (particles ranging from 1 to 100 nm used in certain manufacturing applications) but little is yet known about their general effects.

Natural resource extraction

Logging, or commercial deforestation, is a common precursor to agricultural or urban land use. Deforestation—including removal of riparian vegetation—increases erosion, sediment inputs, and temperature (via increased solar input from canopy removal); alters hydrology and geomorphology; and, eliminates aquatic-terrestrial connectivity and energy subsidies (Sweeney and Newbold, 2014; Kautza and Sullivan, 2016). Typically, macroinvertebrate grazing pressure and light limitation from canopy cover prevents nuisance algae growth from negatively impacting aquatic ecosystems (Sturt et al., 2011). However, anthropogenic removal of vegetation increases light availability and facilitates nuisance algae growth. The relationships among light availability, macroinvertebrate diversity, and aquatic-terrestrial energy subsidies also vary naturally in predictable ways.

Forested or vegetated riparian areas act as natural buffers of LUCC effects that protect waters from a host of impairments including elevated stream temperature and nutrient inputs, loss of organic input (leaf litter) and woody material, bank instability, erosion, and sedimentation (Dosskey et al., 2010). Sweeney and Newbold (2014) established that forest buffers (Fig. 8) ≥30 m are necessary to protect water quality of small to mid-size streams (~5th order streams), but almost half (44%) of riparian systems of all sizes in the United States have disturbed or poor buffers (US Environmental Protection Agency, 2016).

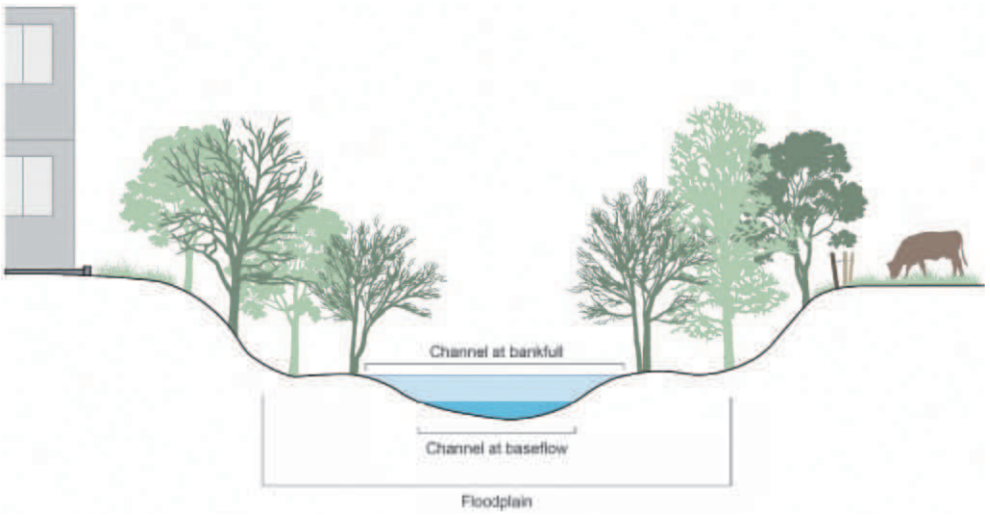

Fig. 8 Sufficiently wide vegetated riparian buffers can ameliorate the negative effects of anthropogenic land use by removing excess nutrients and trapping sediment and contaminants. Illustration: Robert Keast.

Surface and subsurface mining, including mountaintop removal mines and associated valley fills, have also been shown to exert strong negative effects on water quality in streams. For example, Giam et al. (2018) show that streams impacted by surface coal mining (mountaintop mining-valley fill) exhibited 32% lower taxonomic richness, and 53% lower total abundance of invertebrates, fish, and salamanders when compared to reference streams. In areas with extensive subsurface mining, particularly for gold or coal, acid mine drainage (AMD) is a common water- quality problem. Exposed sulfide mineral ores (typically pyrite) are oxidized through multiple pathways resulting in acidic water that dissolves and mobilizes toxic heavy metals (Fe, Al, Zn, Cu, Pb, and Cd), metalloids, and sulfates (Blodau, 2006). Streams receiving AMD have reduced pH (<3) and are coated with heavy metals and metal hydroxide precipitates, such as iron hydroxide FeO(OH), also known as "yellow boy," which is the most common and conspicuous precipitate of AMD (Fig. 9) (Winterbourn et al., 2000). AMD eliminates sensitives taxa through smothering, coating, direct toxicity, and bioaccumulation through food webs, having far reaching effects from macroinvertebrates to top predatory fish (Hogsden and Harding, 2012).

Fossil fuel production and use have myriad impacts on water quality. Oil sand extraction and oil and shale gas drilling (i.e., hydraulic fracturing—"fracking") incur land disturbances that affect water quality through processes of erosion, deforestation, and sedimentation. The storage, import, and export of liquid chemicals at operation sites pose point-source spill risks for streams. For example, a crude oil spill in the Gasconade River, Missouri, United States immediately decreased macroinvertebrate abundance and diversity. Whereas riffles flushed contamination from sediments rapidly and macroinvertebrates recovered, backwaters retained contaminants and showed no recovery after 18 months of monitoring (Poulton et al., 1997). Fracking fluid is mainly a mixture of brine, sand, and various chemical additives such as anti-scalants, biocides, corrosion inhibitors, gelling agents, solvents, and surfactants (for detailed list of chemicals, see Burton et al., 2014). This fluid is injected into wells to fracture rock to facilitate natural gas retrieval and only 10–30% is recovered as wastewater flowback (NYSDEC, 2011). The fate of unrecovered fluids is unknown. Flowback, which is often stored on-site or transported to other wells, contains concentrations of metals, chlorides, sulfates, barium, dissolved solids, organics, and radionuclides that are difficult for WWTP to remove (Entrekin et al., 2011). Between 2005 and 2014, there were 6648 fracking fluid spills reported across the states of Pennsylvania, New Mexico, North Dakota, and Colorado, United States (Patterson et al., 2017). A spill from a ruptured wastewater flowback pipeline impacted Blacktail Creek, North Dakota, United States resulting in elevated levels of Na^+, Cl^-, Br^-, Sr^{2+}, B^{3+}, Li^+, NH_4^+ and hydrocarbons that reduced fish

Fig. 9 Point source acid mine drainage (S) in the Lackawanna River near the confluence with the Susquehanna River in Pennsylvania, United States (41°21′32″ N 75°45′05″ W). Reaches downstream (D) of the point source (S) are visibly contaminated with iron oxide precipitates ("yellow boy") compared to upstream (U) reaches. A historical legacy of anthracite coal mining in the region scars the surface (C) and subterranean landscape. This site is the largest point source of pollution in the Chesapeake Bay and is estimated to discharge 150–380 million liters of AMD per day for the last 60 years (Falchek, 2012). National Agriculture Imagery Program USDA (2021) National Agriculture Imagery Program (NAIP). USDA Farm Service Agency (FSA) Through Aerial Photography Field Office.

survival by 97.5% in some contaminated reaches and caused widespread endocrine disruption (estrogenic inhibition) (Cozzarelli et al., 2017). Streams in northwestern Pennsylvania impacted by fracking, including some directly impacted by fluid spills, had decreased pH, increased methylmercury concentrations, decreased macroinvertebrate and fish diversity, and microbial assemblages enriched in methanotrophic and methanogenic bacteria (Grant et al., 2016; Ulrich et al., 2018).

Other processes related to energy and resource use also come with their own problems for stream water quality. Dams, for example, of all sizes and usages (hydroelectric, reservoir-forming, flood control) directly modify flow regimes causing changes to physical, chemical, and biological aspects of water quality. Fossil fuel combustion either by automobiles or coal/methane burning powerplants emits sulfur and nitrogen oxides (SO_x, NO_x). These oxides hydrolyze in the atmosphere into sulfuric (H_2SO_4) and nitric (HNO_3) acid resulting in acidified precipitation. The bicarbonate buffer system (Eq.1; Fig. 10A) of natural waters resists pH changes, but this system is maintained by the alkalinity provided by underlying carbonate (CO_3^{2-}) lithology (e.g., limestone). Alkalinity is often closely related to water hardness, which is a measure of the mineral content (typically $CaCO_3$ or $MgCO_3$) of water. However, the capacity of the buffer system is quickly exhausted in drainages with limited carbonate reserves (e.g., igneous drainages), leading to a rapid decrease in pH. Acidified streams are directly toxic to organisms, disrupt ecosystem process like leaf litter breakdown rates (Ferreira and Guérold, 2017), and mobilize sorbed metals (Al, Hg, Cu, Pb, Cd, As, Zn) from sediments into soluble toxic forms (Fig. 10B, Gerhardt, 1993). Metals have a variety of toxic effects on aquatic biota. Aluminum is acutely toxic because it disrupts osmoregulation of plasma membranes in plant roots and animal gills. Mercury is converted to highly toxic methylmercury and is biomagnified in the food web causing myriad deleterious effects, most notably on the nervous system (reviewed in Jaishankar et al., 2014). Though acidic precipitation has declined in the past several decades in many regions of the

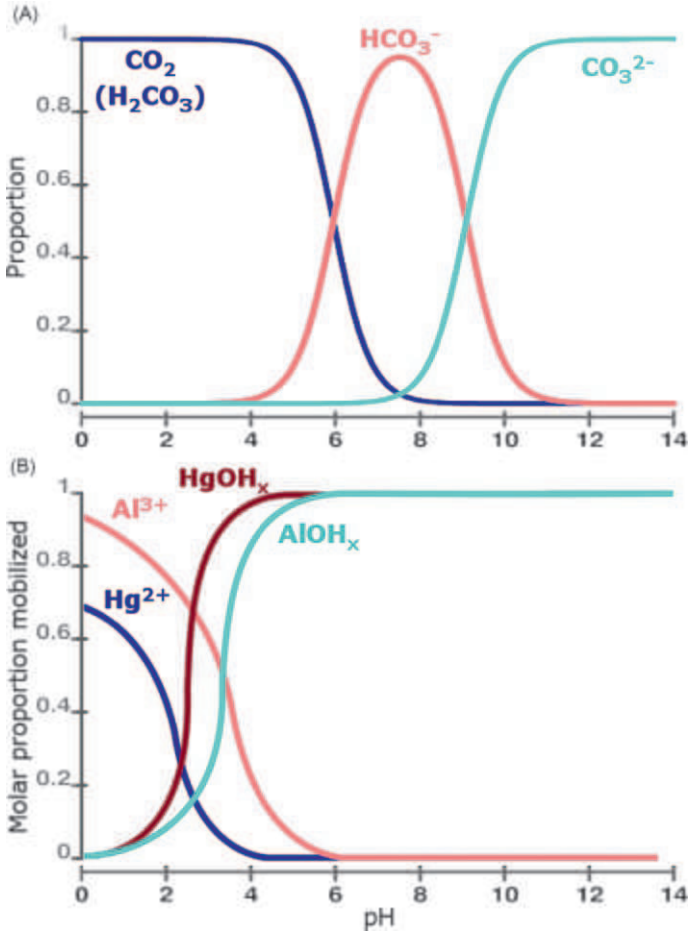

Fig. 10 (A) The bicarbonate buffer system showing the proportion of each dissolved inorganic carbon molecule in relation to pH. The buffer system resists changes in pH, but can be disrupted by excessive acidic pollution. (B) Metals (here, we illustrate Al^{3+} and Hg^2) are mobilized from sediments into more reactive, soluble forms at lower pH. As pH increase, these forms are converted to metal hydroxide forms, that can also be have deleterious effects on organisms. Other heavy metals (As, Cu, Cd, Pb, Zn) show similar patterns relative to pH. (A) Reproduced from Wetzel (2001) *Limnology: Lake and River Ecosystems*. 3rd edn. Academic Press: Sand Diego. (B) Reproduced from Sánchez España J (2007) The behavior of iron and aluminum in acid mine drainage: Speciation, mineralogy, and environmental significance. In: Letcher TM (ed.) *Thermodynamics, Solubility and Environmental Issues*. pp. 137–150, Elsevier: Amsterdam, ch. 7.; Cataldo S, Gianguzza A, Pettignano A and Villaescusa I (2013) Mercury(II) removal from aqueous solution by sorption onto alginate, pectate and polygalacturonate calcium gel beads. A kinetic and speciation based equilibrium study. *Reactive and Functional Polymers* **73**: 207–217.

world and there have been liming efforts to restore the pH of acidified streams (Lawrence et al., 2016), acidification is still an ongoing issue due to inputs from acid mine drainage.

$$CO_2 + H_2O \rightleftharpoons H_2CO_3 \rightleftharpoons H^+ + HCO_3^- \rightleftharpoons 2H^+ + CO_3^{2-} \quad (1)$$

Conclusion

Land-use and land-cover changes continue to strongly affect chemical, physical, and biological characteristics of water quality and represent a global threat to inland waters. The world's burgeoning human population relies on streams, rivers, wetlands, and lakes for the provisioning of multiple ecosystem services and functions that support human health, economic activity, and cultural and recreational practices. This dependence on water will only increase as the human population has grown exponentially over the past century and is expected to continue rising to 9.4–12.7 billion people by 2100 (United Nations, 2019). Over half the world's potable water supply is extracted from rivers (Barnett et al., 2005). Each hectare of land converted to human uses is one lost from its historic natural state. When excluding Antarctica, only 23% of terrestrial land has been unmodified by humans (Allan et al., 2017). River biodiversity is most threatened in landscapes with high agriculture and settlement pressure (Vörösmarty et al., 2010). Indeed, this dramatic reduction in natural habitat is also one of the main contributors to the ongoing sixth mass extinction event (Ceballos et al., 2020).

Here, we reviewed the effects that major anthropogenic LULC types have on inland waters worldwide, with a focus on rivers (Table 1). Human interactions with river catchments are complex and the natural connectivity among waterbodies can lead to far-reaching consequences of LUCC for downstream and downslope waters, including lakes, rivers, and coastal zones. For example, human alterations to headwater streams in the northeastern United States have led to reduced capacity of headwaters to remove nitrogen and to excess nutrient export to downstream waters such as coastal ecosystems (Schmadel et al., 2020). Impairment of aquatic ecosystems is also intimately tied to impairment of terrestrial environments and species. For example, impaired water quality has been linked to declines in species of aerial insectivorous birds across the United States (Manning and Sullivan, 2021) and some contaminants (e.g., mercury) can move from aquatic to terrestrial systems via food-web interactions (Sullivan and Rodewald, 2012).

Water quality is critical to human and ecosystem health, food production, and economic growth. Protecting water quality is, thus, is one of the principal challenges that humanity will face in the 21st century. Individuals to societies will need to be effective stewards of the water and other natural resources, with "beyond government" (i.e., collective governance with state and non-state actors working together) and transboundary (i.e., international teams working together to manage rivers and aquifers that cross borders) approaches increasingly viewed as part of the solution (Cosgrove and Loucks, 2015). Finally, risks to water quality from the interactions among LUCC, climate change, and other stressors will have to be predicted and appropriately managed in order for inland waters to continue to provide the ecosystem services needed for resilient and robust environments, communities, and economies.

Knowledge gaps

- Most of the research on LUCC and water quality comes from North America, Western Europe, Australia, and New Zealand. More research is needed in underrepresented regions like sub-Saharan Africa, South America, and Asia.
- The effects of many, individual anthropogenic stressors are well-studied, but the effects of their interactions have received less attention. Future research should focus on the interaction of multiple stressors to assess their combined effects and evaluate whether they are additive, synergistic, or antagonistic.
- Further integration, research, and monitoring of the physical, biological, *and* chemical components of water quality will be a critical step in long-term sustainability of inland aquatic ecosystems.
- Many solutions have been proposed and implemented to improve riparian ecosystems, but there is a need for long-term evaluation of the efficacy of restorations, policies, and regulations.
- Transdisciplinary approaches that combine both natural (e.g., ecology, toxicology, chemistry, hydrology) and social (e.g., sociology, human dimensions of natural resources, risk decision, etc.) sciences will be necessary effectively protect water quality (Table 2).

Table 2 Examples of recent river case studies addressing land use and their associated anthropogenic stressors.

Topic	*Site*	*Country*	*Coordinates*	*Description*	*Source type*	*References*
Sedimentation Nutrient enrichment Contaminants	Dongjiang River basin	China	22° 21′–25° 12′ N 113° 04′–115° 50′ E	Agricultural and urban land use affected chemical water quality, which impacted macroinvertebrates	NPS	Fu et al. (2016)
Nutrient enrichment	Jordan Lake basin	United States of America	36°45′–36°11′ N 78°56′–79°41′ W	Wastewater treatment plants and urban, but not agricultural, land use contributed most to river nutrient concentrations	NPS	Tasdighi et al. (2017)
Nutrient enrichment Contaminants	Yangtze River basin	China	24°27′–35°54′ N 90°33′–122°19′ E	Agricultural and urban land contributed nutrients and contaminants that negatively impacted chemical water quality	NPS	Xu et al. (2021)
Hydrologic alteration	Chattahoochee River below Buford Dam	United States of America	34°08′19.6″ N 84°05′19.2″ W	Dam hydropeaking altered flow regime and reduced macroinvertebrate functional diversity	PS	Ruhi et al. (2018)
Hydrologic alteration Geomorphic alteration	Shui Wai Nullah and Shan Pui River basins	Hong Kong	22°25′2.57″ N 114° 1′17.03″ E; 22°25′43.30″ N 113°59′40.65″ E	Channelization of urban streams and its effects on macroinvertebrates	PS	Gomes and Wai (2020)
Contaminants	Sacramento River	United States of America	42°′–38° N 123°–120° W	Pesticide mixtures impacted macroinvertebrate assemblages	NPS	Chiu et al. (2016)
Contaminants	Nent River basin	United Kingdom	54°48′53.6″ N 2°23′28.8″ W	Historical mining activities discharged heavy metal pollution into streams and rivers, which impacted macroinvertebrates	PS/NPS	Armitage et al. (2007)
Deforestation Sedimentation Hydrologic alteration	Be River	Vietnam	11°10′–12°16′N 106°36′–107°30′E	Deforestation led to hydrologic alteration and increased sedimentation in the Be river, which climate change exacerbated	NPS	Khoi and Suetsugi (2014)
Deforestation Geomorphic alteration Sedimentation	Rogativa River basin	Spain	38°10′09.9″N 2°13′15.7″W	Reforestation of previously deforested lands reduced erosion, sedimentation, and geomorphological alteration	NPS	Boix-Fayos et al. (2007)
Deforestation Hydrologic alteration	Upper Zagunao River basin	China	30°–33° N 102°–104° E	Timber harvesting increased runoff, but climate change reduce runoff	NPS	Zhang et al. (2012)
Disease	Belém and Barigui Rivers	Brazil	25°22′54.2″ S 49°14′54.6″ W; 25°24′58.3″ S 49°18′29.4″ W	Untreated wastewater effluent increased antibiotic resistant bacteria prevalence in rivers	PS	Böger et al. (2021)
Disease Nutrient enrichment Contaminants	River Nile	Egypt	24°07′05.14″ N 32° 53′50.33″ E	Wastewater effluent had nutrient, heavy metal, and pathogen contamination that decreased fish health	PS	Ali et al. (2015)

See Also: Structures and functions of Inland Waters - Rivers: Ecological Effects of Mining on Stream Ecosystems; Effects of Dams on Rivers; Inputs, Occurrence and Effects of Pharmaceuticals and Microplastics in Freshwater Ecosystems; The Nutrient Spiraling Concept; The River Continuum Concept; Urban Streams and Rivers

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Inputs, Occurrence and Effects of Pharmaceuticals and Microplastics in Freshwater Ecosystems

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Biosolid Solid waste in wastewater treatment facilities. These solids contain residues of pharmaceuticals, personal care products and microplastics.

Microplastic small particles (<5 mm) of plastics that are either designed to be small or are the result of the breakdown of larger plastic particles.

Pharmaceutical Compounds used as prescription and over the counter medications. Use, adoption and regulation of pharmaceuticals can vary by country.

Personal Care Product Compounds that are used in everyday lives such as detergents, skincare products, fragrances, cosmetics, insect repellants, etc.

EcoDC - Ecologically disrupting compound A compound or contaminant, typically a pharmaceutical, that may not be toxic at concentrations present in the environment, but has the capacity to elicit non-lethal effect on organism behavior, ecological processes and functions (Please see Richmond et al. 2017 for further details).

Freshwater ecosystems, especially rivers and lakes, have been exposed to pollution since the earliest human settlements, which were often located near these freshwater ecosystems as they provide drinking water, transportation, hydropower, and waste disposal. The contamination of freshwater ecosystems with a range of pollutants, including human waste, industrial chemicals, and agricultural chemicals, has been studied for decades. More recently, a field of research has developed that focuses on novel pollutants of emerging concern within freshwaters. This class of pollutants includes a wide array of compounds such as pharmaceuticals, including prescription and over-the-counter drugs, personal care products, and microplastics (i.e., particles 1 μm–5 mm), among others. Personal care products include products such as antiseptics, cleansers, skin care products, detergents, insect repellants, fragrances, etc. Many pollutants of emerging concern are found as ingredients in consumer products and many are synthetic chemicals. Synthetic chemicals include a diversity of chemical structures and their increasing variety, global use, and potential biological effects contribute to the recent categorization of synthetic chemicals as agents of global change (Bernhardt et al., 2017). Pharmaceuticals, personal care products, and microplastics are pollutants of emerging concern that are typically discussed together because they enter the environment through normal use of consumer products and thus they are commonly found together when human wastes are discharged into freshwater ecosystems. For this reason, in this chapter we will discuss these pollutants together; however, it should be noted that there are over 3000 pharmaceuticals on the global market today, and microplastics are composed of many different types of polymers and can include a wide variety of chemical additives. Therefore, although these pollutants will be discussed together, their behavior, transformations, fate, and effects on the environment may vary widely.

The sources of novel pollutants such as pharmaceuticals, personal care products, and microplastics to the environment are numerous. At each step in their life cycle (from synthesis to human use and disposal), some fraction may be released into the environment, so exploration of these life cycles can shed light on release dynamics.

Sources and fates of pharmaceuticals and personal care products

Pharmaceuticals and personal care products (PPCPs) are created at manufacturing facilities, and release from these facilities represents a significant source of pollution that is often not regulated. Such releases may occur throughout the world wherever these compounds are produced. In the US for example, some manufacturing facilities are located adjacent to rivers, which subsequently receive discharge from pharmaceutical manufacturing facilities, creating hotspots of pharmaceutical contamination (Scott et al., 2018).

Once sold, PPCPs are used in the day-to-day lives of people and animals, including livestock and pets. PPCPs that are ingested can be metabolized within the body, but many are excreted or egested in urine and feces either entirely or as some fraction of the ingested amount. There is also a large suite of PPCPs that are designed to be used topically in humans or other animals (e.g., antiseptics, sunscreens, insect repellents, analgesics, fungal medications, shampoos, and detergents). After use, these compounds can be released unchanged into wastewater (e.g., via bathing). Some classes of drugs, especially antibiotics, are given to animals in large amounts in confined animal feeding operations (e.g., cows, chickens, and pigs) and to household pets. For example, over two thirds of the medically important antibiotics (for human disease) in the US are used in animal feeding operations (Patel et al., 2020). Antibiotics used in animal agriculture can be readily measured in manure. If livestock manure from animal feeding operations is applied to land for use as fertilizer, as is common, the associated pharmaceuticals can enter the environment and nearby freshwater ecosystems.

The fate of human sewage is also directly related to the fate of PPCPs and their entry into freshwater ecosystems. Direct release of sewage, both through the lack of infrastructure, combined sewer overflows, and leaking of waste from old infrastructure, is a common pathway through which these compounds enter freshwater ecosystems. For sewage that is treated prior to release, the ability of wastewater treatment processes to remove PPCPs varies widely, depending on the specific compound and the specific treatment processes. The incomplete removal of PPCPs by onsite (e.g., septic systems) or centralized wastewater treatment facilities can lead to discharge into freshwater ecosystems through the release of treated effluent. A rich literature exploring the concentrations of PPCPs downstream of wastewater treatment plants and how various treatment technologies mitigate discharges is now available. There is also evidence that in rural areas septic systems are a source of PPCPs to freshwater ecosystems. In addition to the liquid effluent released by wastewater treatment facilities, the solid portion of the wastes (known as sludge or biosolids) may also contain a wide diversity of PPCPs (McClellan and Halden, 2010). The fate of biosolids then provides an additional route for entry of PPCPs into the environment. In the United States, for example, municipal biosolids are applied to land to be used as a fertilizer, disposed of in landfills, or incinerated. Land application of biosolids can be a route by which PPCPs enter the environment as they desorb from the solid materials and potentially enter freshwater ecosystems.

It is also important to note that most human sewage generated around the world is not treated. The World Health Organization (WHO) estimates that more than 80% of human sewage, globally, is discharged untreated to the environment (https://www.unwater.org/water-facts/quality-and-wastewater/). Therefore, although concentrations of pollutants of emerging concern vary depending on the degree of treatment and the specific compounds, many of these compounds are likely discharged, unchanged, into the environment throughout the world and may pose a threat to the health of aquatic ecosystems.

Sources and fates of microplastics

The same principle of exploring the life cycle of a potential pollutant applies to the movement of microplastics to freshwater systems; however, due to their particulate nature, microplastics can enter freshwater systems through a greater variety of pathways than PPCPs, which are typically dissolved in water. Microplastics are categorized as either 'primary', which are particles designed to be small (e.g., 'virgin' plastic pellets or microbeads), or 'secondary', which are particles generated when larger plastic items break apart. Key sources of microplastics in the environment include sewer systems, solid waste management, and direct littering into the environment (Hoellein and Rochman, 2021) (Fig. 1).

Plastics are a ubiquitous part of our everyday lives, thus a major pathway for primary and secondary microplastics to freshwater ecosystems is human sewage (Carr et al., 2016) or brown water discharges. For example, laundry can be a major source of microplastic fibers. As polyester clothes are washed, a fraction of the material ends up as loose fibers in the washing machine water and is discharged with household sewage (Napper and Thompson, 2016). Again, depending on both the sewage treatment process in place and the fate of the biosolids, microplastics can be discharged to the environment directly via direct release of sewage, treated wastewater effluent, land application of biosolids from wastewater treatment plants, or septic systems (Carr et al., 2016; Crossman et al., 2020). In wastewater, plastic may interact with PPCPs and other chemical contaminants, as some plastic surfaces attract chemical pollutants, causing chemicals to sorb onto the plastic.

Another route of entry to the environment that both PPCPs and microplastics share is via solid waste management (i.e., trash). The fate of PPCPs and microplastics depends on how solid wastes are processed in any given area. Some plastics might be recycled, although plastic recycling rates are relatively low at a global scale (Geyer et al., 2017). In municipal landfills, some PPCPs and microplastics in solid waste may enter the environment if there are leaks in the landfill structure. If the solid waste is incinerated, the PPCPs and microplastics associated will be incinerated as well. Landfills and incineration may represent a permanent sink for microplastics, however, some portion of the plastic litter will be converted into smaller microplastics, as well as greenhouse gases via combustion, UV oxidation, or biodegradation (Gewert et al., 2015). Finally, solid waste may be shipped among countries (often to developing nations) as a form of solid waste management, including microplastic and associated PPCPs.

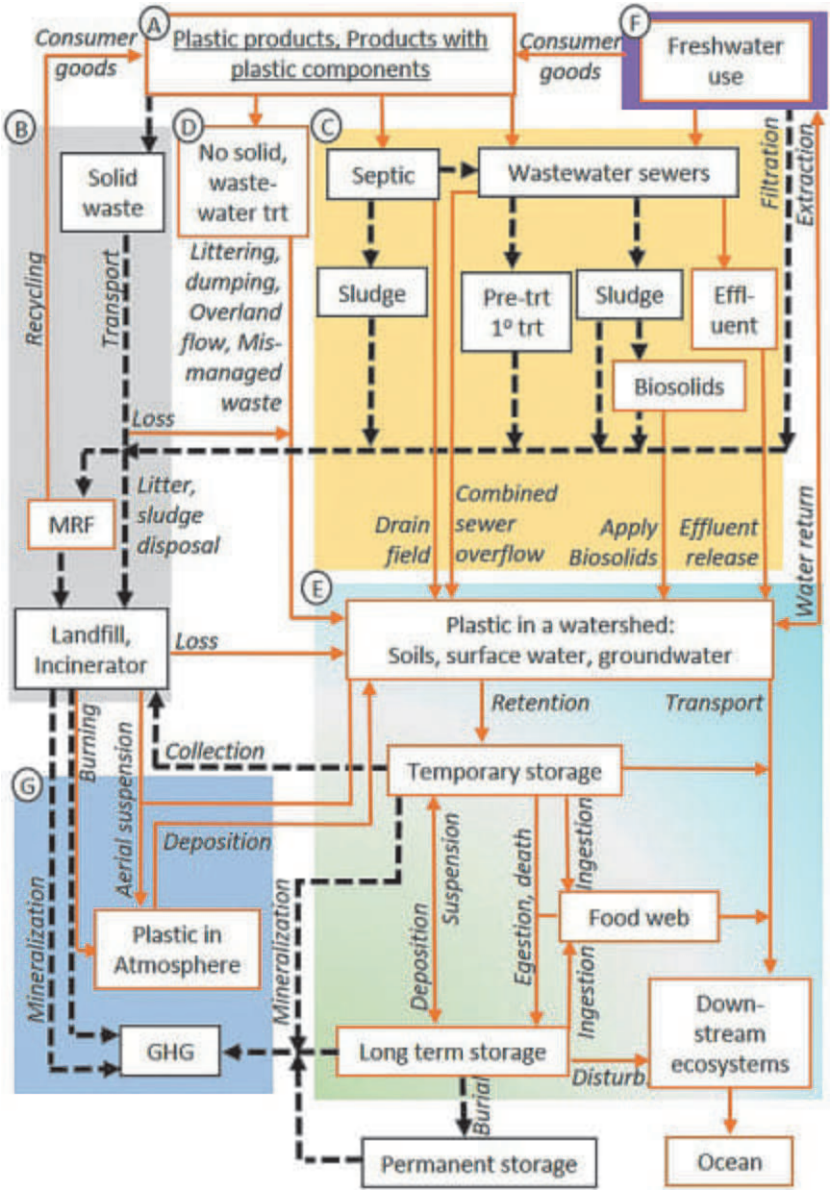

Fig. 1 Conceptual model of the plastic cycle at the watershed scale, including pools (rectangles) and fluxes (arrows). Dashed black lines indicate pathways toward waste containment, storage, or greenhouse gases (GHGs). Solid orange lines show fluxes that represent movement of plastic among pools. Letters A–G correspond to each section of the paper that discusses that portion of the figure, and each letter is placed on a rectangle to coalesce major pools of plastic for a watershed budget. (A) in-use consumer goods; (B) solid waste management; (C) wastewater management; (D) direct littering and mismanaged waste (litter that does not enter solid waste collection or wastewater treatment); (E) watershed litter; (F) freshwater use; and (G) the atmosphere. *MRF*: materials recovery or recycling facility; *trt*: treatment; *Disturb*: disturbance. From Hoellein TJ and Rochman CM (2021) The "plastic cycle": A watershed-scale model of plastic pools and fluxes. *Frontiers in Ecology and the Environment* 19:176–183.

The last major source of plastic litter to the environment is direct littering. In communities without access to solid waste or wastewater management, littering is an informal management process (i.e., dumps, ditches, rivers), however, littering also occurs where waste management is available and can be a major source of plastic litter locally (Vincent et al., 2017). Secondary microplastics are generated from plastic litter once it enters the environment, when larger plastic litter items break down through abrasion, sunlight (UV oxidation), or biodegradation (Gewert et al., 2015).

PPCPs and microplastics in the environment

Once in the environment (via solid waste, wastewater, or littering), PPCPs and microplastics are readily moved throughout the world. Fig. 2 illustrates the microplastic cycle in the environment with pools and fluxes such as deposition from the atmosphere and

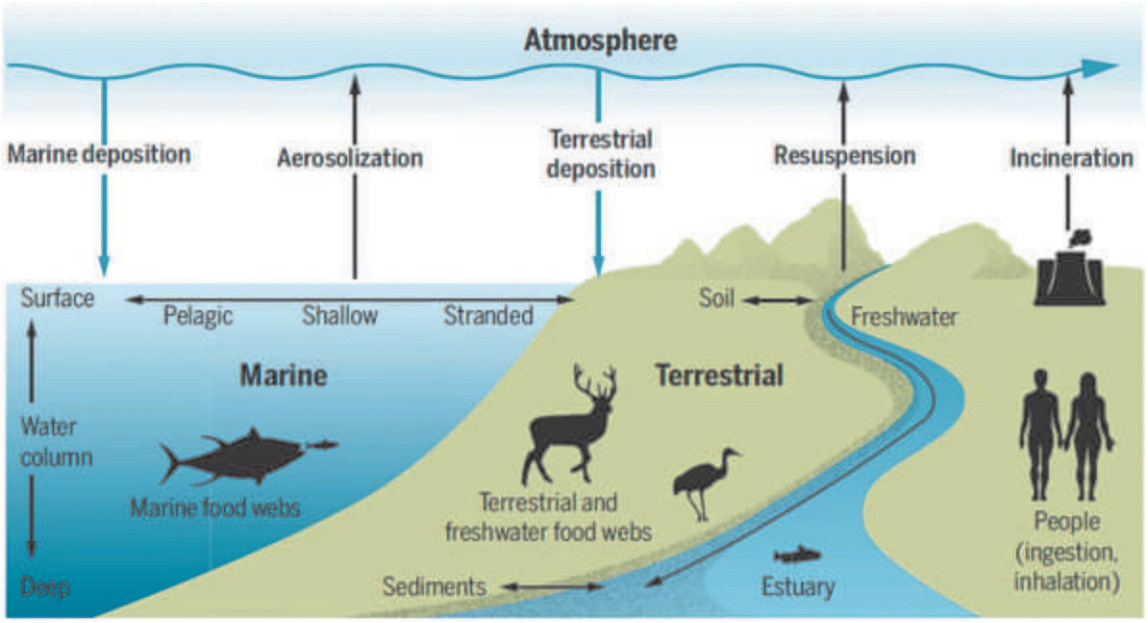

Fig. 2 Microplastic pollution is pervasive. Emerging research pinpoints atmospheric deposition as a mode of microplastic transfer. Mapping microplastic pools (water, land, organisms) and fluxes (arrows) will guide delineation of the global microplastic cycle. From Rochman CM and Hoellein T (2020) The global odyssey of plastic pollution. *Science* 368:1184–1185.

transfer along river corridors, including continual deposition and resuspension accompanied by downstream transfer (Rochman and Hoellein, 2020).

For both PPCPs and microplastics, there continue to be advances in measuring their concentrations in freshwater ecosystems. The challenge has been detecting very low concentrations of PPCPs and collecting and identifying very small plastic particles, including microplastics (<5 mm) and nanoplastics (<1 μm). New methods have revealed some surprising findings, such as detection of PPCPs associated with tourism in US National Parks (Weissinger et al., 2018), in Antarctica (González-Alonso et al., 2017) and in the Alps (Mandaric et al., 2017), and detection of microplastics in Arctic sea ice (Peeken et al., 2018) and in atmospheric deposition in the Pyrenees in France (Allen et al., 2019). Research into the movement of plastic particles through the environment in particular is in its infancy, and the case has been made that much more research exploring these pathways is needed (Rochman and Hoellein, 2020). With respect to freshwater systems, it is important to understand that the sources and fate of PPCPs and microplastics may be varied across the landscape. For example, in urban areas below wastewater treatment plants, the concentrations of PPCPs and microplastics may be high and consistent over time, but in urban streams affected by leaking infrastructure concentrations of PPCPs are highly variable from week to week (Fork et al., 2021). The same is true for rural areas where concentrations of these compounds maybe variable in space and time. Evidence is mounting that there are few places left on earth where these compounds are not detectable in freshwater ecosystems, albeit at low concentrations.

The types of pharmaceuticals detected in freshwater ecosystems represent a wide range of compounds. For the past two decades, most of the information available has been the concentrations of pharmaceuticals and personal care products (PPCPs) in solution in surface waters. In general, if a compound is regularly used by the human population and the compound is relatively persistent, on the order of days to years, it has been detected in the environment, provided there are analytical methods to screen for it. The first detection methods were developed using liquid chromatography combined with mass spectrometry (LCMS). Continual methodological advancement is allowing increasingly more compounds to be investigated. Indeed, non-target analytical approaches are now being proposed as a means for understanding the wide range of synthetic chemicals found in the environment (Singer et al., 2016). In recent years, techniques have expanded to include detection of PPCP compounds in sediments and organisms, including animal tissues. In both cases, sediments and biota tend to have much higher concentrations of PPCPs (Richmond et al., 2018) than are dissolved in water. Moreover, information on the concentrations of PPCPs in biological samples is crucial for understanding their potential to move through food webs via trophic transfer, similar to what has been found for legacy pollutants such as PCBs and DDT. At the time of writing this chapter, our understanding of PPCPs in food webs is limited to a handful of studies, but these suggest that this route may be an important aspect of environmental risk.

In contrast to PPCPs, our measurement of microplastics in the environment has only emerged in the last 10 years. Microplastics are also a highly diverse suite of materials (Rochman et al., 2019). Plastic is a catch-all term for many polymers (e.g., polyethylene, polyvinyl chloride, and synthetic rubber) and plastics are mainly manufactured from petroleum products. The polymer represents the 'skeleton' of a plastic product, but there is also a diverse array of chemical additives embedded within the polymer 'bones' during production. Additives offer properties such as heat resistance, flexibility, and color, and may be leached from plastic litter once in the environment. Some microplastics are semi-synthetic, and consist of mixtures of plastic and other materials. For example, a single microplastic fiber may contain a combination of polyester and cotton. Finally, microplastics are found in a variety sizes

(1–5000 μm) and shapes, such as beads, fragments, and fibers. Techniques for measuring microplastics often involve separating particles from the natural matrix (water, sediment, tissue), and using microscopy to count and measure the particles. Additional analyses (e.g. FTIR) are needed to identify the chemical composition of the plastic polymers.

Ecological effects of PPCPs

In the past 20 years, as the analytical capacity to measure pharmaceuticals and personal care products has increased, the number of studies documenting their occurrence and concentrations has increased in tandem. The first US nationwide survey was published in 2002 by a group of scientists at the United States Geological Survey (Kolpin et al., 2002). This study focused on rivers below wastewater treatment plants in larger cities and detected numerous PPCPs in river water. Since that time, the research on this topic has expanded to include sampling of freshwater ecosystems throughout the world, as well as groundwaters, sediments, and the tissues of insects, fishes, and spiders. Moreover, the number of compounds that have been detected in any given place continues to grow. This suggests that more research is needed to understand the effects of complex mixtures of compounds on biological and ecological endpoints. For example, it is known that drugs can interact in the human body in significantly deleterious ways and drugs are prescribed with drug interactions in mind. In contrast, in the environment, much less is known about how complex mixtures of drugs may interact to affect non-target organisms.

Since the discovery that PPCPs can be detected in surface waters, researchers have investigated whether they also have toxicological and ecological effects on aquatic organisms and ecological processes (Rosi-Marshall and Royer, 2012). The research on this topic has been increasing over the past decade. Much of the work investigating the potential effects of pharmaceuticals and personal care products has used ecotoxicological approaches such as studies of the concentrations needed to result in mortality of aquatic animals. Less work has been done to investigate the ecological effects of these compounds, but as seen in Fig. 3, this work is occurring and expanding our understanding of the potential of these compounds to affect aquatic organisms (Richmond et al., 2017).

Combined with their ubiquity, PPCPs are of particular environmental interest because of their potential to have a biological effect on non-target organisms. Many PPCPs, especially very potent pharmaceuticals, are used in the everyday lives of humans precisely because of their ability to alter biological processes. For example, antibiotics are used to disrupt bacterial growth associated with an infection, and insect repellents are used because they are noxious to insect pests. However, once these compounds are released to the environment, their biological activity does not simply cease to occur. Therefore, these compounds have the potential to disrupt non-target organisms and ecological processes, and for this reason Richmond et al. (2017) made the case that PPCPs should be viewed as ecologically disrupting chemicals.

Recent research has demonstrated that PPCPs at concentrations that have been detected in the environment can disrupt microbial community structure and functions. For example, research has shown that a wide variety of pharmaceuticals can alter algal community structure (Lee et al., 2016; Robson et al., 2020) and the rates of photosynthesis of algal biofilms, e.g., communities of algae and bacteria that grow on solid surfaces in freshwater ecosystems (Rosi-Marshall et al., 2013; Lee et al., 2016; Gallagher and Reisinger, 2020). Moreover, bacterial community structure and function are sensitive to exposure to pharmaceuticals. For example, exposure to the generalized antimicrobial triclosan significantly altered bacterial composition and the proportion of triclosan resistant microbes in a mesocosm study (Drury et al., 2013). An *in situ* experiment comparing the effects of nutrients and drugs on stream biofilms found that increased nutrients led to dominance by a few microbial taxa, whereas pharmaceuticals led to increased richness of microbial taxa (Ogata et al., 2020). There is mounting evidence that a wide variety of PPCPs can influence both the structure and function of bacterial communities (e.g. Rosi-Marshall et al., 2013; Corcoll et al., 2015; Rosi et al., 2017; Robson et al., 2020).

PPCPs have also been shown to affect aquatic animals, even at very low concentrations. The effects of these compounds are highly variable among compounds and the effects represent a wide suite of consequences for animals that are exposed. For example, the insect repellent picaridin caused significant deformities and mortality for salamander larvae (Almeida et al., 2018). A variety of pharmaceuticals have been shown to affect aquatic insect life history patterns such as rates of larval growth and timing of adult insect emergence (Hoppe et al., 2012; Lee et al., 2016; Richmond et al., 2016, 2019). Exposure to illicit drugs significantly altered the oxidative status of zebra mussels, which is indicative of the health of these animals (Parolini et al., 2015). The drug oxazepam significantly altered the feeding behavior and activity levels of European perch, at concentrations found in nature (Brodin et al., 2013). Additional studies continue to demonstrate the effects of numerous drugs on the behavior of aquatic animals (e.g. Jonsson et al., 2014; Reisinger et al., 2021).

As analytical approaches for measuring pharmaceutical concentrations in animal tissues have advanced, recent work demonstrates that pharmaceuticals are accumulating in aquatic animals (Lagesson et al., 2016; Ruhí et al., 2016; Richmond et al., 2018). Fig. 4 illustrates the diversity of drug compounds that were detected in aquatic animals collected from below a wastewater treatment plant in Melbourne, Australia (Richmond et al., 2018). These studies demonstrate that intake of PPCPs via both water and transfer within the food web are likely, and further, PPCPs may be transferred to terrestrial animals that prey on larval or flying aquatic insects, such as riparian spiders, birds, and bats (Richmond et al., 2018). There is also the potential that aquatic animals could serve as an important biomonitoring tool to explore human use of illicit drugs or pesticides (Miller et al., 2019). Recent research also demonstrates that some pharmaceuticals can disrupt aquatic animals' perceptions of their surroundings via chemical signals. For example, it has been demonstrated that drugs disrupt the "smell-scape" by disrupting detection of some compounds and mimicking other compounds. This disruption may have numerous consequences for mating behavior, prey detection, and other species

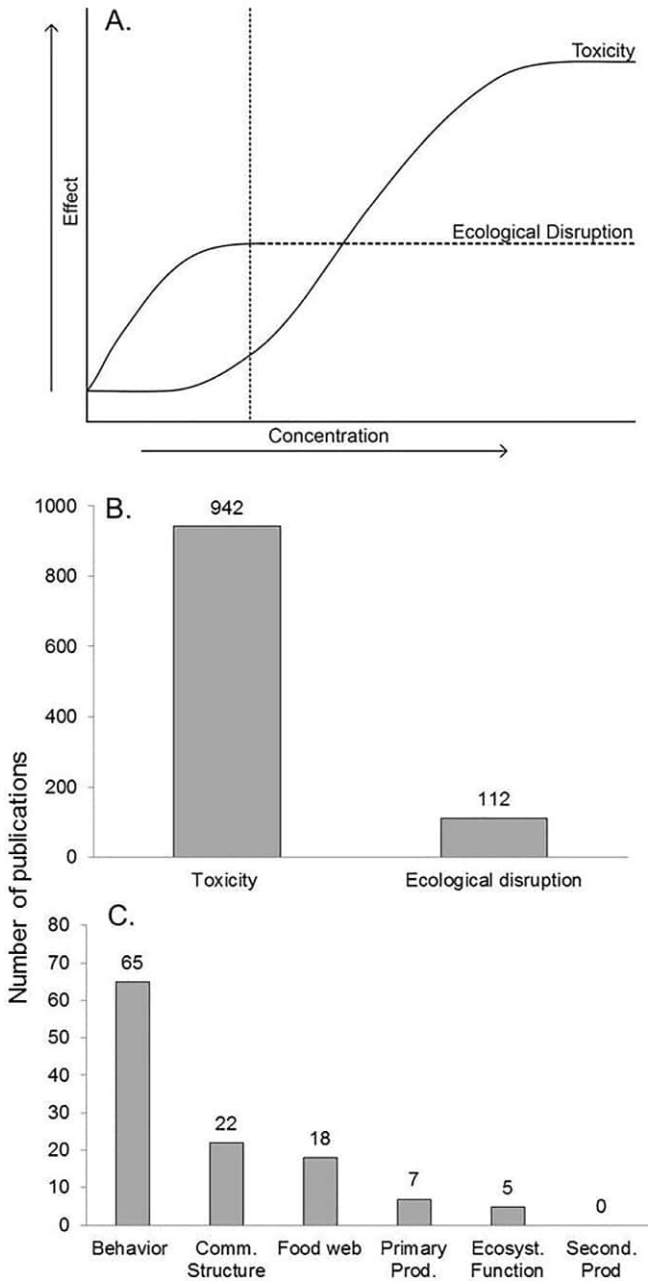

Fig. 3 PPCPs as EcoDCs influence aquatic ecosystem function and biota. (A) Conceptual figure demonstrating the potential non-lethal effects of EcoDCs at low concentrations on aquatic biota and ecosystem function, in contrast to toxic effects observed at high concentrations. The dashed horizontal line at the end of this curve represents uncertainty at high PPCP concentrations. The dashed vertical line indicated where lethality is becoming increasingly important relative to ecosystem disruption. (B) Number of publications indexed in Web of Science measuring toxic endpoints (including LC50 and EC50 toxicity testing) versus those measuring non-lethal, ecological disruption (EcoD) endpoints at environmentally relevant concentrations. (C) Number of publications in Web of Science demonstrating various endpoints related to ecosystem disruption associated with environmentally relevant concentrations of PPCPs. Details of literature search are available in supplementary material. From Richmond EK, Grace MR, Kelly JJ, Reisinger AJ, Rosi EJ, and Walters DM (2017) Pharmaceuticals and personal care products (PPCPs) are ecological disrupting compounds (EcoDC). *Elementa* 5:66, doi:10.1525/elementa.252.

interactions in aquatic food webs (Van Donk et al., 2016). Moreover, there has been a particular focus on the effects of pharmaceuticals on wildlife and growing concern about the general phenomenon of medicating wildlife (see Arnold et al., 2014).

Considerations about the environmental risk of PPCPs and microplastics pose to freshwaters

A few important general principles have been identified with respect to PPCPs. The first is that these compounds can be considered pseudo-persistent (Daughton and Ternes, 1999). This means that although some of these compounds degrade quickly in the environment, because they are continually released or resupplied from various sources, their presence "persists." For example,

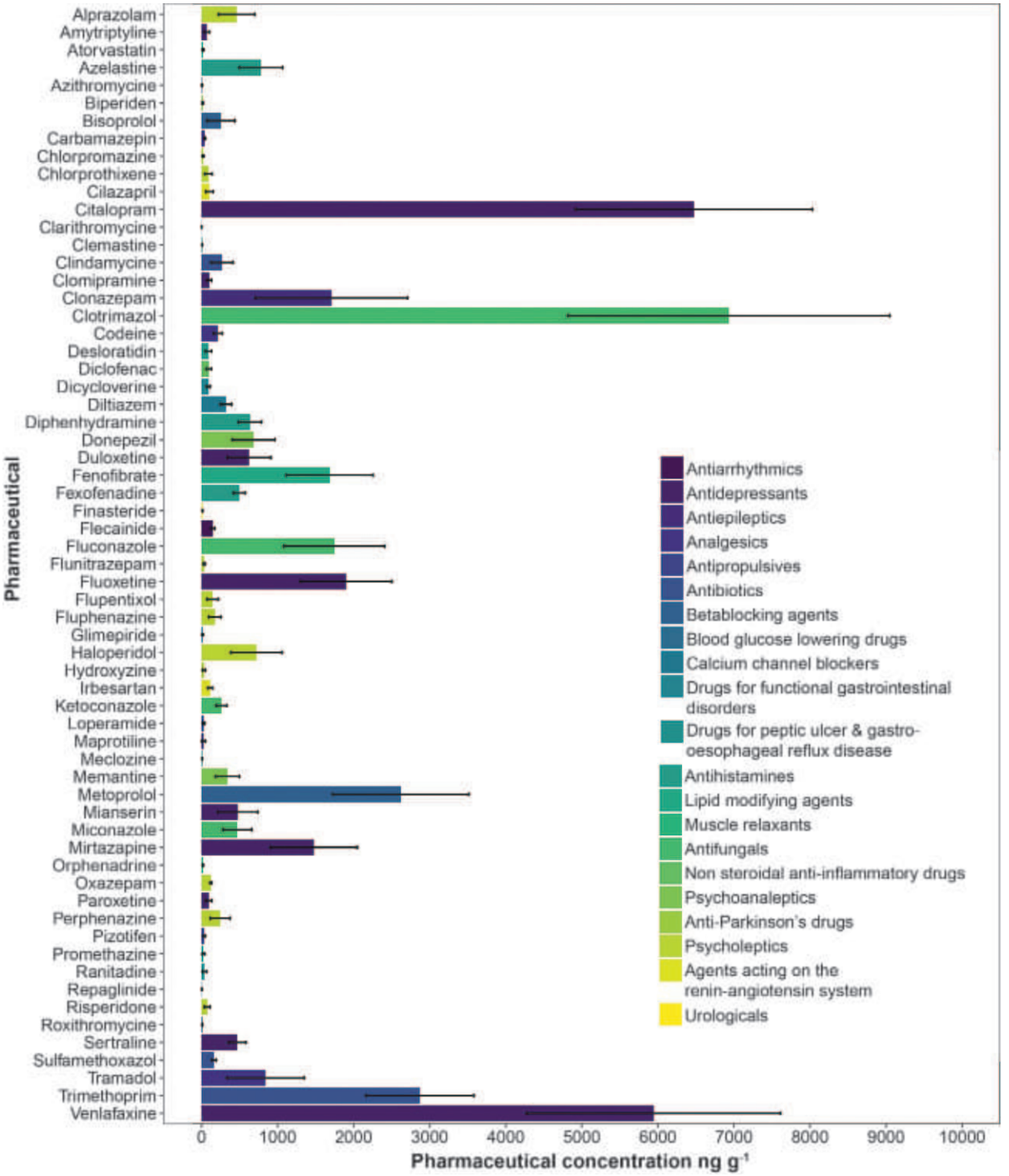

Fig. 4 Pharmaceutical concentrations in caddisfly larvae. Mean pharmaceutical concentrations (ng g^{-1} dry weight ± 1 SE) in caddisfly larvae(Hydropsychidae) ($n = 6$) at wastewater-influenced Brushy Creek. Each bar represents the mean concentration of a pharmaceutical compound in the six individuals collected over two sampling dates. Colors represent therapeutic drug classes. From Richmond EK, Rosi EJ, Walters DM, Fick J, Hamilton SK, Brodin T, Sundelin A, and Grace MR (2018) A diverse suite of pharmaceuticals contaminates stream and riparian food webs. *Nature Communications* 9:4491.

caffeine is readily degraded by microbes and yet it is consistently found in the environment because so many people use this compound in their daily lives. The second important characteristic of these compounds is their role as endocrine disruptors. For example, it has been shown that a number of these compounds can disrupt important endocrine systems in animals leading to problems such as increasing frequency of intersex animals or altered sex ratios in animal populations, both of which have been

shown to have negative consequences for reproduction and long-term population dynamics. For example, the active ingredient in human birth control medication can influence the sex ratios and population dynamics of fishes. When experimentally added to a lake in environmentally realistic concentrations, the active birth control ingredient led to altered sex ratios and population decline of fathead minnow (*Pimephales promelas*) populations (Kidd et al., 2007). Third, there is increasing evidence that PPCPs can lead to ecological disruption (e.g., see Fig. 3) at concentrations lower than those that cause mortality as measured by traditional ecotoxicological approaches. These compounds may disrupt ecological interactions, community structure and/or ecosystem functions. Fourth, there is an increasing need to consider the effects of mixtures and interactions among drugs when investigating the effects of these compounds. Numerous studies demonstrate that a wide variety of compounds can be present in the environment and it is known that drugs interact with each other. Although it is challenging to generalize about such a broad class of compounds, research has demonstrated that, for example, antibiotics disrupt certain members of stream bacterial communities, fungicides disrupt fungal communities, and antidepressants and stimulants can alter algal communities, the life cycles of aquatic insects, and fish behavior, as presented above.

The effects of microplastics on freshwater ecosystems has been very recently emerging as a field of research (Horton et al., 2017; Li et al., 2020). Key ecological dynamics of microplastics in the environment include its movement in the environment, effects on microbial habitat, chemical interactions, ingestion and use by aquatic animals in case building. Plastic particles move through streams and rivers in a fashion similar to natural particles (Fig. 5), so their movement in the environment is akin to naturally occurring particles (Windsor et al., 2019). Microplastics accumulate in stream sediments with fine particulate organic matter (Vincent and Hoellein, 2021), suggesting that organisms that feed on fine particles may be targets for assessing ecological impacts. Plastic surfaces select for very different microbial communities than natural substrates found in the same habitats (McCormick et al., 2016; Harrison et al., 2017). Moreover, the plastic particles harbored a larger proportion of gastrointestinal microbes (e.g., human pathogens) and microbes that may actually degrade the plastic polymers.

Microplastics also interact with chemicals in aquatic ecosystems, including leaching of plastic additive compounds from microplastics to the environment, and sorption of additional pollutants from the environment onto microplastics. Microplastics have especially high capacity to adsorb organic compounds due to their high surface area and hydrophobicity. Consumption of microplastics by aquatic organisms is widespread in aquatic ecosystems and the known effects include a range of ecotoxicological responses including mortality, reproduction, neurotoxicity, and a range of physiological and behavioral effects (see review by de Sá et al., 2018). Microplastics may pass through an animal's gut with no effects, although the presence of plastic in the gut may cause calorie deficits or starvation if microplastics cause animals to feel satiated or microplastics may create intestinal blockage. In addition, compounds adsorbed or embedded within microplastics may pose a threat to animals after ingestion (Foley et al., 2018). Finally, in experimental conditions, macroinvertebrates incorporate microplastics into their cases and incorporation of microplastics destabilized the cases, suggesting an additional threat these compounds may pose to aquatic organisms (Ehlers et al., 2020).

A significant research challenge posed by pollutants of emerging concern such as PPCPs and microplastics is the sheer number of compounds potentially present in aquatic ecosystems. In the United States, for example, the number of pharmaceuticals approved for sale is in the thousands of compounds. Moreover, this does not include the myriad personal care products such as cosmetics, detergents, fragrances, sunscreens, insect repellants, etc. that are used in everyday life. Aquatic ecosystems can have upwards of 500 different compounds (Bradley et al., 2017) with potential varying biological effects. Thus, the ecological consequences will likely be complex and varied, including possible disruption at multiple trophic levels and alterations of ecological interactions and dynamics. For example, a recent study found 69 different compounds, from many different drug classes, in the tissues of caddisflies downstream of a wastewater treatment plant (Fig. 4, Richmond et al., 2018). Recent work has investigated the interactions of PPCPs with other ecological variables such as after a drought (Corcoll et al., 2015) or in response to varying degrees of canopy cover

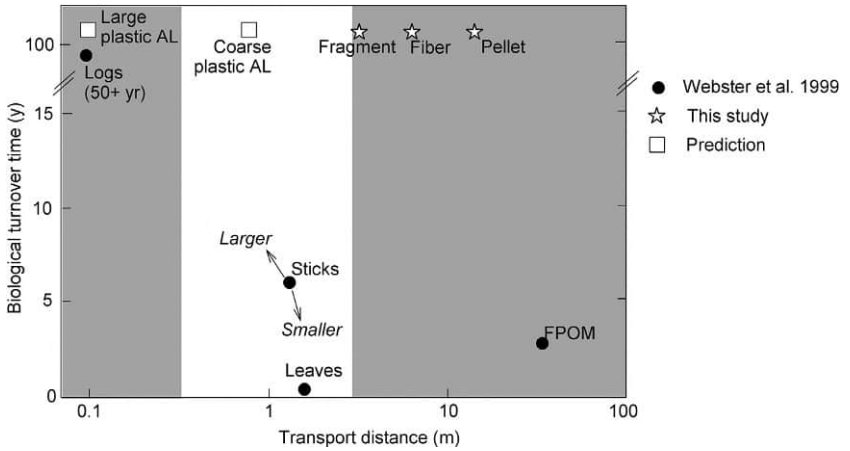

Fig. 5 Transport distance and biological turnover time for naturally occurring allochthonous carbon including leaves, sticks, fine particulate organic matter (FPOM) and wood, originally synthesized in Webster et al. (1999). We added to this diagram by including direct measurements of transport distance for microplastic particles (i.e., fragment, pellet, and fibers), and an estimate of biological turnover time. We also included predictions of transport distance for coarse plastic anthropogenic litter (AL, i.e., shopping bags, bottles, and food wrappers), and large plastic AL (i.e., construction debris, shopping carts). From Hoellein TJ, Shogren AJ, Tank JL, Risteca P, and Kelly JJ (2019) Microplastic deposition velocity in streams follows patterns for naturally occurring allochthonous particles. *Scientific Reports* 9(1): 3740.

(Robson et al., 2020). It has also been shown that the degree of urbanization and the exposure to nutrients influences the effects of pharmaceuticals on algal and bacterial communities (Rosi et al., 2017). We do not yet understand how drugs may interact to potentially pose a threat to aquatic animals. The effects of these compounds are often studied piecemeal, and thus the complexity of effects that may result are both hard to measure empirically, challenging to predict, and extremely challenging to regulate (Kortenkamp and Faust, 2018). Similarly, microplastics are also a complex mixture of chemical types that may have distinct influences on aquatic ecosystems, yet the effects of different types of polymers, plastic additives, and their interactions with other pollutants is yet to be studied and represents a research frontier (Foley et al., 2018). For example, because PPCPs and microplastics share many routes of entry into aquatic ecosystems, there is ample opportunity for these pollutants to interact, e.g. via adsorption of PPCPs to microplastic surfaces, which could have significant implications for the fate, transport, and biological interactions of both of these pollutant types.

Conclusion

A wide variety of pharmaceuticals and personal care products and microplastics are present in aquatic ecosystems around the world. Understanding the effects of these novel compounds and particles represents a significant frontier in freshwater science. In addition, there are many opportunities for researchers to explore the interactions among these novel pollutants and the many types of environmental contexts in which they occur. More research in this area will continue to shed light on the role of these compounds in aquatic ecosystems of the Anthropocene.

Knowledge gaps

- What are the concentrations of PPCPs and microplastics and how do they vary in space and time?
- How persistent are these compounds in different aquatic environments and geographical locations?
- What are the concentrations in food webs both aquatic and terrestrial (e.g. birds, bats, lizards)? What trophic levels are most at risk?
- What are the effects of these pollutants on whole ecosystem processes?
- How do PPCPs and microplastics interact with each other and other stressors like road salt, nutrients, invasive species, climate change, etc.?
- How sensitive are different organisms to PPCPs and microplastics?
- How can we assess the effects of complex mixtures of novel pollutants?
- What are the most effective management and regulation strategies?
- How can we reduce the sources of these pollutants or improve design to reduce inputs?
- Can we make PPCPs and microplastics more biodegradable?
- Are there human health risks when freshwater systems and food webs are contaminated?

Important case studies

Study Site	*Country*	*Main Topic*	*References*
Experimental Lakes Area	Canada	Effects of human birth control medication on fish populations in a whole lake experiment	Kidd et al. (2007)
Streams	Melbourne, Australia	Concentrations of pharmaceuticals in stream food webs	Richmond et al. (2018)
Streams	Various locations, United States	Effects of drugs, land use and nutrients on stream biofilms structure and function	Rosi-Marshall et al. (2013) Rosi et al. (2017) Ogata et al. (2020)
Streams	Illinois, United States	Microplastics source, transport, and fate and microbial communities in association with wastewater	Kelly et al. (2020) Hoellein et al. (2019) Hoellein et al. (2017) McCormick et al. (2016)
Mesocosms	Sweden	Effects of oxazepam on fish behavior	Brodin et al. (2013)
Rivers	Tributaries of Lake Michigan, United States	Microplastic ingestion by fishes is linked to species traits	McNeish et al. (2018)
Meta-analysis	Multiple sites	Meta-analysis exploring the effects of microplastics effects on invertebrates and fishes	Foley et al. (2018)
Drinking water	Multiple Site	Analysis of microplastics in drinking water	Danopoulos et al. (2020)
Urban area	Paris, France	An analysis of microplastics in an urban area	Dris et al. (2018)
Biosolid applications	Canada	Microplastics in biosolid applications	Crossman et al. (2020)
Pyrennes Mountains	France	Atmospheric deposition of microplastics	Allen et al. (2019)

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Relevant websites

https://www.unenvironment.org/resources/report/microplastics—UN Environment Program.
https://www.youtube.com/watch?time_continue=211&v=MTbqrfewuKY&feature=emb_logo—PNW Consortium on Plastics.

Multiple Stressors in Streams

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Additive stressor effect Multiple stressors affect the receptor, with the overall effect being equal to the effect sum of single stressors.

Antagonism The overall multiple stressor effect is smaller than the effect sum of single stressors.

Dominant stressor effect Only one of the multiple stressors affects the receptor despite distinct presence of both stressors.

Interactive stressor effect Multiple stressors affect the receptor, with the overall effect being different from the effect sum of single stressors.

Multiple stressors Two or more co-occurring or sequential stressors.

Phenomenological knowledge In this context defined as knowledge gained from empirical studies measuring the effect of multiple stressors without explicitly examining the underlying cause or pathway of that effect.

Receptor Indicator of stress response, ranging from physiological processes at the cellular level of individual organisms to behavioral patterns of individuals, changes in species populations, biological communities, food webs or ecosystem functions. The term is a synonym for 'biological response.' 'Stressor' and 'receptor' always form a conceptual pair, with one implying the existence of the other.

Stressor interaction Modification of a stressor's intensity or the sensitivity of an organism or ecosystem toward this stressor by another stressor or multiple other stressors. Not to be confused with biotic interactions among organisms.

Stressor Any natural or anthropogenic variable that causes a quantifiable change, irrespective of its direction (increase or decrease), in a biological response. The term 'stressor' is usually associated with an anthropogenic variable that has a negative impact.

Synergism The overall multiple stressor effect is larger than the effect sum of single stressors.

 https://doi.org/10.1016/B978-0-12-819166-8.00102-X

Introduction

Among inland waters, riverine systems are particularly affected by human activities due to their physical structure. They form open spatial networks that cross the landscape, draining higher grounds and concentrating runoff with its associated substance load. The linear shape of streams and rivers determines their tight connection with the surrounding land which often gets in the way of areal land use such as agriculture or urbanization. Rivers form a unity with their floodplain, and the riparian land-water-interface shaped by the fluvial dynamics represents one of the most diverse habitats highly sensitive to anthropogenic stressors. Riverine systems are also longitudinally connected by their directional transport of water, solutes, sediments and biota, with even locally restricted human intervention having potential implications for the entire network. Their very nature thus makes streams and rivers highly susceptible to multiple stressors.

By definition, stressors are external factors modified by human intervention that move a 'receptor' out of its normal operating range (Sabater et al., 2019). Receptors are indicators of stress response, and they range from physiological processes at the cellular level of individual organisms to behavioral patterns of individuals, changes in species populations, biological communities, food webs or ecosystem functions (including implications for biodiversity and ecosystem services). At the scale of river ecosystems, integrative indicators such as 'ecological status' (Lemm et al., 2021) or biodiversity loss represent common stress receptors of societal relevance.

It should be noted that the term 'stressor' differs from the term 'pressure' which is used, for instance, in the conceptual DPSIR framework elucidating socio-environmental relationships. Stressors are conceived as (putative) causes in a cause-and-effect chain, thereby accessible to empirical research and disclosure of mechanistic pathways. Strictly speaking, 'stressor' and 'receptor' always form a conceptual pair, with one implying the existence of the other.

Individual stressors acting on streams

Main stressor categories

A variety of anthropogenic stressors can be active in stream ecosystems worldwide (Table 1). In their study on global threats to human water security and river biodiversity, Vörösmarty et al. (2010) rank physical stressors (water abstraction, river fragmentation) and chemical stressors (water pollution) among the most pervasive in streams and rivers. Reid et al. (2019) complement 12 freshwater stressors threatening biodiversity, which can be grouped into three main categories:

Physical stressors

Agriculture is one key driver accounting for 90% of global water consumption, with about 20% of which is currently abstracted from rivers and other freshwater resources. Further driven by land use and climate change, this share is expected to increase to 25% by the end of the 21st century (Huang et al., 2019). At the global scale, less than 25% of rivers flow uninterrupted to the ocean (Grill et al., 2019), with highly developed regions in the world such as Europe evincing on average 0.74 barriers per kilometer of river length (Belletti et al., 2020). With the global hydropower boom river fragmentation is likely to substantially increase in many regions in the world in the coming decades. With about 90% of natural floodplain habitats lost, Europe also ranks highest regarding the impacts of lateral river fragmentation due to flood control structures (Globevnik et al., 2020). This level of decline is in line with the overall loss of natural wetlands globally, estimated at 87% of natural wetlands lost at end of the 20th century (Davidson, 2014). Other river basins worldwide already show similar degrees of floodplain loss (e.g. along the Mississippi), and substantial increases in other regions are expected for the future (Tockner et al., 2008). Physical stressors are furthermore exerted by the excessive sand and gravel extraction to supply the rapidly expanding building industry especially in the Asian-Pacific region. Severe physical stress manifests at larger spatial scales, allowing for detection and quantification by earth observation (e.g. Globevnik et al., 2020). Many of the physical stressors, however, represent small scale interventions that require costly field inspection to be detected, suggesting that the bulk of physical stressors currently goes undetected (e.g. Belletti et al., 2020).

Chemical stressors

Likewise, water pollution continues to be a major issue in rivers globally, with diffuse pollution mainly from agriculture and point source pollution from households (Ligtvoet et al., 2018). Nutrient stressors generally predominate, originating from aquaculture production, fertilized croplands or incompletely treated waste waters. These sources also increasingly produce pollutants of "emerging concern" such as pesticides, pharmaceuticals, microplastics or industrial chemicals, which may persist conventional sewage treatment and contaminate as parent compounds, metabolites or transformation products. These substances are also referred to as "micropollutants," which are generally present in water bodies in low concentrations but which can have detrimental biological effects in these concentrations. Moreover, the concentrations of inorganic ions in rivers are rising globally. This so-called secondary salinization is mainly caused by agricultural irrigation in arid regions, although mining activities and road de-icing can also play a significant role (Cañedo-Argüelles et al., 2013).

Table 1 Categorization of individual stressors acting on streams and rivers.

Category	*Group*	*Form*	*Main source*	*Main driving factor*
Physical	Hydrological stressors	Flow alteration	River flow regulation	Energy production, Navigation, Agriculture
		Water scarcity	Water abstraction	Agriculture
	Morphological stressors	Longitudinal fragmentation	Dams and barriers	Energy production, Agriculture
		Lateral fragmentation/floodplain loss	Levee dykes	Agriculture, Urbanization
		Channelization	River training	Agriculture, Navigation, Urbanization
		Siltation	Erosion of fine sediments	Agriculture
	Thermal stressors	Water warming	Heat emissions (from thermoelectric power plants)	Energy production
			Lack of riparian shading	Agriculture, Urbanization
		Water cooling	Release of cold bottom water of a reservoir	Energy production
	Radiation stressors	Light pollution	Artificial light; Lack of riparian shading	Urbanization, Agriculture
		Ultraviolet radiation	Stratospheric ozone depletion and climate change	*Drivers of climate change*
		Radioactivity	Nuclear accidents	Energy production
Chemical	Nutrient stressors	Nitrogen, Phosphorus	Soil fertilization; Insufficiently treated wastewater	Agriculture, Urbanization
	Other chemical stressors	Organic matter	Untreated wastewater; Excretion from aquaculture breeding	Urbanization, Aquaculture
		pH	Acid deposition; Acid mine drainage	Energy production, Industry, Mining
		Humic substances	Diffuse emissions from organic soils	*Drivers of climate change*
	Toxic stressors	Salinity	Mining effluents; Road de-icing; Soil fertilization; Water abstraction	Mining, Road transport, Agriculture, Urbanization
		Heavy metals	Acid mine drainage; Storm and surface water runoff; Hull coatings; Soil fertilization	Mining, Urbanization, Navigation, Agriculture
		Contaminants of emerging concern		
		Microplastics	Fragmentation of plastic litter; Untreated or insufficiently treated wastewater	Urbanization
		Pesticides	Diffuse emissions from agricultural soils; Application in aquaculture; Storm and surface water runoff	Agriculture, Aquaculture, Urbanization
		Pharmaceuticals	Insufficiently treated wastewater; Intensive livestock and aquaculture farming	Urbanization, Agriculture, Aquaculture
		Cyanotoxins	Harmful algal blooms caused by nutrient stress	Agriculture
		Other organic chemicals	Insufficiently treated wastewater; Storm and surface water runoff; Hull coatings and bilge water; Oil spills	Industry, Urbanization, Navigation
Biological	Biological stressors	Invasive alien species	Intentional or accidental releases; Bilge water	Navigation, Aquaculture
		Waterborne pathogens	Untreated or insufficiently treated wastewater	Urbanization
		Overexploitation	Commercial fishing	Fisheries

Biological stressors

Biological stressors represent the third category of threats affecting streams and rivers worldwide. Above all, the impacts of invasive alien species on the native biodiversity are noteworthy. Deliberate or accidental introductions of exotic species, mainly by trade and transport, can lead to severe changes of the original communities by out-competing native species, altering food webs and ecosystem functioning. Rivers already affected by physical or chemical stressors may facilitate invasions (Strayer, 2010). The number of alien species in freshwaters strongly increased over the last decades and are expected to exceed today's rate by 20% in 2050 (Seebens et al., 2021). These may go alongside water-related infectious diseases observed to increase in prevalence (Poulin et al., 2011).

The threats of fishery exploitation by humans to large freshwater species such as sturgeons, river dolphins, and turtles are well documented (e.g. He et al., 2018). By-catch rates however, estimated at 40% of total catches globally for marine fisheries, to be detected but assumed to be substantial, leading to species decline and even extinction (Raby et al., 2011). The biological threats of aquaculture include overexploitation of wild fish for feed, introduction of alien species through accidental release, and transmission of pathogens (Martinez-Porchas and Martinez-Cordova, 2012).

Human activities driving multiple stressors

The multitude of stressors in streams and rivers is driven by eight human activities and climate change (Fig. 1): Fisheries, energy production, navigation and quarrying occur in, on or close to the river; agriculture, urbanization, mining and industry take place

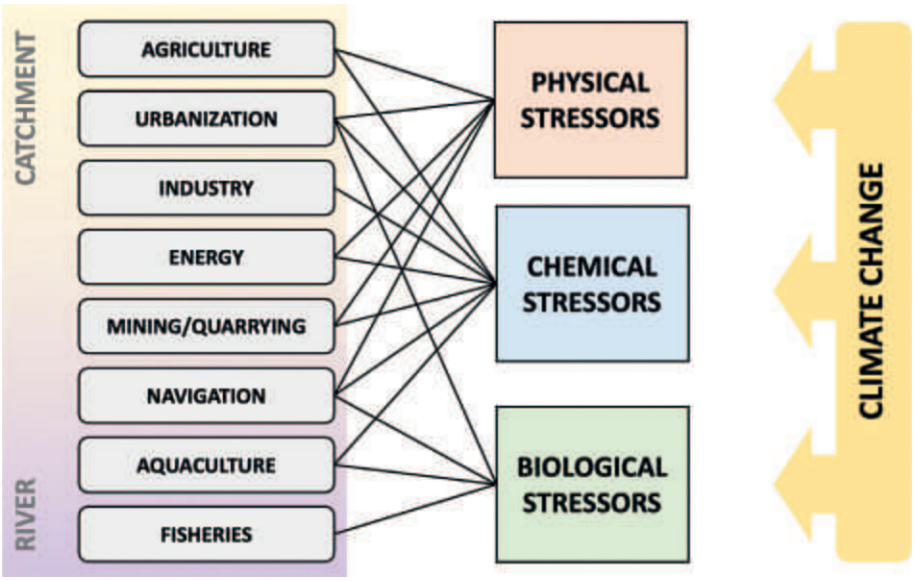

Fig. 1 Human activities and climate change driving multiple stressors in rivers.

anywhere in the catchment; climate change acts globally. Each of these drivers has the potential to cause multiple stressors itself. The "Urban Stream Syndrome" (Walsh et al., 2005) is a case in point: rivers draining urban land feature flashier hydrographs, elevated concentrations of nutrients, fecal pathogens and contaminants (driven by combined sewer overflows), altered channel morphology and complete floodplain loss. The effects of various drivers in the catchment often accumulate and exert more of the same or a spectrum of different stressors. Many of the drivers are closely interlinked by their socio-economic context, calling for a systemic perspective to fully understand all relevant driving forces (e.g. water-food-energy nexus-concept). Stress intensities are likely to increase and exacerbate the multi-stressor situation in the coming decades, in that future models project growing resource demand from the rising world population (EEA, 2020).

The role of climate change

Climate change is not considered a stressor per se, but as a driver boosting individual stressors (Johnson and Penaluna, 2019; see Fig. 1). Direct climate change effects on streams and rivers include increased water temperatures and altered streamflow patterns, locally manifested in extreme events such as floods, droughts and heatwaves. Physical stressors intensify through climate-induced water scarcity or disastrous flooding, which may require climate change adaptation measures such as water reservoirs and conveyance structures, or enhanced flood protection measures. Chemical stressors intensify through reduced dilution of pollutants during dry periods, or flash-flooding which flushes pollutants from urban and rural areas into the rivers. Biological stressors intensify through the spread of alien species and diseases due to warmer climate, facilitated by reservoir constructions. Future models generally predict exacerbated effects of climate change, yet with highly uncertain and variable prospects regarding specific regions.

Multiple stressors acting on streams

Given the wide variety of stressors, river systems are frequently impacted by multiple stressors, especially in densely populated world regions with emerging or high-income economies (North America, Europe, East and South Asia; Vörösmarty et al., 2010). European rivers, for instance, are mainly threatened by the interplay of physical and chemical stressors including hydrological, morphological and nutrient stress (EEA, 2018). Accordingly, these stressor combinations are investigated most often in the scientific literature (Nõges et al., 2016).

Phenomenological knowledge

The effects of multiple stressors are studied on the basis of empirical data covering different stressor intensities, either manipulated in experimental settings or sampled across spatial or temporal gradients under field conditions. Multi-stressor studies often limit their investigations to two stressors acting together, thus simplifying the multi-stressor "cocktail" in favor of paired stressor-response analyses. This allows for separating between three basic multi-stressor effect types:

- Dominant effects: Only one of the two stressors affects the receptor despite distinct presence of both stressors.
  Example: Hydrological stress (river low flow) but not nutrient enrichment showed a significant effect on the benthic macroinvertebrate community composition in a lowland stream experiment (Graeber et al., 2017).
- Additive effects: Both stressors affect the receptor, with the overall effect being equal to the effect sum of single stressors.
  Example: Physical and chemical stressors added up in their effects on various biological community parameters in a mountainous river catchment (Gieswein et al., 2017).
- Interactive effects: Both stressors affect the receptor, with the overall effect being different from the effect sum of single stressors.
  - Synergism: The overall effect is larger than the effect sum of single stressors.
    Example: Increasing nutrient enrichment and temperature amplified/magnified the phytoplankton growth in a boreal river system (Rankinen et al., 2019).
  - Antagonism: The overall effect is smaller than the effect sum of single stressors.
    Example: Hydropeaking (peak flow events from hydropower plant operation) dampened/mitigated the effects of nutrient enrichment on benthic algae biomass in an oligotrophic alpine river experiment (Bondar-Kunze et al., 2016).

A synthesis analysis covering 195 paired stressor-response cases acting on riverine biological community parameters (e.g. diversity, biomass, functional traits mainly affected by morphological, hydrological, toxic or nutrient stressors paired with each other) revealed almost equal shares of multi-stressor effect types (36% dominant, 31% additive, 32% interactive; analysis based on Birk et al., 2020). Data covering larger spatial scales showed higher shares of additive and interactive effects, likely related to the extended stressor gradients investigated. The interactive effects relevant in the cases with significant interactions explained on average about 20% of the community responses, with nutrient and toxic stressors as well as nutrient and morphological stressors interacting most frequently. A recent study analyzing seven stressors acting on the ecological status of European rivers attributed more than half of the multi-stressor response to interactive effects, indicating the complex interplay of the stressors considered (Lemm et al., 2021).

Behind the phenomena: The dearth of mechanistic understanding

Stressor interactions seem to play a significant role in river systems, as they do in other ecosystems (e.g. Brook et al., 2008; Hunsicker et al., 2016). Yet, little is known about the actual mechanisms and pathways underlying stressor interactions. This ignorance obstructs the prediction of multi-stressor effects and gives way to ecological surprises when "perceived reality departs qualitatively from expectation" (Holling, 1986). The inability to predict is one of the biggest scientific challenges, detaining effective policy-making and management intervention (Schindler and Hilborn, 2015).

Three aspects are key to the advancement of multi-stressor knowledge in river systems:

Rivers as hierarchical systems obscuring stressor manifestation

Rivers are natural systems with a hierarchical organization incorporating, on successively lower levels, subsystems from the basin down to the microhabitats (Frissell et al., 1986). This implies that riverine habitats and their biota are controlled by processes acting at different spatiotemporal scales. Human activities often modify these processes at higher scales with cascading implications for the lower scales. Dam construction in the upstream part of a river system, for instance, is an intervention that affects the river system at a high hierarchical level. Its effects on river flow and sediment dynamics downstream alter patterns of flooding and sediment deposition with detrimental consequences for all subsystems. This hierarchical organization complicates the understanding of how, where and when driving forces cause multiple stressors in river systems.

Patterns of stressor interplay

The effect of multiple stressors is dependent on the types of stressors acting together. The biotic response to nutrient stress, for instance, varies when paired with different stressors (Birk et al., 2020). The effect is also dependent on the intensity of co-occurring stressors, with individual stressors at low intensities being ineffective, but at high intensities being potentially no longer effective (e.g. due to saturation effects). This suggests interactive effects are relevant only along certain intervals of stressor intensity. Another likely important factor is the relative duration of individual stressors. Stressor exposure needs to be understood against species-specific life-histories. For example, a stressor lasting a certain time span may be experienced discretely by long-lived species but continuously by short-lived species (Jackson et al., 2021). This suggests varying stressor effects in biological communities will depend on the life-history traits of the different species forming the community. Moreover, the sequential order and frequency of stressor occurrence influence multi-stressor effects, determining specific community vulnerability and recovery potential (Sabater et al., 2021). For example, Brooks and Crowe (2019) demonstrate greater effects on community respiration when copper was applied before the insecticide chlorpyrifos than vice-versa in an experimental treatment. Stressor effects were also influenced by time-lags in the arrival of the two stressors.

Varied responses across levels of biological organization

Multi-stressor effects differ between levels of biological organization, indicating the relevance of different mechanisms at various organizational levels (Galic et al., 2018). At the level of the individual, stressor response is related to the "stressor mode of action". Schäfer and Piggott (2018) distinguish between stressors acting from the outside or from the inside on the individual organism. Stressors acting from the outside affect the whole organism (e.g. physical stress of flooding) leading to destruction or displacement. Stressors acting from the inside affect the organism's physiology, either non-specifically (e.g. salinity, thermal stressors) by

increasing energy costs, or specifically (e.g. toxic stressors) by altering specific physiological processes. Stressors can also be mediated through environmental factors that affect the organism's physiology. Oxygen availability, for instance, is reduced for aquatic organisms at higher temperatures or flow cessation, which can conflict with specific niche or habitat requirements of the organism (Statzner and Bêche, 2010).

At the population level, regulating mechanisms such as density dependence can obscure direct stressor effects by affecting intraspecific competition (e.g. cannibalism and agonistic behavior), predation or increases in food ration. Dispersal dynamics may offset stressor impacts through recolonization (e.g. drift compensation; Chará-Serna and Richardson, 2021) and life-cycle traits determine the species' sensitivity and exposure to stressors. A significant example are insect species whose larval and adult stages occupy different (aquatic and terrestrial) habitats with respective exposition to different stressors.

At the community level, composite biological mechanisms induce more complex responses. Different stress-tolerances among species, for instance, render communities more resistant or more vulnerable to multiple stressors, depending on whether these tolerances are positively or negatively correlated to each other (Vinebrooke et al., 2004). Species interactions are known to mediate community-level responses to multiple stressors, and multi-stressor effects are likely to propagate across the food web. Stressors can have direct trophic effects (top-down on the resource or bottom-up on the consumer) and indirect effects cascading through the trophic levels. Combined with biotic interactions (e.g. competition or facilitation) so-called 'trophic amplification' generates non-trivial multi-stressor responses (Bruder et al., 2019). Besides evolutionary adaptation to stressors including natural selection over multiple generations, potential legacies of past stressors complicate the understanding of multi-stressor effects at community level (Jackson et al., 2021).

Refining the analytical approach to multi-stressor effects

Empirical evidence gained from experiments and field studies provide the critical foundation to the mechanistic understanding of multi-stressor effects. Key is the formulation of appropriate "null models" for the statistical effect analysis (Schäfer and Piggott, 2018). On this basis, more complex mapping and modelling approaches can be conducted as part of an advanced "cumulative effects assessment" (Hodgson and Halpern, 2019). For example, multi-stressor mapping affords insights into species exposure and vulnerability to stressors within their distribution, directing spatial management (e.g. Schinegger et al., 2018). Multi-species modelling allows for integrating direct stressor effects and indirect effects of biotic interactions across the food-web, with ever-increasing predictive accuracy (Schuwirth and Reichert, 2013). Multi-model ensembles, in which multiple alternative models are run and results are compared, would allow for quantifying uncertainties to fortify conclusions.

Orr et al. (2020) aptly summarizes the key issues of multi-stressor research: (1) Our effect understanding needs to integrate ecological complexity and its increasingly intricate patterns from the individual to the ecosystem. (2) The relevance of the temporal scale at which stressors co-act should be scrutinized, with experimental simulations truly striving to imitate real-world stressor situations. (3) Improved analytical models should ultimately enhance our predictive capacity to forecast multi-stressor effects instead being staggered by ecological surprises.

Managing multiple stressors acting on streams

Uncertainty calls for adaptive management

The dearth of mechanistic understanding makes environmental management under conditions of multiple stressors very challenging. Ideally, management is guided by causal diagnosis and prediction. The systematic review of existing evidence for cause-effect hypotheses, a technique adopted from epidemiology, offers support to informed decision making (Norris et al., 2012). This information can feed into probabilistic networks assisting the diagnosis of potential causes for ecosystem deterioration (Feld et al., 2020). In reality, comprehensive system understanding is often scarce, leading to decision making in the face of high uncertainties. This setting calls for an adaptive management approach, that is an iterative process managing the system on the basis of current knowledge while acquiring further information needed to improve future management (Clark, 2002). Yet, "no-regrets" measures, which make the system more resilient toward currently unknown impacts, can be effected immediately (Côté et al., 2016). An example often suggested as a "no-regret" for tackling multi-stressor problems is the establishment of riparian buffers.

Scale of managing multiple stressors

Local action cannot halt global stressors. This poses a dilemma for environmental management, which can only attempt to compensate for the impacts of global stressors by reducing local stressors. Depending on the multi-stressor effect type, such compensation needs to be tackled differently. An additive effect setting, for instance, allows for mitigating any of the relevant stressors, while an antagonistic setting results in worsening of environmental conditions when removing the dampening stressor. In river systems the hierarchy of spatial scales is particularly relevant, with measures to mitigate local stressors (e.g. on river morphology) remaining ineffective if catchment-scale stressors (e.g. diffuse pollution from agriculture) still prevail.

Integrated water resources management

It is a truism that managing multiple stressors acting on rivers falls short when focused only on the watercourse itself. Any effective management of environmental resources requires a landscape-perspective, and in the case of rivers this perspective can be clearly delineated as the watershed or river catchment. From this fundamental landscape unit, the concept of integrated water resources management evolved, recognizing the close linkage of water, energy and food within and across river catchments (Ibisch et al., 2016). Integrated management suggests a comprehensive, participatory planning and implementation approach for managing and developing water resources by embracing all three (social, economic and environmental) "pillars of sustainability" (Purvis et al., 2019). Management solutions should be based on an integrated understanding of the socio-ecological system, in which the interplay of social, economic and environmental matters is respected. Such a "systemic management" is highly ambitious and poses major challenges to implementation (e.g. of the European Water Framework Directive; Voulvoulis et al., 2017).

Nature-based solutions

Multiply stressed rivers are indicative of the environmental crisis increasingly threatening economic and social stability, public health and well-being. In the face of this global crisis manifesting in climate change and biodiversity loss, "systemic solutions" are called for, promoting a shift from human-engineered technical solutions (often employing concrete and steel at high direct and collateral costs) to "nature-based solutions" (Cohen-Shacham et al., 2016). Such solutions are conceived as measures generating multiple benefits by reducing environmental and social vulnerabilities, mitigating climate change, improving human health and well-being, and providing jobs and business opportunities at best (EEA, 2021) — an ideal prospect to meet the pressing global challenges. This is the vision popularized by the Millennium Ecosystem Assessment (2005) and signed up to in the European Green Deal (EC, 2019). At its heart lies the extensive conservation and restoration of riverine (and other) landscapes. In the years to come, the success of this venture will, in no small part, be indicated by the state of rivers, which represent the sentinels of mankind's sustainable relationship with nature.

Conclusions/synthesis

The "great acceleration" (Steffen et al., 2015) describing the simultaneous rise in various human activities and degradation of natural resources is rushing onward across the globe. The surge in driving forces amplifies the intensity of environmental stressors. At the global scale, streams and rivers affected by multiple stressors can now be considered the norm rather than the exception. However, the lack of monitoring data and systems understanding obstructs causal diagnosis and the prediction of effects. The active mitigation of multiple stressors is thus uncertain – it requires approaches that integrate across all (direct and indirect) driving forces within the catchment and beyond, demanding the high price of a societal transformation away from single-purpose sectoral interventions toward multi-benefit sustainability solutions. The words are on everyone's lips these days – truly efficient measures are yet to be taken.

Knowledge gaps

- Mechanistic understanding of the effects of stressor interactions is scarce.
- Causal diagnosis and prediction of multi-stressor effects are highly uncertain.
- The interplay of biodiversity loss and climate is not yet been fully understood.
- The size and combination of measures to mitigate multiple stressor effects are unclear.
- Effective solutions require upscaling to the catchment-level integrating socio-economic factors – such integrative approaches are still in their infancy.
- Necessary governance structures required to mitigate multi-stressor effects are unknown.

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Urban Streams and Rivers☆

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This is an update of JL Meyer, Urban Aquatic Ecosystems, in *Encyclopedia of Inland Waters*, edited by GE Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00236-2.

This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editor LeRoy Poff.

Glossary

Combined sewer system Urban water management system using a single network of pipes that conveys both wastewater and stormwater either to a treatment plant or to a distant, large receiving water (see also Separate sewer systems).
Effective imperviousness The proportion of a catchment covered by effective impervious surfaces (see *Imperviousness*), where "effective" connotes those surfaces that have a damaging effect on the receiving water. Impervious surfaces with direct stormwater drainage connection to a stream are effective; the effectiveness of other surfaces is usually considered to be near zero, but depends on the degree to which their runoff is retained, diverted or treated.
Flashiness (of stream flows) Increased magnitude and frequency of storm flows to streams, and shorter recession times of high-flow events.
Imperviousness The proportion of a catchment covered by surfaces that are impermeable to water (primarily, roofs, roads and paved areas). This may be referred to as 'total imperviousness' to distinguish it from *Effective imperviousness.*
Receiving water The stream, river, estuary, lake or coastal water into which an area of land or a pipe drains.
Separate sewer systems Urban water management system using a network of sewerage pipes that direct wastewater to a treatment plant, and a separate network of stormwater drainage pipes that direct urban stormwater runoff, usually untreated, to the nearest receiving water (see also Combined sewer systems).
Urban karst The network of drainage, sewerage and water-supply pipes, and high-permeability trenches around them and around other conduits constructed under urban areas, which influence groundwater and piped flows to streams.
Urban stormwater Runoff from impervious surfaces during and immediately after wet weather.
Urbanization The process of converting land, either from its native state or from agricultural use, to uses that support the concentrated assemblage of humans and their activities.
Wastewater Sewage, and domestic or industrial effluent.

Introduction

Rivers and streams have been at the heart of human settlements, towns and cities throughout history (Mumford, 1961). Their primary attraction for our earliest cities was as a supply of fresh water, but this ecosystem service was soon compromised by inflows of wastewater and runoff from the settled land. Smaller streams and drainage lines became eroded and polluted by the increased volumes of runoff from roofs, roads and compacted soils of these settlements. These challenges for early human settlements, together with the hazards of riverine flooding for settlements on floodplains, led to an evolution of approaches to urban water

☆*Change History:* October 2021. C Walsh made small updates in all sections.

management that continue to evolve today (Brown et al., 2009b). The deleterious changes to the natural functioning of rivers and streams flowing through our urban lands are the product of those management approaches.

While human population growth is likely to slow over the next century, peaking at 9–13 billion (United Nations, 2019), almost all of the additional 1–5 billion people beyond today's population will be urban dwellers (United Nations, 2018). As a result, the coverage of the world by urban lands will continue to increase over the next century, and many more reaches of many more rivers and streams globally will be affected by the ways urban land and water is managed.

This chapter provides an overview of the effects of urban land, and of urban land and water management, on streams and rivers. I begin by proposing a definition of urban land that quantifies dominant stressors to rivers and streams with urban land in their catchments. I describe the diversity of approaches to urban water management that determine the condition of urban rivers and streams, and the resulting in-stream hydrologic, geomorphic, and biological responses. I conclude by describing emerging approaches to urban water management that show potential for protecting and restoring urban streams.

Defining 'urban' as it affects rivers and streams

Urbanization is the process of converting land, either from its native state or from agricultural use, to uses that support the concentrated assemblage of humans and their activities. Most studies seeking to assess the effect of urbanization on stream ecosystems have used a measure of the density of agglomeration as a proportion of catchment area as the metric of 'urbanization'. Urban areas are most evidently defined by the replacement of vegetation and soil cover by hard surfaces, such as roofs, roads and paving, which are designed to be impermeable to water. These surface changes have led to 'imperviousness' being a primary measure of urban density in many studies of urban impacts on streams and rivers (Arnold Jr. and Gibbons, 1996). Other studies have used composite metrics that include measures such as the density of areas zoned as 'urban' land use or population- or socio-economic--based metrics (e.g., McMahon and Cuffney, 2000; Feist et al., 2017). In most cases, such studies have demonstrated responses in a range of stream indicators as a function of urban density when sites across a gradient of urban density are compared. The general conclusion from such studies has been that urbanization degrades streams.

If the mechanisms that drive the commonly observed degradation of streams with urban catchments are to be understood and better managed, then simple measures of urban density without a direct causal link to stream ecosystems are of limited use. To understand mechanisms of stream degradation, urban land changes need to be measured by the changes in vegetation and soil properties (including conversion to impervious surfaces), and in flow paths for water across (and under) the landscape.

Imperviousness is an important metric for assessing impacts on streams, because impervious surfaces prevent infiltration of water into soils, reducing both water lost to the air by plant transpiration and flows through soils to downstream waters. Less evident superficially than impervious coverage, urban areas are equally defined by networks of underground piped infrastructure for flows of water supply, wastewater disposal, and drainage of runoff. In addition, networks of gravel-filled trenches carrying conduits for services such as electricity, gas and telecommunications, can also act as conduits for subsurface flows of water. These complex underground networks of flow paths, termed the 'urban karst' by Kaushal and Belt (2012) lead to profound changes to catchment hydrology that dominate the impact of urban areas on rivers and streams.

Greater volumes of water run off impervious surfaces than from vegetated land because of reduced soil storage and uptake and loss of water to the air by transpiring plants (Fig. 1). The rapid drainage of this runoff through hydraulically efficient drainage networks greatly increases the frequency and severity of disturbances to receiving streams. Resulting changes to channel form, to in-stream animals and plants, and to ecological processes in streams are observed when as little as 1–2% of a catchment is sealed and drained in such a way (e.g., Walsh and Webb, 2016). Therefore, urban impacts on streams can be detected in streams and rivers that might not obviously be recognized as being 'urban'.

The degree to which stormwater infrastructure is implemented in catchments with only a little urban land is much more variable than in more densely urbanized catchments, because there is often less need for formal drainage at lower urban densities. Several studies have shown that stream degradation is better explained if imperviousness and drainage connection are both accounted for (Walsh et al., 2005a; Walsh and Kunapo, 2009; Hale et al., 2015; Baruch et al., 2018; Blaszczak et al., 2019). The longest-standing metric that does this is effective imperviousness, arising from Leopold's (1968) demonstration that hydrologic changes in urban catchments are a function of both imperviousness and the degree to which impervious areas are serviced by sealed stormwater drainage. The simplest definition of effective imperviousness is the proportion of a catchment covered by impervious surfaces with direct drainage connection to a stream, assuming that only directly connected surfaces are 'effective' (i.e., have a damaging effect on downstream waters). Variants that weight impervious surfaces by their degree of connection have also been proposed (e.g. Walsh and Kunapo, 2009), but directly connected impervious surfaces remain the dominant influence (Walsh et al., 2022). Despite their superior prediction of stream degradation, metrics that account for drainage connection in studies of urban impacts have relatively rarely been used, perhaps because they require drainage infrastructure data that, in many areas, can be difficult to source.

Thus, in this chapter, I define urban land by the increased imperviousness of its surfaces and by features of the underground urban karst, particularly the stormwater drainage network. Rather than defining an urban river or stream, I focus on the nature of urban stressors on streams, and how streams respond to them, noting that these stressors can potentially apply to a stream with even a very small area of urban land in its catchment.

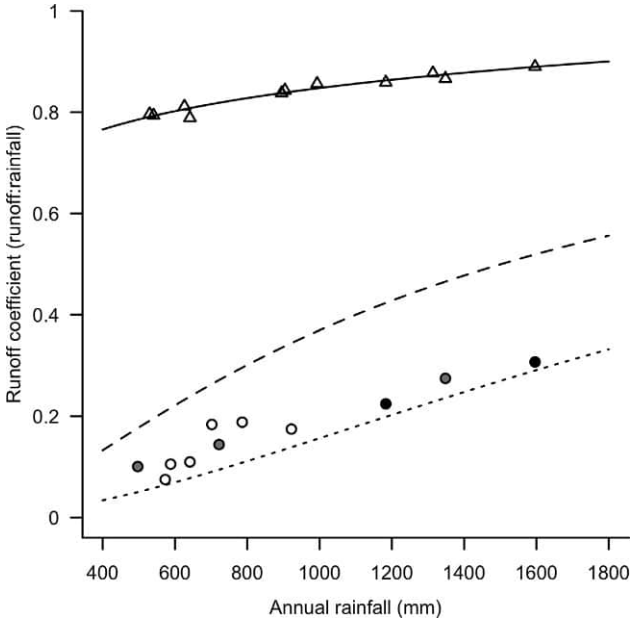

Fig. 1 Impervious runoff and streamflow coefficients for the Melbourne region. Estimated annual runoff coefficients (C) from impervious surfaces (open triangles) from sites across the Melbourne region as a function of mean annual rainfall (MAR). Regression line: $C = 0.230 + 0.206 \times \log_{10}(MAR)$. $R^2 = 0.94$. Annual streamflow coefficients from 11 streams with forested (closed circles), grassland (open circles) or mixed forested and grassland catchments (grey circles) across the Melbourne region as a function of mean annual rainfall. The lines surrounding these stream points are the relationships between streamflow derived by Zhang et al. (2001) for grassland (dashed curve) and forested catchments (dotted curve) of the world. From Walsh CJ, Fletcher TD and Burns MJ (2012) Urban stormwater runoff: A new class of environmental flow problem. *PLoS One* 7(9): e45814.

Urban land and water management approaches that affect rivers and streams

Urban land use alters the water balance of catchments and the resulting flow regimes of rivers and streams primarily through one major influence, impervious runoff (stormwater) generation and the way it is drained or routed to stream channels. These effects can be moderated or compounded by other aspects of urban water management: wastewater and sewage disposal, infiltration of water into catchment soils, extraction of water from streams or the aquifers flowing to them, and channelization to mitigate riverine flooding. In this section, I discuss the history, nature and interactions of these influences.

Stormwater

When the increased runoff from roofs, road and compacted soils of human settlements exceeds the capacity of surrounding soils to absorb it, local flow lines become eroded and polluted. From the earliest human settlements to today, the primary solution to this problem has been to channelize, seal, or more recently, pipe the flow line from the source of the runoff to a downstream drainage line or stream. The cumulative effect of many such small drainage actions in an urban area is to increase flow volumes, erosion and pollution downstream. As the world's cities have grown, the positive feedback of many small-scale drainage actions has led to increasing the size of pipes and channels required to carry the increased flows and to armor or seal the beds and banks of streams and rivers downstream. In many cities, this process has resulted in some streams being obliterated entirely: buried and built over, the dominant flow path of water through stream sediments replaced by hydraulically efficient piped flow (Elmore and Kaushal, 2008; Walsh et al., 2016b).

Other aspects of urban water management (water supply and wastewater disposal) can ameliorate, worsen or displace these effects. However, stormwater drainage systems are fundamentally designed to alter catchment hydrologic processes and rapidly transport runoff and its associated pollutants to streams and rivers. Therefore, the way urban stormwater runoff is managed is a primary determinant of the condition of downstream rivers and streams.

Wastewater

Without reticulated sewerage or water supply, urban settlements historically relied on some variant of cesspools, essentially holes in the ground, for sewage disposal. With the advent of flush toilets and reticulated water supply, unsewered areas today more commonly deal with wastewater using septic tanks, which separate and disperse liquid waste into soil nearby. As long as septic systems, or indeed cesspools, do not overflow into drainage lines, their impacts on streams are likely to be restricted to the slow release of a subset of contaminants that are mobile through soil, such as nitrate (Walsh and Kunapo, 2009).

Reticulated sewerage is needed in more densely populated areas, and such systems are commonly classified into either (a) combined sewers, which convey both wastewater and stormwater either to a treatment plant or to a distant, large receiving water, or (b) separate sewers, where a network of sewerage pipes directs wastewater to a treatment plant, while stormwater drainage is directed in a separate network, usually untreated, to the nearest receiving water. Despite the binary classification, the two systems span a continuum. If their flow capacity is small, combined sewers can overflow untreated into local streams with a small amount of rain, creating hydraulic and chemical disturbances to the stream almost as frequently as separate sewers. At the other end of the continuum, separate sanitary sewers commonly receive some runoff inflows, either through leaky pipes or illicit cross-connections with stormwater drainage, and they are therefore also fitted with overflow structures that allow (infrequent) untreated sewage discharges during large storm events. Combined and separate sewers thus both vary in the frequency of stormwater flows and the frequency of flows contaminated by sewage.

Combined sewers have not been legally sanctioned in most legislatures since the mid-20th century, and are thus often considered characteristic of 'older' cities (e.g., Radcliffe, 2018). Yet the promotion of separate sewerage and drainage networks dates back to the earliest European efforts to formalize urban water management (Chadwick, 1842). Shifts in engineering preference, first for combined systems and increasingly in the 20th century for separate systems, were the result, in large part, of evolving understanding of water-borne disease transmission (Tarr, 1979). Until the late 1800s, it was thought that running waters purify wastewater, so that discharge of sewage effluent untreated into rivers upstream of drinking water intakes was acceptable. Combined sewer systems continue to operate today in North America, Europe and Asia; in most cases, they now include diversion to treatment plants which discharge a constant flow of treated effluent to usually larger receiving waters.

Combined sewer overflows into rivers and streams remain a widespread phenomenon and the focus of considerable municipal expenditure (e.g., USEPA, 2004). Management responses to reduce and mitigate overflows range from increasing the capacity of sewers by constructing bigger pipes (e.g., the Tunnel and Reservoir Plan of Chicago, Dalton and Kenny, 1981, and the underground discharge channel of Tokyo, MLITT, 2014), to increasing stormwater retention using methods discussed below under 'Protection and Restoration', to in some cases, conversion to separate sewers (e.g., Thorndahl et al., 2015). But reducing the impacts of sewer overflows does not address the environmental damage of separate stormwater flows into rivers. Indeed, when sewer overflows are infrequent, their impacts can be secondary and difficult to detect over broader degradation caused by stormwater drainage networks (Kellar et al., 2014).

In most modern cities of the world, sewage and wastewater disposal are well managed by being directed to treatment plants, which discharge treated effluent with reduced loads of pollutants to a larger receiving water downstream or to the sea for coastal cities. For inland cities, the effluent can be a point source of pollution to a river or stream. However, while sewage treatment technologies have improved and become widespread practice in most of the world, untreated sewage draining directly to rivers remains a problem for many cities of low-income countries (Capps et al., 2016).

Infiltration and extraction

Pipes and concrete drains are expensive. It is thus common to direct impervious runoff from at least some constructions into surrounding soils in areas, where the soils have sufficient infiltration capacity to absorb additional impervious runoff. For instance in Perth, Australia, where sandy soils are common, runoff from many roofs and roads drain to soak wells rather than connect to street drainage (Middleton et al., 2020). Where such practices are common, heightened water tables, potentially polluted, may increase groundwater flows to local streams and rivers. The prevalence of such practices in a city is likely to be influenced by a combination of soil properties, rainfall intensities and volumes, potential evaporation, and local regulatory norms. Infiltration into soils is increasingly being used as a 'low-impact' approach to stormwater management (see Protection and Restoration section).

Groundwater is an important water source in many regions of the world, and overextraction has caused land subsidence in areas such as the Mekong Delta (Minderhoud et al., 2017). Groundwater extraction can potentially lead to reduced flows in streams (e.g., Rosburg et al., 2017), but groundwater extraction has not commonly been reported as a cause of reduced stream flows in urban areas.

Channel engineering

The conversion of streams to lined drains and pipes is usually motivated by the increased frequency and intensity of floods caused by runoff from impervious surfaces in urban catchments. Such motivations can extend to engineering larger rivers downstream. However, channelization, leveeing or armoring of large rivers flowing through cities and towns is more commonly aimed at protecting urban lands from riverine flooding, i.e., infrequent large floods from larger, non-urban catchments upstream.

The effects of urban land on stream ecosystems

The changes to catchment processes, arising from the manifold urban land and water management activities, degrade streams and rivers. Around the world, streams of cities and towns are typified by in-stream habitats, biotic assemblages, food webs, and ecosystem processes that are altered, and by ecological values and services, provided by healthy stream ecosystems, that are diminished or lost (Paul and Meyer, 2001; Walsh et al., 2005b). The dominant impact is the increased frequency and magnitude

of disturbance, both *hydraulic* (arising from larger, more frequent high-flow events) and *chemical* (arising primarily from the complex conglomeration of pollutants in impervious runoff and secondarily and more variably, in wastewater and altered groundwater flows). Hydraulic changes also simplify or homogenize in-stream habitat by increasing the capacity of streams to transport sediments. In this section, I first consider the hydrologic changes that drive the hydraulic and chemical disturbances, then the resulting geomorphic and chemical changes, before considering changes to biotic assemblages and ecosystem functions of streams.

Hydrology

Runoff from impervious surfaces through sealed drains tends to increase the total volume of runoff (Fig. 1), and the 'flashiness' of flows: i.e., increased magnitude and frequency of storm flows to streams, and shorter recession times of high-flow events (Fig. 2; Burns et al., 2012). While increased flashiness is commonly observed, it is reduced in regions where precipitation falls as snow, and runoff is buffered by snow-melt (Hopkins et al., 2015). The degree of flashiness from impervious runoff can also be ameliorated if the runoff is infiltrated into catchment soils. The effect of infiltration and evaporation from retention systems has even been reported to reduce the flashiness of flows compared to non-urban streams in arid Phoenix, Arizona (Hopkins et al., 2015). It has also been noted that urban-induced increases in flashiness of stream flows can be smaller in regions with naturally flashy streams (e.g., the tropical streams of Puerto Rico, Ramirez et al., 2009).

Because impervious surfaces and sealed drains prevent infiltration into soils, urban stormwater runoff and drainage contribute to reduced baseflows in streams. While reduced baseflows are observed in streams of some urban catchments (Fig. 2), baseflow responses vary among urban catchments within and between cities (Bhaskar et al., 2016; Hopkins et al., 2015). The size and direction of change in baseflows downstream of urban areas depend on the complex interactions of the degree of baseflow contribution to the stream before urbanization, the extent to which the stream channel has been incised, the amount of infiltration of urban stormwater runoff in the catchment, the amount of catchment vegetation (which drives evapotranspiration losses), and inflows into the stormwater drainage system or the stream from catchment water supply and wastewater systems (Bhaskar et al., 2016). While stormwater infiltration is likely to increase flows to receiving streams, the extent to which such flows become baseflow similar to a pre-urban catchment is highly unpredictable given the complexities of the urban karst (Bonneau et al., 2017).

Geomorphology

Altered flow regimes resulting from urban runoff increase erosive forces on stream channels. Sediment supply in urban catchments rises rapidly during urban construction, followed by a decrease when development is complete (Wolman, 1967), usually stabilizing higher than pre-construction levels (Chin, 2006; Russell et al., 2017). Supply of coarse sediments from established urban land can

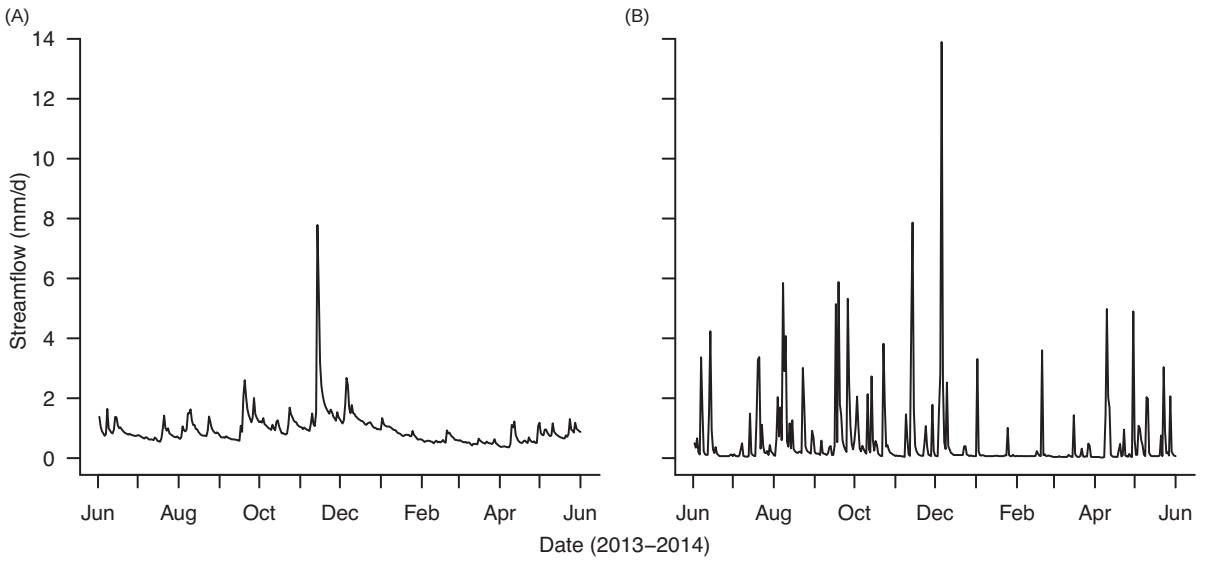

Fig. 2 After Burns MJ, Fletcher TD, Walsh CJ, Ladson AR and Hatt BE (2012) Hydrologic shortcomings of conventional urban stormwater management and opportunities for reform. *Landscape and Urban Planning* **105**: 230–240, contrasting daily stream flow patterns over a typical year in: (A) Olinda Creek with a forested catchment; and (B) Brushy Creek, a comparable, nearby stream with an urban catchment. Note higher baseflows, and much smaller high-flow responses to most rain events, with longer recession times in Olinda Creek. There was a single large high-flow disturbance in Olinda over the year compared to >20 in Brushy Creek. (A) catchment area 9.1 km^2, effective imperviousness (EI) 0.1%, data from research flow gauge used by Walsh et al. (2015). (B) catchment area 14.9 km^2, EI 23.5%, Melbourne Water flow gauge station 229,249.

be substantial, with yields well above those from comparable non-urban land (Smith and Wilcock, 2015; Russell et al., 2018). Increases in sediment supply can persist for decades from informal settlements in poorer cities, because of unsealed roads and poor environmental controls (e.g., Taniguchi et al., 2018). However, the increased sediment supply delivered to streams through stormwater drainage networks is generally moved efficiently through streams by stream flows that are greatly increased by stormwater runoff (Russell et al., 2020).

As a result, eroded, widened, and incised channels are a common characteristic of streams in urban catchments, and such changes reduce habitat heterogeneity, even at low levels of effective imperviousness (Vietz et al., 2014; Hawley et al., 2013). When permitted to erode, "natural" stream channels (i.e., that are not armored, lined or piped) adjust to a new urban flow and sediment regime. The longest-standing, and most commonly reported model of channel evolution in response to urbanization is a sequence of channel incision, and bank failure to create a deeper, wider channel, followed by re-establishment of a lower floodplain or channel system (e.g., Hawley et al., 2020). However, channel responses can vary depending on initial conditions and constraints, such as slope and erodibility of bed and bank materials, multi- vs. single-thread channels (Booth and Fischenich, 2015), and road crossings (e.g., Taniguchi et al., 2018). Concerningly for restoration potential, if a channel has enlarged, erosive hydraulic conditions are likely to persist, even if flashy flows from the catchment are mitigated (Anim et al., 2019).

Water quality

Streams of urban catchments typically carry higher concentrations, and export larger loads of a greater diversity of contaminants than non-urban streams. This results from two overarching attributes of urban areas. First, cities and urban areas in general are remarkable global features for the amount and diversity of materials (e.g., water, food, chemicals, building materials) that their human populations import into them (Kennedy et al., 2007). As a result, urban areas have greatly increased sources and stores of potential pollutants to downstream waters. The second attribute is stormwater drainage, which when designed in its conventional form, greatly increases the likelihood that a spill of a chemical on an impervious surface will flow to its receiving water, or that leaf litter (and other litter), sediments and associated pollutants on urban surfaces will be carried to the stream during a rain event. Chemical and physical weathering of the carbonate-rich materials, such as concrete, that make up much of the urban built environment, add to the cocktail of pollutants that the drainage system delivers to receiving streams (Kaushal et al., 2017). Groundwater flows can also contribute to stream pollution (Roy and Bickerton, 2012), particularly when stormwater (or imported water) are directed to catchment soils at greater rates than can be used by catchment vegetation. Stormwater and groundwater pollution will be worsened if untreated wastewater also mixes with these water sources. And finally, effluents from wastewater treatment plants can be a source of some pollutants.

The combination and quantity of contaminants in urban stream water are highly variable, given the diversity of potential sources and processes. In addition to contaminants, temperature is an important element of water quality, as a fundamental regulator of chemical transformations in catchments and streams (Kaushal et al., 2014a) and of in-stream biological processes. Efficient drainage of water from warm impervious surfaces and the widened channels and often cleared streamside vegetation of streams in urban catchments result in elevated stream temperatures (Somers et al., 2013).

Nitrogen enrichment from human activities is a growing global problem to which streams of urban catchments are significant contributors (Bernhardt et al., 2008). Atmospheric deposition of nitrogen, which is the primary source of nitrogen in natural catchments, is augmented in urban catchments by nitrogen in imported water, food and chemicals. Urban stormwater drainage delivers catchment nitrogen to streams from diverse sources such as: leaks, cross-connections, or combined flow paths with sanitary sewer systems; deposition on roofs and roads, which can be heightened from vehicle exhausts (Bettez and Groffman, 2013); or garden fertilizers through volatilization and deposition or flow to drainage or groundwater (Kaushal et al., 2020). Nitrogen seepage to groundwater, particularly as mobile nitrate-nitrite, from septic tanks (Walsh and Kunapo, 2009; Kaushal et al., 2006) or from leaky sanitary sewers can also contribute to increased dry-weather concentrations. Drainage systems and the compacted soils of urban catchments tend to reduce the opportunity for nitrogen transformation processes, such as denitrification—which reduces dissolved nitrate to gaseous nitrogen—although areas such as urban riparian groundwaters can act as hotspots for such processes.

Urban catchments are also rich in sources of phosphorus (e.g., food, sewage, fertilizers), which can lead to increased concentrations in streams. Phosphorus from these and other sources, particularly fine sediments on impervious surfaces, can be efficiently transported by stormwater drainage systems. Increased phosphorus concentrations can lead to increased algal and microbial growth. Unlike nitrogen, which can be lost from aquatic ecosystems through denitrification, phosphorus can only be removed by biological uptake, sorption onto particles that are then buried, or incorporation into a mineral that is precipitated. Sorption onto particles can be negatively affected by other chemical processes such as increased salinity (Kaushal et al., 2020).

Increased salinity is a particular problem where road salting is common practice (e.g., Wallace and Biastoch, 2016), potentially collecting in groundwater and chronically increasing salinity levels throughout the year (Cooper et al., 2014). However, increased salt concentrations are also observed in urban areas without snow accumulation, as a result of sewage inputs (Kaushal et al., 2014b) and leaching and weathering from built surfaces, particularly concrete (Wright et al., 2011; Kaushal et al., 2017). The weathering of concrete tends to make stream water more alkaline, typically affording streams in urban catchments a strong acid neutralization capacity. As a result, streams of urban catchments can remain alkaline, even in cases where disturbance of catchment soils has resulted in soil acidification (Kaushal et al., 2020).

Streams of urban catchments also tend to be enriched with dissolved organic matter with low molecular weight compared to humic organic matter that is more common in natural streams (Kaushal et al., 2020), potentially driven by increased algal growth

Table 1 Selected sources of trace elements in the urban built environment and the typical dominant elements for each source.

Urban source	*Trace elements*
Gasoline combustion	Pb, Mn
Coal combustion	V, Ni, Cr, Pb, Mn, Zn, Cu, As, Mo, Sb, Ti, Hg, Cd, Se, Mo
Oil combustion	V, Ni, Cr, Pb, Mn, Zn, Cu, As, Mo, Sb, Ti, Cd
Refuse incineration (highly variable)	Pb, Zn, Cr, Mn, Cu, As, Ni, Hg, Sb, Sn, V, Se, Cd
Municipal wastewater treatment	Mn, Ni, Zn, Cr, Cu, As, Pb, Cd
Sewage sludge	B, Cr, Pb, As, Zn, Sb, Sn
Motor oil	V, Zn, Cr, Cu, Pb, Ni, Mo
Vehicular and industrial discharge	Zn, Pb, As, Cr, Cu
Vehicle brake and tire wear	Cd, Cu, Zn, Pb, Sb, Ni, Zn
Leakage from pipes	Sr, Se
Corrosion of metal objects	Mn, V, Co, Mo
Atmospheric deposition	Pb, Zn, Cu, Ni, As, Mn, Cr, V

Adapted from Kaushal SS, Wood KL, Galella JG, Gion AM, Haq S, Goodling PJ, Haviland KA, Reimer JE, Morel CJ and Wessel B (2020) Making 'chemical cocktails'–Evolution of urban geochemical processes across the Periodic Table of elements. *Applied Geochemistry* 119: 104632.

(Imberger et al., 2014). They also typically carry trace-level concentrations of a cocktail of synthetic organic compounds, such as pesticides, polycyclic aromatic hydrocarbons, and legacy contaminants including polychlorinated biphenyls. Compounds such as steroidal hormones, pharmaceuticals and chemicals found in personal care products are also common, presumably associated with sewage contamination.

The complex cocktail of pollutants also includes elevated concentrations of a vast array of metals (Table 1), delivered efficiently to streams by stormwater drainage systems. The mobility and toxicity of metals are modified by interactions with other contaminants, particularly inorganic and organic colloids. More broadly, the complex mixture of pollutants interact in many ways, including potentially synergistic effects in their effects on stream biota. Management of such complexity is likely to only be possible through a holistic approach that seeks shared sources, transport mechanisms and transformation processes (Kaushal et al., 2020).

Biology

The inter-related effects of physical disturbances resulting from altered flow and sediment regimes and altered channel forms, reduced habitat heterogeneity, and the complex changes to stream chemistry in both storm and base flows result in substantial changes to in-stream biotic communities. These changes are typified by loss or reduced abundance of sensitive species, increased abundances of (usually fewer, often cosmopolitan or invasive) tolerant species, and altered ecosystem processes (Paul and Meyer, 2001; Walsh et al., 2005b).

Microbial assemblage composition both in the water column and in stream sediments shifts with increasing urban impacts, including altered composition of denitrifying bacteria assemblages, possibly mediated by changed sediment size (Perryman et al., 2011). Hosen et al. (2017) concluded that microbial community composition in the water column is driven by regional factors related to watershed land use, while sediment bacterial community composition is more strongly controlled by local physicochemistry. Function of microbial assemblages can also be affected by urbanization. Microbial biofilm communities of urban streams in Baltimore streams have developed drug resistance, maintaining respiration rates in response to pharmaceutical exposure that depresses respiration in less urban streams (Rosi et al., 2018). Pathogenic microbes can also be found in streams of urban catchments from variable sources such as animal feces on impervious surfaces washing into stormwater drainage systems, through sewage contamination of stormwater flows, and through discharge of inadequately treated sewage (Ahmed et al., 2019).

Increasing urban impacts also shift the composition of algal assemblages on stream beds, with tolerant species replacing sensitive species, often with little change in species richness, both in streams dominated by stormwater flows (Sonneman et al., 2001; Newall and Walsh, 2005) and those with sewage pollution (Tornés et al., 2018). In severely degraded streams, streambeds can be covered by mats of organic matter, cyanobacteria, iron bacteria, sewage fungus, and algae, replacing the basal food sources such as leaf-litter and biofilms that are typical of less disturbed streams (Faulkner et al., 2000; Yule et al., 2015). Increased light and nutrient concentrations associated with stormwater runoff tend to increase algal growth (Taylor et al., 2004). For example, under controlled conditions of light, algal growth increased with increasing effective imperviousness (Catford et al., 2007). Physical scouring by frequent stormflows can reduce algal growth, but algal regrowth can be rapid (Murdock et al., 2004). However nutrient concentrations in stormwater are variable: a mesocosm study of differing concentrations of collected stormwater found no difference in algal growth, but substantial difference in algal assemblage composition with different amounts of stormwater (Johnson et al., 2011) The effects of nutrient enrichment on algae can also be countered by herbicide pollution (Waite et al., 2019).

The diversity of stream invertebrates declines with increasing urban impacts, with many sensitive species becoming rare or absent in streams with as little as 2.5% effective imperviousness (Walsh and Webb, 2016; King et al., 2011). Mayflies, stoneflies and caddisflies are commonly cited as sensitive taxa, but sensitive species occur in all taxonomic groups, including groups such as oligochaete worms that tend to be dominated by species that are tolerant to disturbance. The diverse group of sensitive species is

replaced by a smaller group of tolerant species dominated by oligochaetes, chironomid midges, and gastropod snails. Where it has been measured, stormwater drainage connection explains the shifts in invertebrate assemblages better than simple measures of urban density (Walsh, 2004; Baruch et al., 2018). The invertebrates that can tolerate urban stormwater impacts tend to contain higher levels of contaminants such as metals in their tissues (Baruch et al., 2018). Stormwater impacts to invertebrates are worsened by intermittent flow (King et al., 2016) and by barriers to dispersal such as road culverts or lack of catchment forest cover (Smith et al., 2009; Blakely et al., 2006). Stormwater impacts on invertebrate assemblages can be ameliorated to some extent by improved habitat afforded by riparian vegetation (Walsh and Webb, 2016). In Perth, Australia, where the landscape is highly permeable, stormwater infiltration is common, and the regional pool of invertebrate taxa is small, riparian vegetation was found to be a stronger determinant of invertebrate assemblages than urban density (Gwinn et al., 2018).

Fish assemblages also shift with increasing urban impacts, with sensitive species being replaced by more tolerant, often exotic species (e.g., Roy et al., 2005; Meador et al., 2005; Pompeu et al., 2005). Fish species of urban streams tend to be backwater, substrate-generalist species rather than riffle specialists associated with boulders and gravel (Brown et al., 2009a). However, such effects are less pronounced in coastal tropical streams, where diadromous species (i.e., those that migrate between the sea and streams) dominate assemblages (Ramirez et al., 2012; Lisi et al., 2018). For such species, local physical habitat conditions can be more important determinants of their abundance than catchment urbanization (Engman and Ramirez, 2012). Exotic species can be more abundant in such urban systems during drought (Ramírez et al., 2018). More broadly, mobile species such as many fish (and the stream-dependent platypus in Australia: Martin et al., 2014) can inhabit streams with high degrees of catchment urbanization if there is connectivity with a meta-population in less disturbed streams (Czeglédi et al., 2020). Nevertheless, there are diadromous species that are very sensitive to urban stormwater impacts (e.g., Puget Sound coho Salmon in Washington USA: Scholz et al., 2011).

Stream-dwelling amphibians are also susceptible to urban impacts. The complex inter-related effects of urban stormwater are likely to be primary drivers of declines in stream amphibian populations. Barrett et al. (2010) demonstrated that increased flow disturbance was a primary mechanism for loss of larval two-lined salamanders, whereas Canessa and Parris (2013) inferred that the effects of urban stormwater were indirect via its negative effect on aquatic vegetation. Other factors potentially causing decline in stream amphibian richness include barriers to movement such as roads (Canessa and Parris, 2013) and predation by invasive species (Riley et al., 2005).

These changes to the structure of biotic communities in streams affected by urban land use are associated with a range of changes to ecosystem function. However, studies seeking relationships between measures of ecosystem function and those of urban land use are less common than studies of biological structure, making generalizations difficult. Gross primary productivity (GPP) was higher in urban streams than reference streams across the US, but there was no difference among land use categories for ecosystem respiration (ER) (Bernot et al., 2010). The ratio of GPP to ER was higher in urban streams than rural streams in Japan (Iwata et al., 2007). GPP and ER are both greatly reduced by stream burial (Pennino et al., 2014). Increased volumes and flashiness of flows with urbanization lead to greatly reduced retention of contaminants in catchments. Contaminant retention, including denitrification, at least during low flows, can be increased where water can interact with sediments, in the catchment, in the stream or through floodplain soils (Newcomer Johnson et al., 2014). Denitrification is also affected by the changes in carbon sources that typify urban areas (Newcomer et al., 2012). Mechanisms by which leaf litter in streams is broken down changes under urban impacts, in that shredder invertebrates tend to be less abundant, but microbial breakdown and physical abrasion from flows both increase (Imberger et al., 2008; Paul et al., 2006). Snails that scrape biofilms from leaf material may also play an increased role in breakdown (Xiang et al., 2019).

Protection and restoration

Despite this chapter's focus on the severe impacts of typical urban land and water management practices, there is evidence that stream ecosystems need not be strongly degraded in urban catchments. For instance, Sassafras Creek on the eastern edge of Melbourne has 8% of its catchment covered by impervious surfaces, but there is very little piped infrastructure, with almost all runoff being directed informally to the deep forested soils of the catchment upslope of the creek. The flow regime, water quality and stream biota of the creek closely resemble those of comparable undeveloped catchments nearby, except for elevated nitrate concentrations from its septic tanks (Walsh et al., 2012; Hatt et al., 2004; Walsh, 2004). This unplanned protection of a stream from its catchment's urban development points to the potential for protection and restoration of other urban streams, if urban water were to be managed differently.

However, this example is a rare exception to the general observation that streams of urban catchments support fewer species and provide lesser ecosystem services than comparable streams without urban impacts. Substantially improving the state of the world's urban streams will require systemic changes to urban land and water management practices. The challenge of reducing loads of pollutants flowing into streams could be aided by reducing imports of resources (water, food, chemicals, building materials) into cities (Kennedy et al., 2007), requiring increased uptake of local production, recycling and reuse. A primary water management imperative is the prevention of untreated sewage or wastewater flows into streams and minimizing treated wastewater flows. However, even with wastewater well managed, streams of urban areas will remain degraded if urban stormwater runoff is permitted to drain uncontrolled to them.

Technologies for low-impact stormwater management are well developed and widely applied around the world (Fletcher et al., 2015). However, they have rarely been applied at a scale and intensity that is required for stream protection. Walsh et al. (2016a)

proposed that stormwater management for stream protection requires mimicking the predevelopment water balance of evapotranspiration, stream flow and infiltration through the application of stormwater control measures that filter runoff from all catchment impervious surfaces, providing filtered flows in a pattern and quality similar to the predevelopment flow and water quality regime. Achieving such aims requires the use or loss of a large proportion of urban stormwater runoff to prevent it from becoming stream flow, which would subsequently present a large, largely untapped freshwater resource for the world's cities (Walsh et al., 2012). Water supply is only one of many co-benefits to human populations that could be gained by stormwater management for stream protection (Walsh et al., 2016a).

Transformation of urban water management is an aim that remains elusive in most of the world. Yet, some benefits to stream ecosystems can be accrued through smaller-scale management actions (Smith et al., 2016). Reduced habitat heterogeneity of streams is often compounded in urban settings by clearing of riparian vegetation. Loss of riparian trees increases erosion of banks, and together with widened channels, increases light falling on the stream and temperature of stream water, and decreases inputs of leaf litter and woody debris. While several studies have found that the effects of riparian vegetation on stream ecosystems are diminished by catchment urbanization (e.g., Roy et al., 2007; Walsh and Webb, 2016; White and Walsh, 2020), taxa that are tolerant to some degree of urban impacts are benefitted by riparian forest cover (Walsh and Webb, 2016; Gwinn et al., 2018) or by an increase in habitat complexity (White and Walsh, 2020). Riparian forest can also improve water quality (Middleton et al., 2020), and re-engaging flow through floodplain soils can increase soil denitrification rates (Newcomer Johnson et al., 2014).

Small-scale restoration of habitat heterogeneity remains a common management action on streams of urban areas despite the overarching mismatch between the small scale of the action, and the large catchment-scale of the problem (Bernhardt and Palmer, 2011). However, examples of stream protection or restoration through better stormwater management at the catchment scale are increasingly common (Roy et al., 2014; Walsh et al., 2015; Hopkins et al., 2020). Increasing uptake of new approaches to stormwater management brings hope that the nexus between cities and towns, and degraded streams and rivers can be broken, but it will require changes to governance and economics. This will require new approaches to planning, including more landscape ecological input into planning processes to permit reservation of important parts of the landscape for ecosystem services of water and contaminant retention. It will also require that construction and maintenance of drainage become an integral part of broader urban water management to allow increased harvesting and use of stormwater. To accelerate the process of change, stronger scientific evidence is required. Such an aim calls for better standardization and adoption of more causal measures of urban impact on streams (such as effective imperviousness), and more experimental studies to assess and improve the efficacy of stormwater control and other management approaches across the world's cities.

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Effects of Dams on Rivers

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Bedload The part of the sediment load transported by a river that occurs near the channel bed and intermittently bounces or rolls along the bed. Typically, bedload is medium and coarser sand, gravel, cobbles, and boulders.
Edge habitat The transition zone between the area directly affected by a dam and reservoir and distant unaffected areas.
Epilimnion The upper layer in a stratified reservoir.
Hydropeaking The practice of releasing water from a reservoir to produce hydroelectricity during times of day when demand for electricity is greatest.
Hypolimnion The lower layer of a stratified reservoir, typically cooler and more saline than higher layers and more stagnant.
Penstocks The pipes at a dam that carry water from a reservoir to the powerplant and turbines where electricity is generated.
River outlets The pipes at a dam that carry water from the reservoir directly downstream and by-pass the powerplant. Typically, these facilities are used in emergencies and to generate occasional controlled floods.
Suspended load That part of the sediment load of a river that is transported aloft in the stream flow and is supported by the turbulence of the fluid. Typically, the suspended load is medium and finer sand, silt, and clay.
Tailwaters The thermally altered regulated river immediately downstream from a dam.

Introduction

Damming of rivers is "one of the most dramatic and widespread deliberate impacts of humans on the natural environment" (Petts, 1984; Dynesius and Nilsson, 1994). A large body of scientific and management literature has emerged during the past 40 years that documents the many ways that dams, and the associated reservoirs and off-channel diversions, have altered natural riverine ecosystems.

The impacts of dams are widespread. The World Commission on Dams (2000) reported that there are more than 45,000 large dams, and the National Inventory of Dams for the United States listed 91,457 barriers (U. S. Army Corps of Engineers, 2020). The total active storage of the world's reservoirs is 9% of the natural flow of the affected rivers, and reservoir storage greatly exceeds mean annual flow in some places, such as the Riviere Manicouagan, Colorado River, Rio Grande, and La Grande Riviere in North America (Hirsch et al., 1990; Dynesius and Nilsson, 1994). Vorosmarty et al. (2003) estimated that 25–30% of the total natural flux of sediment is now trapped in reservoirs and is not delivered to the sea.

Metrics that describe the size and significance of dams

Dams are typically described by their height, reservoir storage capacity in relation to mean annual inflow, the capacity of the dam's withdrawal structures in relation to the pre-dam flood regime, and the elevation and adjustability of the dam's withdrawal structures. The World Commission on Dams (2000) defined large dams as any constructed barrier whose height is at least 15 m, or barriers at least 5 m high and whose storage capacity is at least 3×10^6 m^3. Hirsch et al. (1990) identified the ratio of watershed reservoir storage to mean annual flow as representative of the ability of dams to regulate and transform the natural flow regime. They calculated this ratio for the 36 water resource regions of the United States and Canada and showed that the Colorado River basin has the largest ratio of 3.34. Other regions where the ratio is >1 are the upper Colorado River, Rio Grande, South Saskatchewan, Missouri, and Churchill. Batalla et al. (2004) referred to this ratio as the *impounded runoff index* and calculated this value for 38 gage sites in the Ebro River watershed in northeastern Spain. Singer (2007) modified this ratio by changing the denominator to the median annual flood volume, rather than the mean annual flow. Although there have been no comprehensive classifications of dams by capacity or elevation of withdrawal structures, the ratio of the maximum capacity of the penstocks to the mean annual pre-dam flood characterizes the ability to regulate floods. Dams that can release water from the bottom of reservoirs have the ability to flush sediment downstream, whereas dams with higher elevation release structures cannot. The Three Gorges Dam on the Yangtze River is the largest dam in the world with low elevation river outlets that allow sediment flushing downstream (Ren et al., 2021). Another metric that describes the significance of dams is the proportion of a river's length that has been converted to reservoirs.

The many effects of dams and reservoirs

There are three attributes of dams that affect rivers and river ecosystems: the direct effects of the existence of dams, the effects of depletions or additions of stream flow facilitated by dams, and the effects of reservoir operations (Fig. 1). It is useful to distinguish these different effects, because it is typically cheaper and less controversial to change operations than it is to remove or re-engineer infrastructure.

The primary effect of the existence of dams is fragmentation of the channel network. The degree of fragmentation depends on the height of each structure (Fuller et al., 2015). Tall dams are complete barriers to the movement of most organisms, and the large reservoirs created by these dams transform the river upstream from each barrier. Reservoir releases may affect water quality and ecosystems for 100s of kilometers downstream. Shorter dams, including diversion dams, are typically more permeable barriers, do not block the movement of most organisms at high discharge, and the downstream effects typically extend for shorter distances.

Other effects of dams are caused by the style of reservoir operation that might be for flood control, hydroelectricity generation, or provision of a water supply. Some effects are transitional between those associated with the existence of the infrastructure and those with operations. For example, the existence of large dams allows the incoming sediment and organic matter loads to be trapped, and the trap efficiency partly depends on the size of each reservoir in relation to the magnitude of the incoming flow. However, trap efficiency also depends on how each reservoir is operated, because reservoirs that vary greatly in water storage during the year are less efficient in trapping sediment than reservoirs that maintain relatively constant storage contents (Kondolf et al., 2014a).

Another example of transitional effects of dams concerns the temperature of reservoir releases. These effects depend on both the size of the dam and on reservoir operations. Large reservoirs thermally stratify in summer. If the engineering structures that release water downstream are at a fixed elevation, as is typically the case, then the released water from the reservoir's hypolimnion when the reservoir is relatively full is cooler than is naturally the case in summer. However, the temperature of summer releases is warmer

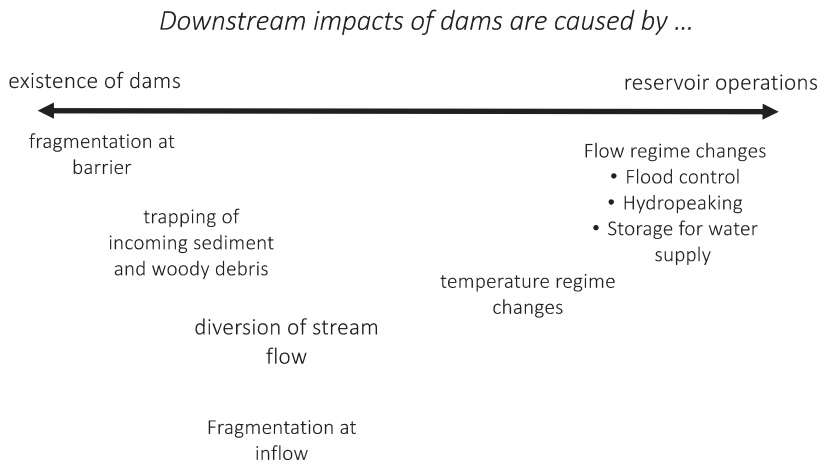

Fig. 1 Types of impacts caused by dams.

if the reservoir is relatively empty, and water is drawn from the epilimnion. Water is warmer in the winter and may reduce the frequency of downstream ice cover. Additionally, releases from the epilimnion have the potential of entraining reservoir fish and delivering those species to the downstream river environment.

Stream-flow diversion is often facilitated by reservoirs, and the reduction in total annual flow may disproportionately reduce the magnitude of floods or base flows. Depletions of flood flow reduce sediment transport and may lead to downstream channel aggradation if the sediment supply exceeds the transport capacity of the regulated flow. Conversely, augmented stream flows associated with trans-basin delivery to an adjoining watershed increases the flow regime of the receiving stream, potentially causing increased sediment transport capacity and channel enlargement.

Reservoir operations are the primary control on the downstream flow regime of regulated rivers. Operations that emphasize flood control maintain relatively low reservoir storage when the flood season begins and have an objective to store the incoming flood within the reservoir. Operations that emphasize water supply typically maintain relatively full reservoir storage. Operations that emphasize hydroelectricity production increase reservoir releases in those months and hours when electricity demand is greatest.

Effects of the existence of dams

Fragmentation

Although river networks can be naturally fragmented by waterfalls, cascades, or beaver dams, barriers constructed or caused by humans have significant impact on the world's freshwater ecosystems (Benke, 1990). Dynesius and Nilsson (1994) found that 77% of the total discharge of the large rivers of the northern third of Earth are strongly or moderately affected by dam-caused fragmentation. Barriers affect biodiversity by blocking the movement of organisms, and the degree of blockage is called barrier permeability. Another way that biodiversity is affected is that the perturbations in flow, sediment supply, and thermal regimes caused by dams and reservoirs that are described below can persist far downstream. The area where these perturbations are significant constitute *edge habitat*, defined as the transition zone between the area directly affected by each barrier and reservoir and distant areas whose flow, sediment supply, and thermal regimes are unaffected (Fig. 2). The entire mainstem of many extensively developed rivers is edge habitat (Fuller et al., 2015).

Large dams are impermeable to upstream migrating fish and aquatic organisms, unless fish passage structures such as fish ladders are constructed. On the Columbia River, for example, such structures have been built at many mainstem dams to facilitate the spawning migration of salmon upstream to the points where Grand Coulee Dam and the Hells Canyon complex of dams completely block migration. Elsewhere, mitigation strategies have been proposed to increase barrier permeability by trucking fish around barriers and reservoirs, such as on the Yuba River in California (Yuba Water Agency, 2020).

Large reservoirs created by high dams may be impermeable to downstream migrating fish and other aquatic organisms, especially where native fish larvae or juvenile fish are prey for nonnative reservoir fish or where larvae cannot swim across long reservoirs. Nevertheless, these barriers are not completely impermeable, and non-native reservoir fish can be entrained in the penstocks that transfer water through turbines that generate hydroelectricity. Even though the survival rate of these fish may be very low, this mechanism is one way that competing and predatory non-native fish invade a native fish community downstream from a dam. Low dams, including diversion dams, may only be impermeable to upstream migration of fish at very low flow.

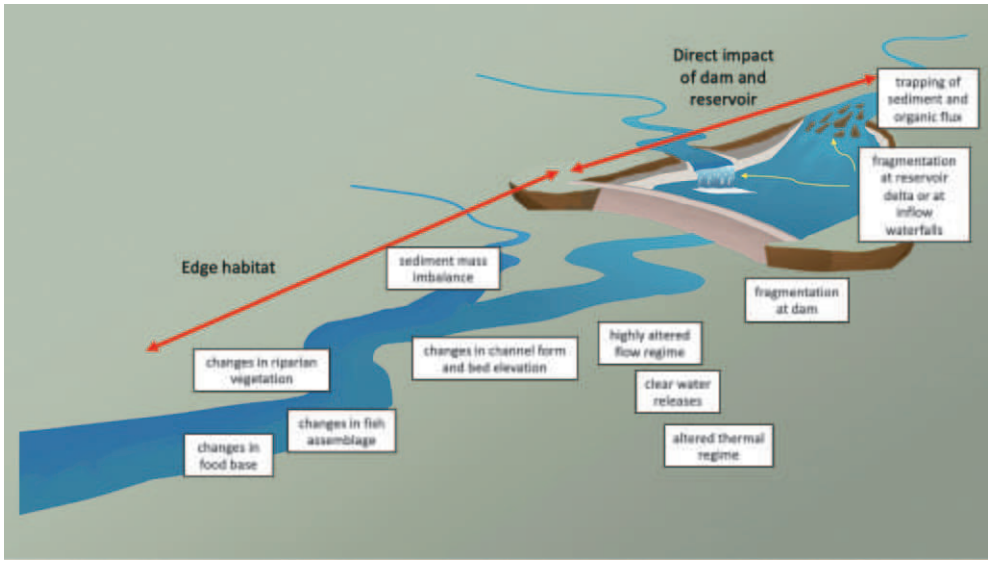

Fig. 2 Diagram showing geographic extent of effects of dams and reservoirs.

In the absence of large tributaries that enter a regulated river downstream from a large dam, edge effects may extend far downstream. For example, the flow regime and temperature of the Colorado River 400 km downstream from Glen Canyon Dam is highly perturbed from natural conditions, because more than 90% of the river's annual flow is released from the dam, and there are few tributaries that contribute supplemental flow.

Another aspect of edge effects is the change in channel form, especially incision or aggradation of sediment and associated changes in channel form that occur where there are large changes in flow and sediment supply regimes. These changes in channel form, and in aquatic and riparian habitat, are discussed below.

Where reservoir storage has decreased due to decreased inflow and/or increased consumptive uses and where there has been a large amount of sediment deposited in reservoirs, fragmentation has occurred in the reservoir inflow areas. For example, the delta of Lake Mead, the largest reservoir in the United States, is 70-m thick. In 2021, Lake Mead was ~30% of capacity and was ~47 m below the elevation when the reservoir is full. The inflowing Colorado River had incised a new channel into the delta, crossing a ledge of resistant bedrock that formed Pearce Ferry Rapid, which is unnavigable. The same had occurred in the San Juan River arm of Lake Powell, the second largest reservoir in the United States (Cathcart et al., 2018).

The ecological implications of this type of fragmentation depends on their longevity, and longevity depends on whether reservoirs remain low or refill and inundate the fragmentation. The waterfalls and steep rapids in the inflow areas are of value to native fish assemblages in some places, because they block upstream migration of non-native, warm water, reservoir fish into the upstream river ecosystems, thereby limiting competition and predation on native species. This is the case in western Grand Canyon, immediately upstream from Lake Mead, where the native fish assemblage is of high value (Kegerries et al., 2020). Conversely, valued native fish successfully occupy reservoir habitat elsewhere but cannot access spawning habitat because of this type of fragmentation, such as in the San Juan arm of Lake Powell (Cathcart et al., 2018).

Transitional effects caused by the existence of dams and by their operation

Changes in downstream sediment supply caused by trapping of sediment and organic flux

The trap efficiency of a reservoir is the ratio of the incoming sediment to that deposited in the reservoir. The proportion of incoming sediment deposited in a reservoir is determined by the size and fall velocity of the incoming sediment, the rate of flow through the reservoir, the distance between the points of significant inflow and the dam, the elevation at which water can be released from the reservoir, and the rules of reservoir operations. Typically, all the bed load and a proportion of the suspended load transported into a reservoir is trapped (Kondolf, 1997), and the trap efficiency of suspended load is generally proportional to the ratio of reservoir storage to inflow (Brune, 1953). Higher ratios of reservoir storage are associated with more effective trapping.

Sedimentation in some large reservoirs of the western United States has the potential to adversely affect water storage. Graf et al. (2010) evaluated 6 dams on the mainstem Missouri River and estimated that the life of these reservoirs varied between 240 and 1250 years. Gavins Point Dam, whose life expectancy is the shortest, is nevertheless estimated to remain functional until the end of the 21st century. The estimated life of Lake Powell is 300–700 years, and the reservoir's delta at the inflow of the Colorado River has advanced ~50 km. This reservoir is ~300 km long at full capacity.

Changes in thermal regime

Most large reservoirs created by large dams thermally stratify in summer, such as at Lake Powell (Vernieu et al., 2005), and released water typically comes from the hypolimnion (Fig. 3). These waters are typically cooler than ambient summer conditions, creating unfavorable conditions if the life history of some native species are dependent on warmer, unregulated conditions. Cool releases, however, may be advantageous to nonnative salmonid species that have been introduced to many tailwaters for sport fishing. The ecological effect on the upper Colorado River's ecosystem was described by Ward and Stanford (Ward and Stanford, 1983; Stanford and Ward, 2001), and Dibble et al. (2021) estimated summer conditions throughout the Colorado River system (Fig. 4). The large dams of the Colorado River were primarily built between the 1930s and the 1960s, and the penstocks that transfer water from those reservoirs to their respective powerplants are at fixed elevations (Fig. 3). As reservoir storage declines, release temperatures are increasing because the penstocks are withdrawing water that is closer to the epilimnion.

Effects by reservoir operations

Changes in flow regime

Changes in the flow regime caused by dams are related to the purpose of each reservoir that determines the rules of reservoir operation (Williams and Wolman, 1984). The ratio of the storage capacity of each reservoir to the inflow determines the flexibility in reservoir operations, and the size of the dam and its reservoir is typically determined by the purpose of the structure. For example, the changes in flow regime downstream from a flood control reservoir differ from a reservoir operated to provide irrigation or municipal water supply. In some cases, water is diverted directly from a reservoir, and the total volume of downstream flow is less that the volume of incoming flow, but, in other cases, the total volume of flow is not changed.

The natural flow regime of any river can be categorized into five components (Poff et al., 1997), and reservoir operations can affect each of these attribute categories. These components are the magnitude, frequency, duration, timing, and rate of change of high and low flows. Richter et al. (1997) identified 21 hydrologic parameters among these five components and proposed a methodology, the *Indicators of Hydrologic Alteration*, to quantify the degree of change in the natural flow regime caused by reservoir

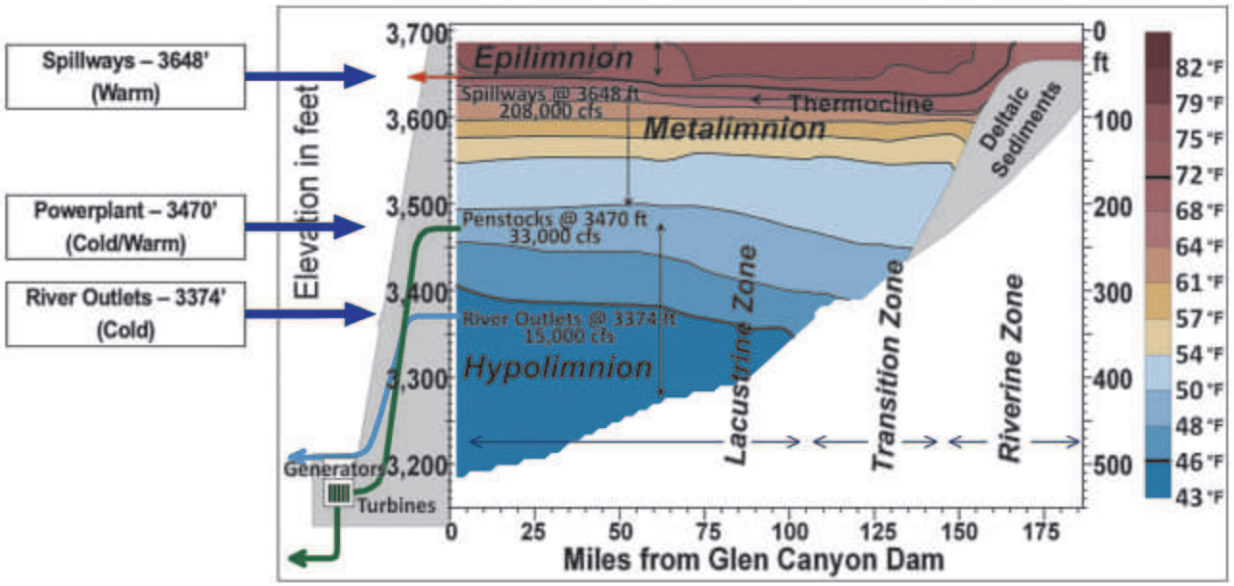

Fig. 3 Diagram showing summer thermal structure of Lake Powell when the reservoir is relatively full. There are three facilities by which water is released downstream. Most water is withdrawn through penstocks into the powerplant where hydroelectricity is produced. The river outlets that by-pass the powerplant are occasionally used to increase releases. The spillways can only be used when the reservoir is completely full. Each facility withdraws water of different characteristic temperature. From Vernieu WS, Hueftle SJ, and Gloss SP (2005) Water quality in Lake Powell and the Colorado River, in *The State of the Colorado River Ecosystem*. Grand Canyon SP, Gloss JE, Lovich and Melis TS (eds.) *U.S. Geological Survey Circular 1282*, p. 69–85. Maximum release volumes (in cubic feet per second) are given for each facility.

operations or other perturbations. Subsequent studies have identified parameters most sensitive to reservoir operations (Table 1). These differences are primarily related to the different purposes of reservoirs, as recognized by Williams and Wolman (1984), who stated "The uniqueness of release policy at each dam precludes simple generalizations about the discharge distributions, except that flood peaks will be decreased." Some recent studies (Batalla et al., 2004; Singer, 2007) characterized the downstream extent of flow regime changes, essentially quantifying the extent of edge habitat. Poff et al. (2007) demonstrated that reservoir operations are homogenizing the natural distinctness of flow regimes that arises from the different climate and geology of parts of the United States.

Another significant change to the flow regime of many rivers is caused by fluctuation of reservoir releases to match hydroelectric power demand, which is called *hydropeaking* or sometimes called load following. The intensity of hydropeaking has been estimated by the hydropeaking index, defined as the daily coefficient of variation in discharge averaged over five or more years (Dibble et al., 2015; Kennedy et al., 2016). Typically, reservoir releases are lowest at night and increase in early morning (Fig. 5). Production of hydroelectricity also affects the monthly flow regime, because reservoir releases are typically highest in months of highest demand. In the Intermountain West, those months are winter to meet heating needs and summer to meet the demands of air conditioning. There is speculation that the shift to renewable energy has the potential to shift the hourly pattern of energy demand, such that the role of hydroelectricity in regional power grids may increase at night or on windless days. Such a change in hydropeaking might cause reservoir releases to vary erratically in response to weather patterns at the sites of renewable power production.

Downstream changes and consequences of dams and reservoirs

The downstream impacts of dams and reservoirs can be distinguished among the physical changes to the stream-flow and sediment-supply regimes that cause change in channel form, changes in water quality especially river temperature, and the biological consequences of these changes (Rood et al., 2005). Changes in the flow and sediment supply regimes may cause disconnection between the river and its floodplain either by reduction in the magnitude of floods or due to incision of the channel bed. The consequences of changes in the hydrologic and geomorphic systems may have significant consequences to the aquatic and riparian ecosystems far downstream from the dam.

Hydrologic and geomorphic changes

Disruption of the flow and sediment delivery regimes causes downstream changes in channel form that may extend hundreds of kilometers (Stevens, 1938; Borland and Miller, 1960; Schumm, 1969; Petts, 1979; Williams and Wolman, 1984; Andrews, 1986; Carling, 1988; Brandt, 2000a; Grant et al., 2003). Typically, channel response immediately downstream from dams involves

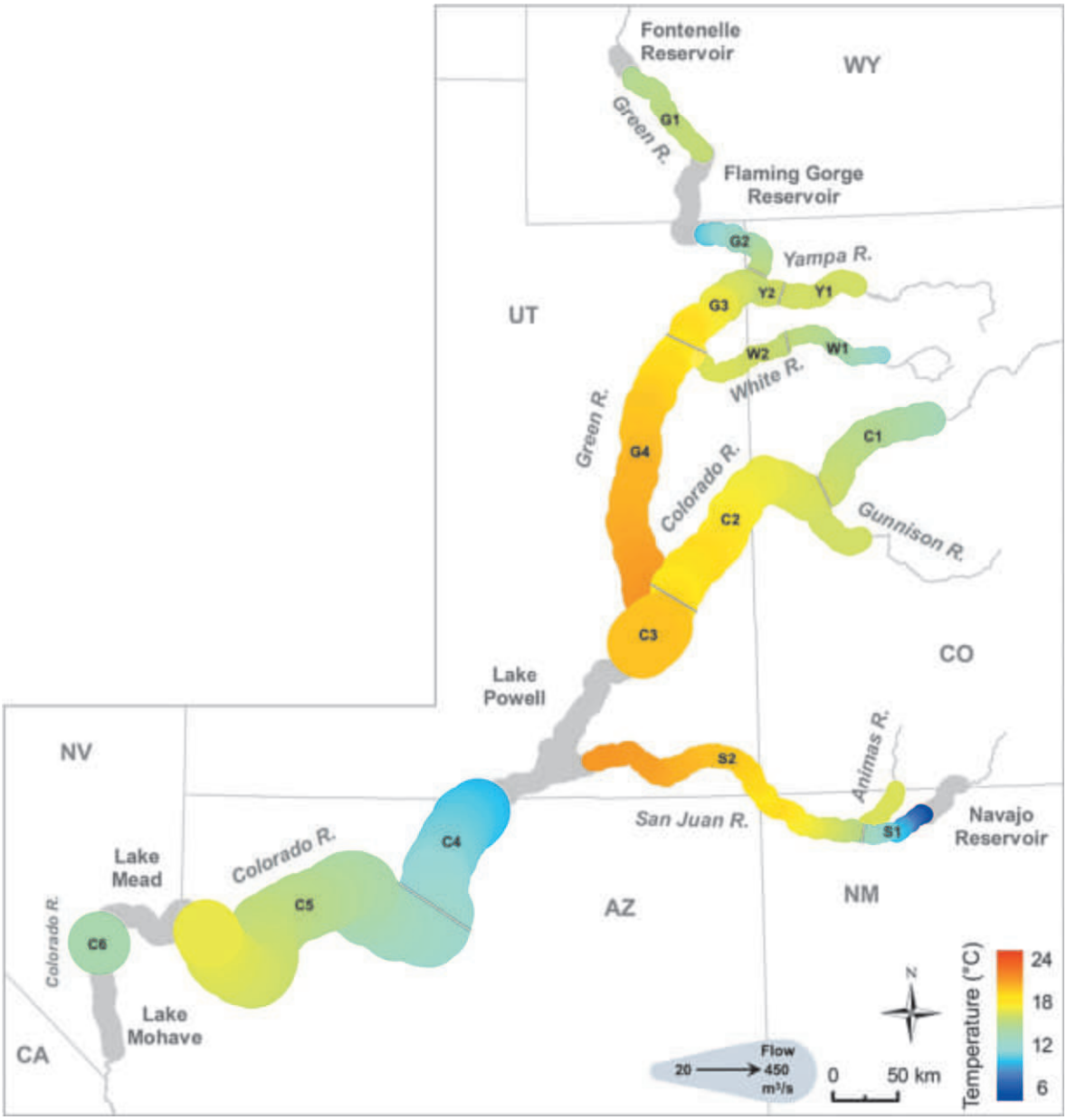

Fig. 4 Diagram showing predicted river temperature for the Colorado River upstream from Davis Dam and Lake Mohave reservoir. This figure demonstrates the releases of cool water that form the tailwaters of each reservoir and shows that river temperature gradually increases downstream from each dam. Color of each river segment represents the warmest growing season months, and the width of each segment is proportional to the mean monthly flow in summer. From Dibble KL, Yackulic CB, Kennedy TA, Bestgen KR, and Schmidt JC (2021) Water storage decisions will determine the distribution and persistence of imperiled river fishes. *Ecological Applications* 31(2): e02279, Fig. 1.

evacuation of sediment and may include incision of the bed (Fig. 6). Channel response further downstream may involve aggradation if unregulated tributaries deliver sediment to a regulated flow regime whose floods have been greatly reduced, as shown by Everitt (1993) (Fig. 7). Williams and Wolman (1984) summarized channel change in degrading reaches downstream from 21 dams in the western United States and developed empirical relations to predict the duration of incision and the magnitude of changes in channel width.

Brandt (2000a) summarized many case studies and identified nine styles of channel change involving either degradation or aggradation. Brandt (2000b) and Grant et al. (2003) suggested metrics that consider changes in both water and sediment supply. Brandt (2000b) predicted post-dam channel form from bed entrainment, sediment transport, extremal hypothesis, hydraulic geometry, and empirical relations. Grant et al. (2003) evaluated the relative effects of changes in flow and sediment delivery. They suggested that channel change is related to changes in the fractional change in duration of sediment-transporting flows and the ratio of sediment supply downstream from dams to the supply upstream from dams. Schmidt and Wilcock (2008) proposed three

Table 1 Hydrologic parameters significantly affected by reservoir operations.

Flow regime characteristic	*Hydrologic parameter (required data)*	
Magnitude, timing	Monthly flow regime (monthly mean flow)	Batalla et al. (2004)
Magnitude, duration	Annual minimum 1-day (mean daily discharge)	Singer (2007)
	Annual maximum 1-day (mean daily discharge)	Richter et al. (1998), Magilligan and Nislow (2001), Magilligan et al. (2003), Batalla et al. (2004), Poff et al. (2007), and Singer (2007)
	Annual minimum 1-day mean daily flow	Poff et al. (2007)
	Annual minimum 30-day flow (mean daily discharge)	Richter et al. (1998)
	Volume of flood flows above a threshold (mean daily discharge)	Singer (2007)
	Total annual flow (annual total flow)	Batalla et al. (2004)
	Flow standard deviation (i.e., annual duration of mean daily flows) (mean daily discharge)	Batalla et al. (2004)
Timing	Date of annual 1-day maximum flow (mean daily discharge)	Richter et al. (1998) and Poff et al. (2007)
	Date of annual 1-day minimum flow (mean daily discharge)	Richter et al. (1998)
Magnitude, frequency/ duration	Mean duration of high flow pulses (i.e., floods) (mean daily discharge)	Richter et al. (1998)
	Number of days mean daily flow exceeds a threshold (i.e., average annual maximum predam mean daily flow)	Poff et al. (2007)
	Number of days mean daily flow less than a threshold (i.e., average annual predam 7-day mean daily flow)	Poff et al. (2007)
Frequency, rate of change	Frequency of hydrograph reversals (mean daily discharge)	Richter et al. (1998)
	number of days in flood rise (mean daily discharge)	Singer (2007)
	number of days in flood recession (mean daily discharge)	Singer (2007)
	Number of days flows less than a threshold (mean daily discharge)	Singer (2007)
	Hydropeaking index (instantaneous discharge)	Kennedy et al. (2016)
Spatial extent of flow regime changes	Downstream persistence of flow changes (mean daily discharge)	Batalla et al. (2004) and Singer (2007)

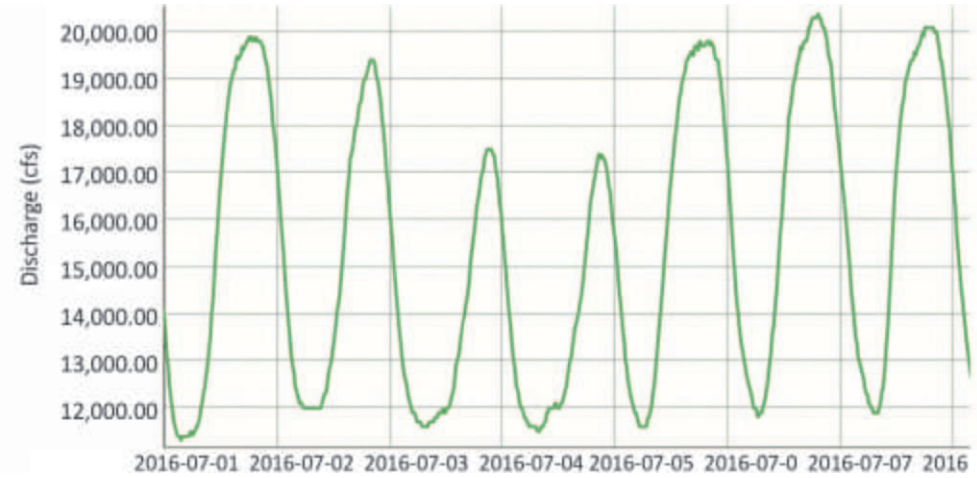

Fig. 5 Graph showing instantaneous hydrograph of 1 week of typical reservoir releases from Glen Canyon Dam in July 2016. July 3 and July 4 (7-03 and 7-04) are weekend and holidays when electricity demand was less.

metrics that they argued were the primary drivers of channel change. One metric represents the shift in balance between sediment supply and transport capacity and, thus, the tendency for sediment to accumulate or evacuate in channels. Another metric characterizes the post-dam stream competence and, hence, potential for channel incision. The third metric is the relative reduction in flood magnitude. Channel incision and flood reduction typically alter the inundation frequency of the pre-dam floodplain, thereby restructuring the disturbance regime and physical template of the riparian ecosystem. Flood reduction is also an important determinant of channel narrowing and the extent to which riparian vegetation invades the post-dam channel.

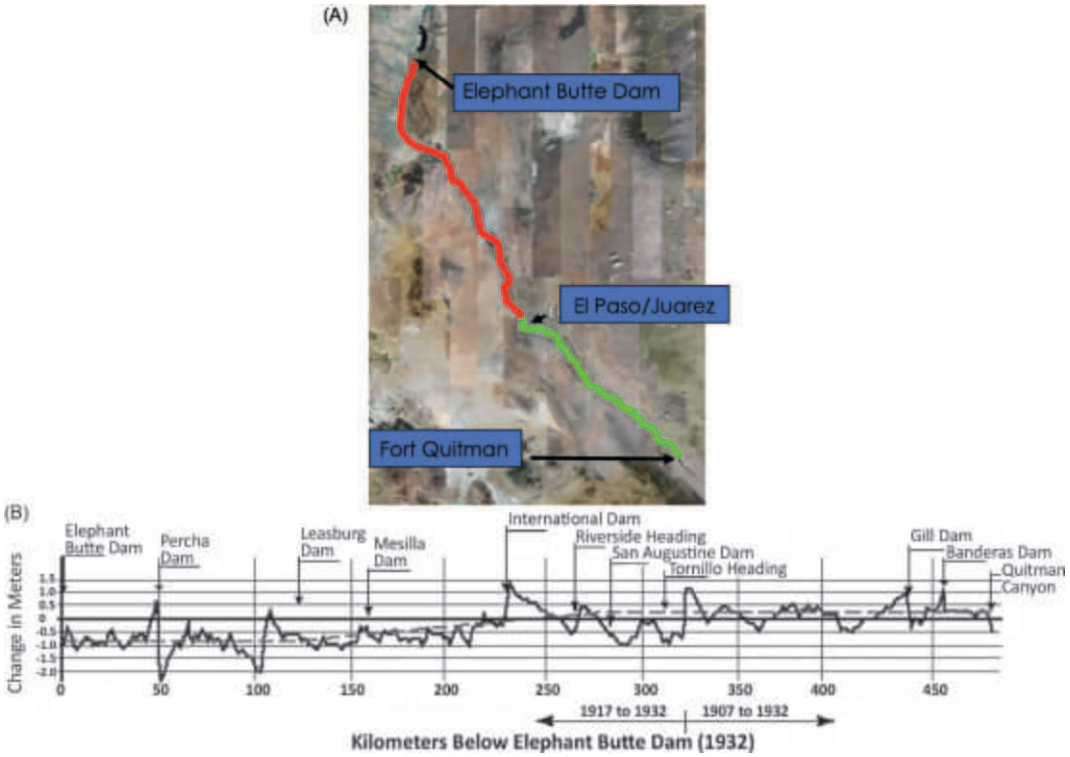

Fig. 6 Channel response to the existence and operations of Elephant Butte Dam and reservoir on the northern branch of the Rio Grande. A. Between 1917 and 1933, the Rio Grande incised its bed (in red) as much as 1 m within 225 km downstream from the dam, and the bed aggraded (in green) about 0.25 m further downstream. B. Change in water surface elevation between 1917 and 1932 for 300 km downstream from Elephant Butte Dam. Grey dashed line is the average change in elevation for 80 km segments. From Stevens JC (1938) The effect of silt-removal and flow-regulation on the regimen of Rio Grande and Colorado Rivers. *Transactions of the American Geophysical Union* 653–659, Fig. 1.

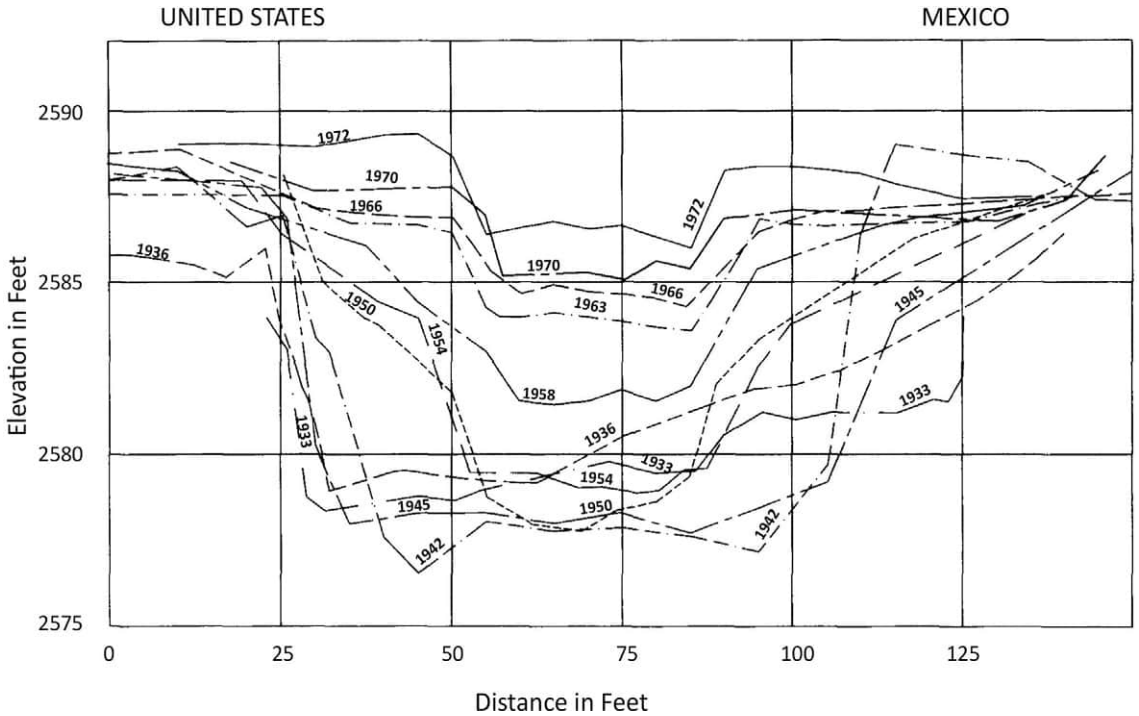

Fig. 7 Graph showing cross-section of the Rio Grande near Presidio, TX, and upstream from the Rio Conchos, surveyed at various times. The channel bed aggraded and the banks narrowed in response to depletion of ~90% of the total annual stream flow, although sediment continued to be episodically delivered to the channel by tributary flash floods. From Everitt B (1993) Channel responses to declining flow on the Rio Grande between Ft. Quitman and Presidio, Texas. *Geomorphology* 6: 225–242, Fig. 3.

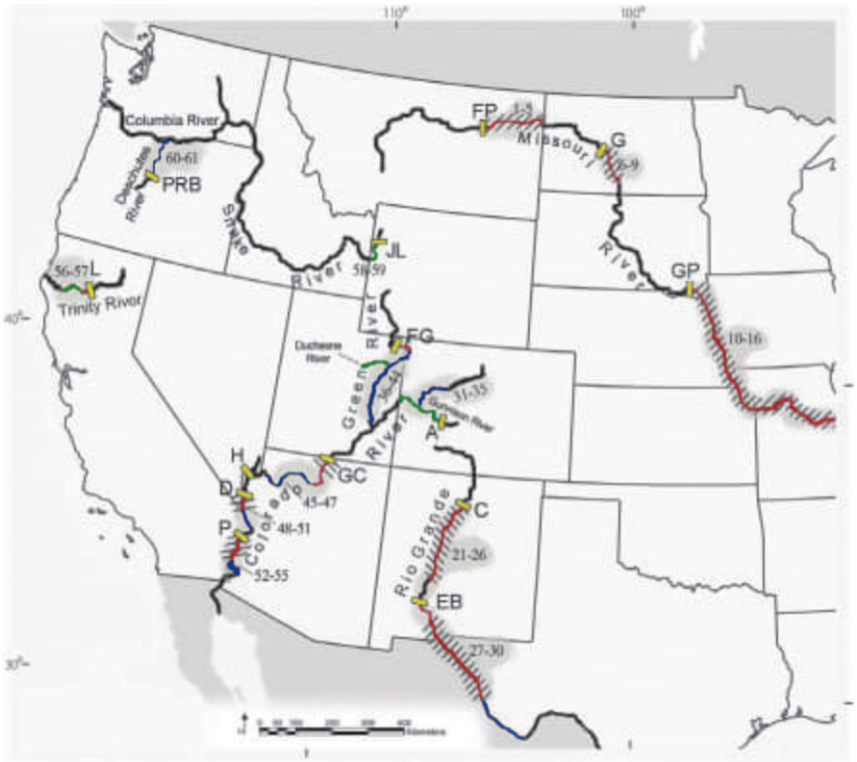

Fig. 8 Map showing perturbations in sediment mass balance of some of the large rivers of the western United States. Red indicates river segments perturbed into sediment deficit, green into sediment surplus, and blue where the perturbation is indeterminate. Cross-hatched segments are those where bed incision is likely. From Schmidt JC and Wilcock PR (2008) Metrics for assessing the downstream effects of dams. *Water Resources Research* 44: W04404. doi:10.1029/2006WR005092., Fig. 1.

Schmidt and Wilcock (2008) computed these metrics for 61 dam-impacted segments of five large river systems in the western United States (Fig. 8). The metrics adequately predict channel changes concerning perturbations in sediment mass balance and post-dam channel incision and poorly predict changes in channel width. Uncertainty in these predictions is caused by a number of factors. Change in the 2-year recurrence flood oversimplifies changes in flow regime, especially where there are large post-dam depletions in total annual flow, and these changes must be estimated between gaging stations. There is uncertainty in the period of record to be used to characterize the pre-dam period, and post-dam reservoir operations change with time. Tributary sediment delivery often must be estimated, although the ratio of post-dam to pre-dam sediment delivery can be more accurately estimated than can the absolute values of the delivery. Changes in the 2-year flood poorly predict changes in channel width, presumably, because factors such as changes in riparian vegetation are not considered in such a simple metric. Nevertheless, these metrics present a spatially robust characterization of the extent to which dams and reservoir operations affect the natural characteristics of river channels.

It is difficult to mitigate the adverse effects of undesirable channel change caused by perturbations of sediment mass imbalance, especially where large dams were built decades ago and completely block the sediment supply once delivered from the upstream watershed. Recently constructed dams in regions of high sediment delivery now include low-elevation release facilities so that sediment laden water can be sluiced through a drawn-down reservoir and delivered further downstream (Kondolf et al., 2014a,b). The Three Gorges Dam on the Yangtze River creates one of the largest reservoirs on Earth, and reservoir sedimentation is being reduced by trapping in smaller reservoirs further upstream, sluicing of high suspended load inflows through the reservoir, and dredging (Ren et al., 2021). To date, sedimentation within Three Gorges reservoir is 33% of what had been predicted, and this success in sediment management has also mitigated adverse downstream impacts of sediment deficit.

In many cases, sediment cannot be rerouted around dams and only clear water can be released, because there is no way to release water from low elevation and there is a very long distance from reservoir inflow to the dam. Intentional large releases of clear water have been released in circumstances where sediment delivery from an unregulated tributary immediately downstream from the dam episodically delivers sediment to the bed of the regulated river. The purpose of these controlled floods is to entrain the sand stored on the bed and redistribute some of that sand to desired locations, such as to eddy sand bars. This management strategy is used to manage sand resources along the Colorado River downstream from Glen Canyon Dam (Webb et al., 1999).

Consequences to aquatic ecosystems

Reservoir operations have the potential to significantly impact aquatic ecosystems, primarily by the effects of thermal changes determined by the temperatures of reservoir releases and by the effects of hydropeaking. Novel, post-dam ecosystems have developed far downstream from many large dams. For example, in the case of the Colorado River, native and nonnative species have developed novel fish assemblages in the cooler releases from the hypolimnion of relatively full reservoirs. Warmer releases that are predicted to occur when reservoir storage declines have the potential to affect the competitive and predatory interactions between native and nonnative species (Dibble et al., 2021). These interactions will also be affected if nonnative reservoir fish species expand their range upstream from each reservoir. In some cases, fragmentation caused by barriers at the upstream end of reservoirs will prevent upstream migration of nonnatives, allowing native fish to prosper in a warming river but elsewhere, nonnatives may outcompete native fish in warming conditions.

Hydropeaking operations significantly affect benthic aquatic insects. Changes in the monthly distribution of flows associated with generation of power during months of high demand, coupled with very cool summer temperatures released from the hypolimnion of Flaming Gorge reservoir on the Green River caused the macroinvertebrate genera to decline from >70 to <30 (Vinson, 2001). Kennedy et al. (2016) demonstrated that aquatic invertebrate abundance is dramatically reduced by hydropeaking operations (Fig. 9), especially wherever flows decrease during the primary hours when insects lay their eggs along the river margin (Poff and Schmidt, 2016). In rivers where there are long segments of edge habitat, it is inevitable that adverse effects will arise due to large fluctuations in river stage. These effects are partially mitigated by eliminating hydropeaking on weekends during spring and summer, thereby providing a 48-h period when invertebrate eggs laid only the river's margin are not desiccated. This management strategy was used downstream from Glen Canyon Dam in 2019 and 2020.

Consequences to riparian ecosystems

Dams and the operations of reservoirs may cause increase or decrease in downstream riparian vegetation. Flood control operations typically lead to a shift in ecosystem function on the pre-dam floodplain from a system dependent on regular flooding or access to shallow ground water to a mesic or xeric ecosystem dominated by upland plants. In some cases, deposition of inset floodplains within the pre-dam channel is the mechanism by which channels narrow, and these new surfaces may be colonized by native and non-native vegetation (Fig. 10) (Dynesius et al., 2004; Merritt and Poff, 2010). Turner and Karpiscak (1980) matched old ground-level photographs and documented the widespread expansion of non-native tamarisk (*Tamarix* spp.) throughout 400 km of the Colorado River downstream from Glen Canyon Dam, and Webb et al. (2007) documented this style of change throughout the Colorado River watershed. Sankey et al. (2015) measured the lateral and longitudinal rate and extent of increase in riparian vegetation throughout the Grand Canyon. Elsewhere, diversion of large amounts of stream flow that are facilitated by dams leads to dewatering of riparian ecosystems and large decreases in floodplain forests (Rood et al., 2005). Numerous field and modeling studies have documented the magnitude and style of riparian vegetation change throughout the western U.S., including in the upper Colorado River watershed (Auble et al., 1994, 2005; Merritt and Cooper, 2000; Grams and Schmidt, 2002), the lower Colorado River watershed (Shafroth et al., 2002), Snake River in Wyoming (Hauer and Lorang, 2004), and the Tietar River in western Spain (Bejarno et al., 2012).

Obviously, different mitigation strategies are required to remove unwanted riparian vegetation that has narrowed channels subject to flood control in contrast to strategies intended to increase riparian vegetation. In most of the Colorado River system, flood control and increased base flows have caused great expansion in riparian vegetation that covers formerly bare fine sediment deposits that are valued as campsites by recreational boaters or that form the architecture of valued low-flow aquatic habitat. In this situation, long-duration high flows have the potential to scour undesired vegetation, but many plant stems have physical characteristics that resist scour. In some circumstances, mechanical removal of undesired vegetation has been followed by high dam releases, such as along the Green River in Dinosaur National Monument.

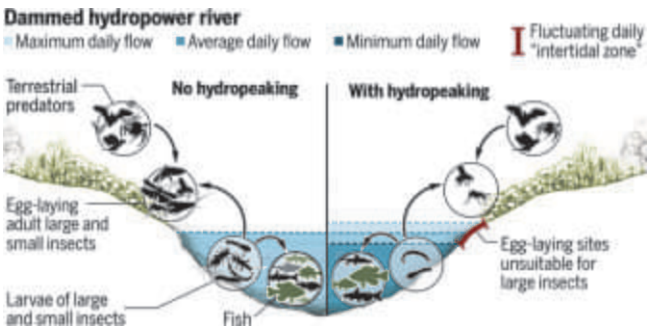

Fig. 9 Dams alter the daily and seasonal flow regime. in cases where reservoir releases are for the purpose of hydropeaking, sites may be desiccated after eggs are laid. From Poff NL and Schmidt JC (2016) How dams can go with the flow. *Science* 353(6304): 1099–1100.

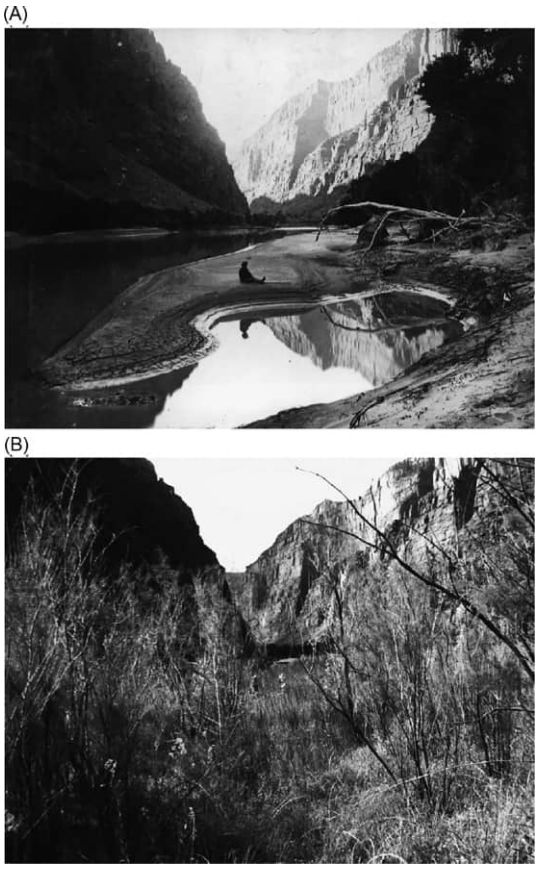

Fig. 10 (A) Photograph taken by E. O. Beaman in 1871 along the Green River in the Canyon of Lodore, downstream from modern Flaming Gorge Dam. (B) Matched photograph taken in 1993 after approximately 30 years after completion of Flaming Gorge Dam. From Grams PE and Schmidt JC (2002) Streamflow regulation and multi-level floodplain formation: Channel narrowing on the aggrading Green River in the eastern Uinta Mountains, Colorado and Utah. *Geomorphology* 44:337–360, Fig. 8.

Where there has been a large loss in riparian forests due to dewatering, establishment of adequate baseflow throughout the year as well as higher "growth flows" that provide additional stream flow to recharge alluvial aquifers during periods of high growth rate of vegetation have been very successful (Rood et al., 2005). Over-bank, flood flows are another critical part of the flow regime needed to rejuvenate riparian forests, because these flows provide a critical disturbance to the riparian ecosystem. The rate of recession of flows from peak flow to base flow are another essential part of re-operating reservoirs to enhance riparian forests. New seedlings of cottonwoods or willows require a gradual flood recession to assure that seedlings survive until the next period of high flow.

The future

The energy demands of underdeveloped societies, changing runoff patterns caused by climate change, and the need to expand renewable energy production all encourage construction of new dams. In regions experiencing an increasing frequency of unusually large floods, dams have the potential to provide some measure of increased flood control. In regions experiencing decreased runoff, new dams have been proposed to provide additional water storage, such as in California and the Colorado River watershed. In the developing world, there are extensive plans for new dams in Africa, Asia, and South America. More than 450 new dams are proposed in the watershed of the Amazon, Congo, and Mekong Rivers (Winemiller et al., 2016). These new projects have the potential to significantly affect the most diverse fish assemblages on Earth (Fig. 11) because of the many impacts described in this review. In the Mekong basin, for example, sediment trapping in new reservoirs is predicted to reduce sediment delivery to the Mekong Delta between 51 and 96%, depending on the number of dams constructed (Kondolf et al., 2014a). Thus, there will be an increasing need to understand, predict, and anticipate the impacts of new dams to identify the best strategies for locating new barriers and whether to build those dams at all.

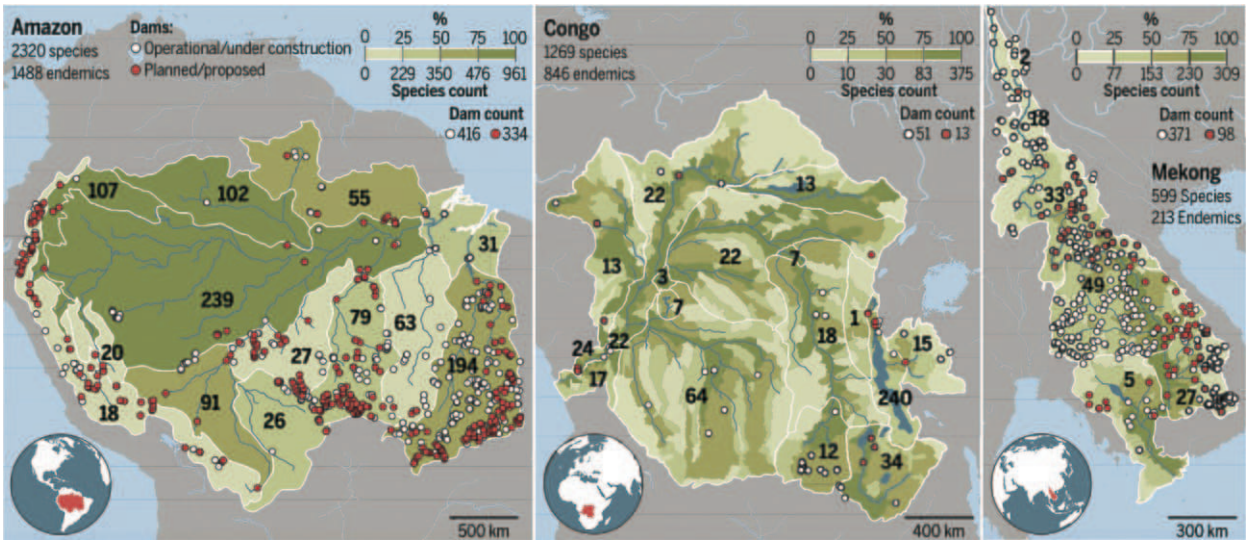

Fig. 11 Maps showing existing and planned dams in the Amazon, Congo, and Mekong basins and the estimated fish diversity in these basins. Basin-wide biodiversity summaries are shown in upper left in first two panels and middle in third panel. The ecoregions (white boundaries) in each basin are also shown. Many species are found only in a single ecoregion (black numbers), and subbasins within each river basin differ widely in their total species richness (shades of green illustrate breakpoints between quartiles in rank order within each basin). From Winemiller KO, McIntyre PB, Castello L, Fluet-Chouinard E, Giarrizzo T et al. (2016) Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* 351(6269): 128–129.

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Ecological Effects of Mining on Stream Ecosystems

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

BACI designs A study design that compares data collected from control and impacted sites before and after a planned perturbation. In restoration studies the design can be employed to measure responses to the removal of a disturbance.
Bioassessment Using biological systems (e.g., populations or communities) to assess the effects of an anthropogenic disturbance such as pollution.
Biotic ligand model (BLM) An integrated physiological and biogeochemical model used to predict the bioavailability of metals to aquatic organisms.
Bioconcentration The uptake of contaminants from water.
Bioaccumulation The uptake of contaminants from food.
Biomagnification The increase in the concentration of a contaminant through a food chain.
Context-dependent responses Spatial or temporal variation in the response of an ecosystem to a perturbation based on the biotic composition of a community.
Remediation Treatment of a watershed that is designed primarily to improve water quality.
Restoration Treatment of a watershed that is designed primarily to improve habitat.
Species traits Physiological, morphological, behavioral, or natural history attributes of a species that can be used to measure responses to natural or anthropogenic factors.
Water quality criteria Established concentrations of chemicals that should not be exceeded in order to protect aquatic life.

Scope and scale of mining contamination

Among the many anthropogenic stressors that negatively impact inland waters, discharges from abandoned and active mines are likely the most widespread and pervasive sources of chemical contamination. Active and abandoned mines are broadly distributed around the world, but over 50% of the mining areas are concentrated in 5 countries: China, Australia, the United States, Russia, and Chile (Maus et al., 2020). The distribution of active mines in the U.S. varies geographically, with the majority of metal mines occurring in western states and the largest concentrations of coal mines located in the central and southern Appalachians (Fig. 1). Although the number of active coal and metal mines have declined since 1983 (by 79% and 69%, respectively), abandoned mines remain a significant environmental threat in the U.S. Accurate estimates of the number of abandoned mines, most of which are located on federal lands (https://www.abandonedmines.gov/), are difficult to obtain. The Bureau of Land Management and the U.S. Forest Service estimate that a total of 52,000 and 29,000 abandoned mines are located on lands they manage, respectively. Between 2008 and 2017 total expenditures to identify, clean up, and monitor hazards at abandoned mine sites exceeded $2.9 billion, with about 90% of these funds used to address environmental hazards. Because discharge of metals and other contaminants from abandoned mines can persist for centuries after mining has ceased, many of these sites will require perpetual on-site treatment. Finally, although the discharge of metals from abandoned mines is generally considered an issue of local concern, mining pollution often has broad regional impacts. For example, approximately 23% of streams in Colorado's central Rocky Mountains were identified as degraded by metals from historical mining disturbance (Clements et al., 2000).

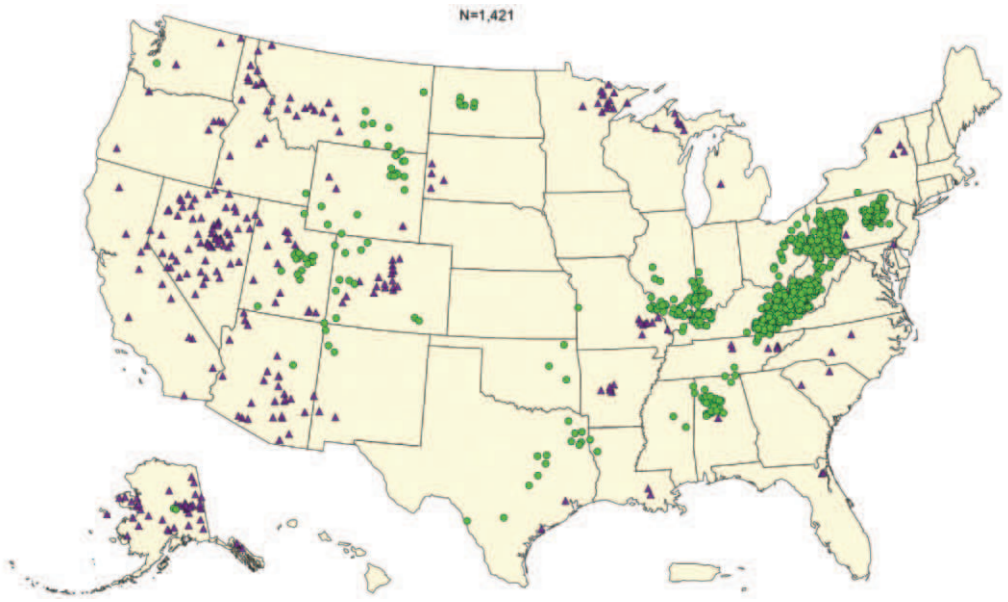

Fig. 1 The distribution of active metal mines (triangles) and coal mines (circles) in the U.S. Data obtained from the Mine Safety and Health Administration, U.S. Centers for Disease Control and Prevention.

Fate and effects of mines on inland waters

Toxicity and bioavailability of metals to aquatic organisms

Many of the chemicals typically associated with mining discharges (e.g., arsenic, cadmium, copper, iron, lead, mercury, nickel, zinc) have severe detrimental effects on aquatic species and ecosystems. Although some of these constituents are associated primarily with physical habitat alterations (e.g., iron deposition), others are highly toxic to aquatic organisms at very low concentrations. For example, the U.S. EPA water quality criterion value for cadmium, defined as the concentration that should protect 95% of aquatic species, is less than 0.5 $\mu g\, L^{-1}$ (parts per billion) in waters that are typical of many western streams where mining occurs. Concentrations of Cd significantly exceeding this safe threshold are frequently measured in discharges downstream from abandoned mines.

Because the toxicity and bioavailability of metals are determined by numerous water quality characteristics, simply measuring the concentration of a metal is not sufficient to predict potential effects. For example, the toxicity of many metals is strongly influenced by water hardness, typically expressed as mg L^{-1} $CaCO_3$. As water hardness increases, the toxicity of metals such as Cu, Cd and Zn decreases. A similar relationship between the toxicity of metals and the amount of dissolved organic carbon (DOC) that occurs naturally in water has also been demonstrated. These complex relationships between potential effects of metals and water quality characteristics have been employed to develop site-specific modifications to water quality criteria for metals from mine discharges. For example, the biotic ligand model predicts the likelihood that metals will accumulate on gill surfaces of organisms based on factors such as pH, water hardness, DOC, water temperature, and concentrations of major ions (Paquin et al., 2002). Although the influence of these water quality characteristics on metal effects have been demonstrated in laboratory experiments, our understanding of how these factors influence toxicity of metals in nature is limited.

Distribution of metals in biotic and abiotic compartments

Once discharged into an aquatic ecosystem, metals and other chemical constituents become associated with one of several abiotic or biotic compartments. Metals dissolved in the water column are readily bioconcentrated by primary producers (phytoplankton, attached algae, including diatoms), invertebrates, and fish (Kim et al., 2012). The major pathways for metal uptake from water vary among these groups. Passive absorption is responsible for elevated levels in algae, whereas bioconcentration of metals by fish occurs primarily across the gills. The bioconcentration of metals by invertebrates typically occurs through the exoskeleton but is also influenced by respiration mode (cutaneous versus gills) and body size. The effects of body size on metal bioconcentration reported in the literature are likely determined by surface area to volume relationships, as small invertebrates have greater relative surface area for metal adsorption and absorption (Kiffney and Clements, 1996).

Sediments represent a second major compartment where metals occur in aquatic ecosystems, with concentrations typically several orders of magnitude greater than those in the water column (Burton, 1991). In systems receiving mine discharges, it is not

unusual for metal concentrations in water to be below levels known to cause harm, whereas sediment concentrations in these same systems can significantly exceed toxic thresholds. In fact, contaminated sediments may continue to contribute metals to the water column long after of the original source of metals has been eliminated. Because of significantly elevated metal concentrations, benthic organisms associated with sediments are at especially high risk of exposure. Most of our understanding of how metals in sediments affect aquatic ecosystems was derived from studies with benthic organisms. In addition to dietary exposure to metals (described below), much of the metal uptake in benthic organisms occurs through interstitial water.

Direct and indirect effects of metals

To characterize the impacts of mine discharges on aquatic systems, it is necessary to distinguish between the direct toxicological effects of metals from the physical effects that cause habitat loss (Fig. 2). As noted above, many of the metals associated with mining discharges are highly toxic to aquatic organisms. Typical responses of aquatic communities to elevated metals include reduced species diversity and abundance, shifts in the composition of communities, and the loss of sensitive species (Clements et al., 2000). Although some aquatic organisms are relatively tolerant to metals (e.g., some caddisflies and many dipterans), others will be eliminated at relatively low metal concentrations (e.g., many mayflies). These differences in relative sensitivity among groups are routinely employed in stream bioassessments to characterize degradation associated with mining discharges. In addition, because these different groups of organisms play different functional roles, shifts in the composition of communities downstream from mining discharges have implications for ecosystem processes such as nutrient cycling, detritus processing, and energy flow. We also know that organisms affected by exposure to metals have lower resilience when challenged by other stressors. For example, experiments have shown that in systems recovering from the long-term effects of mining pollution, metal-tolerant communities are more sensitive to other physical (acidification and UV-B radiation) and chemical (hydrocarbons) stressors compared to reference communities (Wolff et al., 2019).

In addition to these direct toxicological effects of metals, indirect effects from active and abandoned mines can occur as a result of reduced food quality and the loss of prey resources. Lower quality of basal food resources (e.g., algae and biofilm) and reduced prey abundance alter aquatic food webs and limit the transfer of energy to higher trophic levels. In addition, metals that are readily bioconcentrated (through water) and/or bioaccumulated (through food) will be transferred through food webs (Landers et al., 2019). However, unlike many organic contaminants, with a few important exceptions (e.g., Hg and Se) most metals associated with mining discharges do not biomagnify. In fact, because of relatively inefficient transfer, concentrations of most trace metals are usually lower in predators than in other trophic levels. For example, data collected downstream from California Gulch, a U.S. EPA Superfund site on the Arkansas River (Colorado, U.S.), demonstrates how inefficiently Zn in transferred through an aquatic food web (Fig. 3). Although metals were bioconcentrated >6000 X from water to biofilm, concentrations in caddisflies, a major prey item for brown trout in this system, were much lower, and levels in brown trout were ~70% lower than in caddisflies (Kiffney and Clements, 1993). It is important to note that inefficient transfer through aquatic food chains does not imply metals are not harmful to higher trophic levels. Because basal food resources such as biofilm in mining-impacted watersheds are often highly contaminated, even the inefficient transfer of metals can result in elevated and potentially harmful concentrations in consumers.

Emerging adult insects represent an important pathway by which metals can be transferred from aquatic ecosystems to riparian consumers (Fig. 4). Ecologists have long recognized the role of emerging adult insects in providing aquatic-derived subsidies in the form of nutrients or energy to adjacent riparian communities (Fausch et al., 2002). Metals (and other contaminants) are also readily transferred to terrestrial systems and elevated concentrations have been detected in riparian predators, including spiders, birds, and bats that consume emerging aquatic insects (Kraus et al., 2014). Similar to the bioaccumulation of metals within aquatic food webs, the transfer of metals to riparian communities is relatively inefficient, in part because metals are shed in the exoskeleton of emerging

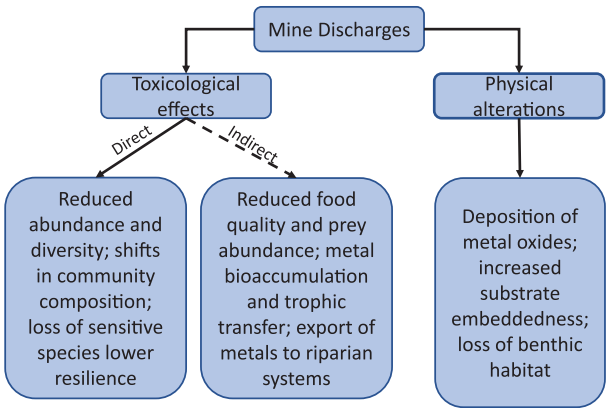

Fig. 2 Conceptual model of the major direct and indirect toxicological effects and physical alterations commonly associated with mine discharges to inland waters.

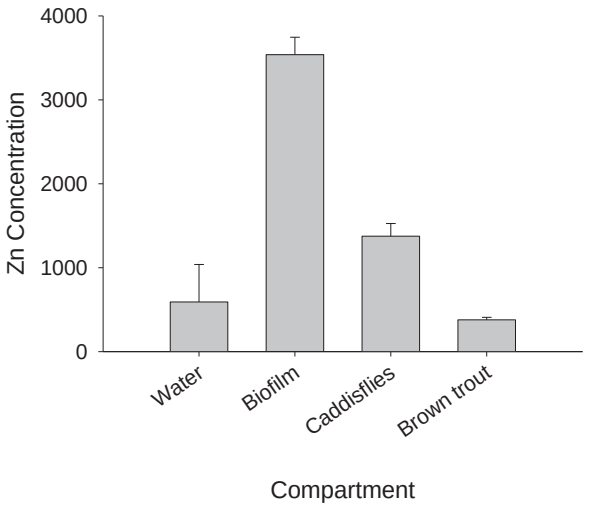

Fig. 3 Concentrations of Zn in water, biofilm (algae and diatoms), caddisflies and brown trout (*Salmo trutta*) measured in the Arkansas River, Colorado (USA). Data were collected downstream from California Gulch, a U.S. EPA Superfund Site in 1993 prior to remediation. Note that metal concentrations in water are shown in μg L^{-1} (ppb) whereas concentrations in other compartments are in μg g^{-1} (ppm).

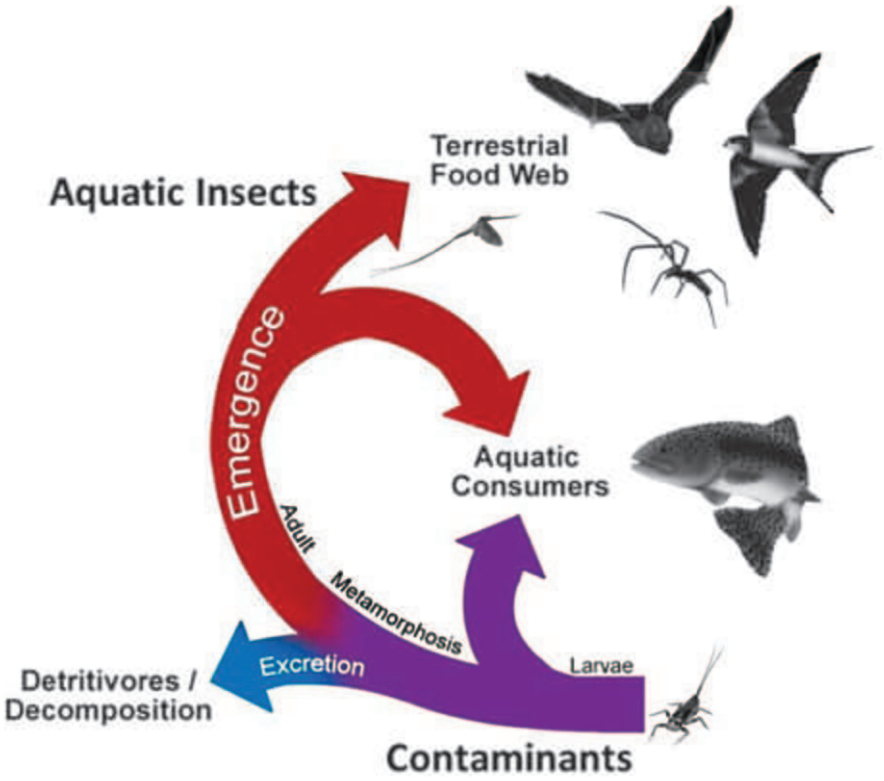

Fig. 4 The movement of contaminants within aquatic ecosystems and the export of these materials to riparian consumers. From Kraus JM, Walters DM, Wesner JS, Stricker CA, Schmidt TS, Zuellig RE (2014) Metamorphosis alters contaminants and chemical tracers in insects: Implications for food webs. *Environmental Science & Technology* 48: 10957–10965.

adults are therefore often much lower than in aquatic life stages. However, as described above, the inefficient transfer of metals in highly contaminated systems can result in elevated concentrations and potential effects on riparian consumers, a phenomenon coined as the "dark side of ecological subsidies" (Walters et al., 2008).

Physical effects of mine discharges

The direct and indirect toxicological effects of mine discharges have received most of the attention in the literature. However, the physical effects of mine effluents can also significantly degrade aquatic habitats, especially for benthic organisms (DeNicola and Stapleton, 2002). The formation of ferric hydroxide, commonly referred to as "yellow boy," occurs through a series of chemical reactions when iron sulfide (pyrite) is exposed to air and water:

$$FeS_2 + O_2 + H_2O \rightarrow\rightarrow Fe(OH)_3 + H^+$$

As pH of a receiving system increases (e.g., beyond approximately 3.5), ferric hydroxide precipitates from the water column as a yellowish-orange solid, staining the substrate, filling interstitial spaces, and resulting in significant degradation of benthic habitats (Fig. 5). Experiments conducted in mine-polluted streams have shown that even in situations where the materials deposited on substrate are not directly toxic, macroinvertebrate colonization of substrate coated with metal oxides can be significantly reduced (Courtney and Clements, 2002).

Assessing the effects of mining discharges on aquatic ecosystems

Study designs and bioassessment approaches

A variety of study designs and bioassessment approaches have been used to quantify the effects of mine discharges on aquatic ecosystems, but most involve comparisons of abundance, species richness, diversity, and/or community composition of aquatic organisms along a gradient of contamination within a single watershed. An alternative but less common approach is to sample a large number of reference and polluted streams in an area with a high density of mines. This study design has been employed in the southern Appalachians to measure the effects of coal mining (Cormier et al., 2013) and in the Rocky Mountains to assess effects of abandoned hard rock mines (Schmidt et al., 2012). An alternative design employed in the Rocky Mountains as part of the U.S. EPA Environmental Monitoring and Assessment Program (EMAP), was to sample a large number of randomly selected streams (Clements et al., 2000). Because these sites were selected randomly, investigators were able to make much broader generalizations about the total number of streams within the region that were affected by abandoned mines.

Studies of the effects of abandoned mines commonly include assessments of algae, benthic macroinvertebrates, and/or fish and have been conducted across multiple levels of biological organization from individuals to populations to communities. In one of the earliest field assessments of metal mining effects on streams, Carpenter (1924) investigated several rivers in the U.K. polluted by lead, concluding that "The correlation of fauna lists with tables of analyses of water samples shews that poverty of fauna, with absence of fishes in particular, always accompanies the presence of lead salts in diffusible form." In what is likely the first study to

Fig. 5 Photograph of North Fork Clear Creek, a U.S. EPA Superfund Site near Blackhawk, Colorado (U.S.). The orange-yellow color of the stream and the staining on the substrate is a result of iron hydroxides that precipitate in the water column.

employ a before-after design to investigate recovery of a stream from mining pollution, Carpenter concluded that "The cessation of the last of the lead mining and washing operations affecting the Rheidol and Ystwyth was followed by a marked and rapid increase in the flora and fauna of the rivers." Since the publication of Carpenter's study, literally thousands of papers have documented the effects of metal or coal mining on inland waters. In addition to the "poverty of fauna" describe above, these studies have identified consistent and predictable shifts in the composition of algal, macroinvertebrate and fish communities downstream from mine discharges.

With respect to which organisms should be sampled in these assessments, there has been some debate in the literature regarding the suitability of using algae, macroinvertebrates or fish for measuring effects of mining discharges (Namba et al., 2020). Difficult taxonomy often precludes the assessment of algal communities by non-experts, whereas logistical considerations and difficulties obtaining sampling permits may limit the use of fish assessments by some organizations. In the U.S. there appears to be a distinct geographic preference for which group to include in stream bioassessments. Because of greater species diversity, responses of fish communities to coal and metal mining have been much better characterized in watersheds of the eastern U.S. In contrast, because of naturally low diversity of fish communities in mountain streams of the western U.S., there has been more emphasis placed on macroinvertebrate communities in this region.

Effects of mines and mining effluents on aquatic ecosystems have been measured across different levels of biological organization. Responses at lower levels of organization, such as elevated levels of metal-binding proteins, have been observed in a wide range of taxonomic groups. Similarly, morphological deformities (e.g., chironomid mouthparts) and anomalies in the capture nets of caddisflies have also shown strong correlations with elevated metal concentrations (Hudson and Ciborowski, 1996; Balch et al., 2000). These responses are often specific to metal exposure in mining-polluted streams. In contrast, responses at higher levels of organization, such as reduced species diversity, are more general and could result from the direct toxicological effects of metals, increased acidification, or the loss of habitat. Surprisingly, despite the well-documented importance of assessing functional characteristics of aquatic ecosystems and their connection to ecosystem services, far fewer studies of mining-polluted watersheds have measured effects on ecosystem processes (e.g., production, nutrient cycling, and detritus processing). The general but largely untested perception that ecosystem processes are less sensitive to contaminants and other stressors compared to population and community responses may account for this disparity (Schindler, 1987).

The use of species traits to assess mining effects

A relatively recent approach derived from basic ecology that is being employed in stream bioassessments is to use species traits to quantify effects of metals and other stressors associated with mine discharges (Poff, 1997; Verberk et al., 2013). Instead of measuring responses of individual species to a contaminant, the idea is to examine how species traits, such as physiological, morphological, behavioral, life history, and functional characteristics are affected (Clements et al., 2021). The assumption is that species traits are more closely linked to attributes that confer sensitivity or tolerance to a particular stressor and therefore provide a mechanistic link between stressors and responses. For example, we know that the toxic mode of action for many metals is damage to gill structures. Therefore, we would expect organisms that respire by gills would be especially sensitive to metals. Similarly, because metal concentrations are often significantly elevated in algae and biofilm, we expect organisms that graze on these materials to have greater exposure to metals. The use of species traits offers distinct advantages over traditional taxonomic approaches when assessing effects of stressors over broad geographic regions. Comparisons of abundance and distribution among regions are often difficult because of natural variation in community composition. In contrast, we expect species traits, which are presumably responding directly to environmental conditions, would be less influenced by natural biogeographic variation compared to taxonomic abundances. The use of this approach in bioassessment is much more effective if species traits are selected a priori based on expected sensitivity to a stressor rather than analyzing data and then providing mechanistic explanations for patterns of individual traits post hoc.

Effects of metals within the context of water quality criteria

Water quality criteria developed in the U.S. are designed to protect aquatic organisms from the adverse effects of chemicals (Adams et al., 2020). These criteria are based primarily on results of laboratory toxicity tests and typically use organisms that are easily cultured in the laboratory (e.g., *Cladocera*; fathead minnows; rainbow trout). Not surprisingly, there has been considerable debate in the literature regarding the ecological relevance of short-term toxicity tests for guarding against adverse effects in nature (Cairns, 1986). The major criticisms of laboratory tests include their short duration (typically 4–7 days), failure to consider dietary exposure to chemicals, and the inability to account for either indirect effects (e.g., competition; predator-prey interactions) or responses at higher levels of biological organization. We also know that most watersheds contaminated by mine discharges receive multiple metals, and the potential additive or greater than additive effects of individual chemicals are not considered when developing water quality criteria. In addition, despite a highly sophisticated understanding of how site-specific variation in water quality characteristics influences metal toxicity and bioavailability (Paquin et al., 2002), we know very little about how populations or communities from different watersheds will be affected by metals. Research into these context-dependent responses has shown that the composition of communities strongly determines their responses to contaminants (Clements et al., 2012).

Finally, certain groups of organisms are poorly represented in the database used to develop water quality criteria for metals. For example, toxicity tests conducted with aquatic insects, a diverse and dominant group of organisms in most inland waters, are quite limited because of difficulties rearing and culturing these organisms in the laboratory (Brix et al., 2011). The data available on effects of metals derived from laboratory experiments suggest that aquatic insects are relatively tolerant to metals. In contrast, field studies of streams receiving mining effluents have shown that some aquatic insects are highly sensitive to metals and often the first group eliminated. Explaining these discrepancies between laboratory-based responses to metals versus what is observed in the field remains a significant research need.

Despite these criticisms and the inherent limitations of single species toxicity tests, much of the research conducted with metals suggest that laboratory-derived criteria are reasonably protective of aquatic ecosystems. Their effectiveness in protecting species in the field is in part because they are ultimately based on experiments conducted with highly sensitive (although ecologically irrelevant) test species. However, there is evidence that even a modest exceedance of metals criteria in streams (~2X) can result in significant loss aquatic insect biodiversity (Clements et al., 2021).

Recovery of aquatic ecosystems from effect of mining

Although thousands of active and abandoned mines continue to discharge metals and other contaminants globally, there are examples where remediation at these sites has significantly improved water quality and restored their natural ecological integrity. Remediation of mine sites involves a variety of approaches, including active or passive treatment of mine effluents, removal or treatment of mine tailings from riverbank and floodplain soils, and revegetation of riparian areas. Assessing the effectiveness of mine remediation requires regular monitoring of physical, chemical, and biological conditions. Ideally, monitoring would be conducted before, during, and after completion of remediation and would include both control (non-remediated) and treated sites. This particular monitoring approach allows investigators to employ a highly effective before-after control-impact (BACI) study design whereby improvements in water quality and biological conditions can be causally linked to the remediation treatments and compared with natural variation in control sites. BACI designs have been traditionally used to quantify impacts of anticipated perturbations and are considered the "gold standard" in aquatic bioassessments (Stewart-Oaten et al., 1986); however, in the situation described above the "impact" is actually the removal of stressors associated with the mine. The basic expectation of a BACI design is that reference sites would show little difference before versus after remediation, whereas treated (remediated) sites would show significant improvements in biological conditions (Fig. 6).

Unfortunately, because of budget constraints or other logistical challenges, these ideal study designs are rarely employed to assess remediation effectiveness. In fact, despite significant expenditures on remediation and restoration programs across the U.S. (and other countries), our ability to quantify their effectiveness is often limited by poor study designs, insufficient post-remediation monitoring, and a lack of broadly accepted criteria that define success (Bernhardt et al., 2005). This is unfortunate because in those instances where appropriate study designs have been implemented and sufficient post-remediation monitoring has occurred, results show that aquatic communities in heavily contaminated streams can rapidly recover after the discharge of mine effluents has been eliminated. For example, investigators comparing recovery of streams located in California, Colorado, Idaho, and Montana reported similar recovery trajectories, despite very different watershed characteristics, discharged metals, and remediation techniques (Clements et al., 2021). The fact that these streams, all former U.S. EPA Superfund sites and among the most metal-contaminated watersheds in the western U.S., rapidly returned to reference conditions demonstrates the potential for restoration success under the most extreme conditions.

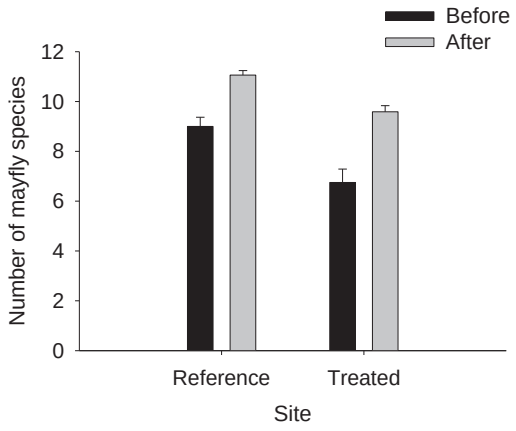

Fig. 6 Example of a before-after control-impact design showing the total number of mayflies (Ephemeroptera) in the Arkansas River, Colorado (U.S.), upstream and downstream from a former U.S. EPA Superfund Site. Data were collected from an upstream Reference site and a downstream Remediated site before and after mine cleanup. Data from Clements et al. (2021).

Conclusions

Discharges from abandoned and active mines are a widespread and pervasive source of contamination in aquatic ecosystems. Metals released from abandoned mines are readily bioconcentrated by aquatic organisms, transferred through aquatic food chains, and can be exported to riparian ecosystems. Typical responses of aquatic communities exposed to elevated metals include reduced species diversity and abundance, shifts in the composition of communities, and the loss of sensitive species. In addition to these direct toxicological effects of metals, indirect and physical effects of abandoned mines can occur as a result of reduced food quality and the loss of prey resources. Although aquatic insects are poorly represented in the database used to derive water quality criteria for metals, these standards appear to be protective of most aquatic organisms. However, modest exceedances of metals criteria in streams can result in significant loss of aquatic insect biodiversity. Finally, several studies have demonstrated that streams can rapidly recover following improvements in water quality. The success of these projects is encouraging and demonstrates the importance of continuing to invest in stream remediation and restoration programs.

Knowledge gaps

- What is the relative importance of dietary versus aqueous exposure of aquatic organisms to metals from mines?
- Why are some aquatic communities more sensitive to metals than others?
- Why do laboratory experiments conducted with aquatic insects show relatively high tolerance to metals, whereas field studies of mine-polluted streams show that insects are highly sensitive and often the first group eliminated?
- What are the likely effects of climate change on the responses of stream ecosystems to mine pollution?
- Does the exposure to metals from mines alter the relative importance of species interactions in aquatic communities?

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Biological Assessments of Aquatic Ecosystems

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Assemblage A subset of the species in a community. The species in an assemblage are typically within the same taxonomic group (e.g., algae, invertebrates, or fish).

Biological criterion Either a narrative description or a numerical value used to judge if a waterbody is biologically altered or legally impaired (i.e., not meeting its designated use).

Biological integrity The capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a composition and diversity comparable to that of the natural habitats of the region. This term is used in the United States and is similar in concept to the term ecological status used in the European Union.

Biotic index An index that measures the average tolerance of an assemblage to pollution or habitat degradation.

Causal analysis The process of identifying the stressor or stressors causing biological impairment.

Ecological status An expression of the quality of the structure and functioning of aquatic ecosystems. This term is used in the European Union and is similar in concept to the term biological integrity used in the United States.

Endpoint Either an ecological good or service that society seeks to protect (an assessment endpoint such as biodiversity) or the value of an index that is used to represent the assessment endpoint (a measurement endpoint such as taxa richness).

Harmonization The process of comparing and scaling different types of indices that may differ in what indicator groups are used, how raw data were collected, and how indices are calculated so that they produce similar assessments of ecological quality.

Index of biotic integrity (IBI) An additive multimetric index that incorporates several metrics selected on theoretical grounds that collectively are thought to characterize biological integrity.

Index of taxonomic completeness A ratio index (O/E) that measures the degree to which the taxonomic composition observed at an assessed site (O) matches the composition expected (E), via model prediction, to occur if the site were in reference condition.

Indicator A species, group of species, or functional property used to assess the ecological status of a waterbody.

Metric A numeric measure of some biological structural or functional attribute or trait typically derived from taxonomic counts obtained from a sample of a biological assemblage. Metrics may be in different units – e.g., richness, relative abundance of individuals, mean tolerance of species.

Multimetric index (MMI) An additive index that incorporates several different types of standardized biological metrics. MMIs are similar to IBIs but often differ from IBIs in that the selection of specific metrics is usually guided by how well individual metrics discriminate degraded sites from reference-quality sites rather than a priori selection based on ecological theory.
Reference condition The naturally occurring (i.e., pre-development) or desired condition used to judge the ecological quality of assessed sites.
RIVPACS River Invertebrate Prediction and Classification System – the original method developed in Great Britain to measure taxonomic completeness and other derived indices.
Typology Classification of waterbodies based on similarities in physiography. Typologies are used to control or adjust for naturally occurring differences in aquatic life that may otherwise confound biological assessments.
Water quality standard A regulation that may include specific numeric criteria used to protect designated uses (such as aquatic life) of waterbodies.

What is bioassessment

Most modern societies have laws or policies designed to protect the ecological wellbeing of water resources. Biological assessments include a variety of activities and analyses that provide water resource managers and policy makers with the information needed to infer if, and how, human activities are harming aquatic life. The type and amount of information produced by biological assessments has greatly evolved in response to both changing societal needs and improvements in our scientific understanding of the structure and function of aquatic ecosystems and the goods and services they provide. For example, over a hundred years ago aquatic biologists discovered that the presence and absence of specific aquatic species were often associated with pollution (Cairns and Pratt, 1993; Moog et al., 2018). Such indicator species provided information regarding the potential harm different waterbodies could cause to human health. Since then, scientists and policy makers have recognized that the goods and services provided by healthy aquatic ecosystems are also essential to the well-being of human societies and need to be protected. Laws and policies such as the 1972 United States Clean Water Act and the 2000 European Union's Water Framework Directive recognize both the intrinsic value of aquatic species and the need to maintain healthy, sustainable freshwater ecosystems that support human wellbeing. To meet these societal goals, aquatic scientists needed to develop more comprehensive ways to measure the status of aquatic life and the effects that human-caused stressors have on different levels of biological organization (Fig. 1). Not surprisingly, specialized language evolved to facilitate communication between specialists and managers, but which can often be confusing to non-specialists. We define some of these terms in the Glossary.

Legislatively mandated biological assessments often are conducted within an adaptive management framework (Fig. 2) in which aquatic life is monitored over time to determine if desired conditions within a waterbody are being achieved and maintained. In general, all biological assessments are conceptually straightforward in that they require (1) selection of one or more biological or ecological endpoints that represent valued aquatic resources of interest and (2) establishment of a benchmark or criterion by which to judge if a waterbody is biologically altered or legally impaired. In addition, if the assessment leads to the conclusion that aquatic life is impaired, further analyses may be needed to identify the factor(s) causing impairment. However, the specific measures used to

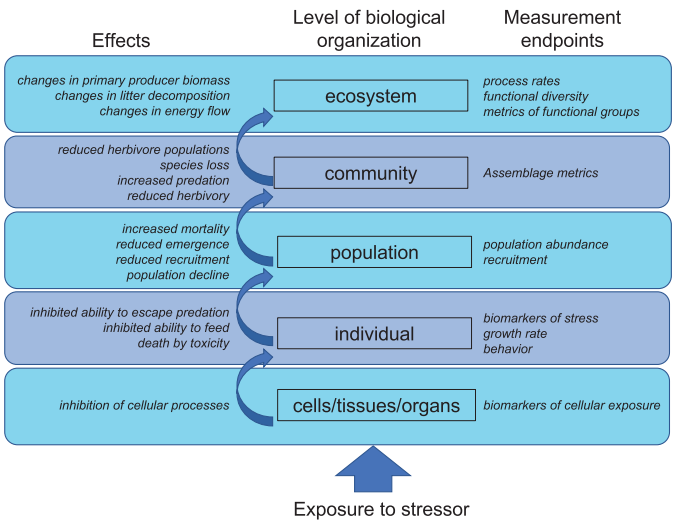

Fig. 1 Diagram illustrating how the effects of a stressor can cascade through different levels of biological organization and the types of measurement endpoints used to quantify its effects at each level.

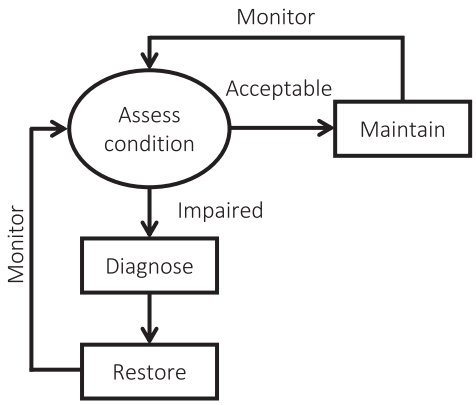

Fig. 2 Diagram illustrating how biological assessments are used within an adaptive management framework to protect and restore the ecological status of aquatic ecosystems.

quantify aquatic life, the approaches used to establish benchmarks or criteria and infer impairment, and the ways used to identify which factors – hereafter stressors – are causing biological impairment vary markedly among programs and practitioners. In this chapter, we summarize the ways aquatic scientists have addressed each of these core aspects of biological assessment as applied to natural water bodies and conclude by highlighting outstanding issues that are currently being addressed and could improve the performance of biological assessments in the future.

Quantifying the status of aquatic life - endpoints, indicators, and indices

Most people have a general, intuitive understanding of what aquatic life is and, perhaps, what biological integrity or ecological status means. Aquatic life includes the set of species (from microbes to vertebrates) that inhabit aquatic ecosystems, and the terms biological integrity and ecological status refer to the level of biological condition or health exhibited by aquatic life. In the United States, biological integrity was defined as "the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a composition and diversity comparable to that of the natural habitats of the region" (Frey, 1977). The Water Framework Directive uses similar, although briefer and broader language to define ecological status as "an expression of the quality of the structure and functioning of aquatic ecosystems" (European Commission, 2000). The latter definition explicitly recognizes that functional processes are an important aspect of ecological status, whereas functional processes are implied but not specifically mentioned in the definition of biological integrity. Because the term ecological status is explicitly more inclusive than the term biological integrity, we will use ecological status in the rest of this chapter when referring to the overall condition, or health, of aquatic life and the ecological processes supported by aquatic life.

Aquatic scientists largely assumed the responsibility for mapping broad policy language to specific scientific concepts and deciding what to measure and how. Ecological status is a general assessment endpoint (i.e., the ecological goods and services that society seeks to protect) that is targeted by water resource legislation and policies. However, aquatic scientists have not agreed on a standard list of measurement endpoints (i.e., specific biological attributes or features) to use when characterizing ecological status, and decisions on what to measure have varied across national and state jurisdictional borders for many legal, historical, scientific, and practical reasons. The result has been a sometimes confusing mix of hundreds of combinations of indicators, sampling methods, indices (measurement endpoints), and analysis techniques (Friberg et al., 2011; Birk et al., 2012) that have made cross-program comparisons of ecological status difficult (Cao and Hawkins, 2011). Moreover, even if all aquatic scientists agreed on a common set of indicators and measurement endpoints, it is not clear how they should be weighted to produce an overall measure of ecological status. In addition, some measurement endpoints are much more difficult or expensive to quantify than others, which limits their practical application. Despite these challenges and lack of complete consensus, broad similarities have emerged in the specific types of measures that have been developed for use in biological assessments. Fish, macroinvertebrates, algae, and macrophytes have been frequently selected to serve as indicators of overall ecological status, but several ways of measuring or quantifying status (measurement endpoints such as an index) have been developed (Bonada et al., 2006).

Many bioassessment programs recognize that selection of the type of indicator used can influence institutional and public support. For example, aquatic vertebrates, specifically fish, are a conspicuous component of aquatic life that are generally valued by society because they provide both food and recreation. In contrast, the public is less aware of the importance and value of less conspicuous species (such as invertebrates, algae, and microbes) to human wellbeing. Consequently, fish are frequently used as an indicator to assess the broader endpoint of overall ecological status. However, fish abundance and diversity may be naturally too low or variable to serve as a good indicator of overall ecological status in some regions, so many bioassessment programs use macroinvertebrates as an indicator group because they are cosmopolitan in distribution and both locally and regionally diverse.

In general, bioassessment practitioners have tried to select taxa groups as indicators that have both public recognition and ecological attributes that make them good indicators. Research has shown, though, that no single taxa group adequately represents how all other groups respond to human-caused stress (Carlisle et al., 2008; Bae et al., 2014). More than one group of taxa must therefore be used collectively to provide a robust assessment of overall ecological status. Moreover, static measures of status based on assemblage structure and species composition may not provide much insight regarding how functional processes respond to stress (Friberg et al., 2011), although strong relationships have been observed in some studies (Wallace et al., 1996).

Indices

Regardless of the indicator group(s) used in assessments, managers need measurement endpoints that quantify ecological status. Several different methods have been developed to do so, the choice of which was driven by specific sociopolitical needs coupled with the current state of scientific understanding of aquatic ecosystem structure and function. Six broad approaches emerged over time: the use of indicator or sentinel species, diversity indices, biotic indices, multimetric indices, measures of taxa loss or shifts in taxa composition, and functional indices. Regardless of the measurement endpoint used, the assessment of ecological status is usually based on the degree to which index values observed at an assessed site deviate from values observed at one or more reference sites considered to be in high, or desirable, ecological condition (see the section on Benchmarks and baselines for details).

Indicator/sentinel species

Indicator or sentinel species are those species that are highly sensitive to environmental disturbance and are sometimes used in aquatic biological assessments to provide an early warning that more severe water quality conditions are likely to occur unless mitigation measures are taken. However, the response of single species cannot quantify overall ecological status because they occupy only a small part of the overall niche space represented by an entire ecological assemblage. As a consequence, bioassessment programs typically favor the use of indices that assess the overall condition of entire assemblages.

Diversity indices

The first of the assemblage-wide indices used in bioassessments were species diversity indices, such as the Shannon-Wiener index. With the emergence of theoretical ecology in the 1970s, aquatic scientists promoted the use of these indices, which measure aspects of alpha diversity (i.e., at a site) and whose values are jointly influenced by variation in both taxa richness and evenness. Two potential advantages of these indices are that they had a theoretical foundation and did not require specific identification of taxa (just the ability to assign individuals into unique taxa – e.g., morphospecies). High diversity values were interpreted as implying better ecological status than lower diversity values. However, use of these indices as a sole basis for quantifying ecological status was soon abandoned both because natural systems vary substantially in both of the key diversity components of richness and evenness and because little consensus emerged regarding the broader ecological significance of observed differences in diversity values. Recent studies have questioned the extent to which diversity indices like the Shannon-Wiener index can be interpreted and compared (e.g., Jost, 2010) and suggest that they may obscure signals based on simple measures of taxa richness and evenness (Cao and Hawkins, 2019). Despite difficulties in their interpretation, diversity indices are still frequently included as one of several metrics incorporated in more contemporary multimetric indices (MMIs). There is evidence, though, that simple measures of taxa richness, after adjusting for the effects of natural environmental setting, may be an effective index of ecological condition (Bailey et al., 1998).

Biotic indices

Biotic indices quantify assemblage-wide tolerance to organic pollution. The original biotic indices were based on tolerance of species to reduced oxygen associated with organic pollution (Chutter, 1972; Hilsenhoff, 2017). Biotic index values can represent either the simple or weighted average of tolerance values assigned to species. Tolerance values were often assigned based on expert knowledge derived from observations of species distributions across known organic pollution gradients, and low tolerance values were assigned to sensitive species and high values were assigned to tolerant species. This approach assumes that waterbodies with lower biotic index scores (i.e., relatively more sensitive species) are in better ecological status than waterbodies with higher biotic index scores (i.e., relatively fewer sensitive species). However, aquatic scientists soon pointed out that species tolerances can vary markedly across natural environmental gradients and that values calculated from appropriate sites in reference condition were needed to avoid misinterpretation of ecological status. Moreover, biotic indices measure just one aspect of ecological condition and may therefore be less robust than desired.

Multimetric indices

Multimetric indices are additive indices in which several aspects of assemblage structure (e.g., trophic structure, taxa composition, tolerance, richness/diversity) are first standardized to a common scale and then summed to represent a more ecologically comprehensive measure of ecological status than any single metric provides. The first multimetric index, an *Index of biological*

integrity (*sensu* Karr, 1981), was specifically designed to include measures that spanned the types of community attributes mentioned in the definition of biological integrity. However, the selection of the individual metrics used in more recently developed multimetric indices have been driven more by their ability to discriminate reference-quality waterbodies from those believed to be degraded or stressed (e.g., Hering et al., 2006; Stoddard et al., 2008), thus MMIs have lost some degree of connection to the original concept of biological integrity that stimulated their development and use. However, MMIs are widely used and much progress has been made in improving their performance (Ruaro et al., 2020).

The use of biological traits that describe species autecology beyond the standard metrics used in many MMIs has been proposed for use as metrics in MMI-type indices (Dolédec and Statzner, 2010; den Brink et al., 2011). A theoretical advantage of using biological traits as metrics is that variation in biological traits should be more independent of geography than variation in taxa. Theoretically, indices based on biological traits should also lead to more direct mechanistic interpretation of the causes of biological degradation than is possible from taxonomic-based indices (Poff et al., 2006; Culp et al., 2011). Trait-based indices should also be more comparable across regions than taxa-based indices because convergent evolution has led to species possessing the same types of traits globally.

Indices of taxonomic completeness

The last major approach to assessing ecological status focuses on quantifying species loss or shifts in taxonomic composition. In this approach, the taxonomic composition observed at an assessed site is compared with that expected to occur in the absence of human-caused environmental alteration. Two main approaches have emerged in their use: a numerical expression of the degree of departure of assemblage composition from reference conditions, and a graphical approach. In the prior case, originally developed in the United Kingdom as RIVPACS (River Invertebrate Prediction and Classification System) (Moss et al., 1987), the proportion of the specific taxa predicted (expected, E) to occur at an assessed site that are observed (O) provides a quantitative measure of the loss of endemic taxa (O/E). O/E theoretically scales from 0 to 1. In contrast, the graphical approach shows the position of an assessed site in taxa-defined ordination space relative to the distribution of reference sites in that ordination space (Reynoldson et al., 1995). In the latter case, the degree of impairment is based on a more general measure of differences in compositional similarity between an assessed site and a set of appropriate reference sites. Both the assessed site and the reference sites are plotted in taxa-defined ordination space, and confidence ellipses around the reference sites are used to assign the degree of departure by the assessed site. The modeling to adjust E for the effects of natural environmental gradients and the standardization of assessment values as a ratio (O/E) means this approach can potentially be used to directly compare ecological status across regions without the extensive intercalibration and harmonization needed when comparing different MMIs and other types of indices (Furse et al., 2009). In addition, because the modeling modules within RIVPACS approaches are essentially multitaxon distribution models, the main model outputs (probabilities of capture) can be used to estimate which taxa have increased and decreased within regions in response to land use and waterway alteration (Hawkins and Yuan, 2016).

Conceptual and practical differences between MMI and O/E approaches

The MMI and O/E approaches are the most frequently used indices globally, and they differ in three major ways that have produced scientific debates regarding their use and interpretation. First, they differ in what assemblage-level attribute(s) are used to characterize biological status as described above. Second, they differ in how biological reference conditions are determined as described below. Third, they differ in how indices are calibrated. MMIs are calibrated by selecting metrics that best discriminate between reference sites and sites considered to be physically or chemically degraded, hence their performance is potentially dependent on the specific stressor conditions occurring at the degraded sites used in calibration as well as sampling variability and the degree to which typologies or models account for natural variability across reference sites. In contrast, O/E indices do not use degraded sites for calibration, and their performance and interpretation are influenced by those factors that affect model predictive accuracy and precision – e.g., sampling variability, the predictor variables used, the type of model used, and the inherent variability of the reference state.

Indices of ecosystem function

Indices based on snapshots of assemblage composition provide no direct assessment of the ecological processes that provide goods and services. Some traits or metrics have been used to characterize trophic roles of species (e.g., functional feeding groups), which theoretically should indicate shifts in the relative importance of different food resources available to consumers and the relative magnitude of different processes involved in energy flow and material transformations (e.g., shredding of leaf litter, consumption and regulation of algal standing crops, filtering of seston). However, few MMIs include functional feeding group metrics, primarily because they seldom discriminate between reference and degraded sites as strongly as other metrics, which implies that functional feeding group assignments may be too coarse or inaccurate to adequately reflect differences in ecosystem processes. Direct estimates of ecosystem processes are therefore needed. The rate of leaf litter processing has been suggested as one useful ecosystem function index (Wallace et al., 1996; Gessner and Chauvet, 2002; Gulis et al., 2006; Young et al., 2008). Differences in processing rates have been detected associated with changes in nutrient inputs, sedimentation, and the presence of contaminants, but such measures have yet to be routinely incorporated into large-scale biomonitoring programs, probably because they can be either too expensive or time consuming.

Benchmarks and baselines

Modern biological assessments measure ecological status as the magnitude of departure of the value of an index of choice from a baseline value. Ideally this baseline (or reference) value would describe the range of natural variation expected at each individual waterbody (Stoddard et al., 2006; Hawkins et al., 2010). Historical data collected over many years at sites prior to human-caused alteration would provide the best estimates of reference condition. However, such data are rarely available, although past assemblages have been reconstructed from fossil organisms observed in sediment cores from lake bottoms. Furthermore, this approach is largely limited to standing waters and may not be practical for routine bioassessments. Instead, the biota expected to occur under natural or desirable conditions are usually estimated via some type of control-impact design or a space for time substitution. The control-impact design requires that one or more reference sites be selected for each assessed site and both the reference and assessed site must be sampled over the same time period. Control-impact designs, though, are expensive, susceptible to serious statistical limitations, and most applicable to targeted assessments of individual sites rather than regional surveys. Some type of space-for-time substitution is used in most regional surveys, but they also have limitations as described below.

The more common approach that can be used in both targeted assessments and regional surveys is to select a large number of high-quality (natural condition or reflective of desirable condition) reference sites within a region of interest. The spatial variation in aquatic life observed across these high-quality sites is then used to estimate natural spatial variation in aquatic life. In the MMI approach, reference condition was originally estimated directly as the variation among reference sites within a homogeneous landscape – e.g., an eco- or bioregion or within a geomorphic or hydrologic type of waterbody, and no attempt was made to specifically estimate temporal variability at individual sites (Hughes et al., 1986). If the index value observed at an assessed site fell outside of a specified range of values observed at the reference sites (e.g., 10th and 90th percentiles), that site was considered to be in non-reference condition and likely to be biologically impaired. Effects of natural environmental gradients within a region or waterbody type were often implicitly ignored, except for stream size in some cases. In the O/E index approach, the relationship between species composition and naturally occurring environmental gradients is modeled in an attempt to more accurately and precisely estimate the reference condition that best matches each individual assessed site (Moss et al., 1987; Bailey et al., 2004; Hawkins et al., 2010). In this approach, model residuals estimate the range of natural variability expected at each site in the region (i.e., a space-for-time substitution), although these residuals also include unexplained variation in E associated with sampling variation and model error. This approach has also been used to adjust simple measures of taxa richness for the effects of natural environmental variation (Bailey et al., 1998). More recently, modeled MMIs and biotic indices have been developed in which either each individual metric of an MMI is modeled (Cao et al., 2007; Vander Laan and Hawkins, 2014) or the MMI or biotic index as a whole is modeled (e.g., Hawkins, 2006) as a function of natural gradients to better parse the effects of stressors and natural environmental features on index values. The primary limitation of this approach is that the quality and number of reference sites can vary across regions, and without post hoc adjustments for reference site quality, assessed sites in some regions can be held to a higher or lower standard than sites in other regions. This issue is not as problematic, though, if reference sites in a region are mainly used to establish an anchor or benchmark that can be used to assess if sites are improving or not over time. An active area of research focuses on how to predict reference conditions in the absence of (high-quality) reference sites – i.e., in regions that are generally degraded or altered by human activities (Chessman and Royal, 2004; Paulsen et al., 2008).

Establishing physical/chemical water quality standards protective of aquatic life

The protection of ecological status generally requires regulatory policies that set limits to physical and chemical conditions beyond which aquatic organisms are harmed. Water-quality standards are regulations that may include specific numeric criteria used to protect designated uses of water bodies – such as the maintenance of aquatic life. In theory, numeric criteria are the concentrations of pollutants (or the degree of habitat degradation) in water bodies beyond which substantive or unacceptable ecological harm occurs, and they are therefore considered allowable limits for regulatory purposes. Traditionally, these criteria were established by conducting bioassays that expose a standardized set of species to different concentrations of a pollutant in a highly controlled laboratory setting for a standardized period of time (e.g., 96 h). Biological responses to pollutant exposure are then measured, which may be either acute or chronic, lethal or sub-lethal. The resulting dose-response relationship is then modeled and used to estimate the pollutant concentration at which a measurable biological response is initiated (e.g., Lowest Observed Effect Concentration, or LOEC). For practical reasons, bioassays are often limited to acute, single-species exposures, and the resulting LOEC is divided by a safety factor to better protect against chronic exposures. If LOECs are available for many different experimental organisms, the LOEC protective of 95% of species, or some other agreed-upon number, could be estimated and used as the water quality criterion—an approach known as species-sensitivity distributions (Posthuma et al., 2001). A common criticism of bioassays is that they lack realism, largely because they are derived from a set of species that are conducive to laboratory rearing rather than representative of the species native to the waterbodies of interest. Moreover, controlled testing is not representative of exposures and responses under natural conditions over the full life-cycle of most species (Clements and Kotalik, 2016). However, large-scale survey data are being increasingly used to either construct field-based species-sensitivity distributions or describe how the values of indices of choice (e.g., MMIs or O/Es) vary across gradients of specific stressors. These relationships coupled with laboratory data and information produced during stressor identification (see below) can be used to better estimate criteria that more fully protect

aquatic life. Indeed, some studies that integrate more realistic experimental exposures – such as on multi-species assemblages within microcosms – with field data have shown that water-quality criteria based on bioassays alone are not sufficiently protective of natural systems (Miller et al., 2020).

Stressor identification

Knowledge of ecological impairment is fundamental in identifying waterbodies in need of restoration, but that knowledge by itself provides insufficient information to guide the specific management actions needed to achieve restoration goals. Therefore, a critical next step is to identify the stressor(s) causing impairment of ecological status – often described as diagnosis or causal analysis (Norton et al., 2009). Diagnosis typically occurs on a site-specific basis because sites (e.g., river segments) are usually the management unit of concern. But insight into potential stressors can also be gained by analysis of survey data across many sites and stressor gradients (Vander Laan et al., 2013).

Diagnostic approaches to stressor identification can be based solely on biological data, on empirical relationships between biological data and measured stressors, or combinations of both. The most common approach, however, is limited to the use of the biological data collected at monitored sites, largely because many stressors simply cannot be adequately characterized with a single discrete sample—as is typically employed in large-scale bioassessment programs. For example, characterizing the modification of hydrologic or thermal regimes or episodic exposure to pesticides requires continuous monitoring over many months, which presents major logistical and economic constraints. Diagnostic approaches that rely on biological data typically include the computation of metrics based on external information, such as species sensitivities to specific stressors from bioassays, or species traits derived from life-history studies. Both approaches assume that patterns observed in impaired biological communities provide clues about potential causative factors.

Diagnostics based on known species sensitivities consider the extirpation of sensitive species as diagnostic evidence. Indeed, this is the premise for some biotic indices that are computed from assemblage data based on relative sensitivities of taxa to specific stressors. In theory, these indices respond to changes in assemblage composition driven by declines in taxa that are sensitive to a specific stressor and increases in taxa that are tolerant of that stressor (e.g., salinity). This specificity in response is an important assumption in the use of these diagnostic indices. This approach has promise, but many taxonomic groups appear to be sensitive or tolerant to multiple types of stressors. For example, experimental evidence shows that the mayfly family Heptageniidae is among the most sensitive aquatic insect group to heavy metal exposure (Clements et al., 2002). However, reductions in the diversity or abundance of this group at a monitored site does not reliably indicate the presence of heavy metals because many species in this family are also sensitive to sedimentation or the modification of hydrological and thermal regimes (Carlisle et al., 2011).

Diagnoses can also be based on trait signatures such as shifts in body morphology, phenology, desiccation resistance, or dispersal abilities (den Brink et al., 2011; Culp et al., 2011) as discussed earlier. The assumption is that changes in trait signatures at ecologically impaired sites are indicative of exposure to specific types of stressors. For example, if the relative abundance of desiccation-resistant species is higher than expected at an ecologically impaired site, then dewatering could be considered a potential cause. Researchers are evaluating the potential utility of extracting causes of degradation from overall trait profiles (e.g., Culp et al., 2011) as well as developing stressor-specific indices for causal diagnosis (e.g., Murphy et al., 2015). These approaches show promise, but major limitations of trait-based approaches are (1) the limited autecological and natural history information available for many species and (2) the coarseness at which many trait categories are described (e.g., cold, cool, and warm water taxa). Traits for fish are better known than for other taxonomic groups, except for the European insect fauna (Schmera et al., 2015). Another limitation is that the environment often acts on groups of interrelated traits (adaptive syndromes), many of which are also linked to phylogenic history. The assumption of specificity, as described above, also applies to trait-based approaches. In summary, trait-based, diagnostic indices have intuitive appeal as they are based on ecological theory, but more research is needed to demonstrate their diagnostic power.

Integrated approaches may be more reliable in diagnosing stressors given the limitations of individual stressor-specific indices. For example, the SPEAR (SPEecies At Risk) index developed in Europe uses information on relative sensitivities of taxa to organic chemicals obtained from bioassays, combined with information on estimates of relative risk of exposure based on life histories (e.g., timing of emergence relative to season of pesticide applications). Such integrated indicators are promising (Bray et al., 2021), but their reliability at diagnosing causes of ecological impairment has yet to be widely established.

Diagnostic evidence from indices derived from sensitivities or traits can be substantially enhanced where stressors have also been reliably characterized at monitoring sites. However, measures of stressors require context to be useful for stressor diagnosis. Potential stressors that also occur naturally, such as sediment deposition, streamflow alteration, temperature modification, and nutrient concentrations, need to be placed in context of the natural range of conditions at the assessed site. Even potential stressors that are entirely anthropogenic, such as many pesticides, need to be viewed in the context of how variation in natural factors influence responses to novel stressors. Moreover, responses need to be interpreted in context of whether acute or chronic lethal concentrations have been estimated and, if so, how. Benchmarks for many stressors do not exist, but those for some well-known stressors, such as salinity and maximum water temperature, may be inferred from existing water-quality criteria, although they have known limitations (see previous section). Despite the challenges of characterizing stressors, integrated analyses that include the use of stressor-specific indices can provide strong diagnostic evidence. For example, consider again the site with a higher-than-expected

frequency of species with desiccation-resistant traits. If measured daily flow data indicated that the duration and magnitude of low-flow periods are outside the bounds of natural variation for that site, both lines of evidence lead to a stronger case for flow modification being the stressor causing ecological impairment (Carlisle et al., 2011).

In general, the strongest diagnostic evidence emerges when multiple lines of evidence are obtained through integrated analyses of biological, physical, and chemical survey data, as well as information from follow-up monitoring and investigations (Clements et al., 2002). Integrated analyses as describe above can lead to hypotheses regarding the causative factors responsible for observed biological impairment, which can be subsequently tested with new survey data or more intensive stressor monitoring at a site. In addition, integrated data analyses from region-wide surveys may provide additional evidence regarding the stressors that are most likely influencing an individual site. In addition to multiple lines of empirical evidence, the diagnostic process requires critical thinking about the direct and indirect effects of stressors on biological assemblages—often obtained via conceptual models—as well as thorough reviews of relevant literature.

Outstanding issues and challenges

Fully characterizing aquatic life

Biological assessments of waterbody condition rely on estimates of what species occur in a specific waterbody. Ideally, we would detect all species present in a waterbody, but practical constraints require that we sample (rather than census) the species that are present. Sampling seldom captures all species present, especially for small, diverse taxa such as algae and invertebrates of which we collect a very small fraction of the total individuals present. Moreover, some taxonomic groups (e.g., microbes, protozoans, microcrustaceans) are not typically used in bioassessments because of the expense and time it would take to determine what taxa occur at a site. Even for those taxa frequently used in bioassessments, imperfect detection associated with the use of small sample counts can lead to distorted estimates of taxa richness and other metrics and endpoints. Fortunately, the use of either DNA extracted from benthic samples or environmental DNA (DNA shed by species and suspended in the water column) samples holds great promise in improving the detection of species in all taxonomic groups while simultaneously reducing the time and expense to produce usable data (species counts) from raw samples and the costs of sample processing (Elbrecht and Leese, 2017; Macher et al., 2018). The use of DNA in bioassessments is a very active area of current research (see Baird et al., 2022).

Expand the types of aquatic ecosystems that can be reliably assessed

Another vexing issue is the absence of reliable methods for bioassessment of non-perennial systems such as temporally intermittent streams and ephemeral wetlands (Mazor et al., 2014; Soria et al., 2020). Non-perennial streams represent a significant portion of the headwaters of stream networks in mesic regions, but they constitute the majority of the networks in arid and semi-arid regions. Ephemeral wetlands are critical reproductive habitat for many invertebrates and vertebrates. However, most state and federal programs are unable to assess the ecological status of these important ecosystems because bioassessment methods have not yet been fully developed and evaluated for these aquatic systems. Active research has started in arid and semi-arid regions of the world (see Compson et al., 2022), but much more is needed, especially given that these systems appear to be much more dynamic and unpredictable than their perennial counterparts (see next section). In addition to non-perennial water bodies, perennial ponds, small lakes, and bogs also are often overlooked in regional bioassessment programs.

More thorough incorporation of ecological theory in index development and interpretation

Reference condition approaches to biological assessment require that practitioners predict the biological condition that would be expected at a waterbody if it was in reference condition. Both classification (typologies) and continuous modeling approaches to predicting biological reference conditions essentially assume biota-environment relationships are deterministic and that taxa or their traits are inherently predictable as long as the classification is correct or the appropriate environmental predictors have been measured. The increasing availability of refined environmental data (e.g., stream temperatures, hydrologic regimes, background water chemistry) and sophisticated statistical tools (e.g., random forest and other machine learning predictors) have improved the accuracy and precision of predictions to some extent, but considerable prediction error still occurs, especially in highly dynamic landscapes that experience frequent natural disturbance. Aquatic scientists now recognize that ecological communities vary in the extent to which they are predictable because the relative importance of niche processes (deterministic biota-environment relationships), dispersal-driven processes, and stochastic colonization and establishment can vary considerably across regions. The development of metapopulation and metacommunity theory (Leibold et al., 2004) has provided the bioassessment community with great insight regarding how to use this understanding to potentially improve assessments (Brown et al., 2011; Heino, 2013; Cid et al., 2020; Brown et al., 2022). For example, depending on the environmental setting, niche processes can vary in their strength with strong niche effects expected in relatively stable environments and weak niche effects occurring in frequently disturbed systems. Variation in dispersal strength can also affect predictability. For example, the mass effects associated with high dispersal pressure can cause environmentally different waterbodies to harbor assemblages that are more similar to one another than would arise from niche sorting, whereas weak dispersal between environmentally similar, but isolated, waterbodies can cause assemblages to be less similar than expected from niche sorting. Incorporating these processes into biological indices may help improve their performance,

but if the predictability of either species or their traits is fundamentally limited by high, naturally occurring environmental variability, additional predictor variables or new modeling techniques will not likely improve index precision. However, simply recognizing that ecosystems naturally vary in how dynamic and predictable they are can help managers set more appropriate index thresholds for regulatory purposes. For example, knowledge of regional variability in the predictability of assemblages is required to set regionally-specific impairment thresholds from the frequency distributions of reference-site index values observed in different regions.

Other research has focused on the evaluation of different measurement endpoints than those currently represented by the six types of indices discusses earlier. For example, a few researchers have proposed biological indices based on phylogenetic diversity (Keck et al., 2016; Weglarz et al., 2021). They argue that phylogenetic indices can more fully assess the completeness of the functional diversity expected at a site or in a region. Maintaining phylogenetic diversity is a goal of many conservation programs. Such new ideas need to be fully evaluated both in terms of their overall ability to detect biological impairment and with respect to how well the assessment and measurement endpoints match to and address specific policy and management directives.

Moving beyond site-specific assessments

Some biological assessment programs are also starting to recognize the need to move beyond site-specific assessments. Site-specific assessments will continue to be a central focus of most programs because most management activities occur at the site level. However, society also needs to know the spatial extent of biological degradation and if certain types of landscape settings are either more or less sensitive or resistant to human-caused stressors, including climate and other global environmental changes. Answering questions about the status and trends at regional to global scales requires that programs adopt statistically valid survey designs that can estimate regional conditions with known certainty (Paulsen et al., 2008). These designs require that programs assess sites other than those known or expected to be impaired. From these designs, site-specific assessments can simply be scaled up to express mean conditions and the likely distribution of different assessment classes across a region of interest. When biological, chemical, and physical sampling occurs, information from such programs can also be used to identify likely stressors of regional importance as mentioned above. However, other, more regional-specific measures of biological condition can provide additional insight. For example, the predictive models used in O/E assessments can be used to quantify what taxa are decreasing and increasing in frequency of occurrence (Hawkins and Yuan, 2016). This information can help us understand what individual taxa may be most susceptible or responsive to human activities in general. Both sensitive, native taxa as well as tolerant, invasive taxa may require specific conservation actions. Information on the taxa composition at multiple sites can also be used to estimate aspects of regional beta diversity – i.e., how similar or different sites are in taxonomic (or functional) composition. Such measures may be especially useful in assessing the degree to which individual sites within a region may be becoming more or less homogenous in response to human-caused alteration of waterways and their surrounding landscapes (Bini et al., 2014; Hawkins et al., 2015).

Cross-regional comparisons of ecological status are often required to support both national and international policies and legislation. Such comparisons assume that the indices used are either the same or that they can be compared in a straightforward and valid way. Unfortunately, these comparisons are a particularly vexing issue for many programs. For example, the US Clean Water Act requires individual states and tribal nations to assess and monitor the status of their surface waters, but individual states and tribes can choose which scoring tools they use. A similar situation exists across countries in the European Union. Index harmonization efforts have met with limited success, which emphasizes the likely need for states and nations to eventually adopt standard approaches to biological assessments.

Better characterization of stressors

A long-standing issue in bioassessments is the incomplete characterization of stressors, which severely limits the ability to understand causes of ecological degradation. In general, stressors that require continuous or frequent sampling are either inadequately characterized with a single sample, or simply not measured. For example, insecticides are designed to be toxic to invertebrates and are ubiquitous in freshwater ecosystems, but they are almost never characterized in bioassessment programs. Similarly, water temperature is a controlling factor of many ecological processes, but it is typically only measured once during site visits, which provides little information about overall thermal conditions. Fortunately, technological advances and innovative research is starting to provide useful and economical tools for characterizing stressors. For example, the recent development of passive samplers has streamlined the collection and characterization of organic compounds such as pesticides. These devices are essentially containers of media that accumulate organic contaminants through time and were designed to be a standardized way to evaluate bioavailability. Samplers are deployed in a water body for several weeks, such as a period of expected pesticide use in the watershed, and therefore require only two site visits and a single laboratory analysis. Pesticide concentrations extracted from passive samplers were strongly associated with indices of ecological status and more representative of exposure than multiple discrete samples (Waite et al., 2021). A variety of cost-effective methods have also been evaluated for characterizing streamflow. Although it is unlikely that technology will replace the need to deploy and retrieve monitoring devices, which requires at least two site visits, better characterization of stressors is necessary to improve bioassessment programs.

The critical need for effective science communication

The main challenges to effective water resources protection and restoration are social, political, and economic rather than scientific. Aquatic scientists can enhance the development and application of successful bioassessment programs by developing effective ways of engaging and communicating with nonscientists. Doing so requires that scientists clearly communicate their knowledge (and its relevance) to stakeholders and decision makers – a process recently termed translational ecology (Enquist et al., 2017). In many respects, biological assessment programs are the poster children of translational ecology in that regulatory agencies have convened meetings between scientists, stakeholders, and regulators to improve the scientific foundations of biological assessment programs for many years (Adler, 2020). However, the success of any translational ecology approach depends heavily on how well different constituents communicate with one another, and a chief impediment to communication in the past has been the inability, or reluctance, of scientists to explain in simple, direct terms both the need for biological assessments and how to use and interpret the tools they develop. Many scientists increasingly recognize the need to improve their communication skills and are seeking training (Brunson and Baker, 2016). Aquatic scientists are also learning at an earlier career stage that science is just one piece of the information ultimately used by decision makers to develop water resources policy and management goals. That understanding, coupled with an ability to more effectively communicate their knowledge, should allow aquatic scientists to be better advocates for the protection and restoration of the planet's critical aquatic ecosystems and the species that depend on them – including humans.

See Also: Structures and functions of Inland Waters - Rivers: Dispersal in Stream Networks: Meta-populations and Meta-communities; Dryland Rivers and Streams; eDNA and Bioassessment of Rivers

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eDNA and Bioassessment of Rivers

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

eDNA An abbreviation of the term 'environmental DNA.' eDNA is the DNA that can be extracted from an environmental sample, such as from bulk sediment, filtered water, or mixed communities actively or passively collected (e.g., kick-net sampling and periphyton scraping), as opposed to DNA that is extracted from one individual at a time.

DNA metabarcoding A method to support species-level identification of organisms from bulk or mixed environmental samples via marker gene sequences, without the need to isolate individual specimens.

DNA barcoding The use of DNA sequences from a signature region of the genome to make species-level identifications.

Operational taxonomic unit (OTU) A cluster of similar sequence variants for a marker gene, usually defined by some measure of sequence similarity (e.g., 97%) or dissimilarity (e.g., 3%). OTUs are sometimes used as a proxy for 'species' even though thresholds needed to group sequences from a taxonomically defined species may vary across taxonomic groups and genomic markers. OTUs are usually represented by a single centroid sequence. A synonym is molecular operational taxonomic unit (MOTU).

Exact sequence variant (ESV) Similar to an OTU that is defined by 100% sequence similarity, but ESVs are generated by a denoising algorithm. Denoising methods commonly attempt to remove or correct errors generated during PCR and/or sequencing, remove artefactual chimeric sequences generated during PCR, and remove other artefactual sequences commonly found in rare sequence clusters. Synonyms include amplicon sequence variant (ASV) or zero-radius OTU (ZOTU).

Bioinformatics An interdisciplinary field that integrates aspects of biology, computer science, statistics, and mathematics to automate the analysis, modeling, and visualization of biological data in "pipelines" of software algorithms.

Polymerase chain reaction (PCR) A process used to amplify millions to billions of copies of a DNA fragment via thermal cycling (i.e., repeated cycles of heating and cooling).

Quantitative polymerase chain reaction (qPCR; also called "real-time" PCR) A laboratory technique akin to PCR, but one that involves the monitoring of the DNA amplification during the PCR (i.e., in real time). qPCR involves either fluorescent dyes or DNA probes to detect the amplified DNA fragment.

Droplet digital PCR (ddPCR) A method used for performing digital PCR that is based on water-oil emulsion droplet technology. Samples containing DNA to be amplified are fractionated into 20,000 droplets, and PCR amplification of the DNA occurs in each individual droplet.

High-throughput sequencing A term referring to DNA/RNA sequencing platforms that are capable of sequencing DNA/RNA in parallel, processing up to millions of sequences simultaneously.

DNA sequence capture An approach that targets enrichment of specific regions of a genome. Coupled with NGS, sequence capture technology enables high-throughput screening of genomic regions of interest.

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Introduction

Since the advent of the Industrial Revolution, anthropogenic activities, such as agriculture, mining, and rapid urbanization have severely degraded the world's rivers (Echols et al., 2009). As rivers play a critical role in global biogeochemical cycling (e.g., carbon, nitrogen, and phosphorus cycles) and provide essential ecosystem services for society, significant alterations to either the physical and/or biological components of these important habitats are an omnipresent cause of concern, requiring increased understanding of their scale and potential consequences (Limburg, 2009; Norris and Barbour, 2009). The first step in addressing degradation of rivers is to assess the nature and extent of the damage through an understanding of the current state of the ecosystem. In an attempt to reduce and ultimately reverse decades of river degradation, bioassessment programs have been launched in many countries to evaluate the biological condition of aquatic ecosystems (e.g., US Clean Water Act and the European Water Framework Directive) (Buss et al., 2015; Norris and Barbour, 2009). Such bioassessment programs observe the state of river ecosystems through biological surveys (Bailey et al., 2014; Buss et al., 2015) or other direct measures (e.g., field experiments) of the biological elements of the ecosystem (Norris and Barbour, 2009). For example, fish, algae, plants, and most commonly, benthic macroinvertebrates are targeted as units of bioassessment in rivers (Buss et al., 2015).

River macroinvertebrate organisms are sensitive to environmental stressors and have been routinely used as biological indicators of river and stream health (Buss et al., 2015). Yet, current bioassessment programs often rely on microscopy methods based on morphological characters of mature specimens for identification (Elbrecht and Leese, 2017; Emilson et al., 2017). This can be a laborious practice, slowing the delivery of timely results to bioassessment programs. Moreover, misidentifications of closely related taxa with differing tolerances to environmental stressors could have consequences for bioassessment, introducing error and potentially compromising study conclusions (Macher et al., 2016). Thus, there is an unmet need to produce rapid, robust bioassessment data to improve river management.

With the advent of high-throughput gene sequencing technologies, coupled with a maturing program to build reference libraries of marker gene sequences that can facilitate accurate species identification, we can now harvest biodiversity information from environmental samples rapidly and cost-effectively by analyzing their constituent DNA. This extracted DNA is termed environmental DNA, or eDNA. The accessibility of eDNA in traditional bioassessment samples presents a major new opportunity to increase the efficiency and accuracy of bioassessment programs supporting river ecosystem policy development and management (Baird and Hajibabaei, 2012; Deiner et al., 2017). In this chapter, we present an overview of the current state of the science concerning observation of riverine biodiversity using eDNA, and how current and future bioassessment programs could profit by employing this new approach.

eDNA and bioassessment

Although various definitions of eDNA exist in the literature (e.g., Deiner et al., 2017; Pawlowski et al., 2020; Taberlet et al., 2018, 2012a, b), here we define eDNA as all of the DNA that can be extracted from an environmental sample, such as from bulk sediment, filtered water, or mixed communities actively or passively collected (e.g., kick-net sampling and periphyton scraping), as opposed to DNA that is extracted from one individual at a time (Fig. 1). DNA extracted from environmental samples includes both the intra- and extracellular DNA of living, decaying, or dormant cells, including cells that are shed by organisms, gut contents, and excrement (Deiner et al., 2017; Pawlowski et al., 2020). Once eDNA has been extracted from the river environmental sample, signature DNA sequences from target species (e.g., invasive species, pathogens), target assemblages (e.g., Ephemeroptera, Plecoptera, Trichoptera), or whole communities (e.g., plants, macroinvertebrates, bacteria, fungi, diatoms—see Deiner et al., 2017; Hajibabaei, 2012; Kelly et al., 2020) can be enriched for DNA gene sequence analysis for bioassessment of rivers. While the detection of a species from eDNA does not necessarily indicate the presence of a living organism at a sampling site, it does provide a biological signal for an organism in the broader study area. In essence, the assessment of eDNA in rivers can provide a snapshot, within a relatively narrow time window, of a target species, assemblage, or community that can be used for bioassessment.

The Environmental Protection Agency (EPA) defines bioassessment as, "the process of evaluating the biological condition of a body of water using biological surveys (i.e., biosurveys) and other direct measurements of the resident biota, and those organisms living in the surface water, including fish, insects, algae, and plants." Traditional means of generating biodiversity data for bioassessment, such as morphology-based identification of freshwater benthic macroinvertebrates, were established decades prior to the implementation of eDNA methods. While DNA-based methods are often advantageous over traditional methods for generating biodiversity data for bioassessment (e.g., detection of rare, cryptic, or low- density taxa and identification to genus or species level; Ruppert et al., 2019), there are also instances where eDNA approaches fall short of traditional methods for detection (e.g., for semi-aquatic snakes; Rose et al., 2019), and there are benefits in combining these approaches. Bioassessments for freshwater health have been enhanced through the application of eDNA due to the ability to identify a greater number of bioindicator taxa to lower taxonomic ranks (i.e., to genus and species level). Likewise, morphological approaches enable direct abundance and body size measures of identified taxa and assessment of life history characteristics (e.g., whether it is a larval, pupal, or adult form), and thus these approaches provide valuable information for biobanking of biodiversity data (Sheth and Thaker, 2017).

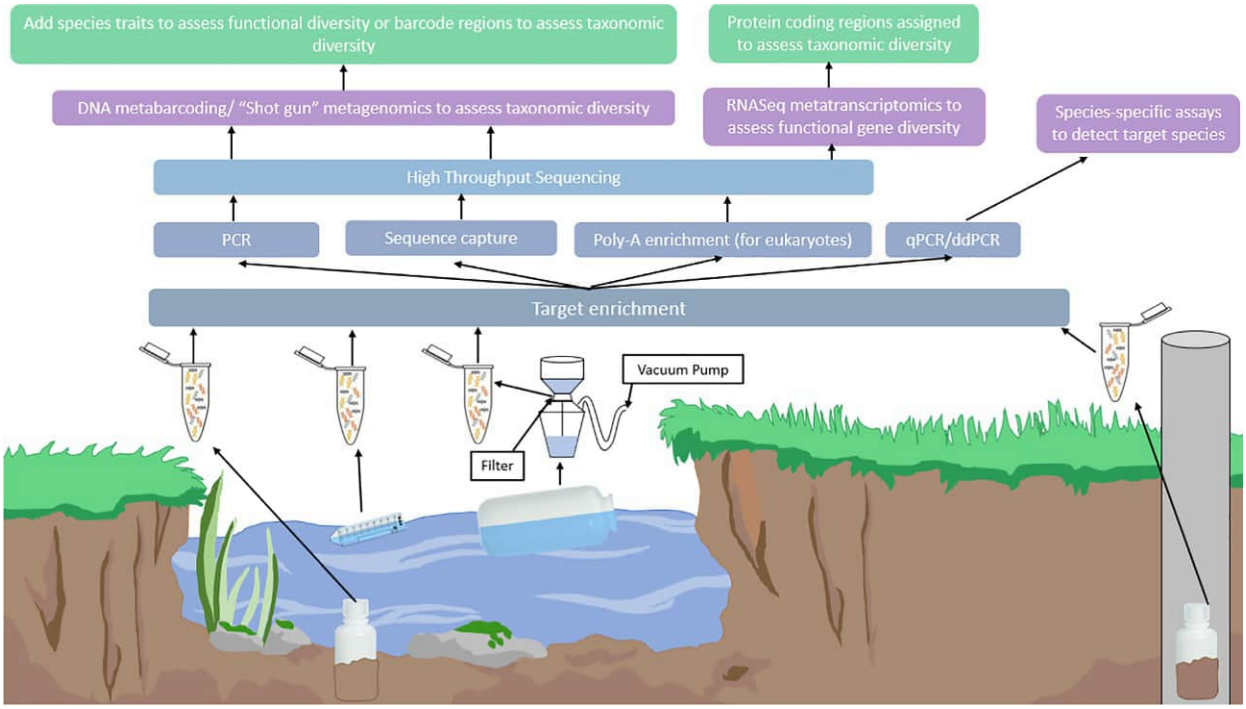

Fig. 1 eDNA workflows for bioassessment in freshwater ecosystems to assess taxonomic or functional diversity.

Observing river biodiversity with eDNA

DNA barcoding and DNA metabarcoding of eDNA has revolutionized the way we observe biodiversity and detect biological change in river ecosystems. The term 'DNA barcoding' refers to the use of DNA sequences from a signature region of the genome to make species-level identifications (Hebert et al., 2003). The process involves the use of reference sequence libraries from individual specimens identified by experts. Collection information, referred to as metadata, is deposited into a database that houses barcode sequences from such specimens along with the trace file of the sequence itself (Ratnasingham and Hebert, 2007). The Barcode of Life Database (BOLD) can be accessed from https://www.boldsystems.org/ and holds about a million DNA sequences representing freshwater biomonitoring taxa of interest (Porter and Hajibabaei, 2018b). DNA barcode sequences from taxonomically identified specimens. DNA barcodes, when linked to confirmed specimen identifications, can form the basis of a reference database for the species-level identification of marker gene sequences that are generated from bulk or mixed environmental samples, i.e., without the need to isolate individual specimens. This has been termed DNA metabarcoding (Hajibabaei et al., 2011; Hajibabaei, 2012; Taberlet et al., 2012b).

For animals, the official barcode region is ~658 base pairs (bp) of the cytochrome *c* oxidase subunit I (COI) gene found in the mitochondrial DNA; other signature DNA regions may be more appropriate for other organisms (Table 1). For example, other suitable DNA regions include: the internal transcribed spacer (ITS) rRNA for fungi; the ribulose-bisphosphate carboxylase (rbcL) and maturase K (matK) region for plants, and 16S rRNA for prokaryotes. While these are the most commonly targeted genes for a vast array of organisms, 5.8S rRNA, 18S rRNA, and large subunit rRNA (LSU rRNA) have been used for other microbial-eukaryotic groups, and 18S rRNA for other eukaryotes. There are also other genomic markers, such as small and large subunit rRNA as well as a suite of "housekeeping" genes, which have been useful for fungal species and even strain-level identification (Taylor and Fisher, 2003). For plants, there are a number of genomic regions that have been used for phylogenetic studies, and these have in turn been used as targets for marker gene studies (Hollingsworth et al., 2011). The current consensus is that rbcL and matK cpDNA together may provide species-level resolution for plants; however, it has also been suggested that ITS rDNA may be needed as well to be able to make species-level identifications (Hollingsworth, 2011).

Albeit both DNA barcoding and metabarcoding are procedures to detect and identify organisms, DNA metabarcoding is more feasible for bioassessment, as this approach can process 96 taxonomically diverse environmental samples (96-well plate) at a time, as opposed to separating and sorting 96 individual organisms for downstream DNA sequencing (Hajibabaei et al., 2011). Environmental samples often contain a plethora of phylogenetically diverse organisms, and this can be inconvenient for sorting and separating organisms quickly. Because many bioassessment programs need to repeat biological monitoring regimes over large-scales and frequent time intervals (Hajibabaei et al., 2011), a DNA metabarcoding approach for multi-species bioassessment

Table 1 Commonly used DNA barcode markers and databases.

Target organism	*DNA marker*	*Databases*	*Websites*
Any	Any	National Centre for Biotechnology Information (NCBI)[a]	https://www.ncbi.nlm.nih.gov/nucleotide/
Animals	COI mtDNA	Barcode of Life Data (BOLD) System	https://www.boldsystems.org/
Diatoms	SSU rDNA (18S), ITS2, rbcL cpDNA, COI mtDNA, LSU rDNA (28S)	Diat.barcode	https://www6.inrae.fr/carrtel-collection/Barcoding-database
Fungi	ITS rDNA	UNITE	https://unite.ut.ee/
Eukaryotes	ITS2 rDNA	ITS2 database	http://its2.bioapps.biozentrum.uni-wuerzburg.de/
Eukaryotes	SSU rDNA (18S)	SILVA	https://www.arb-silva.de/
Prokaryotes	SSU rDNA (16S)	SILVA	https://www.arb-silva.de/
Prokaryotes	SSU rDNA (16S)	Ribosomal Database Project (RDP)	http://rdp.cme.msu.edu/index.jsp
Prokaryotes	SSU rDNA (16S)	Greengenes	https://greengenes.secondgenome.com/

Abbreviations: COI, cytochrome *c* oxidase subunit I; mtDNA, mitochondrial DNA; ITS, internal transcribed spacer region; rDNA, ribosomal DNA; SSU, small subunit (SSU); rRNA, ribosomal RNA; ITS, internal transcribed spacer region 2; rbcL, ribosomal bisphosphate carboxylase large subunit; LSU, large ribosomal subunit.
[a]The NCBI is part of the International Nucleotide Sequence Database Collaboration along with the DNA Data Bank of Japan (DDBJ) and the European Bioinformatics Institute (EMBL-EBI).

can overcome bottlenecks for routine biomonitoring in times of when biodiversity information is urgently needed. However, for single-species approaches and/or for adding to library reference databases, DNA barcoding and other technologies, such as quantitative PCR (qPCR) and droplet digital PCR (ddPCR), may be applicable for river bioassessment.

Environmental DNA workflow

In Table 2, we outline several bioassessment targets and illustrate appropriate eDNA methods by 'use cases,' and in Fig. 1, we provide a schematic for eDNA workflows for bioassessment in freshwater ecosystems. The detection and identification of organisms from eDNA typically involves 5 procedures (Fig. 1): (1) environmental sample collection; (2) extracting DNA from environmental samples; (3) performing polymerase chain reaction (PCR) to amplify the DNA in the sample(s); (4) DNA/RNA sequencing; and (5) bioinformatic analysis. For collecting eDNA from water, samples are typically either collected in small volumes (i.e., $\sim$ 15 mL) and precipitated in ethanol (Ficetola et al., 2008), or collected in larger volumes (i.e., $>$ 250 mL) and filtered (Tsuji et al., 2019). A range of different filter styles and sizes have previously been applied to eDNA sample collection (e.g., see Majaneva et al., 2018). Bulk-benthos or river sediment samples can be collected via direct surface sediment collection (e.g., Turner et al., 2015), sediment coring (e.g., Shaw et al., 2016) or via benthic kick-net sampling (Hajibabaei et al., 2011). After environmental samples are collected, DNA is extracted from these samples using a DNA extraction kit. Several DNA extraction kits exist but can differ in quality, DNA yield, and cost. Moreover, studies have shown that the type of environmental sample from a river (e.g., water vs benthic sample) is known to yield differing concentrations of DNA and should be taken into consideration for bioassessment programs, as this can influence the number of taxa detected in a sample type (Macher et al., 2018; Hajibabaei et al., 2019a).

Once eDNA has been extracted from the environmental sample, the DNA is amplified via PCR to produce millions of copies of this DNA. To target different taxonomic hierarchies with PCR, gene regions (i.e. DNA 'barcodes') specific to these hierarchies are achieved using a 'universal' primer set (e.g., see Folmer et al., 1994). However, universal primer sets are not without their limitations and no single universal primer set is, in fact, universal. Using species-specific primer sets may be warranted in bioassessment studies in order to analyze species distributions and dispersal mechanisms (Elbrecht et al., 2018) (Table 2). Moreover, for single-species bioassessments (as opposed to a broad suite of taxa) other technologies could provide a useful approach.

Followed by DNA amplification of specific gene regions for target taxa via PCR, DNA is then sequenced using high-throughput gene sequencing technologies. The most commonly used platforms include Illumina, Ion Torrent, Pacific Biosciences, and Oxford Nanopore platforms (Reuter et al., 2015). These technologies typically involve DNA sequencing-by-synthesis in parallel to read DNA fragments ranging from 200 to 400 bp in length. Due to the limitations of current high-throughput sequencing platforms, it is common for DNA metabarcodes to range from $\sim$200–400 bp – only a fraction of the barcode region for most primers, including COI. Where the sequencing platform permits, and where the environmental sample makes this feasible, longer DNA metabarcodes could result in more reliable taxonomic assignments (Porter and Hajibabaei, 2018a, b). The recent development of new sequencing technologies, such as LoopSeq (compatible with Illumina platforms) and circular consensus sequencing (PacBio), may facilitate the generation of DNA metabarcodes that are at least as long as the standard DNA barcode region and that have the potential to sequence even longer regions (Heeger et al., 2018; Tedersoo et al., 2018).

Table 2 Major use cases for the application of eDNA in river bioassessment.

Use case	*eDNA/RNA method*	*Challenge*	*References*
Assessing overall sample diversity	DNA metabarcoding using PCR primers that target the barcoding region of interest. If the community is 'known' and detections only need to be counted, microarray methods would be appropriate.	Taxon detection may vary depending on DNA extraction method, primers chosen, technical replicates, sequencing depth	Majaneva et al. (2018), Baird and Hajibabaei (2012), Taberlet et al. (2012b), Hajibabaei et al. (2019a, b)
Assessing presence of indicator groups (e.g. EPT)	DNA metabarcoding or ddPCR using primers that target the 'barcoding' region for the target taxonomic group(s). Ex. For EPT target the COI region using primers that target arthropods	Working with eDNA extracted from bulk benthos may recover greater diversity than from water samples. Detections from water samples can be improved by using taxon specific primers that exclude detections from non-target taxa. Taxonomic detections will only be as complete as the underlying reference sequence databases.	Hajibabaei et al. (2019a, b) and Leese et al. (2020)
Identifying the presence of single target species	Quantitative PCR (qPCR)	Need to develop species-specific primers. Abundance after qPCR/ddPCR reflects abundance in DNA template which may or may not correlate with species abundance/density	Hernandez et al. (2020)
Analyzing species distribution and dispersal	DNA metabarcoding with species specific primers.	Extra care needs to be taken to ensure sequence quality and removal of artefactual sequences (denoising) to avoid haplotype inflation.	Elbrecht et al. (2018)
Estimating the abundance or biomass of target species.	Quantitative PCR can be used to estimate relative abundance of the same species across samples. In some systems, read abundance has been shown to be correlated with species abundance.	Primer binding efficiency to different DNA templates in a mixture may result in skewed template to product ratios after PCR. This may be less of a problem for quantitative PCR where primers are designed to be species-specific or digital droplet PCR where the PCR reactions occur in their own individual droplets. In eDNA from water, water temperature has been shown to affect release rates of eDNA. The quantitative use of DNA counts/relative read abundance may not be appropriate for macroinvertebrates that may vary by orders of magnitude but may be appropriate for taxa with a smaller range of sizes/DNA release rate such as diatoms or fish.	Polz and Cavanaugh (1998), Elbrecht and Leese (2015), Di Muri et al. (2020)
Assessing functional composition of a target community	This can be done by: (1) identifying functional genes; (2) assigning functional traits. DNA metagenomics targets environmental DNA and can be used to assess whole community genomic content directly from environmental samples. Metatranscriptomics targets environmental RNA, and can be used to assess whole community gene expression. Quantitative PCR can be used to assess or verify gene functions present in environmental samples one gene or species at a time. DNA metabarcoding can be used to identify taxonomic diversity, then traits/function can be mapped from public databases such as EPA Freshwater biological traits database (USA), freshwaterecology.info (Europe), or the primary literature.	Taxonomic identification from non-barcode genes/regions may be difficult as database representation for taxa tends to be most diverse for barcoding markers. Gene function from metagenomic or metatranscriptome sequences may be possible using public databases. Ecological traits can be mapped onto taxonomically identified metabarcodes, but databases are not necessarily complete and some databases are not formatted for easy parsing.	U.S. Environmental Protection Agency (2012)
Assessing ecological interactions	DNA metabarcoding coupled with trait-matching and probabilistic methods to infer species interactions	Incomplete trait databases/co-occurrence does not always mean taxa interact	Reviewed in Compson et al. (2020), Makiola et al. (2020), and Blanchet et al. (2020)

Identification of biodiversity from eDNA

DNA from many organisms is present in mixed community or bulk samples, and individual species are identified using computational algorithms that compare the 'anonymous' DNA sequences from signature DNA regions to a reference sequence database of known DNA 'barcodes.' This process is referred to as taxonomic assignment, and there are a variety of methods and tools available for this purpose that vary in ease of use, accuracy, and speed (Table 3). Some of these methods (e.g., using Bayesian classifiers—see, Lan et al., 2012; Wang et al., 2007) can produce a measure of confidence for a taxonomic assignment, thus reducing the risk of false positive assignments. However, not all methods used to identify DNA metabarcodes are equally effective, and some methods have difficulty assigning identity with confidence for short query sequences. For example, sequence similarity-based methods such as the, 'top BLAST hit' approach (e.g., see Table 3) is susceptible to short, spurious matches that can lead to false positive assignments, but this can be minimized by employing high query coverage and sequence similarity cutoffs to filter out spurious matches. For COI, the consensus is that metabarcodes at least 200 bp in length can be reliably assigned to species (Porter and Hajibabaei, 2018a). Even without species-level assignments to reference databases, DNA metabarcoding can produce statistically defined sequence clusters, e.g., operational taxonomic units (OTUs) or exact sequence variants (ESVs), that can be used to assess richness and beta diversity in ecological studies (Porter and Hajibabaei, 2018a, b, 2020). Nevertheless, the scalability of bulk sample processing, as well as the speed and statistical confidence of taxonomic assignments based on DNA sequence analysis, addresses some key bottlenecks in conventional biomonitoring studies (Porter and Hajibabaei, 2018a).

The phylogenetic breadth of marker sequences and their reference databases is important so that target taxa can be identified. Existing reference sequence database coverage is highest for small subunit (SSU) ribosomal RNA (rRNA) prokaryotes, as microbial ecologists have been using marker gene sequencing for phylogenetic and specimen identification for decades (Pace, 1997). Many SSU rRNA sequences can be found in the International Nucleotide Sequence Database Coalition (INSDC), which links the National Center for Biotechnology Information (NCBI), DNA Data Bank of Japan (DDBJ), and the European Bioinformatics Institute (EMBL-EBI). There are numerous community-led efforts to build curated prokaryote SSU reference sets, each with their own criteria for sequence inclusion and underlying taxonomy, such as the Ribosomal Database Project (RDP), GreenGenes, and SILVA. For fungi, reference sequence databases have especially high coverage for the internal transcribed spacer (ITS) region of rRNA, as this region has been used for to study fungal molecular ecology and to identify unknown specimens for decades (Bruns et al., 1991). These sequences can be found in the INSDC, and curated reference sets are also available (Kõljalg et al., 2019; Ankenbrand et al., 2015).

The freshwater invertebrates, including water quality indicators (i.e., Ephemeroptera, Plecoptera, and Trichoptera (EPT), chironomids, and Odonata) are typically targeted using the COI mtDNA marker, which has the largest curated reference set available and has been growing since the advent of 'DNA barcoding' for sequence-based, species-level identification (Hebert et al., 2003; Porter and Hajibabaei, 2018b). These sequences are available from the NCBI, but the largest highly curated repository is available from the BOLD database (Ratnasingham and Hebert, 2007). Gap analyses have been conducted for North American freshwater invertebrates (Curry et al., 2018), European aquatic biota (Weigand et al., 2019), and for biomonitoring in general (McGee et al., 2019). Generally speaking, existing databases are heavily biased toward sample records collected in Canada and the USA (Curry et al., 2018), but work is also ongoing in Europe (Weigand et al., 2019) and Australia. Biodiversity research involving rivers and lake benthos on the other hand, is disproportionately focused on polar or tropical regions (McGee et al., 2019). The consequence is that many endemic species, or rare species in tropical or polar regions will lack a reference sequence to permit species-level identification. In these instances, the importance of geographically-expanded reference library building is crucial (Wilson, 2017).

Specific applications: Single-species and multispecies bioassessment

Experimental approaches can vary from single-species assays to multiplexed assays for a handful of target species to approaches using multiple non-specific primers for DNA sequence generation of broad taxonomic groups, such as macroinvertebrates or diatoms (e.g., Ficetola et al., 2008; Hajibabaei et al., 2011; Kelly et al., 2020). DNA metabarcoding approaches, by contrast, are employed to target phylogenetically diverse taxon assemblages, which can be used to study freshwater community ecology, to create

Table 3 Commonly used methods for identifying DNA metabarcodes.

Method	*Examples*
Sequence similarity	The top BLAST hit approach is one of the most widely used methods to identify unknown sequences. A query is compared with a reference database by aligning their sequences and adopting the taxonomic assignment from the top hit with the best alignment metrics such as sequence similarity, query coverage, bit score, e-value.
K-mers	The naive Bayesian classifier is an example of a k-mer based taxonomic assignment method (Wang et al., 2007). Confidence in an assignment is assessed using a bootstrapping procedure.
Phylogeny	Phylogenetic based methods involve assigning taxonomy based on the evolutionary relatedness of a query sequence with reference sequences. Confidence in an assignment is based on statistical support at the nodes obtained from a bootstrapping or posterior probabilities.

food web networks, and to conduct bioassessments (Compson et al., 2020). In Fig. 1, we provide a schematic representation of these methods. Single-species approaches are typically employed for routine monitoring of a particular species of interest, such as conservation monitoring for rare species, environmental screening for newly introduced aquatic invasive species, or assessing the successful eradication of invasive species (Ruppert et al., 2019).

EPT macroinvertebrates comprise the orders Ephemeroptera (mayflies), Trichoptera (caddisflies) and Plecoptera (stoneflies). These taxa groups are generally highly sensitive bioindicator orders in river systems. Presence of these orders at high family/genus/species richness in eDNA samples can indicate that the local freshwater system is "healthy" (Bush et al., 2019). Conversely, high prevalence of particular families from Diptera that are tolerant to low oxygen levels and larvae of Odonata often indicate the degradation of freshwater wetland systems (Kutcher and Bried, 2014), through poor water quality (Fierro et al., 2017). Certain diatom species within the genera *Navicula*, *Epithemia*, and *Achnanthidium* are classed as highly sensitive to changes in aquatic systems, and they are a focus of bioassessment for freshwater health studies worldwide. There are certain orders and genera of diatoms and macroinvertebrates that are either highly tolerant or highly sensitive to low water quality and poor aquatic conditions, and these specific groups are used as biological indicators for freshwater health bioassessments (Apothéloz-Perret-Gentil et al., 2020; Bush et al., 2019).

eDNA bioassessment metrics

To disentangle natural biodiversity variation and anthropogenic-induced biodiversity assemblage fluctuations, long-term (i.e., 10+ years) datasets are required, which are often lacking from DNA-derived data due to the recent introduction of these methods (Jourdan et al., 2018). In addition, creating policies and implementing management decisions based on freshwater biodiversity data requires robust and established datasets (Jourdan et al., 2018). Embracing the combined efforts of traditional and DNA-based methods overcomes the shortcomings of each standalone approach and facilitates integration of new DNA data with long-term morphological datasets (Porter and Hajibabaei, 2018a; Sheth and Thaker, 2017). One such example is the Canadian Aquatic Biomonitoring Network (CABIN), which has been generating biodiversity data for freshwater health bioassessments since 2006 through community-based water biomonitoring. Previously, CABIN solely employed morphological analyses for identifying invertebrates to (mostly) family or genus level; however, CABIN has begun to integrate DNA sample collection methods for downstream DNA metabarcoding as part of a new pan-Canadian biomonitoring project, STREAM (Sequencing The Rivers for Environmental Assessment and Monitoring; Fig. 2). Established in 2018, STREAM seeks to generate data on benthic macroinvertebrates in watersheds across Canada to address data-deficiencies and to create a better understanding of freshwater health (Robinson et al., 2021). The STREAM project involves DNA metabarcoding of river benthos, following the standardized CABIN kick-net sample collection method (Environment and Climate Change Canada, 2012). Combining traditional taxonomic identification and DNA-based sample processing enables resulting data to form the baseline for bioassessment models such as the River Invertebrate Prediction and Classification System (RIVPACS) (Armanini et al., 2013), which facilitates bioassessment comparisons within and between watersheds.

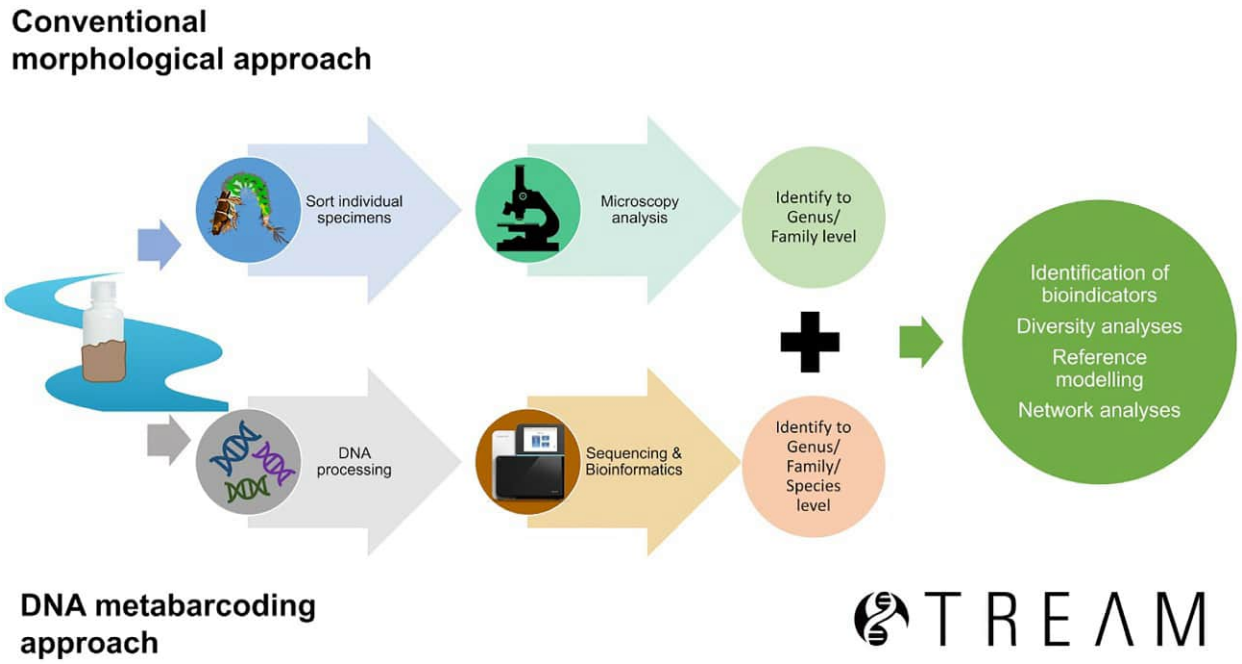

Fig. 2 Workflow of the integration of conventional morphological and DNA metabarcoding approaches for Sequencing the Rivers for Environmental Assessment and Monitoring (STREAM).

The unique properties of DNA mean that there are many opportunities for development of novel bioindicators for environmental disturbance. Traditionally, morphological approaches have relied on relatively simple metrics (e.g., the EPT Index, Indices of Biotic Integrity, Miller et al., 1988), which depict the presence or prevalence of taxa known to be sensitive or tolerant to particular environmental disturbances. The most common application for many of these metrics, however, is by resource managers and scientists who use them to generally classify a system as "healthy" or "impaired" without a real sense of whether a single or multiple stressor–or what particular stressors–are influencing the presence, absence, or prevalence of the indicator taxa. The information embedded in DNA code holds the potential for deeper assessment from eDNA samples, including phylogenetic and functional gene analysis (e.g., Beermann et al., 2021; Compson et al., 2020; Makiola et al., 2020). It is worth noting, however, that at this time the lack of a quantitative signal from metabarcoding data places a significant obstacle in its immediate application in routine bioassessment programs, as many metrics require not only information on composition, but also measures of taxon relative abundance. Some progress has been made in this area for macroinvertebrates (e.g., Elbrecht and Leese, 2015) and also for freshwater diatoms (Kelly et al., 2020).

Another approach to bioindicator metric development is to use the rich taxonomic information revealed by eDNA metabarcoding for ecological network analysis (e.g., food webs). Food web networks can be generated using co-occurrence data from DNA metabarcoding surveys. While this approach can be done with any dataset that has co-occurrence data at many sites, DNA metabarcoding again provides much higher taxonomic resolution (Gibson et al., 2015) with more complete coverage of species present, allowing more complex networks to be created. While co-occurrence networks do not definitively identify what taxa are interacting in a sampled community (e.g., Blanchet et al., 2020), the topological structures of these networks can provide useful information about those communities, and this can be strengthened by linking to other lines of evidence, such as stable isotopes (e.g., Compson et al., 2019).

One way of improving ecological network analysis based on co-occurrence data is to refine the set of possible interactions to a subset of more probable interactions, enabling more accurate food web descriptions. Methods for refining these networks range from empirical approaches that infer true interactions among taxa from information in empirical interaction databases (e.g., Global Biotic Interactions (GLOBI): https://www.globalbioticinteractions.org/) or interactions documented in the literature (e.g., Gray et al., 2014, 2015) to theoretical methods that infer interactions through probabilistic modeling (e.g., Morales-Castilla et al., 2015). Other information, such as species traits (e.g., trophic habit, functional feeding guild, body size) or abundance measures, can be used to further refine interactions (e.g., by calculating probabilities of interaction) to predict actual food web connections. This hybrid approach has been used to create heuristic food webs from DNA metabarcoding observations (e.g., Compson et al., 2018, 2019), and these models have been used to predict properties of real food webs, such as the trophic position of consumers and maximum trophic position of the food web (Compson et al., 2019). Since these heuristic models rely on real observations, they offer potential to develop novel, sensitive metrics for trophic interactions, food web dynamics, and ecosystem health and function (reviewed in Makiola et al., 2020).

Considerations for using eDNA

eDNA is essentially ubiquitous in nature, and standard methods of field sampling (see previously described above), will yield varying quantities of eDNA, itself of variable quality, potentially affecting the likelihood of detecting taxa in bulk environmental samples. For example, 3 L of water is more likely to contain eDNA of target taxa than 15 mL of water, depending on target taxa, due to the likelihood of a greater number of DNA copies in the system. However, collecting and filtering large volumes of water is more time-consuming and requires more handling (i.e., switching out DNA filters once full), which may result in higher chances of reduced sample integrity (e.g., via accidental contamination) as compared to direct extraction of DNA from a small volume (Muha et al., 2019). With eDNA research, there are trade-offs between sample effort, risk of contamination, and likelihood of detecting target taxa; the optimal sampling method is likely to differ depending on the research question and desired downstream DNA processing method (i.e., qPCR, ddPCR, or DNA metabarcoding). Different yields of eDNA in the environment can also arise from both the habits of target taxa and associated environmental and ecological factors. Details of taxa life cycles (e.g., mating, molting, emergence, migration) create seasonal changes that can result in eDNA 'boom-bust' cycles and influence likelihood of detection (de Souza et al., 2016). In addition, determining the exact geographic source of eDNA and whether DNA is derived from a living or recently deceased individual is difficult (e.g., Shogren et al., 2017). Abiotic factors, including light, temperature, oxygen saturation, pH, salinity, and existing substrates influence the rate of DNA degradation (Shogren et al., 2017).

For freshwater macroinvertebrates, several studies have shown that a variety of biological and technical factors affect the template for reading numbers and proportions of sequence reads after sequencing, such as water temperature, primer-bias, DNA polymerase mixes, template GC content, specimen biomass, and larval stage (Elbrecht and Leese, 2015; Fonseca, 2018; Hajibabaei et al., 2011). This is in line with the microbial and fungal literature that identified a suite of technical and biological issues potentially affecting accurate quantification using marker gene sequencing: primer bias, PCR cycle number, annealing temperature, DNA template concentration, and nuclear ribosomal repeat number (Bellemain et al., 2010; Polz and Cavanaugh, 1998). In nematodes, the number of ribosomal repeats can have up to 6-fold variation and this could affect quantification of metabarcoding reads if not accounted for (Bik et al., 2013). Depending on the target organism, it is debated whether DNA metabarcoding can provide insights beyond detecting presence/absence to generate a quantitative signal of biomass or abundance. For example, read counts have previously been shown to correlate with fish abundance and biomass (Di Muri et al., 2020) but have produced equivocal results for other organisms such as macroinvertebrates (Elbrecht and Leese, 2015) or fungi (Amend et al., 2010). In ecological studies, species

richness, distribution, and abundance are key biodiversity measures. Species richness is often used as a simple metric of ecosystem health; however, this simple measure is not straight-forward to calculate using DNA metabarcoding. By only employing the sequences that can be assigned taxonomically using existing sequence databases, we risk underestimating true richness, simply because current databases are incomplete. In the literature, clusters of similar sequences are sometimes used as a proxy for species; for example, clustering DNA sequences with 97% similarity could in theory emulate a 'species' unit based on phenotypic identification. Yet, this is only an estimate of species richness, as the phylogenetically-defined species concept was not conceptualized to support the use of COI sequence diversity for taxonomic discrimination. Generally, metabarcoding results in the detection of many more rare species than typically encountered using conventional methods, so it yields higher richness estimates, and thus may detect species not detected using conventional methods. For this reason, the method adds value to conventional methods (Deiner et al., 2017). For example, in a study of stream chironomids collected from leaf litter and assessed from sequences using COI metabarcoding, specimens were identified to the family rank using conventional methods (Chironomidae), yet 183 metabarcoding sequence clusters were detected and responded to a greater number of response patterns, revealing higher explanatory power using metabarcoding data (Beermann et al., 2021). For macroinvertebrates in water samples, primers should be designed to target species of interest, while excluding non-target taxa (Leese et al., 2020).

Conclusion

River bioassessment has struggled to move beyond binary 'pass/fail' assessments toward a more nuanced interpretation of risk prioritization that acknowledges the presence of multiple stressors derived from a range of anthropogenic pressures simultaneously affecting the ecological condition of rivers, all in the context of accelerating climate warming. Species detection methods using eDNA that are capable of being applied at scale, and allow consistent observation of the existing biological community can support bioassessment outcomes. Moreover, they provide important additional information, enabling insight into the distribution of rare species, supporting the early detection of invasive species or those of public health concern. The recent rapid adoption of eDNA as a biodiversity detection tool has resulted in many well-documented use cases which can be applied to all aspects of riverine aquatic (and riparian) life - from microbes to mammals (Compson et al., 2020). We are at the early stages of a scientific revolution in bioassessment practice, as new biodiversity insights offered by this tool open up new possibilities in the design and application of indicators and metrics that were not previously practicable for routine application outside highly-specialized research laboratories. What is also clear is that the need for such a tool has never been more pressing, but its potential as a game changer in our search for nature-based solutions to reverse decades of river habitat destruction is illustrated by its rapid and widespread uptake by bioassessment practitioners across the globe.

Knowledge gaps

- Significant gaps still exist in reference sequence databases for major taxa groups. To fill these gaps will require 'boots on the ground' to collect and identify local taxa to improve the representation of reference sequence databases when using DNA sequence based taxonomic-assignment methods
- More effort is required to understand the fate and degradation of eDNA in specific systems, keeping in mind that individual studies in this area will not likely be definitive, due to variation in factors determining DNA decay (e.g., microbial action, temperature) across diverse habitats and ecosystems.
- As our understanding of the behavior of eDNA in varying habitats and ecosystems improves, this should inform new designs for field studies in terms of the required spatio-temporal aspects of sampling in relation to habitat heterogeneity.
- eDNA offers exciting opportunities to provide more complete measures of taxonomic and functional diversity in sampled habitats, which in turn can greatly improve species coverage and accessibility of functional trait databases (e.g., EPA Biological Traits Database, freshwaterecology.info, Global Biotic Interactions).
- Although it is clear that DNA metabarcoding is not yet suitable for generation of quantitative observations of biomass or abundance of species for many groups, the application of machine learning algorithms to large datasets of matched DNA sequence and traditional observational data could yield valuable insights as data accumulate (Di Muri et al., 2020; Elbrecht and Leese, 2015).
- eDNA has an important role to play in the area of metapopulation theory and dynamics, supporting alternate methods of quantification based on probability of species detection/non-detection, which can be facilitated by recent advancements in Bayesian-based multi-species occupancy models.
- There are still many questions of how to incorporate biodiversity-rich eDNA data into ecological network and food web analysis. While these types of approaches work with any biodiversity data, the high-resolution taxonomic data the DNA metabarcoding approach affords provides opportunities to model (e.g., through trait-based food webs) or measure (e.g., through metabarcoding consumer stomach contents) food web dynamics in unprecedented detail, and the utility of these approaches for estimating and measuring these topological and trophic processes has not been fully realized. Important ways forward in these areas include (1) expansion of trait and trophic linkage databases (e.g., Global Biotic Interactions database), (2) exploration of new methods for predicting trophic linkages, including using machine learning to extract graph embeddings to predict linkages in real food

webs and using Bayesian approaches to improve probabilistic modeling of linkages, (3) development of novel, taxonomy-free bioassessment metrics from network or food web models that can be more sensitive measures of community change to disturbances and better indicate changes in ecosystem functions (e.g., trophic position, trophic vulnerability, degree of omnivory), and (4) a better understanding of DNA persistence in the guts of consumers and how this affects our measures of trophic linkages in studies that use metabarcoding to illuminate consumer stomach contents.

- Perhaps the greatest challenge of all is the incorporation of these transformative new techniques within highly conservative government bioassessment programs in the areas of biomonitoring, toxic substance monitoring, and impact assessment. This will require open minds to support development and adoption of protocols that will quickly evolve with the rapid pace of change exhibited in molecular technology and techniques. This will include new bioinformatic pipelines, sequencing platforms, and processing algorithms used to 'denoise' and estimate error, as well as taxonomic assignment methods.

Acknowledgments

This Chapter is a joint effort of the Baird and Hajibabaei labs. DJB, TP and KM wish to acknowledge funding support from Environment and Climate Change Canada through the Government of Canada Genomics Research and Development Initiative 'Ecobiomics' Project, and an NSERC Discovery Grant to DJB. MH would like to acknowledge funding by the Government of Canada through Genome Canada, Ontario Genomics and Environment and Climate Change Canada.

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Restoration Ecology of Rivers☆

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This is an update of B.G. Laub, M.A. Palmer, Restoration Ecology of Rivers, in Encyclopedia of Inland Waters, Edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00247-7.

This article was reviewed for the Encyclopedia of Inland Waters, Second LeRoy Poff.

Glossary

Best Management Practices Standard land management approaches that help to mitigate impacts on stream ecosystems from land uses such as agriculture and urban development.

Ecosystem Goods Food, drinking water, wood materials and other products provided by river and riparian ecosystems.

Ecosystem Services Processes provided by river ecosystems that are valued by humans, such as filtering of pollutants from water by aquatic biota and riparian vegetation.

Eutrophication Degradation of aquatic ecosystems caused by excess inputs of nutrients that typically lead to algal blooms, increased turbidity, reduced dissolved oxygen availability, and often loss of biodiversity.

Process-based restoration An approach to river restoration that attempts to recover river and watershed processes necessary to promote river self-sustainability.

River and watershed processes The physical, chemical, and biotic forces, fluxes, and reactions that shape and modify river ecosystem features and properties. Examples of important processes include infiltration of precipitation into the soil, erosion of sediment from hillslopes, surface runoff of precipitation to streams and rivers, river flooding, uptake and transformation of nutrients by aquatic biota, migrations of aquatic organisms, and morphodynamic processes of sediment transport and deposition by flowing water that alter the morphology of river channels.

River restoration The assisted recovery of the biophysical processes that support river self-sustainability.

River self-sustainability The ability of a river to adjust, without human intervention, to disturbances and variability in environmental conditions without compromising natural river processes.

Socio-environmental systems Ecosystems influenced by both natural processes and human activities. Nearly all river ecosystems are socio-environmental systems and river restoration must account not only for natural processes, but also the needs, values, and constraints of human systems.

State-based restoration Restoration that focuses on recovering particular features of river systems, such as habitat heterogeneity, channel morphology, desired water quality levels, or esthetic features.

Stormwater management A watershed-based river restoration approach to deal with increased runoff from urban developed areas. It typically involves construction of features such as ponds, wetlands, rain gardens, bioswales, and other features around impervious surface cover in order to capture runoff from precipitation and allow the water to slowly infiltrate into soil instead of running directly into streams. Stormwater management is designed to reduce the intensity of floods in urban rivers and allow water to be purified naturally by filtering through soil and groundwater.

Watershed management An approach to managing aquatic resources that uses whole watersheds as the unit of management. Aquatic resources are managed in a watershed approach by looking not just at river and stream channels, but also all upland land area within the watershed boundaries.

☆*Change History*: January 2021. BG Laub and MA Palmer updated the text, glossary, further reading, and relevant web pages to this entire article and added Tables 1 and 2 and Figs. 1–4.

Introduction

Ecological restoration of rivers and the science supporting effective practices remain vitally important for meeting societal goals for sustainability in the 21st century (Brierley and Fryirs, 2008). People the world over rely on goods and services provided by natural river ecosystems including food, energy production, transportation, recreation, and clean freshwater supplies (NRC, 1992). Yet human activities have degraded many river systems worldwide to such an extent that they no longer function to provide goods and services valued by people, or at least not at historical levels. Water has frequently become undrinkable and incapable of supporting healthy biotic communities and the esthetic and recreation value of many rivers has declined or been lost completely. For example, the U.S. Environmental Protection Agency (2020) estimated that in 2014 only 30% of the nation's rivers and streams ranked as good condition for stream invertebrate communities, and 43% rated poor for nitrogen conditions. In Europe, only 40% of the rivers and streams are ranked good based on biotic assessments – the remainder are ranked moderate, poor, or bad (Büttner et al., 2020). Where desired goods and services have been lost or degraded, people often turn to river restoration to recover the ecological integrity of river ecosystems.

Global development and biodiversity conservation goals provide examples of the important roles river restoration and restoration science will play in securing sustainable freshwater resources in the coming decades. The United Nations (UN) sustainable development goal number six (SDG6) emphasizes the need for clean water and sets targets for improving water quality and protecting and restoring aquatic ecosystems. Drinking water and wastewater treatment can help improve water quality, but centralized treatment plants in urban areas require large amounts of energy, materials, and chemicals. Thus, in places where water quality has been degraded, restoration of natural processes that provide clean water will also be needed to ensure sustainable water security (Palaniappan et al., 2010). The UN Convention on Biological Diversity also defines conservation and recovery of biodiversity a global goal through the Aichi Biodiversity Targets. Rivers hold a disproportionate amount of diversity relative to their land area, and thus represent a key ecosystem for biodiversity conservation (Dudgeon et al., 2006). Restoration of many river systems will likely be needed to ensure sufficient ecological integrity to support sustainable populations of currently rare and threatened species. The UN has recognized the importance of restoration globally by declaring the 2020s as the decade of ecosystem restoration, and improving the health of rivers and streams is a priority (Palmer and Stewart, 2020).

The use of restoration to achieve defined development and biodiversity goals highlights the role of river restoration for sustainability and also the fact that the process of river restoration takes place within a socio-environmental system, meaning that people and the environment are inextricably linked. Decisions about when to undertake restoration, where, and for what reasons are ultimately societal decisions informed in part by science, but also by the knowledge, values, and needs of people. Human use of water resources, though often damaging to river ecosystems, benefits society in some way, and thus, restoration only becomes an option when some segment of society decides that environmental degradation outweighs the benefits provided from human resource use. In some cases, national or international laws mandate restoration, but laws would not be enacted unless people valued river ecosystems or the goods and services provided by river ecosystems. Local citizens also often have important knowledge of river ecosystems including historic conditions and how conditions have changed over time (Szałkiewicz et al., 2020). For this reason, people besides scientists must be involved in any river restoration project, including local citizens, decision-makers, and resource managers (Brierley and Fryirs, 2008; Naiman, 2013; Schmutz and Sendzimir, 2018; Szałkiewicz et al., 2020). Ecological science and scientists play an important role in the restoration process, by providing knowledge of the extent of degradation, the causes of degradation, and how to recover biophysical processes that support valued goods and services.

Restoration of impacts to rivers caused by hydroelectric dams provides a good example of how ecological science informs the restoration process. The decision to try and restore a river impacted by a dam, either by modifying dam operation practices or through dam removal, is ultimately made by political leaders, resource management professionals, or by citizens. Citizens may participate in decision making directly through voting or indirectly through pressure on local leaders and decision-makers. However, ecological science can inform the decision to restore by providing information on the impacts from the dam to aquatic resources such as fish populations, and the potential for recovery under different management or removal scenarios. Ecological science may also inform the details of restoration, such as what specific flow patterns would be needed to best support migration, reproduction, and survival of particular fish species. For example, ecological research in the Colorado River delta region of Mexico has provided recommendations for flow releases to accomplish specific restoration objectives, but providing flow releases requires bilateral cooperation between Mexico and the United States (Pitt et al., 2017; Schlatter et al., 2017; Shafroth et al., 2017).

The role of people in river restoration, and the reality that river restoration is not solely a scientific undertaking, is important to keep in mind. However, the focus of this chapter will be on the ecological science of river restoration and its role in the restoration process. There are several sources that discuss the role of people in aquatic ecosystems, including several chapters in this encyclopedia (Naiman, 2013; Roni and Beechie, 2013; Riley, 2016; Perini and Sabbion, 2017; Schmutz and Sendzimir, 2018; Szałkiewicz et al., 2020). In addition, river restoration science is inherently multidisciplinary, and fields including hydrology, geomorphology, and biogeochemistry are all vital for informing effective river restoration.

The aim of this chapter is to describe current ecological understanding of how best to restore river ecosystems toward self-sustainability and how ecological science is applied in practice. Self-sustainable rivers are able to recover from disturbance and respond to climatic and landscape changes while maintaining ecosystem goods and services. Self-sustainability is emphasized as a key target for river restoration from an ecological perspective (Hawley, 2018). Rivers that are not self-sustainable will require continual active management, and thus, cannot be considered fully restored to the equivalent of natural functioning ecosystems.

Achieving self-sustainability may not be possible for many rivers, yet the application of ecological principles can still improve them (Riley, 2016). In such cases, river restoration becomes one tool used in a watershed management approach rather than a goal itself. Nonetheless, we define river restoration as the assisted recovery of the biophysical processes that support river self-sustainability, because from the restoration ecology standpoint, self-sustainability represents the ultimate end goal of full river ecosystem recovery (Simon et al., 2011).

Process-based river restoration

A process-based restoration approach emphasizes the need to recover natural processes, because loss or alteration of natural processes is very often the cause of river degradation (Kondolf et al., 2006). To achieve continued success in the long-term, river restoration must mitigate or reverse causes of degradation, and this makes process-based restoration a necessary approach to recover river self-sustainability (Beechie et al., 2010). Another advantage of process-based river restoration is that it often addresses multiple causes of degradation simultaneously. To understand how process-based restoration is beneficial in these ways, it is helpful to first provide a definition of river processes and how they are impacted by human activities.

What are river processes?

A fundamental concept in restoration science is that recovery of natural processes is required to achieve ecosystem self-sustainability (Wohl et al., 2005, 2015; Roni and Beechie, 2013). Natural processes are the physical, chemical, and biotic forces and reactions that shape and modify ecosystem structures and properties. In their natural state, rivers are dynamic, with processes continually modifying river features such as channel shape and position on the landscape. Spatial and temporal variability in processes and their rates create further heterogeneity in river features (Kondolf et al., 2006). For example, the concentration of nutrients in a river, a property of concern for drinking water standards and potential downstream eutrophication, is determined by processes including the movement of water through soils and the uptake and transformation of nutrients by microbial communities in the river. Nutrient concentrations fluctuate naturally during precipitation events and in response to changes in stream biotic communities such as algal growth. The processes of hillslope erosion and sediment transport within river channels continuously shape and reshape river and riparian habitat.

How are processes impacted by human activity?

Human activities can degrade river ecosystems directly and by altering natural processes (Table 1). For example, direct discharge of untreated sewage or industrial wastewater to rivers will increase nutrient concentrations, and direct modification of river channels such as dredging, straightening, installation of levees, or even burial, has degraded river habitat in many regions. However, perhaps an even more pervasive cause of river degradation is alteration of watershed and river processes. One common example is urban land development, where impervious cover alters the process of runoff from substantial infiltration of precipitation into soils to primarily surface runoff directly into stream channels (Paul and Meyer, 2001). The shift in runoff from infiltration to surface runoff often causes greater flooding and erosion in stream channels, incising or widening stream channels and degrading physical habitat (Walsh et al., 2005b). Dams are another pervasive modifier of river processes, substantially changing the patterns of river flow, sediment movement, and downstream temperature fluctuations. Altered flow and sediment regimes in turn alter channel and riparian habitat and often cause loss of river and riparian species that depend on natural patterns of flow to complete their life histories (Collier et al., 1996; Nilsson and Berggren, 2000). Altered temperature regimes can disrupt organism lifecycles, including juvenile growth rates as well as cues for spawning and migration timing (Olden and Naiman, 2010).

Process vs. state-based restoration

A process-based restoration approach may be contrasted with a state-based approach (Fig. 1). A state-based approach focuses on directly restoring the degraded properties of a river system, whereas a process-based approach focuses on the processes that caused degradation. In settings where large dams have curtailed the processes of floodplain inundation and sediment deposition that sustain riparian vegetation species, direct planting of riparian species is an example of a state-based restoration approach. The approach may sometimes recover riparian vegetation temporarily but will require continued maintenance to persist over the long term. The process-based restoration approach would emphasize the need to modify dam operations or remove the dam entirely to help recover the processes of flooding and sediment deposition (Kondolf et al., 2006). Process-based restoration efforts like these, that initialize morphodynamic processes and result in enhanced spatial variability in flow velocities and depths, can help recovery of aquatic, as well as semi-aquatic and even terrestrial species (Muhar et al., 2016).

In addition to focusing on causes of degradation, a process-based approach can often help address multiple limiting factors preferentially or simultaneously, which is less often the case for state-based restoration. For example, if the restoration goal is to increase biotic diversity in a section of river, a state-based approach attempts to identify features of the river section that might be limiting for diversity. Where features are found to be modified compared to pre-disturbance conditions, restoration is implemented to try and recreate pre-disturbance conditions, such as installation of missing habitat features. Habitat restoration approaches such

Table 1 Examples of common anthropogenic activities that degrade river ecosystems, the societal benefits provided, and the direct impacts and processes that are altered by each.

Common Anthropogenic Activities	
Dams	
Benefits	Hydroelectricity
	Flood protection
	Water storage
Direct Impacts	Replacement of river habitat with reservoir
	Blocks migration of aquatic organisms
Impacts to natural processes	Upstream to downstream connectivity disrupted
	Altered patterns of flow downstream
	Traps sediment, disrupting delivery and transport of sediment downstream
	Altered temperature regimes below some dams
Water abstraction	
Benefits	Water use for agriculture, municipalities, and industrial activities
Direct Impacts	Organisms can become stranded in canals
Impacts to natural processes	Altered patterns of flow downstream, including river drying
	Increased concentration of pollutants and nutrients due to reduced dilution
Agriculture	
Benefits	Production of food and natural products
Direct Impacts	Riparian vegetation may be cleared in some cases
	Some aquatic ecosystems such as wetlands may be filled
Impacts to natural processes	Altered patterns of interception, infiltration, and runoff
	Increased runoff of sediment and nutrients
Urbanization	
Benefits	Housing
	Transportation
	Economic and cultural amenities
	Industrial production
Direct Impacts	Channel burial, straightening, and hardening
	Riparian vegetation removal in some areas
	Direct inputs of waste and pollutants
Impacts to natural processes	Decreased infiltration and increased surface runoff
	Increased erosion during the construction phase or urban growth
	Increased temperature of runoff
	Increased delivery of pollutants through runoff

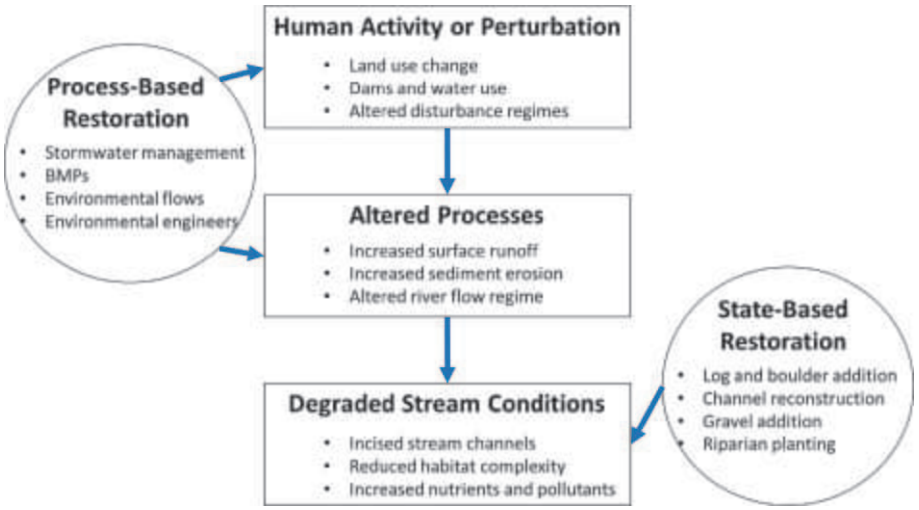

Fig. 1 Diagram comparing process and state-based restoration approaches. Human activities alter watershed and river processes that degrade river and stream conditions. Bullet points in each box and circle give examples. Process-based restoration attempts to restore stream conditions indirectly by recovering natural process rates, whereas state-based restoration attempts to directly modify stream conditions. Process-based restoration will usually be necessary to recover river self-sustainability, but both approaches may be useful in many watersheds where socio-environmental systems pose constraints to full recovery of natural processes. BMPs = best management practices.

as placement of logs or boulders, installation of hydraulic features such as weirs or riffle-pool sequences, and full construction of a new channel with desired features has, despite some failures, improved habitat diversity in many cases (Roni et al., 2008). However, invertebrate and fish diversity often does not increase even with structural habitat improvements (Lorenz et al., 2018). Research has found that other limiting factors, such as water quality, or availability of source populations to serve as a colonization source, often prevent biotic recovery (Palmer et al., 2014) – in other words, watershed scale degradation can override the effectiveness of reach-scale habitat restoration (Leps et al., 2016).

Restoration of natural processes often improves several features of river ecosystems simultaneously because multiple issues often have the same cause of degradation. For example, a common cause of habitat degradation is land use change, such as forest clearing or urban or agricultural development that leads to excessive runoff and erosion of stream channels, large inputs of fine sediments and nutrients, and often loss of wood inputs to streams (Allan, 2004). A process-based approach to habitat restoration would attempt to recover processes such as infiltration in the watershed, hydraulic retention and filtering in a recovering floodplain, and soil stabilization through upland vegetation recovery (Beechie et al., 2010). This approach better addresses watershed-scale impacts and would help recover not only degraded habitat, but degraded water quality as well and thus would be more likely to recover biotic diversity in the long-term (Palmer et al., 2014).

Application of process-based river restoration

Example applications of process-based restoration have been steadily increasing. Four common activities that have developed from process-based approaches to restoration include environmental flow programs, stormwater management in urban areas, agricultural best management practices (BMPs), and assisted recovery of environmental engineer species. Environmental flow programs are often developed to help rehabilitate degraded river systems below large dams. An environmental flow program is a recommended set of flows that can be released from dams to recreate or mimic at least some important elements of the historic natural flow regime (see chapter on environmental flows by Arthington, 2022). Flows often targeted include some minimum flow level to maintain key habitat elements, for example during droughts, and floodplain inundation flows to help maintain riparian vegetation communities and allow for completion of life history events for flood-dependent species. Flood releases from Glen Canyon Dam for the Colorado River in Grand Canyon National Park are a good example of an experimental flows program. Several times over the past 25 years, flow release gates on the dam have been opened to mimic flood occurrences. The flow releases do not fully replicate historic flooding, but are experimental in nature, designed to study how aspects of the river ecosystem, such as non-native fish species and sand bar habitat respond to flooding (Melis, 2011).

Stormwater management in urban landscapes, also referred to as green and blue infrastructure, attempts to recover natural runoff processes that are altered when natural ground cover is converted to impervious cover (Perini and Sabbion, 2017). Altered flowpaths caused by increasing impervious cover in urban areas can contribute to both increased nutrients and degraded habitat by bypassing the natural hydrologic retention and filtering processes that occur when precipitation infiltrates into soils and water makes its way slowly to the stream via belowground pathways (Paul and Meyer, 2001; Walsh et al., 2005b). Examples of stormwater management devices include bioswales, bioretention basins, rain gardens, cisterns, and pervious pavement (Fig. 2). Each of these devices is designed to intercept runoff from impervious surfaces during precipitation events, increase hydraulic retention, and direct the water into soils through increased infiltration, rather than having the runoff flow directly to the stream channel (Walsh et al., 2005a). In many of these devices, a special mix of soil, sand, and organic matter is added and vegetation is planted to help filter nutrients and pollutants out of the stormwater as it infiltrates into soils. By reducing surface runoff from impervious surfaces and restoring more natural flow patterns, stormwater management can help address multiple issues including degraded habitat and water quality, though full recovery to pre-urbanization conditions may be difficult to achieve on a watershed scale, especially in highly urbanized watersheds (Walsh et al., 2005a).

Agricultural best management practices (BMPs) are similar to urban stormwater management approaches, in that they are applied to mitigate the impacts of agricultural land use development on river and stream ecosystems. Conversion of naturally vegetated landscapes to agricultural land use often increases runoff, hillslope erosion, and delivery of sediments to streams, due to soil compaction and reduction in vegetation that would otherwise intercept rainfall and promote infiltration into soils. In addition, delivery of nutrients and other contaminants to stream channels usually increases due to application of fertilizers and other chemicals such as pesticides. Increased runoff, erosion, and nutrient delivery frequently degrades stream ecosystems by reducing habitat heterogeneity and promoting eutrophication (Allan, 2004). Typical examples of agricultural BMPs include cover cropping during fallow periods, no-till farming, crop rotation, multi-cropping, and contour plowing, all of which are designed to help keep vegetation and soil structure intact and reduce runoff and erosion. Crop rotation and multi-cropping can also help reduce applications of fertilizers and pesticides by improving soil nutrient content and reducing damage by pests and weeds (Liebman and Dyck, 1993; Lötjönen and Ollikainen, 2017) Another important BMP applied in agricultural and urban watersheds is the preservation or restoration of a vegetated riparian buffer zone along the length of stream channels, which provides multiple benefits including interception of nutrients and sediments from runoff, shading to help keep stream temperatures lower, and provision of wood material for habitat. The common purpose of all BMPs is to help recover natural rates of processes such as runoff and erosion by mitigating impacts to these processes caused by agricultural land use.

Assisted recovery of environmental engineer species has been used for multiple decades, but has become increasing popular recently as a restoration strategy. Assisted recovery of North American beaver (*Castor canadensis*) and Eurasian beaver (*Castor fiber*) in

Fig. 2 Examples of a bioretention basin (top left) and cisterns (top right), two types of stormwater management features. The cisterns capture runoff from rooftops and the bioretention basin captures storm runoff from the urban landscape, allowing the water to filter through a sand filter media before flowing downstream. Stormwater management is intended to improve water quality and reduce runoff volume from stormwater events, such as seen in the bottom image.

North American and European rivers is one well-researched example (Pollock et al., 2014; Brown et al., 2018). Beavers substantially modify small stream and river systems through the process of dam-building. Dam-building provides unique habitat for aquatic species and increases local groundwater levels, which can in turn expand riparian habitat and enhance riparian vegetation growth. Dams also trap sediment and have been observed to raise streambed elevations, restore floodplain connectivity, and improve fish habitat in incised channels. In many regions in North America, beaver populations were severely reduced in the late 1800s during the fur trade. *Re*-establishment of beaver may be as simple as reintroducing beaver to streams where they were previously extirpated, but in incised channels, structures may be needed to help beavers maintain dams through high-energy flood events. The installation of structures has been successful in at least one incised stream at restoring channel-floodplain connectivity and increasing available habitat for fish (Bouwes et al., 2016). Re-establishment of beaver in rivers and streams represents a self-sustaining restoration, because the beavers will continue to modify stream and river channels without further human intervention (Pollock et al., 2014). It should be noted, however, that beavers are not always an appropriate restoration strategy, and beaver removal is a restoration strategy where beaver are non-native, such as South American river systems (Jusim et al., 2020). Ecological engineer species are found worldwide, ranging from the very large, such as hippopotamus in Africa (Mosepele et al., 2009), to the very small, including microbial biofilms that stabilize sediment (Battin et al., 2003), but with the exception of beavers, riparian vegetation, and some anadromous fish species, relatively little research has been conducted on their use in river restoration.

Restoration in a watershed management context

In the ideal ecological situation, river restoration would remove all human impacts on the river ecosystem and fully recover natural self-sustaining processes. However, rivers are part of complex socio-environmental systems, with often long histories of human use, which often pose justified constraints to full recovery of self-sustainability (Naiman, 2013; Wohl et al., 2015; Brown et al., 2018). In rare cases, full recovery of natural processes, or at least near-full recovery, may be achievable. One example is restoration of the Elwha River on the western coast of the U.S., where complete removal of the only two large dams on the river was completed in

2011–2012. The Elwha River watershed is located primarily within the boundaries of the protected Olympic National Park. Dam removal, coupled with the protection of natural hydrologic and biotic processes through most of the watershed, has allowed the river to transport sediment downstream and alter river, floodplain, and estuarine habitat (East et al., 2015; Foley et al., 2017). Native vegetation communities have reestablished on former reservoir sediment (Prach et al., 2019), and salmon have resumed spawning activities in river sections upstream of the former dams (Tonra et al., 2015). In most cases, river restoration requires a compromise between full recovery of natural processes and preserving human use of river ecosystems for societal benefit. Thus, in most cases, restoration should be viewed as one tool in a program of active watershed management (Wohl et al., 2005).

In watershed management, rivers and streams are managed as components of the overall landscape within watershed boundaries (Schmutz and Sendzimir, 2018). The focus is not just on rivers and streams but on the suite of processes and landscape patterns that influence the movement of water, sediments, chemicals, and organisms from upland areas to and through river channels. Under a watershed approach, land management, such as preservation of forested areas in an unimpacted tributary, become important tools for protecting and restoring river ecosystems. Other tools in watershed management may include controlling hillslope erosion, managing disturbances such as fire and other upland-associated activities, in addition to active stream channel restoration. In this context, river restoration is not applied as a standalone management activity but is instead part of a suite of activities applied at a broad scale to manage the natural processes that create and maintain healthy aquatic ecosystems (Wohl et al., 2005). Such approaches to restoration usually require changes to policies and regulations and can be quite successful ecologically (Viswanathan and Schirmer, 2015). For example, one effective way to limit impacts of further land use development is through altered zoning and other regulations. This illustrates the socio-environmental nature of river restoration – in many cases human actions that caused river degradation can best be reversed with changes in policy or economic incentives.

Whether watershed management incorporates active river restoration, upland land management, or changes in policy, the goals should still target protection or recovery of processes. For example, reforestation efforts on degraded landscapes can be successful at improving stream habitat and water quality conditions, because they recover natural watershed hydrologic processes, thus helping to reduce delivery of solutes and sediments to stream channels (e.g., Paudyal et al., 2017). While most restoration goals require actions outside of the channel, for some, direct manipulation of river channels or riparian zones may be necessary, at least in the short term. Installation of required habitat for an aquatic species with restricted range to prevent imminent extinction during an extreme event, such as a severe drought, is one example of a situation where direct manipulation may be required (Hammer et al., 2013). In such cases, the restoration activity can be viewed as a type of emergency intervention, where immediate actions are needed to save a population or species. In addition, approaches that work within constraints are often more easily implemented from a political, economic, and feasibility standpoint, at least in the short-term. For example, adding gravel to a river below a hydroelectric dam to recover fish spawning habitat lost by sediment retention above the dam is often more expedient than efforts to fully recover flow and sediment transport processes, such as full dam removal (Wheaton et al., 2004). Although such manipulations may provide essential habitat for threatened species in the short-term, they should not be viewed as a substitute for recovering the processes needed to self-sustainably create and maintain required habitat.

In many watershed management cases, ecological or social constraints make it necessary to couple active river manipulation and process-based restoration in some capacity. For example, active manipulation may be necessary in some rivers to maintain appropriate water temperatures for particular aquatic organisms under climate change. One way to maintain cold water as air temperatures rise is to maintain flow releases from large dams, because the water at the bottom of large reservoirs is much colder compared to surface water and incoming river water (Null et al., 2013). Sometimes, continual active management may be needed to ensure conditions are appropriate to take full advantage of natural processes when they occur or are restored. For example, in the Colorado River delta region, the natural flow regime has been altered to such an extent that former lush marshland completely dried up. A recent dam release flow in the region attempted to mimic, albeit on a much smaller scale than natural, historic floods that occurred in the region (Shafroth et al., 2017). Recruitment of native vegetation such as cottonwood trees did occur in response to the flood, but was facilitated by more active restoration measures in the highly modified ecosystem, including maintenance of seed-source trees by irrigation and nonnative vegetation removal (Schlatter et al., 2017). While this flow release was a one-time event, commitments to revisit the 1922 Colorado River Compact are under way, with a 2026 deadline. In addition to the potential for redistribution or further regulation of water rights, some have goals of keeping more water in the river, with the hope of restoring ecosystems including the Colorado River delta (Pitt et al., 2017).

In other cases, active manipulation may be needed initially to assist recovery of natural processes that could eventually become self-sustaining. Installation of structures to assist recovery of dam-building activity by beaver, as described above, is one example. As another example, restoration of small headwater streams can help recover processes that maintain healthy rivers downstream. Attempts to restore Coastal Plain rivers and streams on the eastern coast of the U.S. with poor water quality and low biodiversity have involved converting small tributaries to wetland-stream complexes. Wetlands can provide watershed-wide water quality benefits, particularly by reducing the flux of nutrients to downstream waters (Golden et al., 2019). So while the small channels must be reconfigured, stabilized, and then replanted, if established properly the wetlands should persist, and there is hope the downstream benefits exceed the ecosystem service losses of converting small streams to wetland complexes. To date, these practices have had mixed results and suggest that appropriate siting of the projects is critical, such as placing them in physiographic settings that allow for increased infiltration and water storage in the wetland (Williams et al., 2017).

Whether applied as part of watershed management or relatively independently, a formal process of planning, implementation, and monitoring should be followed for any river restoration project (Fig. 3). One key step in restoration planning, as highlighted in the above example about converting streams to wetland complexes, is to prioritize where on the landscape restoration activities will

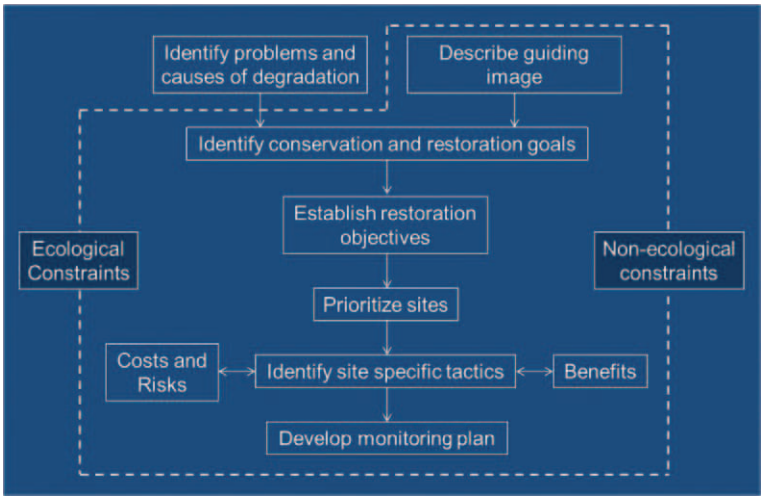

Fig. 3 Flowchart depicting key steps in the restoration planning process. Unless resources, time, and space are nearly unlimited, all restoration projects will have to occur within socio-environmental constraints, such as non-native species, changing climate, and human land and water use. Although not shown here, this process is iterative, with monitoring data feeding back to reconsider goals, objectives, site prioritization, and tactics.

have the most benefit and to prioritize the order of any restoration actions. Prioritization is not necessarily needed in small watersheds or in cases where funding and personnel resources are not limiting. But in large watersheds where resources are limiting, identifying locations and activities that will have the greatest improvement in desired conditions is useful. An example where spatial prioritization is obviously useful is a case where multiple dams or other barriers could potentially be removed or modified to increase connectivity within a watershed or other hydrologically connected region. Removing the furthest upstream dam is likely to have little benefit to downstream river sections if other dams still regulate flow and sediment delivery downstream and block upstream-migrating fish. On the other hand, if the downstream dam is blocking colonization of upstream river sections by a non-native species, leaving the downstream dam in place and removing the upstream dam may provide some benefit to native species while preventing spread of the non-native species (Fig. 4). Prioritizing the order of restoration actions can also be important. Keeping with the same example, removing the non-native fish population first would allow dam removal to proceed without the risk of further expansion of the non-native population.

The complexity of addressing aquatic resource management issues at the watershed scale make an adaptive management approach useful for many river restoration projects. A key part of adaptive management is engaging stakeholders and monitoring the outcome of restoration activities over time to determine if the restoration project achieved the goals and objectives. The plan can be revised repeatedly with stakeholders if it needs adjusting. Ecological effectiveness monitoring must be planned carefully, because evaluation of restoration success can be difficult in practice for several reasons (Table 2), and effectiveness monitoring is still an area of important research in river restoration ecology. Depending on the goals for restoration, other types of monitoring information besides ecological effectiveness may also be important. For example, if restoration goals are to improve the esthetic appeal of a river

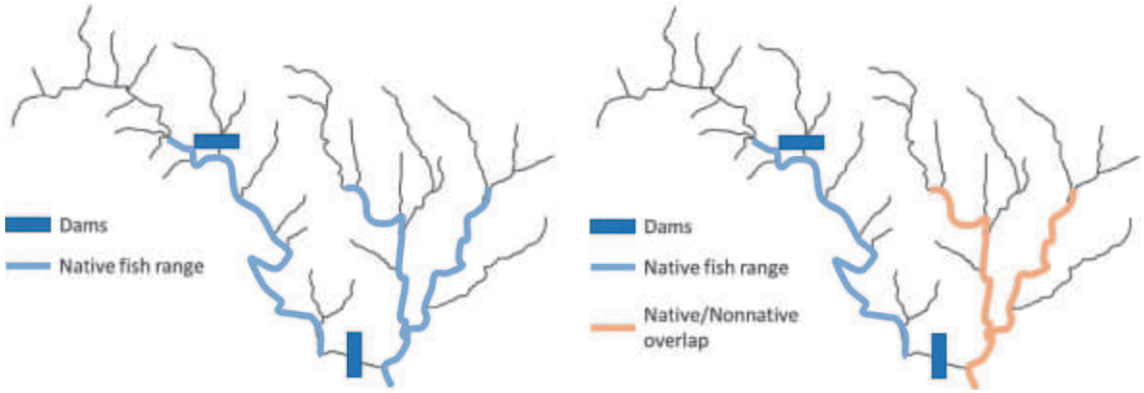

Fig. 4 A hypothetical example showing the importance of prioritizing dam removal. In both cases (left and right), the goal is to improve the conservation status of a native fish population, but there are only enough resources to remove one of the two dams in the watershed. The dams completely block upstream fish passage. In the left panel, removing the lower dam would likely be prioritized, because this would increase connectivity between the two ranges of the population by allowing upstream fish passage. In the right panel, removing the upper dam might be prioritized instead, because it allows access to some new habitat and prevents a non-native species from colonizing the full range of the native species.

Table 2 Potential pitfalls when evaluating restoration effectiveness and some best practices for avoiding pitfalls.

Pitfall	*Pitfall description*	*Best practices*	*Best practices explanation*
Lack of comparison for post-restoration outcomes	Post-restoration monitoring alone does not indicate whether a restoration project changed ecological processes or conditions	Collect pre-restoration data for multiple years on both the restored river and several similar rivers not undergoing restoration	Rivers are highly variable in time and space, thus to determine conclusively that restoration was effective, the amount of change caused by restoration and whether changes were greater than natural variability must be determined
Lack of data on how processes respond	Ideally, post-restoration monitoring will provide information on how processes respond, but monitoring processes can be more difficult than monitoring conditions	Collect pre-restoration data and develop a guiding conceptual or mathematical model of the system that captures important processes and how they will be restored	Process monitoring must be tailored to the restoration project, and having a clear set of objectives and expected outcomes regarding processes can help guide development of needed information. Technological improvements are making process monitoring more feasible, but research on standards for process monitoring is still ongoing.
Monitoring data collected at too small a spatial or temporal scale	Monitoring of individual restoration activities may not translate to effectiveness at the watershed scale. Effects of restoration may not be noticeable for multiple years after implementation, or effects may be short-lived.	Incorporate monitoring into watershed management	Watershed management is a continual process in most locations, thus if monitoring is incorporated as part of the management process, appropriate monitoring to determine watershed-scale and long-term impact of any watershed management activity, including restoration, is more likely to be in place. Increasing availability of remote-sensing data is helping to improve large-scale and long-term monitoring.
Lack of non-ecological monitoring data	Because restoration occurs in a socio-environmental system, monitoring of human systems is also usually important to determine restoration impacts and effectiveness.	Collaboration with social scientists and other non-environmental fields.	Evaluating whether restoration goals such as user experience or recreational value will require monitoring of human systems that interact with rivers, and social scientists have developed tools to evaluate these elements.

in an urban environment, surveys of river users and the surrounding neighborhoods would be appropriate. Matching monitoring to the identified goals is important, because success in one objective does not imply success in all objectives. For example, people's experience recreating in a river corridor could improve without any improvement in stream biodiversity.

If river restoration goals are not achieved, properly-designed monitoring can be used to help identify the reasons for failure and adjust restoration practices in the future. Of particular importance is to monitor the targeted natural process of restoration – if it is moving in the right direction but the ultimate goal (e.g., increase biodiversity) is not yet achieved, this may indicate that not enough time has passed. In this way, restoration projects can be seen as experimental manipulations that help provide understanding about river ecosystems and about how to better manage river ecosystems. Even the best planned restoration project faces uncertain outcomes due to the variability and complexity inherent to socio-environmental systems (Darby and Sear, 2008), and there are many reasons, both ecological and non-ecological, that restoration projects can fail to accomplish goals. For example, a program to address urban impacts on a river through installation of stormwater management practices may be an appropriate restoration approach for addressing altered processes, but it could fail to improve river conditions if stormwater features are not installed properly, or if climate changes alter precipitation patterns and overwhelm any benefits provided by installed stormwater features (Barbosa et al., 2012). In these cases, if monitoring is conducted and the reasons for failure identified, the project can still be considered a learning success even though ecological goals were not accomplished.

Synthesis

To consider a river fully restored from an ecological standpoint, natural river and watershed processes that create and continually alter the physical, chemical, and biotic conditions of river ecosystems must be recovered. Undertaking such a process-based restoration of river systems is the only way to ensure self-sustainability of river ecosystems over the long term. However, river

ecosystems are components in complex socio-environmental systems that often pose constraints to full recovery of natural processes. Thus, in practice, river restoration is best approached as one tool in an overall process of managing whole watersheds for sustainability. In watershed management, human use of river and watershed resources may still continue, and natural watershed processes are preserved or restored to the extent possible, but some forms of active river restoration may be included. Improving river restoration in the context of watershed management will require monitoring and learning from implemented projects, so that restoration approaches can be adapted to help achieve sustainability goals in these complex socio-environmental systems.

Knowledge gaps

- How much habitat or natural area is needed to ensure a sufficient level of processes to sustain desired features or services?
- What are optimal restoration strategies for ensuring resilience to future disturbances such as climate change?
- How do restoration actions impact ecosystem functions?
- What role do feedbacks between restoration and societal goals and values play in the design and application of restoration projects through time?
- Does restoring habitat complexity improve ecosystem functions?
- How long does it take for different components of river ecosystems to recover following restoration?
- How can ecosystem engineer species most effectively be incorporated in river restoration, especially outside of North America?
- What are the unique challenges associated with restoration of intermittent and ephemeral rivers and streams?

Important case studies

Name of Site	*Country*	*Coordinates*	*Main topic/concept covered*	*Key references*
Colorado River in Grand Canyon	USA	36.925 −111.48	Experimental environmental flows Adaptive management	Melis (2011)
Colorado River delta	Mexico	32.152 −115.19	Environmental flows Coupled process and active restoration	Pitt et al. (2017) Schlatter et al. (2017) Shafroth et al. (2017)
Bridge Creek	USA	44.689 −120.282	Environmental engineers in restoration	Bouwes et al. (2016)
Elwha River	USA	48.000 −123.600	Recovery of natural processes following dam removal	East et al. (2015) Foley et al. (2017) Prach et al. (2019) Tonra et al. (2015)

See Also: Structures and functions of Inland Waters - Rivers: Environmental Flows: Ecological Effects of Hydrologic Alterations, Assessment Methods for Rivers, Challenges and Global Uptake

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Relevant websites

www.cbd.int/sp/targets—UN Convention on Biological Diversity.
www.decadeonrestoration.org—UN Decade of Ecosystem Restoration.
https://sdgs.un.org/goals—UN Sustainable Development Goals.

Environmental Flows: Ecological Effects of Hydrologic Alterations, Assessment Methods for Rivers, Challenges and Global Uptake

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Introduction

Human activities have modified the natural hydrologic and ecological processes of catchments, wetlands, rivers, floodplains and estuaries for thousands of years. Early Mesopotamian civilizations constructed dikes, levee banks and barriers made of earth, rocks and logs to redirect water for flood control, and to capture water for irrigation (Arthington, 2012). Dam construction to impound water flows followed and eventually became a fundamental global water management technology. Dams store, regulate and deliver water collected during wet cycles for use during dry cycles. They are constructed and managed to provide water for agricultural production, industry and urban development, to generate electricity, for flood control, to store mine tailings, to foster fish and wildlife populations, and for recreation. Whist the contributions of dams to human development have been enormous, their effects on biodiversity and the ecological goods and services of freshwater ecosystems, such as clean water, fisheries and wildlife, are of global concern. Today most of the world's major river systems, including the 20 largest and the eight with highest biological diversity—the Amazon, Orinoco, Ganges, Brahmaputra, Zambezi, Amur, Yenisei and Indus—are impounded by dams. Moreover, growing energy demands, and a Rio + 20 commitment to the use of Kyoto-compliant energy resources, have triggered a new era of dam construction, with over 3700 proposed or under construction (Zarfl et al., 2015). Globally, impoundments are estimated to have a cumulative storage capacity somewhere between 7000 and 10,000 km^3, the equivalent of five times the total volume of the world's rivers (Vörösmarty et al., 2013). The effects of dams on river basin flow patterns and hydrological connectivity are catastrophic. Only 37% of rivers >1000 km in length remain free-flowing over their entire length, and a mere 23% flow uninterrupted to the sea (Grill et al., 2015).

Flow regime alterations resulting from these major hydrological disturbances have impacted the biodiversity and ecological functioning of rivers, floodplains, wetlands and estuaries worldwide (Vörösmarty et al., 2010). For example, a systematic review by Poff and Zimmerman (2010) reported ecological effects associated with flow regime alterations in 92% of studies. Negative responses to flow regime alteration were recorded in terms of population or community change of riparian vegetation, aquatic primary producers, macroinvertebrates, fishes, birds, and amphibians, primarily in terms of flow magnitude. The remainder reported an increased value for ecological response metrics, such as an increase in non-native species or non-woody plant cover on dewatered floodplains.

The deteriorating condition of freshwater ecosystems and loss of freshwater biodiversity from dam construction, barrier effects and altered flow regimes has led to the science and management of water for the environment (Tharme, 2003; Poff and Matthews, 2013). Originally termed in-stream flows, water allocations that maintain the biophysical and ecosystem processes of rivers and estuaries are now known almost universally as environmental flows (e-flows). A recent definition gaining traction forms part of the 2018 Brisbane Declaration and Global Action Agenda on Environmental Flows (Arthington et al., 2018a) which states: "Environmental flows describe the quantity, timing, and quality of freshwater flows and levels necessary to sustain aquatic ecosystems which, in turn, support human cultures, economies, sustainable livelihoods, and well-being."

This definition recognizes that sustaining water regimes, freshwater ecosystem health and resilience is the foundation for achieving human water security and flourishing livelihoods, for all societies in all regions and across all economic realms (Vörösmarty et al., 2013; United Nations (UN), 2015). Including "freshwater flows and levels" in the 2018 definition is intended to embrace the water requirements of all aquatic ecosystems that experience natural spatial and seasonal patterns in water-level fluctuations, wetting and drying, and connections with groundwater (Arthington, 2012; Kath et al., 2018).

The ecological effects of flow regime alterations and the water requirements of rivers are the main themes of this chapter. It traces the history of environmental flow assessment methods, the emergence of holistic ecosystem level environmental flow frameworks, the framing of two of these (DRIFT and ELOHA), and examples of recent developments. The chapter continues with a discussion of emerging issues for the future of environmental flows under shifting climatic and other regimes, when new scientific knowledge and different perspectives on planning and managing environmental water will often be needed (Capon et al., 2018). The chapter ends with recent efforts to increase the global profile and social-ecological relevance of the environmental flows enterprise. It presents the 2018 Brisbane Declaration and Global Action Agenda on Environmental Flows and examples of the uptake of e-flows within global spheres of influence, such as achievement of the Sustainable Development Goals (United Nations (UN), 2015), and planning for the Post-2020 Global Biodiversity Framework.

Ecological effects of flow regime alterations

Liquid fresh water covers less than 1% of the Earth's surface, constituting only 0.03% of the world's water. This tiny fraction of global water is absolutely vital for human life support and the provision of many ecosystem services—clean water, food organisms, fuels, pharmaceuticals, flood regulation, recreation and spiritual health. Flowing freshwater habitats range from headwater springs and streams to rivers, vast floodplains, and estuaries, all connected through space and time by the dynamics of water. Taken together, flowing and standing freshwater ecosystems support an extraordinary diversity of aquatic life forms—at least 126,000 species out of approximately 1.8 million described globally (Strayer and Dudgeon, 2010).

The dependence of freshwater biota on surface and linked groundwater habitats makes them vulnerable to natural and man-made changes in the availability of water and other drivers of aquatic habitat loss and change. River impoundment (dams, weirs), off-stream farm dams, surface water diversions, groundwater extraction, and modification to natural drainage networks for flood protection have some of the most destructive effects on flow regimes, aquatic habitats and ecosystems (Stewardson et al., 2017). Land clearance, afforestation and urbanization also alter patterns of catchment runoff and hence stream flow regimes.

Ecologists have long conceptualized and documented relationships between prominent features of river flow regimes, their ecological roles, and the effects of flow regime alterations. In 1997, a seminal publication captured the importance of river flows in the "Natural Flow Regime Paradigm" (Poff et al., 1997). This paper shows that the structure and functions of riverine ecosystems, and many adaptations of aquatic biota, are dictated by temporal patterns of river flow and disturbance regimes. Papers by Richter and colleagues contributed to the identification of important "facets" (often termed "components") of river flow regimes, and set out statistical methods to estimate alterations to 64 metrics using the Range of Variability Approach or RVA (Richter et al., 1996).

Understanding of the ecological consequence of alterations to river flow regimes burgeoned. Building on examples from Poff et al. (1997) and other literature, Bunn and Arthington (2002) developed four fundamental principles to summarize the importance of river flows to the maintenance of aquatic biodiversity, and then explored ecological consequences of alterations to natural flow regimes (Fig. 1). Informative summaries of quantitative relationships between particular flow facets, alterations to them and consequent negative ecological effects soon followed (e.g., Lytle and Poff, 2004; Poff and Zimmerman, 2010).

Ecological impacts from alterations to river flow regimes involve a range of mechanisms driven by the functional ecological roles of water in river networks. These roles include water as a habitat and source of food, a vector for transport of materials and organisms, a medium for active movement along connectivity pathways, and an agent of disturbance and geomorphic change. The effects of flow regime alterations span a broad range of taxa, including algae and biofilms, aquatic and riparian plants, zooplankton, invertebrates, fishes, amphibians, reptiles, waterbirds and mammals. Adverse effects have been recorded at individual, population, community and ecosystem levels of ecological organization (Poff and Zimmerman, 2010).

Rolls and Bond (2017) review common types of flow regime alteration linked to ecological consequences for riverine species and ecosystems (Table 1).

While a focus on the effects of alterations to individual components of flow regimes is useful, flows are rarely impacted in complete isolation from one another. For example, dam construction and flow management can produce syndromes of flow alteration involving changes in flow magnitude (e.g., reduced flood peaks, less frequent floods) combined with dramatic changes in the seasonal timing of high and low flows coupled with elevated, more stable baseflows (e.g., Fig. 2).

Stewardson et al. (2017) present a useful guide to how land and water management activities combined with climate change can alter flood regimes, channel flows, baseflows and flow variability. They caution that there can be great variation in the magnitude of these impacts and even the direction of change, resulting from variation in the climatic and hydrological setting, the type and size of water management infrastructure, and policies that guide water management operations. Accordingly, ecosystem responses to flow regime alterations tend to reflect the particular suite of circumstances, historical flow patterns and individual flow events. This particularity adds to the complexity of understanding and quantifying flow-ecology response relationships for use in river management (Stewart-Koster et al., 2014). Multivariate analysis of relationships between facets of flow regime alteration and ecological patterns and processes can reveal interactions as well as dominant responses, and help to unravel the mechanisms underlying syndromes of impact (e.g., Kennard et al., 2007; McManamay et al., 2013).

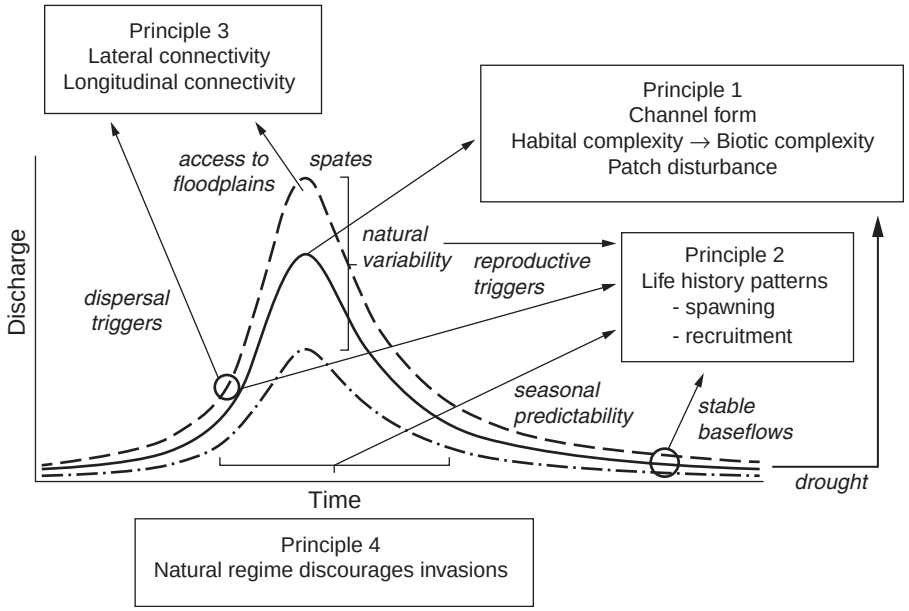

Fig. 1 The natural flow regime of a river influences aquatic biodiversity via several interrelated mechanisms that operate over different spatial and temporal scales. The relationship between biodiversity and the physical nature of the aquatic habitat is likely to be driven primarily by large events that influence channel form and shape (**Principle 1**). However, droughts and low-flow events are also likely to play a role by limiting overall habitat availability. Many features of the flow regime influence life history patterns, especially the seasonality and predictability of the overall pattern, but also the timing of particular flow events (**Principle 2**). Some flow events trigger longitudinal dispersal of migratory aquatic organisms and other large events allow access to otherwise disconnected floodplain habitats (**Principle 3**). The native biota have evolved in response to the overall flow regime. Catchment land-use change and associated water resource development inevitably lead to changes in one or more aspects of the flow regime resulting in declines in aquatic biodiversity via these mechanisms. Invasions by introduced or exotic species are more likely to succeed at the expense of native biota if the former are adapted to the modified flow regime (**Principle 4**). Redrawn from Fig. 1 in Bunn SE and Arthington AH (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity, *Environmental Management*, 30: 492–507, with permission from Springer-Verlag; reproduced with permission from University of California Press, publisher of the text *Arthington AH (2012) Environmental Flows: Saving Rivers in the Third Millennium. Berkeley: University of California Press.*

Table 1 Summary of common alterations to specific components of river flow regimes, linked to ecological mechanisms underlying ecological consequences for riverine species and ecosystems.

Alterations to components of flow regimes	*Ecological mechanisms*	*Ecological consequences*
Reduced base flow magnitude	Reduced or complete loss of fast-flowing, turbulent habitats (riffles) and run habitat	Decline in density and aquatic species richness, or local extinction of species (Kupferberg et al. 2012).
	Reduced wetted habitat area	Encroachment of terrestrial organisms into the riparian and channel zone (Stromberg et al., 2007).
	Loss of longitudinal aquatic connectivity	Flow regulation and fragmentation imperil riverine fishes (Dudley and Platania, 2007)
Reduced flood size and frequency	Decline in life-history cues stimulating reproduction	Decline in richness and functional diversity of birds, aquatic plants, and microfauna (Nielsen et al., 2013)
	Reduced disturbance frequency and severity	Increased biomass and reduced diversity of aquatic macrophytes (Mackay et al., 2003)
	Loss of nutrient inputs and productivity from floodplains	Lower ecosystem productivity such as fisheries yields (Gillson et al., 2009)
Reduced floodplain inundation	Loss of flood pulse advantage	Reduced density of floodplain-dependent organisms, e.g., fish (Welcomme et al., 2006)
	Decline in flooded wetland area used for feeding, reproduction and rearing	Lower species richness of waterbirds (Kingsford and Thomas, 1995)
Increased base flow - artificial perennialization	Absence of non-flowing and low-flowing habitats	Altered species composition reflecting permanently flowing habitat (Rolls and Arthington, 2014)
	Loss of drying events	Increase metabolic activity of biofilms and productivity of chlorophyll *a* which in turn can increase density and biomass of consumers such as macroinvertebrates (Miserendino, 2009)
- anti-droughts		

(*Continued*)

Table 1 (Continued)

Alterations to components of flow regimes	*Ecological mechanisms*	*Ecological consequences*
Increased discharge variability, e.g., hydropeaking	Frequent drying and flooding of stream channel act as disturbances	Population declines due to increased mortality of eggs, larvae, and adults (Casas-Mulet et al., 2015) Reduced species richness and altered species composition (Perkin and Bonner, 2011)
Reduced discharge variability	Reduced flow velocity and flooding disturbances	Promotes invasion of some non-native vegetation (Stromberg et al., 2007) and fish (Rolls and Arthington, 2014)

Adapted from Rolls RJ and Bond NR (2017) Environmental and ecological effects of flow alteration in surface water ecosystems. *Chapter 4 in Water for the Environment: From Policy and Science to Implementation and Management.* Cambridge, MA: Elsevier.

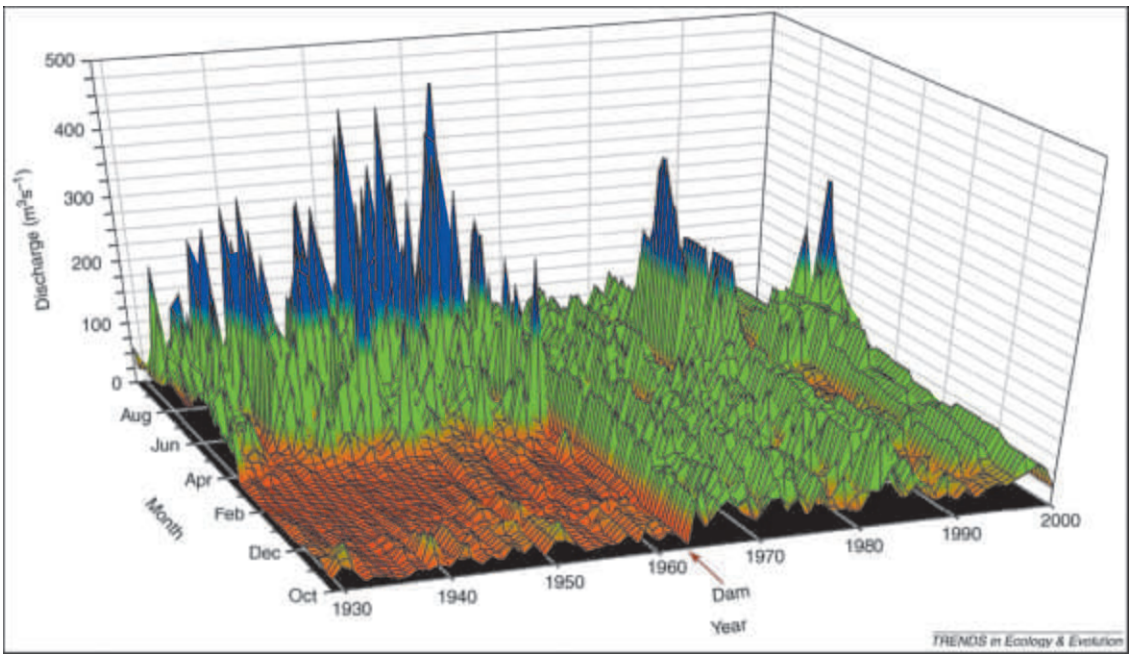

Fig. 2 Hydrograph of the Green River, Utah, United States from 1929 to 2000. Before the Flaming Gorge Dam was completed in 1963 (arrow), the river experienced floods from spring snowmelt and droughts during autumn and winter. Damming has caused both floods and droughts to become less frequent and smaller in magnitude. Lack of spring snowmelt floods in rivers of the western USA has halted recruitment of riparian cottonwoods, which had evolved to depend on these predictable seasonal events. Data from US Geological Survey. Reproduced from Fig. 1 in Lytle DA and Poff NL (2004) Adaptation to natural flow regimes. *Trends in Ecology & Evolution* 19: 94–100, with permission from Elsevier.

Environmental flow assessment methods

Assessments of environmental flow requirements began in the late 1940s in snow-melt streams and rivers of the western United States, initially to protect valuable cold-water fishes, especially salmonids. As the need to manage water flows in streams and rivers grew in prominence, many methods were devised. They are described in a comprehensive global review (Tharme, 2003), in numerous journal publications, two academic books (Arthington, 2012; Horne et al., 2017), and a recent book chapter (Poff et al., 2017). Fig. 3 captures the timeline of critical developments in the evolution of the environmental flow enterprise, beginning in the 1990s and followed by periods of consolidation, expansion, and global uptake (Poff and Matthews, 2013). This framing has helped to shape the present account, with slight adjustments in Fig. 3 to capture recent dimensions of global developments.

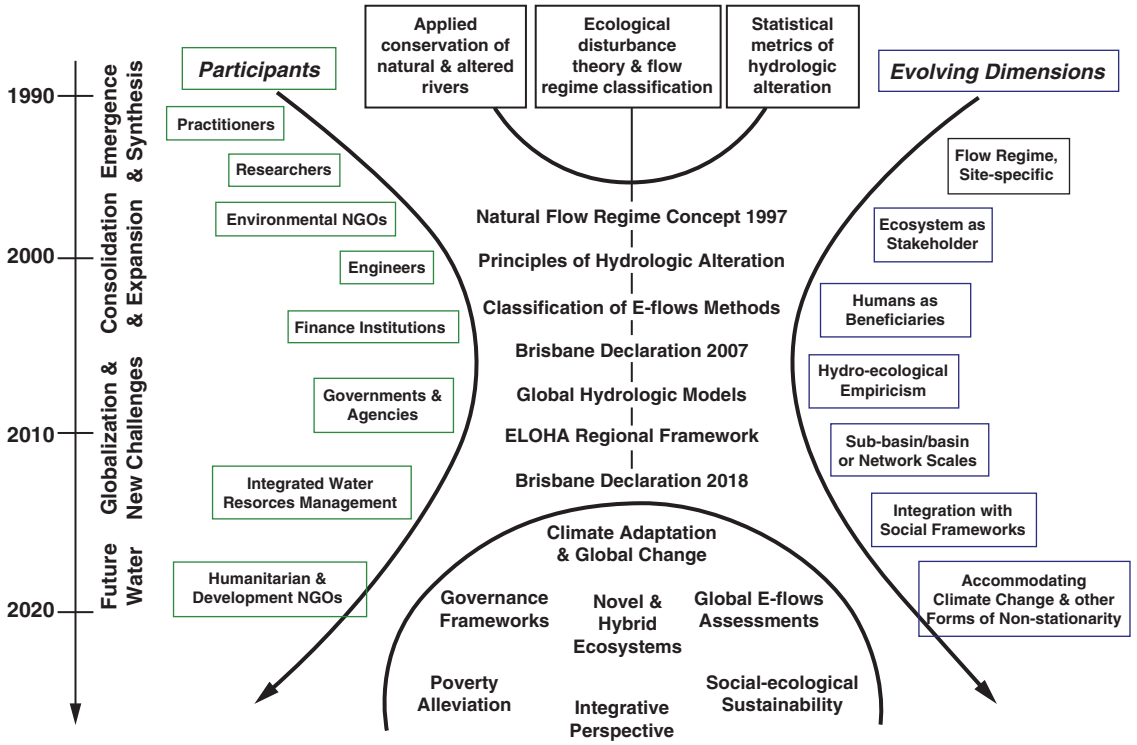

Fig. 3 Historical timeline for "modern" environmental flows (e-flows), showing emerging directions in the principles and concepts that underpin the science, and the growth in number and diversity of engaged institutions and practitioners. Timelines fall into relatively discrete periods of types of activities. The flow chart shows participants engaged in e-flows over time, benchmark achievements (central column), and evolving dimensions of e-flows. NGO—Non-Governmental Organization, ELOHA—Ecological Limits of Hydrologic Alteration. Adapted from Fig. 1 in Poff NL and Matthews JH (2013) Environmental flows in the Anthropocence: Past progress and future prospects, *Current Opinion in Environmental Sustainability* 5: 667–675, with permission from Elsevier.

Four main categories of environmental flow assessment methods were recognized by Tharme (2003) and this typology is still relevant today (Table 2).

The majority (70%) of methods provide simple flow rules founded on the characteristics of the surface water flow regime (e.g., the Montana Method of Tennant 1976), or quantify the discharge needed to maintain hydraulic habitat for selected species, usually fish of commercial or recreational value. PHABSIM, the Physical Habitat Simulation module of IFIM (In-stream Flow Incremental Methodology) is the prime example of these hydraulic habitat methods (e.g., Anderson et al., 2006). Often the flow recommended to support habitat was, and still is, termed a "minimum flow"—the lowest discharge that could maintain a wetted channel and provide opportunities for local movement and maintenance feeding for fish.

As the foundation of environmental flow assessments, these early habitat methods, and improvements in two and three-dimensional habitat modeling linked to habitat preference models, have proved immensely useful in protecting aquatic habitats and species (Poff et al., 2017). Recent advances offer more sophisticated applications at scales larger than river reaches, and encourage greater integration of physical and eco-hydrological models (e.g., Lamouroux et al., 2017; Curry et al., 2020).

Suitable wetted habitat is only one dimension of the needs of aquatic species and the ecosystem processes that support them, leading to the demand for methods that apply flow-ecology principles (e.g., Poff et al., 1997; Bunn and Arthington, 2002) and applications to a wider range of riverine and riparian taxa. A riverine ecosystem perspective on the assessment of environmental flows began to take shape in the 1990s, particularly in Australia and South Africa (Arthington et al., 1992; King and Louw, 1998). New directions in geomorphological theory contributed to these developments (Newson and Newson, 2000). Ecosystem frameworks proliferated rapidly such that after a decade of trial and error they represented around 8% of global methods (Tharme, 2003).

Table 2 Comparison of the four main types of methods and frameworks used worldwide to estimate environmental flows (e-flows) for rivers from site to regional levels.

Method type	*River ecosystem attributes/components addressed*	*Knowledge and expertise required*	*Resource Intensity*	*Resolution of output (environmental flow)*	*Appropriate level(s) of application*
Hydrological	Whole system, river or reach condition/ health, or non-specific	Primarily desktop, with modest data needs (e.g., virgin/naturalized (or other reference state) historical flow records (daily, monthly, or annual) Single flow indices or multiple ecologically relevant flow metrics characterizing flow regime Some use hydraulic habitat or ecological data, or meta-analysis of results of multiple e-flows assessments to derive rules	Low time, cost, and technical capacity	Mostly simple flow targets for maintaining river health, based on estimates of the percentage of annual, seasonal or monthly volume that should be left in a river to maintain acceptable habitat and river condition Often expressed as % of monthly or annual flow (median or mean); or as limits to change in vital flow parameters, commonly low flow indices Variable resolution, complexity and confidence	Reconnaissance/planning level of water resource developments Unsuitable for high profile, negotiated cases, or where flow regime dynamics are critical As a tool within habitat simulation or holistic methods For highly data deficient systems with limited ecological information Regionalization potential for different river ecotypes
	Used widely in many developed and developing countries/basins. Simple single index, rule-of-thumb and look-up table approaches (e.g., Tennant, 1976*) becoming less common. Shifting towards ecologically relevant flow metrics addressing multiple aspects of hydrological regime* (*e.g.,* Richter et al., 1996)				
Hydraulic rating	Aquatic (in-stream) physical habitat for target species or assemblages	Modest data needs, desktop or field surveys Historical flow records linked to single or multiple hydraulic variables at single river cross-section/transect Limited to moderate expertise	Mostly low, sometimes moderate time, cost, and technical capacity	Hydraulic variables (e.g., wetted perimeter) used as surrogate for habitat-flow relationships/models for target species or assemblages Low, sometimes moderate resolution, complexity, flexibility and confidence	Water resource developments where little negotiation is involved As a tool within habitat simulation or holistic methods
	Used widely historically, mostly in developed countries (see Tharme, 2003*), but nowadays largely superseded or used as one of several integrated habitat modeling tools in habitat simulation or holistic methods*				
Habitat simulation	Primarily in-stream physical habitat for target species, guilds or assemblages Some consider channel form, sediment transport, water quality, riparian vegetation, wildlife, recreation and esthetics	Moderate-high data needs, desktop, and field surveys Historical flow records, typically average daily discharge Few to many hydraulic variables are modeled at a range of discharges at multiple river cross-sections. Physical habitat availability, utilization and preference data, or similar models, for target biota	High to sometimes moderate time, cost, and technical capacity	Output in form of Weighted Useable Area (WUA) or similar habitat metrics for target biota (fish, invertebrates, plants) Often includes comparative analyzes of time-series of habitat availability, use and duration Moderate to high resolution, complexity, and confidence, moderate flexibility	Water resource developments, often large-scale, involving rivers of moderate to high strategic importance, often with complex, negotiated tradeoffs among users Commonly used as a method within holistic approaches and frameworks. Useful to examine a variety of alternative environmental flow scenarios for several species/life stages/assemblages
	*Move away from single species focus to increasing use for species, guilds and assemblages (*Tharme, 2003*). Primarily applied in developed countries, using increasingly sophisticated and multi-dimensional (eco)hydraulic habitat modeling*				

Holistic (ecosystem) methods and frameworks *Site level*	Entire ecosystem, river or several reaches, all or several ecological components Most consider in-stream and riparian components, some also consider groundwater, floodplain and other wetlands, deltas, estuaries and lagoons A few consider ecological functions/ processes (e.g., sediment flows, nutrient dynamics) Several explicitly address social and economic dependencies (e.g., livelihoods of rural subsistence users, health) on species, and ecosystem services (e.g., fisheries)	Typically moderate to high knowledge and expertise, but several used in data poor contexts Desktop and often field studies (seasonal, or more intensive), or mix of data. Expert judgment and traditional knowledge Use virgin/naturalized historical flow records, or rainfall records/other data for ungauged sites Several use hydraulic habitat variables from multiple cross-sections Biological data on flow-ecology relationships for lifecycle stages of aquatic and riparian species, assemblages and ecological processes	Moderate-high time, cost, and technical capacity	Recommended hydrological regime linked to explicit quantitative or qualitative ecological, geomorphological, and sometimes, social and economic responses and consequences Some address modified e-flow regimes for dry or wet years Moderate-high complexity and confidence Typically, high resolution and flexibility Several with potential to generate outputs for multiple scenarios (past, future) Some explicitly address probabilities, interaction effects, risk and/or uncertainty A few incorporate climate change	Water resource developments, typically large-scale, involving rivers of high conservation and/or strategic importance, and/or with complex, negotiated tradeoffs among stakeholders Simpler approaches (e.g., expert panels) often used in basin contexts where flow-ecology knowledge is limited, limited tradeoffs exist among users, and/or time and capacity constraints exist Potential for use in very modified or novel ecosystems, with focus on flow regime to deliver specific objectives
Regional level	As for other holistic methods, but for whole system(s)	Designed to use existing data sets and knowledge In some cases, includes collection of new data, or modeling for system locations of interest for which hydrological and/or ecological data are absent	As for other holistic methods	Quantified e-flow rules or standards for rivers of contrasting hydrological type or ecotype and points of management interest, at user-defined regional scale(s) Flow alteration-ecological/social response relationships by river type	As for other holistic methods Large systems/basins or aggregations of smaller ones, regions, entire states, or multiple projects May be integrated with water management systems

*Increasingly common in developing and developed countries. Recent attention in developed regions focused on in-depth analysis of ecosystem components and, less commonly, functions/processes. Used regularly in developing countries, including for capacity development, and in complex basins with development pressures and, in many cases, communities with clear dependencies on aquatic systems (*e.g., Arthington et al., 2003; King et al., 2003; King and Brown, 2010, 2018*). At regional scale, most applications are adaptations of a single framework, the* Ecological Limits of Hydrologic Alteration (ELOHA, Poff et al., 2010*) or derived approaches (*e.g., Kendy et al., 2012; Arthington et al., 2012; McManamay et al., 2013)

Current practice is summarized below each method type, with selected application examples from various world regions (references are provided within the body of the text).

Adapted from Tharme RE (2003) A global perspective on environmental flow assessment: Emerging trends in the development and application of environmental flow methodologies for rivers. *River Research and Applications* 19: 397–441, and Poff NL, Tharme RE and Arthington AH (2017) "Chapter 11: Evolution of environmental flows assessment science, principles, and methodologies," in *Water for the Environment: From Policy and Science to Implementation and Management*. Cambridge, MA: Elsevier.

Ecosystem frameworks for environmental flow assessment in rivers

Environmental flows can be assessed in two major contexts—flow regimes to support conservation of minimally impaired rivers, and flow regimes to guide restoration of regulated rivers. Two environmental flow frameworks, DRIFT and ELOHA, have been particularly effective in addressing these contrasting circumstances. Both are derivatives of early ecosystem approaches and flow-ecology principles.

DRIFT (Downstream Response to Imposed Flow Transformation)

King et al. (2003) developed the DRIFT framework during environmental impact studies in the montane rivers of the Kingdom of Lesotho, South Africa. Details of the original framework, such as the fish component, can be found in Arthington et al. (2003) and a fuller account of DRIFT applications is available in King and Brown (2010). DRIFT is comprised of four modules: (1) a biophysical module used to describe present ecosystem condition, and to predict how biophysical river components will change under a range of flow alterations; (2) a sociological module designed to identify subsistence users of river resources and to quantify the uses of river goods and services, including river-dependent health profiles; (3) a scenario development module which links the first two modules and generates ecological and social outcomes of specified flow alteration scenarios; and (4) an economic module to generate the costs of mitigation and compensation for each scenario.

Building on the Lesotho Highlands project, DRIFT has become a robust collection of field and desktop procedures, database systems and decision support tools for proactive planning of environmental flow provisions for rivers and estuaries. It now provides a platform for Integrated Basin Flow Assessment (IBFA), which can illustrate, for any future development option, potential changes in a wide range of river characteristics (e.g., channel configuration; bank erosion; water chemistry; riparian forests; river, estuarine and near-coastal fisheries; rare and pest species), and river-related human health and well-being (e.g., King et al., 2014). Most recently, King and Brown (2018) have promoted basin-wide environmental flow assessments of planned new hydropower developments, at a time of great concern for rivers and biodiversity threatened by new hydropower dams (Zarfl et al., 2015). DRIFT can be used to evaluate the biodiversity and ecosystem service consequences of different permutations of dam numbers, locations, designs, operations and power generation. "Such information is invaluable in helping guide decisions on whether or not to build, the design of meaningful mitigation measures, the fine-tuning of dam operation and, in some cases, identification and design of biodiversity offsets" (King and Brown, 2018).

ELOHA (Ecological Limits of Hydrologic Alteration)

The ELOHA framework (Poff et al., 2010) also aims to set limits on levels of ecological change in rivers as a consequence of flow regime alterations, and its outcomes can be applied in river flow restoration as well as protection of valued rivers and assets. A central concept is that eco-hydrological relationships can be developed for a selection of rivers with distinctive flow regime characteristics (distinguished by classification procedures) and transferred to other rivers of the same hydrological type, rather than managing for the "uniqueness" of each river's flow regime (Poff et al., 2010). The framework provides a multi-step process: (1) building a hydrologic foundation (including modeled hydrographs for ungauged stream segments), (2) classification of river segments into ecologically relevant types based on selected flow metrics, a further geomorphic sub-stratification (if necessary), (3) assigning flow-altered streams to pre-impact "reference" (unregulated) stream types, (4) and testing hypotheses (preferably mechanistic or process-based) about the likely ecological responses to flow alterations for each river type (Fig. 4).

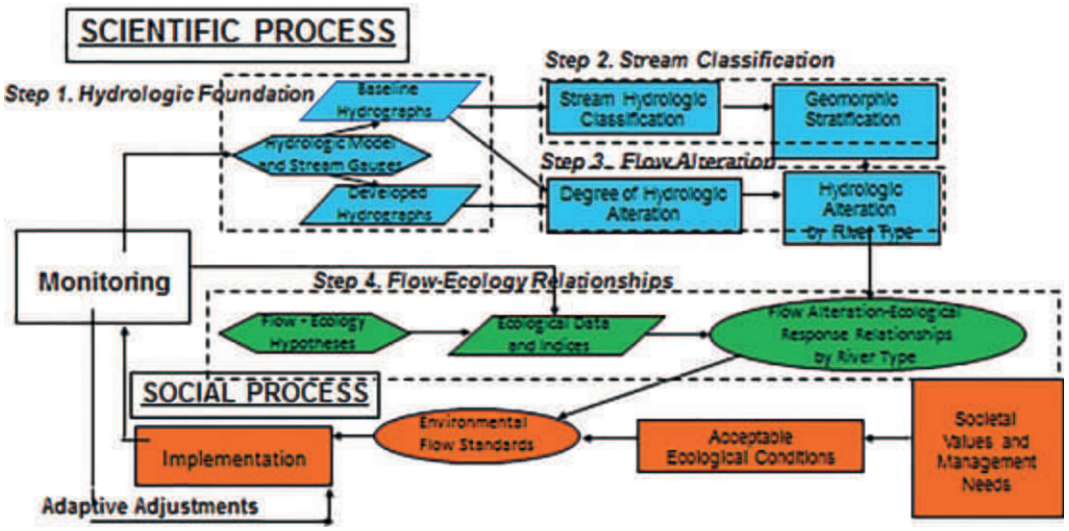

Fig. 4 The ELOHA framework comprises a scientific and a social process. Hydrological analysis and classification (blue) are developed in parallel with flow alteration–ecological response relationships (green), which provide scientific input into a social process (orange) that balances this information with societal values and goals to set environmental flow standards. Redrawn from Fig. 1 in Poff NL, Richter BD, Arthington AH, Bunn SE, Naiman RJ, Kendy E, Acreman M, Apse C, Bledsoe BP, Freeman MC, Henriksen J, Jacobson RB, Kennen JG, Merritt DM, O'Keeffe JH, Olden JD, Rogers K, Tharme RE and Warner A (2010) The ecological limits of hydrologic alteration (ELOHA): A new framework for developing regional environmental flow standards. *Freshwater Biology*, 55: 147–170, with permission from John Wiley & Sons Inc.; reproduced with permission from University of California Press, publisher of the text *Arthington AH (2012) Environmental Flows: Saving Rivers in the Third Millennium. Berkeley: University of California Press.*

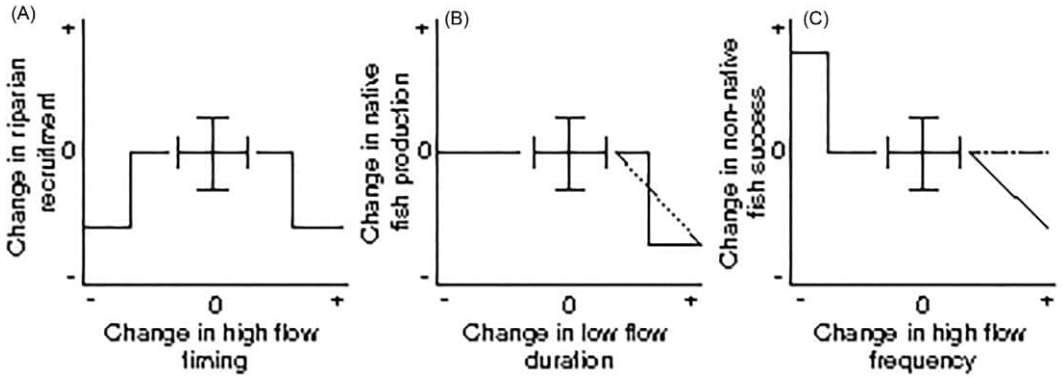

Fig. 5 Flow alteration–ecological response relationships for three river types: snowmelt (A), groundwater-fed (B) and flashy (C). Change in the flow metric (X-axis) ranges from negative to positive with no change representing the reference condition. The response of the ecological variable (Y-axis) to the flow alteration measured across a number of altered sites ranges from low to high. The bracketed space in the center of the graph represents the natural range of variation in the flow variable and ecological variable at the reference sites. Redrawn from Fig. 1 in Poff NL, Richter BD, Arthington AH, Bunn SE, Naiman RJ, Kendy E, Acreman M, Apse C, Bledsoe BP, Freeman MC, Henriksen J, Jacobson RB, Kennen JG, Merritt DM, O'Keeffe JH, Olden JD, Rogers K, Tharme RE and Warner A (2010) The ecological limits of hydrologic alteration (ELOHA): A new framework for developing regional environmental flow standards. *Freshwater Biology*, 55: 147–170, with permission from John Wiley & Sons Inc.; reproduced with permission from University of California Press, publisher of the text *Arthington AH (2012) Environmental Flows: Saving Rivers in the Third Millennium. Berkeley: University of California Press.*

When eco-hydrological relationships from ELOHA studies are expressed graphically, they provide information that can be used to set 'threshold' levels of change in flow alteration and species response in rivers of contrasting hydrological character (Fig. 5). In the final stages of an ELOHA application, a social process balances scientific information and impact risk assessments with societal values and goals, thus enabling environmental flow standards or "rules" to be negotiated for each distinctive river type.

Development of the hydrologic foundation has dominated applications of the ELOHA framework (e.g., Belmar et al., 2011; Kennard et al., 2010; Zhang et al., 2012) and prompted new approaches to accurately simulate flows and estimate flow metrics at many ungauged locations across broad geographical areas. Further developments have incorporated geomorphic features (e.g., Reidy Liermann et al., 2012) and water temperature (St-Hilaire et al., 2021) into river classification schemes. The framework has been applied in six US states and three interstate river basins to determine environmental flow needs at the regional scale (Kendy et al., 2012). It has been tested in Australian sub-tropical rivers to inform the possible development of new headwater dams to augment domestic water supplies (Arthington et al., 2012). McManamay et al. (2013) used flow-ecology relationships from an ELOHA study to predict fish and riparian responses to flow restoration in the regulated Cheoah River, Tennessee. This application demonstrated that recommended increases in flow magnitude reduced riparian encroachment 4 years after flow restoration, as predicted.

Like DRIFT, the ELOHA framework can be used in differing societal, governance and management contexts (Pahl-Wostl et al., 2013). ELOHA is being piloted for a collection of small coastal basins in Chiapas State, southern Mexico, and foundational studies are underway in China (Zhang et al., 2012). A further development has enhanced the social process within ELOHA by addressing indigenous people's beliefs, knowledge and socio-cultural relationships to water and rivers (Finn and Jackson, 2011). This long overdue recognition of indigenous values, knowledge and needs, initiated in the Lesotho DRIFT study, is becoming the norm in several countries (Anderson et al., 2019).

Future challenges for environmental flows

A founding principle of environmental flows assessment methods and implementation in river management is that the maintenance of critical features of the historical natural flow regime will sustain or restore associated ecological features and processes (Poff and Matthews, 2013). However, it is now clear that the hydrologic baselines and flow regimes of past eras are changing in many locations experiencing climate shifts (e.g., Laize et al., 2014). The implications of "non-stationary" climate regimes (Milly et al., 2008) are likely to be severe for many freshwater ecosystems. For example, Pound et al. (2020) forecast potentially devastating impacts of climate change on U.S. stream ecosystems, "with the restructuring of diatom, insect and fish communities, diminished distributions of functionally important taxa and widespread expansion of warm-water taxa, giving rise to biotic homogenization." Furthermore, natural ecological communities have been gravely impaired by the spread of non-native species (Bunn and Arthington, 2002; Rahel and Olden, 2008) and other forms of river and catchment degradation (Tickner et al., 2020).

A consensus is emerging that aiming to maintain or restore the historical patterns of flow variability, biodiversity and ecosystem structure in highly altered river systems that are also under duress from climatic shifts is typically unrealistic, even undesirable (Acreman et al., 2014; Poff et al., 2017). Scientists and managers are now faced with difficult social-ecological choices, trade-offs and decisions around the kinds of ecosystems (and e-flow regimes) that may be desirable, and manageable, now and in changing climatic futures (e.g., Poff et al., 2016).

In this context, should environmental flows be "designed" to sustain or improve particular features, such as fish catches of high value, as demonstrated for vital fisheries of the Mekong River Basin (Sabo et al., 2017)? This study found that a statistically optimized seasonally timed "designer flow regime" would lead to a two- to fourfold increase in fisheries catch compared with the historical (pre-dam) natural flow regime. Capon et al. (2018) comment that environmental flows can be designed to enhance ecological functions beyond their historical limits, such as the creation of new aquatic refuges or migration corridors where climate change has negatively impacted historical patterns of habitat, connectivity and organismal movement.

Given the potential for expansion of the "designer" environmental flow concept, river scientists urge caution and careful evaluation of the consequences of selective designs for broader freshwater biodiversity. Efforts to promote particular outcomes, such as sustainable fisheries, or to rescue and protect particular threatened species, may compromise other taxa, communities, even ecosystem processes. Tonkin et al. (2020) assert that "designing flows for the benefit of entire ecosystems requires long-term perspectives that embrace hydrologic dynamism involving critical flow events that occur at multiple temporal frequencies. While returning to the historical natural flow regime is an increasingly distant option in highly managed rivers in a non-stationary world, environmental flows must remain founded on the principles of the natural flow regime paradigm."

A capacity to predict possible future river ecosystem states and processes under changing climatic regimes is now demanded of river scientists and environmental flow managers. Yet the dynamic processes that underlie the assembly of ecosystem states are typically ignored in environmental water science and assessment (Poff et al., 2017). Envisioning the next developments in environmental flow science, Poff (2018) recommends several major areas of research: (1) shifting from static, regime-based flow metrics to dynamic, time-varying flow characterisations; (2) expanding the ecological metrics (and space–time scales) used in e-flows from primary reliance on ecosystem states to include process (e.g., population) rates and species traits; (3) incorporating other "non-flow" environmental features (e.g., temperature, sediment) to guide prioritization of e-flows applications with a likelihood of success; (4) broadening the ecological foundation of e-flows to incorporate more ecological theory that will contribute to a more predictive river science. Tonkin et al. (2019) call for a fresh global campaign to gather data on the dynamic responses of freshwater species and biodiversity to changes in river flows, preferably creating process-based models. They envisage that targeted interventions to avoid population collapse during extreme flows will be a cornerstone of managing rivers for resilience in future. "Freshwater biodiversity is disappearing on our watch. As the crisis deepens, we must model and manage rivers to safeguard the services they provide."

Capon et al. (2018) take a broader view of the implications of challenges associated with climate change and shifting hydrological and ecological baselines. They propose three guiding principles as "critical to avoiding perverse outcomes of environmental water management (EWM)": (1) climate change highlights the imperative for EWM to extend its scope beyond conventionally narrow ecological objectives, to encompass "functional, social, economic and cultural aspects"; (2) the scale of, and uncertainties associated with, climate change effects require that EWM adopt both "a broader and more nuanced consideration of its spatial and temporal framing"; (3) effective adaptation of EWM, and ultimately its transformation, will depend on its "successful alignment and integration, with respect to both water management more broadly and other sectors such as agriculture and energy production." The next section of this chapter moves into this broader policy arena.

Globalization and social-ecological sustainability

Frameworks such as DRIFT and ELOHA have expanded the geographic, socio-economic and governance contexts of environmental flow assessments and water management (e.g., Arthington et al., 2018b; King and Brown, 2018). Their incorporation into other policy and management frameworks is already under way; for instance, Integrated Water Resources Management (Overton et al., 2014), systematic conservation planning (Nel et al., 2011), climate change adaptation strategies (Poff et al., 2016; Capon et al., 2018) and implementation of the United Nation's Sustainable Development Goals (SDGs).

In an effort to increase the visibility and social-ecological relevance of the environmental flows enterprise as a powerful scientific and policy platform, the influential 2007 Brisbane Declaration and Global Action Agenda (www.eflownet.org) has been refreshed and expanded as the 2018 Brisbane Declaration and Global Action Agenda on Environmental Flows (Arthington et al., 2018a, see Box 1). The refreshed Global Action Agenda presents 35 actionable recommendations to guide and support implementation of environmental flows through legislation and regulation, implementation and water management programs, and research. The Declaration gives particular emphasis to integrated partnership arrangements that ensure full and equal participation for people of all cultures, and respect for their rights, responsibilities and systems of governance in environmental water decisions (see Anderson et al., 2019). The intent is that the Declaration and its actionable recommendations will guide a new era of shared visions, research and innovation, collaborative implementation programs, and adaptive governance of environmental flows, suited to diverse social, economic and environmental contexts.

The renewed 2018 definition has been incorporated (with the omission of water quality) into the Food and Agricultural Organization (FAO) Guidelines for inclusion of environmental flows into the SDG "Water Stress" Indicator 6.4.2. As custodian UN agency for this SDG, the FAO is required to collect global data on water stress and environmental flow allocations annually or at least every 3 years, following an agreed protocol for estimation of country-wide environmental flow provisions. This high-level process could facilitate a global review of the methods currently applied by every country to estimate environmental water allocations at finer scales (e.g., regions, basins), as well as data on how and where rivers have benefited from environmental water management—a significant information gap in the global literature (Horne et al., 2017). Discussions are underway to address these opportunities.

Box 1 The 2018 Brisbane Declaration and Global Action Agenda on Environmental Flows.

The 2018 Brisbane Declaration and Global Action Agenda on Environmental Flows was developed and endorsed by an international network of environmental flow practitioners comprising civil society, indigenous peoples, the private sector, scientists, water users, businesses, non-government organizations, local, regional and national government agencies and international institutions. It was endorsed by delegates of the 20th *International Riversymposium and Environmental Flows Conference* (Brisbane, September 2017) and numerous colleagues.

Definition: Environmental flows describe the quantity, timing, and quality of freshwater flows and levels necessary to sustain aquatic ecosystems which, in turn, support human cultures, economies, sustainable livelihoods, and well-being.

The goal of environmental flow management is to protect and restore the socially valued benefits of healthy, resilient, biodiverse aquatic ecosystems and the vital ecological services, economies, sustainable livelihoods, and well-being they provide for all societies.

Aquatic ecosystems include in the e-flow enterprise include rivers, streams, springs, riparian, floodplain and other wetlands, lakes, near coastal water bodies, including lagoons and estuaries, and groundwater-dependent ecosystems (Arthington et al., 2018a).

Global Action Agenda on Environmental Flows (2018)

The Brisbane Declaration on Environmental Flows (2018) calls upon all governments, development banks, donors, water and energy associations, multilateral and bilateral institutions, community-based organizations, research institutions, indigenous groups and the private sector across the globe to commit to the following actions for protecting and restoring environmental flows as a central element of water resources management, and as a foundation for achievement of the water-related Sustainable Development Goals (SDGs).

Declaration Statements	Leadership & Governance	Management	Research
E-flows are essential to protect and restore biodiversity, aquatic ecosystems, and the ecosystem services they provide for all societies	Develop and implement government programs to support provision of e-flows to freshwater-dependent ecosystems, including Groundwater Dependent Ecosystems GDEs) Develop and implement government e-flow programs to support achievement of water-related Sustainable Development Goals (SDGs)	Develop and implement e-flow programs that integrate surface and groundwater processes into e-flow planning, assessment, monitoring and management Integrate e-flows into programs and projects designed to support achievement of water-related Sustainable Development Goals (SDGs)	Quantify flow-ecology relationships and ecosystem services for all aquatic ecosystems that depend on fresh water, including GDE Demonstrate ecological, economic and societal benefits of e-flows and healthy freshwater-dependent ecosystems in programs and projects that support water-related Sustainable Development Goals (SDGs)
E-flows are critical to protect and restore the world's cultural and natural heritage	Develop and implement government programs to generate awareness of cultural heritage values, knowledge and attachments to freshwater-dependent ecosystems	Integrate cultural heritage values, knowledge and attachments to freshwater-dependent ecosystems into e-flow assessment, implementation, monitoring and adaptive management	Improve understanding and quantify relationships between e-flows, healthy aquatic ecosystems and cultural heritage values, and attachments to freshwater-dependent ecosystems
E-flows have been compromised and today many aquatic systems around the world are at risk	Develop and implement government programs to protect and restore freshwater ecosystems Protect healthy freshwater-dependent ecosystems.as early as possible Establish programs to implement e-flows during the planning stage of new dams and other water infrastructure	Apply systematic planning tools to achieve cost-effective protection and restoration of healthy freshwater ecosystem Base protection and restoration of e-flows on scientific and local knowledge within an adaptive management framework that balances human and ecological water requirements	Identify obstacles to implementation of e-flows in different world settings Improve systematic planning tools and trade-off processes that can guide the location, design, and operation of new dams/other water infrastructure, for social-ecological benefit
Implementation of e-flows requires a complementary suite of policy, legislative, regulatory, financial, scientific and cultural norms and values to ensure effective delivery and beneficial outcomes	Develop and implement a legal basis for regulating water use, e-flows, water rights and licenses, including recognition of cultural heritage values, knowledge and customary relationships with water Develop and implement policies and programs to position e-flows as an integral component of water, food and energy security objectives and water-related SDGs Provide sustained funding to effectively plan, design, implement, monitor and adaptively manage e-flows Provide sustained funding for research and training to enhance understanding of aquatic ecosystem functioning, e-flow planning, assessment, implementation, monitoring and adaptive management	Establish environmental water allocation mechanisms appropriate to basin conditions and governance structures Establish a system to manage consumptive water uses at basin and local scales Utilize basin and system-scale infrastructure planning, design and operation to protect and enable e-flows even where dams and other types of water infrastructure are needed, as well as in cases of infrastructure retrofitting and decommissioning Ensure that water management professionals have sufficient technical capacity and knowledge to incorporate environmental flow approaches into water resource management plans, implementation, monitoring and adaptive management	Investigate existing, and propose new, mechanisms for integrating e-flows implementation in broader water and related resource management system Research effective design, monitoring and reporting of e-flow implementation projects and programs, treating them as experiments where feasible Research and identify appropriate indicators of ecological, cultural, and economic outcomes from environmental flows Establish centers of excellence for research and training to enhance understanding of aquatic ecosystem functioning, e-flow planning, assessment, implementation, monitoring and adaptive management

(*Continued*)

Box 1 (Continued)

Local knowledge and customary water management practices can strengthen e-flow planning, implementation, and sustainable outcomes	Develop and implement arrangements for full and equal participation, and respect for the rights, responsibilities and systems of governance of all cultures and stakeholders in e-flow planning, assessment, implementation, monitoring and adaptive management	Empower and ensure the full and equal participation, and respect for the rights, responsibilities and systems of governance, of all cultures and stakeholders in e-flow planning, assessment, implementation, monitoring and adaptive management	Co-develop best-practice models to ensure full and equal participation, and respect for the responsibilities, rights and systems of governance of all cultures and stakeholders in e-flow planning, assessment, implementation, monitoring and adaptive management
Climate change increases the risk of aquatic ecosystem degradation and intensifies the urgency for action to implement e-flows	Develop and implement flexible governance and management arrangements that enable consideration of climatic and other environmental regime change implications for e-flows and ecosystems Establish programs to implement adjustments to e-flows in aquatic ecosystems impacted by changing flow and other environmental regimes	Where climate change may further disrupt e-flows and social-ecological systems, adapt existing approaches to maintain/restore ecological resilience and societal benefits Monitor ecological and societal outcomes of e-flows in relation to changing flow and other environmental regimes, and adjust implementation plans accordingly	Conduct long-term studies of freshwater-dependent ecosystem adjustments and societal responses to changing flow and other environmental regimes in areas experiencing shifts in climate, human demographic patterns and demands for water Research new approaches to maintain/restore ecological resilience and societal benefits in such areas

The year 2021 is notable for visionary global activities to "Halt the loss of species, ecosystems and genetic diversity by 2030; restore and recover biodiversity to ensure a world of people "living in harmony with nature" by 2050" (Post-2020 Global Biodiversity Framework Mission, https://www.iucn.org/theme/global-policy/our-work/convention-biological-diversity-cbd/post-2020-global-biodiversity-framework). To this end, governments are reviewing international agreements relevant to biodiversity loss—the Convention on Biological Diversity (CBD), the Sustainable Development Goals (SDGs), and the UN Framework Convention on Climate Change (UNFCCC).

The 2018 Brisbane Declaration and Global Action Agenda forms part of a submission to the CBD (SBSTTA—Subsidiary Body on Scientific, Technical and Technological Advice) on actions needed to support the Global Biodiversity Framework). Signatories to this submission urged SBSTTA to consider an Emergency Recovery Plan to "bend the curve" of freshwater biodiversity loss (Fig. 6).

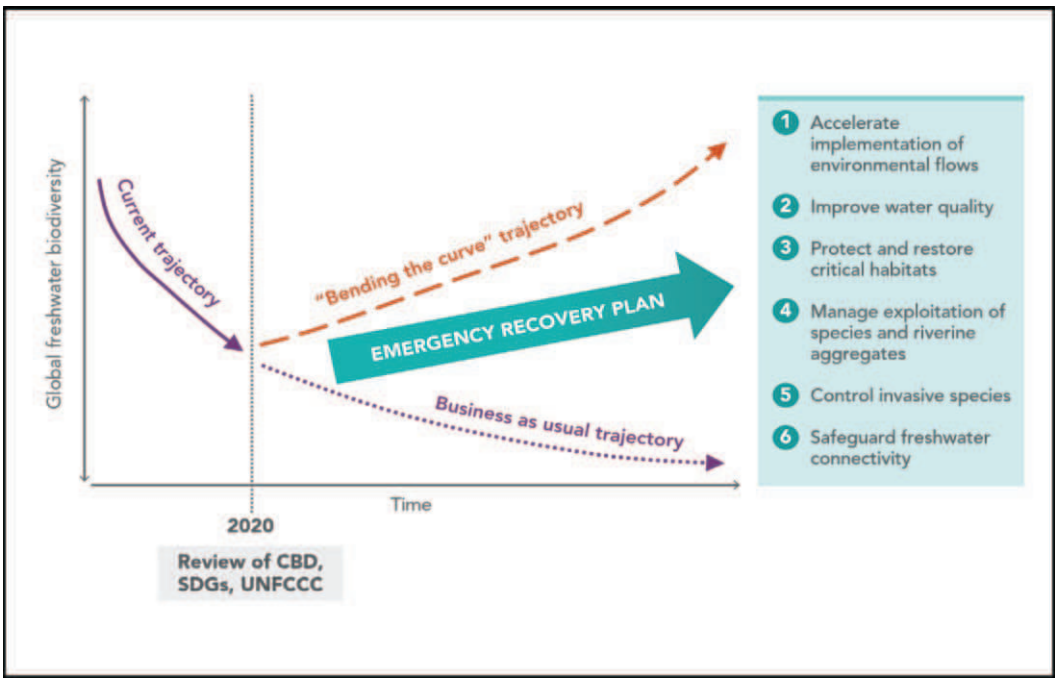

Fig. 6 The Emergency Recovery Plan for freshwater biodiversity: Six priority actions for global action to bend the curve of freshwater biodiversity loss that should be reflected in the post-2020 Global Biodiversity Framework. Threats to freshwater biodiversity are often synergistic so coherent planning of interacting priority actions to address such threats is necessary. Creative Commons License.

In this plan, six priorities for action start with the need to accelerate implementation of environmental flows globally (see Tickner et al., 2020). Other major actions to halt freshwater biodiversity decline include: improving water quality; protecting and restoring critical habitats; managing exploitation of freshwater species and riverine aggregates; preventing and controlling non-native species invasions; and safeguarding and restoring river connectivity.

In further support of the environmental flows aspects of the Emergency Recovery Plan, Tharme et al. (2020) published a BLOG to highlight the grave threat to freshwater biodiversity and river health from these multiple, interacting stressors (https://blog.oup.com/2020/09/bring-living-waters-back-to-our-planet). Its message is that Planet Earth "has shown unimaginable resilience, but at a cost we have not fully reckoned—precipitous declines in the health and biodiversity of freshwater ecosystems will undoubtedly push us beyond the bounds of sustainability. We have reached a pivotal moment when all of us, whether policymakers, indigenous and business leaders, resource managers, engineers, scientists, and the public, must re-evaluate priorities and mobilize to protect and recover our freshwater ecosystems for the long term. Meeting the imperative for accelerating implementation of environmental flows is central to that path and that potential."

Conclusion/Synthesis

The challenge of protecting or restoring the water regimes and biodiversity of rivers and other freshwater ecosystems is urgent and it is global. The evolution of the environmental flow enterprise has produced a remarkable array of methods, models, decision support tools and policy instruments to guide the management of environment water (Poff and Matthews, 2013; Horne et al., 2017). The development of ecosystem frameworks such as DRIFT and ELOHA has enabled quantification, evaluation and implementation of environmental flow regimes at reach, river, basin and regional scales. These framings and decision support tools can help to guide which aquatic ecosystems should be protected versus those that can be rehabilitated, re-engineered or even re-designed across diverse natural and developed landscapes (Poff et al., 2016; King and Brown, 2018; Tickner et al., 2020). Achieving a societally acceptable balance between the provision of environmental flows for wild and formally protected rivers and the return of flows to selected regulated rivers should be a major goal.

Shifting climatic regimes and associated effects on river hydrology, water temperature, water quality and ecological dynamics are creating new challenges across the full spectrum of river science and environmental water management (Capon et al., 2018; St-Hilaire et al., 2021). Predicting ecological configurations and outcomes from environmental flow allocations against a background of shifting climatic and other regimes, and diverse societal perspectives, is challenging but necessary. To this end, a more dynamic, process-based river science and new modeling techniques are emerging (Poff, 2018; Tonkin et al., 2019, 2020). The "designer environmental flow" concept may have merit in particular circumstances, but each application will require careful evaluation to ensure that freshwater biodiversity and valued ecosystem services are not compromised.

Continuing efforts to enhance and promote environmental flows science and implementation in diverse contexts, countries, systems of governance and policy arenas are essential. The 2018 Brisbane Declaration and Global Action Agenda on Environmental Flows and the 2020 Emergency Recovery Plan for Freshwater Biodiversity provide examples of what can be achieved by collaborative international teams speaking with one voice. The Post-2020 Global Biodiversity Framework offers a perfect window of opportunity to bring freshwater ecosystems to greater prominence in global policy arenas. Continued efforts will be needed to keep up the pressure on world governments and other sectors to ensure recovery of freshwater biodiversity and resilient ecosystems for the long-term benefit of people and nature.

Acknowledgments

The author acknowledges the many sources of information and examples cited throughout this chapter, which draws from the work of numerous colleagues and friends. Thanks are due to each and every individual for their dedication to research on rivers and environmental flows, and their commitment to sustaining healthy rivers for people and nature. I am especially grateful to Samantha Capon, who re-drew most of the figures from original sources for my book (Arthington, 2012) and to Paul Godfrey for his assistance with the preparation of figures for this chapter.

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Dam Removal and River Restoration

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Benthos Refers to the collective community of aquatic organisms that lives or forages at the bottom of an aquatic habitat like lakes, rivers, or the ocean.
Connectivity Represents the ability of water, organisms, and other materials to move among the main dimensions of a river, including longitudinally (upstream and downstream), laterally across the floodplain, and vertically through the interaction between surface water and ground water.
Dam removal mitigation A project, program, or structure designed to off-set the effects of dam removal, such as planting of vegetation, removal of exotic species, or installation of a water treatment facility.
Ecological memory The ability of past ecosystem states or events to influence present or future ecological condition.
Ecological response trajectory The path through time followed by an ecosystem or its fundamental properties after a major disturbance or restoration action.
Fish passage The modification or removal of barriers to allow fish and other aquatic organisms to swim and migrate unimpeded through a river system.
Instantaneous dam removal A dam removal project that proceeds following a relatively rapid drawdown (hours to days) of the impoundment.
Sedimentation The process of sediment transported in suspension by a river settling out once the water enters an impoundment, reservoir, or barrier.
Species turnover The change in taxonomic composition among habitats, time periods, or areas.
Staged dam removal A dam removal project that proceeds in stages, drawing out the reservoir drawdown by incrementally dismantling a dam.
Thermocline A relatively thin zone of stratification in a reservoir where layers contain markedly different water temperatures.

Introduction

We begin our discussion of dam removal by focusing on the importance of rivers. Rivers provide vital ecosystem services, largely through the provision of food, energy, and water. For millennia, humans have been attracted to rivers for these resources, settling near rivers and developing their floodplains. In the geologic record, signatures of human development on river systems date back to the earliest Mesopotamian civilizations of the 3rd millennium BCE, and elsewhere during the 1st and 2nd millennia BCE in Europe, Asia, and South America (Williams et al., 2014). Today, the intricate connections between societies and rivers occur across many socio-political boundaries and spatial scales. At the local scale (100s to 1000s of m^2) indigenous fishing communities harvest fish and use water for drinking and bathing; at continental scales, governments wrestle with river management—water scarcity, storage, irrigation, organic and inorganic pollution, eutrophication, disease, flood control, navigation, and sedimentation. Globally, rivers have sculpted the earth by weathering rock and mineral deposits, transporting sediment and nutrients to floodplains, river deltas, and oceans. They connect the atmosphere to the ocean via the water cycle and are a central geographic feature of many of the world's most populated cities.

Dams have become one of the most prevalent agents of change to the world's rivers. Early dam construction was largely driven by human needs for mechanical power, reliable water supplies, irrigation, and protection from floods, with little concern for the environmental consequences. As technology advanced in the modern industrial era, the form and magnitude of changes to rivers resulting from dam construction accelerated. The ability of human engineering to harness larger, more powerful rivers has advanced resulting in the damming of many of the world's rivers to maximize the provision of resources or infrastructure for providing flood protection, navigation, and recreational opportunities (Grill et al., 2019). Despite engineering feats that allow for the construction of mega-dams, the vast majority of the world's dams have heights of less than 10 m. Several national and global databases of larger dams exist (e.g., Mulligan et al., 2020), although the exact number of dams worldwide is unknown. Estimates using known databases of larger reservoirs and statistical projections of smaller reservoirs suggest that the number could exceed 16 million (Lehner et al., 2011). This number is expected to increase in the coming decades as developing countries build large dams on big rivers and small dams on tributaries for hydropower, irrigation, and water supply (Zarfl et al., 2015).

The different kinds of dams can be categorized into five groups (USSD, 2015). *Arch dams* are constructed of stone, brick, or concrete. They are curved in an upstream direction, which transmits the major part of force from the water load to the abutments (typically bedrock canyon walls or concrete). Arch dams facilitate a taller structure, which increases the reservoir storage capacity. A *buttress dam* is usually made of concrete, with a solid water-tight side upstream supported by concrete buttresses on the downstream side. A *gravity dam* depends upon its own weight for stability and can be constructed from concrete, stone masonry, timber cribs filled with rock, or roller-compacted concrete. An *embankment dam* is constructed of earth materials such as rock and soil, with an impervious core to control seepage. Finally, a *composite dam* consists of both embankment and concrete.

Effects of dams on rivers

Although dams produce societal benefits, they also impact the structure, function, and ecology of rivers and can have a range of impacts on indigenous communities both upstream and downstream of the dam structure. Dams instigate other potential socio-ecological impacts, such as population displacement, loss or inundation of agricultural lands, evaporative water loss, and greenhouse gas emissions. The ecological effects of dams occur both upstream and downstream of the structure; larger dams eliminate a free-flowing section of river by replacing it with a reservoir, while low-head dams may slow water velocities and create impoundments within the banks of the river channel. The magnitude of these effects depends upon the size of the dam and its impoundment, the operation and purpose of the dam, the geography and hydrology of the river system, and whether any additional drivers of change are present in the watershed, including other dams. Thus, each dam has a unique set of interacting factors contributing to the types and levels of impact on a river (Poff and Hart, 2002).

Immediately upstream of a dam, some of the free-flowing river is eliminated and replaced by an impoundment. The shallower and faster moving *lotic* habitat is replaced with deeper, slower moving *lentic* habitat. Although there may be some overlap, the organisms adapted to life in these two contrasting environments are different; therefore, creating an impoundment can cause a turnover in the assemblages of plant, invertebrate, and vertebrate species occurring in that segment of river. Reservoirs can also change the temperature regime of downstream waters. By absorbing more of the sun's heat and having a longer water residence time than an equivalent length of river, reservoirs can store heat. When water that passes through the dam originates from above the thermocline, the heated water can increase the temperature of waters downstream. In other cases, when the dam draws water from below the thermocline, a cooling effect can occur in downstream waters. In both cases, the change from the normal temperature regime can have consequences for downstream aquatic life. For dams without any provisions for fish passage past the dam (e.g., fish ladders, smolt bypass), migrating fish can no longer ascend or descend the river. This disruption of connectivity leads to loss of habitat availability, often extirpating upstream migratory fish and potentially leading to population declines across the whole river system.

Downstream of a dam, most of the changes to the river are driven by physical factors, which can indirectly affect organisms. A natural flow regime—defined by the magnitude of discharge, the timing and duration of peak flows, and the rate of change of flow events—determines the ecological character and integrity of a river (Poff et al., 1997). A river's natural flow regime is disrupted by dams when they are used to regulate discharge through water storage, withdrawals, and running turbines. Naturally occurring floods or pulses of seasonally high flows from snow melt, for example, that serve to reset the structure of gravel bars or create and transport large woody debris, may no longer occur with enough frequency or strength. Because many organisms are adapted to these habitat-forming processes and their timing, the effects on downstream organisms can cascade through freshwater food webs. In addition, the transport of sediment may be altered or eliminated, causing riverine habitat downstream to degrade and coarsen, which in turn affects the benthos and the ability of fish to spawn (Wohl et al., 2015).

A brief history of dam removal

As the effects of dams became more widely recognized and understood, the notion of deliberately removing them slowly emerged into the zeitgeist of river management and conservation. For much of human history, the removal of dams occurred unintentionally through failure during floods—whether due to old and degraded structures no longer able to withstand the forces of nature, or because new dams were improperly constructed or maintained. Such failures resulted in economic damage, environmental

degradation, and in some tragic cases the loss of human life. Despite modern safety standards and monitoring, structural and catastrophic failure of dams still occurs, sometimes with lethal consequences.

The advent of dam safety regulations has helped propel the recent increase in dam removal. In some countries, modern safety standards, policies, and laws require regular inspections of dams to assess risk, resulting in the identification of deficient dams and potential candidates for removal. Some states and municipalities have dedicated funding to remove obsolete, unsafe, or hazardous dams. In other cases, especially for privately-owned dams, economics may cause owners to remove some dams when the return on investment is inadequate to justify costly repairs, upgrades, or other mitigation measures to resolve environmental effects and legal mandates (e.g., fishways for adult fish, trap-and-haul structures for juveniles).

Increasingly, river restoration has spurred dam removal because the return of a natural flow regime and increasing connectivity have repeatedly resulted in restoration of river functions (O'Connor et al., 2015). Sedimentation has also led to dam removals in cases where reservoir water storage capacity has been lost due to the accumulation of sediment. Largely propelled by these factors, dam removals in the U.S. have steadily grown in number since the mid-1970s (Foley et al., 2017). A comprehensive list of U.S. dam removals shows that as of 2019 about 1700 dams have been removed (American Rivers, 2020), while Europe has documented over 4900 barrier removals, many of them dams and weirs (Dam Removal Europe, 2020).

A large share of dams removed in the U.S. are small, generally less than 10 m in height. Based on available data, the median height of dams removed in the U.S. was ~3 m (Bellmore et al., 2017). The skew toward small dams in the size distribution of dam removals is driven by a suite of factors. There are many more small dams in the world than larger dams and they are, on average, older than large dams. Thus, in addition to being structurally deficient, their purpose is often tailored to a bygone era. Such small dams are now less likely to generate significant economic benefits compared with larger dams that store water or produce hydroelectricity, increasing their likelihood for removal. In contrast, the bias against larger dam removals stems from there being fewer of them; moreover, they are, on average, younger and are more likely to provide economic and societal benefits, although many are older than 50 years (Perera et al., 2021). Additionally, it is generally more arduous, time consuming, fraught with socio-economic challenges, and expensive to remove large dams and in some cases, like flood protection, to replace their function.

Not all dam removal projects fit neatly into the categories described above. There are exceptions, for example, to the prevalent small- versus large-dam rules of thumb associated with the reasons and primary cost drivers for dam removal decisions. Some low-head dams can impound large volumes of water, making their operational footprint considerable. Although the potential risks for property damage and loss of life associated with catastrophic failure are generally greater with larger dams, fatalities at hydraulically dangerous low-head dams (to swimmers, boaters, and other river recreationists) are also a public safety issue.

Considerations for dam removal

Several factors must be considered when evaluating potential dam removal projects. These can include legal requirements such as obtaining the necessary federal and local permits. Other practical issues surrounding project management include obtaining funding, identifying and getting input from stakeholders, and determining whether mitigation projects are necessary or required to minimize dam removal effects. Technical difficulty, expense, and time horizon of a proposed dam removal project contribute to its feasibility. Additional factors include whether the dam is publicly or privately owned, the purpose and size of the dam, level of reservoir sedimentation, the status and ecology of the river and surrounding project lands, the infrastructure downstream of the dam, and any necessary environmental compliance mandates. These all contribute to the complexity and unique scope of each dam removal project.

Existing manuals and technical documents provide recommendations for planning and conducting a dam removal project (e.g., Graber et al., 2015; USSD (U.S. Society on Dams Committee on Dam Decommissioning), 2015; Randle and Bountry, 2017; Georgia Aquatic Connectivity Team, 2020). For any given project, consultation with local experts and regulators who can provide information appropriately tailored to local conditions is prudent. Below, we briefly outline the main issues for consideration when scoping a dam removal project.

- *Assembling a project and stakeholder team*. Regardless of the scope and complexity of the dam removal project, planning will involve both the creation of a project team and engagement with stakeholders who have an interest in project details. A project team will be multidisciplinary and likely include a manager, engineers and restoration designers, biologist, geomorphologist, outreach specialist, and construction-engineering specialist. The main goal of a project team will be to define project objectives, obtain necessary funding and permits, conduct the removal and any necessary mitigation and post-project monitoring. Larger, more complex projects may require several intermediate steps, including feasibility studies, preliminary design analyzes, and alternative scenario plans (e.g., no action, refurbishing, rebuilding). There could be many potential stakeholders, including local, state, tribal, and federal agencies who have legal jurisdiction. Other parties—public utilities, business and industry groups, environmental and watershed groups, heritage and historical societies, indigenous communities and residents—also have an interest and differing viewpoints on how ecosystem services may be impacted by the dam removal project. The success of many dam removal projects has depended upon successfully navigating such complex socio-political relationships through the building of successful partnerships and institutional coordination (Johnson and Graber, 2002).

- *Determining the ownership of the dam and surrounding lands upstream and downstream of the project*. The potential ownership of dams spans a gamut of possibilities, from privately owned structures to those owned by local, state, or federal entities. In less common situations, older dams may have been abandoned, and their ownership is unclear or unknown.
- *Assembling historical and technical details about the dam and its structure*. These include obtaining information and technical drawings (i.e., "as-built plans") or photographs showing how the dam was constructed, the history of any modifications or rebuilds, and the materials used in the dam's construction. This key information (albeit often lacking for older structures) is helpful for planning the mechanical removal of the structure, especially for determining equipment needs and methods for removal. Additionally, other infrastructure associated with the project (e.g., roads, bridges, utility lines, water intake structures) or within the influence of the dam removal project area should be identified in the early stages of planning. This information is necessary for determining levels of risk from the dam removal and potential liabilities and mitigation needs.
- *Understanding project scope, including river hydrology and sedimentation*. Determining the amount of sedimentation and the concentration of possible contaminants is vital, as these factors are perhaps the most significant drivers of project cost, complexity, and the strategy for conducting a dam removal (Randle and Bountry, 2017). Such reconnaissance will set the boundaries of the sediment management planning and any mitigation measures required to protect downstream resources. The length and width of the reservoir, coupled with the characteristics of the stored sediments, play a role in predicting how much sediment will ultimately erode from the reservoir during and following dam removal (Major et al., 2017). Hydrological conditions of the river, including the magnitude and seasonal variability of flows and the hydraulic capacity of the river to erode the reservoir sediment are crucially important, as this will determine the rate of scour, deposition, and river channel evolution in the former reservoir area and downstream river channel (Doyle et al., 2002). Providing additional context to the issues of hydrology and sediment, detailed geomorphological assessments upstream and downstream of the dam, including cross-section surveys and longitudinal profiles, can be vital for project planning.
- *Identifying needs for infrastructure and species protection*. Assessing the potential impacts to infrastructure or biological species of special concern within the project area is necessary, as this will influence the planning, permitting and conduct of the dam removal project. Many of the concerns surrounding infrastructure are focused upon how reservoir drawdown and sediment release will impact the function of existing water-related infrastructure. For example, development of reservoir shorelines can follow construction of a dam, creating infrastructure like wells, surface-water intake pipes, and septic systems. Once a reservoir is drained, concerns arise for this infrastructure. In their review of this topic, Tullos et al. (2016) noted that the effects of dam removal on wells were dependent upon whether the water table was hydraulically connected to the reservoir. For many locales, existing databases indicate the potential presence of sensitive aquatic species, including plants, fish, amphibians, invertebrates, and mammals, but additional local-scale surveys for potentially impacted taxa of concern may be necessary. For cases where sensitive species are present, actions may be required to reduce or eliminate potential negative effects. These include scheduling dam removal activities to avoid biologically sensitive times of year, utilizing abatement strategies to minimize noise from construction equipment, and relocating sensitive sessile and mobile animals from the project area into safer habitats.
- *Identifying regulatory statutes and environmental compliance mandates*. This includes obtaining the necessary permits to conduct the dam removal. Requirements vary among jurisdictions and consulting with local experts would be beneficial. In the United States, federal regulations that may apply to a dam removal project might include: (1) the Clean Water Act (Sections 401, 402, and 404) to protect water quality and regulate the discharge of dredged or fill material into navigable waters of the United States (administered by the U.S. Army Corps of Engineers and Environmental Protection Agency); (2) the Endangered Species Act (administered by either the National Marine Fisheries Service or the U.S. Fish and Wildlife Service); (3) the Magnuson-Stevens Act if commercial fish species are present in the project area, and (4) the Federal Power Act, which gives the Federal Energy Regulatory Commission (FERC) the exclusive authority to license non-federal hydropower projects. Some dams are designated as historical or culturally significant sites and may be protected by laws like the National Historic Preservation Act. State and local regulations may also apply.

Case-studies and conducting a dam removal

Once permitting and other logistical preparations are completed, the deconstruction phase of dam removal can proceed following one of three possible pathways—partial dam removal, instantaneous dam removal (also referred to as "sudden") or staged ("phased") dam removal. These pathways differ in the rate and extent of removing the structure from the river (given the needs and constraints of the project, as described above) and determine the time horizon of the project.

A partial dam removal is applied in cases where logistical (e.g., sediment retention) or socio-political (e.g., dam is a historically significant site) factors call for retention of some portion of the dam. For example, the portion of a dam blocking fish passage might be removed while other portions of the dam and related structures are left in place for historical preservation. Three different case-studies highlight the different factors that might lead to a partial dam removal. The first example involves the Kent Dam on the Middle Cuyahoga River in Ohio, where significant water quality degradation was caused by a dam no longer serving its intended purpose. Dam removal was considered necessary to improve the water quality status of the river. Yet, the historically significant dam was one of the oldest arch masonry dams in the U.S. and by creating a picturesque waterfall it was a culturally important feature for the citizenry (Tuckerman and Zawiski, 2007). A compromise was reached where a partial dam removal allowed part of the dam and its waterfall to be retained, while a bypass channel reconnecting the downstream and upstream portions of the river improved water quality.

A second example of a partial removal comes from Banff National Park in Canada. In this case, the town of Banff dug wells, thus negating the 8-m high water-storage dam's primary purpose, even as it remained a liability requiring costly annual maintenance and inspections. A flood washing out the dam's access road led to proposals for dam removal, but due to funding limitations the town managers decided to pursue a partial dam removal where only a portion of the dam was removed, but a bypass channel was engineered with both concrete and natural substrate that allowed fish passage (Sullivan et al., 2019). This was particularly beneficial for bull trout (*Salvelinus confluentus*), a protected migratory species in the province.

The final example of a partial removal comes from Taiwan, where a series of sediment retention check dams were limiting the available migration corridor of the land-locked Formosan salmon (*Oncorhynchus masou formosanus*). The most downstream and largest dam (Number 1 Dam, 16 m) on the Chichiawan River was slated for removal to increase connectivity for the last remaining population of this critically endangered fish species (Chang et al., 2017). Project planning identified that a main road would be impacted by full removal of the dam, but a partial removal allowed the western abutment to remain and protect the road while still restoring fish passage.

Full dam removals are cases where the dam is removed, the stream bed is returned to its original elevation and course, and all portions of the dam that could influence hydrological conditions of the river are removed. A full dam removal can be accomplished in two ways, differentiated mainly by the speed of the removal process and the rate of reservoir drawdown. In an instantaneous dam removal, reservoir draw down occurs in a matter of hours to days. Some of these projects are informally described as "blow and go," where a portion of the dam is first removed, sometimes with explosives, so that rapid and complete draining of the reservoir follows. Such instantaneous dam removal using explosives occurred with the 38-m high Condit Dam, on Washington State's White Salmon River, where a detonation of explosives in a tunnel bored out of the bottom of the dam caused a rapid and complete drawdown of the reservoir, releasing a large volume of sediment downstream. This minimized the duration of high sediment concentration experienced by fish populations downstream of the dam, limiting impact to a single spawning season instead of multiple seasons (as in some phased removals, see below). After the breach, the remains of the dam were mechanically removed in stages over the next 12 months. Note however that for smaller dams a rapid reservoir drawdown is usually achieved with more conventional methods using construction equipment.

A second type of full dam removal is staged dam removal which, by design, is drawn out over months or years. This is a method often used for taller dams where large amounts of sediment are contained within the reservoir, raising environmental or infrastructure concerns for accepting waters downstream. A staged removal allows the pace of reservoir drawdown to be controlled, which is a major determinant of the rate and timing of sediment mobilization. By maintaining the reservoir as the dam is removed in stages, the project managers can retain some level of control over the timing, duration, and amount of sediment released downstream. It also gives time for erosive processes and lateral channel migration to mobilize and redistribute sediment within the reservoir. Factors such as the presence of sensitive species and infrastructure, or a limited capacity of the receiving channel downstream to accept sediment, can initiate the need for a staged dam removal.

A good example of a staged dam removal comes from the Elwha River in Washington, where two dams were removed using two different staged dam removal strategies. The downstream Elwha Dam was a 32-m tall concrete gravity dam. Its staged removal was accomplished by alternating the river's flow through one of two constructed channels, using temporary coffer dams to route water through one channel at a time. The second dry channel was excavated to a lower elevation than the one with water, so that when the flow was switched between channels, the elevation of the reservoir was reduced by an amount equivalent to the difference in elevation between the wet and dry channels. A total of 10 channel switching events were used to remove the dam over an 8-month period. The taller 64-m Glines Canyon Dam was a concrete arch dam with a reservoir that contained about 75% of the 21 million m^3 of stored sediment contained behind both dams (Randle et al., 2015). Gradual removal of this dam was accomplished over a three-year period by notching the dam, at first mechanically with hydraulic hammers and then with explosives. The depth of each notch reduced the water elevation of the reservoir to a set amount, determined by limits of reservoir slope stability and levels of sediment to be released downstream to minimize negative effects to fish and their habitats. This incremental workflow also enabled project managers to control and manage sediment within the former reservoir, allowing the river time to erode, deposit, and redistribute sediment within the former reservoir.

Alternatives to the strategy of river erosion may be required when sediment cannot be released downstream. Removal of sediment, via dredging or mechanical removal, can minimize the downstream impacts or mitigate issues with contaminated sediments. However, this usually dramatically increases project cost because in addition to sediment dredging, project planners must find a location to dispose of the material and a method for transport. Mechanical sediment removal strategies were required to remove contaminated sediment stored behind the Milltown Dam on the Clark Fork River in Montana, a U.S. Superfund site, before dam removal could proceed (Brooks, 2015). In the case of the 32-m tall San Clemente Dam on the Carmel River in California, the aging dam was a safety risk, with a reservoir filled to 95% of its capacity with sediment. Dam removal was necessary, but the stored sediments posed a sediment management dilemma because downstream development, infrastructure, and limited channel capacity imposed unacceptable risks from a large sediment release. The creative solution involved leaving the reservoir sediments in place and constructing a bypass channel to reroute the river around the former reservoir reach. This approach allowed for sediment transport from river reaches upstream of the reservoir while sequestering reservoir sediment that may have created downstream issues for roads, houses, and other infrastructure (Harrison et al., 2018).

Physical and ecological outcomes of dam removal

As the number of dismantled dams has grown, the scientific community has increasingly studied the outcomes of dam removal (Table 1), including whether the environmental changes caused by dams can be reversed. Nearly 10% of the dams removed in the U.S. have been scientifically evaluated, through assessing changes to a suite of physical, water quality, and biological variables (Bellmore et al., 2017). Although many studies collect before and after dam removal data, some only collect post-removal data. Most of these studies, no matter their experimental design, have lasted for relatively short durations, and they have evaluated outcomes for a few years around the initiation of dam removal. Long-term evaluations are rare, as most studies have focused upon the time period where rapid physical changes take place in the upstream and downstream vicinity of the dam. As the number of case studies evaluating river outcomes has increased, synthesis of the physical and ecological responses has emerged alongside tools like numerical hydrodynamic and sediment modeling to allow predictions about how a river's condition will change over time following dam removal.

When conceptualizing responses to dam removal, it is helpful to segregate—in both space and time—the processes that affect the structure and function of the river ecosystem (Hart et al., 2002; Bellmore et al., 2019). Spatially, the most straight forward case involves a single dam that effectively creates three distinct zones that behave differently following dam removal. These zones are the river segment upstream of the reservoir, the reservoir section from the river inlet to the dam, and the reach downstream of the dam. Within each of these spatial domains, different sets of physical and biological factors and processes drive change, which collectively impact the shape of the ecological response trajectory following dam removal. This trajectory is also shaped by differences in temporal dynamics, as both short-term and long-term responses are dependent upon a suite of factors, including the size of the dams, amount of sediment, and ecological context (Fig. 1).

Changes to the upstream spatial domain are driven by restoration of connectivity following dam removal. The ability of organisms to travel past the dam location into upstream waters can increase species richness and life history diversity. This is especially true for migratory fish populations, which can be lost from upstream reaches following the placement of a dam unless significant mitigation (e.g., fish ladders for adults to pass the dam) is taken. Once passage is returned following dam removal, migratory fish from reaches downstream of the dam can swim up past the former dam, often rapidly repopulating upstream reaches, which over time can increase upstream species richness (Wippelhauser, 2021). Given the right conditions, in terms of environmental suitability and genetic memory, life-history diversity can re-emerge in upstream populations. This was seen when summer run Steelhead (*O. mykiss*) that were rare for decades prior to dam removal returned to the Elwha River following dam removal (Fraik et al., 2021). The return of fish to upstream reaches can also drive changes indirectly, as seen when Pacific Salmon (*Oncorhynchus* spp.) provide marine-derived nutrients to their freshwater spawning grounds. These marine-derived nutrients can be seen in both aquatic and terrestrial food webs (Tonra et al., 2015). Salmon can also transport freshwater mussel larvae to upstream areas and significantly alter the stream benthos through bioturbation disturbance from their spawning activity. A potential downside to restored connectivity occurs in cases where significant risk exists from invasive species migrating into upstream waters. This has deterred some potential dam removals, such as in streams draining into the Great Lakes in the U.S., where significant resources are directed toward eliminating Sea Lamprey (*Petromyzon marinus*), which spawn in rivers and as adults parasitize commercially important fish species in the lakes (Jensen and Jones, 2018).

The most dramatic changes to physical, biological, and ecological factors occur in the former reservoir reach. This spatial domain experiences a wholesale change from a lake-like (lentic) ecosystem to a river ecosystem (lotic). Once a dam is removed, the reservoir drains, stored sediment is transported downstream, and a new channel emerges within the former lakebed. Initially, the re-emergent river channel (or braided channels in wide reservoirs) is unstable. As the sediment interacts with hydrological flows, a stable channel will eventually reform. The pace of this physical transformation varies, depending on the size of the impoundment, stored sediment volume, and hydrological conditions. As the river channel reforms, the aquatic communities adapted to pelagic conditions and lentic fish species are replaced by benthic production and lotic fish species. For some systems, such species turnover can be considerable, but the absolute number of species may not change, and some generalist species can be found in the same area before and after dam removal (Bellmore et al., 2019). A driving force that determines the reassembly of species following dam removal is the "ecological memory" of the system, defined here as the current and future influence of the cumulative past impacts to

Table 1 Case studies with key citations illustrating some of the concepts of dam removal discussed in this chapter.

Name of site	*Country*	*Main topic/concept*	*Key citations*
Elwha River (Elwha + Glines Canyon dams)	Washington, United States	Large-staged dam removal Multi-dam project Reservoir sedimentation Fish passage	Ritchie et al. (2018) Duda et al. (2020) East et al. (2015)
Sandy River (Marmot Dam)	Oregon, United States	Large-instantaneous dam removal Sediment transport	Major et al. (2012) Cui et al. (2014)
Clark Fork River (Milltown Dam)	Montana, United States	Contaminated sediment Downstream geomorphology	Woelfle-Erskine et al. (2012) Evans and Wilcox (2013) Brooks (2015)
Kaoshan Steam (Kaoshan I-IV)	Shei-Pa N.P., Taiwan	Multi-dam project Fish passage	Battle et al. (2020) Chang et al. (2017)

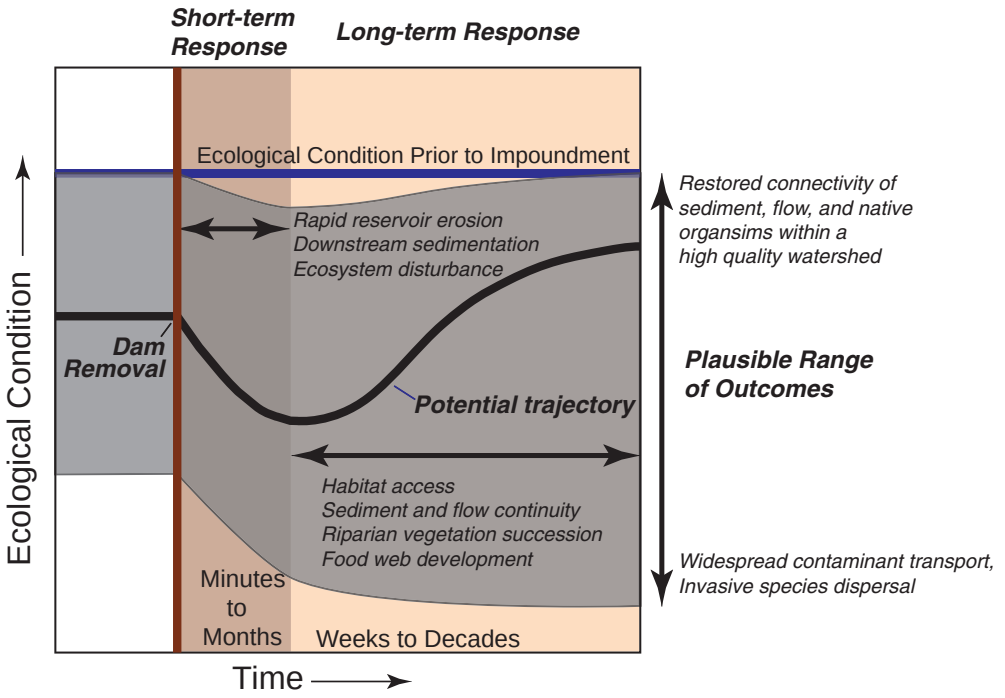

Fig. 1 Conceptual model of the ecological trajectory of a river following dam removal. Considerable variability exists in the condition of the river prior to removal (gray area to the left of the dam removal line). Following the initiation of dam removal, a short-term disturbance effect is caused by the dam removal, but conditions improve in the long-term as natural flow and sediment regimes are restored and habitat access in the former reservoir and upstream areas is resumed. A range of plausible outcomes (gray area to the right of the dam removal line) exists due to a suite of possible factors influencing the river condition outcome, such as existing watershed condition, size of the dam and sediment released, and strategy of dam removal From Foley MM, Bellmore JR, O'Connor JE, Duda JJ, East AE, Grant GE, Anderson CW, Bountry JA, Collins MJ, Connolly PJ and Craig LS (2017) Dam removal: Listening in. *Water Resources Research* 53: 5229–5246. Used with permission.

the ecosystem. In cases where upstream, downstream, and tributary reaches retain a high level of species and life history forms available for repopulating the reservoir reach, the system will more closely approach the pre-dam condition. Conversely, if these species and life history pools are diminished, due to the age of the dam or via other disturbances in the watershed, the river ecosystem might not approach the state that existed prior to dam placement (see Fig. 1). Natural revegetation within riparian and upland zones, sometimes assisted by seeding and planting, further stabilizes former reservoir surfaces, over time reducing erosion. With the return of riparian and upland vegetation, wildlife species also return and can further assist in normalizing habitat structure and function, as well as re-establishing trophic ecological interactions within the former reservoir reach.

Downstream of the dam, changes to the river are driven by fluxes of water, sediment, organic material, and nutrients caused by the dam removal. As the reservoir base level declines, either rapidly or in stages, fine sediments from the reservoir are eroded and transported downstream, even with modest river flows. Much depends on the amount of sediment stored in the reservoir, the characteristics of the sediment (e.g., bulk density, grain size), frequency and magnitude of floods, and the characteristics of downstream river reaches that are receiving and transporting the sediment (Major et al., 2017). Given the wide range of sediment volumes and dam conditions previously observed, a common theme among dam removal projects is that even large changes in geomorphology are relatively short-lived. A river will process the stored sediment, sometimes in amounts that are multiples of the river's naturally occurring annual sediment load, by transporting it downstream. Temporary changes in elevation, channel morphology, and grain size of the stream bed will occur. Over time, as supply from the reservoir diminishes to background levels, an equilibrium condition will emerge in the downstream reach to the point that the river channel approaches the pre-dam condition. From a physical standpoint, most rivers are resilient to the dam removal disturbance and largely recover their form and function soon after dam removal (Magilligan et al., 2021).

The downstream response of individual species, biological assemblages, and their trophic structure are also impacted by perturbations brought about by dam removal (Lake et al., 2007). The fluxes of water and sediment can have both direct and indirect effects on aquatic and riparian organisms, as well as significantly altering or entirely removing their habitats, at least for a time after the initial sediment pulse. Again, context—in terms of the size of the dam, amount of sediment released, dam removal strategy, and how altered the downstream ecosystem is from its pre-dam condition—matters (Foley et al., 2017; Bellmore et al., 2019). Burial of the benthos by sediment can directly impact organisms, particularly sessile organisms that cannot disperse to other less impacted areas. It is typical to see a rapid change in the species assemblage and the density of aquatic macroinvertebrates following dam removal (Carlson et al., 2018), with species tolerant of finer sediments and scour favored over sensitive taxa intolerant of such conditions. Also, sediment release usually increases the turbidity of the river, which reduces light availability and can affect the taxonomic composition of benthic primary producers and their capacity for production. Reductions in the densities of

benthic algae and invertebrate communities have been widely reported and are usually most significant in the reaches closer to the removed dam. These changes are often temporary, with recovery occurring once the dam removal effects diminish. Fish have been shown to be less directly impacted by sediment release from dam removal than organisms of the benthos, although mortality and damage to gills from abrasion are possible. Unlike sessile organisms or those with narrow habitat requirements, many fish species can avoid or move to refuges to escape the highest impacts associated with dam removal. Yet, indirect effects can affect fish and their habitats. A reduced food supply from reductions in benthic production, a diminished capacity to visually forage in high turbidity conditions, and diminished suitability of spawning habitat can all lead to decreased fitness of individual fish and reductions in population size during and following dam removal as the river processes the physical changes (Stanley and Doyle, 2003).

Despite the short-term disturbance caused by dam removal, a growing body of research suggests that rivers, given the opportunity, can recover substantially from having been dammed. However, the structure and function of the ecosystem may not be the same as what existed prior to dam emplacement. Changes in ecological communities caused by dams, such as extirpation of native species and harboring of invasive species, can limit the capacity for the ecosystem to reassemble into the pre-dam condition following dam removal (see Fig. 1). Moreover, land use, the presence of other dams, sediment contamination, climate change, and numerous other factors may constrain both physical and ecological trajectories. The ability to go back to a pre-dammed state will likely depend on how long the dam existed and the magnitude of its many-faceted effects on the ecosystem. Even if all elements of the ecosystem still exist, it is unlikely they will reassemble in the exact fashion that existed previously.

Future outlook of dam removal

It is likely that the number of dam removals and communities removing dams will increase into the future, for both practical and aspirational reasons. Given the immense number of dams and their age, there will be a number of candidates for removal, particularly dams that have aged beyond repair and outlived their usefulness. In places where the practice is well established, these dams (especially smaller dams) will continue to come down, probably with greater efficiency and less controversy. In regions or countries with few dam removals, translating the knowledge and experience gained from past projects could lessen the learning curve and institutional barriers to applying the practice where applicable. Coupling predictions about expected outcomes with a wide range of experience in conducting dam removal should see dam removal emerge as an accepted practice in areas where it is currently rare, especially when applied to dams that are beyond repair or pose a significant risk to life and property.

The opportunity to build on past successes and intensify river restoration efforts is gaining momentum, in terms of scientific expertise, practical experience, and public policy. This has led to a reassessment of policies and practices involved with the management of rivers. As an example, a recent joint statement from a working group representing the U.S. hydropower industry and the environmental and river restoration community recognized the need to remove dams that, "no longer provide benefits to society, have safety issues that cannot be cost-effectively mitigated, or have adverse environmental impacts that cannot be effectively addressed" (U.S. Hydropower: Climate Solution and Conservation Challenge 2020). The statement also acknowledges that hydropower is an important component of renewable energy strategies and that rehabilitating and retrofitting existing dams will also be important tools for addressing the myriad of challenges facing the wise use and conservation of the world's rivers.

Knowledge gaps

Considerable progress has been made in the field of dam removal over the last three decades. The action of physically removing a dam from particular river is a relatively straight forward construction-engineering process. Yet, additional knowledge and advances in key areas are still needed, largely in decision making and predicting the long-term outcomes of individual dam removal projects.

- Decision making
  - o Prioritization and optimization tools to aid decision making and selecting dam removal projects.
  - o Numerical modeling, in particular for tracking the fate of stored sediment and ecological outcomes.
  - o Tools for estimating the cost of dam removal projects.
- Outcomes of dam removal
  - o Assessing cumulative impacts of removing multiple dams from a single watershed.
  - o Long-term outcomes of river response and restoration
  - o Quantifying socio-economic effects, such as long-term outcomes to property values, economic trajectories of communities near dam removal projects (e.g., recreation, commercial fishing), cultural resurgence of indigenous peoples, communities, and river economies, as well as other societal benefits.

Conclusion/Synthesis

Dam removal is an important tool for river restoration and addressing aging infrastructure. It is an ongoing activity that will continue as a large number of aging dams that are no longer serving their original purposes, have become safety liabilities, or represent potential for significant restoration action are taken down. The increase in the number of dams removed has led to a

greater understanding about the outcomes to the river and its ecosystem. Rivers are resilient to the changes and disturbance that accompany the removal of a dam, with many of the changes occurring rapidly and representing an improvement in water quality, hydrological flows, and migratory movement of aquatic animals. Yet, some of the outcomes of dam removal may play out over longer time periods, depending on such factors as the life-history of key species or implementation of other complementary river restoration actions. In the future, as societies are faced with changing hydrologic and land-use drivers that influence water use and conservation, dam removal will be an important option for maintaining or enhancing the values and ecosystem services of the world's rivers.

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High Latitude Rivers: Ecosystems Shaped by Environmental Extremes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Anadromous Fish that migrate from salt water to freshwater to spawn including various salmonid species such as the Arctic charr (*Salvelinus alpinus*).
Arctic Council An international forum comprised of the Indigenous people and the eight countries of the Arctic that interact and coordinate on joint aims such as sustainable development and environmental protection of the Arctic.
Atmospheric transport The transfer of pollutants via the atmosphere such that these materials are dispersed and deposited large distances from their source.
Eurythermic Refers to organisms that live in a wide range of temperatures.
Freeze-up The process of a body of water freezing at the surface in winter.
Global distillation A process whereby volatile contaminants (e.g., persistent organic pollutants) evaporate and are transported from warmer to colder areas where the vapors condense and are deposited as precipitation (i.e., the "grasshopper effect").
Ice breakup The collapse of winter ice on rivers that can cause extreme flood events and often is an annual ecosystem reset event due to streambed and bank erosion.
Permafrost The thick layer of soil in polar regions that remains frozen throughout the year.
Stenothermic Refers to organisms that are only capable of living in a narrow temperature range.
Thaw slump Landslides that develop on hillslopes in areas of ice-rich permafrost that can deliver large volumes of sediments and organic debris downslope to stream channels.
Thermokarst Characteristic land-surface configuration in polar regions caused by subsiding ground due to thawing of ice-rich permafrost.
Tundra Biome where tree growth is limited by cold temperatures and short growing season with a characteristic vegetation of dwarf shrubs, sedges, mosses, and lichens.

Introduction

This chapter provides a broad overview of food web structure and composition in high latitude streams of the circumpolar Arctic and describes how the biota are affected by major environmental variables and the pressure of climate change. This region includes 12 major river basins that flow into the Arctic Ocean, and it can be subdivided into the Sub-, Low, and High Arctic. The Sub-Arctic is a boreal forest zone with discontinuous permafrost located immediately south of the treeline, the High Arctic is the most northerly region of the Arctic, characterized by barren tundra landscapes with continuous permafrost, and the Low Arctic is a transition zone between the forested region to the south and treeless polar region to the north (Fig. 1). Key environmental variables affecting Arctic river systems include the hydrological and ice regimes of cold-region environments, cold thermal conditions, and water quality

 https://doi.org/10.1016/B978-0-12-819166-8.00128-6

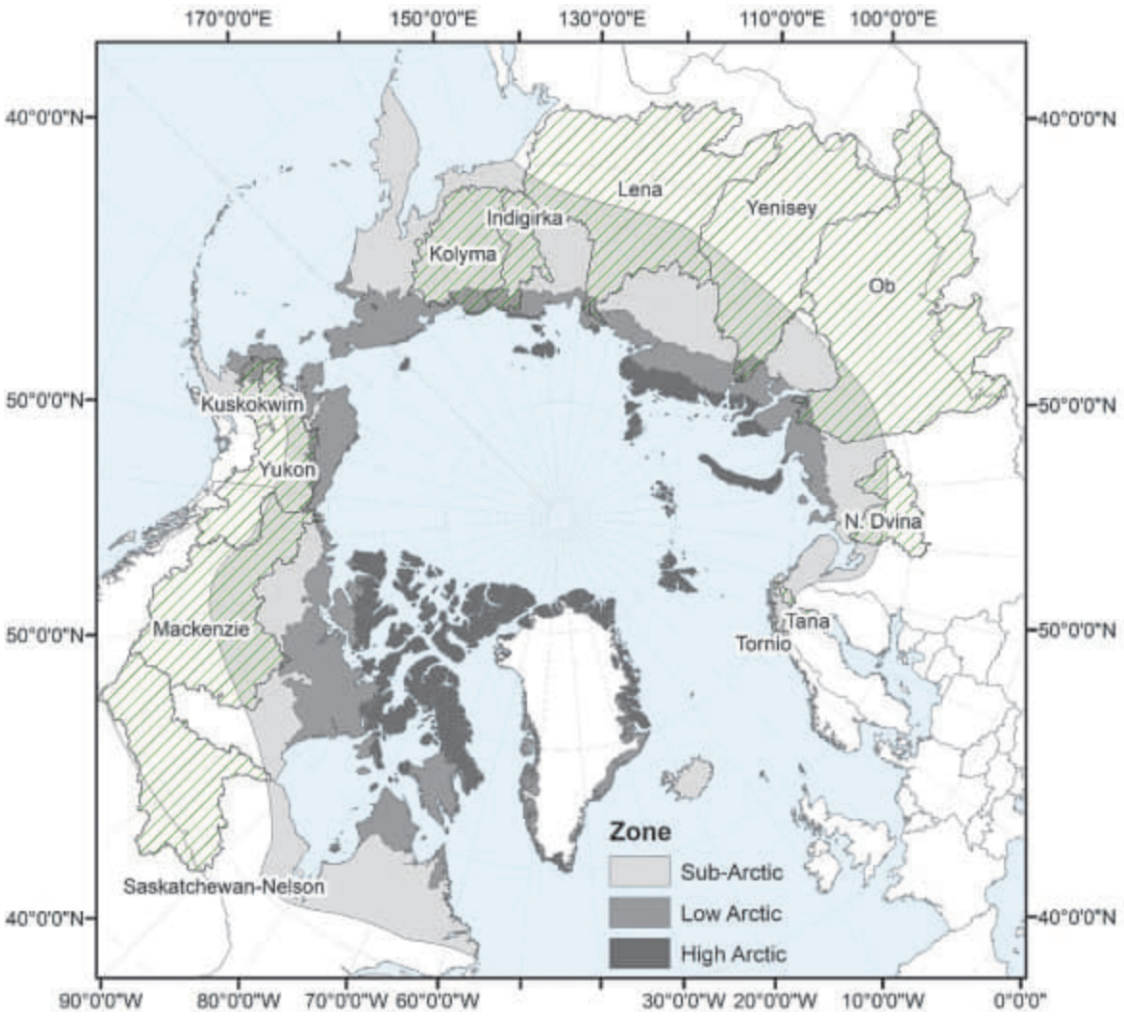

Fig. 1 Map of circumpolar Arctic showing Sub-Arctic, Low Arctic, and High Arctic regions as well the catchment area of 12 major river basins flowing to the Arctic Ocean. Basin watershed boundaries are indicated by dashed line, while area within the basins are shown by diagonal crosshatched fill. Basin boundaries after GRDC (2020). Arctic boundary layers from https://nam11.safelinks.protection.outlook.com/?url=http%3A%2F%2Fcaff.is%2F&data=04%7C01%7Cmrw-inw2%40elsevier.com%7C9d006d04aa7f4c27e91708d9b1052fef%7C9274ee3f94254109a27f9fb15c10675d%7C0%7C0%7C637735458104205575%7CUnknown%7CTWFpbGZsb3d8eyJWIjoiMC4wLjAwMDAiLCJQIjoiV2luMzIiLCJBTiI6Ik1haWwiLCJXVCI6Mn0%3D%7C3000&sdata=yRSXlPS0GNnQ6H25RMT7FYvtxYjh%2FlDZw6qHp6T7OOg%3D&reserved=0.

variables such as nutrients and sediments (Culp et al., 2021a). Our understanding of such stream ecosystems is nascent as much of the Arctic region is remote, sparsely populated, and relatively unstudied, as also noted by Huryn (2021). Given the breadth of the topic, this overview aims to provide an advanced introduction to the current knowledge of these systems.

The overriding environmental variable that establishes the abiotic template for biota in these rivers is related to water discharge, with the hydrological regimes of high latitudes varying significantly from those of temperate regions. This difference is related to the sources and pathways of snow and ice from a landscape often underlain by permafrost that limits infiltration below the land surface (Peters et al., 2021). Distinct cold-region hydrographs include (1) proglacial conditions with seasonally dominant spring snowmelt followed by runoff from glaciers and occasional rainstorms, and (2) nival hydrographs in regions of permafrost where spring snowmelt is the only major annual flow event (Peters et al., 2021). Winter flows of such high latitude rivers progressively decline from Sub- to High Arctic regions as discontinuous permafrost is replaced by continuous permafrost. Additional hydrologic regimes include (3) spring-fed environments that have more consistent flow throughout the year (Huryn, 2021), and (4) wetland conditions where spring snowmelt is followed by the summer and fall period where flow inputs from rainfall are greatly attenuated by the water-retaining capacity of muskeg.

A second critical driver of biotic pattern in high latitude rivers relates to the extreme cold temperatures and ice regimes of these ecosystems. Several investigations demonstrate that diversity of biota declines with latitude (e.g., Culp et al., 2019), with Lento et al. (2021) showing strong negative associations of macroinvertebrate diversity with decreasing temperature at higher latitudes. Across the circumpolar Arctic, macroinvertebrate composition of high latitude rivers is predominated by cold-tolerant macroinvertebrate taxa such as chironomids and oligochaetes. Similarly, Castella et al. (2001) found sharp decreases in species richness of glacial streams with increasing latitude.

Such extreme, cold thermal regimes lead to river ice playing a major role in affecting the physical and chemical environment of high latitude rivers. For example, headwater streams (<1–2 m in width) can be completely frozen in winter, while deeper channels downstream generally contain unfrozen water capped by floating ice (Huryn, 2021). Ice-covered rivers lack a direct exchange with the atmosphere and can experience substantial decrease in dissolved oxygen over the winter. Where streams freeze completely to the bottom, macroinvertebrate communities may be dominated by taxa with freeze tolerance or freeze avoidance traits, whereas fish typically employ seasonal migration to avoid freezing during these periods (Huryn, 2021). The annual breakup of river ice can cause streambed scour, extreme suspended sediment loads, and a rapid rise in water temperature, which together create an ecosystem reset event unique to these environments (Prowse and Culp, 2003). The resultant input of organic material and sediments, and post-breakup deposition of these materials, can reduce habitat quality and impair biological production. River ice breakup also adds nutrients (including phosphorus and nitrogen particulates) from the shoreline and floodplain. One study discovered that up to 30% of the annual phosphorus input to a small river in Alaska occurred during ice breakup (Whalen and Cornwell, 1985). Notably, ice breakup can also have important effects on the input and transport of contaminants, such as metals and organic compounds (Beltaos, 2018; Culp et al., 2021b).

As global warming progresses, the pressure of climate change will affect virtually all key environmental variables associated with river ecosystems. Climate change assessments indicate global warming is amplified at high latitudes (Box et al., 2019) and is occurring at twice the global average rate (Walsh et al., 2011). This climate shift is leading to permafrost thaw (Spence et al., 2020) and glacial retreat, which together modify downstream river environments, and to higher inter-annual variability in extreme precipitation events that modify hydrological regimes and exacerbate the growth of permafrost thaw slumps (Kokelj et al., 2015). Climate models predict that the Arctic will experience a reduction in snowfall and increase in precipitation falling as rain, including increased precipitation in the winter, which is expected to have strong effects on the hydrology of Arctic rivers (Box et al., 2019). Warming also affects the release of key nutrients from the terrestrial landscape such as dissolved organic carbon (DOC) and total phosphorus (Levenstein et al., 2018; Huser et al., 2020). Of importance is the increased occurrence of permafrost thaw slumps that augments sediment and nutrient input to high latitude rivers (Kokelj et al., 2015; O'Donnell et al., 2019; Huser et al., 2020), with sediment inputs in particular leading to shifts in the composition of river biota (Chin et al., 2016). Heino et al. (2020) conclude that most recent environmental changes in high latitude freshwater ecosystems are the result of human activities associated with climate warming, long-range transport of pollutants, and local or regional land use change. As these high latitude ecosystems continue to warm, it is expected that southern species will expand their ranges at the expense of cold-adapted species (Culp et al., 2012), resulting in changes to the biodiversity of these systems that will affect the ecosystem services on which Indigenous Peoples of the Arctic rely (Heino et al., 2020; Culp et al., 2021a).

Ecology of high latitude Rivers

Overview of abiotic and biotic structure and function

The physical-chemical environment of high latitude rivers forms an abiotic template for biotic activity that is vastly different than that of rivers in temperate regions. Freeze-up occurs in early fall, causing a reduction of light entering the water column and of oxygen exchange with the atmosphere (Prowse and Culp, 2003; Wrona et al., 2013). Cold thermal conditions dominate, with many smaller rivers of northern latitudes freezing completely to the streambed during winter (Peters et al., 2021). In contrast, larger rivers flowing north from temperate headwaters (e.g., Mackenzie River in Canada, Ob in Russia) can have significant discharge year-round (Peters et al., 2021), although they experience floating surface ice in winter. Winter flow can also remain continuous in springs, habitats that can be an important refuge for biota during winter (Wrona et al., 2013). Depending upon the latitude, these conditions combine with cold temperatures from fall through spring to either greatly reduce or halt biological activity during winter. Following the harsh winter, rapid warming produces the spring freshet that causes dynamic river ice breakup, which creates a short, but intense, physical disturbance that sorts the river substrate and affects river chemistry (Fig. 2). Such ice movement can cause substantial bank erosion and sculpting of the riparian zone. In addition, the concentrations of dissolved inorganic nutrients (including C, N and P) are generally extremely low due to low mineralization rates that result from the cold, Arctic temperature regime and because permafrost limits groundwater development (Huryn, 2021). This unique cold region regime produces a suite of environmental conditions that shape the diversity and biological traits of biota across all trophic levels.

Algae and bryophytes form an important basal component of food webs in Arctic rivers. Production and biomass of primary producers in these systems is typically low due to oligotrophic conditions (Peterson et al., 1985; Deegan et al., 1997). While animal diversity at higher trophic levels shows strong latitudinal declines (Culp et al., 2019; Laske et al., 2019), species richness of riverine benthic algae of the circumpolar Arctic is largely associated with nutrient concentrations and geology, with only weak negative associations with latitude (Lento et al., 2020). At the circumpolar scale, Kahlert et al. (2020) found that diatom community composition was lowest at the highest latitudes, but it was not dominated by endemic taxa. Rather, the strongest community shifts across the Arctic were associated with changes in substrate, velocity, alkalinity, pH, and the concentrations of several water quality variables, including nutrients, dissolved organic carbon and calcium. Bryophyte production in high latitude rivers also is limited by low nutrient concentrations; long-term nutrient enrichment experiments show bryophytes become the dominant component of autotrophic biomass in fertilized reaches of the Kuparuk River, Alaska (Bowden et al., 1994). However, macrophyte communities shift towards a greater dominance of bryophytes at the highest latitudes, which suggests that they are better adapted to the harsh

Fig. 2 Bank-to-bank ice rubble on the Mackenzie River, Northwest Territories near the mouth of the Arctic Red River, Northwest Territories, Canada. Note the large ice blocks causing erosion of the bank. River flow is from left to right. Photo credit: S. Beltaos, Environment and Climate Change Canada, Burlington, ON.

environmental conditions than are vascular plants (Lento et al., 2019). Both the abundance and community structure of benthic macroinvertebrate communities can be profoundly affected by bryophyte biomass (Stream Bryophyte Group, 1999).

A second important basal resource for food webs of cold region rivers includes energy sources flowing from microbial decomposition of terrestrial and aquatic carbon sources. For example, Peterson et al. (1985) demonstrated that in a tundra stream, heterotrophic processes dominated system metabolism with dissolved and particulate material from tundra soils being the predominant organic matter fueling the food web. Autotrophic carbon from aquatic primary producers also contributed carbon to decomposition pathways, with autotrophy becoming the dominant pathway when this stream was experimentally fertilized with phosphorus. Both rate and variability of decomposition of a standardized carbon source decline with latitude indicating that temperature limits this process at high latitudes. Recent studies show the following: soil organic carbon represents an important fraction of the organic carbon in rivers (Cole et al., 2007); biofilm communities can play a crucial role in the breakdown of this material; old carbon (5255 years before present to modern) from permafrost is incorporated into benthic biofilms; and, this carbon can be an important energy source for Arctic food webs (O'Donnell et al., 2019). Finally, Sub-Arctic rivers such as the Mackenzie River, Canada, can exhibit highly diverse microbial communities (Galand et al., 2006), the importance of which is only recently being revealed through the application of molecular techniques (Cavaco et al., 2019).

Benthic macroinvertebrate communities are a critical component of energy flow in high latitude food webs and are supported by the primary producer and decomposer trophic levels. The diversity of such macroinvertebrate communities decreases with latitude such that High Arctic rivers are dominated by the most cold-tolerant groups of dipterans (e.g., Chironomidae, Diamesinae, Tipulidae) and oligochaetes (Culp et al., 2019; Lento et al., 2021). These taxa are largely consumers of algal and detrital material associated with the streambed. In the Low Arctic, riverine invertebrate communities include many of the groups that dominate temperate streams including mayflies, caddisflies, and stoneflies (Lento et al., 2013, 2021). This northern decline in species richness is similar to the physiological thresholds observed along thermal gradients in glacial streams (Milner et al., 2001). Moreover, Culp et al. (2019) concluded that diversity declines with latitude were the result of the increased dominance of cold-tolerant taxa rather than being explained by the energy-richness hypothesis that links food limitation with latitudinal declines in richness (see Currie et al., 2004). Brittain et al. (2020) recently showed that the environmental drivers of macroinvertebrate communities of high latitude rivers in Fennoscandia are mainly related to climate variables including temperature and precipitation. However, both local and landscape scale environmental variables do play an important role in affecting alpha and beta diversity as also shown for Sub- and Low Arctic rivers in Northern Labrador, Canada (Lento et al., 2013). It is notable that these latitudinal trends in diversity and taxonomic composition of macroinvertebrates are mirrored in the harsh environment of glacial rivers, where cold thermal regimes, and low nutrient conditions dominate along a gradient from downstream to glacier snout (Milner et al., 2001).

High latitude rivers present harsh environmental conditions for fish survival (Wrona et al., 2013). Thus, the diversity of fish species that complete their entire life history in riverine environments of cold regions is low relative to lakes of this region (Wrona et al., 2013). For example, many species utilize small rivers for spawning but remain in lentic habitats for much of their life cycle. Such fish species utilize benthic macroinvertebrates for food. Riverine fish, such as the Arctic grayling (*Thymallus arcticus)*, also have the potential to modify food web structure through the top-down, cascading effects of predation on the benthos (Golden and Deegan, 1998). Although fish diversity is unrelated to latitude in the Sub- and Low Arctic regions (Lento et al., 2020), diversity decreases with latitude above 70°N as temperature regimes decrease. Moreover, richness of fish species is limited by historic or contemporary barriers to colonization (Laske et al., 2019). These discontinuities are caused by the ongoing species recolonization following Pleistocene glacial events and spatial gaps related to island geography (Wrona et al., 2013; Laske et al., 2019). Species

diversity in rivers of the High Arctic is often limited to landlocked Arctic char (*Salvelinus alpinus*), nine spine stickleback (*Pungitius pungitius*), as well as anadromous populations that can colonize islands via movement through the brackish water of coastal pathways (Laske et al., 2019).

Fish species in Arctic rivers, including Arctic char, inconnu (*Stenodus leucichthys*), Arctic grayling, Arctic cisco (*Coregonus autumnalis*), northern pike (*Esox Lucius*), and lake whitefish (*Coregonus clupeaformis*) are important food sources for Indigenous Peoples (Knopp et al., 2020). Indeed, research on Indigenous Knowledge indicates that various species of whitefish are a valuable food resource for the people of the Arctic Red River, Northwest Territories, Canada. Thus, although diversity and production of high latitude rivers is low relative to lake habitats, these rivers provide critical habitat for fish life cycle completion and production, and often are valued cultural locations.

Effects of climate change on biodiversity

Climate change has caused substantial alteration to Arctic freshwaters, with these shifts often occurring relatively rapidly and having long term ecological consequences (Heino et al., 2020). Increased temperatures and changes to the timing and magnitude of precipitation cause glacial retreat and hydrological shifts, and lead to permafrost thaw that increases sediment and nutrient levels (Fig. 3). These ecosystem shifts modify the biota of high latitude river systems through changes in the range distribution of biota and alterations in community structure and function.

Climate warming impacts

Cold temperatures are a defining feature of the Arctic and have been shown to limit diversity of freshwater organisms (Lento et al., 2019). For example, macroinvertebrate richness decreases in northern latitudes (Lento et al., 2021) and the lowest observed abundance of diatoms occurs at high latitudes (Kahlert et al., 2020). Fish species richness also follows this trend of low diversity at the highest latitudes, with species often limited to anadromous, cold stenotherms (Laske et al., 2019). Thus, climate-related water temperature increases are likely to cause directed changes in biotic composition of Arctic freshwaters as the physiological tolerances of stenothermic species are exceeded and eurythermic species adapted to warmer temperatures extend their range northward (Vincent et al., 2011; Culp et al., 2012).

An example of the mechanism that may lead to such biotic shifts with climate warming is related to how metabolic rates is affected by temperature (Lento et al., 2021). For fish and invertebrates, this relationship can modify ecological interactions such as

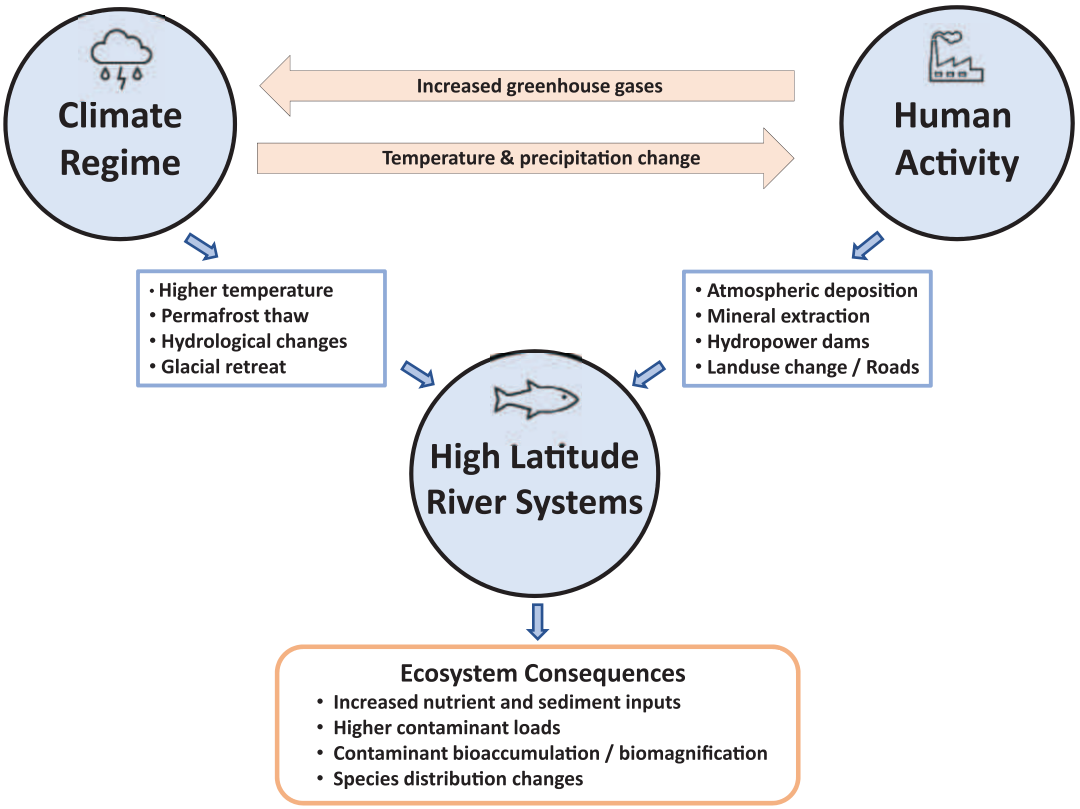

Fig. 3 Conceptual diagram showing the synergistic interactions between the pressures of climate change and human activity. These interactions result in modification of key environmental drivers that impact the physical and chemical environment of high latitude rivers and, ultimately, affect biological diversity.

competition and predation if body size changes with thermal regime, ultimately leading to shifts in species composition (Lento et al., 2021). As range expansion of southern species occurs, the loss of cold stenotherms that prefer temperatures $\leq$20 °C and have low physiological tolerances for higher temperatures may be coupled with increasing abundance of southern eurythermic species (Vincent et al., 2011). For example, model predictions for stream invertebrates suggest that species richness will rise at higher latitudes as warming progresses. Moreover, fish species such as Arctic char will likely be negatively affected by increasing water temperature, as well as by negative interactions with southern species that expand their range northward (Wrona et al., 2013). For example, analysis of long-term catch statistics from Iceland and Norway indicated a decrease in the relative proportions of Arctic char and concurrent increase in the relative proportion of brown trout (*Salmo trutta*) that was associated with increasing temperatures (Svenning et al., 2021). While there will be a net increase in species richness in Arctic areas, this change will cause the irreversible loss of unique Arctic biodiversity as 'climate change winners' replace 'climate change losers' (Heino et al., 2020).

Permafrost thaw impacts

One of the most important impacts of climate warming on high latitude rivers will result from permafrost thaw and the resultant mobilization of dissolved organic carbon (DOC), phosphorus, nitrogen, and major ions (Kokelj et al., 2015). This trend of warming is projected to continue (Wrona et al., 2013; Peters et al., 2021); thus thawing of thermokarst soils is anticipated to continue over all polar regions, impacting freshwater systems of the circumpolar Arctic (Spence et al., 2020). In low relief topography, or at a distance from rivers, the dominant effect of this thaw process will be from the release of large amounts of nutrients (e.g., DOC, nitrogen), ecosystem components that often are in short supply and that limit biological production. For example, Bowden et al. (2008) found that nutrient effects were confined spatially in some headwater streams, with biological uptake hypothesized as an important factor in restricting downstream export of nutrients. It is notable that the nutrient concentrations from thermokarst features were similar to those observed when experimental fertilization of an Alaskan stream increased benthic algal and macroinvertebrate production (Slavik et al., 2004).

In contrast, thawing of thermokarst soils in regions of steep topography or high ground ice content can lead to slope instability along stream valleys and significant input of terrestrial materials, with mud slurries flowing downslope into stream systems (Kokelj et al., 2015; Levenstein et al., 2020). A dramatic example of such slope failure is the case of retrogressive thaw slumps where large amounts of sediments, nutrients, soil organic matter (Chin et al., 2016), as well as contaminants (St. Pierre et al., 2018), flow into rivers and drastically alter these environments (Fig. 4). This phenomenon is predicted to increase in frequency and magnitude with increasing precipitation in the Arctic (Kokelj et al., 2015). This physical disturbance causes significant declines in benthic macroinvertebrate abundance (Chin et al., 2016) and periphyton biomass (Levenstein et al., 2018). Although the origin of thaw slumps is localized, the impact on the aquatic community can be observed at considerable downstream distances. For example, Levenstein et al. (2020) demonstrated that the sedimentation events associated with such slumps increased the relative proportion of

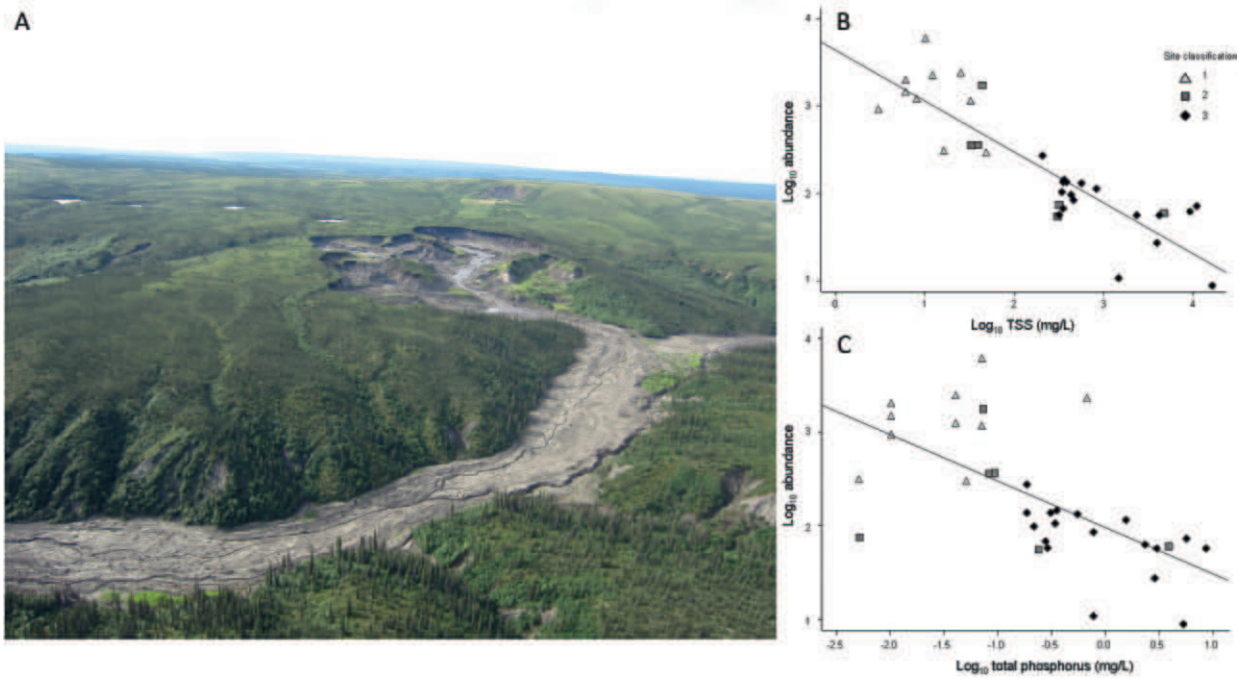

Fig. 4 Retrogressive thaw slumps can introduce large amounts of sediments, nutrients and soil organic matter to high latitude rivers (Chin et al., 2016). (A) Mega slump in the Peel Plateau region of the Northwest Territories with debris flow from the slump filling the river channel. Panels to the right show abundance of invertebrates in undisturbed (class 1), minimally disturbed (class 2) and heavily disturbed (class 3) streams in the Peel Plateau, plotted as a function of (B) total suspended solids (regression $p < 0.001$ and $r^2 = 0.76$) and (C) total phosphorus (regression $p < 0.001$ and $r^2 = 0.41$). Photo credit: J. Lento.

macroinvertebrates entering the drift even after prolonged (>3 years) exposure and lowered invertebrate abundance relative to upstream undisturbed sites. Finally, in several riverine environments, the impact of sediment loading appears to be more important than nutrient enrichment (Fig. 4). For example, suspended sediments were a more important driver of biotic change in a western Canadian river relative to nutrients, and algal biomass accumulation was more sensitive to thaw-slump sedimentation than was microbial decomposition (Levenstein et al., 2018).

Environmental change in glacial rivers

Glacier-fed rivers have a unique ecology that is shaped by longitudinal gradients in flow, temperature, nutrients and sediment load downstream of glacial inflow (Milner et al., 2001). These rivers are an important freshwater component in the Arctic with the largest global mass of glaciers occurring in Alaska, the Canadian Arctic and Greenland, and they are particularly susceptible to climate warming. Shifts in the abiotic template of high latitude, glacial rivers will produce structural changes in riverine flora and fauna, as well as modification of ecosystem functions. For example, both the diversity of species and their traits are predicted to increase as glaciers recede or as percentage of glaciers decrease in the basin, with these shifts mirroring existing downstream longitudinal patterns below glacial margins (Milner et al., 2001).

Effects of human development

Although Arctic ecosystems are often remote, these regions receive contaminants derived from external sources that are transported long distances from outside the Arctic region and deposited on the landscape, or that originate within the region from various sources including mineral extraction, landuse change, road development and hydropower generation (Gregor et al., 1998) (Fig. 3). Long-range transported compounds predominately arrive through atmospheric processes; however, northerly flowing rivers, such as those in Russia or Canada (Fig. 1), also can be important sources of contaminants bound to sediments or in water. In contrast, regional sources of such compounds are released directly in wastewater discharge from various industrial developments (e.g., mining, oil and gas), or within municipal waste waters (Gregor et al., 1998). Impacts to rivers of the above contaminants include biomagnification and toxic stress in biota, acid deposition and altered water chemistry that causes shifts in community structures, and nutrient enrichment that shifts community composition and biotic production (Culp et al., 2012). Importantly, contaminant stressors in Arctic freshwater are likely to interact with aspects of climate change such as increases in temperature and precipitation to produce cumulative impacts on ecosystems that will be difficult to predict (Wrona et al., 2013) (Fig. 3).

Long-range transport of pollutants

The long-range transport of contaminants has included persistent organochlorines (OCs) such as polychlorinated biphenyls (PCBs) and pesticides (e.g., DDT, chlordane, toxaphene), which are known to bioaccumulate in food webs of remote high latitude freshwaters, with examples for lakes being the most well studied (e.g., Kidd et al., 1998). Such contaminants can be extensively deposited across the catchment landscape or through air-water exchange (Gregor et al., 1998), and can bioaccumulate from primary consumers (invertebrates), to secondary Arctic char, nine spine stickleback and tertiary (lake trout, *Salvelinus namaycush*) consumers. Although the accumulation of contaminants in rivers is not well studied, OCs would be expected in riverine food webs because of the extensive connectedness of lake and river ecosystems in the Arctic.

Mercury is also a potentially toxic contaminant of concern that reaches high latitude freshwaters via long-range atmospheric transport, with enhanced atmospheric deposition occurring in spring and early summer as biological activity is increasing. Chételat et al. (2014) provide an extensive review of the cycling and fate of mercury in Canadian Arctic freshwaters, including detailed assessment of concentrations and processes in key ecosystem compartments of water, sediment, and food webs. An important finding is that large rivers transport considerable mass of aqueous and sediment-bound mercury, with concentrations increasing substantially in spring as tributary rivers erode and deliver material to downstream mainstem channels (e.g., Mackenzie, Yukon, Nelson, Churchill rivers). These sources of mercury provide opportunity for microbial transformation to the bioavailable and toxic form of methyl mercury in the environment (Chételat et al., 2014). Finally, research in the Mackenzie River Basin indicates that climate warming over the last 50 years appears to have mobilized mercury in this northerly flowing river system leading to striking increases of total mercury concentration in burbot (*Lota lota*), a food fish used by northern communities. Such mobilization of mercury will only increase as permafrost thaw slump frequency and magnitude increases.

Acid deposition through long-range atmospheric transport has also historically impacted high latitude freshwaters, primarily in Fennoscandia and northwest Russia (Moiseenko, 1994; Skjelkvåle et al., 2001). Acidification of freshwater systems in these regions led to the decrease of fish stocks, particularly in Norwegian lakes where Arctic char, brown trout, roach (*Rutilus rutilus*), and perch (*Perca fluviatilis*) were lost (Tammi et al., 2003). Legislation put in place to reduce sulfate emissions has led to large reductions in sulfate deposition in the region since the 1980s, and this was followed by the onset of recovery of water chemistry (Skjelkvåle et al., 2001). In parts of the southern Arctic such as Sweden, declines in sulfate deposition appear to increase the binding of phosphorus in soils, thereby reducing transport to freshwaters. In a recent circumpolar assessment, Huser et al. (2020) concluded that this process enhances terrestrial primary production at the expense of aquatic producers in the near and Sub-Arctic.

Regionally derived pollutants

Internally produced sources of contaminants in the Arctic region originate largely from mineral extraction (e.g., base metal mining, placer mining, oil and gas development), legacy effects such as abandoned mines, and municipal wastewater discharge. These types

of developments can affect food security of Indigenous communities and cause long-term environmental degradation that may be difficult to mitigate given the remote location of this activity and the unknown interactions of these impacts with climate change (Tolvanen et al., 2018). The expected responses of riverine biota to extraction activity includes the bioaccumulation and biomagnification of contaminants leading to selection for taxa more tolerant of contaminants, as well as nutrient enrichment (Culp et al., 2012). For example, input of heavy metals from mining operations is known to have negative effects on stream communities, with fish species in the Arctic being particularly vulnerable to heavy metals and associated contaminants in mine waste (Lemly, 1994). Placer mining for gold and other precious metals also impacts Arctic biota through substantial increases in sediment loading, with Reynolds et al. (1989) describing the avoidance by Arctic grayling of impacted stream habitats in Alaska, as well as reductions in carrying capacity for fish in summer. Explosives used in the mining process are also suspected to have increased nutrient concentrations in Sub-Arctic streams in northern Finland, resulting in changes in diatom and macroinvertebrate communities (Mykrä et al., 2021). Legacy effects of abandoned mercury mines in Alaska have been shown to raise contaminant concentration in Arctic grayling, Dolly Varden (*Salvelinus malma*) and northern pike, though the tissue mercury levels did not cause a health risk for humans (Gray et al., 2000). Finally, nutrient enrichment from wastewater discharges occurs in the relatively few urban areas in the High Arctic region, as well as from discharge associated with industrial and mining operations (Gregor et al., 1998). Classic experiments by Peterson et al. (1985) have highlighted the vulnerability of Arctic streams to nutrient addition, emphasizing that nutrient increases that may arise from municipal wastewaters released to high latitude rivers can shift these systems from heterotrophy to autotrophy and increase the size of dominant insects.

Hydropower dams

Hydropower generation and capacity have been expanding across the Arctic and Sub-Arctic including in Alaska, Canada, and much of Fennoscandia since 1980 (Cherry et al., 2017). This development has important environmental impacts that can cause striking regional change to the local landscape and riverine habitat. A key example of the environmental effects of hydropower impoundments on high latitude rivers is the dramatically altered discharge regime downstream, with reduced summer flows and enhanced winter flows in basins of Siberian Russia (Yang et al., 2004). Moreover, such modification of flow regimes and dynamic ice breakup in spring can reduce the periodic inundation of biologically important floodplain areas, such as perched wetlands of the Mackenzie River Basin, far downstream from impoundments (Peters et al., 2021). Further information on the importance of defining the required environmental flows to sustain the aquatic ecosystem in permafrost regions is provided in Peters et al. (2021). Hydropower regulation also modifies the water quality regime as materials transport is shifted from the spring flood pulse to winter with potential consequences to the riverine food web (Siergieiev et al., 2014).

The biological effects of hydropower include impacts at multiple trophic levels. A global synthesis of dam impacts on river macroinvertebrates found declines in taxonomic richness in relation to dams, with the strongest evidence of this pattern found in cold regions (Wang et al., 2020). Furthermore, Wang et al. (2020) noted that stoneflies, caddisflies, and true bugs were most affected by the presence of dams. Other studies have found that fish growth is negatively affected by hydropower reservoirs because of lowered ecosystem productivity (Milbrink et al., 2011). Habitat for juvenile salmon is often degraded or eliminated as observed for rivers in Finland, and restoration efforts to restore stream substrate quality as well as the installation of fish ladders are applied to increase fish stocks (Erkinaro et al., 2011). As hydropower development increases at high latitudes, it will be necessary to further examine the potential impacts on the ecological function of high latitude rivers.

Conclusion/synthesis

High latitude rivers present extremely harsh environments to aquatic species. The cold temperatures that occur much of the year limit dissolved nutrient concentrations required by basal producers and restrict biological production of river food webs. Moreover, these rivers are ice-covered for up to 8 months with many smaller, headwater streams freezing to the bed. Atmospheric reaeration of oxygen is also reduced during winter ice cover (Peters et al., 2021). Much of the landscape is underlain by permafrost, which is a major driver of river flow and greatly limits groundwater formation (Peters et al., 2021) and rates of mineralization of key elements (e.g., phosphorus). Environmental harshness is exacerbated in spring when river ice breakup often causes a major annual disturbance that resets many ecosystem processes by resorting the substrate and causing bank erosion that reintroduces deposited materials including key nutrients required for basal metabolism (Prowse and Culp, 2003). Following the spring freshet, biological production can increase quickly as temperatures rise reaching a peak in late summer prior to fall freeze-up. This harsh abiotic template of high latitude rivers restricts basal production by algae and microbes and limits biological diversity at all trophic levels, with many fish and other aquatic organisms being cold adapted (Lento et al., 2019). The harshness of the physical-chemical environment tends to increase with latitude (Culp et al., 2019), a gradient that mirrors the environmental regime observed for glacial rivers where production and diversity are at a minimum near the glacier terminus (Milner et al., 2001). Due to the remoteness and seasonal extremes of high latitude rivers across the circumpolar Arctic, our knowledge of these systems is poor relative to rivers of other geographical regions (e.g., temperate ecosystems).

The accelerated warming of Arctic landscapes will cause substantial change to high latitude river ecosystems. Because temperature is a primary driver of biodiversity in the Arctic freshwaters (Lento et al., 2020), climate-related warming will lead to modification of biotic composition of all trophic levels as cold adapted stenothermic species are replaced by southern eurythermic species that extend their range northward (Culp et al., 2019). Thus, while an overall increase in future biodiversity is expected, there will be an irreversible loss of unique Arctic biodiversity as 'climate change winners' replace 'climate change losers' and changes in

ecosystem functioning (Heino et al., 2020). Finally, permafrost thaw produced by climate change will mobilize various nutrients (e.g., DOC, phosphorus, nitrogen) that can alleviate nutrient limitation in some river systems (e.g., regions of low relief topography). However, in regions with steep valley slopes, thaw slumps and the downslope movement of substantial sediment input will degrade river habitat.

High latitude rivers are under further threat from increased human development, facilitated by climate shifts, and this increase in development may contribute regionally derived pollutants (Fig. 3). These remote environments also receive contaminants from distant sources through the processes of global distillation of persistent organic pollutants (POPs) transported from warmer regions, and the cumulative effects of pollutants and climate warming are likely to cause substantial environmental stress that will be difficult to forecast. A common plea from assessments of Arctic freshwaters is that there is an urgent need for improved coordination and standardization of the monitoring of physical-chemical and biological components of these ecosystems (Heino et al., 2020; Culp et al., 2021b). Improved monitoring approaches also need to fully engage Indigenous Peoples of the region to integrate their knowledge and perspectives of climate-induced change, thereby developing more rigorous assessments. With greater effort and focus on monitoring approaches and circumpolar Arctic cooperation via institutions such as the Arctic Council (https://arctic-council.org), our baseline knowledge of these understudied ecosystems will improve substantially. The result of these actions will be the increased ability to model the future state of these systems, which will improve planning, the conservation of biodiversity, and the associated ecosystem services provided by high latitude rivers.

Knowledge gaps

- Knowledge of the energy flow of high latitude food webs is in a nascent form. This gap requires determination of the relative importance of carbon supplied to consumers by algae and aquatic plants compared to that of microbial decomposition.
- Climate warming is predicted to increase the biodiversity and productivity of high latitude rivers. Will such increases lead to a greater or lesser importance of top-down predation versus bottom-up stimulation of basal food resources as drivers of food web structure and function?
- Improved models are required to predict the rate of northward expansion of southern species into high latitude rivers, the potential extirpation of cold adapted species related to this range expansion, and the effects these changes in biodiversity will have on ecosystem services on which Indigenous Peoples of the Arctic rely. These models must consider the extent to which spatial discontinuities (e.g., Arctic islands) will hinder the northward range expansion of taxa.
- Permafrost thaw will continue to accelerate as climate warming progresses, thereby releasing nutrients, sediments, and contaminants. The relative importance of these environmental stressors is poorly known, requiring investigation to better understand and predict landscapes where effects of each stressor will predominate (e.g., steep versus low gradient topography, role of ground ice composition).
- As permafrost thaw progresses, what will be the effect of the release of old carbon from ancient soils on decomposition pathways and ecosystem productivity?
- Future contaminant loading to high latitude rivers will increase through long-range transport and regional release of pollutants. What specific predictions can be made related to the cumulative effects of such pollutants and climate change? There is a need to produce improved models that can forecast change to riverine community structure and function.
- For the various biological, physical, and chemical impacts associated with climate change and human development, it will be important to determine critical ecological thresholds where abrupt change in ecosystem structure and function may occur.
- Monitoring at high latitudes must become routine to establish time series observations and allow for the detection of temporal changes in biodiversity and habitat conditions, as well as address questions related to range expansion of taxa and shifts in the boundaries of Arctic regions. Improved monitoring approaches can provide important baseline information for modelling and should fully engage Indigenous Peoples of the region.

Important case studies

Site	*Country*	*Coordinates*	*Topic/Concept*	*References*
Peel Plateau	Canada	67°N 135°W	Permafrost thaw slumps (physio-chemical and biotic responses)	Kokelj et al. (2015), Chin et al. (2016), and Levenstein et al. (2018)
Kuparuk River	USA	70°N 148°W	Hydrology and water chemistry, experimental fertilization	McNamara et al. (1998) and Slavik et al. (2004)
Hengill	Iceland	64°N 21°W	Experiments with geothermal streams to test warming effects	Woodward et al. (2010)
Disko Island and Kangerlussuaq	Greenland	69°N 53°W (Disko) 67°N 50–51°W (Kangerlussuaq)	Effect of water source on macroinvertebrate communities	Friberg et al. (2001)
River Tana	Norway	70°N 28°E	Atlantic salmon migration	Økland et al. (2001) and Karppinen et al. (2004)

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Relevant websites

https://caff.is/freshwater—Home of the Circumpolar Biodiversity Monitoring Program's Freshwater group, including links to the State of the Arctic Freshwater Biodiversity Report.
https://www.arcticbiodiversity.is/—Arctic Biodiversity Assessment website, including links to the report and education resources.
https://www.amap.no/—Home of the Arctic Monitoring and Assessment Programme, including links to numerous reports about snow, water, and ice in the Arctic.
https://www.arctic.noaa.gov/Report-Card—NOAA's Arctic report card, released annually since 2006, which provides updates on change in the Arctic.

Alpine Streams and Rivers

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Alpine zone The zone above the treeline.
Braided channel A network of river channels separated temporary by islands of unconsolidated sediment (called braid bars), usually occurs on glacial floodplains.
Cryosphere Regions of the Earth's surface where water is in solid form (i.e., snow or ice).
Discharge The volume of water moving past a given point in the river per unit time (usually liters per second).
Meltwater Water (specifically runoff) that has come from melting snow or ice.
Permafrost Any ground that remains completely frozen for at least 2 years consecutively.
Water source A distinct source of water that generates river flow (e.g., groundwater, snow or ice).

Introduction

Alpine streams and rivers are found on all the Earth's continents. The alpine zone is located above the treeline in mountain ranges but below the permanent snow-line (Körner et al., 2003). The term "alpine stream" is often applied where glacier-fed streams extend below treeline, as occurs in many large mountain ranges. The geomorphology of alpine regions is a product of glacier activity over millennia. Significant ice movement during Quaternary glaciations has created a landscape characterized by U-shaped valleys, hanging valleys and over deepening of valley floors. These landscapes host poorly developed soils interspersed with bare rock, where vegetation typically forms herbaceous meadows with a high diversity of endemic plants and shrubs. However, at higher altitudes, vegetation is sparse, valley slopes are steep and snowpacks and glaciers become a major feature of the alpine zone.

Alpine running waters are diverse, ranging from turbid torrents fed by glacier melt to small groundwater-fed springs (Fig. 1A). There are four key hydrological stores in the alpine zone—permafrost, glacier ice, snow and groundwater—individually and jointly water sourced from these stores produces characteristic discharge regimes and a distinctive suite of physicochemical habitat properties (Brown et al., 2003). Spatiotemporal variability in the magnitude, timing and duration of meltwater production and groundwater recharge leads to mixing of these water sources in differing proportions, producing gradients of habitat harshness

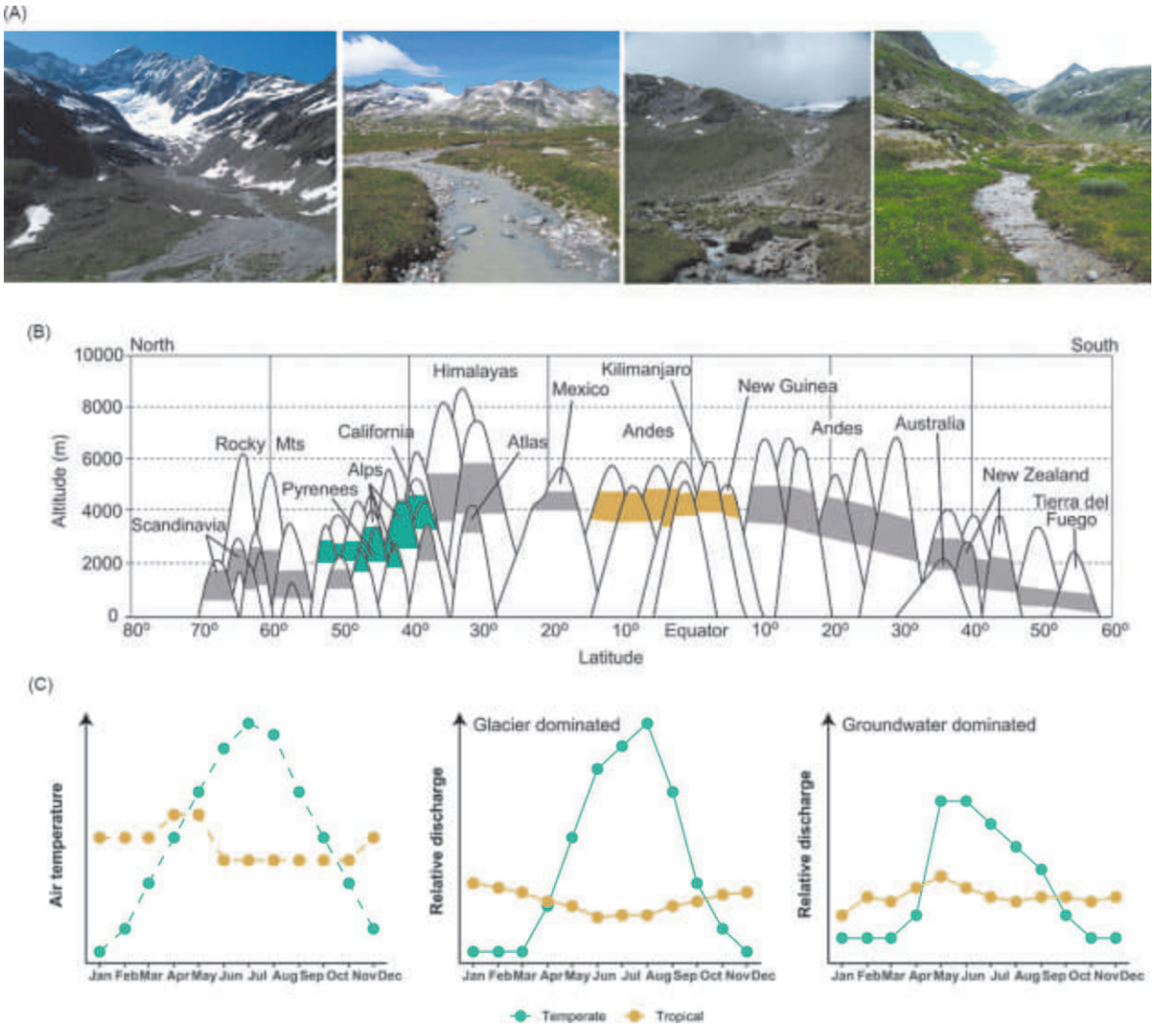

Fig. 1 (A) Images of glacier-fed streams (left and left-center; Austrian Alps), snowmelt fed (right-center; Austrian Alps) and a groundwater dominated stream (right; Austrian Alps). (B) The distribution of the alpine zone (gray shading) across a global latitudinal gradient. (C) Schematic representation of seasonal air temperature and discharge for a temperate (e.g., Alps) and tropical (e.g., Equatorial Andes) alpine region. Hydrographs are displayed for glacier-fed and groundwater dominated streams. (B) Modified from Körner C, Paulsen J, and Pelaez-Riedl S (2003) A bioclimatic characterisation of Europe's alpine areas. In: Alpine Biodiversity in Europe. Berlin: Springer, pp. 13–28.

(e.g., variations in thermal maxima, turbidity, primarily productivity and river bed and channel stability). This gradient can, at the river basin or regional scale, be conceptualized as a harsh (pure glacial meltwater)—benign (pure groundwater) gradient with mixtures of different stores creating intermediate harshness (Khamis et al., 2016). Permafrost can complicate this harsh-benign gradient though, with meltwater outlet streams that are often small and stable hydromorphologically, but with very low water temperature (Brighenti et al., 2021). The strong gradients in habitat properties create high species turnover between sites (beta diversity), with increasing specialization of aquatic fauna in meltwater-dominated streams and isolated spring brooks.

In many regions, particularly (semi)-arid, the generation of river flow in alpine regions is important for ecosystem functions and services downstream, such as hydroelectric power, irrigation and water supply (Milner et al., 2017). Given the high climate sensitivity of alpine regions and the cryospheric processes that dictate streamflow, understanding the structure and function of alpine river systems is particularly important as anthropogenic pressures intensify and the cryosphere shrinks.

This chapter provides an overview of current understanding of alpine stream and river ecosystems. The global distribution of alpine rivers and streams is discussed initially. The different stream types and associated habitats and the concept of dynamic water source contributions (snow, ice, groundwater) are introduced, followed by current knowledge of biodiversity patterns and ecological processes. A discussion of anthropogenic threats and future predictions for alpine rivers concludes the chapter. Examples are drawn from a broad range of biogeographical zones, from temperate to tropical/equatorial regions.

Alpine lotic ecosystems: Links between climate and habitat

Distribution

The alpine zone has a broad geographic coverage—from temperate to tropical mountains (Fig. 1B). In undisturbed areas, the treeline approximates the 10 °C July (Northern Hemisphere) or January (Southern Hemisphere) mean temperature isotherm (Remmert, 1980). Hence, the elevation of alpine streams can vary markedly according to location, from near sea level at high latitudes to >4000 m a.s.l (meters above sea level) near the tropics (see Fig. 1B).

Hydroclimatological conditions

There is strong seasonality in temperate alpine zones with predictable shifts in hydroclimatology. During winter, air temperature is low with precipitation in the solid phase and accumulation of snow and ice is apparent (Fig. 1C). When temperature and solar radiation increase during late spring and summer, snowpack and glaciers melt and feed stream flow and recharge groundwater (Milner et al., 2009). A characteristic annual hydrograph for temperate alpine streams, with a summer peak and winter minimum is evident (Fig. 1C). For example, the main glacier-fed channel of the Val Roseg in Switzerland (46°N, ~2100 m a.s.l) is perennial, but a difference in discharge of two orders of magnitude exists between the winter (<0.5 $m^3 s^{-1}$) and summer peak (>10 $m^3 s^{-1}$). Similar patterns have been recorded for the Upper Rhone catchment (46°N, ~2000 m a.s.l) with <0.2 $m^3 s^{-1}$ recorded during winter and >10 $m^3 s^{-1}$ in summer (Uehlinger et al., 2003). While the difference between winter and summer is not as extreme for groundwater streams, shallow alpine aquifers are recharged by snowmelt and hence peak flow is observed in late spring/early summer. Catchment storage is sufficient for most springs to maintain baseflow during winter months when precipitation falls primarily as snow (Mackay et al., 2020).

Tropical alpine regions experience less hydroclimatological variability over the year due to relatively constant solar input, but daily variability in meteorological conditions (particularly air temperature) can be extreme. Precipitation can occur year-round but with distinct wet and dry seasons depending on latitude (Buytaert et al., 2011). Local elevation and topography are important; for example, there are strong gradients across the equatorial Andes from less than 500 mm $year^{-1}$ on the dry eastern slopes to more than 3000 mm $year^{-1}$ on western slopes (Buytaert et al., 2011). In contrast, in the East African Rift Valley precipitation is related inversely with elevation. Accumulation usually exceeds melt during the wetter seasons with differences between dry and wet season flows, but these are less pronounced than seasonal variability for temperate regions (Jacobsen, 2009). While discharge records for equatorial and tropical alpine streams are limited, a few monitoring sites have captured marked annual flow variability. For example, differences between dry and wet season flow were apparent for the glacier-fed River Mubuku, Uganda (0.2°N), 0.002 vs. 0.017 $m^3 s^{-1}$, and runoff from the Zongo Glacier, Bolivia (16°S), 0.07 vs. 0.21 $m^3 s^{-1}$ (Taylor et al., 2009; Wagnon et al., 1999).

Climate-habitat-ecology linkages

Regardless of elevation or latitude, alpine rivers exhibit some general features that differentiate them from lower altitude streams. Within the river channel, there is typically a lack of woody debris and allochthonous matter due to limited riparian vegetation and low in-channel retention. Alpine streams typically accumulate fewer annual degree days, have a shorter growing season and contain limited nutrients, all of which result in low relative stream productivity (Ward, 1994). There is also a strong coupling between meteorological, cryospheric, hydrological and ecological conditions in alpine regions. These links can be conceptualized as a deterministic process chain with climate dictating the contribution of the major hydrological stores to runoff (Hannah et al., 2007). These differing water sources impart a distinct signal in the river habitat (sediment, habitat stability, flow variability) and thus structure the species assemblages and ecological functioning (Fig. 2). However, it is important to consider regional and local conditions that potentially modify the relationships between different stages in the process chain. These can be either natural (e.g., geology, river basin aspect, topography and biogeography) or anthropogenic (e.g., land use change, flow storage alteration, livestock grazing, and species introductions). For example, in the Southern Alps in New Zealand, storms are often so intense that the summer part of the hydrograph for many alpine glacier-fed rivers is totally dominated by rainfall events (Anderson et al., 2016).

Changing flow regimes

Anthropogenic warming is generally strongest at high altitudes and latitudes. Alpine hydrology is changing in response to this warming, and model predictions suggest major changes in flow magnitude, timing of peak and water source contributions. However, the amplitude of this seasonal cycle is currently increasing under climate change, with higher summer air temperature increasing meltwater production and stream discharge. Over longer timescales (decades) as negative mass balance dominates (summer melting of snow and ice exceeds winter accumulation), the volume of runoff generated by glaciers and permanent snowpacks will decline and consequently the magnitude of the summer discharge peak will diminish and shift to earlier in the season (Hock et al., 2019; see Fig. 3). Rainfall patterns are likely to become less predictable seasonally, and the frequency and magnitude of extreme events are also expected to increase. These patterns are already becoming apparent for many regions as a reduction in cryospheric water stores in alpine basins will potentially lead to low flow periods during late summer and a less predictable flow regime that is influenced more by episodic precipitation as buffering by the cryosphere (meltwater production) is reduced (Milner et al., 2017).

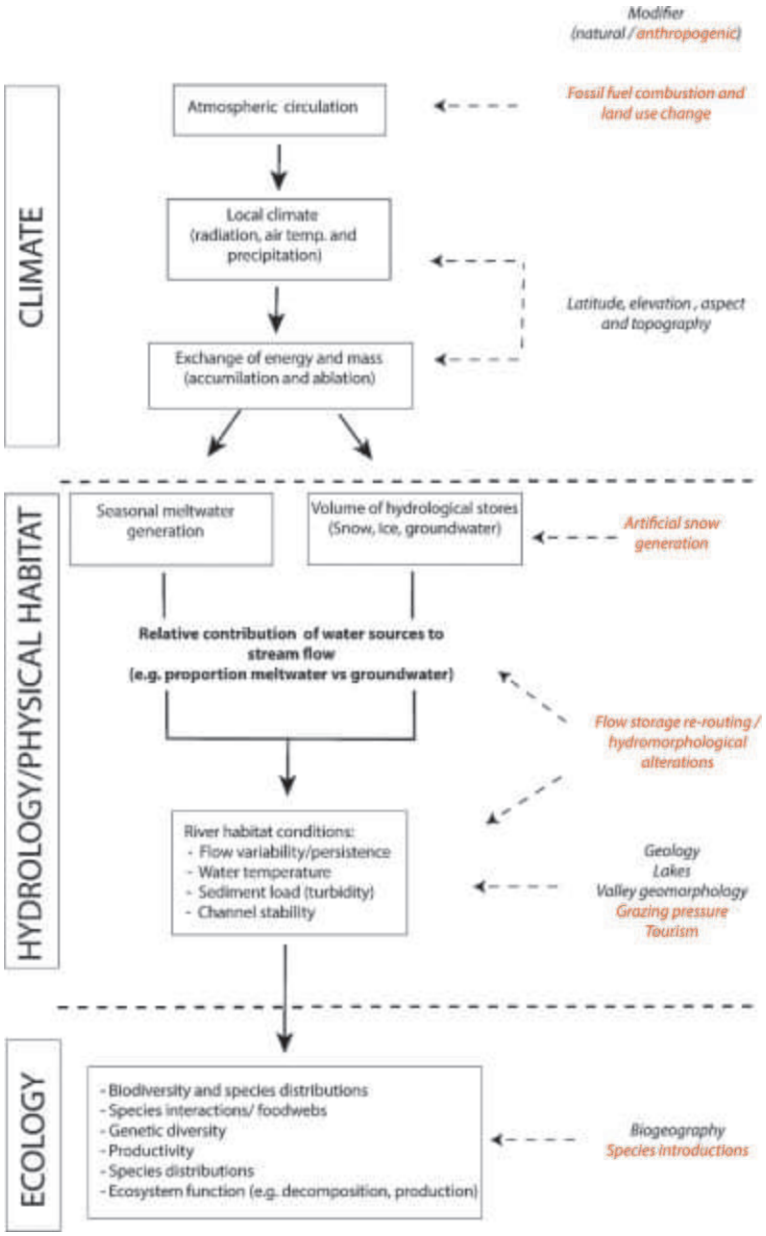

Fig. 2 Flow diagram depicting the conceptual linkages in the climate-hydrology-ecology process chain. Potential modifiers to the links are highlighted in italics (black for natural and red for anthropogenic).

Alpine stream types

Traditional approach to alpine stream classification

In alpine regions, water source is a major control on stream flow dynamics, habitat properties and biotic communities. Early approaches to group or classify alpine stream types were based on perceived water source, with three general stream biotypes: *kryal* or glacier-fed, *krenal* or groundwater fed and *rhithral* or seasonal snowmelt fed (Fig. 1A; Ward, 1994). There are distinct differences in physicochemical habitat properties associated with *kryal*, *krenal* and *rhithral* streams, particularly regarding water thermal regimes, discharge, suspended sediment dynamics, solute concentrations and bed/channel stability (Table 1). While there is increasing evidence that permafrost is an important water source in alpine regions (Brighenti et al., 2021), more research is needed to constrain conceptual understanding of associated habitat conditions. In addition, most permafrost melt provides recharge for local groundwater.

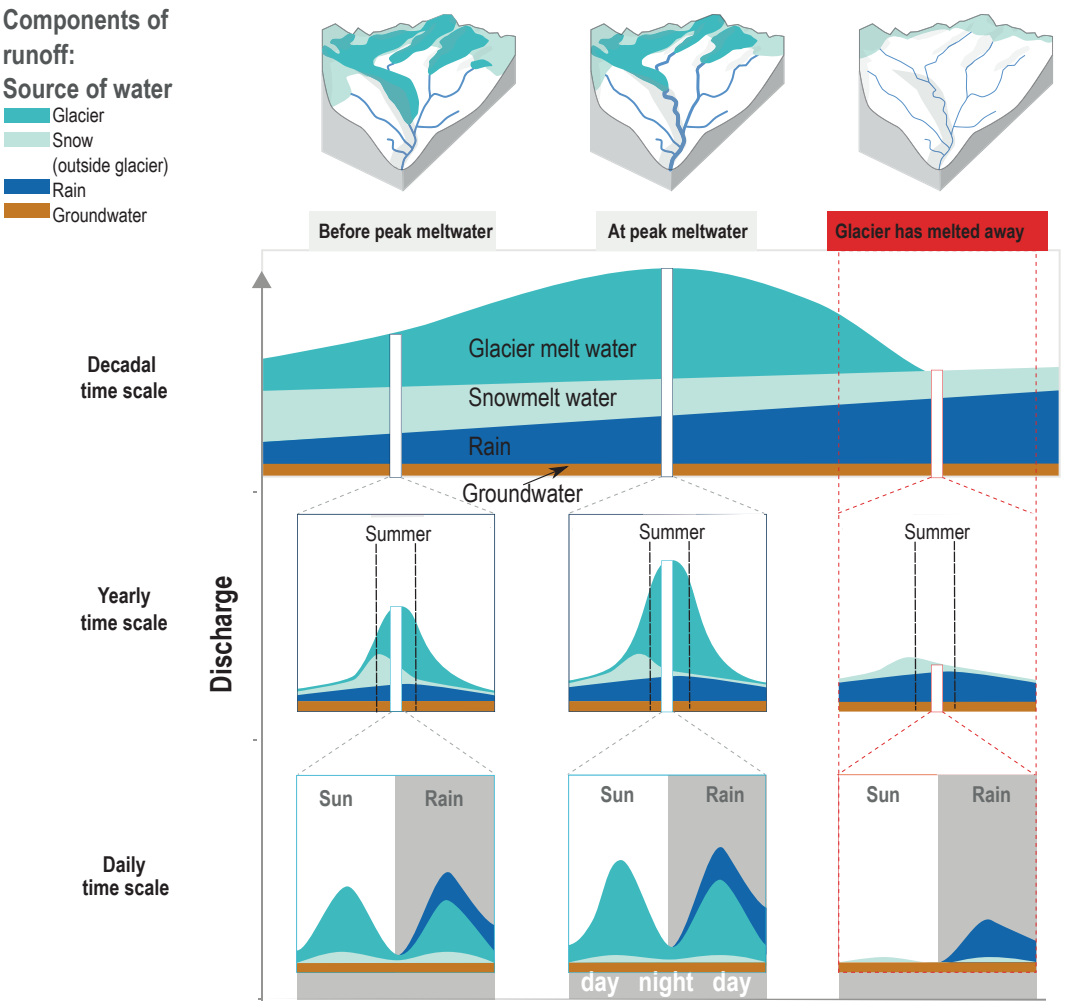

Fig. 3 Conceptual representation of the predicted changes in discharge and water source contributions across a gradient of cryosphere shrinkage. Note that the summer pattern for temperate alpine zones reflects the year-round pattern for aseasonal equatorial alpine regions, both at the annual and daily time scales. Modified from Hock R, Rasul G, Adler C, et al. (2019) High Mountain Areas. In Pörtner HO, Roberts DC, Masson-Delmotte V, et al. (eds.). *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. Geneva, Switzerland: IPCC.

Table 1 Physical and chemical properties of the three major stream types in alpine environments based on water source.

Variables	*Kryal (glacier fed)*	*Rhithral (snowmelt fed)*	*Krenal (groundwater fed)*
Discharge	Summer peak, diurnal variations sustained through melt season	Spring snowmelt causes peak flow. Also, peaks following rainfall events	Relatively constant but attenuated peaks following precipitation events
Channel stability	Frequently unstable, braided or wandering. Stability a function of distance from glacier and time since deglaciation	Typically more stable and less braided	Stable, single thread channels. With significant riparian vegetation
Water temperature	Diurnal variability lower than rhithral; <2 °C close to glacier margins, increases with reducing glacier influence	High in summer, range from 0 °C to 12 °C. Large diurnal variation	Related to air temperature at source, typically low diurnal and seasonal variation
Suspended sediment	High suspended sediment concentrations during summer melt season with peaks over 500 mg L^{-1}	May be elevated during high flows, but much lower than kryal	Low suspended sediment concentration
Hydro-chemistry	Conductivity usually low but sulfates can be elevated due to erosion processes	Ionic enrichment related to snowpack concentrations of solutes. Intermediate between kryal and krenal	Generally high conductivity. Chemistry related to the geology of groundwater store but usually enriched in carbonates and silicates
Macro-nutrients	Phosphorus concentration can be high and dissolved organic carbon (DOC) concentration low but highly labile	Generally low nutrient concentrations but nitrate can be high during initial snow melt	Low nutrient concentration, particularly phosphorus and DOC

Adapted from Brown LE, Hannah DM and Milner AM (2003) Alpine stream habitat classification: An alternative approach incorporating the role of dynamic water source contributions. *Arctic, Antarctic, and Alpine Research* 35: 313–322.

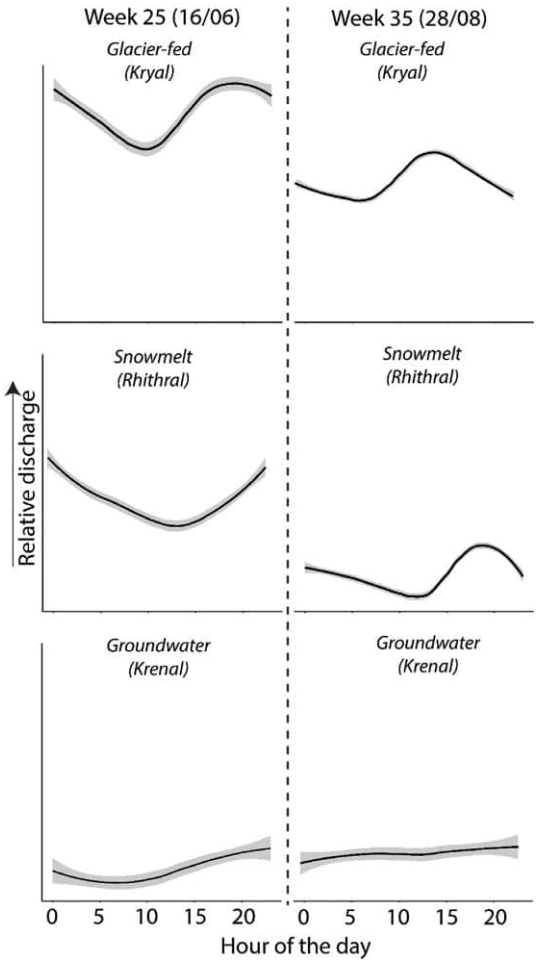

Fig. 4 Locally weighted smoothing (LOESS) of daily discharge recorded for the Taillon glacier-fed stream (French Pyrénées, 42°N) a snowmelt dominated stream Vignemale (French Pyrénées, 42°N) and groundwater spring (Austrian Alps, 47°N). Note that the curve is based on the daily pattern over a week (gray band = 95% CI) during early melt season (week 25) when snow cover is extensive and during late summer (week 35) when extensive glacier ablation is apparent.

Kryal streams can be considered more environmentally "harsh" in terms of habitat properties when compared to *krenal* and *rhithral* streams, with lower water temperature, more unstable riverbeds and channels, less riparian vegetation, and higher suspended sediment loads (Table 1). The daily variation in flow is particularly pronounced for *kryal* streams and is always greater than observed in stable *krenal* streams but can be comparable to *rhithral* streams in summer before seasonal snowpacks have melted (Fig. 4). *Krenal* streams can be considered the most stable stream type in terms of habitat characteristics but this can vary with aquifer volume and recharge dynamics. *Rhithral* streams are generally intermediate between *krenal* and *kryal* (Table 1).

For equatorial mountains, the discharge regime of *kryal* streams varies on a diurnal basis due to diurnal melting and nocturnal freezing. Seasonal variability in the amplitude of diel (24 h) cycles is less pronounced than for temperate streams and is a function of air temperature/solar radiation input (control on meltwater generation), precipitation (increased albedo due to snowfall) and wind (sublimation). For *krenal* streams groundwater recharge is not strongly seasonal with inter-annual variability more pronounced than annual changes in flow. Hence, variability is more a function of longer-term changes in climate, such as El Nino cycles (Jacobsen, 2009). Equatorial *rhithral* streams have a more stochastic flow regime with no seasonal snow accumulation apparent and rain showers occurring throughout the year.

Novel stream classification approaches

The stream classification approach outlined above provides a basis for understanding alpine stream habitats, but it is static temporally in that the seasonally dynamic nature of water source contributions to flow are largely ignored, and some water sources such as permafrost or cold rocky landforms (CRL; Brighenti et al., 2021) are not explicitly incorporated. There have been some efforts to create sub-groupings within these broad classifications, e.g., groupings based on the presence of lakes or macroinvertebrate assemblage composition (e.g., *metakryal* vs. *hypokryal* based on chironomid community composition). Other approaches have

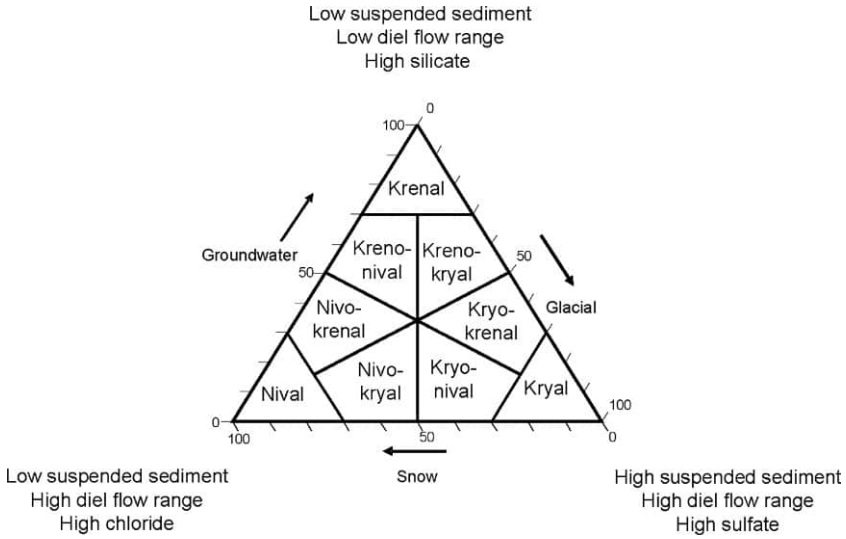

Fig. 5 Alpine stream classification system based on water source contributions. Key physicochemical characteristics of the water source end members (snow/glacier/groundwater) are highlighted in gray boxes. modified from Brown LE, Hannah DM and Milner AM (2003) Alpine stream habitat classification: An alternative approach incorporating the role of dynamic water source contributions. *Arctic, Antarctic, and Alpine Research* 35: 313–322.

considered the importance of quantifying the influence of glacial runoff on a given river reach based on estimation of glacier cover in the upstream catchment (aerial imaging; Jacobsen et al., 2012) or through the calculation of indices based on habitat conditions (e.g., suspended sediment, water temperature and river bed stability) or periodicity in diel flow variability (Cauvy-Fraunié et al., 2013).

An alternative classification system was proposed (ARISE: a classification tool for Alpine RIver and Stream Ecosystems) based on the premise that streams are not fed by a single water source but over time can have a combination of sources. Hence, alpine streams can be grouped based on quantification of these relative water source contributions to streamflow at a given point in space and time (Brown et al., 2009b). Building on the three groupings outlined above (*kryal*, *krenal*, *rhithral*), streams can be placed into nine categories based on the relative contribution of glacier melt, groundwater and snowmelt (Fig. 5). These categories relate water source contributions with physicochemical habitat variables such as stream discharge, suspended sediment concentration and hydrochemistry. As this approach involves quantitative measurement of water source contributions through use of mixing models there is potential for accurate comparisons between stream reaches across different river basins, regions and climate zones. ARISE does not, however, consider flow generated from rainfall, a feature that becomes more of an issue in basins with less snow and ice cover (i.e., climate change and glacier retreat). Furthermore, permafrost contributions are still absent from this model but rivers fed predominantly from this source are likely to exhibit characteristics of *kryal-krenal* streams (Brown et al., 2009b).

Intermittent alpine streams

There are other modifiers to the expected patterns based on water source contribution which need to be considered. Lakes, have a significant influence on the physicochemical properties of alpine streams. For example, in glacier-fed streams, lakes increase channel stability, thereby buffering flow variability and reducing suspended sediment load (Milner et al., 2001). It is also important to consider the interaction between water source and geomorphic/landscape properties (Weekes et al., 2012). For example, valley scale depositional processes can influence streamflow regimes and water temperature dynamics in ways that depart from expectations based on water source (Weekes et al., 2015). Flow intermittency occurs naturally in alpine environments and while it is a feature of significant ecological importance, it has only been relativity recently that the occurrence of natural intermittent rivers and ephemeral streams (IRES) have been assessed systematically (Paillex et al., 2020). The seasonal variability in climate and water source availability are important drivers of seasonal intermittency, with the landscape heterogeneity and limited storage potential/shallow aquifers contributing to the relatively high proportion of IRES in temperate alpine regions (see Robinson et al., 2016). Conceptually, the dominant water source of streamflow can provide an indication of intermittency likelihood (Fig. 6). Despite this, it remains difficult to generalize patterns of intermittency across basins with contrasting climate, geology and geomorphology. The occurrence of IRES in tropical/equatorial alpine regions remain largely unknown but it is likely that the frequency will increase with climate change.

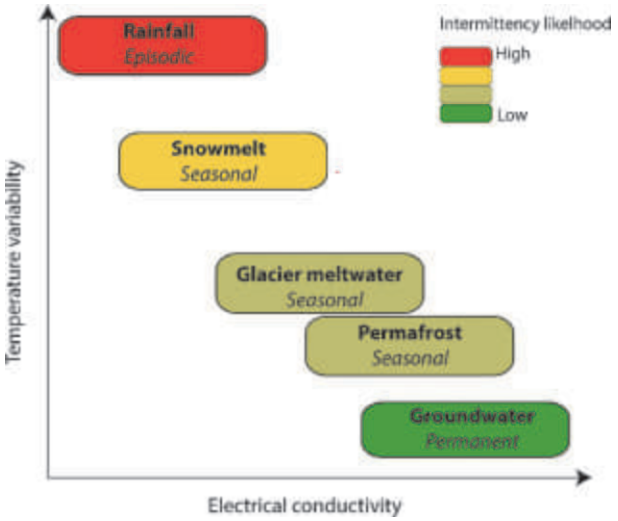

Fig. 6 Conceptual representation of the relationship between water source and intermittency for temperate alpine streams. Electrical conductivity and water thermal variability are the physicochemical habitat variables that display the greatest variability over the flow permanence gradient. Adapted from Paillex A, Siebers AR, Ebi C, et al. (2020) High stream intermittency in an alpine fluvial network: Val Roseg, Switzerland. *Limnology and Oceanography* 65: 557–568.

Ecological structure of alpine streams

Alpine streams support a unique flora and fauna with high levels of endemism (Brown et al., 2009a) due to isolation and marked changes in environmental gradients over short spatial scales. Despite having relatively low local diversity (alpha diversity), alpine streams contribute significantly to regional scale biodiversity (gamma diversity). Equatorial and subtropical—tropical regions potentially have high levels of endemism and rarity, e.g., in Japan over 50% of the freshwater taxa are endemic, many in alpine streams (Yoshimura et al., 2005). However, taxonomic limitations in many other countries prevent a full understanding of the true diversity.

Across different biotic groups and trophic levels, some general patterns of biodiversity are apparent across alpine stream types. Alpha diversity is generally lowest for high meltwater sites (particularly those close to glaciers), and generally peaks at intermediate to low meltwater contribution or glacier influence. This pattern is associated with decreasing environmental harshness and mass effects (more upstream sources of colonists). Community structure in groundwater sites is more varied and is driven by biotic interactions and flow permanence (Brown et al., 2007). Despite low alpha diversity, high meltwater sites support a unique, specialized flora and fauna and thus make a significant contribution to beta diversity (turnover between sites). Historically, macroinvertebrate communities have been the focus of study in alpine regions, however, surveys of algal and microbial diversity have increased in recent years (Fell et al., 2017). In the following sections, we consider community structure, diversity and distribution of major taxonomic groups across the alpine stream types identified above.

Microbes and fungi

Alpine streams are important repositories for microbial diversity with communities associated with either attached biofilms (epilithic) or the water column. In alpine glacier-fed streams, bacterial diversity generally increases with distance from the glacier margin, with Proteobacteria, Cyanobacteria, Bacteroidetes and Actinobacteria dominating the benthic communities (Freimann et al., 2013; Ren et al., 2017a). The stream water column has greater species richness than attached biofilm communities, likely due to mass effects and the influx of cells from a variety of sources (e.g., cryoconite holes, glacial ice, groundwater and the adjacent terrestrial environment). However, only a subset of taxa recorded in the water column are able to successfully colonize benthic biofilms principally due to short water residence time and transient environmental conditions (Wilhelm et al., 2013). Nevertheless, bacteria within the phyla Firmicutes and Tenericutes are typically only found in glacier-fed channels in alpine regions. Furthermore, rare taxa are particularly important components of biofilms in glacier-fed streams (Wilhelm et al., 2014), with significant turnover of community composition in space (i.e., longitudinal) and time (i.e., optimal environmental conditions in spring or summer).

Average microbial biomass, carbon production and diversity are higher in groundwater-fed tributaries compared with glacier-fed streams (Battin et al., 2004), with bacterial diversity correlated positively with water temperature. Taxonomic diversity in snowmelt channels is comparable to groundwater channels, with bacterial biomass and abundance being lower than groundwater but higher than glacier-fed channels (Hotaling et al., 2019). Icy seeps or outflows from rock glaciers also represent important habitats for microbial communities, particularly cold water specialists, and they may represent refugia as glaciers and permanent snow packs recede and disappear (Hotaling et al., 2019). There is limited data regarding the microbial communities associated with tropical or equatorial alpine rivers. However, studies from the glacier ice of Mt. Kilimanjaro have identified rich bacterial assemblages with a particularly high diversity of endemic taxa, suggesting the river networks may also have unique microbial communities (Vimercati et al., 2019).

Aquatic hyphomycetes dominate alpine-river fungal communities often as a component of complex microbial biofilms. They represent an important functional component of alpine riverine communities, acting as a nutrient source for higher trophic levels and as the principal microbial decomposers of allochthonous organic-matter inputs (Gessner and Robinson, 2003). Some specialists show adaptation to cold water temperature and high suspended-sediment concentrations, with biomass, taxonomic richness and diversity in glacier-fed rivers comparable to temperate rivers (Gessner and Robinson, 2003). Recent large-scale studies have linked OM decomposition rates to specific fungal taxa, saprotrophic groups (those that obtain nutrients from the decomposition of detritus) and functional genes (Fell et al., 2021). Over 1000 unique fungal Operational Taxonomic Units (OTUs) were identified from a study spanning mountainous regions of Alaska, Austria, Ecuador, France, New Zealand and Norway (Fell et al., 2021). Reductions in catchment glacier cover were associated with increased fungal (ITS) abundance across all mountain river sites. A total of 294 fungal OTUs was found exclusively in rivers with >52% catchment glacier cover, highlighting the potential vulnerability of fungal diversity to ice loss. Decomposition rates of organic matter increase in rivers as glacier cover decreases (Fell et al., 2021), reflecting increases in temperature, channel stability and reduced sediment transport. Responses of fungi and other biofilm species to glacier retreat are also thought to be mediated by local factors including nutrient supply and hydrodynamics (Battin et al., 2004; Wilhelm et al., 2013).

Algae

As alpine streams are predominantly located above treeline, their allochthonous organic inputs are typically low. Hence, primary producers (autotrophs) represent the main energy source, particularly in glacier-fed stream ecosystems. Yet, despite alpine springs having been identified as hotspots of benthic algal biodiversity, there is a relative paucity of knowledge regarding algal communities compared to groups such as invertebrates (Fell et al., 2017).

Strong seasonal variations in stream discharge, channel stability, turbidity, water temperature and hydrochemistry are recognized as the key drivers of fluctuations in benthic algae biomass. Biomass typically peaks during spring when nutrient input from snowpacks and water clarity is highest. This period represents a "window of opportunity" for primary producers in the otherwise highly turbid and unstable glacier channels (see Milner et al., 2001). For example, the golden alga, *Hydrurus foetidus*, can dominant in glacier-fed rivers in early summer (Rott et al., 2006). Rapid growth at this time of low water temperature (<1 °C) indicates *H. foetidus* growth is not temperature limited, and that it resists increased river flows by forming a gelatinous cover on the substrate. Other taxa with differing growth strategies are also found, such as the patch-forming cyanobacterium *Phormidium autumnale* and less frequently the tubular tissue-forming red alga *Lemanea fluviatilis* (Rott et al., 2006).

In alpine streams, benthic diatoms are often the most species rich component of the algal community, and they play a major role in primary production and energy transfer to higher trophic levels (e.g., major food source for macroinvertebrates; Clitherow et al., 2013). The diatom community of glacier-fed rivers across the Northern Hemisphere is dominated by *Hannaea arcus* and taxa from the genera *Achnanthidium*, *Fragilaria* and *Odontidium* (Cantonati et al., 2001). At the species level, diatoms show a range of responses to catchment glacier cover reductions; for example, *Eunotia trinacria*, found exclusively in European Alps rivers with ≥52% glacier cover, may be affected negatively by loss of glacier ice. In contrast, seven taxa found only at sites with no glacier cover, including *Gomphonema calcareum*, may benefit (Fell et al., 2018). However, new species are being recorded (for example *Odontidium* spp. in the Himalayas) as sampling efforts have increased for alpine streams in recent years (Jüttner et al., 2017). Species richness (alpha diversity) is generally highest at sites with low glacier/meltwater influence and community composition divergence is greatest. Cold adapted specialists that can thrive in oligotrophic conditions are well represented across a range of stream types. However, *Achnanthidium* spp. are found closest to the glacier margin as they can also tolerate stream bed instability. Conversely, taxa from stable channels with low glacier influence exhibit a greater range of growth strategies; for example, chain-formation (e.g., *Staurosirella pinnata*) and motility (e.g., *Nitzschia soratensis*) are common. A study from the Austrian Alps (Fell et al., 2018) found that there was a high proportion of Red List species (rare or threatened taxa) at groundwater or low glacier influenced sites and two taxa, *Fragilariforma constricta* and *Staurosira construens*, were exclusively found at sites with higher glacier influence (>28% glacier cover in the catchment).

Invertebrates

There has been significant interest in the longitudinal zonation of invertebrate assemblages downstream from glaciers. Studies from both temperate and tropical regions highlight consistent increases in species richness with increasing distance from the glacier margin (Crespo-Pérez et al., 2020; Kuhn et al., 2011; Milner et al., 2001). This pattern has been linked to increasing channel and bed stability, water temperature, groundwater input and basal resource retention. However, longitudinal patterns can be punctuated by tributary inflows with biotic diversity responses depending on water source of the input (e.g., a high groundwater tributary increases diversity while a high meltwater tributary may decrease diversity) or the presence of lakes. This change in habitat conditions (and associated community changes) can be conceptualized across the continuum of stream types in alpine environments from meltwater to groundwater dominated as a gradient of environmental harshness (Khamis et al., 2016; Fig. 7).

Relatively predictable downstream changes in community composition have been observed for macroinvertebrates of temperate streams in the Northern Hemisphere. Chironomids are generally the most abundant and diverse family in glacier-fed streams. Species of the sub-family Diamesinae are found closest to the glacier margin (i.e., *Diamesa* spp.) and can complete their lifecycle even when channels are unstable and maximum water temperature is <2 °C; due to minimal competition and predation these

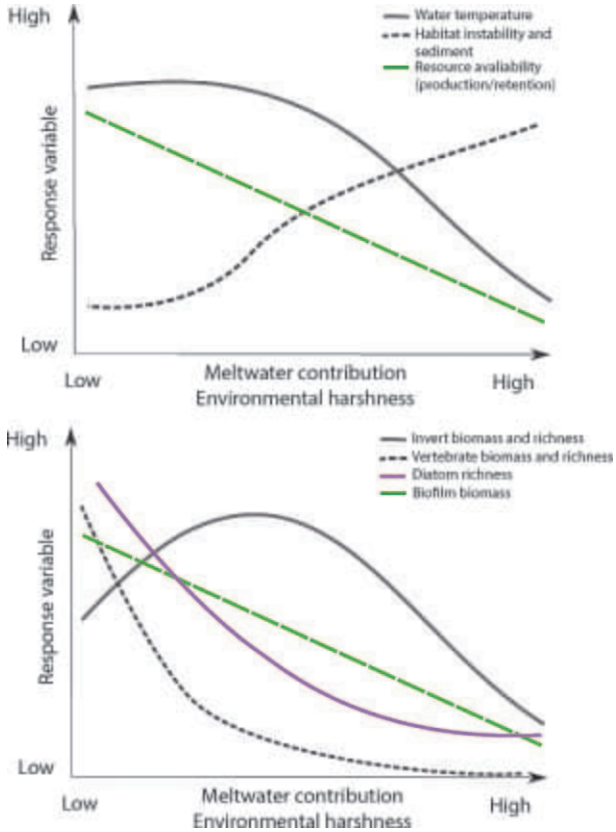

Fig. 7 Conceptual representation of alpine benthic habitat properties and biota responses along the meltwater (glacier influence) gradient. Curves are based on data from Khamis et al. (2016) and Fell et al. (2017).

species are often very abundant. Orthocladiinae can also tolerate low channel stability where water temperature reaches 4 °C, whereas Oligochaeta and other Diptera (e.g., Tipulidae and Empididae) can colonize more stable channels at these temperatures (Milner et al., 2001). Further from the glacier snout Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa become increasingly abundant and diverse along with Simuliidae and other chironomids (e.g., Chironominae). In the Southern Alps (New Zealand), *Diamesa* spp. are absent due to biogeographical constraints, and here *Deleatidium* spp. (Ephemeroptera: Leptophlebiidae), are found near to glacier margins at low temperatures. (Fig. 8A; Cadbury et al., 2011). Similar longitudinal patterns are apparent in equatorial glacier-fed systems, with an increase in EPT taxa correlated to distance from the glacier, while a notable difference is the presence of Podonominae and absence of *Diamesa* spp. at sites closest to the glacier margin (Jacobsen et al., 2010). Thus, differences are largely attributed to biogeographical variability in the regional species pool (Fig. 8B). Although less is known about meiofauna communities, diversity patterns for copepods, tardigrades and rotifers broadly follow macroinvertebrates (e.g., increasing diversity at sites of decreased glacier influence; Eisendle-Flöckner et al., 2013).

Differences in habitat conditions between streams fed by different water sources is a key control structuring the associated macroinvertebrate assemblages. Generally, abundance and total taxonomic richness is higher (2–8 ×) in groundwater-fed streams. Alpine spring-fed systems are often associated with a unique fauna (Brown et al., 2009a). For example, in the Val Roseg, Switzerland, Heteroptera, Coleoptera, Gastropoda and Bivalvia were restricted to spring-fed streams. Similarly, of five endemic Pyrénéan species found in the Taillon-Gabiétous basin, French Pyrénées, four were strongly associated with groundwater streams (Brown et al., 2006). Sites with more stable physicochemical habitat variables (e.g., groundwater-fed streams) may not necessarily support the most stable communities though, perhaps because species abundance patterns are influenced more by changes in resource availability and biotic interactions. These studies suggest alpine groundwater springs and streams are important contributors to biodiversity. Furthermore, groundwater-fed streams may be potential sources of macroinvertebrates for the more physically disturbed meltwater-fed streams (Robinson et al., 2004). Groundwater streams can even act as refugia for specialized cold-water macroinvertebrates providing the thermal conditions are suitable (Muhlfeld et al., 2020). A comprehensive survey of streams in Glacier National Park (Montana, USA, 48.7°N) identified most of the regional species pool in non-glacial channels (110 of 113 species) suggesting few glacier obligate species (Muhlfeld et al., 2020). This highlights the need for increased sampling effort in alpine regions to better constrain species distributions and ultimately help guide targeted conservation efforts.

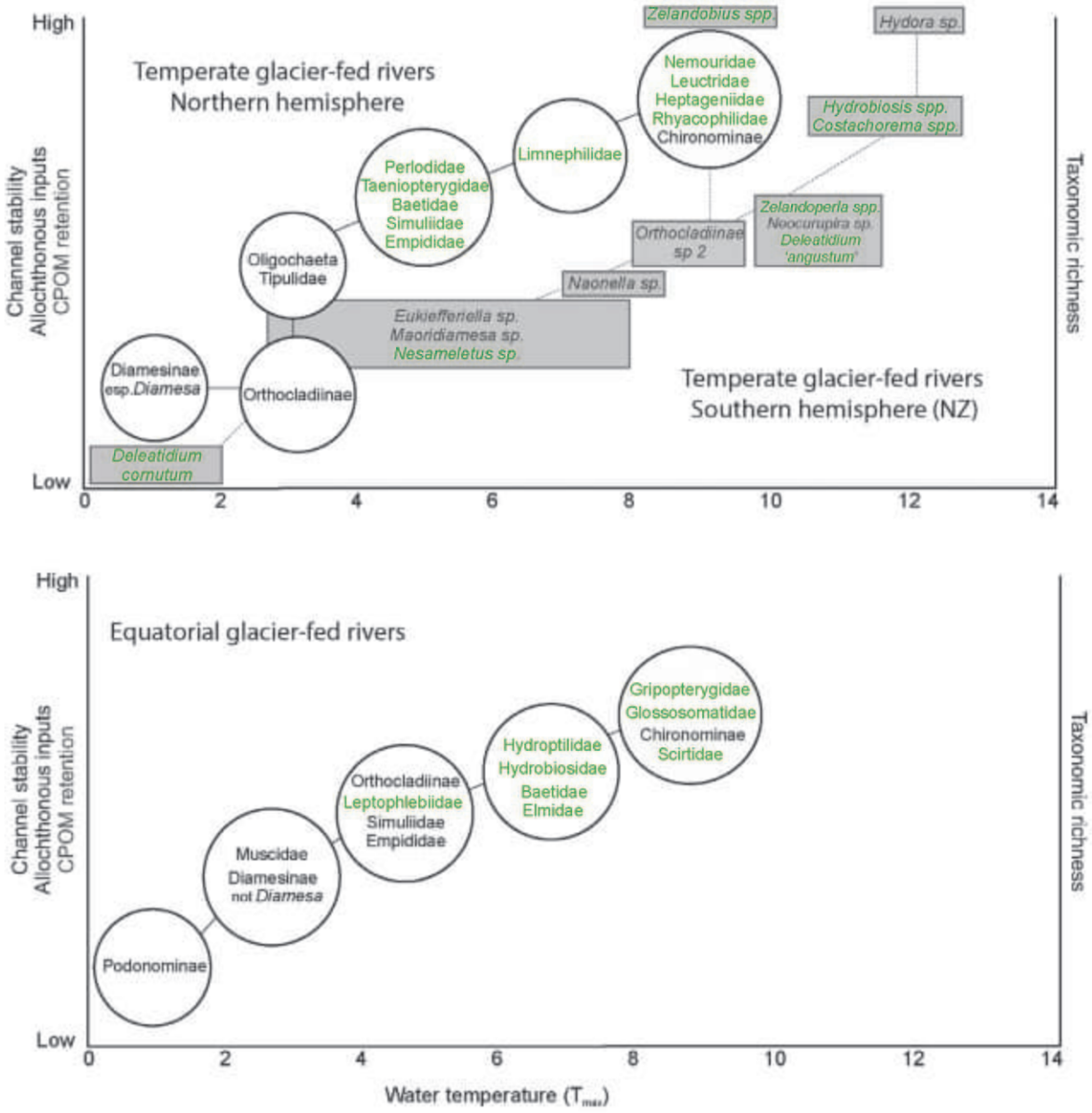

Fig. 8 Conceptual representation of macroinvertebrate community composition patterns in glacier-fed streams in relation to water temperature, channel stability and organic matter retention. The top panel represents temperate regions in the Northern and Southern Hemisphere after Fell et al. (2017) and Milner et al. (2001). The lower panel represents community patterns in equatorial streams based on Kuhn et al. (2011) and Crespo-Pérez et al. (2020). Green text is used for non-dipteran taxa (Ephemeroptera, Coleoptera, Plecoptera, Trichoptera) taxa. Gray fill on the upper panel represents patterns for streams in New Zealand.

The increasing use of molecular and genetic techniques in ecology are identifying significant cryptic diversity among invertebrates in mountainous and alpine regions. This is particularly prevalent where refugia communities have persisted during Pleistocene glaciation. For example, the mayfly *Baetis alpinus*, a well-studied species in temperate regions, has been shown to consist of reproductively isolated units in the Alps and Pyrénées, with limited genetic overlap between sites of high and low glacier influence (Finn et al., 2014). This suggests subspecies with distinct evolutionary histories are likely linked to extreme environmental differences between sites. Interestingly, these patterns have not been identified in tropical alpine streams in the High Andes, with gene flow apparent between groundwater and glacier melt streams for *Andesiops peruvianus*, a baetid mayfly. This is thought to reflect the legacy of volcanic activity in the region leading to environmental and demographic instability on evolutionary time scales (Finn et al., 2016).

Fish

Few native fish species are able to colonize and inhabit alpine rivers due to the harsh environment and cold water temperature (Milner et al., 2009). In the Colombian Andes only six species were found above 1250 m and diversity decreased at higher elevations (Carvajal-Quintero et al., 2015). In Europe, the dominant native alpine fish are brown trout (*Salmo trutta*), in eastern North America brook trout (*Salvelinus fontinalis)*, and in western North America the cutthroat trout (*Oncorhynchus clarkia*) and the bull trout (*Salvelinus confluentus*). In New Zealand, alpine galaxias species are native in alpine rivers. However, non-native cold stenothermic species have been introduced, in particular European brown trout for sport fishing, which have eliminated or severely reduced the range of native species (Boddy and McIntosh, 2017).

Climate change has and will affect cold stenothermic alpine fishes markedly, due to warmer water temperatures and to downstream fishes expanding their range and out-competing species at higher elevations (Bruno et al., 2019). In addition, contraction of suitable range habitat also occurs as species cannot migrate upstream into colder waters due to barriers such as dams. Conversely dams may restrict upstream movement of downstream cool water fishes. Interestingly rock glaciers are ubiquitous in alpine environments and their springs can reduce maximum daily water temperature by up to 5 °C, thereby providing a cold water refugia (Harrington et al., 2017).

Biogeochemical and ecological functioning

Nutrient cycling and microbial processes

Glaciers play an important role in the carbon cycle, both storing and transforming organic carbon. Much of the carbon exported from glaciers is "ancient" with radiocarbon dating estimates suggesting ages of 600–8500 year BP (Singer et al., 2012). Interestingly, carbon age is related positively to bioavailability (i.e., readily available fuel for microbial processes; Hood et al., 2015). The highest DOC concentrations are usually found in basal ice and cryoconite (surface sediment) holes reflecting localized accumulation of organic material from deposited material and in situ production (Singer et al., 2012). Local soils and vegetation are the primary source in high altitude systems with longer distance atmospheric transport of aeolian dust (e.g., Saharan dust to European Alps) and anthropogenic aerosols (e.g., polycyclic- aromatic carbon—a measure for black carbon associated with industrial emissions). Rock glaciers and permafrost represent important stores of labile carbon with potential to provide bioavailable DOC to alpine rivers over the coming decades (Fegel et al., 2019). For groundwater channels DOC concentration is generally higher than for glacier channels (Tockner et al., 2002) and is likely to increase with permafrost melting. The depth of the aquifer channel is an important control with streams fed by deeper groundwater flow paths displaying lower DOC concentrations that are more refractory than those fed by shallow karst systems or with connections to the soil layer/riparian zone (Boix Canadell et al., 2019).

The flux of DOC from snowmelt or runoff channels (cf. Jacobsen, 2009) is highly seasonal—during winter and spring soluble organics accumulate beneath the snowpack and are preferentially flushed during the early melt season from the upper soil horizons. This first flush or snowmelt freshet is associated with complex humic carbon (aromatic) reflecting the terrestrial origin. As the melt season progresses a reduction in DOC concentration and aromaticity is apparent as connectivity between the stream channel and surface soils is reduced and flow paths become associated with mineral layers (Hood et al., 2003). The transport of glacier carbon to the stream network is limited to the summer melt season and is controlled by atmospheric forcing (e.g., air temperature, solar radiation and precipitation). Hence, labile carbon can only provide a stimulus for downstream heterotrophic activity in glacier-fed streams during summer melting. However, seasonal differences in carbon composition exist with terrestrial, vascular plant-sourced material dominating during the early melt season and shifting to a more microbial protein-dominated signal as supraglacial channels link cryoconite holes to the drainage network (Hood et al., 2015). Despite seasonal shifts in composition, the age of the exported carbon remains relatively consistent across seasonal melt cycles.

While nutrient concentrations are generally low in alpine streams, there are distinct seasonal dynamics associated with the predictable shifts in water sources (Tockner et al., 2002). It is thought that most nutrients (N, P and C) are linked to short term atmospheric deposition. This results in the seasonal snowpack representing the major nutrient source (Mladenov et al., 2012). Hence, the mass associated with fluxes varies spatially but the mechanism by which the nutrients are delivered—i.e., through snowmelt—is consistent. This results in distinct seasonal pulses of nutrient release into the alpine river network (Fig. 9). Soluble Reactive Phosphorus (SRP) concentrations are generally highest in glacier meltwater and associated with phosphorus release via glacier rock weathering and reduced potential for instream uptake (Hood et al., 2009). Glacier runoff can also act as a source of N and may be associated with ammonium (NH_4^+) sorption to suspended sediments (Milner et al., 2017). Studies assessing nutrient uptake in alpine streams are limited; however, a study by Scott et al. (2010) found that N and P travel conservatively in supra glacier-fed streams, suggesting demand for nutrients was either limited or saturated. In snowmelt and groundwater dominated alpine streams in N. America, uptake velocities of N and P were comparable to those observed for headwater streams in lowland regions but N uptake was reduced when lakes were present (Arp and Baker, 2007).

Primary production does not appear to be N-limited in temperate alpine regions and is generally only P-limited during spring (Robinson et al., 2002). During the summer melt season physical factors (e.g., turbidity, scouring and bed stability) appear to override any nutrient effects on primary production in snowmelt and glacier-fed streams. Hence, water source can be seen as the key control on metabolic regime of alpine streams (Fig. 10; Canadell et al., 2020), with a distinct window of opportunity for benthic production in meltwater streams apparent in early and late melt season when turbidity and bed movement are lower

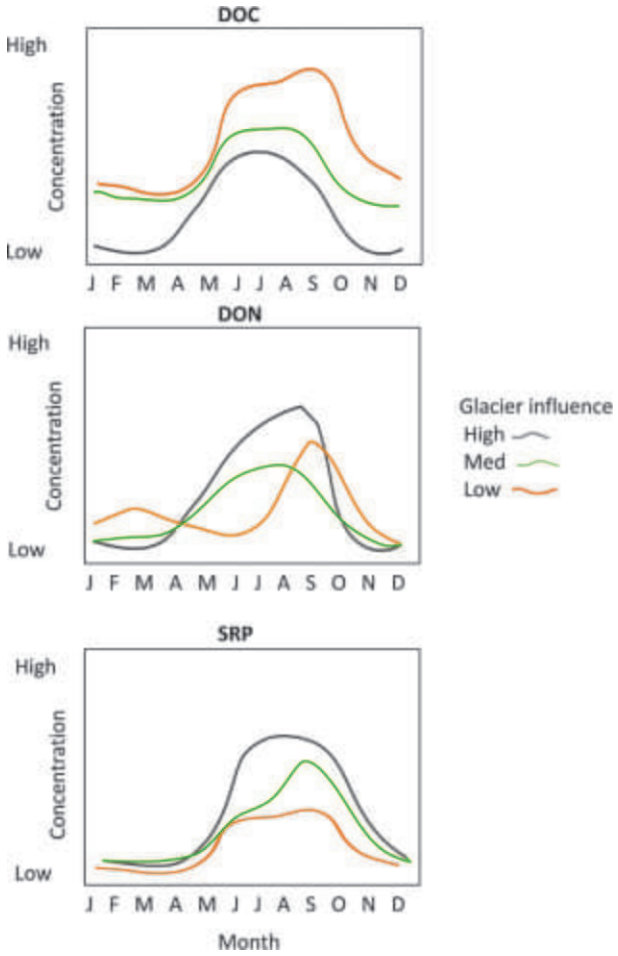

Fig. 9 Conceptual representation of the release of nutrients in alpine rivers with high (~50%), medium (~25%), and low (<1%) glacier cover in the upstream catchment. SRP = soluble reactive phosphorus, DON = dissolved organic nitrogen and DOC = dissolved organic carbon.

(Milner et al., 2001). Similarly, for decomposition of particulate organic matter (larch needles), groundwater-fed streams display faster breakdown rates than meltwater dominated channels (Robinson et al., 2000). This pattern of increasing breakdown with decreasing meltwater appears to be due to more rapid colonization by aquatic hyphomycetes and shredding macroinvertebrates. A study by Fell et al. (2021) found cellulose decomposition increased with decreasing glacier cover and was largely associated with changes in the fungal community, particularly an increase in the abundance of fungal a cellulose-degrading gene. While detailed microbial functional data remain limited, some patterns are emerging highlighting that glacier loss could increase the activity of bacterial functional genes important for N cycling (e.g., denitrification, nitrification, and anammox; Ren et al., 2017b). Bacteria associated with glacier-fed streams displayed highly specialized enzyme activity, whereas krenal sediments were dominated by generalists that displayed enzyme activity more similar to communities from lowland streams (Freimann et al., 2013). This loss of specialization in enzyme activity provides an interesting analogy to the biotic homogenization expected for higher organisms (e.g., macroinvertebrates) as glaciers retreat under climate warming (Milner et al., 2017).

Species interactions and food webs

Alpine river food webs reflect the diversity of feeding interactions between trophic groups characteristic of mountain streams and from the emergent properties that arise from complex ecosystem networks (Fell et al., 2017). They are predominately supported by primary production, with the majority of feeding linkages occurring between macroinvertebrate and fish consumers and epilithic diatom and algal resources (Füreder et al., 2003). As the availability of these resources is often patchy and constrained by the low water temperature of mountain streams, alpine aquatic macroinvertebrates adopt highly variable feeding strategies to opportunistically exploit resource availability (Clitherow et al., 2013), which itself fluctuates with season, water source (Sertić Perić et al., 2021) and flow intermittency (Siebers et al., 2021). For example, detritus (particularly the attached fungi) is a variable but often significant source of nutrients, particularly in many groundwater-fed streams, and the ancient carbon released from melting ice can contribute

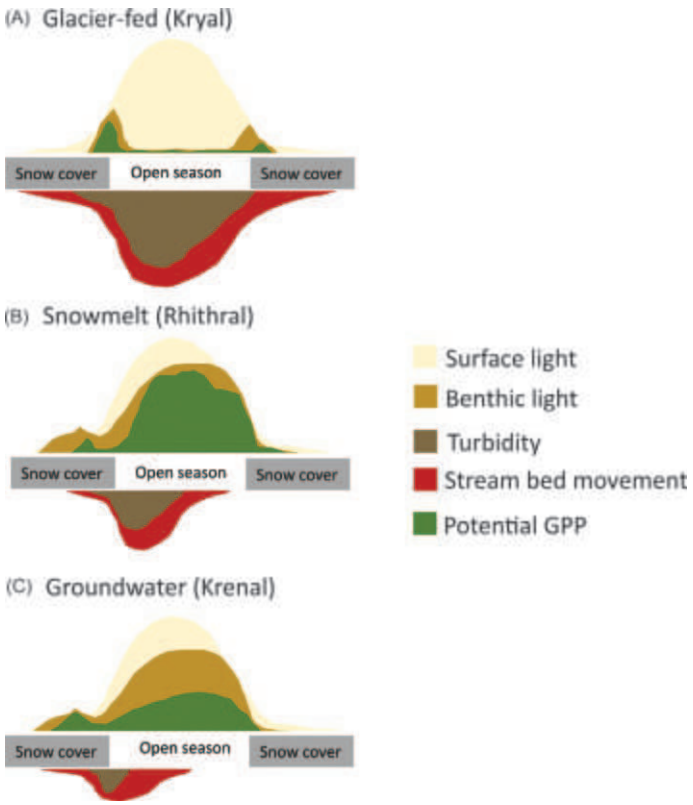

Fig. 10 Conceptual model of productivity regimes and physiochemical controls for the major stream types in alpine regions: (A) glacier-fed, (B) rhithral and (C) krenal stream. Modified from Canadell MB, Gómez-Gener L, Clémençon M, et al. (2020) Daily entropy of dissolved oxygen reveals different energetic regimes and drivers among high-mountain stream types. *Limnology and Oceanography* DOI: 10.1002/lno.11670.

to the diet of microbial consumers in glacier-fed waters (Zah et al., 2001). These opportunistic, generalist and omnivorous feeding behaviors were identified through stable isotope studies (e.g., Zah et al., 2001) and then confirmed by gut contents analysis. A meta-analysis of food webs from a wide range of river ecosystems found the highest directed connectance (proportion of possible feeding connections) in a glacier river food web from the Austrian Alps (Clitherow et al., 2013). This suggests the effects of local extinctions will rapidly propagate through food webs in glacier-fed rivers.

Cold water temperature, turbidity and bed instability of alpine streams typically limit productivity (Fig. 10) and associated abundance and biomass of many taxa, ensuring that alpine river food webs have low numbers of nodes and feeding linkages (Clitherow et al., 2013). This is particularly the case for glacier-fed rivers, where colonization by large predators is minimized by low temperature, repeated channel shifting disturbances and low availability of prey (Fell et al., 2017). As a result, many alpine river food webs are characterized by shorter mean food chain lengths and weaker size structuring when compared to streams and lakes from lower elevation (Clitherow et al., 2013). As glaciers retreat and the relative contribution of groundwater, springs, and precipitation increase as post peak-flow ice melt inputs decline, alpine river food webs can be expected to have increased number of nodes, links, and chain lengths (Niedrist and Füreder, 2017; Fig. 11). However, additional gut contents studies are required to determine the implications for species-level interactions (Fell et al., 2017). Changing water sources may also have implications for body mass as glacial-river specialists (*Diamesa* spp.) are larger in glacier dominated streams than more benign groundwater streams. This difference in body mass is likely due to the environmental conditions in glacier-fed streams limiting colonization by potential competitors and adaptation of *Diamesa* to the cold water temperature (Niedrist et al., 2018).

Anthropogenic threats and conservation priorities

Alpine regions are considered sentinels of global change that are generally more "pristine" than lowland regions and more sensitive to environmental variability (Hannah et al., 2007). The cryospheric component of alpine regions is particularly important for alpine river ecosystems (see Fig. 2), but it is also particularly sensitive to climate change. Alpine regions across the globe have reported a shrinking cryosphere with declines in snow, ice and permafrost extent impacting seasonality and river flow volume (Hock et al., 2019). Changing flow regimes have implications for a range of ecosystem services ranging from irrigation and water supply to hydropower production and fisheries (Milner et al., 2017). As the flow regime becomes more unpredictable, and the frequency and magnitude of extreme high and low flow events increases, specialist cold stenotherm taxa are likely to go extinct or see substantial

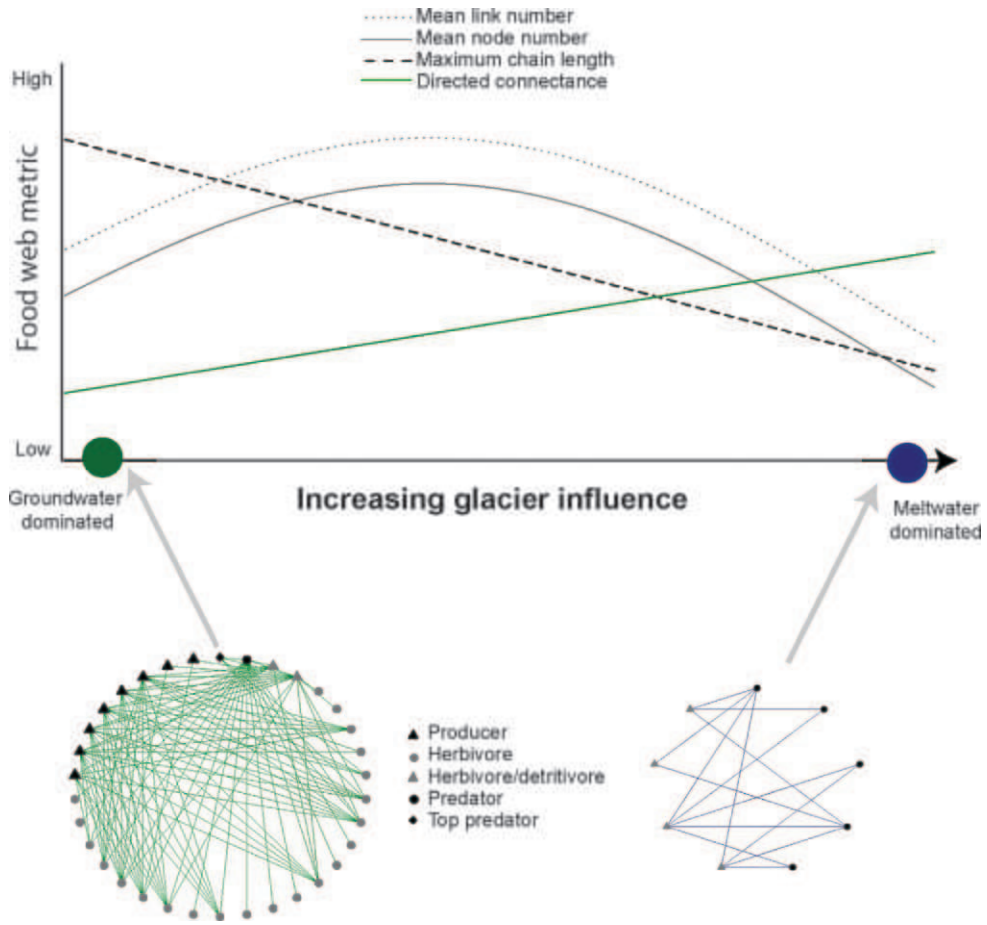

Fig. 11 Schematic representation of changes in river food-web connectance and web metrics as a function of increasing glacier melt contribution to bulk discharge. Observed connectance food webs are displayed for sites along a gradient from low to high glacier influence. Modified from Fell SC, Carrivick JL and Brown LE (2017) The multitrophic effects of climate change and glacier retreat in mountain Rivers. *BioScience* 67: 897–911.

reductions in range (Muhlfeld et al., 2020). Warmer temperatures and lower flows are likely to result in an increase in emission of CO_2 to the atmosphere from in-stream processes (Fell et al., 2021) and a reduction in transport of autochthonous organics to downstream ecosystems (Ulseth et al., 2018). Legacy contaminants (e.g., black carbon, mercury, pesticides, and other persistent organic pollutants) locked in glacier ice have increased downstream as glaciers recede, but their impacts are largely unexplored (Milner et al., 2017).

Hydropower developments are prominent features of alpine regions in Europe, North America and Asia and, while a renewable energy source, they result in the unsteady release of water to rivers (i.e., hydropeaking). This has significant implications for both the physical habitat and biotic communities with potential to have major impacts on ecosystem structure and function (Bruno et al., 2019). However, recent work has highlighted that water abstraction alone can improve habitat conditions further downstream through an increase in the relative contribution of less turbid and groundwater sources (Gabbud et al., 2019), but habitat directly below the intakes (~1 km) is devoid of fauna. Furthermore, intake flushing that generates sediment-laden flows can destabilize large areas of stream bed with significant impacts on macroinvertebrate abundance and diversity. As alpine glaciers retreat they will provide new opportunities for damming and hydropower (Milner et al., 2017) so careful management of operations are required to optimize energy production while minimizing environmental impacts.

Seasonal tourism in alpine regions has obvious implications for water quantity associated with peak water demand during winter coinciding with the period when water availability is lowest (Vanham et al., 2008). Implications for water quality have also been noted with increased concentrations of pharmaceuticals and personal care products recorded in streams close to major tourist resorts (Mandaric et al., 2017), with the impact on river water quality most pronounced in winter when stream flows are lower. In addition, the increased use of salt to de-ice roads and other impervious surfaces to facilitate winter tourism results in increased salinization of alpine river systems with currently unknown impacts on biota (Niedrist et al., 2021).

Given the complex nature of climate change impacts on alpine ecosystem structure and function, current legislative and conservation policy mechanisms need to be realigned. In particular, a shift in focus towards holistic ecosystem functioning conservation is required (Khamis et al., 2014). Due to limited potential for preventative intervention in these systems, conservation

strategies should focus on: (i) the maintenance and enhancement of connectivity within and between alpine river basins, (ii) protecting refugia for cold stenotherm (e.g., rock glacier-fed streams), (iii) improvement of hydropower operations to minimize impacts on river ecosystems, and (iv) where possible control and reduction of additional anthropogenic stressors such as erosion associated with ski-run creation and water pollution from tourist resorts.

Conclusion/Synthesis

This chapter has provided an overview of the varied nature of alpine river ecosystems from small stable springs to turbid glacier-fed torrents and has highlighted the important linkages between climate, hydrology and ecology. As a consequence of the strong coupling between climate and hydrology in alpine regions, the stream and river ecosystems are particularly sensitive to climate change. Currently biodiversity patterns (across multiple groups of organisms) are largely deterministic with meltwater contribution to flow a major control on alpha diversity and community structure. However, reductions in meltwater generation will have implications for stream habitat properties and could promote biotic (and functional) homogenization, a reduction in beta diversity and loss of cold stenotherms. The cryosphere melt dynamics in alpine regions are an important control on solute and nutrient concentrations, with loss of ice likely to lead to increased DOC export but a reduction in SRP and N. This change in water source will also have important implications for stream metabolism as the open season or "window of opportunity" for algal growth is extended, which in turn can facilitate an increase in secondary production and food web complexity. Beyond climate induced cryosphere shrinkage and the associated changes in water source dynamics, a number of other threats to alpine stream ecosystems have been identified. The most poignant of these threats are associated with the expansion of infrastructure for hydropower generation and tourism. As we move into an era of accelerated environmental change and biodiversity loss there is a clear need to realign legislation and conservation efforts for alpine streams, focusing on enhancing connectivity between and within river basins, promoting better management of hydropower activities and development for tourism. An additional challenge to implementing successful conservation strategies is linked to gaps in knowledge of ecosystem functioning, largely due to the logistical challenges associated with sustained monitoring campaigns, particularly during the winter months, or at the high altitudes associated with equatorial alpine environments.

Knowledge gaps

Despite increased research interest in alpine stream ecology over the last 30 years, gaps in our knowledge and understanding still exist. These can be split into four key groups with some of the most poignant questions outlined below.

Biodiversity and zoology. What is the extent of cryptic biodiversity in alpine streams (particularly among invertebrates) and is it more pronounced for equatorial regions? What is the distribution of aquatic alpine mammals and amphibians and are these ranges shifting with climate? How important are under snow/winter dynamics and processes for maintaining biodiversity?

Ecosystem function and species interactions. Do we see consistent patterns in connectance based food webs across latitudinal gradients, and do inferences made from quantitative assessments of energy transfer provide new insights into community resilience? Does the biofilm function and nutrient cycling of a given stream reach follow predictable patterns based on habitat conditions? To what extent does our understanding of ecosystem structure and function from temperate regions hold for alpine regions in the tropics/sub-tropics?

Impacts of anthropogenic activity. What is the impact of legacy contaminants (i.e., those released from melting glaciers) on biodiversity and ecosystem function? What are the implications of extinction of cold stenotherms for species interactions in alpine streams? How are the suite of anthropogenic pressures modifying the climate-environment-ecology cascade outlined in this chapter?

Methodological. Are there implications of making inferences based on time-series vs. chronosequences and do these vary with latitude? How well have we constrained the uncertainty associated with projections of change and what does this mean for conservation activity?

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Dryland Rivers and Streams

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor, LeRoy Poff.

Glossary

100-year flood A storm event that has less than a 1% chance (frequency) of being exceeded in intensity (rainfall rate) and duration (length of storm) in any given year.
Aridity index Numerical index of the degree of dryness of a region's climate, or, mathematically, the ratio of the average annual precipitation to the potential evapotranspiration.
Dryland river A river that occurs in regions that have an aridity index <0.65.
Ephemeral A non-perennial river or stream without a substantial groundwater connection that flows for a short period of time, typically only after precipitation events. These waterways are hydrologically losing surface water the majority of the time when considering long-term flow patterns.
Hydrological persistence Significant temporal dependence between flow observations over a long time span in a river.
Intermittent A non-perennial river or stream with a considerable connection to the groundwater table, having variable cycles of wetting and flow cessation, and with flow that is sustained longer than a single precipitation event. These waterways are hydrologically gaining surface water most of the time when considering long term flow patterns.
Non-perennial Any lotic, freshwater system that periodically ceases to flow and/or is dry at some point in time and/or space.
Perennial A continually flowing system.
Potential evapotranspiration (PET) The amount of evaporation and transpiration from a surface to the atmosphere that would occur given sufficient water availability (e.g., ground saturation).

Introduction

Dryland rivers are those that occur in hyper-arid, arid, semiarid, and dry-subhumid climates of the world, or regions that have an aridity index of <0.65 (U. N. E. P., 1992). Drylands make up 40–50% of the Earth's surface and sustain 30–40% of Earth's population (United Nations, 2016; Heritage et al., 2019). The term "dryland rivers" has historically been used to describe lotic

 https://doi.org/10.1016/B978-0-12-819166-8.00156-0

ecosystems that do not continuously flow, but this is a misnomer as non-perennial rivers and streams are not unique to drylands and exist in all climates and biomes (Busch et al., 2020). Further, perennial waterways are present and important in dryland climates. For our purposes, we use the definitions for "non-perennial," "intermittent," and "ephemeral" rivers as recommended by Busch et al. (2020), who based this terminology on a systematic literature search of all terms used to describe these types of non-flowing rivers and distinguish them from flowing rivers (see *Glossary* for definitions).

The major driving force that generates and maintains drylands is the climate of these areas, particularly the temporal dynamics of water gains and losses. Water is a key currency in drylands (Allen et al., 2014) and plays four key roles in dryland environments: (1) maintenance of biodiversity, (2) chemical solvent for other substances, usually salts, (3) medium of mass transport, and (4) direct energy source, which can govern runoff by impacting infiltration (Thornes, 2009). High-pressure and dry air masses dictate the regional climate by impeding low-pressure, precipitation-bearing air masses. Topographic barriers also form drylands by constraining these air masses and creating rainshadows (e.g., deserts in the southwestern U.S. and on the Tibetan plateau). In addition, drylands can be formed in the center of large continents (e.g., Eurasia) due to large distances from oceanic moisture. Storms in drylands are often characterized as explosive, localized convective systems due to uneven surficial heating. But frontal systems can also be dominant, as seen in Western Australia (Cordery et al., 1983) or in northern and central Australia, where monsoon incursions from the Indo-Pacific basin dominate precipitation patterns (May and Ballinger, 2007). Irregular oscillations of sea surface temperatures, such as El Niño–Southern Oscillation (ENSO) (Evans and Boyer-Souchet, 2012) and the Indian Ocean Dipole (Ashok et al., 2003), can be the main contributors to shifts of rain- or snow-bearing systems on many continents. In regions where rainfall is relatively high, the even higher potential evapotranspiration (PET) becomes the first-order control in forming drylands (Bull and Kirkby, 2002). Here, the sheer deficit between precipitation and PET, along with their pronounced temporal variability, often makes rainfall run off quickly, leaving these rivers dry for many months at a time.

Even though deserts are not considered global biodiversity hotspots (Durant et al., 2012), they have high endemism (Sosa et al., 2020). Within these arid biomes, dryland rivers (especially perennial dryland rivers) house a disproportionate amount of the regional biodiversity (Stromberg et al., 2009). Because water is such a severely limiting resource in these systems (Allen et al., 2014), the structure and functioning of intermittent rivers and ephemeral streams (IRES) in drylands are governed by the timing and magnitude of water delivery (Datry et al., 2018a), with dramatic increases of ecosystem productivity (Fisher et al., 1982) and local recruitment (Boulton and Lake, 1992) after hydrological events.

Dryland rivers are unique from perennial, intermittent and ephemeral streams in more mesic biomes (Fig. 1). First, dryland rivers are some of the most variable and unpredictable systems in the world (Bunn et al., 2006a; Petts, 2017). Second, these rivers

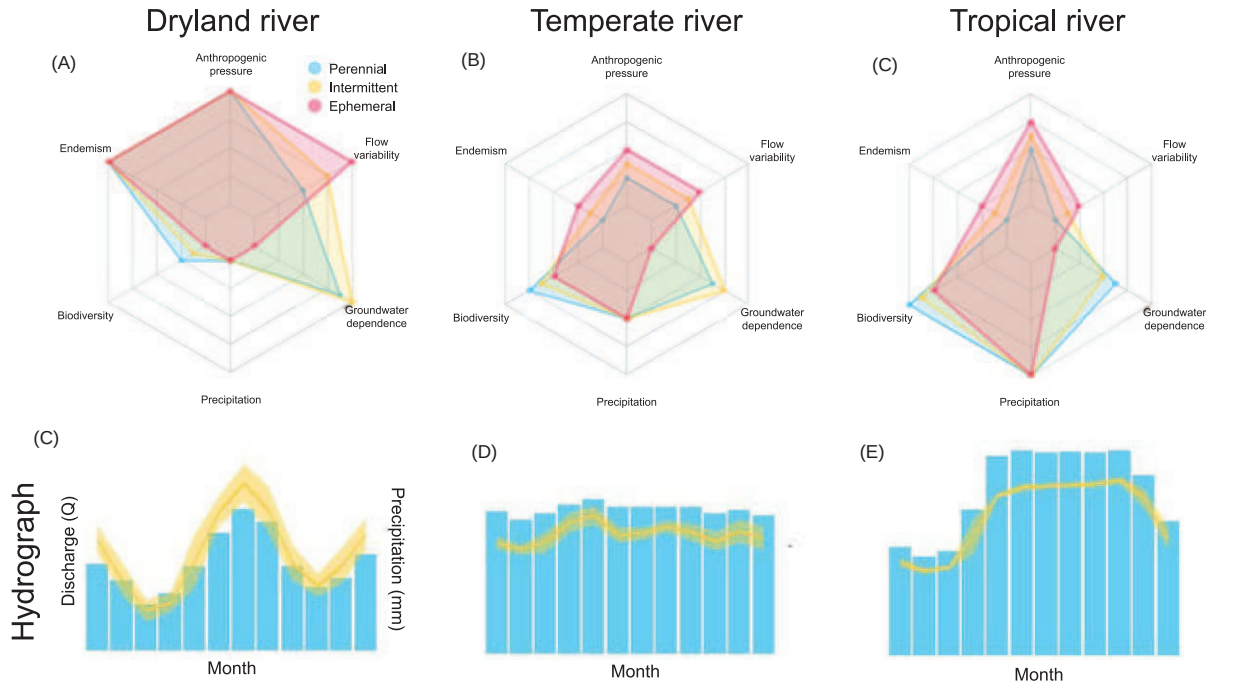

Fig. 1 Conceptual radar plots of key features of typical perennial (blue), intermittent (yellow), and ephemeral (red) rivers in dryland (A), temperate (B), and tropical (C) regions. Axes depict relative values of each variable for each river type and include flow variability (measured on an annual scale), groundwater dependence (or the proportion of stream flow that is supported by groundwater sources), precipitation (or the relative annual precipitation for a given watershed), biodiversity (associated with the stream and surrounding riparian zone), endemism (or the number of unique species in the watershed), and anthropogenic pressure (measured as the degree to which human activities are currently impacting these systems globally). Values increase moving out from the center of each radar plot. Overlapping colored contour lines highlight key differences in perennial, intermittent, and ephemeral streams within each region. Conceptual hydrographs depicting typical 20-year flow regimes for dryland (D), temperate (E), and trophic (F) rivers, including monthly precipitation (blue bars) and discharge (yellow lines with 95% CI bands).

have a higher dependence on aseasonal factors (e.g., catchment area, ENSO) compared to perennial rivers (Puckridge et al., 2000; Walker et al., 1995). Consequently, these rivers are likely to experience more intense effects of natural and anthropogenic disturbances, such as climate change. Dryland rivers also provide important ecosystem services, such as water security in arid regions (Petts, 2017). They provide water supply for agriculture, and their wetlands protect cities from the frequent, high magnitude flash floods to which these systems are prone. Pressure to develop water resources in dryland regions is increasing, threatening their under-appreciated resources and services (Kingsford et al., 1998; Petts, 2017). This pressure has led to some of the greatest examples of hydrological interference by humans, with large over-allocation of these resources for human uses in the 1970s, including in Australia (Petts, 2017) and the western United States (Young, 2014).

Here, we outline the key features of dryland rivers that distinguish them from temperate and tropical rivers and explore knowledge gaps in our understanding of how these systems function. Specifically, we outline the unique geomorphology, hydrology, biogeochemistry, and biology of these systems, highlighting key differences (e.g., flow variability, groundwater dependence, annual rainwater inputs, biodiversity, and endemism) in relation to temperate and tropical systems (see Fig. 1). Next, we detail how anthropogenic drivers will impact these systems (e.g., urbanization and climate change; collectively "Anthropogenic pressures," Fig. 1), and how these systems can be used as ecological laboratories to understand and advance fundamental research in metacommunity theory. Finally, we identify key knowledge gaps and provide a conceptual framework synthesizing key aspects of these systems, how their unique geomorphology, hydrology, biogeochemistry, and biology interact to influence their provisioning of ecosystem functions and services, and how global change is expected to alter these systems (Fig. 2).

Geomorphology of dryland rivers

The fluvial geomorphology of rivers differs by climate, with large differences between tropical, periglacial, and dryland rivers (Graf, 1988). Yet, few morphological features are unique to dryland rivers (Powell, 2009). This lack of distinctive features, coupled with the high amount of variation in their geomorphic forms that range from high-energy, high-gradient upland rivers prone to flash flooding to low-energy, low-sediment-load lowland systems with languid flows, makes classifying these systems difficult (Powell, 2009). The features that do make these systems distinct result from the variability and magnitude of their flow regime.

Flow variability is a key aspect of the flow regime shaping geomorphology (Graf, 1988). Highly variable flow regimes, which are typical of dryland rivers (McMahon, 1979), create geomorphic complexity and greater in-channel complexity (Thoms and Sheldon, 2002). For example, increases in extreme floods (i.e., magnitude and/or frequency) could trigger geomorphological state changes from mixed bedrock-alluvial systems with high geomorphic and ecological diversity to bedrock dominated channels with lower diversity and altered ecosystem function (Heritage et al., 2019; Milan et al., 2018). Further, since infiltration is a major threshold in dryland morphological development (Thornes, 2009), variability in delivery of flow to these systems leads to further morphological distinction and heterogeneity. Collectively, these aspects of flow variability and heterogeneous geomorphology lead to high levels of habitat patchiness and variable connectivity in space and time, supporting biodiversity (Quinn et al., 2000).

The magnitude of high-flow events also structures the geomorphology of dryland rivers. Because there is frequently little vegetation to buffer runoff from the surrounding landscape, dryland rivers worldwide are subject to episodic, extreme flood events, with channel scouring and stripping of streambed sediments. Flash flooding influences the architecture of dryland river deposits, and frequent, local, deep-scour events dramatically alter their geomorphic structure within short periods of time, making them difficult to study (Carling and LeClair, 2019). These restructuring events provide physical refugia important for sustaining biota through long-duration dry spells and sporadic precipitation events. Further, flood-flows enhance the relationship between flow variability and in-channel complexity (Thoms and Sheldon, 1997). The intensity of flow events dictates the transport of sediment downstream, with large flash floods capable of moving large bedloads for long distances in a short time. This means that the geomorphic structure of dryland river channels can change rapidly, and in extreme events leading to an entire rerouting of the channel (Field, 1994).

Hydrological regimes of dryland rivers

The high flow variability of dryland rivers is controlled by a climate characterized by extended dry periods that are punctuated by intense storm seasons (e.g., monsoons), or episodic events that provide most of the annual moisture during relatively short periods of time (Dare et al., 2012; McGrath et al., 2012; Fig. 1D). The hydrological inputs can be similar for dryland rivers as for other systems, but the relative importance of these factors can vary greatly compared to those of temperate systems, and their relative roles can change much more spatiotemporally compared to temperate systems (Thornes, 2009). In dryland rivers, gross water inputs occur at high intensities, but low relative volumes, with rain events coming at irregular intervals and exhibiting strong seasonal and interannual variability (Thornes, 2009). Low volume rain events and low soil moisture coupled with patchy vegetation adapted to rapidly uptake moisture means that interception rates (i.e., rates at which water is stored above the ground surface, primarily in vegetation) are low and variable in dryland systems, meaning that these systems are particularly vulnerable to changes in moisture patterns.

Dryland rivers exhibit unique characteristics compared to rivers in more humid regions. The primary trademark of dryland rivers is a flashy hydrograph with steep rising limbs, with delayed but sharp peaks, followed by steep falling limbs. The steep rising limbs mostly result from the explosive, convective rainfall typical of dryland areas. High evapotranspiration causes low antecedent soil moisture content, and thus a high initial abstraction into low-moisture soil, which can delay runoff responses to rainfall, especially low- or moderate-volume events. This results in a low runoff coefficient (i.e., total runoff volume divided by total rainfall). Another contributing factor is re-infiltration, a signature process in dryland hydrology, where upstream surface runoff is routed to and then infiltrates the dry streambed of downstream river sections (Nahar et al., 2004). Re-infiltration leads to transmission loss, or abstraction into the dry streambed, shortening the period of runoff, as reflected by the steep falling limbs of hydrographs. Re-infiltration is also important because the intense storms in dryland areas are often very localized, which means rainfall only occurs in a fraction of the whole watershed, and dry, downstream sections reduce those flows through re-infiltration. Because much of the excess surface water is directly lost to evaporation, inputs into dryland rivers are generally low and sub-alluvial aquifers (i.e., those just below the streambed that are often connected to groundwater sources) assume a more significant hydrological role in these systems, especially for non-perennial streams (Thornes, 2009). The infiltration that does occur in dryland rivers is largely controlled by soil and bedrock surface characteristics, and systems dominated by hard bedrocks and clay soils, for example, are prone to flash flooding; consequently, channel flow through these systems can range widely based on the frequency and magnitude of precipitation events as well as the channel geology and boundary conditions, including saturation of alluvium (Thornes, 2009).

Previous researchers used three major approaches individually or jointly to characterize intermittent flow regimes: in-situ monitoring, remote sensing, and hydrological simulation. In general, the first two estimates are essentially visual observations that lack spatial and temporal continuity (Zimmer et al., 2020). Given the highly varied nature of rainfall processes, hydrological modeling—when validated by in-situ and/or remotely sensed observations—promises to bridge the spatio-temporal gaps in assessment of these flow regimes in dryland areas.

Biological properties of dryland rivers

Environmental flows and the maintenance of biodiversity

Flow regulation—or the process of controlling stream flow through diversions, dams, and impoundments—is a common practice in dryland regions of the world, both for flood mitigation and water storage. Flow regulation in dryland rivers is highly divisive, providing both an important role in maintaining water supply for human use (e.g., irrigation) but also representing one of the most hydrologically destructive impacts in these sensitive ecosystems (Petts, 2017). For example, over 90% of the exploitable flow of the Murray-Darling river (south-eastern Australia), generated from only 21 mm of annual runoff, is often extracted for irrigation use within the basin, causing significant ecological impacts (Wedderburn et al., 2017). Indeed, dryland systems are more sensitive to flow alteration than perennial systems because of the ecological interplay between their hydrology and biology (Kingsford et al., 1998; Leigh et al., 2010).

The unique geomorphic and hydrological characteristics of dryland rivers are important for maintaining and regulating ecological interactions in these systems. For example, flow variability and flood timing are critical for sustaining biodiversity across the river-floodplain mosaic (Leigh et al., 2010). Biodiversity in these systems is strongly linked to rainfall-driven pulses (Free et al., 2013), which can cause dramatic booms in secondary production (Leigh et al., 2010; Free et al., 2013) that sustain aquatic and terrestrial biota over large spatial scales (Bunn et al., 2006b). Another ecologically important feature of the dryland river hydrological regime is hydrological persistence, or the significant dependence between flow observations a long time span apart (see Puckridge et al., 2000). Thus, the patchy wetted habitats that persist during dry periods require periodic hydrological recharge to replenish downstream nutrients and production (Petts, 2017), thereby sustaining biodiversity in these systems (Puckridge et al., 2000). Indeed, organisms in dryland systems often display traits that respond to periodic delivery of water and dissolved nutrients (e.g., increased ability to tolerate dry periods as well as strong dispersal ability; Sheldon et al., 2010). Further, hydrological persistence can play a role in exotic species invasions, as serial flooding favors recruitment of native species that are adapted to these highly variable flow conditions (Puckridge et al., 2000). Collectively, the biota of dryland systems are particularly susceptible to hydrological alterations that abstract river flow or reduce high flow variability.

With increasing human demand and climate change leading to increasing water stress, there is a clear need to better manage the water resources provided by highly stressed dryland systems, to minimize the negative social-ecological outcomes of water management. By directly integrating the different components of the hydrological regime—quantity, timing, and variability of flows—environmental flows aim to sustain and promote both the health and function of aquatic ecosystems and their biodiversity as well as the human cultures, economies and livelihoods that rely on these systems (Poff et al., 2010; Arthington et al., 2018). The move toward more integrated approaches to managing water is even more critical within dryland environments: the successful development and implementation of these frameworks reflects a collaborative approach that includes discussion of risk and balance of water needs (e.g. Chen and Olden, 2017; Conallin et al., 2018). These frameworks come with a clear need for consistent and long-term monitoring, but effective methods are not always in place for dryland rivers which limits their formal assessment (Chessman et al., 2010).

Ecosystem function and biogeochemical processes

Overview and processes in flowing systems

Biogeochemical processes in dryland watersheds are controlled by the degree of hydrological connectivity through the stream network. Variation in hydrological connectivity across dryland watersheds controls the downstream movement of dissolved oxygen, organic matter, nutrients, and microbial colonizers. Low allochthonous inputs and high light availability make many flowing desert streams autotrophic (i.e., gross primary production > ecosystem respiration) and net exporters of organic matter (Fisher et al., 1982; Fellows et al., 2009). A paucity of allochthonous organic matter means that ecosystem respiration in dryland systems can be highly linked and dependent on organic matter released from primary producers (Fellows et al., 2007; Townsend et al., 2011). Aerobic respiration occurs in porous hyporheic and parafluvial zones that are well connected to the stream surface and thus oxygenated, but anaerobic processes such as methanogenesis can occur in less well-connected bank sediments (Jones et al., 1995). Further, spring and groundwater inputs of bioavailable dissolved organic carbon (DOC) and dissolved inorganic nitrogen (DIN), can stimulate both rapid mineralization and algal growth (Burrows et al., 2020; Fellman et al., 2014).

Ponded and dry phases

Flow cessation has large impacts on the ecosystem function and biogeochemistry of dryland rivers. Gross primary production can remain high in residual pools (Fellows et al., 2007), but high turbidity can limit algal production to a narrow littoral band (Bunn et al., 2003). However, even small inputs of allochthonous resources can induce heterotrophy, particularly in nutrient-poor pools (Siebers et al., 2020). As aquatic environments recede and benthic sediments become exposed, particulate organic matter breakdown may decrease (McIntosh et al., 2017) and CO_2 released (Keller et al., 2020). Evaporative processes often control biogeochemical dynamics in ponded systems (Townsend, 2002), but the degree of groundwater-surface water connectivity can moderate this through dilution. For example, in the semi-arid northwest region of Australia, pools with higher evaporative losses and lower alluvial connectivity had higher nutrient (C, N, P) concentrations and higher proportions of humic and protein-like organic matter than pools with greater alluvial connectivity (Siebers et al., 2016).

Flow pulses after dry and low-flow phases

Flow pulses play a major role in shaping ecosystem metabolism, biogeochemical characteristics, and ecosystem processes of dryland rivers. Flow velocities and turbulence can drastically reduce primary productivity over days to weeks by scouring benthic surfaces (Fisher et al., 1982) and increasing water-column turbidity (Bunn et al., 2006a). Further, high-flow periods can cause a temporary increase in allochthonous DOC concentrations by increasing hydrological connectivity of the watershed (Wise et al., 2019). Although flow pulses can temporarily suppress algae production and alter biogeochemical conditions, they also reconnect isolated waterholes and floodplains, delivering water and dissolved and particulate resources that are key to the long-term persistence of dryland river ecosystems (Bunn et al., 2006a). Further, particulate organic matter accumulated in channels during dry phases, or delivered during flow pulses, can be subject to enhanced microbial activity upon wetting and lead to significant CO_2 fluxes to the atmosphere from dryland rivers at local scales (Datry et al., 2018b).

Food web dynamics

Due to the combination of extreme hydrological variability and opportunistic biotic responses to flood pulses, dryland rivers have unique food webs. Primary productivity and heterotrophy are important for sustaining food webs in these systems (McIntosh et al., 2017; see also "Biological properties of dryland rivers" section). Yet, because flows that provide rewetting and the delivery of upstream dissolved and particulate resources are episodic, autochthonous production often occurs in dramatic booms that generate a large biomass in a short time (Bunn et al., 2006a). This biomass boom can translate to high amounts of secondary production; in fact, one of the highest estimates of stream annual secondary production ever measured (i.e., 120.9 ± 18.0 g m^{-2} $year^{-1}$) occurred in Sycamore Creek, Arizona USA (Jackson and Fisher, 1986).

Consumers in dryland systems are often generalists that have adaptations to exploit pulses in resources that correspond with the changes in resource availability. Most consumers in dryland rivers have traits either allowing them to capitalize on a wide range of resources or to persist until favorable conditions and resources return. For example, traits like desiccation tolerance or burrowing can allow some organisms to persist during drying conditions, while strong dispersal ability can enable mobile predators (e.g., dragonflies) to track resource availability and boom cycles (Boersma et al., 2014; Bogan et al., 2014). Many consumer trophic interactions (e.g., fish predation) are excluded by temporary flow regimes, making these interactions less important in dryland rivers lacking fish, causing many of these systems to be driven by bottom-up trophic forces. Even in perennial dryland rivers, the effects of fish predation are likely to be weaker than in temperate systems. For example, in many perennial, low-gradient dryland rivers, waters are turbid due to large influxes of sediment, especially during the wet or monsoon season, and these systems naturally lack the large, visual predators typical of rivers in more temperate regions.

Yet the interactions that do exist in dryland rivers are likely to be strong given their adaptations to variable flow regimes characterized by periods of zero flow and drying. Whereas organisms in perennial streams are subject to faunal devastation during droughts (Hynes, 1958) that can lead to trophic rewiring (Lu et al., 2016), organisms in dryland rivers are adapted to extended periods of drying. There is some evidence that while the food webs in these systems contract during these periods, core ecological interactions persist, resulting in similar topologies as regional food webs (Peralta-Maraver et al., 2020). Additionally, aquatic

consumers in dryland rivers can exhibit relatively strong trophic connections to terrestrial food webs. This is, in part, because as drying intensifies, more and stronger linkages with terrestrial systems are created (McIntosh et al., 2017). Experimental evidence suggests that aridity enhances terrestrial consumer responses to water additions (Sabo et al., 2008; Allen et al., 2014), which has led to the idea of water as a "trophic currency" in drylands (Allen et al., 2014). Collectively, this evidence suggests that dryland river food webs might have resistant "multiscale backbones" (sensu Serrano et al., 2009) that enable core ecological functions to persist in these systems during drought conditions, but more research is needed to test this hypothesis.

Dryland river riparian ecosystems

The presence of a river can have profound consequences for dryland terrestrial landscapes. Riparian ecosystems are the portion of a terrestrial landscape immediately surrounding rivers and streams. Although riparian systems are important habitats everywhere (Selwood and Zimmer, 2020), they are especially unique in dryland climates (Free et al., 2013; Selwood et al., 2017). The presence of water in the river channel and its shallower water table can lead to a drastic difference in the dominant terrestrial vegetation in riparian compared to upland ecosystems. For example, in the drylands of the southwestern US, riparian areas are marked by mesic cottonwood and willow species that can access shallow groundwater through deep taproots. These trees create gallery forests in dryland streams that are vastly different from the scrub habitats upslope of the floodplain, which are dominated by more xeric shrub, grass, and succulent species (Lite et al., 2005).

Riparian zones in drylands can be of paramount importance to terrestrial animals. They are typically more productive habitats than uplands, and therefore have elevated energetic resources for consumers. Many bird species rely on riparian corridors in drylands. In the arid Southwestern US, for example, riparian zones in desert areas are key stopover sites for migrating birds during the spring, as woody riparian vegetation offers more perching sites than upland scrub vegetation and provides increased water and energetic resources (Skagen et al., 1998, 2005). Further, mammals often preferentially forage in riparian areas, even those that live in upland areas. For example, in drylands, mammalian carnivores have been shown to prefer riparian areas during especially dry times of year when productivity of upland habitats is limited (Soykan and Sabo, 2009). Finally, terrestrial invertebrates can be more abundant and diverse in riparian than upland habitats due to the availability of aquatic insect resource subsidies that many riparian arthropods prey upon (Ramey and Richardson, 2017). Within the riparian zone, river drying can alter the composition of terrestrial arthropods and lower their diversity (McCluney and Sabo, 2012). Because of the importance of riparian habitats to many different terrestrial taxa, they are often a high value area for conservation and management (Riis et al., 2020).

Environmental factors that influence water availability in floodplains and riparian zones are important determinants of riparian plant community composition and abundance. Accordingly, variation in streamflow in the river itself is a critical factor for riparian ecosystems at both ends of the hydrological spectrum. Flood magnitude, duration, and timing can be critical for the recruitment of certain pioneer riparian plant species. For example, in western North America cottonwood seed dispersal generally occurs after peak streamflows in the spring, and the receding stream exposes bare, moist soils in banks and bars where seeds germinate (Mahoney and Rood, 1998). But the vast majority of seedlings die if water table declines outpace root growth, such that only floods large enough to scour and generate bare soil, but also have gradual streamflow declines after the peak flow, allow cottonwoods to successfully recruit (Mahoney and Rood, 1998).

On the dry end of the hydrological spectrum, the lack of continuous surface flow can also be important for riparian ecosystems. Surface-flow permanence is related to groundwater table depth, such that when the river dries the groundwater table lowers as well. Some riparian tree species may require the presence of shallow groundwater, whereas other species may be able to access much deeper groundwater with longer taproots (Lite and Stromberg, 2005). Because water table depth typically varies with streamflow, this can lead to different riparian plant communities at continuously flowing river reaches versus those that are not. For example, in the Sonoran Desert in the US Southwest, riparian vegetation along perennial streams is more diverse compared to intermittent riparian plant communities, which are dominated by a less diverse assemblage of herbaceous and shrub species (Stromberg et al., 2007). These differences can reverberate throughout the rest of the riparian ecosystem. For example, changes in riparian plant communities associated with groundwater declines led to reduced avian diversity in one study (Merritt and Bateman, 2012), and another showed that ground-dwelling arthropods varied with riparian vegetation type at perennial vs. non-perennial reaches of the same river (Allen, 2016).

Despite their ecological importance, dryland riparian ecosystems are among one of the most imperiled ecosystems worldwide. One of the most common threats to these systems is invasive plant species, which can impact both riparian and stream ecosystems. For example, nonnative *Tamarix* spp. (salt-cedar) is widespread in riparian areas across the western US, and this species has been shown to alter the composition of riparian lizard, small mammal, and bird communities (Bateman and Ostoja, 2012; Fleishman et al., 2003). As discussed earlier, riparian vegetation and its inputs of leaf litter into the stream are critical to the food web and biogeochemical dynamics in streams, so changes in dominant riparian vegetation species can influence these aspects of stream ecosystems as well. Russian olive (*Elaeagnus angustifolia*) is another invasive riparian tree species in the western US, and its presence is associated with 25 times more leaf litter input to streams, increasing benthic organic matter storage while decreasing the efficiency of stream respiration relative to organic matter input (Mineau et al., 2012). In-stream nutrient dynamics are also affected by the Russian olive as it is a nitrogen-fixer, and stream reaches invaded by it have greater N concentrations and reduced N limitation of

stream biofilms (Mineau et al., 2011). Dryland riparian ecosystems are also being negatively impacted by changes in streamflow. Indeed, flow modification by dams typically reduces the frequency and magnitude of floods, this can prevent cottonwood recruitment and alter riparian vegetation community structure (Goodale et al., 2002; Stromberg et al., 2007). Water withdrawals and diversions that reduce stream flow can impact riparian vegetation, but efforts to restore streamflows have shown that flow resumption can reverse these effects and restore riparian habitat (Bigelow et al., 2020; Hillman et al., 2016).

Dryland rivers provide ideal case systems for advancing metacommunity theory

Temporal and spatial changes in aquatic habitat availability drive population and community dynamics not only locally but also regionally, as species interact within a river network or a landscape as part of a metapopulation and metacommunity, respectively. Metacommunity theories assume that changes in population trajectory or community composition are driven by interacting local (e.g., species interactions, environmental changes) and regional (e.g., dispersal of individuals) drivers.

In drylands, where aquatic habitats are scarce, dispersal and connectivity between remnant aquatic habitats is likely central in determining population and community structure of, for example, fishes (Jaeger et al., 2014) and invertebrates (Cañedo-Argüelles et al., 2015). Although the main pathways of recolonization post-drying are still debated, dry temporary streams can serve as dispersal corridors linking aquatic habitats, particularly for flying insects (Cañedo-Argüelles et al., 2015). Some invertebrates (Stubbington et al., 2019) and fishes (Rodríguez-Lozano et al., 2019) can also migrate vertically to the hyporheic zone where moisture is preserved and where they can persist during the dry season to recolonize when water resumes. Aquatic organisms typically are little resistant to drying; however, some strategies, such as diapause or dormancy (e.g., the burrowing tree frog, *Cyclorana alboguttata*, that can exist for years buried in mud in a state of torpor), can allow species to persist locally and maintain diversity under drying conditions (Boersma et al., 2014). These resistance strategies can be considered as "temporal dispersal" since dormant forms can persist in situ, sometimes for years and develop after local conditions become favorable (Buoro and Carlson, 2014). Local persistence and colonization capacity from refuges are thus key in determining dryland communities, but it remains unclear which of the temporal and spatial dispersal strategies maintain diversity in different locations within the landscape and among hydrological phases.

Learning from these approaches, management strategies should focus on preserving the aquatic habitats central to the metasystems, which provide sources of spatial and/or temporal colonizers (Ruhí et al., 2017). A better understanding of the pathways connecting populations and communities – and the effect of fragmentation on those – could also help in designing integrative management plans which sustain regional diversity under climate change.

Dryland rivers in urban systems

The behavior of rivers and streams in urban areas is regulated by human activities, including land cover, and infrastructure, especially stormwater management infrastructure. Until the late 20th century, with the adoption of the U.S. Clean Water Act in 1972, urban stormwater systems functioned primarily to shed water from the landscape as quickly as possible through drainage infrastructure consisting of concrete and pipes, often replacing natural riparian zones and ecosystems with concrete-lined channels optimized for maximum flow (Shuster et al., 2005). These developments increased discharge of roadway and urban pollutants into rivers (Booth and Jackson, 1997), reduced riparian areas (Walsh et al., 2005), and increased the velocity of runoff flows through the system, among other problems (Miller et al., 2014). In the USA, the intensity-duration-frequency (IDF) framework (Hershfield, 1961) for design of urban river and drain systems has led to systems that can shed or retain discharge from 100-year floods. Because much of the land development in the United States has occurred in drylands since the introduction of regulations associated with Low Impact Development (LID, Dietz, 2007) and Green Infrastructure practices (Fitzgerald and Laufer, 2017), newer southwestern dryland cities tend to support relatively modern, ecologically adapted riparian systems compared with older, well-watered eastern cities.

A remarkable feature of rivers, streams, and wetlands in dryland cities is the phenomenon of artificial riparianization, in which the large volumes of water delivered to dryland cities are released into dryland stream channels through wastewater discharge, causing perennial wetlands and streams to appear (Palta et al., 2017). This artificial riparianization process alters the hydrologic regime and thus species composition and ecosystem function. Additionally, it enables species that are uncommon in arid environments to establish in these ecosystems. These "accidentally restored" systems can serve as biodiversity hotspots in their own right, maintaining other ecosystems in decline (Bateman et al., 2015).

Dryland rivers in a changing world

Dryland rivers, which are among the most variable, unpredictable rivers in the world (Bunn et al., 2006a), are also subject to some of the most intense pressures from anthropogenic disturbances (Jaeger et al., 2014; Burrell et al., 2020). A major reason for this is water security. Not only are dryland rivers a source of water for a growing number of people (e.g., due to people disproportionately

moving to warmer, drier climates; Samson et al., 2012), but they also ensure food and economic security in arid regions by providing water for agriculture. Consequently, some of the most dramatic examples of hydrological interference can be seen in these systems (Petts, 2017).

Given the tremendous pressures on dryland rivers, there will likely be major impacts on the biodiversity of these systems and the services they provide. Because biodiversity in these systems is adapted to unpredictable, dynamic hydrological events, organisms endemic to these systems will likely be disproportionately affected by hydrological alterations (Ruhí et al., 2016). For example, flow regulation homogenizes flow regimes of these systems, which has been linked to factors that impact endemic species, including disrupting natural environmental cues native organisms use for reproduction and emergence (Ruhí et al., 2015). Mismatches in environmental cues, for example, can result in failed recruitment events in fish (Perkin et al., 2019) and alter consumer-resource linkages (Asch et al., 2019), which themselves link aquatic and terrestrial food webs (Nakano and Murakami, 2001). Moreover, many of the water column changes that impact endemic species favor invasive species, making it easier for species invasions to further threaten and reduce local biodiversity (Propst et al., 2008).

In conjunction with these anthropogenic pressures, climate change is expected to have disproportionate effects on systems in extreme environments (e.g., high latitude ecosystems, high-elevation deserts), including arid regions where climate change has already been associated with extreme changes (Birrell et al., 2020; Vincent, 2020). While the long-term average of climatic variables defines and characterizes dryland environments, unpredictable short-term variability (i.e., intra-annual variability) may be even more important for shaping river intermittency and altering river forms in diverse ways (see "Geomorphology of dryland rivers" section).

These complications require that climate change effects in dryland rivers be studied in context of predictions of increasing temperature and less frequent, higher magnitude flood events, as well as under different scenarios of change. These considerations are especially important given the profound, nonlinear changes expected for both ecosystems and human populations in dryland regions (Koutroulis, 2019). Additionally, intensifying droughts coupled with increasing water withdrawals is expected to decrease connectivity in dryland rivers, potentially altering fish dispersal and stocks, both seasonally and in the long term (Jaeger et al., 2014). Collectively, more extreme drying and flooding events will test the phenotypic plasticity (i.e., genetic-independent changes to an organism's behavior, morphology, or physiology in response to environmental change) of dryland river organisms to endure extreme changes, which in many cases are happening too fast for them to adapt (Woodward et al., 2010). Finally, with climate change expected to enhance the duration and intensity of drying in arid regions while increasing the frequency and duration of large magnitude floods, this uncertainty will lead to an intensifying struggle among stakeholders with competing interests, including those of indigenous peoples who use dryland rivers for social, cultural, and economic reasons (Barber and Woodward, 2018; Poelina et al., 2019). These issues will require proactive forms of inclusive communication and legislation to ensure environmental justice among all stakeholders (Shiva, 2016).

Conclusions and synthesis

Dryland rivers are highly variable, unpredictable systems that provide critical ecosystem functions and human services. Given that these systems have historically been understudied, and that their biodiversity has likely been underestimated (Ruhí et al., 2017), more focus on these systems is warranted, especially in context of how climate change will disproportionately affect them and interact with other anthropogenic disturbances to affect biodiversity and human wellbeing in the decades to come. Key knowledge gaps about dryland rivers include (1) how geomorphic (e.g., sedimentation, surface-groundwater exchanges) and biotic processes (e.g., dispersal and recruitment of organisms, food web dynamics) interact in these systems, particularly in high gradient systems prone to flash flooding, and (2) how these interactions relate to metacommunity dynamics, ecosystem functioning, and the provisioning of ecosystem services, and (3) understanding dryland rivers occurring in high latitude and high elevation regions, including in high- and low-elevation deserts and arctic regions, especially since these regions are expected to be disproportionately impacted by climate change (Birrell et al., 2020; Vincent, 2020).

Despite these knowledge gaps, progress can be made to better manage dryland rivers through better integration of knowledge we do have into adaptive management plans, which will require better communication among scientists and other stakeholders. Dryland rivers lack large-scale, long-term adaptive management programs, and there has been a general failure to integrate dryland rivers in whole-watershed management plans (Petts, 2017). Further, recent policy changes threaten the health and service provisioning of dryland rivers, including efforts to change the classification of dryland rivers to relax their environmental regulation (Popovich et al., 2021). These problems are compounded by piecemeal regulation across state, provincial, and national boundaries, which is particularly problematic for dryland rivers reliant upon infrequent pulses of water and nutrients (Kingsford et al., 1998).

Given the need for a of more holistic, collaborative resource management for dryland rivers, including management that crosses political boundaries and includes all stakeholders in management decisions (Kingsford et al., 1998), we propose an integrated nested-DPSIR framework (sensu Atkins et al., 2011) for understanding and adaptively managing these systems in the face of climate change and other anthropogenic pressures (Fig. 2). The DPSIR framework includes drivers (human activities impacting a system), pressures (causes of the human problems), state changes (the change in background status), impacts (impacts on ecosystems, ecosystem services, and human society), and responses (the human response). Key anthropogenic drivers causing pressures, state changes, and impacts to dryland river systems include (but are not limited to) urbanization, flow regulation, agricultural practices,

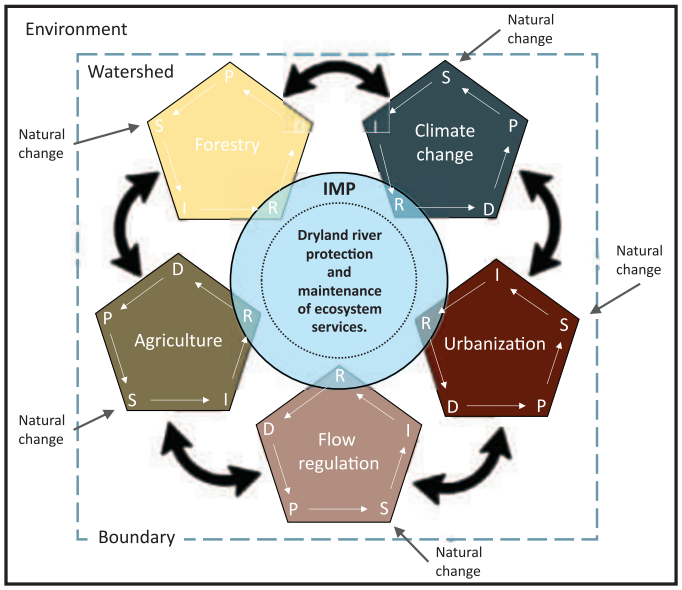

Fig. 2 Adaptive management framework for dealing with key anthropogenic system drivers expected to affect dryland rivers. This nested DPSIR framework shows the relationship of five key system drivers (D) and associated pressures (P), state changes (S), and impacts (I), which require management in the form of human responses (R). The dashed blue line depicts the watershed boundary, with everything outside this line representing the natural environment and changes associated with natural processes. Pentagons within the watershed boundary depict five key anthropogenically driven processes impacting dryland rivers. Effective management of dryland river systems will require adaptive human responses (to these and other drivers) and consider these processes together in a single, integrated management plan (blue circle). Modified from Atkins JP, Burdon D, Elliott M, and Gregory AJ (2011) Management of the marine environment: Integrating ecosystem services and societal benefits with the DPSIR framework in a systems approach. *Marine Pollution Bulletin*, 62(2): 215–226.

forestry practices, and climate change, which themselves are impacted by natural environmental change (Fig. 2). The adaptive, nested-DPSIR approach integrates existing management practices for key impacts to dryland river systems, while remaining flexible to the rapid accrual of basic knowledge about these systems that is important for proper management and protection in the context of an uncertain, changing world.

See Also: Structures and functions of Inland Waters - Rivers: Dispersal in Stream Networks: Meta-populations and Meta-communities

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Intermittent Rivers and Ephemeral Streams

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Disturbance An event in which physical forces alter habitats, change resources and cause a biotic response characterized by the loss of organisms. Floods and drying are common disturbances in rivers.
Dry phase A period of time in which a channel has no flowing surface water, although isolated pools can persist, and water may be present beneath the sediment surface.
Ephemeral A flow regime in which flowing water occurs only in response to rainfall events, and flowing phases are thus unpredictable and typically short, lasting hours to weeks.
Flow cessation The point at which water in an IRES channel stops flowing from upstream to downstream.
Intermittence The state or quality of being *intermittent*, *ephemeral*, or having any other flow regime in which surface water sometimes stops flowing.
Intermittent rivers and ephemeral streams (IRES) Rivers and streams with ephemeral, intermittent or other flow regimes in which surface water sometimes stops flowing and is often partly or completely lost, resulting in channel drying, with or without isolated pools.
Intermittent A flow regime typically characterized by relatively long, predictable flowing phases and shorter, seasonal dry phases. Intermittent flow typically resumes in autumn/winter and continues until spring/summer, reflecting changes in precipitation and temperature.
Perennial rivers and streams Rivers and streams in which surface water never stops flowing from upstream to downstream.
Resilience The capacity of a biological entity (e.g. a species) to recover by colonization after a disturbance (such as drying, for an aquatic organism) ends.
Resistance The capacity of a biological entity (e.g. a species) to tolerate a disturbance (such as rewetting, for a terrestrial organism) in situ.

Intermittent rivers and ephemeral streams: Dynamic aquatic-terrestrial ecosystems

Intermittent rivers and ephemeral streams (IRES) are all rivers and streams in which water sometimes stops flowing, and many dry in part or completely (Datry et al., 2017a). The world's most widespread type of river ecosystem (Messager et al., 2021), IRES range from small ephemeral streams that occasionally flow for a few days after heavy rain to large intermittent rivers that recede to isolated

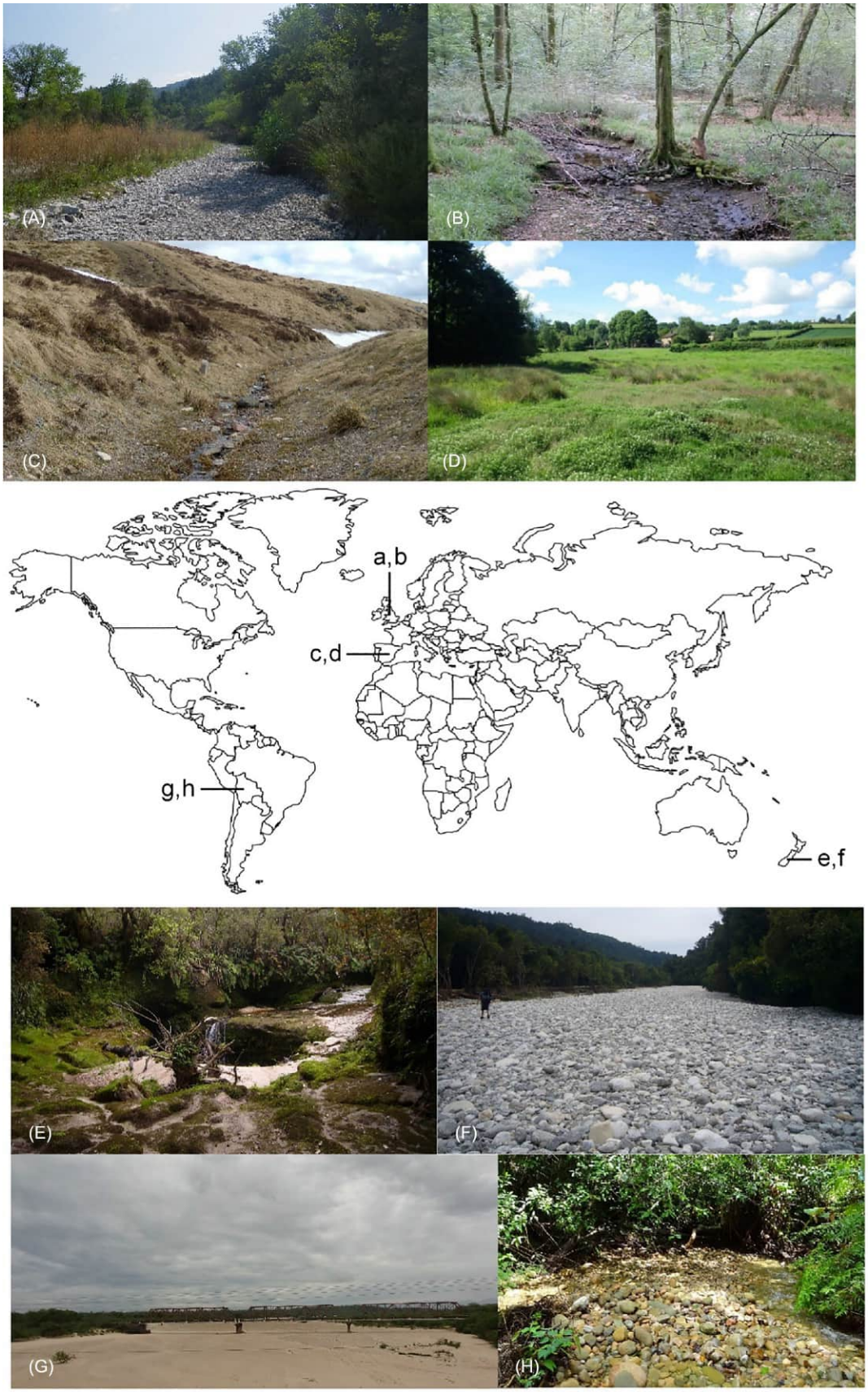

Fig. 1 Intermittent rivers and ephemeral streams are dynamic ecosystems in which habitat diversity varies within and among regions. Dry phases are shown in: (A) an alpine system and (B) a wooded Jura mountain stream, France; (C) a near-dry channel in the uplands of Scotland as snow recedes and (D) a vegetated 'winterbourne' stream in the lowlands of England, United Kingdom; (E) a karst limestone stream and (F) an alluvial cobble-bed river, New Zealand; and (G) a sand-bed channel and (H) an Amazonian stream, Bolivia. Photos: (A–B) and (E–H) T. Datry; (C) C. Macadam; (D) © Environment Agency of England; map © J. Bruce Jones (2019).

pools or dry only during severe droughts (Datry et al., 2017a). Also known globally as temporary or non-perennial rivers, the local names for IRES that exist around the world—such as arroyos, ramblas and winterbournes—highlight the physical diversity and cultural importance of this biome to people living in IRES basins (Steward et al., 2012). Several studies have assigned names to IRES classes in which flow ceases for differing durations and with varying predictability (e.g., Uys and O'Keeffe, 1997; Williams, 2006; Gallart et al., 2012), but terminology remains inconsistent, due to the considerable environmental variability within and between IRES subtypes (Fig. 1; Datry et al., 2017a; Shanafield et al., 2020; Zimmer et al., 2020).

IRES show complex alternations between aquatic and terrestrial conditions in both space and time, with important consequences for physical and biological processes (Datry et al., 2017a). They thus comprise dynamic, shifting mosaics of flowing, ponded and dry habitats, the extent and connectivity of which continually vary across drainage basins in response to groundwater levels and/or surface runoff and thus river discharge (Stanley et al., 1997; Datry et al., 2014; Jaeger et al., 2014). During long, uninterrupted flowing phases, physical habitats and ecological communities can become increasingly similar to those in nearby perennial rivers or streams. Equally, drying can have effects on communities and ecosystem processes that persist long after flow resumes (e.g., Datry et al., 2011; Piano et al., 2019), due to the replacement of drying-sensitive species by those with adaptations to drying (Armitage and Bass, 2013). After flow ceases, lentic waters ranging from extensive ponded reaches to tiny isolated pools are soon colonized by aquatic species from nearby surface waters such as ponds (Argyroudi et al., 2009). During dry phases, although riverbeds can remain distinct from adjacent soil-based environments (Arce et al., 2019), they can support a diverse range of terrestrial organisms.

In this chapter, we explore the hydrological, biogeochemical and ecological features that characterize a diverse range of IRES. We first present the global distribution and diversity of these ecosystems and outline their flow permanence regimes, including shifts between flowing, ponded and dry phases. We then explore how spatial and temporal heterogeneity in environmental conditions influence biogeochemical processes, aquatic and terrestrial communities and thus ecosystem functioning in IRES. Lastly, we identify major knowledge gaps, to stimulate further research that advances our understanding of, and thus our ability to protect, these unique ecosystems.

The global diversity of IRES ecosystems

IRES occur on all continents and dominate arid, semi-arid, and dry sub-humid regions, which represent more than half of the Earth's land surfaces (Messager et al., 2021). For example, 70% of Australian rivers are IRES (Sheldon et al., 2010), as well as up to 94% of river lengths in southwestern USA (i.e., Arizona, California, Colorado, Nevada, New Mexico and Utah; Levick et al., 2008). IRES also occur across alpine, boreal, continental, mediterranean, oceanic, polar and tropical regions (Datry et al., 2017a; Stubbington et al., 2017b). It is likely that every river network includes IRES, because small headwater streams—which are estimated to represent more than 70% of the total river network length—typically experience flow cessation and drying events (Benstead and Leigh, 2012).

IRES are increasing in space and time due to interactions between climate change and other human impacts (Larned et al., 2010; de Graaf et al., 2019). Climate-driven shifts from perennial to intermittent flow are predicted in the next decades for streams and rivers across global regions including Australia, Brazil, the southwestern USA, the Caribbean, southern and western Africa and the Mediterranean Basin (Döll and Schmied, 2012). In addition, in many natural IRES, dry phases are increasing in duration, frequency and spatial extent (e.g., Larned et al., 2011). Conversely, some natural IRES are predicted to become perennial in the Alps, Siberia, Canada and Alaska due to warmer winters, snowmelt and glacial melting (Döll and Schmied, 2012; Paillex et al., 2020).

The hydrological template of IRES

IRES are dynamic mosaics of lotic (aquatic, flowing), lentic (aquatic, ponded) and dry (terrestrial) habitats (Fig. 2). Integrating concepts and methods from lotic, lentic and terrestrial ecology can therefore enhance understanding of these unique ecosystems (Datry et al., 2014; Stubbington et al., 2017a,b).

Changing in-channel conditions: From wet to dry

Following a decline in surface runoff and/or groundwater levels (Fig. 2A), flow ceases and aquatic habitats within IRES channels typically fragment into pools (the ponded phase, Fig. 2B). The loss of flowing water exerts a strong pressure on biogeochemical processes and associated biota (Boulton, 2003). In isolated pools, water quality can quickly decline due to high temperatures, low dissolved oxygen and high nutrient concentrations (von Schiller et al., 2017), especially in pools without a connection to subsurface flow. Isolated pools often disappear as the duration of the dry phase increases, resulting in the complete loss of surface water (Fig. 2C). From this point, the surface channel no longer includes aquatic habitats, although it rarely resembles adjacent terrestrial habitats, instead retaining riverine characteristics (von Schiller et al., 2017; Arce et al., 2019). Sometimes, the subsurface sediments can remain saturated throughout a dry phase, offering a potential refuge in which aquatic organisms can survive (Stubbington, 2012). However, these subsurface sediments typically dry—but may retain moisture in interstitial spaces, especially in regions with year-round rainfall, enabling them to support aquatic organisms with some degree of desiccation tolerance (Boulton, 2003; Stubbington and Datry, 2013; Pařil et al., 2019). This sequence of in-channel changes crosses several critical thresholds, notably the loss of flowing water and subsequent loss of surface water (Boulton, 2003), although drying can also be considered a 'ramp' disturbance in which conditions gradually intensify over time (Lake, 2003).

Fig. 2 (A–D) Intra-annual and (E–H) interannual variability in dry, ponded and flowing phases in IRES. Alternating wet and dry phases in the Calavon River, southern France, in 2016: (A) a flowing phase in April; (B) a ponded phase in June; (C) a dry phase in August; and (D) just after rewetting in November. Within-season hydrological conditions can vary at single sites between years: a 'winterbourne' chalk IRES, United Kingdom, during: (E) winter flowing; (F) winter dry; (G) summer low-flow; and (H) summer dry phases. Photos: (A–D) B. Launay; (E–H) © Environment Agency of England.

Changing in-channel conditions: Flowing water returns

In many IRES, rewetting extends from upstream to downstream as inputs from surface runoff and groundwater springs increase, but where the water table rises above the bed, rewetting can occur locally then extend in either direction (Arscott et al., 2010). Rewetting can coincide with the rapid onset of sustained flow or be a slower process in which isolated pools first fill then gradually become linked by surface flow (Fig. 2D; Jaeger and Olden, 2012, Godsey and Kirchner, 2014). Rewetting is typically more rapid than drying, although some IRES experience 'false starts' in which flowing surface water is fleetingly present or pools repeatedly fill and dry for weeks or months before flow establishes in earnest (e.g., Corti and Datry, 2012; Bhamjee et al., 2016). Sometimes, rewetting coincides with floods that generate novel habitats and scour mats of desiccated benthic algae and leaf litter, washing them downstream (Corti and Datry, 2012; Rosado et al., 2015).

Drying and rewetting patterns occur at multiple spatial scales

Drying and rewetting patterns in IRES occur at multiple spatial extents from the microhabitat to the regional scale (Costigan et al., 2016; Hammond et al., 2021). At regional scales (i.e., biogeographical regions), patterns are determined by interacting environmental factors including climate and geology, with greater evapotranspiration to precipitation ratios promoting intermittence as aridity increases (Fig. 3A; Costigan et al., 2016, Messager et al., 2021). Permeable surface geologies that enable infiltration and groundwater recharge after rainfall subsequently deliver water that sustains surface flow, whereas impermeable geologies rapidly deliver water to channels, creating short flow pulses separated by long dry periods (Costigan et al., 2016, Hammond et al., 2021). However, substantial variation in IRES flow regimes occurs both within and among regions and climatic zones, often preventing robust generalizations (Boulton et al., 2017).

At intermediate scales (i.e., from the river segment to river basin), rainfall can increase sediment moisture or cause rewetting and flow resumption in some streams while adjacent channels stay dry, and the predictability of flow is particularly low in arid and semi-arid regions (Boulton et al., 2017). Such spatial variability in flow varies among events, seasons and years, which contributes to IRES habitat heterogeneity (Figs. 2 and 3B; Costigan et al., 2016). Differences in patterns and rates of drying and rewetting also occur in response to spatial variability in bedrock, overlying sediments and climatic conditions, which collectively influence infiltration and evapotranspiration and thus transmission losses along channels (Boulton et al., 2017).

At local scales (i.e., within reaches), drying and rewetting can be asynchronous among adjacent habitats due to local variation in channel microtopography and sediment permeability: low-lying, fine-grained microhabitats fill earlier, hold water for longer, and dry more slowly than coarse-grained riffle crests (Costigan et al., 2016). These fine-scale patterns generate heterogeneous mosaics of habitat patches of varying size and permanence, and with varying physicochemical, biogeochemical and biological conditions (Fig. 3C; Boulton et al., 2017).

The biogeochemical template of IRES

River networks transport a variety of dissolved and particulate materials such as inorganic nutrients (e.g., nitrogen and phosphorus) and organic matter, which constitute the base for stream food webs and thus support wider ecosystem functioning. River networks play key roles in global biogeochemical cycles (Raymond et al., 2013), but the occurrence of ponded and dry phases alters processes in IRES, and our understanding of their contribution to global cycles is still developing (von Schiller et al., 2017). Most biogeochemical cycles, which result from the input, transformation, production, export and removal of dissolved and particulate materials, are controlled in IRES by factors such as free water availability and sediment humidity, temperature, and flow velocity (Shumilova et al., 2019). Shifts between dry and wet phases generate pulsed nutrient and organic matter inputs, processing periods, and transport events (Fig. 4; von Schiller et al., 2017, del Campo et al., 2021).

Biogeochemical responses to changing in-channel conditions: Ponded and dry phases

When flow ceases, so too does the transport of dissolved and particulate materials from upstream to downstream. Particulate matter is deposited and accumulates in pools and on dry sediments (Datry et al., 2018), potentially including leaf litter from riparian plants and stranded aquatic organisms such as fish and invertebrates (Fig. 4). Evapotranspiration continues during ponded and dry phases, further reducing water levels in surface pools and consequently increasing concentrations of dissolved substances including inorganic nutrients, supporting algal growth.

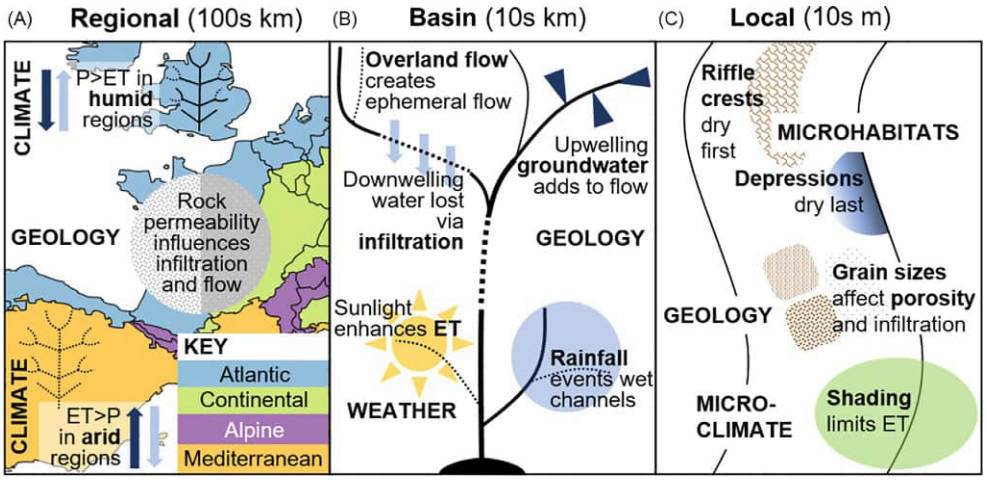

Fig. 3 Geology and climate are the key natural drivers that influence flow intermittence at multiple, nested spatial scales from (A) large, regional scales to (B) intermediate, segment-to-basin, scales and (C) local, reach scales. ET, evapotranspiration; P, precipitation. Solid lines, perennial rivers; dotted lines, IRES. Base map in (A) adapted from: © J. Reis, 2006, CC BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0/).

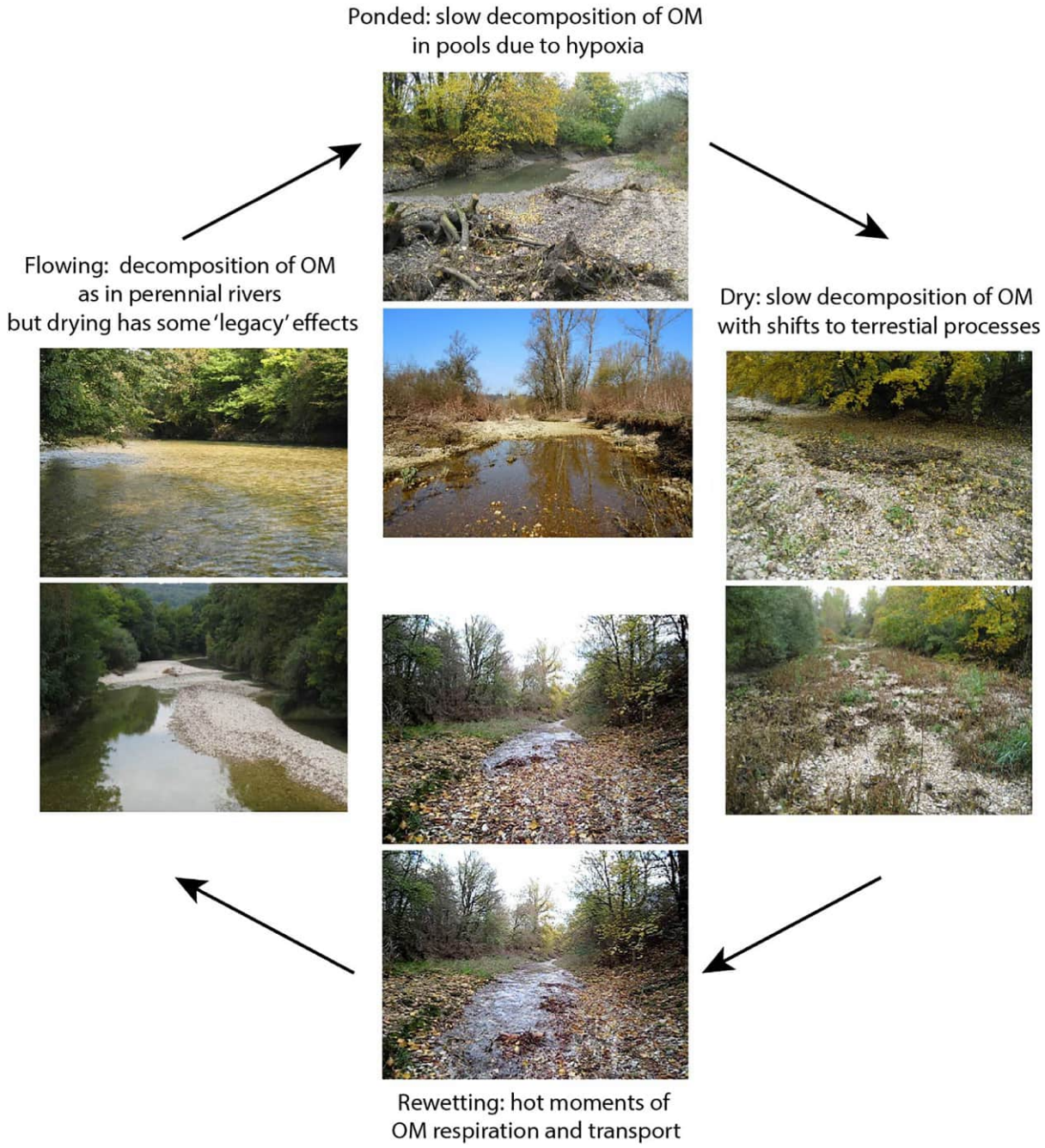

Fig. 4 Changes in the rates and modes of organic matter (OM) decomposition in the Albarine River, France, during flowing, ponded, dry and rewetting phases. The temporal sequence can vary (e.g., some IRES do not have ponded phases). Photos: T. Datry.

Biofilms associated with 'dry' sediments may slowly continue to process organic matter and nutrients, with rates limited by sediment moisture (von Schiller et al., 2017). Organic matter is decomposed very slowly during dry phases, due to reduced activity of aquatic invertebrates and microorganisms (Fig. 4; Corti et al., 2011, von Schiller et al., 2017). However, when exposed to solar radiation, organic matter on the dry riverbed can be partly decomposed by photodegradation (von Schiller et al., 2017). In addition, the activities of terrestrial animals (e.g., insects and mammals) and plants that colonize dry riverbeds can modify the quantities and types of organic and inorganic resources (Fig. 4; Steward et al., 2017, Masese et al., 2020).

In pools and in saturated and/or moist sediments beneath dry riverbeds, the activity of some anaerobic microbes can continue, leading to spatial and temporal variation in the concentrations of inorganic nutrients (Merbt et al., 2016). Accumulations of organic matter can also promote high respiration rates in isolated pools, depleting dissolved oxygen as temperatures rise, and generating

hypoxic conditions that cause shifts in biogeochemical processes (von Schiller et al., 2017). For example, methanogenesis can replace aerobic respiration when dissolved oxygen concentrations become low (Gómez-Gener et al., 2016, 2021). Hypoxia can also promote denitrification processes in pools, with the reduction of nitrate ions associated with an increase in ammonium concentrations (von Schiller et al., 2017; Gómez-Gener et al., 2021).

Biogeochemical responses to changing in-channel conditions: Flowing water returns

When flow resumes, rewetting of dry organic materials and riverbed sediments reactivates dormant organisms within biofilms, triggering pulses of microbial activity (Fig. 4; von Schiller et al., 2017). Experimental inundation of dry sediments (Shumilova et al., 2019; von Schiller et al., 2019) and accumulated terrestrial leaf litter (Datry et al., 2018) has shown that rewetting is associated with high respiration rates and thus rapid leaching of nutrients from dry organic matter. Acting as 'hot moments' of metabolic activity, these rewetting events can emit considerable CO_2 to the atmosphere (Fig. 4; Datry et al., 2018; Keller et al., 2020). These periods of intense microbial respiration can also send pulses of anoxic waters downstream, killing animals including fish (von Schiller et al., 2017) and reducing water quality in receiving waters including reservoirs, large rivers and estuaries.

The aquatic-terrestrial biodiversity of IRES

Diverse aquatic and terrestrial communities inhabit IRES during wet and dry phases, respectively, including representatives of all major taxonomic groups: vertebrates encompassing fish, amphibians, reptiles, birds and mammals; macroinvertebrates and microinvertebrates; plants including flowering plants and bryophytes; and microorganisms (Datry et al., 2017a). Macroinvertebrates are particularly abundant, diverse and well-studied, and have important ecological roles. This group includes mollusk, flatworms, worms and arthropods, the latter including major contributors to the IRES fauna, namely insects, crustaceans and arachnids (Steward et al., 2017; Stubbington et al., 2017a,b). Microorganisms also make notable contributions to IRES ecosystem functioning, with the biofilms that cover IRES substrates including algae, with particular biodiversity noted for diatoms; bacteria, including a diverse range of cyanobacteria; and fungi and archaea, although these two groups are poorly known (Sabater et al., 2016; Romaní et al., 2017).

Resistance and resilience traits promote species persistence in IRES

IRES communities experience profound shifts in composition between flowing, ponded and dry phases, encompassing species across a continuum of environmental preferences from obligate aquatic to fully terrestrial (Stubbington et al., 2017a,b). Although often predictable, dry and wet phases represent disturbances that disrupt aquatic and terrestrial biotas, respectively. As such, all IRES inhabitants require adaptations that enable their use of these dynamic habitats. Adaptations can be considered as functional traits that promote resistance, defined as the capacity to tolerate a disturbance—i.e., dry and wet conditions for aquatic and terrestrial species, respectively—in situ, and those confer resilience, which describes the capacity to recover after a disturbance (McGill et al., 2006; Bogan et al., 2017). Both resistant and resilient organisms thus contribute to post-disturbance community recovery. Traits promoting resistance typically involve physiological tolerance of either inundation or drying, whereas resilience is enhanced by behaviors enabling refuge use during unfavorable conditions and/or facilitating dispersal after favorable conditions return (Bogan et al., 2017).

Biotic responses to changing in-channel conditions: Flowing water returns

When a dry channel rewets and flow resumes, mobile terrestrial organisms with behavioral adaptations can avoid advancing wetted fronts; for example, many adult ground beetles (Carabidae) are winged and can escape by flight (Bonn, 2000). Others are engulfed by water and are either washed downstream or stranded in inundated sediments (Corti and Datry, 2012), alongside the submerged roots of terrestrial plants. Here, terrestrial organisms that lack escape mechanisms or inundation tolerance will die and can become prey for aquatic scavengers and generalist feeders (Nakano et al., 1999).

Concurrent colonization by aquatic organisms can be rapid (Bogan et al., 2017). First, water triggers the development and emergence of resistant organisms such as desiccation-tolerant microorganisms in dry biofilms and lifeforms within aquatic invertebrate 'seedbanks' (see below). At the same time, resilient species with strong dispersal abilities colonize from nearby refuges, including drifting diatoms, actively swimming fish and flying insects, which arrive from upstream, downstream and nearby perennial waters, respectively (Peterson and Bayley, 1993; Robson et al., 2008; Bogan and Boersma, 2012). Others migrate short vertical distances from saturated subsurface sediments (Kawanishi et al., 2013; Vander Vorste et al., 2016). Over time, as flowing phases continue, communities become increasingly similar to those in nearby perennial rivers if species with weaker dispersal abilities join the early colonists (Stubbington et al., 2017a,b). However, communities remain distinct where colonist sources are limited by widespread drying (Davey and Kelly, 2007) or are disconnected from rewetted reaches by barriers (Labbe and Fausch, 2000). IRES biodiversity thus typically remains lower than in perennial streams when peak aquatic taxonomic richness is compared at small spatial scales (Soria et al., 2017), because the absence of drying-sensitive species that fail to colonize after water returns (Davey and Kelly, 2007; Chadd et al., 2017) is offset by the localized occurrence of just a few IRES specialists (Armitage and Bass, 2013).

Biotic responses to changing in-channel conditions: Flowing waters recede, dry habitats expand

Perhaps days later in some ephemeral streams but months later in intermittent rivers, water depths decline, submerged habitats shrink, and mobile aquatic organisms become concentrated in remaining wetted areas (Boulton, 2003), causing a brief increase in population densities during flow recession (Stubbington et al., 2011). The loss of flow represents a critical ecological threshold that imperils obligate lotic species, such as invertebrate filter-feeders that consume fine particles of organic matter delivered by flowing water (Boulton, 2003). As ponded reaches contract into connected then isolated pools, the decline in water quality—and in particular, low dissolved oxygen concentrations—can kill sensitive species including fish and mayfly and stonefly juveniles (Chadd et al., 2017; Kerezsy et al., 2017). At the same time, biotic interactions intensify, with predators feasting on oxygen-deprived prey (Boulton, 2003). These predators include persisting lotic species with broad environmental tolerances such as gammarid amphipods, lentic species such as dragonfly juveniles, and terrestrial species, notably piscivorous birds and mammals such as herons and otters (Steward et al., 2017). Despite these interacting abiotic and biotic pressures, pools are an important refuge for groups including aquatic invertebrates (Bogan et al., 2017), fish (Rodríguez-Lozano et al., 2019) and turtles (Leidy et al., 2016).

The shrinkage of submerged habitats equates to the expansion of exposed, drying sediments, and mobile terrestrial organisms soon arrive to exploit resources including subsurface water (Kiss, 2016), stranded aquatic organisms (Paetzold et al., 2005) and humid microhabitats (Langhans and Tockner, 2014). Many colonists are resilient and originate from marginal, riparian and wider terrestrial habitats, but others may persist in situ during wet phases as inundation-resistant forms (Steward et al., 2011; Corti and Datry, 2016). Predatory invertebrates including ground beetles prowl the surface of drying sediments, devouring stranded dead and dying aquatic invertebrates (Fig. 5; Paetzold et al., 2005); fish carcasses may also attract terrestrial organisms from fungal decomposers to vertebrate scavengers (Steward, 2012). Springtails span the surface and subsurface sediments, feeding on newly exposed biofilms (Langhans and Tockner, 2014), and themselves becoming prey for ground beetles—some of which are specialist springtail predators (Riddick, 2008). This transfer of aquatic-derived energy through trophic levels into mobile animals might create dry-phase food webs that extend deep within the beds of riverine ecosystems and far into their surrounding basins (Paetzold et al., 2005; O'Callaghan et al., 2013). As well as energetic resources, IRES channels can represent relatively cool, humid corridors that

Fig. 5 Terrestrial animals use the resources in IRES channels: (A) a wild elephant digs to access subsurface water resources in South Africa; (B) a domesticated cow drinks from a ponded reach in England; (C) a deer walks through a shaded channel in France; (D) a predatory lycosid spider searches for stranded aquatic prey in drying sediments. Photos: (A) © Gabriella Kiss; (B) © Environment Agency of England; (C) B. Launay; (D) T. Datry.

attract terrestrial vertebrate and invertebrate animals seeking shelter from heat and access to drinking water in either surface pools or subsurface sediments, in particular during long migrations (Fig. 5; Langhans and Tockner, 2014, Kiss, 2016, Sánchez-Montoya et al., 2016).

Biotic responses to changing in-channel conditions: Surface water is lost

With or without the persistence of scattered pools, the loss of surface water is a fundamental threshold in the drying process, at which many aquatic organisms die (Boulton, 2003). However, where subsurface sediments remain saturated, many invertebrates (Vander Vorste et al., 2016) as well as vertebrates including fish (Kawanishi et al., 2013; Rodríguez-Lozano et al., 2019) and juvenile salamanders (Feral et al., 2005) may respond to surface drying by migrating downwards into saturated interstices—if sediment characteristics permit (Stubbington, 2012). If interstices remain saturated, long-term survival then partly depends on whether abiotic factors such as oxygen concentrations remain tolerable for the days, weeks or months for which a dry phase continues.

Many aquatic species survive in sediments that have lost free water but remain humid (Strachan et al., 2015; Pařil et al., 2019). IRES biofilms commonly support desiccation-tolerant organisms including cyanobacteria and algae whose metabolism slows in accordance with interstitial humidity (Romaní et al., 2017). In addition, some eggs, juveniles and adults of aquatic invertebrates have some degree of desiccation tolerance, and a diverse range of insects (including beetles, and true fly and caddisfly juveniles), crustaceans, molluscs and mites thus form a so-called 'seedbank' or egg bank (Stubbington and Datry, 2013). The moisture requirements of some active seedbank residents are surpassed as dry phase durations increase, and they perish (Datry et al., 2012; Stubbington and Datry, 2013). Others—in particular microcrustaceans from the Cladocera, Copepoda and Ostracoda—become the 'living dead', entering dormant states in which water requirements are minimized by slowing metabolism to below detection levels (Ricci and Fontaneto, 2009). In IRES that have experienced seasonal drying over evolutionary timescales, vertebrates have also evolved desiccation tolerance. Notably, killifish (order Cyprinodontiformes) persist for months as desiccation-tolerant diapausing eggs in the dry sediments of African IRES (Furness, 2016).

As dry habitats extend in space across the channel, from upstream to downstream and sometimes into the subsurface, and as dry durations increase from hours to years, terrestrial colonists may collectively form complex assemblages. Terrestrial invertebrates are the best-known group, with common dry-channel inhabitants including springtails; ants; spiders, in particular wolf spiders; and beetles, especially ground and rove beetles (Steward et al., 2017). Collectively, these taxa may make a greater contribution to overall channel biodiversity than the aquatic invertebrates active during wet phases (Corti and Datry, 2016). However, biodiversity estimates to date have typically been constrained by coarse, variable taxonomic resolution (but see Sánchez-Montoya et al., 2020). In addition, we know little about how the structure and functioning of dry-phase communities respond to environmental variability. In particular, biotic responses remain uncharacterized for a fundamental habitat transition: from the dry riverine channels of intermittent systems with short dry phases, to the terrestrialized channels of ephemeral streams in which drying is extensive enough to support sediments and vegetation characteristic of adjacent riparian habitats (Arce et al., 2019).

Responses to changing environments create high biodiversity

Despite their lower aquatic alpha diversity (Soria et al., 2017), IRES have higher spatial and temporal habitat heterogeneity than perennial rivers and streams, due to the occurrence of flowing, ponded and dry habitats at multiple points throughout a river network. This heterogeneity enables these dynamic ecosystems to support ever-changing assemblages of species with a wide range of environmental preferences (Larned et al., 2010; Stubbington et al., 2017a,b). This compositional variability in space and time (i.e., spatial and temporal beta diversity) may enhance both the aquatic biodiversity of IRES compared to equivalent perennial systems (Datry et al., 2016; Tonkin et al., 2017) and their terrestrial biodiversity compared to that in the surrounding land (Sánchez-Montoya et al., 2020). However, further research is needed to quantify how intermittence affects regional (i.e., gamma) biodiversity in riverine networks with varying extents of IRES reaches (Sarremejane et al., 2020).

IRES communities interact within meta-ecosystems

Much research characterizing biotic responses to flow intermittence has considered communities sampled at local spatial scales, i.e., at a few sites within one IRES. In contrast, recent conceptualizations have positioned populations, communities and ecosystems within meta-populations, meta-communities and meta-ecosystems linked by dispersal (Datry et al., 2017b; Cid et al., 2020). In IRES, flowing phases that extend throughout river basins create landscape-scale networks of longitudinally connected habitats in which aquatic biota can move (Fig. 6C), but which may represent barriers to lateral migration of ground-dwelling terrestrial organisms (Fig. 6A). Accordingly, surface water loss can restrict movement by obligate aquatic species to the subsurface sediments (Fig. 6D) while creating opportunities for ground-dwelling terrestrial organisms to venture across channels that dissect terrestrial habitat patches when wet (Fig. 6B; Stubbington et al., 2017a,b).

Meta-community dynamics thus influence community resilience, with local communities situated within well-connected meta-communities recovering most rapidly after a disturbance ends, then experiencing reductions in spatial beta diversity due to community homogenization (Datry et al., 2017b). For example, after rewetting in IRES reaches positioned between perennial upstream and downstream waters, aquatic communities soon resemble those in adjacent reaches (Storey and Quinn, 2008; Datry et al., 2014). Equally, aquatic communities in isolated headwaters may return to a pre-drying state more slowly after flow resumes,

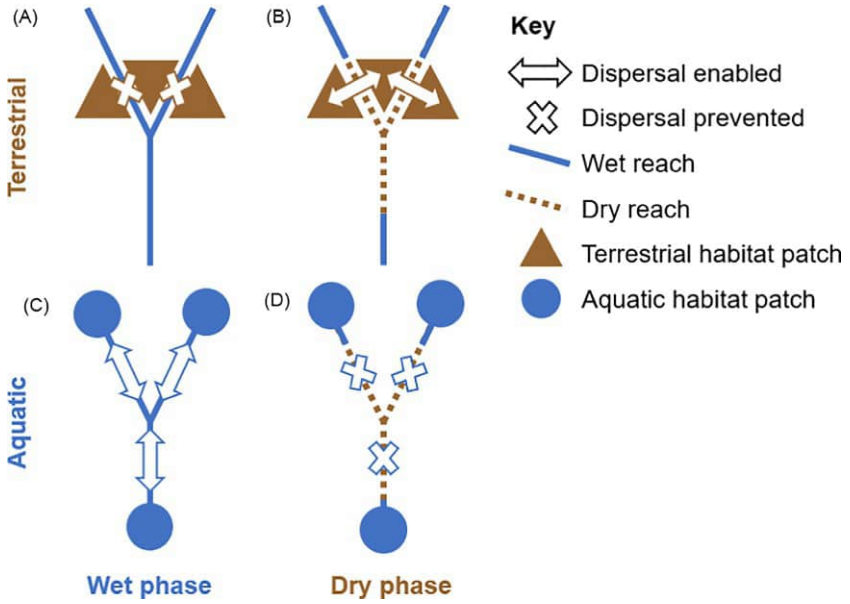

Fig. 6 A conceptual model comparing the effects of wet and dry phases on the dispersal of fully aquatic and ground-based terrestrial organisms among comparable habitat patches within meta-ecosystems: dispersal of terrestrial organisms is prevented (A) and enabled (B) during wet and dry phases, respectively; conversely, aquatic dispersal is enabled (C) and prevented (D) during wet and dry phases, respectively.

and then remain distinct from those at perennial sites—as well as from nearby IRES, if early colonists have a long-term influence on community assembly (Davey and Kelly, 2007). The role of drying as a source of fragmentation in river networks that alters dispersal is still poorly explored, but it could be as important a determinant of riverine biodiversity as the effects of local drying on local communities (Phillipsen and Lytle, 2013; Gauthier et al., 2020).

Because drying facilitates dispersal by ground-dwelling organisms, terrestrial meta-community succession and associated heterogeneity can be overridden by mass effects in dry riverbeds (Steward et al., 2017). Mass effects may be amplified as channels dry if resources including stranded aquatic prey motivate riparian predators and scavengers with strong ground-based dispersal abilities to enter habitats that otherwise align poorly with their environmental preferences (Corti and Datry, 2016). Mass effects may also introduce passive aerial dispersers such as spiders into channels, and gravity may then impede their windblown return to riparian habitats (Tonkin et al., 2015). The temporal trajectories that in-channel terrestrial communities follow as dry phases extend in time remain uncharacterized (but see Corti and Datry, 2016, Sánchez-Montoya et al., 2020), with variability expected from diurnal to seasonal scales, as well as in response to changing habitat conditions (Steward et al., 2017). Differences in both the spatial and temporal organization of colonist sources within IRES, their riparian corridors and the wider landscape are therefore likely to have contrasting effects on aquatic and terrestrial meta-community dynamics, with consequences that reverberate through aquatic-terrestrial food webs. Whereas the terrestrial predators that consume aquatic prey in dry riverbeds transfer trophic resources from in-channel to riparian habitats during dry phases (Corti and Datry, 2016), terrestrial organisms engulfed by advancing wetted fronts supply energy to aquatic organisms (Corti and Datry, 2012; Rosado et al., 2015). Further research is needed to determine how these shifts in trophic interactions influence the flow of energy through IRES meta-ecosystems.

Towards better understanding and protection of IRES

Although our understanding of IRES has advanced considerably in recent years (Larned et al., 2010; Datry et al., 2017a; Stubbington et al., 2017a,b; Allen et al., 2020), knowledge gaps still limit our capacity to manage these diverse ecosystems (Datry et al., 2017c). First, locating and mapping IRES remains challenging because discharge gauging networks are strongly biased towards perennial rivers and streams (Beaufort et al., 2018), although alternative methods are emerging, such as citizen science initiatives (e.g., Allen et al., 2019), spatial interpolation based on point measurements (e.g., Beaufort et al., 2018) and remote sensing technologies (e.g., Borg Galea et al., 2019). The lack of continuous discharge data also limits our ability to classify the considerable diversity within IRES flow regimes and identify the underlying drivers of intermittence (Costigan et al., 2016; Hammond et al., 2021), hindering the implementation of environmental flows in IRES (Acuña et al., 2020).

Second, IRES aquatic-terrestrial biodiversity is still poorly explored at regional scales (Soria et al., 2017). Interactions between aquatic and terrestrial organisms are a major feature of perennial rivers (e.g., Baxter et al., 2005) and are probably even more significant in IRES, particularly during drying and rewetting phases (Steward et al., 2017). This includes exchange of materials and

energy through reciprocal subsidies and intertwined food webs between channel and riparian habitats. The extent to which our developing knowledge of biodiversity in natural IRES can be applied to new, artificial IRES is also unclear, but contrasting responses may be observed for biotas experiencing flow cessation and drying for the first time due to climate change and other anthropogenic drivers (Pařil et al., 2019; Crabot et al., 2021). Equally, ecological responses to artificial flow perennialization (Hassan and Egozi, 2001; Steward et al., 2012), notably caused by wastewater effluent releases (Luthy et al., 2015), have not yet been quantified.

Third, the role of IRES in global biogeochemical cycles remains poorly understood, although some studies have suggested that IRES could contribute disproportionally to carbon cycles due to the hot moments of carbon processing that occur during rewetting events (Datry et al., 2018; von Schiller et al., 2019; Keller et al., 2020). The consequences of the pulsed processing of carbon, nitrogen and phosphorus within IRES require exploration, in particular to inform the management of IRES in urban areas (Luthy et al., 2015). How flow intermittence shapes biodiversity-ecosystem function relationships is also a promising and timely research avenue, with IRES representing model ecosystems in which to examine the effects of disturbance on these relationships, which is still an open question in ecology (Gamfeldt and Roger, 2017; Barnes et al., 2018).

Finally, despite recognition of widespread degradation due to human activities, the legislative status of IRES remains ambiguous, inadequate or non-existent across nations, which contributes to their ongoing degradation (Acuña et al., 2014; Fritz et al., 2017). For example, the future legislative protection of most IRES remains uncertain in the USA (Marshall et al., 2018, United States Environmental Protection Agency, 2021), and in Europe, IRES challenge implementation of the Water Framework Directive (Stubbington et al., 2018; Acuña et al., 2020). Following recognition of their global prevalence, their considerable physical and biological diversity, and their key contributions to wider ecosystem functioning, now is the time for scientists to unite with environmental managers and policy makers to integrate IRES into updated legislation that grants these dynamic ecosystems the protection they deserve.

Acknowledgments

TD was supported by the H2020 European Research and Innovation action Grant Agreement No 869226 (DRYvER).

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Biodiversity Conservation of Aquatic Ecosystems

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Area-based conservation strategies These cover management or governance approaches that are applied to specific geographic areas and have objectives and/or outcomes relevant to conservation and sustainable use.
Conservation feature Biophysical attributes that can be mapped to a planning unit. Examples are a class in a classification, a certain vegetation type or a single fish species.
Cost In conservation planning terminology, cost is a summary term used to describe constraints in the optimisation. A typical example is planning unit area; however, cost can also include measures of ecological condition, vulnerability or pre-determined priorities. Multiple constraints can be combined to a single cost.
Drivers of biodiversity loss The main causes of biodiversity loss are demand for food, energy, water, as well as increased urbanization, international trade, climate change.
Integrated catchment management Management of freshwater ecosystems requires strategic decision-making to integrate multiple and often conflicting objectives, such as exploitation of freshwater resources and biodiversity conservation.
IUCN Redlist The world's most comprehensive inventory of the global conservation status of biological species. Species are assigned a rating from "Extinct," through various threat categories to "Least Concern."
Pressures Mechanisms by which the drivers act in biodiversity loss, for example water abstraction, river regulation, species exploitation, pollution, land-use transformation.
Restoration The assisted recovery of the biophysical processes that support river self-sustainability.
Systematic Conservation Planning A structured, step-wise and iterative approach to identify priority areas for conservation management actions to best represent and sustain the biodiversity of areas in the most cost-effective way (often used synonymously with spatial conservation prioritization, etc.). Most modern systematic planning approaches are based on the CARE principles: comprehensiveness, adequacy, representativeness and efficiency. Efficiency is usually provided by a complementarity-based strategy.
Wetland Is used analogously to the Ramsar definition, including all lakes and rivers, underground aquifers, swamps and marshes, wet grasslands, floodplains and peatlands.

Introduction and status of global protection

Freshwater systems are among the most endangered biomes globally (Dudgeon et al., 2006; Dudgeon, 2019). This is partly due to the connected nature of rivers, streams, lakes and wetlands. Threats to freshwater systems are often non-localized and can be propagated both longitudinally—along the river, usually from up- to downstream—but also laterally from the river to the associated floodplains (Linke et al., 2019a). Often, human populations reside close to freshwater systems, for the services provided by rivers, lakes and wetlands. These services include clean water for drinking and sanitation, carbon sequestration, erosion

prevention and local climate regulation. Another key service is food production, both instream through harvesting fish populations, crustacea and aquatic plants but also using irrigated agriculture (Green et al., 2015; Boulton et al., 2016).

A recent review identified key drivers and pressures to freshwater ecosystems and biodiversity (Acreman et al., 2020; Fig. 1). The drivers and pressures include

- Increased demand for food, energy and water: Abstraction for drinking water and irrigated agriculture will lead to river regulation and changed flow regimes. Demand for hydropower—often falsely seen as "clean green energy" can change flow regimes greatly. Overharvesting of aquatic populations, especially fish by a growing population is another pressure.
- Expansion of urban area leads to changes in hydrology and water chemistry, with flows becoming flasher and pollution washing into waterways.
- Climate change is an overarching threat, changing not only flow, but also thermal regimes and through increased flooding also exchange between the river and the surrounding floodplain. In some areas of the world, river habitat can disappear completely through greatly reduced inflow.

This leads to habitat loss and degradation, a decrease in native biodiversity and a change in species movements between habitats, driving a decline in species populations and ultimately species extinctions.

While protected areas are not the only strategy to conserve freshwater ecosystems and biodiversity, national parks and other areas designed to conserve nature represent an important contribution to conservation. Most protected areas were designed with terrestrial biodiversity in mind. They thus lack "integrated protection"—a term recently coined for adequate protection of upstream areas (Abell et al., 2017). A few rivers still have high rates of integrated protection, for example in the Amazon basin where 42.5% of river kilometers are assessed as adequately protected. That said, the lower reaches of the Amazon where flow exceeds 10,000 m^3/s are only 17% protected. Other large rivers yield lower protection, for example the Mekong (15.8%), the Yangtze (12.6%) and the Danube (9.2%). Among the lowest protection rates are the Volga (3.5%), the Rio Grande (3.3%) and the Mississippi at only 1.9%. The case of the Murray-Darling—the largest river in Australia—demonstrates that configuration of protection matters. While a total of 8.1% are protected, only 3.5% have adequate upstream protection (Fig. 2).

A global tally of wetland protection painted a similar picture of underrepresentation (Reis et al., 2017). While South America protected 17% of their wetlands, only 7% are covered in the highest IUCN categories with the remainder mainly in the frequently unenforced IUCN Category VI. Oceania and Central America yielded similar number, while North America and Europe showed similar protection percentages. Asia—where a large percentage of the population relies on freshwater services, has the lowest percentage of protection, with only 5% in the strictest category.

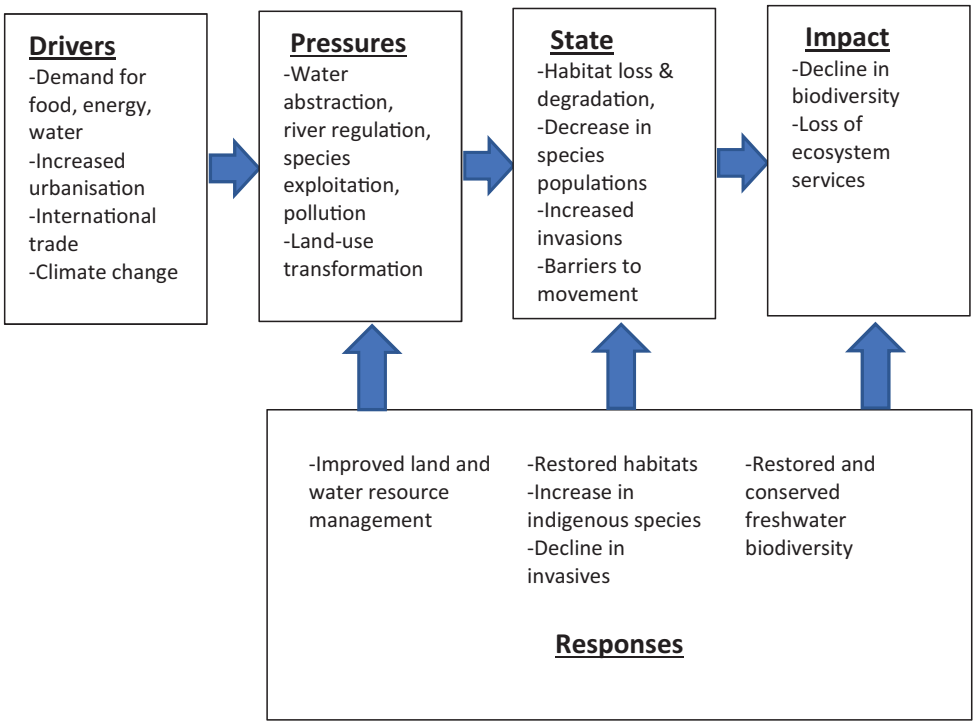

Fig. 1 Drivers, pressures, state, impact and responses to freshwater ecosystems. After Acreman M, et al. (2020) Protected areas and freshwater biodiversity: A novel systematic review distils eight lessons for effective conservation, Conservation Letters 13 (1), e12684.

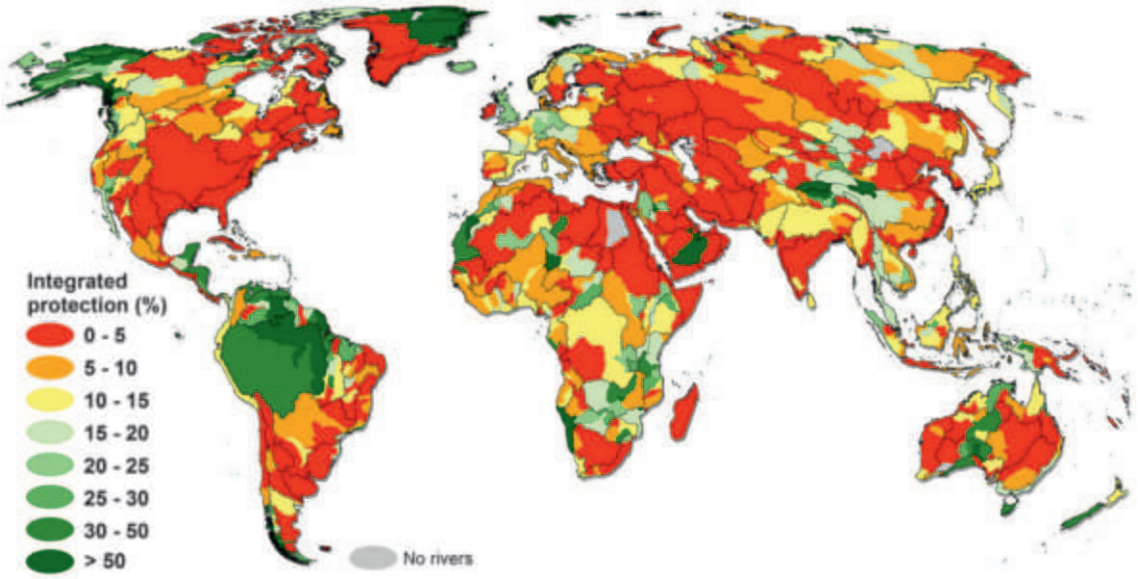

Fig. 2 Global protection status of rivers. From Abell R, Lehner B, Thieme M and Linke S (2017) "Looking beyond the fenceline: Assessing protection gaps for the world's rivers. *Conservation Letters* 10(4): 384–394.

In this chapter, we will detail the significance of these threats for the conservation of freshwater biodiversity, discussing the conservation status of freshwater biodiversity, key threats to freshwater systems and biota and strategies to conserve freshwater systems.

Status of freshwater biodiversity

While data about both the status and the distribution of freshwater biodiversity have been lagging behind their terrestrial and marine counterparts, the last 10 years saw high activity in assessments for the IUCN Redlist (Bland et al., 2019). Some taxonomic groups—freshwater shrimps and crabs for example—have complete global assessments. Other groups are slightly lagging behind, but have complete continental assessments. Fish, for example now have complete assessments for North America, Africa, Europe and Oceania (bar Papua New Guinea). Assessments of South American and most parts of Asia are underway, bar smaller areas in the Levant and Central Asia. In total, in late 2021, out of a total of ~18,000 fish species globally, 11,022 species have their assessments completed.

The IUCN Redlist is a homogenized rating system that classifies the relative risk of extinction. Categories range from "least concern" (LC), to vulnerable (V), to endangered (E) and critically endangered (CE). Note that the statistics we are reporting on will be based on all freshwater dependent taxa from the IUCN website, including the "freshwater & marine" and "freshwater & terrestrial" categories. In contrast to previous studies, which included the near threatened category, such as the "Bending the Curve of Global Freshwater Biodiversity Loss" opinion piece (Tickner et al., 2020), we will only include taxa that are vulnerable, endangered or critically endangered.

In 2021, out of a total of 35,000 species, 7529 were classed as threatened. This by itself is a staggering—and worrying—statistic, as 21.5% of all freshwater species are threatened. The number is likely higher than this as 7000 additional species are data deficient, some of which are certainly also endangered. While there is certainly bias in the coverage of the assessments, threat assessments differ both by regions and by between taxa.

Unsurprisingly—given the density of development and human population—Europe has an above average percentage of threatened species, with 27% of taxa in the V, E or CE category. Europe also has the highest assessment rates with only 9% classed as data deficient, lending high confidence to the percentage. North America—with a lesser population density—has an even higher assessment coverage (5%) and classes 15.5% of freshwater taxa as threatened. That said, North America has the highest extinction rates with a total 108 species extinct, amounting to 2.5% of total taxa. Nineteen of these extinct species are fish taxa, for example Silver Trout (*Salvelinus agassizi*) and the recently extinct Blackfin Cisco (*Coregonus nigripinnis*; Fig. 3), which was last sighted in 2006.

South America, South-East Asia and Oceania all have around 16% of endangered freshwater dependent taxa. Coverage for these areas is highly variable however. While in Oceania only 9% of the taxa are data deficient—indicating a higher certainty in the estimate, a total of 21% and 26% are data deficient in South America and South-East Asia, respectively. This indicates that the number of threatened species in South-East Asia could still increase once more fish are assessed. According to a 2016 analysis of change in human influence on ecosystem—measured by the change in "Human Footprint"—South America and South-East Asia are still in a trajectory of degradation (Fig. 4; see Venter et al., 2016; Linke et al., 2019b). We therefore expect a further degradation of

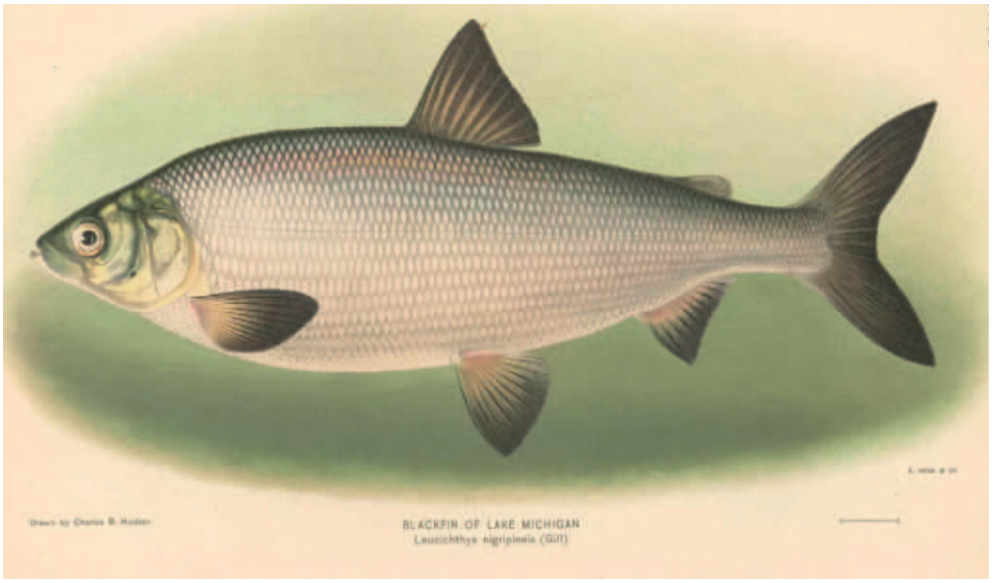

Fig. 3 The recently extinct blackfin cisco (*Coregonus nigripinnis* Painting by C.B. Hudson (1911) courtesy of the Freshwater and Marine Image Bank, University of Washington), last seen in 2006.

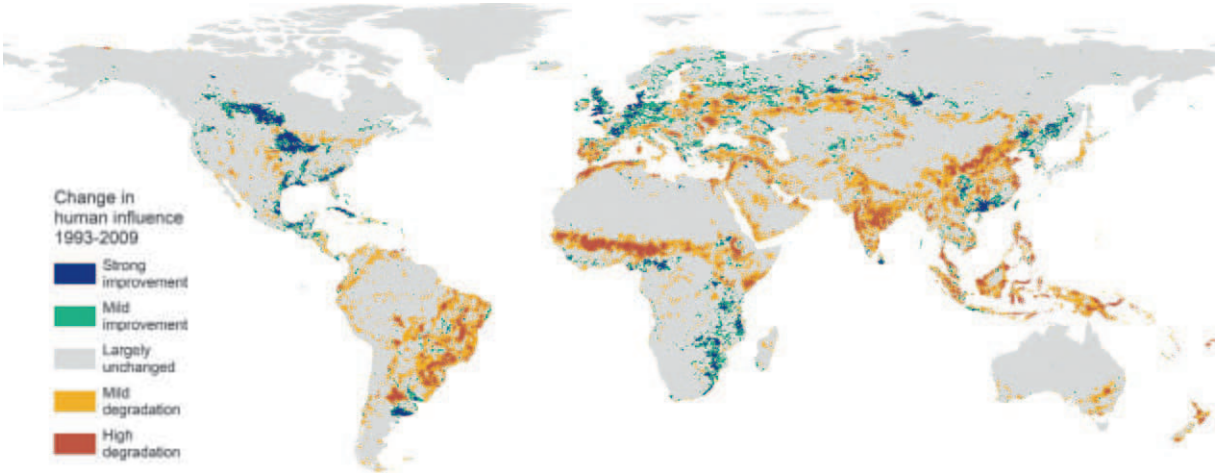

Fig. 4 Change in Human Footprint 1993 to 2009 by Level 8 Hydrobasins. Data from Venter O, Sanderson EW, Magrach A, Allan JR, Beher J, Jones KR, Possingham HP, Laurance WF, Wood P, and Fekete BM (2016) Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications* 7: 12558; Linke S, Lehner B, Ouellet Dallaire C, Ariwi J, Grill G, Anand M, Beames P, Burchard-Levine V, Maxwell S, Moidu H, Tan F, and Thieme M (2019b) Global hydro-environmental sub-basin and river reach characteristics at high spatial resolution. *Scientific Data* 6(1): 283.

habitat and hence an increase of taxa classed as endangered in these areas, as opposed to many regions in Europe and North America that are either in a stable condition or have either succeeded in mitigating threats.

Taxonomic groups also display differing trends. Aquatic molluscs are heavily endangered with 25% of Gastropods and 31% of Mussels and other bivalves being classed as endangered. The real number could be even higher as these benthic organisms are harder to survey and are 20% and 31% data deficient, respectively. Aquatic mammals are also often highly endangered (37.5%) but have a high assessment rate, with only 10% being data deficient. Fish, which that are 80% assessed, have a slightly lower rate with 23% classed as endangered. Waterbirds and insects have lower rates, with 12% and 11%, respectively.

A second indicator is the Living Planet Index—an index of published population surveys of marine, terrestrial and freshwater organisms (Almond et al., 2020). The index is constructed by using the year 1970 as a baseline (=100%) and then tracking increases or declines in population. The last release in 2020 tallied populations until 2016 and showed a decline by around 62%, to a value of 38% of populations remaining. The plight of freshwater systems is especially clear in the index: When only counting freshwater-dependent species, the index is reduced to 22.5%, indicating that 77.5% of freshwater populations have been lost (Fig. 5).

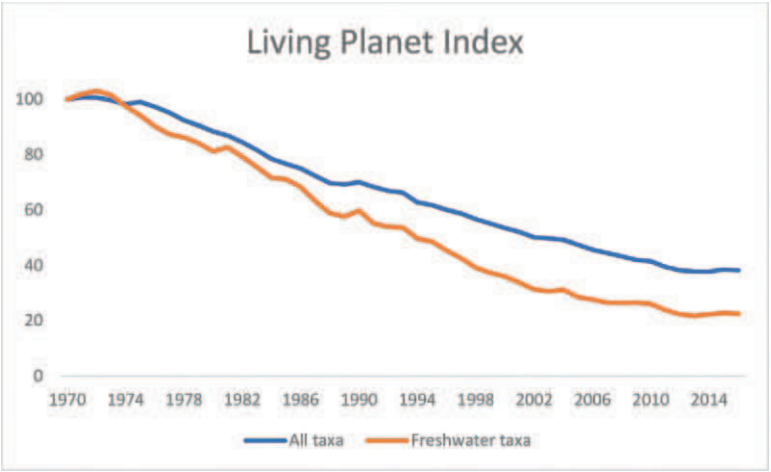

Fig. 5 Trajectory of the Living Planet Index 1970–2016. Data from Almond R, Grooten M, and Peterson T (2020) *Living Planet Report 2020-Bending the Curve of Biodiversity Loss*, World Wildlife Fund.

Major threats

Threats to aquatic ecosystems can stem from a diverse array of human activities. Some threats are direct and localized impacts of human activities on freshwater biota. An example of this is overfishing, a threat in which the impact is mainly local and occurs at the site where fish are extracted. Similarly, invasive species are a threat that is primarily a local threat, although of course invasives can spread across catchments. Other localized threats are, for example, habitat loss triggered by either changes to the river channel or the surrounding catchment, including the riparian zone. Similarly, point source pollution has its greatest impact in the local reach; however, like habitat loss, pollutants can have non-localized negative impacts. Flow regulation is a threat that can act on river health and biodiversity for thousands of kilometers. All of the above can be exacerbated by the overarching non-local threat—climate change, which can act as a driver detrimental to both thermal and hydrological regimes (Dudgeon, 2019; Reid et al., 2019).

Overexploitation of freshwater systems is mainly related to fishing impacts. Inland fisheries are an important source of nutrition globally (Funge-Smith and Bennett, 2019). The most recent estimate by the FAO was a catch of 11.9 million metric tonnes per annum. While this is only 12.9% of the overall catch—the remaining being marine fisheries—it still represents a sizeable amount of the total biomass. Often, the total impact of inland fisheries can be severely underreported. A recent study tallied 42 low and middle income countries in Asia, South America and Africa and found a net underreporting rate of 64.8%. Although the actual number harvested matters, the fishing techniques used are also important (Fluet-Chouinard et al., 2018). While no doubt a lot of the catch adheres to regulatory frameworks, a small number of extractions using illegal fishing practices (e.g., fishing with explosives) will cause additional damage. In addition to fish, amphibians, turtles or crocodiles are caught for food or traditional medicine, and these are poorly reported.

Invasive species are one of the hardest threats to control (Gallardo et al., 2016). Unlike most other endangering processes, invasive species are self-perpetuating. Single invasion events can lead to infestations of waterways that are extremely hard to control in the future. Impacts of invasive species can influence aquatic ecosystems in multiple avenues. Invasive species can change habitat, including water chemistry, and they often invade waters that display increased water temperature, nitrogen or organic matter concentrations. This of course depends on the context, as well as the species. For example the zebra mussel infestation in the Great Lakes led to major shifts in the Lakes' foodwebs. As the mussels filtered most of the primary producers from the water column, zooplankton populations declined, as did fish populations. In turn, submerged macrophytes increased as light penetration improved due to increased clarity. Invasive species can also directly act on other biota by predation, competition or increased grazing. Thus, the impact on the guild of natives depends on the trophic state of the invader. Invasive filter feeders have more of a grazing impact on plankton, whereas predators can decimate fish and benthic invertebrates. Apart from ecological losses, invasive species also have a major detrimental impact on the economy. A 2021 study estimated the global costs of invasions to aquatic systems to be at least $23 billion, 99% of which is in the freshwater realm (Cuthbert et al., 2021).

Land use change is one of the most complex proximate drivers of decline, as it can act through multiple avenues (Di Marco et al., 2019; Dudgeon, 2019). Habitat loss in freshwater systems can be caused by land-use changes around the river channel, for example by clearing riparian vegetation. Riparian corridors can filter nutrients and other pollutants, preventing them from reaching the river channel. Removing riparian vegetation will not only hinder this retention capacity but also reduce the input of terrestrial organic matter. Leaf litter is an important source of external energy inputs to river ecosystems, as are fallen branches and other woody debris that can act as nursing habitat for fish. Run-off from agricultural land often contains fertilizer that leads to excess nutrients being washed into the river, hence increasing primary production and often leading to algal blooms. Agricultural inputs can also increase fine sediment which can clog important habitat, an effect also observed by poor forestry landuses.

Unlike broader land-use effects, *point source pollution* stems from input contained in a defined area. This can be organic input—for example untreated sewage, which can lead to eutrophication, similar to land-use runoff. As point source pollution is localized, concentrations can often be higher. This can increase the direct impact at the local runoff point before dilution can attenuate concentration and lead to major damage. This is often not just restricted to organic inputs, but also includes chemicals from industrial runoff, as well as pathogens. Some of the most concerning chemicals are persistent organic compounds that do not degrade or cannot be metabolized in the food chain. An example for long-term exposure is the dioxin legacy in Sydney Harbour in Australia—an estuarine system in which fish harvest is forever banned due to high contamination.

The hydrological regime is a key influence on health, function and biodiversity of inland waters. Modifications to stream hydrology by *flow regulation* can influence the ecosystems thousands of kilometers downstream, and it can also present barriers to migratory species upstream of dams and weirs. A recent global study found that 67% of rivers had their flow intercepted to a significant level and only 23% of rivers flow uninterrupted to the ocean (Pittock et al., 2018; Grill et al., 2019). Hydrological change by either abstraction or seasonal reversal of flow can affect all types of organisms. Fish for example, need flows as spawning triggers but then often require overbank flow events to connect to nursery habitats. Floodplain vegetation requires regular watering events and overbank flows. Thermal regimes are often disturbed by regulation so spawning cues are missed. Invertebrates can also be affected by flow regulation as flushing flows that clean out sediment from interstitial spaces can be reduced.

Climate change will affect aquatic ecosystems through a combination of direct and indirect pathways (Knouft and Ficklin, 2017; Pittock et al., 2018). Primary drivers such as changes in rainfall and snow patterns lead to decreased flows and increased frequency and extent of drying. Air and water temperatures can have a direct effect on the ecology and life cycles of biota, but also on biogeochemical cycling, altering carbon and nutrient dynamics in aquatic system, which in turn affects aquatic systems. Water quality issues, such as increased frequency of algal blooms is a consequence of extended periods of increased temperature and reduced flows. The intensity of weather events (flooding and erosion) leads to direct physical effects on aquatic systems through elevated turbidity. Increasing salinity can also affect some freshwater systems as a secondary consequence of decreased dilution flows, but more directly in freshwater coastal systems that are under threat from sea-level rise.

The interaction between different threats can greatly exacerbate single detrimental effects (Dudgeon, 2019). Climate change, for example, can foster the establishment of invasive species by extending their range. Flow modification can be exacerbated by climate change when inflows are reduced. Flow modification can also increase effects of point source pollution when dilution is not present. Land-use change can add to a changing hydrograph and climate change can drive land-use change—when for example more land is needed for the agricultural production under climate change. These interactions call for a holistic approach to remediating actions, both in the nature of the remediation, but also the type of action taken (Fig. 6).

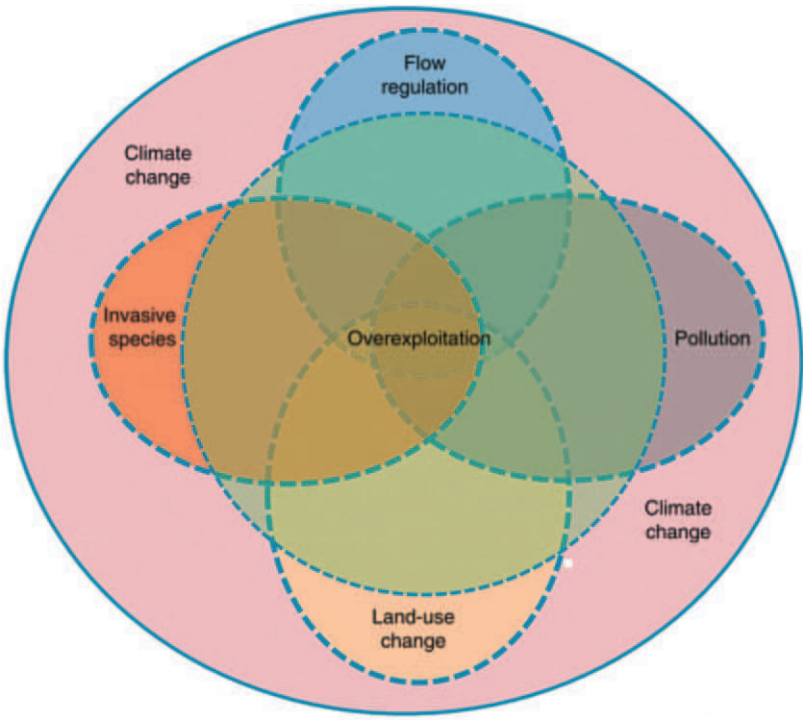

Fig. 6 A conceptual diagram of global threats to freshwater ecosystems. From Dudgeon D (2019) Multiple threats imperil freshwater biodiversity in the Anthropocene. *Current Biology* 29(19): R960–R967.

Conservation challenges

Freshwater conservation needs to be rooted in effective and efficient management. This is especially important in the face of rising pressures due to increasing demand for freshwater resources (e.g., clean water, construction material) and availability due to the impact of climate or land use change. Improving effectiveness and efficiency of conservation action in freshwater ecosystems faces important challenges that must become a priority to reverse the steep decline that freshwater ecosystems and biodiversity are now experiencing.

Some of these challenges are related to the special nature of freshwater ecosystems: they are systems that drain and accumulate impacts along full hydrological catchments. For example, the development of infrastructure to exploit freshwater resources might compromise the effectiveness of conservation action in lower regions in the catchment because of altered hydrological regimes and water quality. It is for this reason, that full catchment management plans are necessary. Moreover, in many cases freshwater ecosystems cross administrative boundaries, which makes the management of environmental problems and biodiversity conservation even more complex (Allan et al., 2019). Catchment management plans need to harmonize multiple (often conflicting) objectives that converge in freshwater ecosystems, for example water extraction of agriculture, hydropower production and biodiversity conservation. Management plans must identify the most suitable areas in the catchment to achieve these different objectives, while trying to minimize impacts of each objective on the others. Developing management plans requires the use of analytical tools and data to help make better informed decisions, negotiation and broad agreements across a multiplicity of stakeholders. There have been advances on the former, so tools and data are currently available to carry out prospective analyzes that help prioritize the allocation of different uses across full catchments to maximize the achievement of all objectives collectively while minimizing potential trade-offs between them (Hermoso et al., 2018). However, there is no single solution to facilitate negotiations and agreements across stakeholders. Multi-jurisdictional catchment-wide coordination exists, for example the Mekong River Commission that coordinates the development of catchment-wide management plans across Cambodia, Lao PDR, Thailand and Vietnam.

More effective conservation of freshwater biodiversity also needs full recognition of freshwater ecosystems as a unique realm in international and national agreements and policy as a step forward to setting meaningful targets and adequate management (van Rees et al., 2021). Freshwater ecosystems have been traditionally included as part of terrestrial systems (for example in the United Nation's SDGs), overlooking the particularities mentioned above. This has led to poor designs of freshwater protected areas and, therefore, important gaps in representation of freshwater habitats and species within protected areas There are initiatives, such as the Post-2020 Global Biodiversity Framework or the EU Biodiversity Strategy for 2030 (EC, 2020), that specifically set recovery targets for freshwater ecosystems and that are currently leading the path towards a better recognition for freshwater conservation needs.

Effective conservation must be supported by adequate and sufficient knowledge on the status of freshwater biodiversity, drivers of its decline and the effectiveness of different management options to address the impacts of those drivers. There are currently large gaps in all these different pieces that need to be addressed to enhance the effectiveness of conservation action in the future. For example, a large proportion of the described freshwater species lack adequate assessment of their conservation status following IUCN standards (see above), and there are many species, including vertebrates, that still to be described. These knowledge gaps are especially important in the regions that harbor the highest richness of freshwater biodiversity, such as large river systems in the tropics (e.g., Congo, Amazon or Mekong). There is also is insufficient knowledge of how different management strategies help abate the drivers of biodiversity loss. This lack of adequate information constrains our capacity to fully grasp the magnitude of the problem faced by freshwater ecosystems. It also hinders our capacity to raise awareness and plan action to reverse the decline of biodiversity in these systems. Monitoring programs are critical to fill some of these knowledge gaps. There are international initiatives, such as the Biodiversity Observation Networks (BON), as well as the development of indicators to track changes in ecosystem health or trend in populations of species, such as the Essential Biodiversity Variables; however, there is still support needed for systematically collecting and sharing data (Turak et al., 2017). An opportunity to address the challenge of better monitoring nature comes from emerging technology, such as e-DNA and bioacoustics, and citizen science. The development of these technologies is making them more accessible and cheaper, which will facilitate their use in the near future.

Freshwater ecosystems and biodiversity have also traditionally received less attention by the public, which has translated to less support to conservation action (Kochalski et al., 2019). A large proportion of freshwater biodiversity is out of sight under the water, and there are fewer examples of charismatic species commonly used to raise awareness of conservation problems and attract attention and funds. It is, therefore, a challenge of future conservation in these systems to improve public knowledge of the value of freshwater ecosystems and biodiversity and understanding of the specific problems that affect them through education and dissemination programs. In this sense, initiatives like the Alliance for Freshwater Life are needed to outreach society and educate on values and problems of freshwater biodiversity (Darwall et al., 2018).

Finally, although more knowledge is desirable, action is urgently needed. Given the complexities of managing freshwater ecosystems depicted above, this action needs to be supported by adequate planning at catchment scale and agreed among stakeholders: think globally to act locally.

Conservation strategies

Protected areas

Protected areas, as defined by the International Union for the Conservation of Nature (IUCN), are "clearly defined geographical spaces, recognized, dedicated, and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values." These are the most commonly used conservation tool worldwide and, consequently, the number and extent of protected areas has been growing constantly over the last decades.

The effectiveness of existing protected areas for freshwater biodiversity is often uncertain, given that there has been little emphasis on declaring or managing protected areas for the primary purpose of conserving freshwater ecosystems and biodiversity. A few exceptions to this place-based conservation approach do exist such as RAMSAR sites that are specifically designated to protect wetlands (not only freshwater). These sites have also experienced an important growth in area, but insufficient to halt the decline of natural wetlands (Gardner and Finlayson, 2018).

Although the majority of the world's protected areas are managed by governments at all levels, the importance of privately protected areas and mixed models is becoming increasingly recognized. Alternatives to conventional place-based approaches are quickly rising in freshwater systems. Some of these alternatives arise from recognition of the strategic value of freshwater resources for human wellbeing and development and to make the most of the opportunity of new markets that arise from the payment for ecosystem services. These alternatives go beyond designing place-based conservation efforts for biodiversity values alone and incorporate key ecosystem services provided by freshwater systems, for example water provision through different initiatives such as Water Funds and Water Reserves (Goldman-Benner et al., 2012).

To provide effective freshwater conservation, protected areas must consider some particularities of freshwater ecosystems which pose unique challenges to the implementation of effective conservation. For example, spatial-temporal connectivity plays a key role in maintaining important ecological processes, such as periodic migrations or dispersal from refuge areas, gene flow, or transport of energy and matter essential for the persistence of populations and species. To ensure conservation efforts in freshwater systems are effective, these connectivity components need to be considered when designing and managing freshwater protected areas. Freshwater ecosystems are extremely dependent on the surrounding terrestrial landscape, and the same connectivity that defines functional ecosystems also facilitates the propagation of impacts along river networks. For this reason, adequate management for conservation of freshwater biodiversity needs to go beyond the limits of the freshwater ecosystem and extend to the terrestrial realm, and sometimes even far distant areas. Finally, a key aspect to conservation in freshwater ecosystems is the need for water, often flowing but also standing water in lakes and connections to underground sources. However, as for connectivity, natural flows have been deeply transformed by human intervention: modification of the quantity, timing and variability of flows due to river regulation by dams, water abstraction and overexploitation of aquifers.

The designation of protected areas alone is therefore insufficient to halt freshwater biodiversity loss and must be accompanied by measures to ensure adequate habitat quality and connectivity at appropriate spatial scales. Additional management options are needed to expand management beyond the boundaries of protected areas and ensure effective conservation. These include maintaining and restoring free-flowing rivers key to ensure the maintenance of key ecological processes or environmental flows important to allow the transport of energy and material along the river network (Grill et al., 2019).

Integrated water resources management and integrated river basin management

Management of freshwater ecosystems requires strategic decision-making to integrate multiple and often conflicting objectives, such as exploitation of freshwater resources and biodiversity conservation. Integrated management needs to be sustained by strong objective setting and adequate planning. Objectives should be agreed on by all relevant stakeholders to reflect the diversity of interests and needs that converge in a particular freshwater ecosystem (Cañedo-Argüelles et al., 2019). As mentioned above, reaching agreements across stakeholders is still the most common challenge that hinders effective management of freshwater ecosystems and that deserves further attention and innovative solutions. Decision-making, to achieve those objectives, should be rooted in adequate planning, not only to help minimize potential trade-offs between conflictive objectives (e.g., construction of dams for the exploitation of freshwater resources and cultural/recreational ecosystem services), but also to promote co-benefits across objectives whenever possible (e.g., conservation of riparian forests for regulation ecosystem services such as carbon storage of flood retention and biodiversity conservation). There are multiple approaches to addressing this complex task of deciding what to do, where to do it and when to do it that span from expert elicitation to multicriteria and optimisation methods. Each approach, with its own pros and cons, can contribute to disentangling those complex questions and, therefore, help achieve conservation goals.

Integrated management for multiple objectives at catchment scale is challenging to implement, not only because of potential conflicts and trade-offs between objectives, but also because of the transboundary and cross-sectoral nature of freshwater ecosystems (Allan et al., 2019). Rivers often drain through different administrative boundaries, from regions to countries, which makes coordination across them essential to ensure effective management. Coordination of different sectoral administrations with different competencies and responsibilities within the same administrative unit can include catchment management authorities, National administrations (such as Ministries for the Environment) or even supra-national institutions (e.g., European Commission in the European Union) with competences and legislative capacity in biodiversity conservation issues. Catchment coordination agents, like the Mekong River Commission, can help disentangle the management conundrum by promoting both discussions on objectives and planning at catchment scale across jurisdictions and administrations.

Retaining wild or free-flowing rivers

Given the key role of connectivity in maintaining functional freshwater ecosystems, effective conservation of freshwater biodiversity needs to focus attention on maintaining (and restoring) free-flowing rivers (Grill et al., 2019). These are "rivers where ecosystem functions and services are largely unaffected by changes to fluvial connectivity." They are essential for maintaining populations of freshwater migratory species and megafauna, such as the European eel (*Anguilla anguilla*), the Chinese paddlefish (*Psephurus gladius*) or the Amazon dourada (*Brachyplatystoma rousseauxii*), that in many cases need to migrate over large distances (>1000 km) between spawning and adult foraging grounds. The cumulative impact of thousands of small infrastructures, such as small dams and weirs, can cause even larger impacts than a single large dam on freshwater ecosystems and their biodiversity (Lange et al., 2019). It is therefore crucial to adequately plan future development of infrastructure that impacts longitudinal connectivity of rivers, ideally following the mitigation hierarchy: whenever further impact cannot be avoided (prevent development) or minimized (corrective measures), restoration of connectivity in similar rivers (off-setting) must be warranted to ensure no net loss of free-flowing rivers. Under offsetting schemes, loses derived from new project developments that cannot be avoided need to be counterbalanced by generating an equivalent biodiversity benefit somewhere else. More importantly, restoration needs to focus on similar habitats to avoid net loss.

The protection of the free-flowing rivers can be operationalized through different policy tools, beyond formal designation of protected areas. For example, in the United States, the designation of Wild and Scenic Rivers provides protection for wild rivers with outstanding scenic, recreational, geologic, fish and wildlife, historic, cultural, or other conservation values, including the prohibition of dam construction. Protection of free-flowing rivers materialize through other means like granting rivers legal status similar to persons or adequate catchment management plans. For example, the Whanganui River in New Zealand was first in the world to be considered a legal person, providing traditional owners with legal instruments to protect the river's integrity (Charpleix, 2018). Catchment management plans are, on the other hand, a widely implemented instrument that can aim to harmonize contrasting objectives such as exploitation of freshwater resources and conservation of biodiversity and maintenance of free-flowing rivers. For example, the Strategic Environmental Assessment for hydropower in Myanmar recognizes the value of some mainstem rivers for maintaining critical basin processes and, therefore, proposed to be specially managed for their connectivity value. This recognition implies that no future dam development projects that impact longitudinal connectivity are allowed.

Dams: Operation, design, removal

The widespread impact of barriers makes them a focal point for effective freshwater conservation point of view. Preserving free-flowing rivers, as mentioned above, is key to freshwater biodiversity conservation but could not be sufficient to warrant the long-term persistence of freshwater biodiversity, as most rivers are already impacted by these infrastructures (see introduction). Dams can act as water storages and generate and store power, and they can also act to mitigate floods. Numbers on dams globally vary: global datasets like GOODD or GRanD contain 35,000–55,000 dams. These of course leave out many smaller impoundments like farm dams on agricultural properties. The AMBER barrier atlas currently contains 63,0000 dams and other artificial barriers globally—an exact number will be almost impossible to find.

As stated in the previous sections these structures can impede fish migration, for example upstream movement of anadromous fish to spawning grounds. Barriers can be mitigated by fish ladders—structures that can be used to bypass dams and move upstream. Fish ladders unfortunately are not a perfect solution as often only a limited pool of species can use them and they incur ongoing maintenance costs (Zarfl et al., 2019).

Thermal pollution is a key problem with dams globally. When lakes stratify in summer, the lower layer can be 5–15 °C colder than the surface layers. Upon release of the colder water river sections downstream of the dam will be unseasonably cold in summer (Miara et al., 2018). This can not only interfere with spawning behavior, but also stunt growth in fish larvae, as well as change aquatic food webs. Multiple mitigation strategies can temper the impact. Instead of releasing water from dams at the—usually cold—bottom of the late, multi-level offtakes near the dam wall can mitigate thermal pollution by drawing water from one of the top layers near the thermocline. Also, destratification measures are often used to mix the colder water from the lake bottom with surface water. This can be achieved using mixer structures to blend the water layers. Cheaper approaches include bubble plume destratification in which air flow from a bubbler hose can break the stratification (Helfer et al., 2011).

Altered flow regimes downstream of a dam can gravely affect ecosystems by changing many aspects of the flow regime and river ecology in general (Arthington et al., 2006; Arthington, 2012). Depending on the location and nature of the river, the natural flow regime shapes a river's ecology in multiple ways. In tropical rivers for example, large flood pulses shape the wet season hydrograph. This is similar in snow-fed rivers, where spring melts result in high volumes. Dams can change seasonality, volume but also the magnitude of high- and low-flow periods. Changes to seasonality, for example, can change trophic status of rivers, and also reverse spawning cues. Tempering of high flood pulses may protect downstream low-lying habitable areas, but it may also impact and reduce important flushing flows that clean sediment deposits out of in-stream habitat and reduce connections to the floodplain. This can impede movement to safe spawning habitats for biota and can also reduce nutrient fluxes between the floodplain and the rivers. Dam releases and other man-made interventions to restore these regimes are termed "environmental flows" (Poff and Zimmerman, 2010).

Despite optimal operational design and best management practises, dam impacts can sometimes not be sufficiently minimized and dam removal becomes the only option for biodiversity conservation. Dam removal has gained momentum over the last decades, with over 1000 dams been removed in the United States (O'Connor et al., 2015), see Duda and Bellmore this volume) or

the commitment made by the European Union of reconnecting at least 2500 km of rivers by 2030 in its recently adopted Biodiversity Strategy. Barrier removal projects can be expensive and can involve significant opportunity costs associated with the socio-economic benefits of dams and reservoirs. Restoration of natural connectivity needs to be carefully planned to maximize the recovery benefit while minimizing socio-economic trade-offs, ideally at the whole catchment scale. Although opportunistic decision-making at reduced scales can leverage local interests, it is only at large scales that the cumulative impact of barriers can be tackled in an efficient way.

Restoration

Given the poor conservation status of freshwater ecosystems worldwide (see "Major threats" section) restoration often needs to complement conservation efforts. River and wetland restoration projects have gained momentum in the last decades, not only to restore intrinsic biodiversity values, but also because of the importance of these systems as providers of services to humans (e.g., clean water, flood control, food or recreational opportunities). More than US$ 1 billion is spent annually on rehabilitation projects in the United State alone, and the number of projects has increased exponentially in the last decades (Allan et al., 2013). Despite these efforts, freshwater biodiversity continues to decline alarmingly. Compounding factors are behind this insufficient improvement, although the failure to address the true driving causes at a scale adequate to capture the ecological processes involved in the degradation could be some of the leading factors—along with failure to include socio-economic considerations.

Traditionally, decisions on where and what to restore were implemented following ad-hoc approaches, mainly making the most of opportunities (e.g., removal of obsolete barriers) that do not necessarily address the roots of the problem (the key drivers) at the adequate spatial scale. This results in resources invested in restoration poorly effective and, in some cases, redundant. For example, the removal of a barrier that impedes the movement of migratory species might be insufficient if habitat quality in the areas where the species need to migrate to is in poor condition and not restored simultaneously. It could even cause more harm than good if the infrastructure removed was an effective barrier containing the spread of invasive species. To overcome these issues and enhance efficiency of restoration investment in freshwater ecosystems, adequate planning is needed, to identify priority areas where restoration can help tackle the drivers of degradation at the adequate scale. Catchment scale planning of restoration seems the more adequate approach to overcome these problems (Hermoso et al., 2012).

International conventions on conservation

Since the last edition of the Encyclopedia of Inland Waters a number of international conventions have been ratified at a global level. Historically, the key conventions were the Ramsar Convention and early drafts of the Convention on Biological Diversity. The Ramsar Convention, ratified in 1971, aimed to halt worldwide loss of wetlands by conserving representative, rare or unique wetlands. Ramsar wetlands are not designed for exclusive use as national parks, but as a mixed-use conservation feature for which the imperative is to maintain its ecological character. A global wetland analysis in 2017 demonstrated that the Ramsar convention is reasonably effective—human pressures to wetlands protected under the convention Wetlands was higher compared to strict protection regimes (IUCN I-IV), but on par or even less than IUCN V-VI (Reis et al., 2017).

Since then, two major conventions were ratified—the Aichi Targets in the Convention on Biological Diversity (CBD), as well as the targets set by the UN's Sustainable Development Goals (SDGs). The Aichi Targets cover recommendations on habitat loss (Target 5), fisheries management (6), pollution reduction (8), invasive species (9), protected areas (11) and ecosystem services (14) (Juffe-Bignoli et al., 2016). The protected areas target for example recommends 17% of freshwater systems to be protected. As discussed above this is often not does include enough as upstream areas, and surrounding wetlands may need to be protected. The "Emergency Recovery Plan" outlined by a broad coalition of NGOs and academic partners (Tickner et al., 2020) also encourages extension of the Aichi targets by explicitly emphasizing freshwater systems and their connectivity requirements in Target 5, explicitly setting targets for inland fisheries (6), focusing on pollutants to freshwater systems (9) and considering the full range of freshwater ecosystem services (Juffe-Bignoli et al., 2016).

The same recovery plan discusses the SDG targets 6, 14 and 15. SDG target 6.3 mandates an improvement of water quality by reducing all sources of pollution including chemical pollution. This target, as well as target 6.4 (water use efficiency and sustainable withdrawals) align with the recovery plan. Target 6.6 (protection of water related ecosystems) as well as Target 15 (protection, restoration and sustainable use of ecosystems) suffer from a similar shortfall as Aichi 11: the spatial context in these targets is not explicitly dealt with, so pollution or water withdrawal upstream can adversely affect downstream ecosystems (Green et al., 2015; Harrison et al., 2016; Harper et al., 2021). Currently intergovernmental bodies, NGOs and the research community are working on longer term strategies to address these shortcomings, including re-framing quantitative targets.

Conclusions and further directions

Over the last 20 years, conservation of freshwater ecosystems has faced both renewed challenges (e.g., increasing population growth and consumption) and a drive towards systems science to conserve freshwater biomes at the landscape scale. Both governments and intergovernmental organizations have started to adopt large-scale conservation frameworks that are underpinned by science. That said, the biophysical realm is only one aspect of the conservation puzzle. A recent review that highlighted

25 essential research questions for freshwater conservation found that implementation of the science, as well as embedding conservation science in a broader social context, is essential for bending the curve on biodiversity loss (Harper et al., 2021).

Key areas this chapter highlighted include lessons from successful efforts of translating conservation research into policy. Communication of the importance of pollution reduction to industry, as well as incentives to embrace nature-based solutions, were highlighted as important to remediation efforts. Trade-offs in balancing resource needs between food production both on land and via aquaculture with freshwater biodiversity need to be identified and acted on. Policy and investment need to be made aware of the economic consequences of biodiversity loss and long-term funding stability for conservation management needs to be addressed. Integration with social scientists and the general public is needed to translate scientific findings into action, especially in areas that are underrepresented in standard scientific circles. Finally, acceptance that conservation science is not a one-way street needs to be fostered as indigenous and multicultural perspectives can contribute greatly to conservation.

Knowledge gaps

- *Distribution and threat status for biodiversity*: As species are less visible than their terrestrial counterparts, often distributions are not known. It is also harder to estimate threat status to trigger statutory protection.
- *Adequate monitoring*: Freshwater monitoring has been a key scientific discipline for decades, however with technological advances such as eDNA or autonomous sensor technology, higher spatial and temporal resolutions can be achieved.
- *Interaction of existing threats and climate change*: Climate change can exacerbate other threats, such as water extraction or invasive species. Factors that cannot be mitigated need to be included in proactive planning to minimize the effects on threatened species.
- *Effectiveness of protected areas*: Few studies have examined overall effect of protected areas on rare and threatened species. This is partially due to a relative lack of properly designed aquatic protected areas that integrate longitudinal and lateral protection.
- *Coordination across administrative boundaries*: Rivers often divide countries. There is a clear need for proper policy instruments that can help coordinate freshwater conservation between states or countries.
- *Trading off multiple objectives of conservation and human demand*: Both modeling approaches and policy processes need to develop better integrated workflows that trade off multiple objectives of biodiversity and human demand and human benefit.
- *Inclusion of socio-economic processes*: While not covered in this article, socio-economic processes, such as knowledge transfer between agents and general stakeholder engagement need to be included. Both processes, but also research insights are currently lacking.
- *Translating conservation into policy*: Clear avenues need to be developed that translate conservation knowledge and research into policy. These are currently lacking, with intergovernmental organizations acting as mediators, but often resolutions are not binding.

See Also: Structures and functions of Inland Waters - Rivers: Dam Removal and River Restoration

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Climate Change and Extreme Events in Shaping River Ecosystems

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This is an update of B. Finlayson, M. Peel, T. McMahon, Climate and Rivers, in Encyclopedia of Inland Waters, edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00042-9.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor LeRoy Poff.

Glossary

Beta diversity Differences in ecological communities among multiple locations. More specifically, variability in species composition among locations within a region.
Ecological trap A situation where rapid environmental change leaves organisms in poor-quality habitats. Whether the habitat quality or the environmental cue changes rapidly to the point that one no longer reliably indicates the other, organisms mistakenly prefer habitats where their fitness is lower than in other habitats.
Extreme event "A rare or unusual weather or climatic occurrence (e.g., extreme of precipitation, temperature or wind) and/or the resultant extreme physical phenomena in river catchments (e.g., fluvial floods, hydrologic droughts, storm surges, fire or cryosphere-related effects)"; taken from Ledger and Milner (2015). See "Extreme events defined" section for full explanation.
Flow regime The long-term sequence of high (floods) and low (droughts) flows, characterized by five key components: magnitude, frequency, duration, timing, and rate of change.
Nonstationarity Generally, where a system no longer fluctuates within a range of variability that persists through time (no longer fixed underlying probability distribution). More specifically, differences in statistical characteristics, such as mean or variance, or in statistical relationships, through time.
Press disturbance Disturbances that arise rapidly and then maintain a constant level, such as the building of a dam to alter a flow regime or river connectivity.
Pulse disturbance Short-term and sharply delineated disturbances, such as flood events.
Ramp disturbance A disturbance where the strength of disturbance steadily increases over time, such as gradual land-use change, the spread of an invasive species, or long-term drought.
Resilience The capacity of a population or community to recover following a disturbance event.
Resistance The ability of a population or community to withstand a disturbance event.
Species range shift Changes in the distribution limits of a species, generally along altitudinal or latitudinal gradients.

Introduction

In June 2021, a large low-pressure mass built up over the Tasman Sea to the west of New Zealand before proceeding to pick up moisture-rich air from the Pacific Ocean to the north and slamming into the east coast of New Zealand's South Island. This event caused widespread destruction across the Canterbury region of New Zealand, with many of the large rivers draining the eastern slopes of the Southern Alps flooding, damaging critical infrastructure and putting lives at risk. Although this was described as a

one-in-two-hundred-year event, the reality of climate change means these kinds of events will recur at much higher frequencies than in the past (IPCC, 2021). In the weeks that followed this event, we witnessed catastrophic floods unfolding elsewhere in New Zealand, as well as across Europe and China. This is a recurring trend: over recent years, we have seen increasing frequencies of various extreme climatic events, including high profile drought and wildfire events across western North America and eastern Australia, causing tens of billions of dollars of economic losses, severe losses of biodiversity, and loss of human life (WMO, 2020).

Such events serve as a reminder that the main way in which humans will feel climate change is via increasing frequencies of what we currently consider extreme events. Climate change-driven disturbances are predicted to continue to intensify by more than an order of magnitude over the next 100 years (IPCC, 2021). We continue to see records being broken in terms of heat across the globe (WMO, 2020), with July 2021 being the hottest month ever recorded on Earth (NOAA, 2021). The threats to human infrastructure are clear. More nuanced, however, are the threats to freshwater biodiversity and to the ecosystem goods and services provided by rivers.

Rivers and streams are highly dynamic environments, with natural cycles of floods and droughts (Poff et al., 1997). Organisms that inhabit these ecosystems have evolved life histories to cope with, and indeed capitalize on, these natural disturbance regimes (Lytle and Poff, 2004). However, these regimes are rapidly changing in terms of their magnitude, frequency, timing, and duration (Blöschl et al., 2017, 2019; Stewart et al., 2005).

Climate change and extreme events are dynamically entwined in river ecosystems. In addition to magnifying and increasing the frequency of extreme events, climate change has the potential to alter many other aspects of river ecosystems, such as modifying temperatures and inducing species range shifts, or interacting with various other anthropogenic stressors, including invasive species, land-use change and flow alteration (Dudgeon et al., 2006). The physical basis of climate change has never been clearer: with an increasingly high level of confidence, science indicates that climate change will continue to intensify in coming decades (IPCC, 2021). The need to understand the effects of climate change on riverine ecosystems has, therefore, never been more pressing. In this chapter, I review the broad ways in which climate change will influence river ecosystems, and the role of climate-driven extreme events in shaping river ecosystems, including their structure and function.

The physical basis of climate change and extreme events

Extreme events defined

Climate change research has often focused on shifting mean conditions, but one of the key ways in which climate change will impact freshwater ecosystems is via increasing variation around increasing means; i.e., by amplifying the magnitudes and frequencies of extreme events. There is no consistent definition for what constitutes an extreme event in running waters. This lack of coherent definition is an issue that has transcended disciplines, which may have hampered our ability to understand and manage extreme events (McPhillips et al., 2018). Extreme events in rivers are typically considered statistically rare or unusual events (often climatically-driven) that translate into extreme physical effects, such as through floods or droughts, which may or may not have extreme consequences on the ecosystem. Extreme climatic events include prolonged droughts, heatwaves, or rainfall events associated with unusually large and infrequent storms.

Many have used probability-based definitions, such as extreme floods being those with a 100-year return interval or 1% excedence probability; or threshold-based, such as temperature crossing certain thresholds (Ledger and Milner, 2015). However, what is considered an extreme event in the present day based on certain thresholds or magnitudes will likely be revised as the climate continues to warm (McPhillips et al., 2018).

For the purpose of this chapter, I will focus mostly on climate-related extreme events, which largely reflect flood and drought regimes (flow regimes). My definition of an extreme event is deliberately broad, with no particular threshold or probability. Thus, I will loosely define an extreme event following the definition used by Ledger and Milner (2015): "a rare or unusual weather or climatic occurrence (e.g., extreme of precipitation, temperature or wind) and/or the resultant extreme physical phenomena in river catchments (e.g., fluvial floods, hydrologic droughts, storm surges, fire or cryosphere-related effects)." It is important to note that this definition also considers more than just the magnitude of events. For instance, if a major event falls well outside the typical timing of such events historically, it may have just as detrimental an effect as an extreme event defined by magnitude alone.

From historical range of variability to novel future regimes

Research has now demonstrated considerable change has already occurred to flow regimes across the world in recent decades (Blöschl et al., 2017, 2019; Stewart et al., 2005). Extreme flood events have increased substantially in frequency over the 20th century (Milly et al., 2002). These changes play out differently across the globe and within regions. Existing water stressed regions (Fig. 1) are set to become more challenged by water shortages. For instance, floods are arriving earlier in northeastern Europe due to warmer temperatures driving earlier snowmelt, later around the North Sea and parts of the Mediterranean coast due to delayed winter storms, and earlier in western Europe due to earlier soil moisture maxima (Blöschl et al., 2017). Similarly, flood magnitudes are increasing in northwestern Europe due to increasing autumn and winter rainfall, and decreasing in both southern and eastern Europe due to decreasing precipitation and increasing evaporation in southern regions, and decreasing snow cover and melt in eastern regions (Blöschl et al., 2019). In western North America, the onset of spring snowmelt and associated increases in river discharge is occurring earlier across the region (Stewart et al., 2005). Similarly, increases have been found in river temperatures over a 30-year period in northwestern United States (Isaak et al., 2012), a trend that is set to continue with increased climate change, not

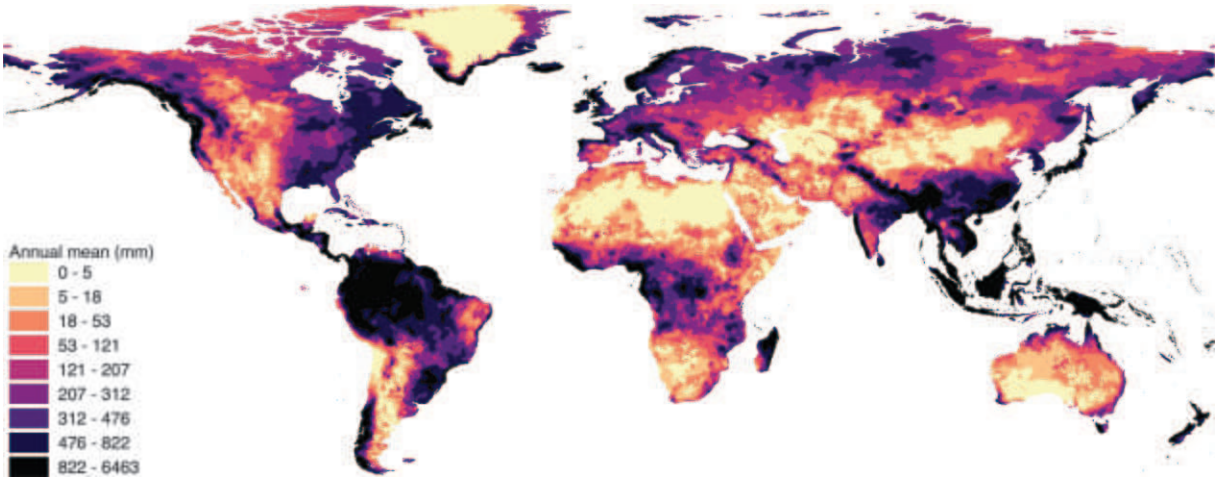

Fig. 1 Global map of land surface runoff (mm year^{-1}), based on long-term (1971–2000) averages, highlighting existing water stressed regions at risk of further climate change. Data were sourced from the HydroATLAS database (Linke et al., 2019).

just in North America, but across the globe (van Vliet et al., 2013). This shifting physical template of rivers presents critical challenges for the species that inhabit them, let alone the management of river flows for human wellbeing.

Effects on river ecosystems

The mechanisms by which extreme events influence biodiversity are varied depending on their nature, and effects can be direct or indirect. Extreme floods can significantly alter the physical template of rivers (Death et al., 2015), or cause direct mortality on individuals, but may also enable previously isolated populations to disperse and reconnect, particularly in arid landscapes where stream drying isolates permanently flowing channels (Datry et al., 2016; Tonkin et al., 2018a). By contrast, extreme droughts can fragment freshwater habitats or push temperatures and pollutant concentrations beyond tolerable limits for organisms (Palmer and Ruhi, 2019). Thus, ecological responses to extreme events, like everything in ecology, are context dependent. However, testing the effects of extreme climatic events on riverine biodiversity is challenging given the rarity of extreme events and the general associated lack of pre-event data (Poff et al., 2018). Thus, case studies on the effects of extreme events on riverine ecosystems are not common.

Nonetheless, evidence of the effects of these climate change-induced extreme events is beginning to accumulate. For instance, unprecedented droughts such as Australia's Millennium Drought or California's recent drought, can completely alter river and riparian ecosystems, shifting ecological communities over new thresholds (Aspin et al., 2019; Bogan and Lytle, 2011; Thomson et al., 2012). Further, the intensity and duration of drying can regulate rates of gross primary productivity (Colls et al., 2019) and litter decomposition (Mora-Gómez et al., 2020). At the other extreme, intensified floods can also have major impacts on the functioning of rivers (Palmer and Ruhi, 2019), including leading to population genetic changes as a result of mass mortality events (Poff et al., 2018).

Coupled geomorphological-ecological responses

Extreme floods resulting from climate change also have the potential to significantly change the geomorphological template of rivers (Death et al., 2015). Beyond the negative direct effects of large floods on organisms, such channel-altering floods, can provide significant benefits for resident biota by resetting physical conditions, opening up habitat for flood-adapted species, and removing nuisance accumulations of primary producers and exotic weeds. However, channel-altering floods can also multiply the effects of other stressors on aquatic life such as by redistributing toxic chemicals, in addition to their direct effects on human infrastructure (Death et al., 2015).

The geomorphological and ecological context can also influence the ecological response of stream ecosystems to extreme events. Robertson et al. (2015) examined the response of meiofauna, macroinvertebrates and fish to an extreme flooding event in southeast Alaska across four recently deglaciated catchments. The ecological responses to this event differed across the four catchments, which reflected both the local intensity of rainfall and factors related to the age of each stream (38–180 years), including channel morphology, and catchment vegetation type and cover. However, many questions remain unanswered regarding the effects of extreme floods on river geomorphology and ecology (Death et al., 2015).

Resistance vs. resilience

Given the inherent dynamism of rivers, riverine species are often relatively resistant and/or resilient to extreme flood events (Blondel et al., 2021; Lytle and Poff, 2004), as a result of the evolution of behavioral, morphological or life-history adaptations (Lytle and Poff, 2004). However, there is often a tradeoff between resistance and resilience to flood disturbances (McMullen et al., 2017). For instance, Poff et al. (2018) examined population genomic responses of aquatic insects to a one-in-500-year rainfall event in

Colorado streams. Local species responses depended on traits related to resistance and resilience, but persistence was lowest at locations with highest disturbance. Persistence was lowest for immobile taxa, with a greater chance of persistence for species with mobile larvae or terrestrial adult stages present during the flood event. Despite a clear role of resistance and resilience traits in determining species persistence, genomic changes were much less predictable for the six species examined. Resistance and resilience to extreme floods can also differ within populations depending on what aspects of the population are considered. For example, Blondel et al. (2021) found genetic diversity and population structure of native riverine guppies to be resistant, and phenotypic diversity, represented by body size and male coloration, to be resilient to extreme flood events. More specifically, minimal changes were observed in genetic diversity and population structure compared to preflood patterns whereas phenotypic diversity was more heavily impacted by the flood events, but these larger impacts were short-lived.

Altered flow regimes

Of the many changes that will occur to flow regimes as a result of ongoing climate change, one of the more concerning for native riverine organisms is changes to the timing of flow events. Flow timing is a critical component of the natural flow regime (Poff et al., 1997), and one for which species have evolved various strategies to capitalize on (Lytle and Poff, 2004). The predictability of flow regimes is a critical structuring agent of riverine biodiversity, with more predictably seasonal flow regimes able to harbor greater biodiversity (Tonkin et al., 2017). Riverine species have adapted to capitalize on these seasonal rhythms. This is not surprising given the predictability of flow regimes in many parts of the world (Fig. 2). For instance, in western North America, cottonwood (*Populus* spp.) release their seeds after the annual peak river flows that come with spring snowmelt, which facilitates dispersal and establishment into the floodplain (Mahoney and Rood, 1998). Shifting the timing of these peak flows may help non-native *Tamarix* to outcompete cottonwoods through time (Lytle et al., 2017), as has been seen below dams that have altered timing and magnitudes of peak flows (Merritt and Poff, 2010).

Fish are also fundamentally attuned to the natural timing of flow events in rivers. For instance, the timing of winter events is often critical for the reproductive strategies of coldwater fish species (Shuter et al., 2012). Given the existing evidence that the timing of flood events has already changed (Blöschl et al., 2017), it is not surprising that phenologies of riverine fish have already shifted (Shuter et al., 2012). Mismatched phenologies are a critical threat to freshwater fish as river flows continue to change, ranging from

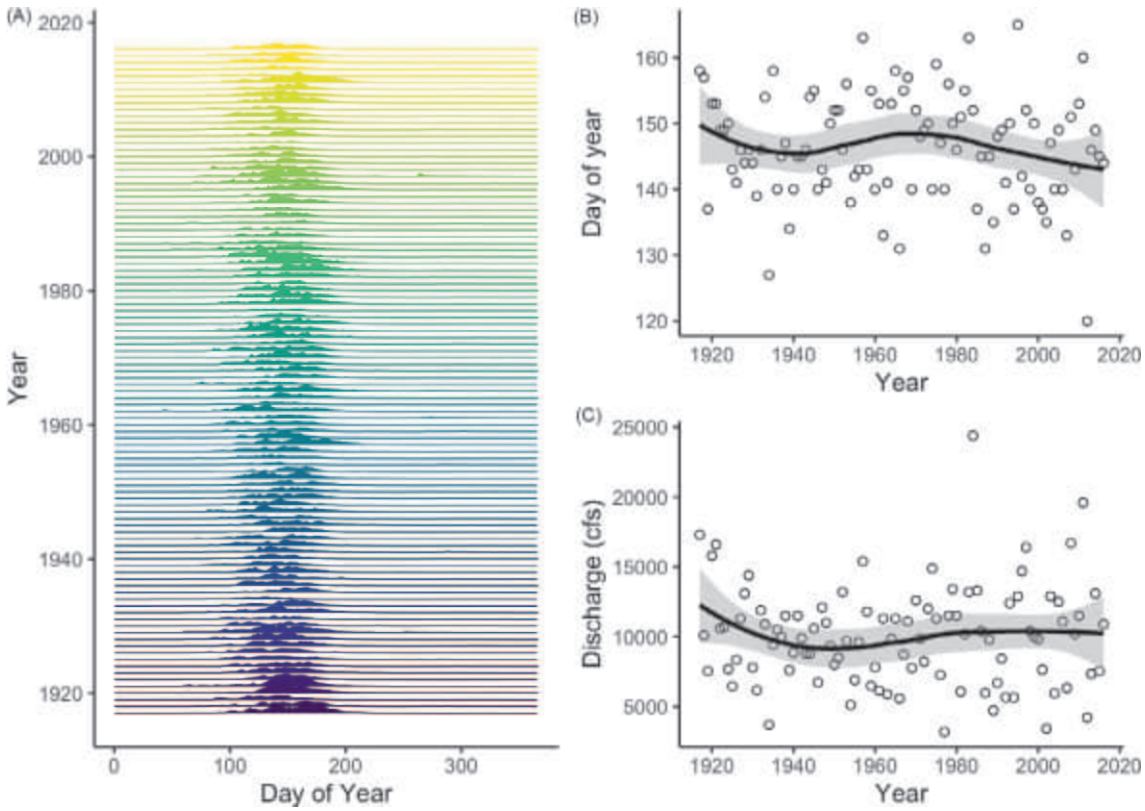

Fig. 2 (A) Ridgeline plot of flows in the unregulated Yampa River, a tributary of the Colorado River at Maybell, Colorado over a 100-year period. Each line is an annual hydrograph demonstrating the consistency of the spring snowmelt flood pulse from 1916 to 2016. Species such as riparian cottonwoods have evolved intricate relationships with these predictable pulses. Although difficult to discern here, climate change is already altering the natural phenology of river flows globally, and bringing spring snowmelt earlier across most of western North America (Stewart et al., 2005). (B) The day at which 50% of annual flow has passed the gage. (C) Annual peak in daily discharge over the 100 years. Trendlines in both B and C represent locally weighted smoothing (loess) curves.

increased larval mortality due to premature hatching to mismatched feeding phenologies between different stage classes shifting interactions between predation and competition (Shuter et al., 2012).

Human-altered flow regimes can be extreme in and of themselves. For instance, hydropeaking, where dams release different volumes of water throughout the day in response to energy demand imparts a novel pattern of flow variability into a river (Ruhi et al., 2018). These flows have been shown to reduce functional diversity of invertebrate communities downstream of a large dam on the Chattahoochee River in Georgia, United States (Ruhi et al., 2018), and lead to the near complete extirpation of mayflies, stoneflies and caddisflies in sections of the Colorado River subject to high levels of hydropeaking (Abernethy et al., 2021). Such alterations are analogous to the effects of urbanization, which can severely alter flow regimes and lead to exacerbation of flow extremes and their effects on riverine biodiversity (Palmer and Ruhi, 2019). Streams draining urban catchments are subject to regular, intense flow events due to their increased impervious surface and more concentrated runoff. In certain cases, this can lead to a cycling between flow extremes and extreme anoxia events (Blaszczak et al., 2019).

Complex and nonlinear responses to change

Biodiversity change in response to changing river conditions is complex and varied. For instance, Larsen et al. (2018) found no change in metrics typically used to detect biodiversity change but uncovered more nuanced underlying changes. Using a 30-year time-series dataset of benthic macroinvertebrates from southern Wales, they found no change in taxonomic or functional alpha diversity or spatial beta diversity. However, underlying this apparent stasis in widely-used metrics of biodiversity change was a temporal change in mean species composition. These changes reflected a systematic decline in mean community specialization, which was associated with a lower rate of recolonization of specialists as opposed to an increased local extinction rate.

Other studies have found clear evidence of change at multiple levels over recent decades attributable to climate change, but trends are often nonlinear. Using a comprehensive 42-year long dataset (1969–2010) of weekly species-level insect abundances from the Breitenbach Stream in central Germany, Baranov et al. (2020) uncovered major shifts in insect community structure, including an 82% decline in overall abundance and a 9% increase in richness. These changes occurred in the absence of any other ongoing stressors beyond a climate change-induced 1.9 °C water temperature increase and an altered flow regime, characterized by the change in four annual discharge patterns: dry years, wet years, aseasonal spate years and extreme spring spate years. Their research, again, uncovered often-missed mechanisms of change: peak insect emergence arrived 13 days earlier over the study period and the duration of emergence increased by 15 days. Understanding these mechanistic changes can enable a more comprehensive picture of how species may or may not adapt to ongoing warming. Although evidence suggests the responses of biodiversity to extreme climatic events is highly idiosyncratic and unpredictable (van de Pol et al., 2017), taking a more mechanistic approach to understand responses will likely uncover generalities that can transcend species, ecosystems and locations.

Understanding ecological responses to environmental regimes is often carried out by focusing on mean environmental conditions as the key drivers of ecological dynamics. However, in reality, one-off or extreme events may play an equal or larger role in shaping biodiversity in running waters than long-term trends through a legacy effect. Jourdan et al. (2018) compared the role of long-term climatic change and antecedent climatic conditions in predicting European stream invertebrate communities across a set of long-term ecological research network (LTER) sites sampled for between 10 and 24 years. They found that antecedent climatic conditions, measured as the mean temperature and daily precipitation, and the number of extreme hot, cold and high precipitation days over the preceding 12 months, were better predictors of community metrics than background long-term change. This highlights the need to both understand the mechanistic responses to individual flow events, including both ecosystem states and rates (Tonkin et al., 2019), and continue investment into long-term monitoring programs to help detect longer-term trends.

Species range shifts, community reorganization and invasion

One of the most apparent responses of biodiversity to ongoing climate change is caused by species moving their range to track shifting isotherms. In Europe, climate change projections have indicated a decline in climatically suitable habitat for more than 50% of invertebrate species and losses could be as great as 40% by late this century (Domisch et al., 2013). These models have indicated that species facing the largest decline in climatically suitable areas were cold-adapted species, whereas warm-adapted species were expected to gain suitable habitat (Domisch et al., 2013). Haase et al. (2019) analyzed changes in stream invertebrate community composition over 25 years across central Europe and found clear evidence of community reorganization, and in particular, evidence of a decline in cold-adapted species, with warm-adapted species appearing to replace them. The biggest distribution shifts were apparent with elevation rather than latitude, and these changes were apparent despite the temperature only having changed by 0.5 °C over this period. Systematic shifts have been found for riverine fish upstream and in elevation across France at rates faster than many terrestrial organisms but not rapid enough to track changing climate (Comte and Grenouillet, 2013).

Flow alteration and temperature change combine to threaten riverine species. Across western United States, projected climate-induced flow alteration has been shown to be equally as important as warming in its risk for stream invertebrate communities (Pyne and Poff, 2017). However, the vulnerability to projected gradients of temperature and hydrologic change varies widely across the ecoregions of the western United States—from the wet forests of the northwest to the desert of Arizona: communities in some ecoregions are more sensitive to warming and others to reduced flow (Pyne and Poff, 2017). Similarly, both increased water temperature and discharge reduction have played a key role in the disappearance of invertebrate species from the Middle Loire River in France over a 30-year period (Floury et al., 2013). During this period, species that specialize in slow flowing or standing waters, including invasive species, increased in number. Similar patterns have been uncovered for riverine fish with species

that prefer warm- and slow-water habitats increasing in dominance across the globe (Comte et al., 2021), changes that are exaggerated in human-modified regions (Comte et al., 2021).

Climate change-induced reorganization is already widespread across the globe. For example, stream invertebrate communities appear to be homogenizing through time in New Zealand (Mouton et al., 2020). Homogenization often accompanies invasion by non-native species, and many have found climate change to help facilitate the invasion of non-native fish species (Radinger and García-Berthou, 2020; Rogosch et al., 2019; Ruhí et al., 2016). Using a community-wide modeling approach, Rogosch et al. (2019) revealed non-native fish species in the southwest United States replaced native species as river flow regimes became increasingly affected by drought. These replacements reflected differences in mortality to the major flow events, including spring and summer floods, and droughts. Ruhí et al. (2016), using time-series techniques on multi-decadal ecohydrological data, uncovered high quasi-extinction risks of native species, and asserted that continuing current stream flow trends would further increase these risks for native species but decrease the risks to non-native species.

Dispersal becomes a critical tool in a species' toolbox for its response to ongoing change. Poor dispersers will be less capable of tracking shifting climatic conditions, and species that are restricted to dispersing along the river network will be more vulnerable to extinction than those that can also disperse overland (Tonkin et al., 2018a). Furthermore, species moving upwards in elevation along the river network are threatened by the "summit trap" effect, whereby further dispersal up hillsides is capped at mountain peaks (Sauer et al., 2011). Thus, the extent to which communities will reorganize will depend on a host of factors, including river network structure, dispersal ability and mode, and barriers to invasion.

Interactions with other stressors

There are very few rivers left in the world that have not been impacted by human activities. Understanding the true effects of climate change on riverine ecosystems requires a much broader understanding of species vulnerabilities beyond thermal tolerances to incorporate flow regimes and various other anthropogenic stressors including land use change (Comte et al., 2021). Human-altered systems are potentially more at risk both ecologically and economically from increased extreme events, such as dam failures that may occur with extreme future floods (Palmer et al., 2008). Dams, by altering the natural temperature regime of downstream flows, can also alter the natural responses of biodiversity to shifting climatic conditions. For example, Bruno et al. (2019) found contrasting changes between cold- and warm-adapted species from the 1970s to the 2010s between free-flowing and dam-altered rivers in alpine catchments of south-eastern France. Cold-adapted taxa decreased in both river types, but there tended to be a replacement of cold-adapted taxa by warm-adapted taxa in the free-flowing catchment over time. Such replacement was less pronounced in the regulated catchment, which led to a decline in taxonomic diversity, potentially due to the direct effect of flow regulation on habitat suitability and heterogeneity (Bruno et al., 2019). Dams or other instream barriers can also fragment rivers, which can exacerbate the effects of climate change on fishes (Marshall et al., 2021; Radinger and García-Berthou, 2020). For instance, instream barriers can limit the potential recovery of stream fishes following prolonged drought due to blocking colonists (Marshall et al., 2021). However, there is also a tradeoff associated with increasing connectivity, whereby the spread of non-native species may be worsened under climate change (Radinger and García-Berthou, 2020).

The relative vulnerability of human-altered ecosystems to species loss or diminished ecosystem function when faced with further environmental change or extremes is well illustrated when various stressors combine, leading to catastrophic ecological effects. Between December 2018 and January 2019, millions of fish died across three separate events near the town of Menindee in the Darling River, Australia. Ultimately, these events occurred as a result of human alteration of the river's water through a series of weirs, including substantial harvesting of water upstream, combined with an extremely hot and dry climate during 2018 (Vertessy et al., 2019). Specifically, the fish die-offs resulted from a series of events, including large fish biomass accrual, algal bloom development and thermal stratification of weir pools leading to hypoxic bottom-water conditions. These events culminated in rapid oxygen deprivation resulting from weir pool destratification following sudden cool weather changes (Vertessy et al., 2019). The result of this is likely to be ongoing impacts on fish populations both locally and potentially in the wider Darling catchment for some time to come. The key take home here is that ongoing (or press) disturbances related to climate change are likely to make a system more vulnerable to combined anthropogenic stressors such as the over-allocation of water that can further increase water temperatures and lead to a cascading series of events similar to those at Menindee.

The effects of large transient (or pulse) disturbances (e.g., extreme floods) on top of existing ramp or press disturbances (ongoing climate change shifting mean conditions over decadal scales) is an area in need of further attention. For instance, heat waves can result in fire regimes that can increase flood intensity due to combustion of forest vegetation. When extreme events of different forms combine, the results can be particularly detrimental. Dahm et al. (2015) found flash floods that followed a catastrophic forest fire led to major reductions in water quality that persisted for 50 km downstream. Indeed, combining events that may not be extreme in isolation can make them extreme via their combination (McPhillips et al., 2018). Vieira et al. (2004) studied the response of stream invertebrate communities to repeated flood disturbances after a wildfire in New Mexico, United States, and found that total insect density and taxonomic richness declined to near zero following the first 100-year flood after the wildfire. However, density returned to pre-fire levels rapidly due to the colonization of aquatic insects including simuliids, chironomids and baetid mayflies; taxa with resilience traits (including high dispersal ability) that are often associated with disturbance regimes (McMullen et al., 2017). By contrast, taxonomic richness and community composition were much slower to return to pre-fire levels as less resilient species slowly recolonized (Vieira et al., 2004).

The interaction between ongoing land-use alteration and climate change presents a key challenge for river ecosystem resilience as rates of change continue to intensify (Van Looy et al., 2019). For instance, catchment-scale land use can mediate the local-scale responses to extreme events (Woodward et al., 2016). Collier and Quinn (2003) found that invertebrate communities in streams draining pastoral catchments (representing an underlying press disturbance) can be more influenced by flooding than those draining forested catchments. Similarly, climate change-driven changes to water temperature and flow alteration are interacting with land-use change to reorganize riverine fish communities around the world (Comte et al., 2021).

Land use alteration and climate change, representing ongoing press or ramp disturbances, can combine to interact both synergistically (amplifying effects) and antagonistically (buffering effects) to affect river ecosystems, and the nature of these interactions is context dependent. For instance, both synergistic and antagonistic interactive effects of climate change and land use change are predicted to influence the future distributions of fish diversity in the Elbe basin in Spain, resulting in a predicted increase in average species richness of 0.7–2.9 species by 2050 across the entire river network (Radinger et al., 2016). Antagonistic effects of land use and climate change were predicted for up to 75% of the network, and synergistic and additive effects up to 20% and 16% of the network, respectively (Radinger et al., 2016). Further, improvement in water quality from historical degradation has been found to mask the long-term effects of changing climate on stream invertebrate communities (Vaughan and Ormerod, 2014), potentially via the arrival of pollution-sensitive taxa (Floury et al., 2013). Such improvements can make detecting climate change impacts challenging for freshwaters. These examples demonstrate that the multi-pronged effects of long-term environmental change must be studied together to get a clear picture of the true effects of climate change on freshwater biodiversity.

Thresholds and regime shifts

Ongoing changes in the environment, such as unprecedented drought, can potentially push communities and ecosystems into novel states. Bogan and Lytle (2011) examined aquatic insect community changes in two stream pools in French Joe Canyon, Arizona between 2003 and 2009 in response to multi-year drought. They found an abrupt shift between community states during this prolonged drought, which reflected a transition from a perennial to intermittent flow regime (Fig. 3). While richness of communities may recover following, or remain stable during, multi-year drought in streams, there is often an underlying reorganization of communities, such as a replacement of long-lived, weaker dispersers with short-lived, strong dispersers (Bogan and Lytle, 2011). Aspin et al. (2019) used experimental mesocosms to examine trait-based responses to drought intensification and found that intensifying stream drying events can push stream invertebrate communities over functional thresholds, a point whereby statistical changes in traits were more rapid than changes in drought intensity. They found that the specific traits responding depended on the intensity of drought: moderate drought levels resulted in shifts in morphological traits, whereas extreme drought, where surface water was lost, saw shifts in morphological and physiological traits including body size, respiration mode and thermal tolerance (Aspin et al., 2019). Riparian ecosystems are similarly at threat from climate-induced changes to flow regimes. Using a mechanistic modeling approach, Tonkin et al. (2018b) found that an increasingly dry future would lead to the collapse of networks of interacting riparian plant species and a loss of keystone species in the southwest of the United States. Unraveling interaction networks could have negative consequences for community stability and resistance to invasion, whereas losing keystone species could lead to the loss of important ecosystem services including habitat provision, flood mitigation and nutrient cycling.

Extreme drought associated with climate change can also lead to previously suitable habitat becoming an ecological trap for native species. Vander Vorste et al. (2020) found that endangered juvenile Coho salmon survival in intermittent Californian stream pools differed markedly depending on the duration of disconnection between upstream and downstream habitats. Approximately half of the pools studied that were previously able to sustain juvenile salmon in non-drought years appeared to transition into ecological traps—defined by survival being markedly reduced—during drought.

Geographic differences

The threats of climate change will likely play out differently around the globe. Scenario projections have predicted up to 75% of local fish biodiversity will be threatened by extinction by 2070 as a result of the combined effects of climate change and human water demand, but these differ geographically due to baseline differences in climatic conditions (Xenopoulos et al., 2005). Based on physiological estimates of thermal sensitivity, more recent research suggests that freshwater fish faunas will be most at risk of climate change in Northern Hemisphere regions, particularly at high latitudes (Comte and Olden, 2017). This disproportionate threat to high latitude biodiversity in rivers is not limited to fishes (Nilsson et al., 2015). Threats include greater temperatures, increased rainfall and altered timing of stream flow events as a result of altered snowmelt dynamics, many of which will translate into extreme forms, such as unusually large floods (Nilsson et al., 2015). Northern regions will also likely see the arrival of many new species as the climate warms. Emergent aquatic macrophytes have already expanded their distributions northwards in boreal regions over the past several decades, and models suggest this will continue over the next century due to increasing growing degree days (Alahuhta et al., 2011).

No region is spared from the ongoing effects of climate change, however. For example, increased drying associated with climate change in dryland regions will further threaten endemic fishes, particularly through hydrologic fragmentation (Jaeger et al., 2014). Reductions in network-wide hydrologic connectivity through drying is expected to be as severe as 6–9% over the space of the year and up to 12–18% during spring spawning season by the mid- to late-century in the Verde River Basin, United States (Jaeger et al., 2014). Tropical regions are particularly threatened by the considerable ongoing habitat loss and agricultural expansion that will

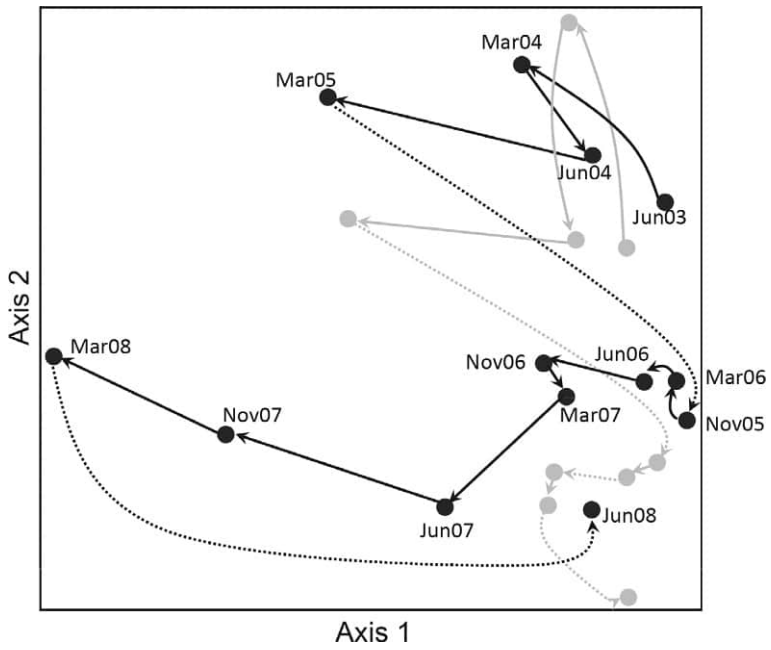

Fig. 3 Ordination plot of aquatic insect community changes in two pools (black vs. gray) in French Joe Canyon, Arizona between 2003 and 2009 in response to prolonged drought. Each point represents a community at one time-point, with those closer together reflecting more similar community composition. Trajectories of change through time are shown by the arrows (dates are labeled only on the black pool). Solid lines reflect times when continuous surface flow was available between both sampling dates. Dotted lines indicate the stream dried in between samples. March 2005 represents a transition from a perennial to intermittent flow regime. Reprinted with permission from Bogan MT and Lytle DA (2011) Severe drought drives novel community trajectories in desert stream pools: Drought causes community regime shifts. *Freshwater Biology* 56: 2070–2081. doi: 10.1111/j.1365-2427.2011.02638.x.

exacerbate the effects of climate change on river ecosystems (Sundar et al., 2020). However, considerable changes have already been observed in tropical Hong Kong stream invertebrate communities over recent decades in the absence of non-climate change drivers (Dudgeon et al., 2020).

Solutions

Many solutions are available for protecting riverine biodiversity, and indeed humans, from the growing threat of climate change and extreme events in river ecosystems. It is clear that the tools are here—the challenge is in the impetus and implementation—and I list a small selection of these tools below. First, in order to be able to better protect freshwater biodiversity from ongoing climate change, we need to go beyond observational data and correlational approaches, and understand mechanistic responses to individual events and whole regimes (Tonkin et al., 2019). This is particularly important for extreme events (van de Pol et al., 2017), and a mechanistic approach will enable a shift towards more robust forecasts and projections of future scenarios. Nevertheless, greater investment into coordinated monitoring programs is required to detect trends across broad regions.

The cost of anticipatory or proactive action will be cheaper than mitigation at a later date (Palmer et al., 2008). By focusing on employing adaptive or anticipatory management policies, much needed flexibility will be promoted to cope with the rapid rate at which systems are changing. Anticipatory or adaptive management aligns particularly well with ecological forecasting. Adaptive management and ecological forecasting can be coupled in an adaptive iterative cycle of model development, prediction and testing (Dietze et al., 2018). Moreover, frameworks such as eco-engineering decision scaling (EEDS) enable a quantitative assessment of trade-offs among potentially conflicting engineering and ecological targets across a variety of possible management regimes under uncertain hydroclimatic settings (Poff et al., 2016).

One key target to build resilience into rivers to rapidly changing futures is to embrace natural riverscape variability. This can be at both local and regional scales. For instance, giving rivers more room to move will enable a greater capacity to self-organize in response to extreme events. Even without the pending threat of climate change altering the frequency of large floods, rivers often naturally overtop their banks at regular frequencies. However, given the likelihood of large-scale river floods becoming more frequent and the fact that human infrastructure is often built on river floodplains, strategic decisions are required about where to give rivers the room they need to move and where to continue to lock in protective structures.

At more regional scales, there is a need to consider streams as metasystems from a dynamic perspective as flow regimes continue to change (Datry et al., 2016; Van Looy et al., 2019). Managing for variability and spatial connectivity across the landscape will

accommodate uncertainty and promote the resilience of river networks to change. Spatial environmental heterogeneity enables broad ecological responses (response diversity) to changing conditions, thereby imparting resilience by enhancing adaptive capacity at the landscape scale.

Designing and implementing spatial ecological networks that enable multiple species to persist, disperse and migrate, and that are robust to multiple climatic and environmental futures is possible using multi-criteria decision making (Albert et al., 2017). Without facilitating unhindered movement of organisms in this manner, managed relocation or assisted migration of species (Olden et al., 2011) or whole communities (Jourdan et al., 2019) will be required in many instances. Balancing local-scale optimal conservation goals while maintaining and promoting the variability that is inherent in natural systems remains key, but it presents major challenges for prioritization in the broader geographic context given the inherent tradeoffs and complexity in decision making required.

Often, the focus of management efforts is too local. Instead, effort should be put into strategic spatial prioritization of management actions for maximizing targets regionally while maintaining resilience at the landscape scale (Poff, 2018). Dammed river catchments may be more at risk from climate change than free flowing rivers via a reduced capacity to reorganize and absorb additional disturbances (Palmer et al., 2008). On the flip side, however, water-control infrastructure, such as dams, provides opportunities for managers to build both resilience and precision into human-altered systems (Tonkin et al., 2021). Although most research on designing environmental flows for human-altered rivers has so far focused on single dams, there is potential to apply this notion to portfolios of hydrologic infrastructure to minimize shortfall risk (in hydropower, water yields) while maximizing regional ecological outcomes. It is, nonetheless, a major societal challenge to achieve an appropriate balance between ecosystem conservation and water resource development.

Conclusions

Humans have extensively exploited river systems for their services, such as food and water supply, power, transport, and recreation, but at the cost of severe ecological degradation (Dudgeon et al., 2006). Climate change is now pushing river ecosystems into new domains of variation by altering regional precipitation and temperature regimes and extremes. The excursion of natural hydrologic variability outside the range of the historical undercuts assumptions of water resources management (Milly et al., 2008) and threatens ecosystems (Tonkin et al., 2019).

The alarming signals we are seeing from Siberian wildfires, extreme floods around the world, to deadly western United States heatwaves each represent the no-analog futures that atmospheric scientists have been predicting for some time. Only time will tell just how devastating these events will be for freshwater biodiversity. But the evidence provided in this chapter highlight that the effects will be wide ranging, from local species extirpations, range shifts, food web collapses, and homogenization. Riverine biodiversity is naturally resilient to dynamic fluctuations in the environment, but we need to be prepared to help increase this resilience through any means possible.

Acknowledgments

JDT is supported by a Rutherford Discovery Fellowship administered by the Royal Society Te Apārangi (RDF-18-UOC-007). N. LeRoy Poff provided useful edits on earlier versions of the manuscript.

See Also: Structures and functions of Inland Waters - Rivers: Ecological and Evolutionary Consequences of Disturbance in Freshwater Ecosystems; Environmental Flows: Ecological Effects of Hydrologic Alterations, Assessment Methods for Rivers, Challenges and Global Uptake; High Latitude Rivers: Ecosystems Shaped by Environmental Extremes; River Resilience

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SECOND EDITION

Encyclopedia of INLAND WATERS

VOLUME TWO

ACADEMIC PRESS
An imprint of Elsevier
elsevier.com/books-and-journals

Set ISBN
ISBN 978-0-12-819166-8
9 780128 191668

Vol ISBN
ISBN 978-0-323-99121-6
9 780323 991216

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Library of Congress Cataloging-in-Publication Data
A catalog record for this book is available from the Library of Congress.

British Library Cataloguing-in-Publication Data
A catalogue record for this book is available from the British Library.

ISBN 978-0-12-819166-8

Publisher: Oliver Walter
Acquisition Editors: Priscilla Braglia
Content Project Manager: Paula Davies
Associate Content Project Manager: Greetal Carolyn
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Klement Tockner is an internationally leading freshwater scientist, in particular in the research domains biodiversity, ecosystem science, and environmental management. He has published about 250 scientific papers including 180 ISI papers. He was editor-in-chief of the journal *Aquatic Sciences* (2005–2014) and is subject editor of the journal *Ecosystems*. He has published about 250 scientific papers including 180 ISI papers. In 2009, he edited a comprehensive book on European Rivers (Rivers of Europe, Elsevier; 2nd Edition in 2021). He is elected member of the Austrian Academy of Sciences and the German Academy of Sciences, Leopoldina.

Photo credit: David Ausserhofer

Thomas Mehner is vice director and senior researcher at the Leibniz Institute of Freshwater Ecology and Inland Fisheries in Berlin, Germany. He is limnologist and fisheries biologist by training, and has got his Diploma and Ph.D. at the University of Rostock (formerly East Germany) in 1992. In 1999, he had received his habilitation and venia legendi in limnology, which allowed him to start teaching as Privatdozent at universities. Since 1997, he has been working at IGB in several positions. He has published about 170 ISI papers, with primary focus on fish communities, lake food webs, and species interactions. However, his topical interests are broader, and he has authored and co-authored several publications on freshwater fisheries management, fish population genetics and evolutionary and behavioral ecology of aquatic organisms. He has been Handling Editor of the journals "*Aquatic Ecology*" and "*Freshwater Biology*" for several years, and he is currently member of the Editorial Boards of "Global Change Biology" and "Limnologica." Since spring 2018, he has been the president of the International Society of Limnology (SIL), the oldest and most international scientific society devoted to the study of inland waters. Thomas Mehner has taught M.Sc. courses at universities on limnology, fish ecology, fisheries management, and behavior and evolution. His one-week course on "Scientific Writing" for Ph.D. students has been run at 3 universities and in total 18 times, with >120 international students participating. He has trained many M.Sc. and Ph.D. students and supervised their theses, and he is actively mentoring undergraduates, graduates, and post-doc researchers.

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Debbie Chapman as a graduate of the University of London, Deborah Chapman started her research career as limnologist at the Freshwater Biological Association in the English Lake District. She subsequently became interested in monitoring the impacts of disposal of sewage sludge on aquatic organism and the potential for human health impacts from aquatic pollution. In 1986 she joined the United Nations Environment Programme's (UNEP) Monitoring and Assessment Research Centre (MARC) in London, participating in the international monitoring and assessment activities of UNEP and the World Health Organization (WHO), and assisting in global environment assessment programs. In 1988 she became the deputy director of MARC and took responsibility for the developing country workshops and training program, and global environment data review and compilation. After moving to Ireland in 1990, she worked as a freelance Environmental Consultant engaged mostly on international and developing country projects for WHO, UNEP, and other international organizations. She has assisted with the compilation of State of the Environment reports and has contributed to, edited, and produced more than 20 books on water resources and environmental management, including the internationally successful *Water Quality Assessments: A guide to the use of biota, sediments and water in environmental monitoring.*

In 1998 she joined UCC becoming the first lecturer in Environmental Science and then Head of Environmental Science in 2013. In recent decades her research interests have focused on water resources management, especially recreational and amenity lakes and reservoirs, developments and current practice in design and implementation of water quality monitoring programs, and human health risk assessment in relation to the use of freshwater resources and wastewater disposal. Drawing on 30 years of international experience, in 2015 she established the UNEP Global Environment Monitoring System for Water (GEMS/Water) Capacity Development Centre at UCC. This center delivers capacity development activities in water quality monitoring and

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Photo by Blythe White

Kendra Spence Cheruvelil is professor of limnology and co-director of the Data-intensive Landscape Limnology Laboratory at Michigan State University (MSU) in the Department of Fisheries and Wildlife (https://www.canr.msu.edu/fw/). She is also serving as Interim Dean of the Lyman Briggs College, which is MSU's residential college for studying the sciences and maths within their societal and global contexts (www.lbc.msu.edu). Kendra co-established the discipline of landscape limnology (https://bigdatalimno.org/research-themes/landscape-limnology/) and co-leads the LAGOS research program that is creating the research infrastructure to conduct big-data research on U.S. lakes (https://lagoslakes.org/). This large, collaborative, and interdisciplinary research program has been funded by the U.S. National Science Foundation and seeks to understand how global changes such as climate change and land use intensification affect lakes across regions and continents and through time. Dr. Cheruvelil also pushes the boundaries of how to conduct limnology research by using data-intensive science, science of team science, and open science approaches, tools, and perspectives to answer complex scientific questions. She also has an active research program to advance diversity and inclusion in the sciences (https://ee-stem.weebly.com/) and serves as an associate editor for the journals *Limnology & Oceanography Letters* and *Frontiers in Ecology & the Environment*. Prior to joining MSU, Dr. Cheruvelil was a faculty member in the Purdue University system. She has a dual Ph.D. from MSU in Fisheries & Wildlife and Ecology, Evolution, & Behavior (2004).

Photo by Shayenna Nolan

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Christian Griebler is full professor and head of the Limnology unit at the University of Vienna, Austria. He is a dedicated groundwater ecologist with core expertise in microbial ecology and biogeochemistry.

Kenneth Irvine has a broad range of multidisciplinary experience working on aquatic ecology, ecological assessment of surface waters, especially lakes and wetlands, and policy and related policies and management. After gaining a Ph. D. in 1987 at the University of East Anglia (U.K.) for a study on trophic ecology of shallow lakes, he worked for the U.K. Nature Conservancy Council, before moving to study ecosystem structure of Lake Malawi in Africa. He moved to Trinity College Dublin in 1994 Ireland. There, he continued work on the African Great Lakes, as well as building a research group working on ecological assessment in support of the EU Water Framework Directive. In 2011 he moved to IHE Delft Institute of Water Education, the Netherlands, as chair of Aquatic Ecosystems. Current work focusses on wetlands and capacity development in Sub-Sahara Africa. Recent work also includes a review of hydromorphology and links to policy. He currently sits on the Board of the Board of the *African Center for Aquatic Research and Education* (ACARE) and on the Scientific Advisory Board of the *Leibniz Institute of Freshwater Ecology and Inland Fisheries* (IGB), Berlin.

Wolfgang Junk was scientist of the Max-Planck-Institute for Limnology, Dep. Tropical Ecology, Plön during 1970–75.He was scientist of National Amazonian Research Institute, leader of the Dep. of Hydrobiology and Inland Fishery at Manaus, Brazil during 1976–79. and leader of the Working Group "Tropical Ecology" at the Max Planck Institute for Limnology in Ploen, Germany during 1980–2007.He is expertise in ecology and sustainable management of floodplains, land-water interactions, wetland classification. His main research areas arestudies on biomass, primary production, and decomposition of wetland plant communities; nutrient fluxes between land and water; adaptations of plant and animals to periodical drought and flooding; ecology of aquatic macrophytes and fish communities; biodiversity; conceptional considerations on river-floodplain systems, sustainable management of wetland resources and wetland protection with emphasis on the Amazon River floodplain and the Pantanal of Mato Grosso, Brazil. He supervised numerous M.Sc. and Ph.D. students and published more than 300 peer-reviewed publications, including several books and book chapters on Amazonian wetlands and the Pantanal of Mato Grosso. He received many honors, among them the Award of the Grande Cruz (the highest distinction of Brazil) for exceptional scientific performance, and the Cross of Merit First Class of the Federal Republic of Germany. He is corresponding member of the Academy of Sciences of Brazil.

Krantzberg is professor and lead for the engineering and public policy in the School of Engineering Practice and Technology at McMaster University offering Canada's first master's degree in engineering and public policy. Gail completed her M.Sc. and Ph.D. at the University of Toronto in environmental science and freshwaters. She worked for the Ontario Ministry of Environment from 1988 to 2001, as coordinator of Great Lakes Programs, and senior policy advisor on Great Lakes. Dr. Krantzberg was the director of the Great Lakes Regional Office of the International Joint Commission from 2001 to 2005. In 2007 she was appointed as an adjunct faculty member of the United Nations University Institute for Water and Environmental Health and participated in the twinning of the Laurentian and African Great Lakes (principally Lake Victoria). She has co-authored and edited 9 books and more than 200 scientific and policy articles on issues pertaining to ecosystem quality and sustainability and is a frequent speaker to media and the public. Her research interests include investigating Great Lakes governance capacity, analyzing interjurisdictional co-management arrangements internationally for application to the Great Lakes regime, and methods to better integrate science and engineering in policy formulation and decision-making.

Marie-Elodie Perga is associate professor of limnology at the University of Lausanne in Switzerland. Since receiving her Ph.D. from the University of Savoie-Mont Blanc (France), she has worked at the University of Victoria in Canada, and the French National Institute for Agronomy and Environment (France), before moving UNIL.

Because she is a Lindeman's groupie, her research lies at the interface of community ecology and biogeochemistry, through lake food webs and carbon processes. More recently, she added a pint of hydrodynamics with the intent to bridge physical and biogeochemical mechanisms, especially in alpine and high-altitude lakes. Her work covers centennial up to minute timescales through the combination of high-resolution paleo-records and high-frequency data from autonomous sensors.

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CONTENTS OF VOLUME 3

Structures and functions of Inland Waters - Wetlands

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Section Introduction: Wetland Ecology

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Biogeochemical cycling Is largely mediated by the microbiota, in particular bacteria and fungi, that are responsible for the degradation of organic matter and the cycling of nutrients, including nitrogen and phosphorus.
Decomposition Is the conversion of plant material at the end of the growing season to detritus and then to carbon dioxide, which can be released to the atmosphere, or remains as recalcitrant compounds (such as hemicelluloses and lignin) in the wetland.
Primary production A measure of the amount of carbon fixed through photosynthesis and released through respiration by the plants and algae (photosynthetic organisms) in a wetland.
Vegetation Succession The consequence of disturbances in the wetlands causing changes in the species composition of the vegetation, with species acting independently of one another.

Introduction

This article provides an overview of key aspects of the ecology of inland wetlands, including their extent and distribution, species diversity, and ecological processes. The range of inland wetland types varies greatly in terms of their size (area and volume), water quality (conductivity, nutrients and trace metals), hydrological patterns (permanency, flows, connectivity), and biodiversity (composition, richness, or abundance). They have also been defined in many ways with many terms used to describe them (Finlayson et al., 2018) and with much discussion over formal classifications (Gerbeaux et al., 2018).

Their ecological condition and management status also varies, with recent global analyses, based on information collated through the Ramsar Convention on Wetlands' Global Wetland Outlook, showing that many are in decline or have been destroyed, their species populations threatened, and their ecosystem services diminished (Ramsar Convention on Wetlands, 2018).

Following the acceptance of the Global Wetland Outlook by the parties to the Ramsar Convention a list of policy suggestions to improve wetland management (Finlayson and Gardner, 2020) was provided. This was based around the concept of maintaining the ecological character of a wetland (Fig. 1) which has been defined by the Convention to include the ecological components (biological, chemical, and physical), ecological processes, and ecosystem services (Pritchard, 2021). Key aspects of the ecological character of inland wetlands are presented with a description of the extent and distribution of wetlands, their species diversity, and vegetation succession, and ecological processes including primary production, decomposition, and nutrient cycling. Ecosystem services are not considered further given that they are derived from the interactions between the ecological components and processes in a wetland and from the associated social interactions and values. The importance of ecosystem services for human

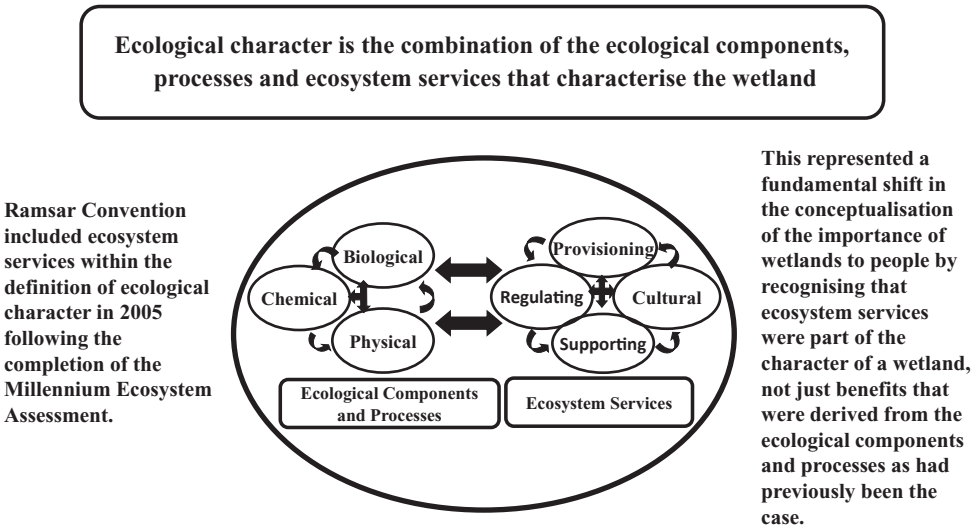

Fig. 1 Pictorial representation of the Ramsar Convention on Wetlands concept of ecological character whereby a wetland is comprised of ecological components, ecological processes, and ecosystem services.

wellbeing and livelihoods is shown by the estimate from Davidson et al. (2019) that the economic worth of inland wetland ecosystem services was US$27 trillion per year at 2011 values, or 25% of the total global value of all ecosystem services.

The ecological processes considered here include the hydrology or water regime, primary production and biogeochemical cycling (nitrogen, and phosphorus). The hydrology of a particular wetland is one of its fundamental features and underpins the occurrence and dynamics of the biodiversity and biogeochemical cycles. Primary production is the balance between the fixation of carbon through photosynthesis and release through respiration by the plants and algae. The text addresses primary production by vascular plants, and not that by the highly diverse phytoplankton population that occur in inland wetlands. Similarly, secondary production is not described. Biogeochemical cycling is associated with the primary production in and wetlands and is largely mediated by the microbiota, in particular bacteria and fungi, that are responsible for the degradation of organic matter and the cycling of nutrients, including nitrogen and phosphorus (Baldwin, 2018).

Wetland extent and distribution

Estimates of the area of wetlands need to be considered in terms of the types of wetlands included, and the method and scale of the analyses (Davidson and Finlayson, 2019). The latter reflects advances in data collection, increasingly from Earth Observation using data obtained from satellite-based remote sensing (Rebelo et al., 2018), while the former can be greatly influenced by the method of data analysis and the types of wetlands that are included. Both are affected by the way in which changes in inundation are considered, whether these occur seasonally, or annually, or stretching to decadal time periods. Davidson and Finlayson (2019) further noted that global estimates based on data collated from multiple sources tended to be greater than those from satellite-based remote sensing data.

A recent collation of data from multiple sources by Davidson et al. (2020) provided an estimate of the area of inland wetlands of approximately12.38 million km^2 including lakes (>10 ha in size), lakes and ponds (<10 ha in size), non-forested and forested peatlands, mixed marshes and swamps on alluvial soils, and forested wetlands on alluvial sources. There is a further estimated 1.90–1.94 million km^2 of human constructed wetlands, including rice paddy, reservoirs, small ponds, aquaculture ponds and wastewater treatment ponds. Based on these sources of inventory information the area of inland wetlands is dominated by peatlands (4.23 million km^2), natural lakes (3.23–4.20 million km^2), and marshes and swamps on alluvial soils (2.53 million km^2) which together comprise 80% of the total. Recent analyses of the area of Arctic wetlands suggest that the area of peatland may be an underestimate, as discussed by Davidson et al. (2020), including consideration of the extent of permafrost wetlands.

It is likely that information on the extent of particular wetland types or in specific areas may not have been included in such collations given limits to literature searching and access to large amounts of information, and discrepancies between definitions of wetland types.

Calls for greater attention to the collation of such information and the creation of reliable global estimates have not resulted in the creation of a reliable inventory repository for wetland inventory data at a global scale. As an example, in a data base proposed by the UNEP as a resource for individual countries, the area of inland wetlands in South America is given as 0.4 million km^2 (Kingsford et al., 2021) compared to higher estimates of 1.96 million km^2 in Davidson et al. (2020) and 2.338 million km^2 from Junk et al. (2018). Junk et al. (2014) report that wetland area in South America could extend to 20% of the area of the continent, namely, about 3.56 million km^2. There are further inconsistencies as to whether floodplains, that are complex systems (Tiner, 2016), are considered as wetlands in all parts of the world, and uncertainties around the area of ephemeral wetlands that may be dry for years or even decades (Parra et al., 2021).

Given that many countries in reporting to the Ramsar Convention on Wetlands (2018) noted the absence of a national wetland inventory there is a need to continue to improve the data resource (Davidson et al., 2020). In addition, greater consistency in the use of wetland definitions would assist with the mapping of wetland areas at continental and global scales.

Recent analyses have highlighted the continuing loss and degradation of wetlands globally with Darrah et al. (2019) reporting a loss of 35% since 1970, where data is available. The latter is an important phrase as there are still gaps in the analysis of wetland extent as well as loss. On this basis the areal estimate is likely to be an underestimate, and extrapolation of the rates of loss to continental or global statements needs to be done with caution. Further data are needed before these values can be considered as definitive. This is particularly so for historical wetland loss where definitive data may be lacking about the extent of wetlands and losses in many parts of the world. Biases could also be introduced by the algorithms used in these analyses, such as recently considered for the use of similar indices for species changes (Leung et al., 2020).

Descriptions of individual wetland types are provided in many publications including continental and global overviews, national and sub-national inventories, and site descriptions. Finlayson et al. (2018) provide a summary of major sources of information, including continental-scale wetland directories and inventories, collations and overviews of wetland types, and national overviews. Milton et al. (2018) similarly provide a summary of information sources for regional compilations of individual or wetland complexes and introduce detailed overview articles that inter alia describe the diversity within the wetland, its distribution and extent. The Ramsar Convention on Wetlands provides a data base of 1977 inland wetlands of international importance (accessed 14 October 2021, https://rsis.ramsar.org/ris-search/?f%5B0%5D=wetlandTypes_en_ss%3AInland%20wetlands) with information on their ecological character and management arrangements. Fig. 2 shows a range of inland wetland types.

Species diversity

The species diversity in many, but not all inland wetlands, is high, with many being populous and dynamic, with wetlands in higher altitudes and latitudes generally less biodiverse. A snapshot of vertebrate diversity in wetlands is given in Fig. 3. Turak and Pittock (2018) used several key sources to provide an estimate of the number of freshwater species in various taxa (Table 1). They used a general definition to include the diversity of species that occur in inland waters, including those that occur in saline wetlands (such as salt lakes and marshes), and which accomplished all or part of their life cycle in these wetlands. This was in line with the Freshwater Animal Diversity Assessment (Balian et al., 2008) which provided a global overview of the diversity of selected animal groups and wetland plants (macrophytes). Gopal and Junk (2001) provide a similar definition of wetland species, namely "all those plants, animals and microorganisms that live in a wetland permanently or periodically, (including migrants from adjacent or distant habitats), or depend directly or indirectly on the wetland habitat or on another organism living in the wetland." The groups covered by Turak and Pittock (2018) are shown in Table 1 and comprised more than 131,000 species with others, such as freshwater fungi and plankton that could be added, as well as an unknown number of microbial species. Estimates of species also vary, with for example, Piedade et al. (2021) conservatively reporting 3457 macrophyte species.

Despite a paucity of information about the ecology of many of these populations their importance is underpinned by their role in the ecological processes that are outlined below.

The population sizes of many species are unknown with estimates constrained by difficulties in measuring them as well as fluctuations due to environmental changes and, increasingly, due to the negative impact of human activities. Population estimates are notoriously difficult to obtain for many species, regardless of whether they are sedentary or migratory, due to difficulties in observing individuals, and for migratory species accounting for both short and long-distance movements and, for some species, rapid changes in numbers in response to environmental stimuli, such as the onset of flooding in seasonal and even more so, in ephemeral wetlands. Difficulties in obtaining estimates of species populations are reflected in the limited application of the criteria used by the Ramsar Convention for listing wetlands as internationally important based on species populations sizes (Stroud and Davidson, 2021). This is well shown for waterbird populations that have been investigated for decades, using extensive networks of observers, but which still lack current population estimates for many species.

Given the range of inland wetland types and the variety of climate and water regimes that influence these it may be fallacious to make generalized statements about the biodiversity in inland wetland types. This is shown by the differences in species diversity recorded in five large wetlands, as recorded in Junk et al. (2006) and shown in Table 2. In these examples it was possible to make reasonable comparisons between vertebrate species, for example, but the data for invertebrate species were inadequate for a meaningful comparison. Meaningful and more detailed comparisons, if required, could be based on wetland types within biogeographic zones, particularly if the biogeographical zonation reflects wetland distribution and is not based on terrestrial features. In this respect the Freshwater Ecoregions of the World (FEOW) proposed by Abell et al. (2008) provide a relevant base for considering the biogeographical distribution of wetlands, as done by Milton et al. (2021) for wetlands of international importance (Ramsar sites). A mapping of inland wetland types across these ecoregions is not available.

Vegetation succession in wetlands

Wetland vegetation comprises a wide range of plant types, including woody and non-woody species that accomplish all or part of their life cycle in the wetlands. As inland wetlands can vary from having permanent water to ephemeral systems that can be dry for years or even decades, a large range of plants can be found in wetlands with Cronk and Fennessy (2001) characterizing them as

Fig. 2 A variety of inland wetlands occur globally with many being freshwater, but some also brackish to saline, others permanently or intermittently filled, and of different sizes and depths. Photographs © C.M. Finlayson.

being able to grow in water or a waterlogged substrate generally deficient in oxygen. They further characterize them as: (i) emergent (herbaceous and woody species) with leaves, stems and reproductive parts above the surface of the water, or the waterlogged substrate; (ii) submerged plants with leaves and stems generally below the water, with flowers that may be above or below the water;

Fig. 3 Examples of vertebrate species in inland wetlands. Photographs @ C.M. Finlayson.

Table 1 Number of species in inland wetlands.

Taxonomic group	*Number of species*
Vascular plants	2614
Vertebrates	
Mammals	>122
Birds	566
Amphibia	4117
Reptiles	500
Fish	15,062 to 15,750
Invertebrates	
Molluscs	3998
Crustaceans	11,990
Arachnids	>6146
Insects	75,874
Others	10,292

Derived from Turak E and Pittock J (2018) Conserving freshwater species in protected areas. In Finlayson CM, Arthington H and Pittock J (eds). *Freshwater Ecosystems in Protected Areas: Conservation and Management*, pp. 110–143. Abbington: Routledge.

Table 2 Estimates of plant and vertebrate animal species numbers in four freshwater wetlands.

Taxa	*Pantanal (Brazil)*	*Okavango (Botswana)*	*Tonle Sap (Cambodia)*	*Kakadu (Australia)*
Algae	337	>50	123	700
Herbaceous wetland plants	248	ca. 350	34	75
Herbaceous terrestrial plants	900	ca. 800	114	126
Woody plants	756	ca. 180	70	21
Mammals	93	122	11	7
Fish	263	71	149	62

Derived from Junk WJ, Brown M, Campbell IC, Finlayson CM, Gopal B, Ramberg L and Warner BG (2006) The comparative biodiversity of seven globally important wetlands: A synthesis. *Aquatic Sciences* **68**: 400–414.

(iii) floating-leaved plants that are anchored in the substrate and may have leaves below the surface as well as floating; and (iv) floating plants that are not attached to the substrate. The range of species and their dominance is greatly influenced by the climate and the water cycle in any particular wetland, and also by the substrate type and chemical composition, and the water quality, including nutrients and salinity (Piedade et al., 2021). Changes in the composition of the plants over time, referred to as ecological succession, occur as a consequence of competition between species, the accumulation of organic matter and sediments, as well as changes to the water regime (water depth, flow rate, period of inundation) and the water quality.

An overview of succession in wetlands is provided by Middleton (2018) who saw succession as the consequence of disturbances in the wetlands causing changes in the composition of the vegetation, with species acting independently of one another. An alternative view that there was a successional progression towards a climax state in wetlands with interlocked species associations is largely disregarded nowadays (Niering, 1987; Anderson, 2018). Rather, disturbances including changes in the water and salinity regimes, as well as the impact of herbivores and fires, climatic events, and earthquakes, are considered as driving succession in wetlands.

Using these concepts and considering the life history traits of dominant plant species, Van der Valk (1981) developed a model for vegetation succession in wetlands based on initial investigations in prairie pothole wetlands in North America and further specifically applied in monsoonal wetlands in Australia (Finlayson, 1991) and in India (Middleton, 1999). The model represents wetland succession as a cycle that maintains wetlands over varying periods of time in response to the abovementioned ecological factors. In tropical wetlands subject to pronounced wet and dry seasons, such as in the monsoonal wetlands of south and east Asia, the drying-flooding cycle occurs across annual time periods whereas in many temperate zone wetlands the cycle may operate over many years. The regrowth or re-establishment of many species following changes in the water regime is dependent on the survival of reproductive propagules in the sediments, in what is simply called a seed bank although it can contain vegetative propagules as well as seeds, and how they respond to the conditions that exist in a wetland at a particular time, or to them being carried into wetlands by water flow, by prevailing winds, or by animals.

Van der Valk (2018) discusses the application of plant attributes to determine successional changes in wetlands whereby the environmental conditions act as a sieve which determines which species can become established and which will persist under specific conditions.

The accuracy and usefulness of such approaches are dependent on understanding the life-history attributes of the species involved and how they respond to changing environmental conditions, and to new species becoming established in a wetland.

The dynamics and growth patterns of wetlands associated with large rivers have been intensively investigated in South America especially those in Amazonia and the Pantanal of Mato Grosso. As described by Junk et al. (2000) and Piedade et al. (2010) wetlands along the Amazon river support forests that contain more than 1000 plant species growing in areas that are flooded annually for up to 8 months in a year, and at depths that reach 10 m. The trees have a wide range of anatomical, morphological and physiological adaptations to the oscillating flood pulses that they experience annually and are highly productive with large amounts of biomass when the nutrient levels in the water and soils are sufficiently high. The importance of pulse flows to the dynamism and ecological changes that occur annually in these wetlands is mentioned further below in this chapter.

As climate change may lead to more species "moving" and becoming established in various wetlands the currently recognized successional paths may be altered. The establishment of the submerged plant *Egeria densa* in the Rio Cruces wetlands in Chile following an earthquake in 1960, and subsequent decline illustrates both the type of changes that can occur as well as the lack of understanding of the drivers of these changes (Marín et al., 2018). The advent of global climate change is expected to drive further change in successional patterns in wetlands.

Hydrology

The importance of hydrology for wetlands is encapsulated in the following statement from Tiner (2018, p. 217) "Hydrology—the frequency, duration, and timing of inundation and/or soil saturation—is the lifeblood of wetlands. The presence of water strongly influences the physical and chemical environment, biota, productivity, and connectivity between wetlands and waterbodies and among habitats within wetland complexes."

A general overview of the hydrology of inland wetlands is provided by Rasmussen et al. (2018). The hydrological pattern or water regime of a wetland shapes its biogeochemical features, from the occurrence and dynamics of the biodiversity and successional patterns to the ecological processes that sustain the biodiversity and cycling of nutrients and other materials. As wetlands are often seen as occupying a transitional zone between permanently saturated aquatic and terrestrial environments, the presence of water in the substrate or sediment can lead to anaerobic conditions that creates specific growing conditions for aquatic plants and the biogeochemical processes such as nutrient cycling and availability.

Inland wetlands tend to occur in low-energy environments and generally experience slower water flows than in adjacent or inflowing rivers, although under high rainfall events this can change quickly with much faster flows and increasing depths. Flood flows can to some extent be stored in wetlands with water being released slowly during subsequent dry periods. The storage and release of water is largely dependent on the morphology of individual wetlands, in particular their size, depth and shape, and to some extent the vegetation that they contain, and the water balance upstream and downstream of the wetland, and in the underlying aquifers. This illustrates the connectivity that occurs between many wetlands, including with floodplains and groundwater systems.

Wetlands tend to form where surface water and groundwater accumulate within topographic depressions, such as those along floodplains, and behind dunes or levees, or in groundwater seepage, and near the shore of streams and lakes. Fringing wetlands can form along the shoreline of lakes, with periodic inundation occurring as water levels rise and fall. Perched wetlands form above substrates with low permeability.

The water regime (or hydropattern) of a wetland is a function of the topography and the difference between the inflows from atmospheric, surface and sub-surface sources, and the outflows. It is characterized by the timing, frequency and duration, depth and spatial extent of the flows. The water regime in some wetlands fluctuate over short time periods, whereas others fluctuate more slowly. Water levels tend to rise following storms with heavy precipitation and subsequent flows, and then decline slowly. The water budget of a wetland is derived from the balance of inflows from precipitation, surface flows, groundwater flows, and seepage, and outflows from evapotranspiration, and surface and groundwater flows. When the inflows exceed the outflows the wetland stores water.

The way in which a wetland fills, or the water is replenished, and retained is an important driver of its ecological features, with many wetlands responding to pulse flows on an annual basis, while others can be dry for long periods, even decades, and then undergo rapid filling with an explosion of biological activity as the hydrological and water quality conditions allow.

The concept of pulse flows, or flood pulses, in wetlands has extended since being ascribed as an important factor driving seasonal changes in Amazonian floodplains, including the inter-relationships between water levels, functional dynamics and species diversity (Junk, 1982). This is particularly the case in tropical wetlands rather than in temperate zone swamps or peatlands that experience more stable or permanent inundation. Flood pulses are important for wetlands in between the contributary channels of large rivers (interfluvial wetlands) as well as for the extensive savanna wetlands in highly seasonal semi-arid environments, which may connect with coastal lagoons and mangrove wetlands. Junk et al. (2018) summarize the variation of flood pulses based on their duration, amplitude, frequency and regularity as monomodal, bimodal, polymodal, of low or high amplitude, predictable or irregular.

- Predictable, monomodal pulse with low amplitude (in large, interfluvial wetlands and coastal lagoons) and high amplitude (along large rivers); or polymodal pulses with variable amplitude (in tidal wetlands);
- Unpredictable, polymodal pulses with variable amplitude (along streams and small rivers, in depressions, or in coastal lagoons); or multi-annual pulses with low amplitude (wetlands in semi-arid zones); or
- Variable anthropogenic predictability, with variable pulses and amplitude (in reservoirs and paddy fields).

Large rivers such as those in the Amazon, the Orinoco River, and the Mekong, have monomodal flood pulses with high amplitudes of up to 8–15 m. In contrast, large savanna wetlands have monomodal pulses with amplitudes of a few meters, and some Andean rivers and the Congo River have a bimodal flood-pulse (Piedade et al., 2021). Middleton (2002) has compiled cases where steps have been taken towards restoring pulse flows in previously degraded wetlands to help with the re-establishment of ecological processes and biodiversity with varying levels of success. The variability in water regimes, including in the features that characterize pulse flows, in individual wetlands is reflected in the primary production and successional patterns that occur over time and across the variety of inland wetland types.

Primary production

As outlined in Fennessy and Cronk (2018), primary production in wetlands is a measure of the amount of carbon fixed through photosynthesis and released through respiration by the plants and algae (photosynthetic organisms) in the wetland. Photosynthesis is a complex physiological process for the conversion of solar energy into chemical energy in plant cells containing chlorophyll, as expressed in the following equation:

$$6CO_2 + 12H_2O \rightarrow C_6H_{12}O_6 + 6O_2 + 6H_2O$$

Photosynthesis is carried out by primary producers, or autotrophs and include a variety of plants (including a variety trees, shrubs, macrophytes, as well as macro-algae and phytoplankton species). Many have specific adaptations to enable them to function in aquatic or semi-aquatic conditions, with fresh or saline water, and in ephemeral wetlands, with periodic drying and wetting.

Photosynthetic organisms (or autotrophs) have vital roles in wetland ecosystems, including influencing the trophic dynamics and the cycling and retention of plant nutrients (Cronk and Fennessy, 2001). Net Primary Production (NPP) is often reported and is the difference between Gross Primary Production (GPP), or the total amount of carbon captured and stored through photosynthesis, and respiration which is the conversion of chemical energy contained in organic compounds to Adenosine Triphosphate (ATP) which maintains cellular activity (Fennessy and Cronk, 2018). The balance represents the net carbon fixed and which can be used to build the biomass of primary producers.

The amount of carbon fixed by global wetlands is estimated to be 137 Tg $year^{-1}$ (Mitra et al., 2005), although as the types of wetlands and autotrophs in them are extremely diverse, their primary production is also highly variable (Kang and Jang, 2018). The rate of primary production varies in response to the wide variation of conditions and climates and in any specific wetland is influenced by the species composition as well as by nutrient availability (e.g., nitrogen and phosphorus), wetting and drying, light intensity, and temperature ranges (Kang and Jang, 2018).

In boreal wetlands and peat bogs, primary productivity typically ranges from 100 to 300 g (dry weight) m^{-2} $year^{-1}$ (Cronk and Fennessy, 2001; Cook et al., 2009), far less than in temperate areas with rates of 1500–4000 g m^{-2} $year^{-1}$, and reaching 5000 to 10,000 g m^{-2} $year^{-1}$ in tropical wetlands (Piedade et al., 1997, 2021). Marshes, both freshwater and saline, dominated by emergent herbaceous vegetation are generally highly productive, with above ground primary productivity of marshes in temperate zones reaching 2000 g m^{-2} $year^{-1}$ and freshwater swamps 1800 g m^{-2} $year^{-1}$ (Kang and Jang, 2018). Given difficulties with sampling, below ground production may not be recorded, but it can represent a substantial amount of the production of a particular species or wetland. Measurements of the total primary production of a wetland require a combination of measures covering *inter alia* algae, submerged and emergent plants as well as trees and shrubs, possibly using different methods with the results converted to the same units and combined in order to reflect whole system productivity (Fennessy and Cronk, 2018; Pezeshki, 2018a, 2018b).

The biomass of plants in wetlands varies greatly with higher values in forested and tropical wetlands than in herbaceous and temperate wetlands. In the United States Cronk and Fennessy (2001) reported biomass from multiple studies being <1300 g m^{-2} across a range of temperate to sub-tropical wetlands for above ground materials.

Vegetation decomposition

The decomposition of vegetative organic matter in wetlands is an important process as it determines whether and how fast inorganic nutrients are cycled and made available for further plant growth, or whether gases (such as carbon dioxide or methane) are released (Whigham, 2018). The high primary production in wetlands can lead to the accumulation of a large amount of organic matter that is decomposed by a variety of invertebrates or microorganisms (such as fungi, bacteria, and prokaryotic microbes). This material, as described by Verhoeven (2009) can comprise: (a) easily degraded materials which decompose over a few weeks or months; (b) cellulose and hemicellulose in plant cell walls which decomposes over a few months to a year; (c) lignins and waxes which can take several years to decompose; and (d) antibiotic polyphenolics which affect the decomposition of the above mentioned.

As described by Whigham (2018) in an overview of ecological processes in wetlands the rate of decomposition is determined by a combination of factors, including the chemical properties of the organic matter, the temperature, nutrient and oxygen supply, microbial properties, and the wetting and drying cycles. Following senescence of the plant material at the end of the growing period, much of the organic material, including the carbon, is converted to detritus which is then decomposed and converted to carbon dioxide, and released to the atmosphere, or to recalcitrant compounds (such as hemicelluloses and lignin). In the drying phase of the hydrological cycle in many wetlands much of the carbon may also be consumed by fire. Hot fires can burn much of the vegetative material stored in organic substrates, including in peatlands and in seasonally dry floodplains.

The fate of the senesced material in a wetland depends on many factors including the absence or presence of oxygen in the substrate, the nutrient and oxygen content of inflowing water, the air and water temperature, and the nutrient content of the plant material. The nutrient content of the plant material varies and is in part related to the type of plants that are included in inflows, including that from rural, urban or industrial landscapes. Decomposition is generally faster in wetlands dominated by herbaceous species compared to wetland dominated by woody trees and shrubs, and also in more nutrient enriched environments.

A general understanding of decomposition is presented by Whigham (2018). The easily degraded materials are decomposed soon after senescence with soluble labile materials retained in the substrate, available for uptake by plants and microbes, or exported to other systems. The more recalcitrant cellulose and hemicellulose, and lignins and waxes decompose slowly and are likely retained in the wetland. Decomposition can also lead to the production of methane (CH_4) through methanogenesis, although under aerobic conditions most is used by methane oxidizing bacteria and very little reaches the atmosphere. Under anaerobic conditions a wetland can be a source of methane to the atmosphere.

Nitrogen cycling

The nitrogen contained within a wetland can undergo a number of transformations, predominately mediated by microbial processes (Baldwin, 2018). Key processes within the nitrogen cycle in a wetland include the following: atmospheric deposition,

fixation of atmospheric nitrogen by microbes and some plants, leaching from biotic sources, ammonification, nitrification, denitrification, and immobilization (Whigham, 2018).

The cycling of nitrogen in a wetland is complex and in part dependent on the particular hydrological features along with the physico-chemical conditions in the water and sediments, and the microbial populations that are present (Deemy et al., 2021). Nitrogen can enter a wetland from a number of sources, including from the atmosphere into the water column of a wetland where it can be taken up by nitrogen-fixing bacteria or by some plants. Surface and groundwater inflows can contain organic nitrogen, dissolved ammonia, nitrate and nitrite, while large numbers of migratory animals, such as the large numbers of waterbirds that are known to annually migrate or move in a more nomadic manner in response to climate triggers, can add pulses of nitrogen. Litterfall from plants adjacent to a wetland can contribute nitrogen, while plants within a wetland can cycle nitrogen through absorption and then litterfall and subsequent decomposition. Nitrogen export from wetlands can occur through the water flows from the wetlands, and by volatilization of ammonia after denitrification, although some of the nitrogen produced by denitrification can be cycled within a wetland by nitrogen-fixing bacteria. Within a wetland organic nitrogen can be deposited and stored in the sediment, with some also being released and exported by outflowing water, or to the atmosphere during drying and burning of the plant material.

As described by Whigham (2018) the conversion from one form of nitrogen to another is tied to the physiochemical characteristics of the sediment or substrate in a wetland, in particular the presence of aerobic or anaerobic conditions and associated microbial populations.

Under aerobic conditions the presence of oxygen enables bacteria and fungi to mineralize carbon-containing compounds to produce carbon dioxide and ammonium-nitrogen which can be assimilated by plants under alkaline conditions. In the presence of oxygen ammonium is converted to nitrate, or to nitrite and then to nitrate. This process can be reversed, and nitrate also converted to nitrogen gas through denitrification which leads to the loss of nitrogen to the atmosphere. Under anaerobic conditions denitrification can also occur in the oxygenated microzones (often referred to as a rhizosphere) around plant roots and rhizomes. Denitrification also releases nitrous oxide that contributes to global warming, although in the presence of water the residence time in the soil is increased.

Phosphorus cycling

The phosphorus cycle in wetlands is described by Baldwin (2018) and Whigham (2018). The main source of phosphorus for wetlands is from the water that enters as surface flow from streams, or as runoff from adjacent landscapes, either associated with organic or mineral particles, or in a dissolved form. Within a wetland the biologically available phosphorus, as orthophosphate (PO_4), can be taken up by plants, algae and microbes, while the rest is adsorbed on inorganic and organic particles. It has a strong affinity for metals such as aluminum, iron, and calcium, and will preferentially bind to suspended particulate matter containing these. About 10–15% of the biologically available phosphorus is taken up by the biota with the rest being sequestered in the sediment or in the litter or detrital material.

The ability of wetland to store phosphorus is largely dependent on the amount of aluminum and iron that is present with a high absorptive capacity for phosphorus when in high concentrations. Alkaline soils with a high calcium content also provide long-term storage. While sediments may represent the largest sink in aquatic systems, they may also represent a major source of phosphorus remobilization. This involves the release of phosphorus from sediment particles to the interstitial water and then to the overlying water column. This process is mediated by iron reducing bacteria that convert ferric (oxidized) iron to ferric (reduced) iron that releases the phosphorus. Additionally, sulfate- reducing bacteria that reduce sulfur to sulfide which reacts with iron minerals can release the phosphorus. The phosphorus enters the water column following disturbance of the interstitial water, such as scouring by high flow events, or by bottom-feeding fish or invertebrates. The phosphorus can also be taken up through the roots of aquatic plants.

Conclusion/synthesis

There is increasing knowledge and understanding about the ecology of the biodiversity in inland wetlands and the ecological processes that support the biodiversity. Global estimates of the area of inland wetlands are in the vicinity of 12.4×10^6 km^2 with a further estimated 1.90×10^6 km^2 of human constructed wetlands. Best available estimates are that 35% of the wetland area has been lost since 1970, although further analyses are needed to confirm this value. Species diversity in individual inland wetlands can be high, but not uniformly across the range of wetland types.

The basics of the key ecological processes of vegetation succession and decomposition, and biogeochemical cycling of nitrogen and phosphorus in wetlands are well known, although the specific details for individual wetland types may need further elaboration. This is particularly so given the major role that the microbial populations in wetlands play in these processes. It is expected that further application of genomic analyses and more sophisticated models will assist in understanding the dynamics of these processes in different wetlands, and how these may respond under changing climatic conditions.

Knowledge gaps

- The extent and distribution of all inland wetland types is unevenly known, described or mapped.
- The populations sizes and dynamics of major species in inland wetlands is poorly known, including sedentary and migratory species.
- The successional patterns of vegetation in inland wetlands in response to changing environmental drivers requires further elaboration and development of descriptive models
- The extent of gaseous emissions to the atmosphere following microbially-mediated decomposition of wetland vegetation and cycling of nutrients is of increasing importance under global change scenarios.

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Structure and Function of Inland Waters-Wetlands: Classification Systems of Wetlands

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This is an update of R.W. Tiner, Ecology of Wetlands: Classification Systems, in Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Elsevier Inc.,2009, https://doi.org/10.1016/B978-012370626-3.00057-0.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Editor Thomas Mehner.

Introduction

Wetlands occur in all continents and are represented by a large variety of types, ranging from simple habitats of a few hectares in size up to complex wetland landscapes with many interacting different habitats extending over thousands of square kilometers. According to general estimates, between 4% and 6% of the Earth's surface is covered by wetlands (Mitsch and Gosselink, 2015), but this may be an underestimate because there is still no clear definition of what constitutes a wetland. Traditional definitions restrict wetlands to those common in temperate regions, such as bogs, fens and mires. By contrast, scant attention has been paid to periodically drying wetlands, which account for the majority of wetlands in tropical and subtropical regions. In South America, they account for roughly 20% of the continent's surface. In addition, while permafrost soils in North America and Asia fulfill the environmental requirements established for wetlands, such as waterlogged soils during the growth season of vegetation and the occurrence of wetland plants, they have not been considered as such in calculations of worldwide wetland area.

In ancient times, wetlands drove the development of high cultures, such as those along the Euphrates and Tigris Rivers, the Nile River, the Mekong River, the Indus and Brahmaputra Rivers and the Huanghe River. In some tropical countries, wetlands are still home for local human populations with distinctive cultural traits. Other important functions of wetlands are water storage, supply and purification. Moreover, wetlands provide favorable habitats for many plants and animals and are thus important to the maintenance of biodiversity (Gopal et al., 2000-2001). Nonetheless, they are among the most threatened ecosystems of the world, and the loss of wetlands is a major concern of the governments in many countries.

A first step in protecting wetlands is their definition, delimitation and classification (summarized in National Research Council (NRC), 1995; Tiner, 1999; Maltby and Barker, 2009; Mitsch and Gosselink, 2015; Finlayson, 2018; Gerbeaux et al., 2018; and others). The authors of those studies used different parameters according to the ecological, geographic and socio-economic peculiarities of the respective country or region, but the different approaches also reflect the preferences of the involved scientists. The development of a classification system that allows comparisons of available scientific data across fields of research would stimulate advances in wetland science, management and protection (Scott and Jones, 1995; Finlayson and van der Valk, 1995). The need for a better wetland classification was also recognized by Ramsar's Scientific and Technical Review Panel, which called for the "development and testing of a hydro-geomorphically-based system of wetland classification" (Davidson and Finlayson, 2007). This chapter provides a summary of the state of the art of wetland classification and a proposal for a unified classification.

Wetlands in ecological theory

The position of wetlands at the interface of terrestrial and aquatic ecosystems

Wetlands are situated at the interface between terrestrial and aquatic ecosystems. They interact with the permanent terrestrial environment and, in those with further connections, with deep-water inland (rivers and lakes) and marine ecosystems.

This intermediary position of wetlands led many scientists to consider them as ecotones. While there are many definitions of ecotones, all of them stress the transitional character between two or more ecosystems. For example, Holland (1988) defined ecotones as "a zone of transition between adjacent ecological systems heaving a set of characteristics uniquely defined by space and timescales and by the strength of the interactions between adjacent ecological systems." This definition certainly holds true for smaller, linear wetlands situated between, for instance, the upland and a lake, referred to as "littoral ecotones" by Hillbricht-Ilkowska (1993). Many wetlands, however, are surrounded by uplands and are not connected with permanent deep-water ecosystems, such as peat bogs and swamps in depressions. Also, the complex geomorphological structures, soil properties and hydrological conditions found in the inner portions of many large wetlands, exemplified by those of the Pantanal and the Amazonian várzeas in Brazil, the Everglades in United States, the Okavango Delta in Botswana and the Sundarbans in India/Bangladesh, result in unique ecological characteristics that distinguish these wetlands from adjacent terrestrial and aquatic ecosystems. As such, they can be considered as specific wetland ecosystems (Odum, 1959). Large wetlands encompass ecotones that bridge major landscape units, which are called macrohabitats in large Brazilian wetlands, for instance in Amazonian large river floodplains (várzeas and igapós), the Pantanal (Junk et al., 2014, 2018), and the Paraná River floodplain (Junk et al., 2021).

Independent of the discussion of the ecotonal character of wetlands, the contributions of the different scientific disciplines have to be considered in wetland studies. Freshwater ecosystems are the focus of limnologists, who very early on developed concepts to explain their structures and functions (Illies, 1961; Naumann, 1932; Thienemann, 1915; Vannote et al., 1980). These differ from the concepts used to describe marine ecosystems but both have to be considered in discussing coastal wetlands (Junk, 1997; Fig. 1).

In flood-pulsing wetlands, large areas are periodically covered by shallow water bodies, which behave ecologically like shallow lakes. Water distribution inside the floodplain and between parent rivers and their floodplains occurs by temporary or permanent channels, thus periodically resembling streams and small rivers. In both subsystems, the processes taking place during the aquatic phase are best explained from a limnological perspective. During the low-water period, formerly inundated areas become dry, in which case terrestrial concepts well explain the ecological conditions, such as the switch from anoxic wetland to oxic dryland conditions.

Organisms in large flood-pulsing wetlands can be similarly subdivided into terrestrial species, deep-water aquatic species and specific wetland species (Gopal and Junk, 2000). The large species diversity in these wetlands is the result of the mosaic of permanent terrestrial, aquatic and flood-pulsing environments. The switch between aquatic and terrestrial conditions in the areas affected by the flood pulse allows the colonization of the same area by terrestrial, aquatic and wetland plants and animals. Consequently, the migration behavior of fishes between deep water habitats and the floodplains in South America can be understood by applying limnological theories, and that of large herds of ungulates between the Okavango Delta and the surrounding upland savannas by the application of both terrestrial and wetland concepts.

Wetland specific concepts

The most common wetland types in temperate regions are oligotrophic peat bogs, eutrophic swamps and different types of coastal wetlands. Their genesis and ecology are well-studied and the conceptional framework is well established but will not be treated here.

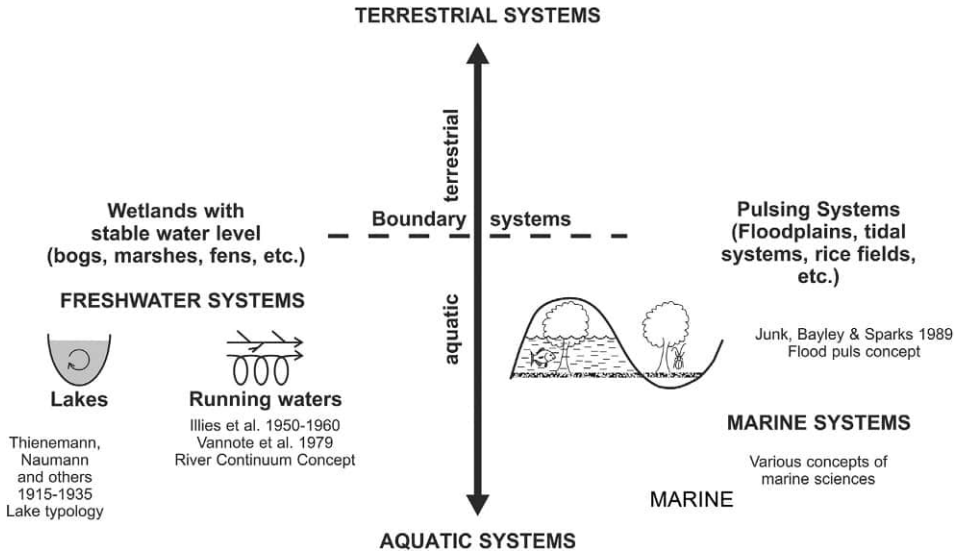

Fig. 1 The position of wetlands in relation to other aquatic and terrestrial ecosystems. From Junk WJ (1997) General aspects of floodplain ecology with special reference to Amazonian floodplains. In Junk WJ (ed.), *The Central Amazon Floodplain: Ecology of a Pulsing System*. vol. 126, Ecological Studies, pp. 3–22, Springer Verlag: Berlin Heidelberg\New York.

By contrast, large river floodplains are of interest to terrestrial ecologists, who focus on the terrestrial phase of these wetlands, and to limnologists, who focus on their aquatic phases, but an integrated approach is for the most part lacking.

The lateral dimension of the river-floodplain system and its ecological implications were first described by fish ecologists and fishery biologists. Lowe-McConnel (1964) showed that the fish communities of rivers and streams were related to the periodically flooded savannas of the Rupununi District in Surinam. Holcik and Bastl (1977) described the impact of floods on fish populations in the Danube River floodplain. Welcomme (1979) analyzed environmental factors in river floodplains and described the importance of floodplains for fisheries in tropical river systems.

Junk and Welcomme (1990) analyzed the data on floodplain systems and identified floodplains as *areas of low-lying land that are subject to inundation by the lateral overflow of water from river and lakes with which they are associated. The floods further bring about such changes in the physico-chemical environment that biota react by morphological, anatomical, physiological or ethological adaptations or by change in community structure. In some cases flooding may directly result from rainfall or snow and ice melt whereby water periodically accumulates in shallow depressions (sheet flooding). While such areas are not true floodplains in that they are not associated with any permanent water body, they do merit consideration as seasonally flooded wetlands*.

Junk et al. (1989) formalized this approach in the flood pulse concept (FPC), in work that was later complemented by Junk and Wantzen (2004) and Junk (2005) and extended to lakes by Wantzen et al. (2008). The FPC treats the river channel and its floodplain as one unit, called the river-floodplain system. Periodic inundation by high river stages or rainfall events is referred to as the flood pulse. The resulting aquatic conditions in the affected wetland area, called the aquatic terrestrial transition zone (ATTZ), links the area with the parent river or permanent lakes by a moving littoral. Aquatic and terrestrial phases influence each other and are thus considered as alternating ecological stages of the same ecosystem. The ATTZ is colonized by plants and animals adapted to the specific conditions. It is also frequented by visitors from the surrounding upland and connected lakes and rivers, which temporarily use the wetland's many resources. Processes switch from terrestrial to aquatic depending on the dry or wet status of the system. The transfer of organic matter and nutrients between terrestrial and aquatic phases complicates the differentiation between allochthonous and autochthonous material. Additions of the FPC were formulated by Ward et al. (1999), Ward and Stanford (1995), Ward et al. (1999), Puckridge et al. (1998), Humphries et al. (1999), Tockner et al. (2000), and others.

Wetland indicators

Wetland hydrology

Hydrology is probably the single most important determinant of the establishment and maintenance of specific types of wetlands and wetland processes. This is reflected in the many wetland definitions discussed in Section "Wetland definition, identification and delimitation" of this chapter, all of which refer to permanent or periodically shallow flooding or water logging. However, the parameters that define wetland hydrology vary in different regions and climatic zones. Classification schemes in the northern hemisphere must consider the impact of hydrology during the growing season of the vegetation and thus the overlap of periodic flooding (flood pulse) with another important ecological driver: the light/temperature or summer/winter pulse. At high latitudes the light/temperature pulse determines the biological activities in wetlands, but its strength diminishes towards the equator. In the subtropics and tropics, the seasonal variations in light and temperature have little or no impact on the biota, but water availability, often driven by heavy rainfall events or by rainy and dry seasons, are the decisive determinants.

The definition of a wetland depends on ecological parameters but also on political/economic requirements. This is well-demonstrated by the definition of the wetland status of areas in the United States. The National Food Security Act Manual (in National Research Council (NRC), 1995) concluded that flooding for 14 consecutive days is sufficient to create wetland conditions. If an area is covered with water or there is saturation to the surface in most years (>50%) for more than 12.5% of the growing season, then the area is defined as a wetland based on its hydrology. If water is present for 5–12.5% of the growing season then it may or may not be a wetland, depending upon other parameters (hydrophytic vegetation and hydric soils). Areas with standing water or water saturation to the surface for <5% of the growing season do not meet the definition of a wetland. The definition of the growing season relies on cultivated crops and varies among regions. Notably, however, ecological aspects are not considered in this definition (Tiner, 1999).

Considering the large importance of hydrology, the minor role of hydrological parameters in wetland classification systems and the larger reliance on other parameters, such as geomorphology, climate, soils, water chemistry, and vegetation, is perplexing. In a recent attempt to counter this discrepancy, Brazilian scientists proposed a hierarchical classification that at higher levels is primarily based on hydrological parameters (Table 1) and only at lower levels on chemistry and vegetation (see Section "Wetland classification"). The classification considers the fact that in large subtropical and tropical wetlands a monomodal flood pulse imposes an annual hydrological seasonality on the biota, which contrasts with the climatic unseasonal rain forest areas around the equator. This approach has been adopted also by Columbian scientists for Columbian wetlands.

Wetland soils

In the first wetland classification system originating from the United States, hydromorphic, halomorphic and alluvial soils were associated with wetlands (Shaw and Fredine, 1956). The National Technical Committee for Hydric Soils (NTCHS) defined a hydric soil as *a soil that formed under conditions of saturation, flooding, or ponding long enough during the growing season to develop anaerobic*

Table 1 Flooding regime and affected wetlands in the Brazilian classification system.

Wetlands with rather stable water levels			
Wetlands with fluctuating water levels			
Flood pulse variables			
Predictability	*Frequency*	*Amplitude*	*Wetland type*
Predictable	Monomodal	High	Large river floodplains
		Low	Large interfluvial wetlands
Predictable	Polymodal	Variable	Tidal wetlands
Unpredictable	Polymodal	Variable	Wetlands along low order rivers
			Wetlands in small depressions
Unpredictable	Multi-annual	Low	Wetlands in arid regions
Variable (human-made)	Variable	Variable	Reservoirs, paddy fields

conditions in the upper part (Federal Register, 1994). This definition emphasizes climate, because it considers the growing season, which is determined by the summer/winter (light/temperature) pulse. While this pulse has a large impact at high latitudes it has none on the growing season in the tropics and subtropics.

Soils are classified into organic soils characterized by an accumulation of organic material at the surface, and mineral soils composed of a mixture of sand, silt and clay. Soil texture has an important influence on the water retention capacity (Vasilas et al., 2018). Soil color is used in classification systems, but it depends on many factors. In the United States, a standardized procedure for measuring and describing soil color using the Munsell Color System has considerably improved the precision of the method (Schulze et al., 1993). However, soil color changes with soil wetness and is thus more relevant in the tropics and subtropics, where many wetland soils are dry during the dry season. All countries provide soil maps with general information on hydric soils. In Brazil, 36 types of hydric soils are distinguished (Dos Santos et al., 2018).

Flooding and water logging lead to anoxic soil conditions that reduce the decomposition of organic material. In temperate regions, the oligotrophic acidic conditions and prolonged waterlogging lead to the formation of extended peat layers, often associated with the growth of moss (*Sphagnum* spp.) and resulting in the formation of large peat bogs with characteristic acidophilic vegetation. Peat accumulation is a slow process, with a rate of only about 1 mm $year^{-1}$. However, after the last glacial period, peat layers of up to 10 m depth accumulated. Under eutrophic conditions, organic matter is produced by highly productive emergent herbaceous plants, such as *Typha* spp. and *Phragmites* spp. In an advanced stage of terrestrialization a swamp forest develops. Peat bogs and swamps are considered long-term sinks for organic carbon. By contrast, in flood-pulsing wetlands the accumulation of organic matter is hindered because during the dry period soil aeration favors decomposition. This is the case for most tropical and sub-tropical wetlands, which therefore cannot be considered as long-term sinks for organic carbon (Junk, 1985).

Water logging affects microbial communities in the soil and thus gives rise to biochemical processes referred to as oxidation-reduction (redox) reactions. Under anoxic conditions, manganous manganese, ferrous iron, methane, ammonia, and hydrogen sulfide, among others, are produced. The reduced compounds are often soluble and available for plants, but some of them, such as aluminum, are toxic at higher concentrations.

Wetland organisms

Wetland plants

Definition of hydrophytes

The morphological and physiological adaptations of aquatic macrophytes to waterlogging of the substrate and flooding, the classification of these plants and their role in wetlands are treated in a separate chapter. Here, only aspects directly related to wetland classification are discussed.

Plants have been and continue to be used as indicators to identify and delineate wetlands. There are innumerous definitions of wetland plants. Scientists working in wetlands recognized early on the problem of separating wetland plants from terrestrial plants. Warming (1909) stated *. . .there is no sharp limit between marsh plants and terrestrial plants. . .the boundary zone represents a gradual transition from terrestrial to aquatic conditions and it is impossible to establish any sharp distinction between swamp-forests and forests on dry land*.

That study distinguished between two major types of wetland plant communities: saline swamps with halophytic vegetation and freshwater swamps with three sub-groups: reed swamps dominated by emergent herbaceous plants, bush swamps characterized by the growth of alders (*Alnus* spp.), willows (*Salix* spp.), birches (*Betula* spp.) and others, and forest swamps (Juniper swamps characterized by the Atlantic white cedar *Chamaecyparis thyoides*, black gum swamps with *Nyssa sylvatica* and bald cypress swamps with *Taxodium distichum*).

Weaver and Clements (1938) stated that . . .*amphibious plants have a wide range of adjustment and may grow for a time as mesophytes or partially submerged....(they are) the least specialized of water plants.*

The definition of hydrophytes varies among countries and authors and has considerably changed since the beginning of modern science. Limnologists and many botanists describe only aquatic herbaceous plants as aquatic macrophytes or hydrophytes (e.g., Sculthorpe, 1967; Cook et al., 1974). Other terms include "aquatic cormophytes" (aquatic plants with roots, shoots and leaves), "aquatic vascular plants, aquatic tracheophytes" (all aquatic herbaceous plants with specialized vascular tissue, excluding algae and bryophytes), "helophytes" (perennial marsh plants whose buds overwinter under water) and "mesophytes" (plants growing in moist soils).

According to the definition of Raunkiaer (1934): *Hydrophytes are plants which have vegetative parts submerged or floating at the water surface, but not emerging into the air, and which survive unfavorable seasons as submerged buds attached to the parent plant or lying free on the substrate.* Thus, it excludes emergent herbaceous plants and woody species.

Dobenmire (1968) introduced oxygen deficiency into the definition: *A hydrophyte is any plant growing in a soil that is at least periodically deficient in oxygen as a result of excessive water content.*

The simplest and most comprehensive definition is that of Weaver and Clements (1938): Aquatic macrophytes are *plants that grow in water, in soil covered by water, or in soil that is usually saturated.*

The definition of Lichvar et al. (2012) includes herbaceous and woody species: *Obligate Wetland Plants almost always occur in wetlands. With few exceptions, these plants (herbaceous or woody) are found in standing water or seasonally saturated soils (14 or more consecutive days) near the surface.*

Animals

The importance of wetlands as habitats for animals is well-documented and the diversity and abundance of these species are one of the strongest arguments for wetland protection. Indeed, the Ramsar Convention for the protection of wetlands of international importance was established for the protection of migrating waterfowl.

According to Gopal and Junk (2000), wetland animals can be classified into six main categories: First, are residents in the wetlands proper. This group covers a wide range of taxa. Vertebrates have been the focus of many studies but very few studies have considered invertebrates. The role of Amazonian river floodplains as important generators of species richness was demonstrated by Erwin and Adis (1982) and Adis and Junk (2002) and many other authors. The second category comprises regular migrants from deep-water habitats and thus mostly fishes. Juveniles of many fish species use the floodplains during the high-water period for hiding and feeding. In Amazonia, however, some turtle species and the manatee (*Trichechus inunguis*) also migrate from deep-water habitats into the floodplains for feeding. In the third group are regular migrants from terrestrial habitats. This group also covers a wide range of species and includes the well-known large migrations of ungulates between the African floodplains and adjacent savanna. Less obvious are the nocturnal visits of bats from the surrounding uplands into the Pantanal floodplain for feeding. In the fourth group are regular migrants from other wetlands, such as the extended migrations of waterfowl between South American wetlands depending on the water level of the respective areas. Some species from northern and southern high latitudes spend the winter in tropical and subtropical South American wetlands, but terrestrial birds may also use the floodplains as stopping points during their migrations (Junk et al., 2006). The fifth group comprises occasional visitors and in the sixth are animals that indirectly depend on wetland biota. The last group, which includes canopy invertebrates and also pathogens and parasites of wetland species, has hardly been studied but it contributes significantly to the overall species diversity of wetlands.

For wetland classification purposes, however, the mobility of animals limits their use as indicators, although the presence of some species can serve as an indicator of the ecological integrity of wetlands or parts of them. In the Brazilian Pantanal, for instance, the presence of top predators such as the jaguar and the giant otter indicates a high level of ecological integrity of the respective region.

Wetland definition, identification and delimitation

The ecological diversity of wetlands is demonstrated by the many definitions put forward by nearly every country. This reflects the fact that: (1) scientists from different disciplines emphasize different parameters; (2) local politicians prefer national or even regional definitions and (3) the local population is more likely to understand and support environmental protection when it is related to landscape units described with local names and thus in familiar terms.

Definitions of wetlands can be divided into two groups. One exclusively considers scientific aspects and is important for scientific work, environmental protection and sustainable management. The other also takes political and socio-economic conditions into consideration. However, these regional approaches often omit scientific definitions, are frequently in conflict with the requirements of environmental protection by favoring economic demands and their use in comparative international studies is difficult.

At the international level, the Ramsar Convention, with 169 signatory countries, plays a leading role with respect to the conservation and wise use of wetlands. The Ramsar definition of wetlands states: *Wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters.*

Semeniuk and Semeniuk (1995) defined wetlands as *areas of seasonally, intermittently or permanently waterlogged soils or inundated land, whether natural or otherwise, fresh or saline.* The authors called attention to Western Australia, where only the permanently

inundated part of the wetland was traditionally considered as wetland area, and thus correctly extended the definition of the peripheral wetland boundary to periodic *dampness, or hydric soils or vegetation indicative of wet conditions*. In arid regions all over the globe, there are depressions that become filled with water only every couple of years (playa, barlkarra of Semeniuk and Semeniuk, 1995), but during that period they fulfill important wetland functions, by providing breeding and feeding grounds for aquatic animals and waterfowl. During the multiannual dry periods, the wetland boundary may be indicated by changes in the salt content of the soil.

At the national level, Cowardin et al. (1979) defined wetlands in the United States as . . . *lands transitional between terrestrial and aquatic systems, where the water table is usually at or near the surface or the land is covered by shallow water. Wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes; (2) the substrate is predominantly undrained, hydric soil; and (3) the substrate is nonsoil and is saturated or covered by shallow water at some time during the growing season of each year*.

In this definition, the inclusion of the growing season is a concession to management interests, because under ecological aspects many wetland processes are not restricted to the growing season but are ongoing during the entire year. Indeed, for management purposes, state regulatory programs in the United States use specific wetland definitions that differ in nearly every state (Tiner, 1999).

For Brazilian wetlands, a consortium of scientists provided the following definition: *Wetlands are ecosystems at the interface between aquatic and terrestrial environments; they may be continental or coastal, natural or artificial, permanently or periodically inundated by shallow water or consist of waterlogged soils. Their waters may be fresh or highly or mildly saline. Wetlands are home to specific plant and animal communities adapted to their hydrological dynamics* (Junk et al., 2014).

Determining the borders of a wetland would seem to be a simple task, assuming that its water level was relatively stable. Hydric soils with an accumulation of organic material and the presence of hydrophytes are good indicators of wetlands, and the transition zone to the upland is normally narrow. In wetlands with an oscillating water level, however, delimitation is very difficult and scientific definitions often contradict political and economic priorities.

Brazilian ecologists proposed the following definition for wetland delimitation: *The extent of a wetland can be determined by the border of the permanently flooded or waterlogged area, or in the case of fluctuating water levels, by the limit of the area influenced during the mean maximum flood. The outer borders of wetlands are indicated by the absence of hydromorphic soils and/or hydrophytes and/or specific woody species tolerant to grow in periodically or permanently flooded or waterlogged soils. The definition of a wetland area should include, if present, internal permanently dry areas as these habitats are of fundamental importance to the maintenance of the functional integrity and biodiversity of the respective wetland* (Junk et al., 2014).

With its citation of the mean maximum flood level, this definition recognizes hydrology as the main determinant in wetlands while also considering the importance of permanently dry areas inside large wetlands as both a periodic refuge for animals during high floods and the source of the large plant and animal biodiversity. However, this wetland definition proposed by Brazilian scientists has been rejected by Brazilian politicians and representatives of agrobusiness, who favor a definition of the wetland border at the low-water level that strongly reduces the size of the wetland area.

Wetland classification

Wetland classification systems rely on different parameters, especially hydrology geomorphology, soils, water chemistry and vegetation. As noted above, many countries, and often many regions, have their own classification systems. In Argentina, the classification system of Neiff (2001) differentiates between nine wetland types, using 12 parameters to describe wetlands according to their geomorphology, soils, fire stress, vegetation, fauna, water origin, and several hydrological factors. Brinson and Malvárez (2002) differentiate between nine types of Argentinian wetlands, but use climate, hydrology, soils and the regional vegetation as criteria.

The current U.S. Fish and Wildlife Service classification hierarchy for wetlands and deep-water habitats distinguishes five major systems, 10 subsystems and 56 classes (Cowardin et al., 1979). Major systems are marine (subtidal, intertidal subsystems), estuarine (subtidal, intertidal subsystems), riverine (tidal, lower perennial, upper perennial, intermittent subsystems), lacustrine (limnetic and littoral subsystems) and palustrine. Classes are described based on different attributes, such as rock bottom, emergent wetland, forested wetland, aquatic bed and unconsolidated shore. The hydrogeomorphic classification of Brinson (1993) relies on geomorphic, physical and chemical parameters to provide a better understanding of the relationship between organisms and their environment.

The classification system used in the Directory of Neotropical Wetlands (Scott and Carbonell, 1986) lists 19 wetland types while that of the Directory of Asian Wetlands includes 22 types (Scott, 1989), using geographic, geomorphological, hydrological and vegetation parameters in a non-hierarchical approach.

The European CORINE Biotopes database (Co-ORdinated INformation on the Environment), established in 1985, lists the following biotopes, including wetlands, in Mediterranean countries: coastal and halophytic communities (10 habitats), non-marine waters (4 habitats), scrub and grassland (2 habitats), forests (1 habitat), bogs and marshes (3 habitats), inland rocks, screes and sands (4 habitats), agricultural land and artificial landscapes (5 habitats) (European Communities - Commission, 1991). The Natura 2000 inventory specifies the CORINE Biotopes database and for 12 EU member states lists 71 habitat types, under the EU Birds Directive or Habitat Directive. The database differentiates between marine and inland habitats, which are characterized mostly by trophic status and communities of higher plants (European Commission, 2014).

Semeniuk and Semeniuk (1995) proposed a geomorphic approach to the global classification of inland wetlands that combines landform types with hydroperiod and distinguishes 13 primary types of common wetlands: permanently inundated basin (lakes), seasonally inundated basin (sumpland), intermittently inundated basin (playa), seasonally waterlogged basin (dampland), permanently inundated channel (river), seasonally inundated channel (creek), intermittently inundated channel (wadi), seasonally waterlogged channel (trough), seasonally inundated flat (floodplain), intermittently inundated flat (barlkarra), seasonally waterlogged flat (palusplain), seasonally waterlogged slope (paluslope) and seasonally waterlogged highlands (palusmont).

The frequently cited Ramsar classification claims to classify wetlands at the worldwide scale but it has been interpreted differently by different authors. Scott and Jones (1995) recognize six major wetland systems: (1) marine (coastal wetlands including coastal lagoons, rocky shores, seagrass beds and coral reefs); (2) estuarine (including deltas, tidal marshes and mudflats, and mangrove swamps); (3) lacustrine (wetlands associated with lakes); (4) riverine (wetlands along rivers and streams); (5) palustrine (i.e., "marshy," including marshes, swamps and bogs) and (6) human-made wetlands (fish and shrimp ponds, farm ponds, irrigated agricultural land including rice paddies, salt pans, dams, reservoirs, gravel pits, wastewater treatment ponds and canals). These systems are subdivided for hydrological characterization using the terms subtidal, intertidal, perennial, intermittent, permanent and seasonal. Subunits are characterized by geomorphological, hydrological and/or botanical parameters.

Matthews (1993) examined the history and development of the Ramsar Convention on Wetlands. The Ramsar classification repeats the differentiation between marine and coastal wetlands (with 12 habitat types), inland wetlands (with 14 habitat types) and human-made wetlands (with 9 habitat types). It uses the same non-hierarchical mixture of criteria for the characterization of habitat types, including hydrological criteria (permanent, seasonal, intermittent), vegetation parameters (shrub-dominated, tree-dominated, marshes, peatlands, mangroves, etc.), geographical parameters (tundra/alpine wetlands, deltas, etc.) and limnological parameters (rivers, streams, lakes, springs, etc.) and others. The attributes for characterization used by Finlayson (2018) were similar to those used by other authors and differentiate between 42 wetland types: marine and coastal wetlands (12 types), inland wetlands (20 types) and human-made wetlands (10 types).

The recent classifications devised for Brazilian and Colombian wetlands (Junk et al., 2014; Ricaurte et al., 2019) are much more detailed than these other approaches but they also differentiate at the system level among coastal, inland and artificial wetlands. Higher categories, consisting of subsystems, orders, suborders and classes, are determined according to hydrological parameters, such as the predictability, frequency and height of the flood pulse (see Table 1). Hydrological, hydrochemical and vegetation parameters are used to differentiate within lower categories (functional units, subclasses and macrohabitats) (Junk et al., 2014; Nunes da Cunha and Junk, 2017), Fig. 2.

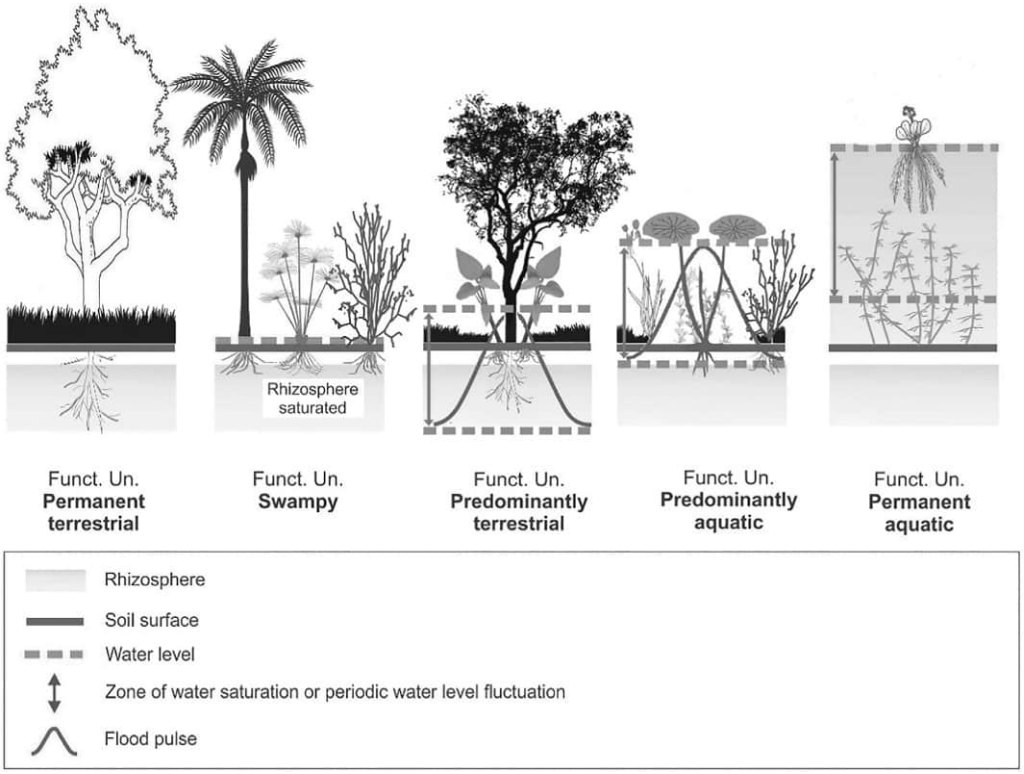

Fig. 2 Functional units in large floodplains according to their hydrological status. adapted from Nunes da Cunha C and Junk WJ (2017) Classificação dos macrohabitats do Pantanal mato-grossense para fins de gestão. In Nunes da Cunha C, Arruda EC, Junk WJ (Orgs). *Marcos referenciais para a Lei Federal do Pantanal e gestão de outras áreas úmidas*. pp. 73–79, Cuiabá-MT: Carlini & Caniato Editorial, EdUFMT. p. 156. ISBN 978-85-8009-177-9 (Carlini & Caniato); ISBN 978-85-327-0604-1 (EdUFMT).

Wetland distribution and contribution in ecosystem coverage

The data in the literature on wetland coverage vary considerably. The UNEP-World Conservation Monitoring Centre has estimated ~570 million hectares (5.7 million km^2), roughly 6% of the Earth's land surface; Mitsch and Gosselink (2015), estimated 4–6% of the Earth's land surface. Mangroves cover some 240,000 km^2 of coastal area, and an estimated 600,000 km^2 of coral reefs remain worldwide. Nevertheless, a global review of wetland resources prepared for Ramsar COP7 in 1999, while affirming that *it is not possible to provide an acceptable figure of the areal extent of wetlands at a global scale*, indicated a "best" minimum global estimate of 748–778 million hectares. The same report indicated that this "minimum" could be increased to 999–4462 million hectares when other sources of information are taken into account.

These figures certainly underestimate total wetland area, because conventional approaches consider only "classic" wetlands (peat bogs, marshes, fens, etc.). New approaches emphasize periodically flooded areas, which includes most wetlands in South America. In Brazil, wetlands account for ~20% of the national territory (Junk et al., 2012), in Argentina 23% (Kandus et al., 2008), and in Columbia 27% (Ricaurte et al., 2019). We estimate similar values for other South American countries, which means that about 20% of South America can be considered as wetland. For the northern hemisphere, estimates of wetland area are restricted to "classic" recognized wetlands. However, if the three criteria for wetland definition are applied, i.e., periodic saturation with water during the growing season and the presence of hydric soils and plants adapted to them, then many areas of permafrost soils have to be considered as wetlands. This approach will greatly increase the current total wetland area estimate of 4–6% provided by Mitsch and Gosselink (2015).

Discussion and conclusions

Scott and Jones (1995) provided a global overview of the many approaches to the classification and inventory of wetlands. They also called for international standards to strengthen international agreements among partner countries regarding wetland protection. Finlayson and van der Valk (1995) noted the difficulties in determining general parameters for wetlands that can be used on a worldwide scale to define and delimit wetland areas, and the need to resolve differences between regional wetland definitions and regional typologies. They also recommended a standardization of data collection and the dissemination of new technologies in order to establish ample international inventories. The Ramsar's Scientific and Technical Review Panel likewise called for the *development and testing of a hydro-geomorphically-based system of wetland classification* (Davidson and Finlayson, 2007).

Indeed, the many wetland definitions and classification systems formulated decades ago for specific purposes do not meet current scientific and regulatory requirements. However, there are two major problems in compiling a general wetland classification. The first is that any classification system must encompass wetlands of different size and complexity. Classification systems that differentiate between specific wetland types, such as shallow lakes, swamps, grasslands, and forests, are not applicable to the large, complex wetland systems that often cover tens of thousands of square kilometers. In *Wetland Indicators*, Tiner (1999) treated floodplain wetlands as hydrologically problematic, briefly considered floodplain forests and called for additional studies. In the Ramsar Convention's typology of wetlands published by Finlayson (2018), floodplains are not considered as a specific category because they are complex and include several wetland types. This shows the limits of most typologies.

Large floodplains, but also other large wetland complexes, are made up of different subunits that interact with each other. Examples are the Everglades in North America (Brown et al., 2006), the Sundarbans Mangrove Ecosystem at the Indian subcontinent (Gopal and Chauhan, 2006), the Okavango Delta in Africa (Ramberg et al., 2006; Ellery et al., 2000), Tonle Sap and connected wetlands in Southeast Asia (Campbell et al., 2006), the wetlands of the Kakadu National Park in Australia (Finlayson et al., 2006), the Pantanal (Nunes da Cunha and Junk, 2014) and the Amazonian várzeas and igapós (Junk et al., 2012, 2015) in South America, the mires of the former Soviet Union (Masing et al., 2010) and the northern peatlands of Canada (Warner and Asada, 2006). These wetlands must therefore be treated holistically, including considerations of the political, social, cultural and ecological aspects of the entire wetland complex.

The second problem is that most classification systems do not organize the hydrological, geomorphological, botanical or soil and water chemical parameters of wetlands hierarchically. While the large majority of scientists agree that hydrology is the main driver in wetlands worldwide, this is rarely reflected in classification systems and comparisons between the different systems are accordingly difficult. These and other challenges, discussed herein, have hindered the development of a wetland classification system that is acceptable worldwide.

Certainly, wetlands in boreal regions differ from those in the tropics, wetlands in arid zones from those in humid regions and wetlands in high mountains from those in the lowlands. Furthermore, at the national level, politicians may require a differentiation of wetlands that takes into account economic aspects, such that a geographic delimitation of major climatic, geomorphological and perhaps also politically defined areas may be necessary. This can be achieved at supra-national and national levels depending on the technical and political requirements, as demonstrated by the Colombian classification. It differentiates between four macro regions: the Amazonia and Orinoco region, inter-Andean lowlands, the Andean range and coastal systems, but uses in all regions the same hydrological criteria for major classification units (Ricaurte et al., 2019).

A serious problem for all wetlands, influenced by strong water level fluctuations, is the delimitation of their areas. In most countries, the wetland area is subjected to specific legal protection measures. This situation creates conflicts of interests between different stake holders. Ecologists extend the wetland borders, pointing to the importance of occasionally flooded areas for the

maintenance of biodiversity, whereas ranchers and planners reduce the borders to permanently wet core areas, accepting the risk of losses in biodiversity but also of crops, domestic animals and even human life during high floods. This problem will increase in future because of the increase of extreme flood and drought events predicted by the Intergovernmental Panel on Climate Change (Intergovernmental Panel on Climate Change (IPCC), 2014).

Many classification systems include permanent aquatic habitats, and even deep lakes as wetlands, but not the permanent "terrestrial islands" within large wetland landscapes. Studies in the Brazilian Pantanal however have shown that permanent terrestrial macrohabitats, such as paleo-fluvial levees and terraces, are of fundamental importance for biodiversity. Yet, they are also the most threatened areas, because ranchers use them for pasture plantation and they are often designated for infrastructure development, typically with the argument that these areas are not wetlands. A modern wetland definition and classification approach should incorporate these areas, as does the Brazilian system (Junk et al., 2014). It defines the wetland area as the area influenced during the mean maximum flood and includes permanent dry areas inside the wetlands as of vital importance for the maintenance of wetland integrity. This definition, however is heavily contested by the Brazilian agroindustry.

An international wetland classification system should, in its higher rankings, be based on hydrological aspects, because hydrology is the only factor of general, worldwide importance, and it can easily be classified, as shown in this review. Lower rankings should refer not only to the regional hydrology but also to other classification parameters of regional importance, such as vegetation and hydrochemical peculiarities. At this level, also economic and management aspects such as the use by agriculture, forestry, cattle ranching and fishery can be established. This approach is simple, user-friendly and satisfies the requirements of scientists, environmentalists, politicians, and local populations.

See Also: Social/societal values of Inland waters: Riparian Buffers and Land Cover Change; Structures and functions of Inland Waters - Groundwater: Karst Groundwater Dependent Ecosystems—Typology, Vulnerability and Protection; Springs—Groundwater-Borne Ecotones—A Typology, with an Overview on the Diversity of Photoautotrophs in Springs; Structures and functions of Inland Waters - Lakes: Origins of Types of Lake Basins; Structures and functions of Inland Waters - Rivers: Hydrology and Classification of Rivers for Management; Structures and functions of Inland Waters - Wetlands: Wetland Plants: Adaptations, Classification, Ecology and Distribution

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Prehistoric Wetlands

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Angiosperms Vascular seed plants that bear flowers and have seeds encased in an additional layer of tissue called a carpel. Includes two major subgroups: monocots (e.g., grasses, palms, lilies) and eudicots (most broad-leaved trees, shrubs and herbs). Early-diverging lines belonging to neither subgroup include magnolias and water-lilies.
Bog A type of wetland in which peat accumulates under waterlogged, low-oxygen, acidic, nutrient-poor conditions, with water from precipitation, sometimes building up above the topography.
Bryophytes Nonvascular, herbaceous land plants. Includes modern liverworts, hornworts, and mosses.
Chert Sedimentary rock composed of microcrystalline to cryptocrystalline silica (quartz, chalcedony).
Cladoxylopsids Extinct vascular plants that are ancestors of ferns and horsetails.
Coal A combustible rock containing more than 50% organic matter (carbon) by weight, and 70% carbonaceous material by volume including inherent moisture, formed from the compaction and alteration of peat.
Cordaitales Extinct vascular woody plants ancestral to conifers.
Facies Characteristic combinations of grain size, bedding, fossil assemblages, etc., in sedimentary strata representing a specific depositional environment.
Fen A type of wetland in which peat accumulates under waterlogged, low-oxygen, nutrient-rich conditions, generally sourced by groundwater in topographic depressions.
Glossopteridales A group of extinct, vascular gymnosperms, named for their most common genus, the shrubby to arborescent genus *Glossopteris*.
Gymnosperms Vascular plants in which seeds are not surrounded by specialized tissue ("naked seeds"). Includes modern conifers, ginkgophytes, gnetophytes, and cycads.
Histosol An organic soil order formed from peat or organic-rich muck in bogs and fens.

Lycopsids Vascular, spore-producing herbaceous to arborescent plants. Includes modern club mosses, quillworts, and spike mosses, and also the extinct scale trees (lepidodendrids and sigillarians).
Maceral The microscopic framework constituents of coal, which are the byproducts of the original plant material from which the coal formed. Macerals are analogous to sediment grains and cements in sedimentary rocks.
Marsh Wetlands with emergent, herbaceous, nonwoody plant cover established on a mineral substrate.
Peat An organic deposit or layer formed predominantly from partly decomposed plant material under acidic, low-oxygen, waterlogged conditions in wetlands like bogs and fens.
Progymnosperms Vascular, woody, spore-bearing plants, which are ancestors to gymnosperms.
Pteridosperms Extinct vascular, seed-bearing, herbaceous to arborescent (tree ferns) gymnospermous plants.
Sphenopsids Extinct vascular, reed-like plants, which are a sister group of equisetales (horsetails).
Swamp Wetlands with trees (>6-8 m in height).

Introduction

Wetlands have a long geologic history. Land plants first colonized, evolved, and diversified in wetlands, changing and altering those environments over geologic history (Hotton et al., 2001). Land plants evolved from freshwater green algae (charophytes) in aquatic wetlands in the early Paleozoic, first as groundcover plants, then herbaceous plants, then shrubs and trees. As plant stature and rooting systems evolved, so did wetlands: from groundcover wetlands, to marshes, to forest swamps on mineral substrates, and then to fens and swamps on peat. The plants and animals that inhabited ancient wetlands were different from those of today, but as different types of wetlands evolved, so did their many critical functions and links to Earth's geochemical cycles (Greb et al., 2006).

Data and methods for interpreting ancient wetlands

Ancient wetlands are interpreted from coals, paleosols and rooting horizons, fossils, and other geologic data.

Coals

Coal is formed from peat, and most banded coals formed from peat accumulated in situ (Fig. 1A and B). Coals of all but the highest ranks contain microscopic spores and pollen (Fig. 1C and D), which can be analyzed through palynology. Similar to modern palynological studies of peat and wetland soils, coal palynology reveals the plants that grew in the original peatland and allows for interpretations of lateral (spatial) and vertical (temporal) variability in plant types in coal beds (Dai et al., 2020). Petrographic analysis of coal macerals provides data on the relative contribution of original botanical tissue components in the peat (Fig. 1E and F), and ratios of degraded and nondegraded macerals can be used to interpret paleowater tables in the original peat (Diessel, 1992). Combinations of petrographic, palynologic, and geochemical data are also used for a variety of depositional interpretations, including interpretations of rheotropic (groundwater-fed) vs. ombrotrophic (rainwater-fed) wetland origins (Eble and Grady, 1993).

Paleosols and rooted horizons

Paleosols are fossil soils (Fig. 1G and H). Many of the physical and geochemical features found in modern soils are preserved in them. Hydric soils, characterized by high water tables, are anaerobic in their upper horizons at least for part of the year. Anaerobic conditions lead to preservation of organic material in paleosols, accompanied by gleying and root halos (Retallack, 1990).

Fossils

Plant fossils (macroscopic and microscopic remains) provide direct evidence of vegetation throughout Earth's history. In some cases, plant fossils are found in growth position. In-place (autochthonous) fossils in wetland facies include buried stumps of wetland trees (Fig. 1I), and coal balls (permineralized peat) in coal beds (Fig. 1J and K). Coal balls can preserve cellular details of the peat-forming flora. In many cases, plant fossils represent transported (allochthonous) elements (Fig. 2A–C). Some fossil plants (megascopic and macroscopic) have extant members that are hydrophytic; hence, interpretation of wetland habitats or ecologies for these taxa is straightforward. Interpretations for other taxa are based on comparisons to related extant plants, on their own morphological features, or on their associations with wetland facies.

Animal fossils are also found in association with wetland strata (Fig. 2D). Most common are invertebrates (bivalves, gastropods, etc.) and invertebrate traces (burrows, tracks, trails), but many famous vertebrate fossils are also associated with ancient wetlands (Greb et al., 2006; Greb, 2013).

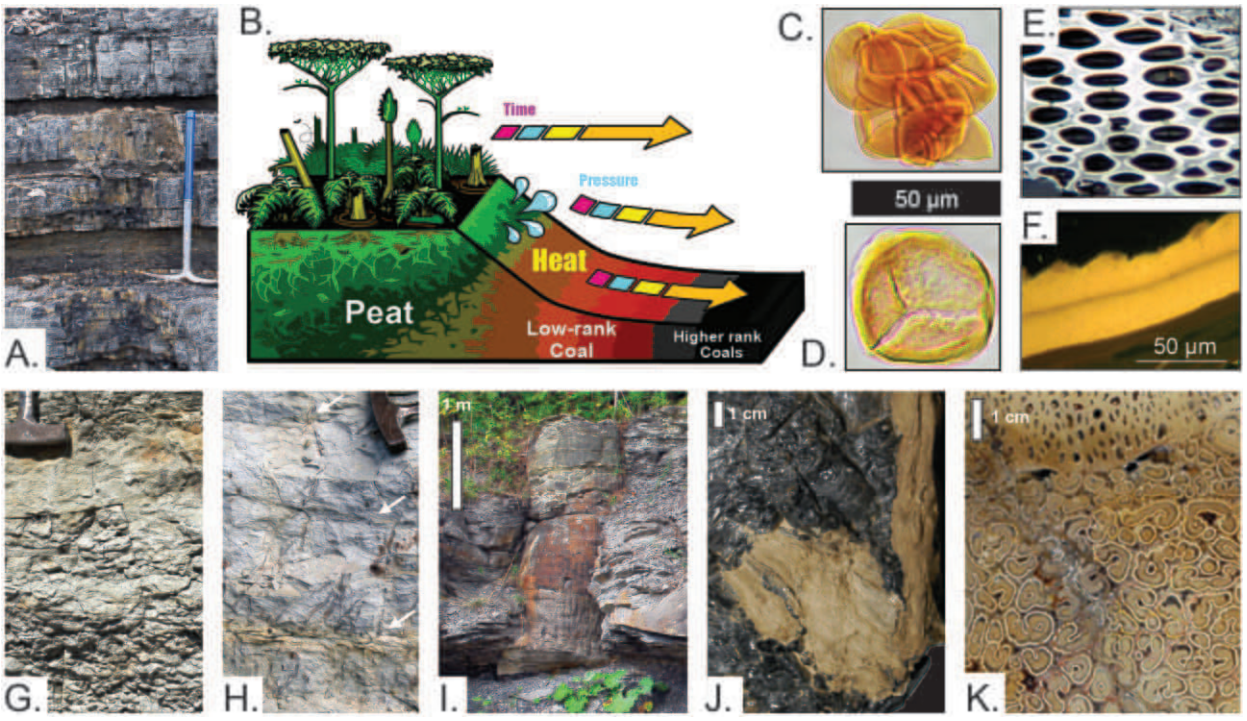

Fig. 1 Some of the types of geologic data collected to interpret ancient wetlands. Examples are from Pennsylvanian coals in Kentucky. (A) Coal interbedded with shale representing alternating peat accumulation and overbank flood deposits. (B) Coal is formed from peat. (C) Microscopic image of tree fern spore, *Punctatisporites minutus*, and (D) *Lepidodendron* lycopod tree spore, *Lycospora pusilla*, from coal samples. (E) Microscopic images of inertinite maceral (charcoal) and (F) sporinite (spores) from coal samples. (G) Gleyed wetland paleosol (soil) with orange root halos. (H) Lycopod forest roots *(Stigmaria)* in a sandstone. (I) In situ lycopod tree stump buried by sandstone splay deposits. (J) Coal ball (calcareous cementation) preserving plant debris in coal. (K) Detail of tree fern internal structure from a coal ball.

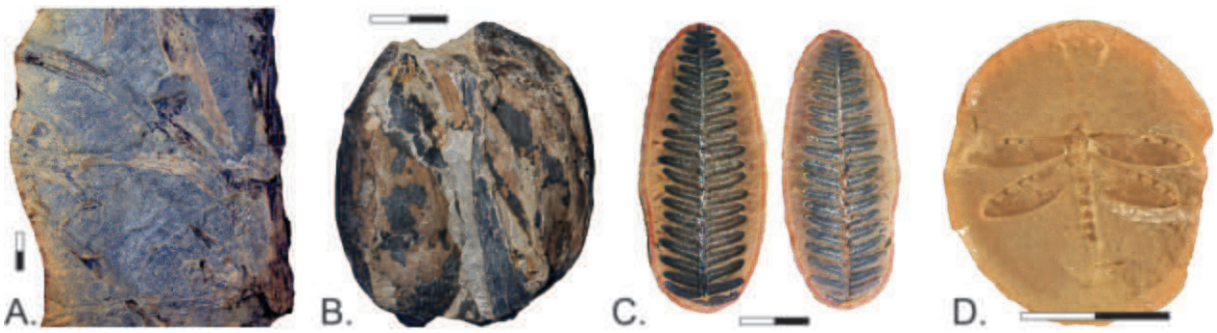

Fig. 2 Examples of transported plant and animal fossils from prehistoric wetlands. Compression fossil of (A) Devonian marsh plant, *Pertica quadrafaria*, Maine, and (B) Paleocene *Nypa* sp. mangrove fruit, Columbia. (C) Pennsylvanian fern, Indiana, and (D) insect, *Eubleptus danielsi* Illinois in siderite nodules. Insect fossil, no. PE40223, with permission Field Museum of Natural History.

Other geologic data

Some rock types, including coals and some organic-rich terrestrial shales, formed only in wetlands. Palustrine limestones and some marls are characteristic of more seasonally wet conditions, including seasonal wetlands (Wright and Platt, 1995). Recognition of facies containing or surrounding coals, organic-rich shales, and palustrine strata allows comparison to original depositional settings (e.g., fluvial, levee, floodplain, etc.). In addition, facies associations are used to infer broader paleogeographic features, including ancient deltas and coastlines, which are important characteristics for many wetland classifications.

Geologic history of wetlands

Pre-Ordovician wet areas

Stromatolite (cyanobacteria) mounds are the oldest fossil life on Earth. Most stromatolites are marine, but some forms from Proterozoic strata more than 2 ½ billion years old are interpreted as inhabiting intertidal areas (Noffke et al., 2006) and freshwater ponds and lakes (Bolhar and van Kranendonk, 2007). Although interpretations of freshwater stromatolites are equivocal (Martín-Closas, 2003), if intertidal or freshwater stromatolites existed in Proterozoic times, and aquatic wetlands are defined to include cyanobacteria mounds in shallow ponds, then the origins of wetlands may extend back into truly deep geologic time.

Ordovician–Early Devonian: Groundcover wetlands

Land plants (embryophytes) are interpreted to have evolved from freshwater charophytes (green algae) in the Late Ordovician to Early Silurian (Graham, 1993; Delwiche and Cooper, 2015) in ponds and aquatic wetlands (Fig. 3). The earliest confirmed, nonspore fossil embrophyte consists of bryophyte-like mats from the Early Silurian (Llandoverian; 443 Ma) of Virginia (Tomescu and Rothwell, 2006). All early embryophytes required moist substrates. The habitats of these low-lying flora come closest to modern moss-lichen wetlands, or wet meadows that lack standing water but have seasonally high water tables, with substantial differences. "Moss-like" wetlands (based on stature) or "groundcover" wetland might describe these primitive wetlands better (Fig. 4).

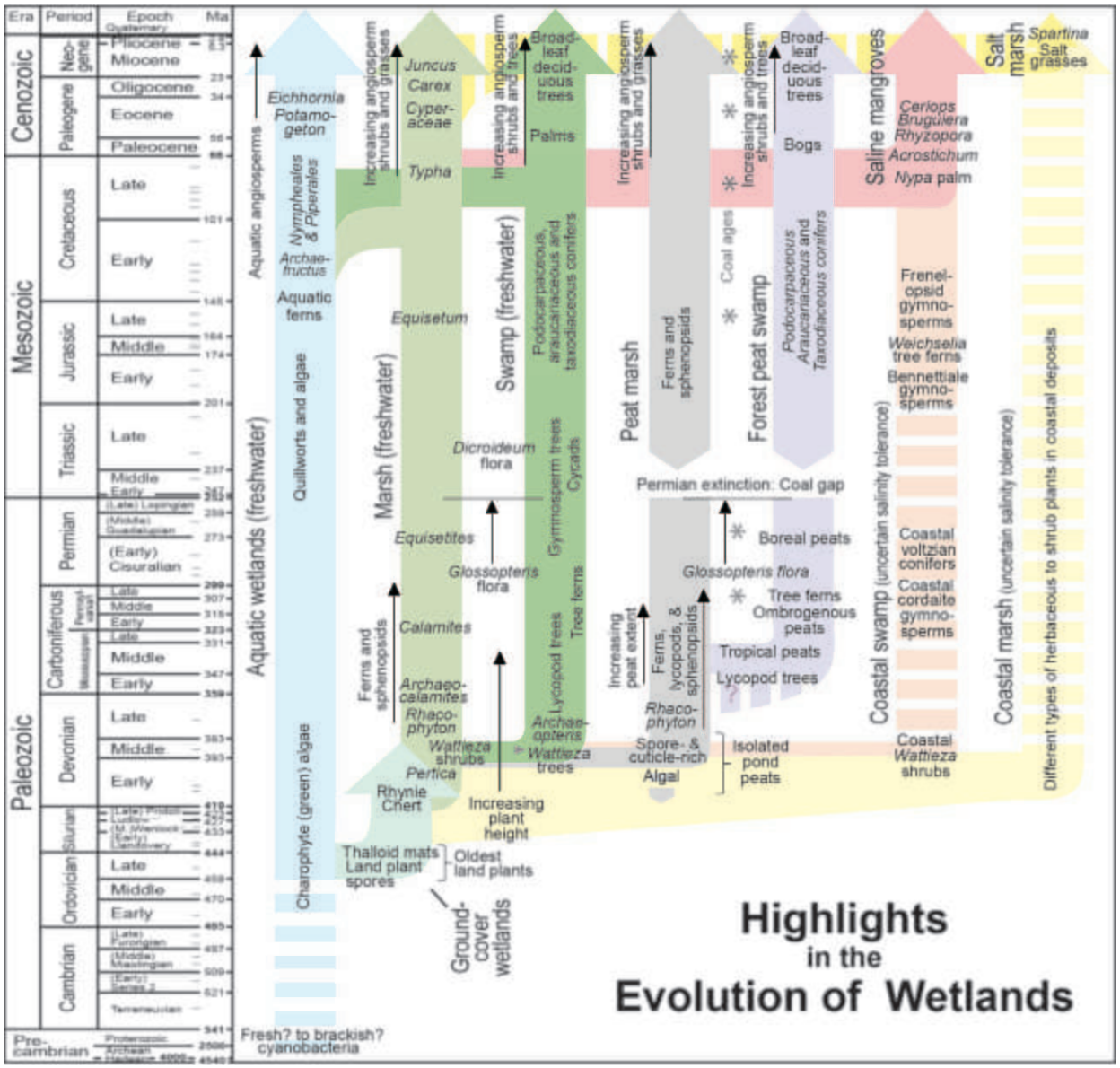

Fig. 3 Wetlands through time. Data are based on flora and fauna discussed in Greb et al. (2006). Ma = Millions of years ago.

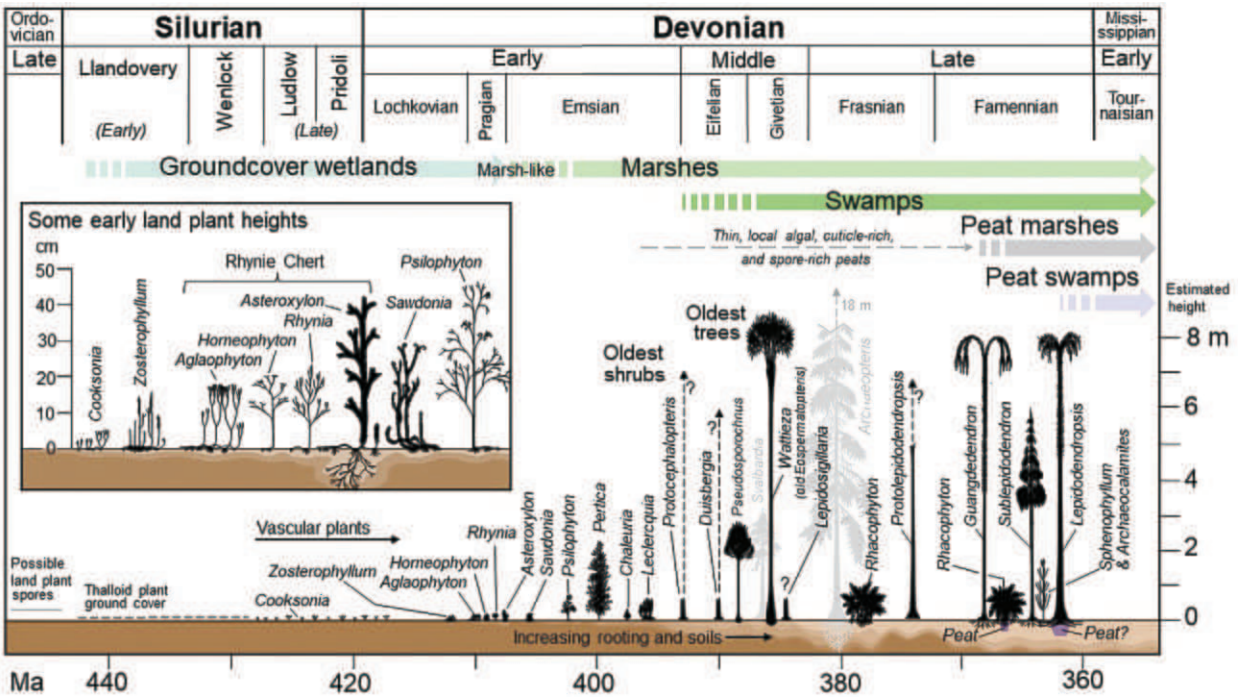

Fig. 4 The early diversification of flora and the wetlands they formed. See vegetation references in text. Modified from Greb et al., 2006, Fig. 1.

By the Early Devonian, a variety of slightly taller plants (mostly <20 cm) occupied wetlands along channel margins, floodplains, coastal areas, and bays (Hotton et al., 2001; Kennedy et al., 2013). The most famous example of Early Devonian (Pragian; 407 Ma) wetlands is the Rhynie Chert of Scotland (Kerp, 2018). The chert preserves fossils of freshwater plants, charophytes, fungi, and tiny invertebrates (Rice et al., 1995). Plants such as *Aglaophyton*, *Horneophyton*, and *Rhynia* were <20 cm tall, but *Asteroxylon* grew to 40 cm (Fig. 4). The Rhynie habitat could be described as a groundcover wetland to wet meadow, or perhaps marsh-like wetland. The association of tiny arthropods with the Rhynie flora shows that even from their origins, wetlands were providing critical habitats for animal life. By the mid-Devonian, the first land vertebrates would emerge from ponds and lakes in wetlands (Clack, 2002). In the Early Pennsylvanian, the earliest reptiles *(Hylonomus)* lived in lycopsid swamp forests (Calder, 2012).

Early–Middle Devonian: Evolution of freshwater marshes

As wetland plant height increased, the first marshes formed and expanded. Early Devonian (Emsian; 407 Ma) plants such as *Pertica* and *Leclercqia* may have grown to heights in excess of 1 m (Fig. 4) and occupied lacustrine-fringing-, floodplain-, and coastal/estuarine-margin marsh habitats (Fig. 4; Allen and Gastaldo, 2006). Wetland marshes with shrubby (<6–8 m) plant taxa evolved by the Middle Devonian (Fig. 4). The cladoxylopsid *Wattieza* (generally <5 m tall) grew in Middle Devonian (Givetian; 385 Ma) marshes on the margins of oxbow lakes (Retallack and Huang, 2011). By the Late Devonian (Famennian; 360 Ma), the pre-fern *Rhacophyton* was widespread in riparian river-margin and lake-margin marshes (Scheckler, 1986). In addition, sphenopsids (horsetails and relatives) such as *Sphenophyllum* and *Archaeocalamites* (Fig. 4) were established with reed-like morphologies and rhizome stems in disturbance-prone riparian and lake-margin marshes (Wang et al., 2005)—habitats their distant ancestors still inhabit.

Mid-Late Devonian: Evolution of forest swamps

The oldest trees evolved in the Middle to Late Devonian and quickly occupied both wetland (Figs. 3 and 4) and non-wetland habitats. Those early trees rooted in wetland paleosols represent the oldest forest "swamps." An example is the Mid-Devonian (Givetian; 385 Ma) tree-fern-like *Wattieza* (previously *Eospermatopteris*), from Gilboa, New York (Driese et al., 1997; Stein et al., 2012). Based on fossil stump diameters, *Wattieza* varied from tall shrubs to trees nearly 9 m tall (Retallack and Huang, 2011). One of the first large trees (18+ m in height), the deciduous progymnosperm *Archaeopteris*, evolved in the Middle Devonian and became common in Late Devonian floodplain and lake margin settings (Scheckler, 1986) marginal to wetlands (Retallack and Huang, 2011). A variety of lycopsid trees also evolved in the Devonian, including *Protolepidodendropsis* (mid-Devonian, Frasnian; 380 Ma) in North America and Europe (Berry and Marshall, 2015) and *Guangdedendron* (Late Devonian, Famennian; 372 Ma) in China (Wang et al., 2019). Lycopsid trees evolved specialized root systems (*Stigmaria*), which allowed them to thrive in flooded substrates.

Expanding marshes and forest swamps in the Devonian and Carboniferous established several wetland functions. River banks were stabilized by vegetation, which changed Devonian stream patterns (Davies and Gibling, 2010). The evolution and expansion of roots likely altered the global nitrogen and phosphorous cycles (Greb et al., 2006). Rooting changed rates of chemical weathering (Algeo et al., 1995). Increased weathering and the deposition of organic carbon from spreading land plants dramatically changed the carbon cycle (Algeo et al., 1995; Berner, 1998; Boyce and Lee 2017).

Mid–Late Devonian: Evolution of peat marshes

The oldest coals are from the Devonian. Thin, laterally isolated, "boghead" coal beds from the Early to Middle Devonian of Siberia and China (Kennedy et al., 2013) represent local freshwater algal peats. Some Middle Devonian non-banded coals represent accumulations of peat from mostly monotypic spores or cuticles from land plants in ponds and lakes (Dai et al., 2020). Organic contributions in these early coals may have been from marsh plants growing along the margins of ponds, and not necessarily growing in the ponds on a peat substrate. By the Late Devonian (Famenian; 360 Ma), thin-banded coals dominated by the pre-fern *Rhacophyton* are recorded (Scheckler, 1986), and may represent plant growth on peat (histosol) substrates. Because *Rhacophyton* had shrub stature, these thin coals may represent the oldest peat marshes, a habitat that became more common into the Carboniferous (Figs. 3 and 4). These early peat marshes could be termed "fens," although they lacked significant contributions from mosses and, of course, the angiosperm reed, rush, and sedges that typify modern fens.

Late Devonian–Carboniferous: Evolution of peat swamps

The oldest peat-accumulating forests or swamps probably spanned the Late Devonian–Mississippian transition (Figs. 3 and 4). Lycopsid swamp trees evolved in the Late Devonian paleotropics and became widespread in the Mississippian on both mineral and peat substrates (Scheckler, 1986). Russian coals from the Middle Mississippian (Visean; 345 Ma) are dominated by lycopsid trees, with some contributions from gymnosperms and sphenopsids (Mosseichik and Ruban, 2010). Although Carboniferous coals are sometimes interpreted as "bogs," that term sometimes implies significant bryophyte contributions, which is not the case for Late Devonian and Carboniferous swamps.

Paleozoic coastal marshes

Many of the Silurian and Early Devonian plants described from early freshwater marshes have been found in coastal and estuarine facies (Fig. 3) or are capped by marine facies, and interpreted as inhabiting possibly brackish- or saltwater coastal marshes (Allen and Gastaldo, 2006; Wang et al., 2019). In coastal and estuarine settings, however, it is not uncommon for wetland plants to occupy local freshwater lenses and ponds, yet be rooted in coastal sediments and subsequently buried in coastal or marine sediments. Hence, it is difficult to definitively interpret the salinity tolerance of fossil plants based solely on characteristics of the strata that encase the fossil assemblage.

Paleozoic coastal mangroves?

Numerous shrub and small-tree taxa are also known from Devonian coastal tropical deposits (Fig. 3). The Devonian cladoxylopsid *Wattieza* has been found in intertidal facies and interpreted as a possible estuarine mangrove (Retallack and Huang, 2011), although it also occupies a variety of freshwater habitats. In the Carboniferous, some Cordaitales are interpreted as possible mangroves (Raymond and Phillips, 1983), although they may have tolerated only occasional brackish incursions, rather than forming true mangrove wetlands (Falcon-Lang, 2005). Voltzian conifers (woody gymnosperms) in coastal deposits from the Permian (Asselian; 295 Ma) are also possible mangroves and have physiological adaptations to drought tolerance, which might have provided salinity tolerance (Falcon-Lang et al., 2015).

Carboniferous: The oldest widespread peatlands

Coals became thicker and more widespread throughout the paleotropics and subtropics during the Late Mississippian and Pennsylvanian (Gastaldo et al., 2020), which demonstrates continued evolution of peatlands. Early to Middle Pennsylvanian coals tend to be dominated by lycopsid trees (e.g., *Lepidodendron*), with subordinate pteridosperms, tree ferns, woody sphenopsids, and small ferns, and variable amounts of Cordaitales (Phillips and Peppers, 1984; DiMichele and Phillips, 1994; Montañez, 2016). Niche partitioning of wetland communities increased through the Mississippian and expanded in Pennsylvanian wetlands among many plant clades (DiMichele et al., 2001). Vertical successions in some coals indicate upward drying and leaching, and floral changes suggest the oldest ombrogenous (domed peats fed by rainwater) peat development (Eble and Grady, 1993) and the oldest hydroseral successions in peat bogs.

Some Middle Pennsylvanian (Desmoinesian; 310 Ma) coals were the oldest to have very large geographic extent. These coals record broad blanket peatlands, approaching the scale of some of the largest modern blanket peatlands (Greb et al., 2003). Because of the many widespread coals in eastern North America and Europe during the Pennsylvanian, it is sometimes called the "Coal Age." The extent of coals has varied through time, however, and coal ages have occurred in different parts of the world at different times (Fig. 3); at other times, there were few coals, and therefore few peatlands (Cross and Phillips, 1990; Thomas, 2002).

Permian: The rise of wetland gymnosperms and high-latitude peatlands

Today, widespread peatlands occur at both high latitudes and in the tropics. In the Permian (299–252 Ma), tropical peats are found in what is now southeast Asia (Wang et al., 2012). Mid- to high-latitude peats are recorded in coal beds from Australia, Brazil, India, South Africa, and Antarctica, which formed part of the Gondwana supercontinent. Gondwana coal beds are dominated by gymnosperms, including glossopterids (like *Glossopteris*), cordaitales, conifers, and cycads but also subordinate horsetails (*Equisitales*), ferns (Filicopsids), herbaceous lycopsids, and bryophytes (Archangelsky, 1986; Cúneo, 1996). Gymnosperms would remain the dominant trees in forest swamps and peatlands in the Permian, and through much of the following Mesozoic (Cross and Phillips, 1990; Wing and Sues, 1992; Graham, 1999).

Some Permian high-latitude deposits represent the oldest conifer-dominated boreal wetland forests. In addition, mid-Permian coals from Antarctica contain clastic dikes, comparable to polygonal soil wedges in modern palsa peats with permafrost cores (Krull, 1999), attesting to cold climates for some high-latitude Permian peatlands. High-latitude peatlands in the Southern and Northern Hemispheres have come and gone since the Permian as landscapes and climates changed through geologic history.

Mesozoic: Aquatic plants, angiosperms, and lacustrine wetlands

Lacustrine wetlands coexisted with the earliest coastal and floodplain wetlands, but a component of modern lacustrine wetlands—truly aquatic vascular plants in open water—did not evolve until much later (Fig. 3). Aquatic quillworts such as *Isoetes* are known from the Triassic (Retallack, 1997) and possibly Permian (Hetherington et al., 2019). These fossils may represent the oldest submerged aquatic vascular plants, and may have contributed to the oldest shallow-water wetlands not dominated by submerged algal macrophytes. Aquatic ferns of the Marsileaceae family evolved in the Late Jurassic to Early Cretaceous, approximately 145 Ma (Yamada and Kato, 2002), and Salviniaceae (floating aquatic ferns) in the early Late Cretaceous (Cenomanian; 94 Ma; Hall, 1974). Angiosperms did not evolve until the Early Cretaceous (Barremian stage; 125 Ma). Floating and emergent aquatic angiosperms are common in two early-diverging orders—Nymphaeales (water lilies and allies) and Piperales (Friis et al., 2003)—as well as among the basal lineages of monocots and eudicots, which constitute the vast majority of extant crown-group angiosperms. The evolution of aquatic (submerged, emergent, and floating) angiosperms through the Cretaceous Period and early Cenozoic Era dramatically altered aquatic (littoral, limnetic) wetlands, which became essentially the same as modern forms by the Eocene Epoch of the Paleogene (Graham, 2011).

Mesozoic–Cenozoic coastal mangrove wetlands

Several small, woody Mesozoic gymnosperms with drought-tolerant (possibly salt-tolerant) adaptations are interpreted as possible mangroves (Fig. 3). Some Bennettitales (extinct cycad-like plants) and conifers of the Late Jurassic (Barbacka et al., 2006), and Early Cretaceous (e.g., *Frenelopsis*; Upchurch and Doyle, 1981) were facultative saline-tolerant plants, but equivocal mangroves (Sucerquia et al., 2015). Some species of the Middle Jurassic (Bathonian; 166 Ma) to mid-Cretaceous (Cenomanian; 94 Ma) tree-fern *Weichselia*, have also been interpreted as mangroves (Retallack and Dilcher, 1981).

The oldest extant mangrove lineage is that of *Nypa* (palm family) known from the Maastrichtian (Late Cretaceous) (Fig. 3, Harley, 2006). Fossils of the mangrove fern *Acrostichum* have also been reported from Maastrichtian (Bonde and Kumaran, 2002), but the assignment to the extant genus has been questioned (Schneider et al., 2004). Most other extant mangrove taxa originated in the Cenozoic Era (Plaziat, 1995; Ellison et al., 1999).

Cenozoic: Saltwater marshes

Continued angiosperm radiation in the Cenozoic involved the evolution of many plants commonly associated with freshwater and saltwater marshes (Fig. 3). Extant saltwater-marsh plants such as cordgrass (*Spartina* sp.), rushes (*Juncus* sp.), and sedges (*Carex* sp.) are angiosperm grasses (Poales), and all have very poor fossil records. Ancestral grasses can be traced back to the Cretaceous, but the crown groups of modern Poales date to the Paleogene (66 Ma) at the beginning of the Cenozoic Era (Bouchenak-Khelladi, et al., 2014). These groups originated in damp, freshwater, infertile substrates (Givnish et al., 2010) prior to expansion into saline habitats. *Carex* spores can be traced back to the mid-Cenozoic (Eocene–Miocene; 56–23 Ma); *Juncus* has a poor fossil record and can only be traced back to the Miocene (23–5 Ma); and *Spartina* also has a poor fossil record, but may postdate the Miocene (Daghlian, 1981). Hence, extant saline marshes dominated by these taxa are geologically relatively recent types of wetlands.

Cenozoic: Return of the bryophytes at high latitudes

Modern high-latitude peatlands are dominated by *Sphagnum* moss. Although bryophytes were among the first inhabitants of wetlands, they remained only very minor components of wetlands until the Cenozoic Era. *Sphagnum* evolved by the Early Jurassic (206–144 Ma), and increased in abundance in the Late Cretaceous and Cenozoic (Cross and Phillips, 1990). Spores and biomarkers (C^{23}/C^{31} *n*-alkane ratio) of *Sphagnum* from a German lignite (Inglis et al., 2015) indicate that ombrogenous sphagnum-dominated bogs existed in the Paleocene (55 Ma), but most species of *Sphagnum* evolved after late mid-Miocene (17 Ma) global cooling (Shaw et al., 2010) and are also relatively recent additions to mid- and high-latitude peatlands.

Cenozoic: Climate and tectonic changes and wetlands

Many of the changes to wetland (and other) biomes through time are influenced by global climate and tectonic changes. During the Cenozoic, separation of South America, India, and Australia from the southern Gondwana supercontinent, and mountain building in South America and the Himalayas led to physical barriers and climate change, which greatly influenced wetland and rainforest distribution in the world (Wing and Sues, 1992; Graham, 1999; Hoorn et al., 2010; Morley, 2018).

Modern-style, closed-canopy, angiosperm-dominated vegetation was present in tropical wetlands of South America by the Paleocene (Wing et al., 2009; Graham et al., 2019). During early Cenozoic "hothouse" climates, wetland floras at middle and high latitudes were dominated by taxodioid conifers (Cupressaceae) and deciduous broad-leaved eudicots, but palms extended to both the Arctic and Antarctic (Williams et al. 2003; Reichgelt et al., 2018). Freshwater marsh habitats became essentially modern in the Middle Eocene to Early Miocene (Graham, 2011). Through the mid-Miocene warm period (17–15 Ma) northern mid-latitude floras continued to include what are today more tropical as well as temperate lineages, but the latter came to dominate during the cooler late Neogene (Tiffney and Manchester, 2001). In North America, cool-temperate forests (and wetlands) at mid and high latitudes changed to boreal forests similar to their modern counterparts by the mid-Miocene (6 Ma) (Graham, 2011; Pound et al., 2012). Northern Hemisphere continental glaciation (waxing and waning) from the Pliocene (5 Ma) through the Quaternary was accompanied by dramatic changes in the distribution and extent of temperate and northern latitude wetlands as great ice sheets advanced and retreated across the continents.

Conclusions/Summary

The history of wetlands is ancient and intricately tied to the evolution of the terrestrial flora. As wetland plants evolved, so did different types of wetlands; from groundcover wetlands, to marshes, to swamps. Increasing morphological adaptations to the physical and chemical requirements of living in wetlands led to increased niche partitioning of flora, and a wide array of wetland habitats through time. Because lowland wetlands have provided habitat for fauna since their earliest beginnings, and have high preservation potential, prehistoric wetlands have been a major source of the fossil flora and fauna geologists use to interpret the geologic past from the Late Silurian to the present. The evolution of different types of wetlands has influenced sedimentation along rivers, lakes, and shorelines, and dramatically influenced several global biogeochemical cycles, including the carbon cycle. Through geologic time, wetlands have fostered evolutionary innovation, but have also been habitats where some species have remained in refugia past their demise in other habitats. Wetlands have expanded and contracted across the globe through history in response to changes in climate, sea level, and tectonics; because of this, prehistoric wetlands are important sources of data for modeling the potential impacts of future climate, sea level, and landscape changes at a variety of scales.

Knowledge gaps

- *Preservational bias*. Much of what we know about the ancient history of terrestrial ecology comes from coastal-deltaic areas in subsiding basins, which have a higher chance of being buried by sediment. Hence, the geologic record of wetlands is biased toward coastal and paludal settings. Wetlands in upland settings and in areas where tectonic subsidence is uncommon have lower preservational potential.
- *Nonpeat wetlands*. Ancient wetland history is biased toward studies of coal because it is fossil peat. Nonpeat wetlands are less commonly studied.
- *Discovery bias*. In many parts of the geologic record, terrestrial fossils are found in association with industrial activities, such as coal mining. This has acted to multiply the biases already described—paleontologists are more likely to find and collect the wetland fossils associated with the artificial exposures created by these activities. The plants and animals living in the less frequently preserved, seasonally dry habitats are also less likely to be searched for and found.
- *Wetland diversity*. The plant macrofossil record only preserves a small proportion of the original systematic diversity of these sites. Fossil pollen and spores recovered from wetland deposits may contain information not only about the plants that grew in wetlands, but also of the regional contribution from communities growing on other substrates. Knowing exactly which plants may have grown under high-watertable conditions and those outside of wetlands is sometimes difficult.

See Also: Fundamental concepts and theories: Egg Banks, Bet-Hedging and Resurrection Ecology; Inland Waters and Limnology; Human pressures and management of Inland Waters: Measuring Impact, Overview and Reference Conditions; Structures and functions of Inland Waters - Lakes: Origins of Types of Lake Basins; Structures and functions of Inland Waters - Wetlands: The Landscape Role of River Wetlands

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The Geomorphology of River Wetlands

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Anabranching Alluvial multi- channel patterns. The channels are separated even at bankfull discharge stage by vegetated semipermanent alluvial islands excised from existing floodplains or formed by within-channel accretions. Anabranching patterns are dominant among the largest rivers in water discharge and also present in a wide range of environments and smaller rivers worldwide.

Avulsion Natural process by which flow diverts out of an established river channel to a new relocated course.

Avulsive rivers Unstable rivers that experience avulsion of long fluvial belts at a variety of time scales, but without the typical conical shape of channels radiating from an apex that characterize the megafans.

Braided Braided rivers are bedload-dominated systems characterized by a network of braided ephemeral bars, unstable channels, and limited riparian vegetation.

Floodplain Depositional surfaces adjacent to the active channel subject to floods, constructed by river processes and built with alluvial sediments. A floodplain is a morphosedimentary unit related to the present-day dynamic. However, older related alluvial units at the same or similar elevation level can also be frequently flooded.

Meanders Sinuous fluvial morphology in a single channel. Meandering rivers wander across a floodplain forming a series of sinuous bends. The water flow patterns through meanders encourage erosion on the outer bank, while deposition and point bars form in the inner bank.

Megafan Megafans are large-scale avulsive alluvial systems formed by unstable rivers that exhibit multiple radial channel patterns (active or abandoned) diverging from an apex. Megafans are >100 km in length and their depositional area ranges from ~7000 to ~200,000 km^2.

Introduction

The global relevance of fluvial systems for inland wetlands is self-evident as wetlands are defined as permanently or seasonally water-saturated land areas, with flowing or stagnant water or saturated soils, and where plant and other biological activity adapted to wet conditions can develop (IUCN, 1971; Cowardin et al., 1979; Brinson, 1993; and many others). Rivers and their landforms/environmental mosaics sustain a significant proportion of inland-continental freshwater wetlands on Earth. Some early classifications of wetlands that incorporated hydrogeomorphology concepts are limited to including descriptions in topography, hydrological, and soil parameters (Brinson, 1993; Neiff et al., 1994; Semeniuk and Semeniuk, 1995; among others), but fluvial wetlands have been dominantly defined under a biological, ecological, and hydrological perspective (Lisenby et al., 2019). Since those pioneer efforts to incorporate hydrogeomorphology into fluvial wetlands research and freshwater conservation, scientists have perceived the relevance to incorporate hydrogeomorphologic concepts into the classification, delimitation, and environmental understanding of wetlands (e.g., Phillips, 1989; Tooth and McCarthy, 2007; Latrubesse, 2012; Sinha et al., 2017; Mu et al., 2021;

Kandus et al., 2017, 2018; Latrubesse et al., 2017, 2021). This chapter reviews and discusses the links between wetlands and hydrogeomorphology, classification systems of fluvial wetlands, the hydrogeomorphologic environmental role of fluvial wetlands, and the global environmental challenges they face. We concentrated on inland fluvial wetlands and did not include wetlands in transitional continental-marine environments, such as deltas and estuaries.

Rivers, fluvial wetlands, and floodplains

Fluvial systems are open physical systems where the primary inputs and outputs of the fluvial system are water, sediment particles, and solutes (solid load and dissolved load). These components are conveyed through the channels that contain water permanently, seasonally, or episodically. Channel development is controlled by the lithological substrate and water and sediment flows, resulting in various channel geometries. The fluvial channels can be shaped by (a) eroding the terrain surface in a self-building channels network; (b) self-formed by alluvial materials the own system transport and deposit, or (c) built by a combination of both processes.

They can be relatively stable or unstable features as erosional and aggradation processes can constantly modify them. Channels adjust and evolve, and a wide range of channels are found in nature. When water flow exceeds the channel capacity during flooding, flooding waters overtop the channel and spread onto the surrounding terrain. Part of the flooded area can be alluvial sediments deposited by the system or terrains formed by rocks and older sediments unrelated to the river's hydro-geomorphologic dynamics. Fluvial flooded areas can be defined from a hydrological or geomorphological point of view. The engineering hydrological definition for floodplains considers a flat surface delineated by the extension of a flood with some particular recurrence interval of flooding (e.g., 100 years). It is also defined as the Special Flood Hazard Area by agencies such as the Federal Emergency Management Agency of the United States (FEMA). Urban planning and insurance companies have thoroughly used the flood-recurrence criterion to delimit the areas of flood risk. However, the delimitation of that area is not necessarily a well-delimited natural unit as "$(x)_{years}$" floods can spread on different kinds of lithology and landscape components. The geomorphologic definition is based on the principle that floodplains are flat depositional surfaces adjacent to the active channel subject to floods, constructed by river processes and built with alluvial sediments. This means that a floodplain is a morphosedimentary unit related to the present-day dynamic. However, older related alluvial units at the same or similar elevation level can also be frequently flooded. It happens because a fluvial system is a natural system with a history, and floodplains are fluvial archives containing recent alluvial units of the Holocene age that can be frequently flooded but not necessarily deposited by the present hydro-geomorphologic regime.

Floodplains are an essential environmental component of the fluvial system and play different functions and services. They are the central fluvial wetlands, support a variety of environments and habitats, act as an erosional-depositional and hydrological buffer area during extreme events, act as aquifers, provide agricultural land and other multiple socio-economic services for humans, and can be a sink of sediments and pollutants.

River's typology

Rivers can be classified in a variety of ways. A simple approach uses the physiographic setting by considering the relief in categories and classifying rivers in mountains, highlands-plateaus, lowlands, and coastal rivers. We can add other factors if the systems reach the Ocean (exoreic basins), if the flows end inland (endorheic basins), and if the flow regime is perennial, seasonal, or intermittent. In some regions, such as in the Amazon, the physical-chemical characteristics of water (water types such as black, clear, and white) have been used to differentiate rivers (Sioli, 1984). In some cases, the kind of environment they drain can also be used to qualify them, as those draining peats and classified as "peat rivers."

Classifying rivers is still challenging, and not a single holistic classification covers all the necessary conceptual and classificatory aspects and their hydrogeomorphologic and environmental diversity. Considering major geotectonic domains of river basins across the planet, many basins spread on more than one geologic domain and climatic zone; therefore, Latrubesse (2015) and Latrubesse and Sinha (2021) proposed four main groups of geological and geomorphological settings of rivers. The main categories are (a) orogenic mountain belts, (b) cratonic areas, sedimentary and basaltic plateaus/platforms, (c) lowland plains in sedimentary basins, (d) and mixed terrains (Table 1). This highlights the complexity of geologic-geomorphic settings of the global rivers, which manifests in morphological diversity and, as a consequence, in the diversity of wetlands.

From the classification above, we can consider two major groups of physiographic settings and two main types of fluvial hydro-sedimentological conveyors. From the physiographic point of view, rivers draining mountain and highlands plateaus are mainly dominated by erosional v-valleys landforms and have considerable stream power and higher slopes than their lowland counterparts. Of course, it is a generalization as some high elevation's settings, such as high plateaus (Altiplano, Tibet), old planation Gondwana surfaces, basaltic plateaus, and a variety of tectonically controlled intra-mountain and inter-mountain basins can also hold rivers that, at a reach/regional scale, exhibit some similar characteristics to those of lowland rivers. Also, medium-size and large rivers can have headwaters in the highlands or mountains and flow downstream through the lowlands. It is relevant as the upper catchment can control the hydrology of the system, and, more relevantly, it usually controls the primary source of sediment load to the rivers. Therefore, generalizing, mountain rivers (or upper catchments of lowland rivers) are mainly flowing on erosional valleys and have relatively large energy with a dominant erosional-transport regime. Consequently, they do not hold a relevant proportion of fluvial wetlands.

Table 1 Geological, geomorphologic settings and fluvial wetlands for large axial rivers, megafans and avulsive rivers.

Category/Description	*Examples*	*Wetlands-floodplains*
1. Linear axial rivers: stable and avulsive fluvial belts		
A. Orogenic belts-linear fluvial belts: rivers with headwaters and long reaches in active orogenic belts, basins' shapes are commonly elongated.		
A.1 Encased in rocky terrain but poorly developed alluvial plain (better developed in the lower reach)	Ayeyarwady, Mekong	Narrow, developed in alluvial reaches, islands, bars and limited floodplain lateral extension Lager rocky-alluvial mixed islands (Mekong)
B. Platforms/Plateau: river draining dominantly platform areas and plateaus (basaltic or sedimentary) bedrock channels, with incised valleys and rapids, bed-load dominant	Upper Parana	Complex-wide wetlands, islands, swamps, paleochannels, paleoislands, lakes
C. Cratonic: headwaters and good part of the river length in low relief areas of stable Pre-Cambrian crystalline basement		
C.1 Confined rivers. Bedrock channels, with incised valleys and rapids, bed-load dominant, v. low suspended load, fragmented, narrow alluvial plain in lower reaches	Tocantins	Narrow, poorly developed with some islands and bars
C.2 Blocked rivers. Large flooded valleys, bed-load dominant, v. low suspended load, rapids in middle or upper courses	Tapajos, Xingú	Blocked valley, large ria-lakes, can have also mixed alluvial-rocky archipelagos.
C.3 Wide valleys with complex islands. Anabranching complex reaches alternating with narrow reaches with rapids or nodal points, bed-load dominant, low suspended load	Negro, Congo	Very wide floodplain, complex huge relict island, sandy fluvial bars.
D. Lowland plains: large aggradational plains- lowlands		
D.1 Meandering belts. Single channel, non-harmonic meanders, muddy banks, high suspended load	Jurua, Purus, Mississippi	Meanders, oxbows, swamps, scroll bars, crevasse splays
E. Mixed: Rivers draining mixed terrains		
E.1a Platforms + cratons. Mainly anabranching with braided tendency, alternating with incised valleys, abundant bed load	Middle Araguaia Middle Parana	Channel dominated anabranching floodplains, impeded floodplains, elongated abandoned-channel lakes, islands, fluvial bars, splays
E.1b Platform + lowlands + Mountains Mainly anabranching with braided tendency in the main multichannel conveyor, large islands, water saturated floodplain, floodplain deltas, meandering floodplain branches		Channel dominated anabranching floodplains, impeded floodplains, elongated abandoned-channel lakes, floodplain deltas, islands, fluvial bars, splays, scroll bars from meandering branches
E.2 Orogenic belts + (or) platforms + (or) cratons + (or) sedimentary lowlands. Complex systems, low to moderate anabranching with braided tendency in some cases, confined reaches and rocky reaches or rapids alternating with wide alluvial reaches, high sediment load (bed load + suspended load) when the orogenic belt is the dominant area, lower sediment load when the platform/cratonic zone is dominant	Orinoco, Madeira, Lena, Obi, Yangtze	Channel dominated dynamics floodplains Related periglacial processes in floodplain wetlands of high latitudes. Can alternate geologically controlled reaches of wide floodplains and narrow floodplains.
E.3 Orogenic belts + lowlands. Headwaters in mountains and well-developed fluvial belts in lowlands		
E.3.1 Stable fluvial belts. Anabranching or meandering systems with stable well defined fluvial belt and terraces	Japura, Içа	Channel dominated anabranching with islands, abandoned channel and swamps. Oxbows and swamps can be present in sinuous reaches
E.3.2 Unstable-avulsive fluvial belts in the forelands		
E.3.2.1 *Avulsive anabranching, high vertical aggradation systems in floodbasins*	Lower Magdalena	Flood basin anabranching system, paleochannels, splays, lakes, swamps, floodplain deltas
E.3.2.1 *Avulsive rivers, lateral migration by avulsion dominant, unstable channels, normally meandering or anabranching with some sinuosity, high in suspended load*	Beni, Ucayali, Pastaza	Paleochannels, lakes, swamps and splays
2. Megafans		
A. Foreland: the whole fan lying in foreland (proximal wedge top-foredeep zone)	Kosi	Shifting fluvial belts and splays
B. Cratonic: Source areas lying in cratonic settings, depositional zone dominantly linked to intra-plate basins	Okavango	Flooded basins and avulsion
C. Complex: Source area in mountains, fan spreading into different settings such as foreland and lowland plains, platforms-cratonic zones	Pilcomayo, Bermejo	Paleochannels, swamps, splays

On the contrary, lowland rivers (rivers with their alluvial tract on lowlands, although the headwaters can or not be in highlands and mountains) are usually characterized by lower valley slopes and less specific energy, well-developed floodplains, and, in many cases, they have bigger rates of lateral migration than the valley-incised mountain rivers. For those reasons, lowland rivers hold the most extensive fluvial wetlands on the planet. Two main groups can be individualized for lowland rivers: (a) axial rivers, (b) avulsive rivers and megafans (Table 1).

Axial lowland rivers flow confined through a valley, their length is typically multiple times (hundreds or thousands of times) larger than their width, and they characteristically exhibit well-developed floodplains. The second group encloses avulsive rivers and megafans. Avulsion is the natural process by which flow diverts out of an established river channel to a new relocated course. Megafans are depositional landforms radiating from an apex. They form when a river debouches from an elevated relief into a plain (apex), depositing the sedimentary load in a radiate conical shape because of the lateral instability and shifting of the channel through time. Other avulsive rivers that are not classified as megafans are those where rivers can suffer avulsion along many significantly long reaches and at a variety of time scales, but without the system presenting the typical conical shape of channels radiating from an apex as in the megafans.

Axial, megafans, and avulsive rivers exhibit in nature a variety of channel patterns. Alluvial channels can be classified in braided, meandering, and anabranching. Straight patterns can be considered, but they are the exception and restricted to short reaches.

Channel patterns in axial rivers and wetlands

Therefore, considering that floodplains are the biggest fluvial wetlands and that there is a link between a channel pattern's style and the floodplain hydro-morphological mosaic, the relationships between channel patterns, floodplains, and fluvial wetlands is analyzed. Though the three patterns can also be found in megafans and avulsive rivers, we discuss braided, meandering, and anabranching patterns specifically for axial rivers. In contrast, megafans and avulsive rivers are presented separately. Thus, questions raise on what is, in the present time, the relative abundance of each type of channel patterns on Earth, what is the size of the rivers (in water discharge and floodplain development) that relates to each channel typology, and how they correlate with the occurrence and extension of fluvial wetlands.

Braided rivers

Braided rivers occur where the flow divides the channel into a series of braided bars by accumulating sediment. Braided rivers are bedload-dominated systems characterized by a network of unstable channels, ephemeral bars, and limited riparian vegetation (Ashmore, 2013). They possess a relatively high slope for the available discharge and a large proportion of bedload concerning the total load. Mid-channel bars are covered by water during the bankfull discharge stage, acting as a single channel system.

Many modern active high bed-loaded axial braided systems are related to mountain-alpine conditions and proglacial systems or semiarid regions. However, some braided systems can be found in mountain zones and foot slopes of tropical areas, India's monsoonal wet-dry seasonal climate, and other climatic zones. But most of the braided rivers in the geomorphologic and sedimentological literature come from rivers with moderate water discharge. Thus, as Latrubesse (2015) claimed, quintessential braided rivers with large water discharges are not found anywhere on the planet. Braided systems are characterized by a high width to depth (w/d) channel ratio, but their channel-floodplain is no more than a few kilometers in width as the fluvial processes are self-contained in the channel-dominated braiding corridor (Figs. 1 and 2). Despite the lack of large braided rivers in present times, it seems that the size and importance of braided rivers have been different during some glacial periods, so larger braided paleochannels and coarse Pleistocene deposits are found across the globe (Latrubesse, 2015).

Meandering rivers

Meandering alluvial rivers wander across a floodplain forming a series of sinuous bends. The water flow patterns through meanders encourage erosion on the outer bank, while deposition and point bars form in the inner bank. It creates asymmetric cross-sections and longitudinal sequences of pools and riffles. As the channel shifts, meander bends tend to expand by lateral migration until chute cut-off and neck cut-off happen, leaving oxbow lakes and scroll bars on the floodplain. Meandering rivers are globally found in any kind of non-glaciated environment.

Meanders are the most studied fluvial channel pattern. Although meandering rivers are not the largest on the planet, several are large rivers and developed big fluvial belts. Even many smaller rivers have formed large meandering floodplains, several kilometers in width. That is possible because of the capacity of meandering rivers to shift laterally through time. Therefore, large meandering rivers develop wider floodplains belts than the largest braided rivers (Figs. 1 and 2). Typical hydrogeomorphic environments and landforms in meandering rivers are point bars, scrollbars, oxbow lakes, levees, back swamps, and crevasse splays.

In some meandering rivers, lateral shifting can be coetaneous with local avulsion of the meander belts, increasing the coverage of the fluvial mosaic of wetlands through large areas. Floodplains characterize several of the largest meandering rivers and recent episodically flooded lower terraces that can reach more than 10 km in width. In water discharge, the largest meandering river is the Mississippi River, but islands are common in some channels' reaches. The most emblematic and most significant wetlands in a meandering system are those of the middle Mississippi River. In western Europe, wetlands in meandering rivers and floodplains are also present locally (oxbows and swamps). Some remarkable examples of wetlands in meandering reaches are those of the upper Loire, the upper Rhine at the German-French border, and the trilateral floodplains of the Morava-Dyje-Danube Ramsar site.

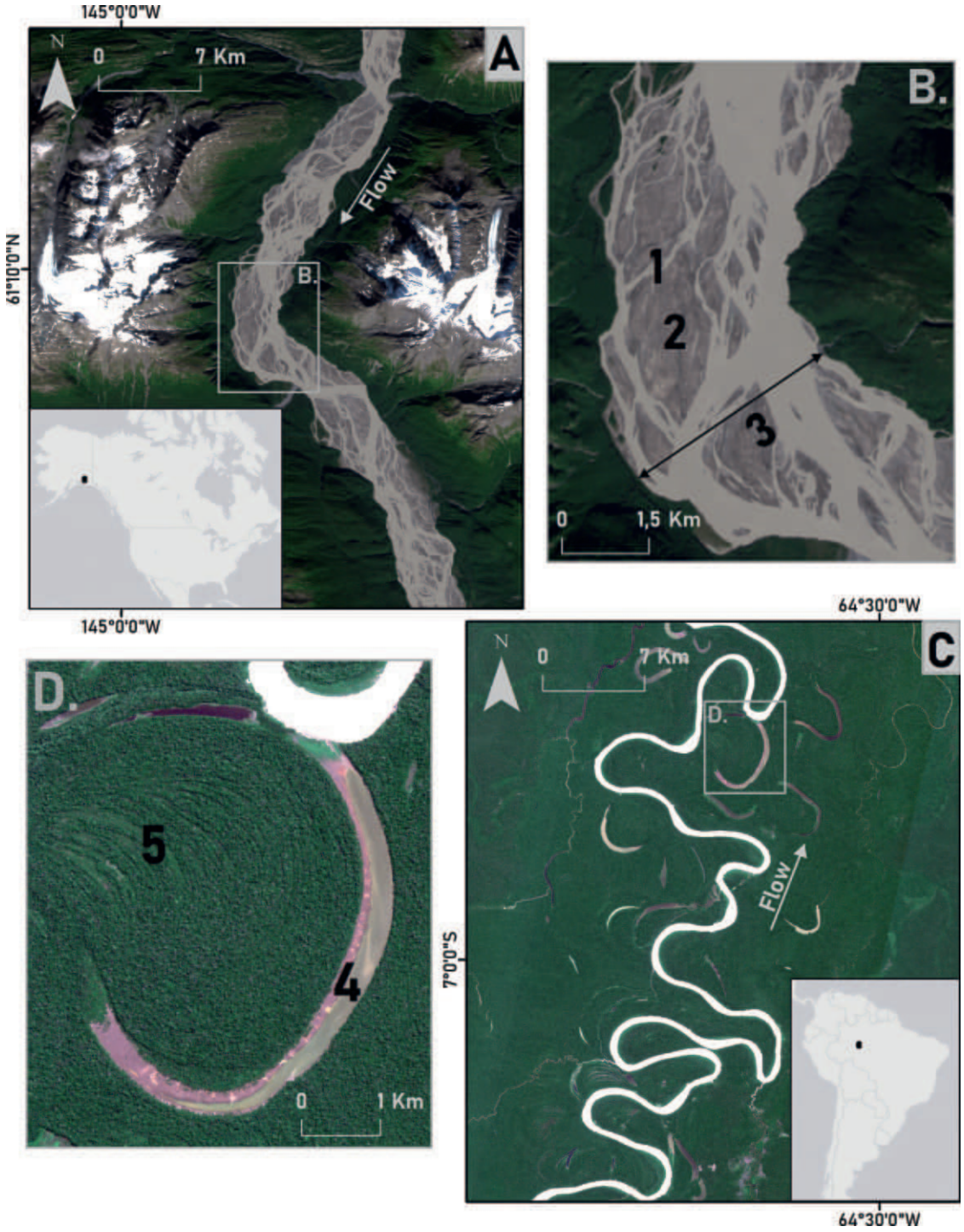

Fig. 1 (A and B) Channel-dominated braiding corridor of the Copper River, Alaska (B1,secondary channel; B2 and B3, fluvial bars), taken on 21 August 2021. (C and D) Meandering floodplain of the Purus River,Amazon basin, over 2nd July 2021. Background Sentinel-2 image downloaded from Google Earth Engine (GEE) platform. D, Oxbow lake (4 abandoned channel; 5 scroll bars).

However, river engineering and land-use changes have affected all those systems in Europe and North America, big or small. We can consider that the most extensive, natural flow, non-engineered single-channel meandering river of the planet in water discharge is the Purus River, a tributary of the Amazon.

Anabranching rivers

Anabranching rivers consist of multiple channels separated even at the bankfull discharge stage by vegetated, semi-permanent alluvial islands that are excised from existing floodplains or formed by within-channel accretions. The islands effectively divide flows into branches, even at bankfull discharges. These rivers are also present in a wide range of environments, from the subarctic to

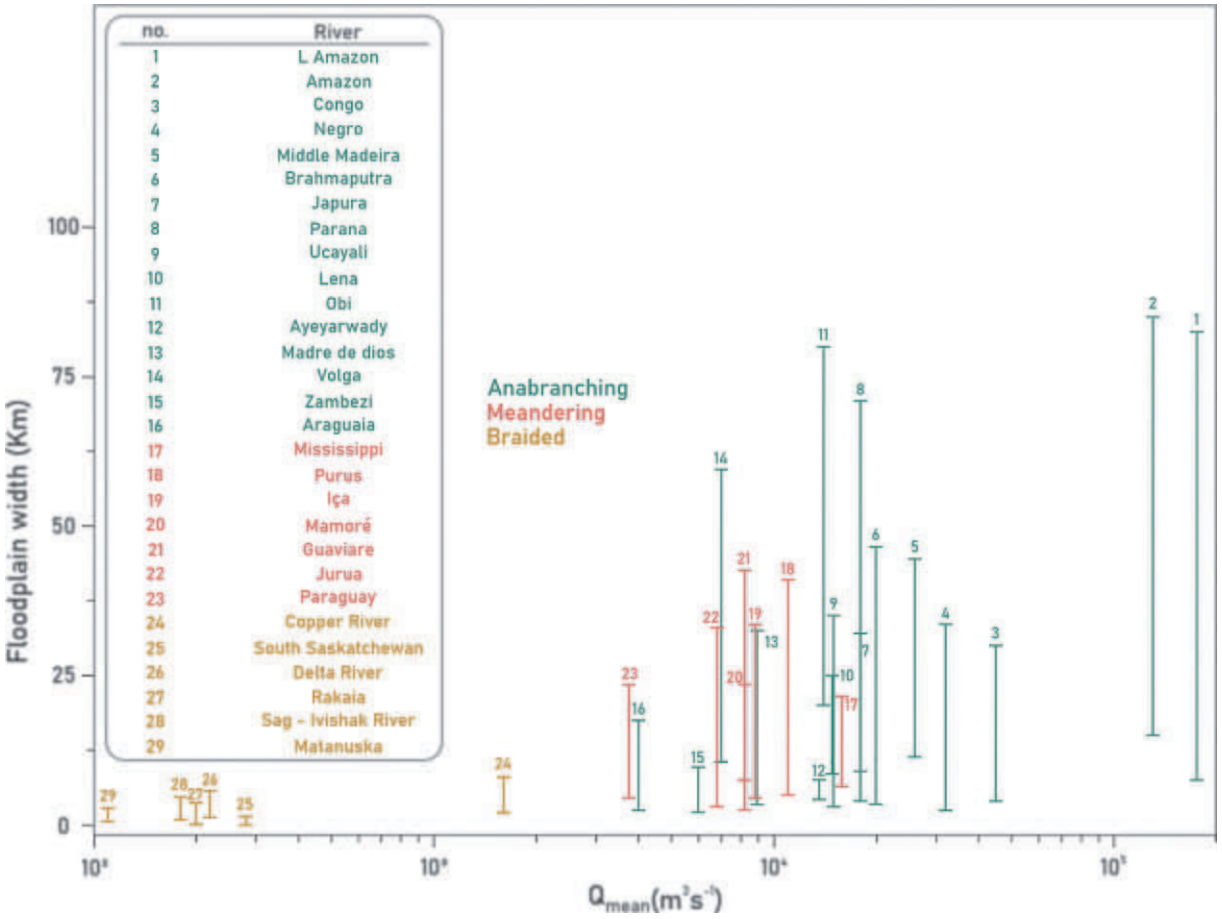

Fig. 2 Representative floodplain width (approximated minimum and maximum widths) of present braided, meandering, and anabranching rivers and the related mean annual discharges (Qmean). Chanel patterns are highlighted with different colors. Figure adapted and expanded from Latrubesse E (2015) Quaternary megafans, large rivers and other avulsive fluvial systems: A potential "who is who" in the geological record. *Earth Science Reviews* **146**: 1–30.

the tropics and temperate regions to the drylands of Africa and Australia. Anabranching rivers consist of multiple semi-permanent channels that concentrate streamflow and maximize bedload transport by constantly adjusting the optimum channel width-to-depth ratio under conditions with little or no opportunity to increase gradient (Nanson, 2013). Branches of the anabranching rivers can show different geomorphic styles and even tend to meander or braid. Islands in large rivers can persist for more than a century, and anabranching floodplains are in many cases a palimpsest of units of different Holocene ages that were generated by a variety of morphological processes (e.g., Santos and Stevaux, 2000; Ramonell et al., 2002; Latrubesse and Franzinelli, 2002, 2005; Sarma, 2005; Lahiri and Sinha, 2012; among others). Vegetated islands are distinctive morphosedimentary components in anabranching rivers, from densely vegetated with alluvial forest in tropical rivers to scarce lines of trees in arid systems of Australia.

The vegetation produces an arial anchoring effect on the floodplain/channel landforms where sediment trapping by vegetation helps stabilization and vertical accretion, and contributes to the floodplain mosaic's variable roughness. Although vegetation is not a prerequisite to developing an anabranching pattern, it could significantly contribute to sustaining and triggering a diversity of anabranching patterns and landforms in multichannel-floodplain systems and play a relevant role in the development and stabilization of islands (Latrubesse, 2015).

Islands and parts of the floodplain can hold swamp lakes, scroll bars, levees, paleochannels, diverse types of elongated straight and sinuous lakes formed on paleochannels, floodplain channels, and internal deltas that generate from the connection between the main channels and big lakes in the floodplain.

The nine largest rivers on Earth in water discharge have anabranching channel patterns (Latrubesse, 2008) and anabranching patterns are also dominant among the world's 15 largest rivers (Latrubesse, 2015). Thus, they have the most extensive floodplains, and consequently, their wetlands are the largest and hydro-geomorphologically diverse among axial fluvial rivers (Fig. 2).

The Amazon and its main anabranching tributaries contain the largest and most diverse belt of continuous floodplain wetlands of the planet (Figs. 2 and 3) (Latrubesse, 2012). The Amazon floodplain "várzea" forests are the most species-rich wetland forests globally (Wittmann et al., 2006). Other iconic wetlands in anabranching systems found in the literature are the Columbia River floodplains, the Saskatchewan River delta-Cumberland marshes in Canada, the upper Brahmaputra floodplain, the Rio Negro and its flooded forest (igapó), the vast middle-lower Paraná River floodplain, the Lena River floodplain, among many others.

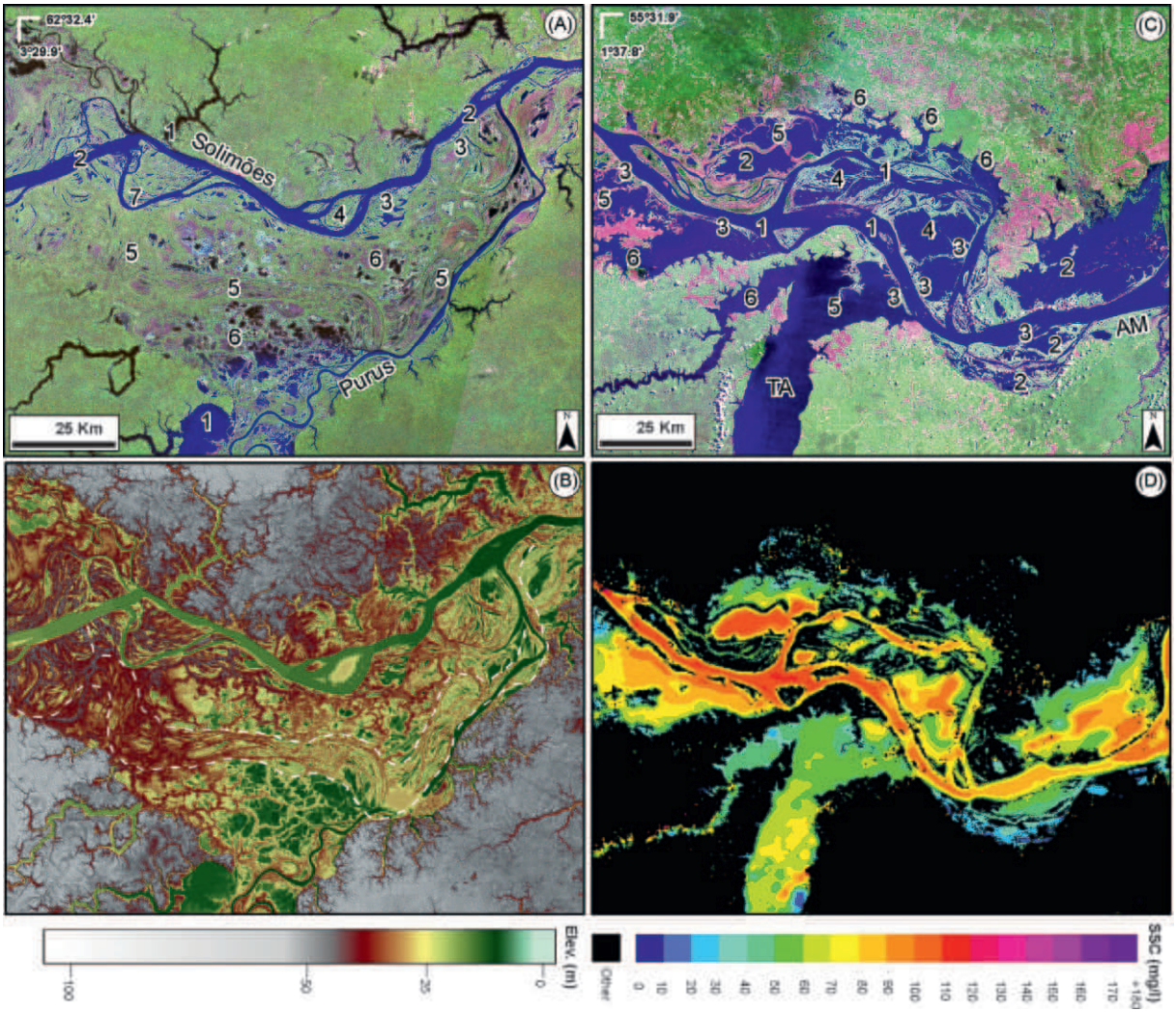

Fig. 3 The Solimões (upper Amazon) River (A and B) complete floodplain with an abandoned belt by avulsion in a tectonic sunken block upstream of the confluence with the Purus River. (A) The sedimentation of the floodplain dammed several tributaries generating blocked valley lakes (1). The Solimões River channel is anabranching (2) with levees (3) and large islands (4). A large alluvial belt of the Solimões River was abandoned by avulsion (5). Numerous small rounded lakes form the impeded floodplain unit (6) while secondary sinuous branches scrolled topography (7) (Geocover image). (B) Digital elevation model (SRTM) of the same area than (A). The dashed line indicates the original position of the Solimões River before avulsion. (C and D) The lower Amazon River at the confluence with the Tapajos River. The Amazon at this reach is an example of incomplete floodplain that is still storing more than 140 Mt. y^{-1} of muddy sediment load (Park and Latrubesse, 2019). (C) The Amazon River is anabranching with large islands (1). The floodplain is characterized by rounded lakes in an impeded drainage floodplain (2). Long and well-developed levees confine the river flow along a surrounding water saturated floodplain (3). Large islands and island lakes characterize the anabranching pattern (4), and floodplain deltas sourced by the main channel system splay into the floodplain lakes (5). The sediments of the Amazon block the lower valley of tributaries (6) which behave as lake systems (Geocover image). (D) Surface sediment concentration maps during rising water stages (April, 15, 2006) around and downstream Obidos, showing the channel–floodplain interactions and the impact of sediment inputs from the main channel toward the floodplain. Values of suspended sediments were calculated with the suspended sediment concentration model by Park and Latrubesse (2014). Reproduction with permission from Latrubesse E (2015) Quaternary megafans, large rivers and other avulsive fluvial systems: A potential "who is who" in the geological record. *Earth Science Reviews* **146**: 1–30.

Although the anabranching pattern is the ultimate planform adjustment of large rivers, small to mid-sized anabranching rivers are found extensively in different climatic and geological regions around the world and exhibit a diversity of peculiar patterns (Nanson, 2013). It points that far from an oddity, as previously assumed by fluvial specialists, a variety of anabranching patterns are, perhaps, the most dominant in our planet.

Megafans and avulsive rivers

Megafans and plains formed by large avulsive rivers are fluvial aggradational mega-landforms that can be found in many climatic settings, but they reach maximum extent in the tropical-subtropical systems (Latrubesse et al., 2005; Leier et al., 2005; Sinha et al., 2012; Latrubesse, 2015) and develop in a variety of tectonic, sedimentary basins, such as foreland and internal continental basins.

Some use a standard >100 km length to define megafans (Gohain and Prakash, 1990; Wilkinson et al., 2006; Chakraborty and Ghosh, 2010; among others), and a depositional area that ranges from ~7000 to ~200,000 km^2 (Wilkinson et al., 2006).

Both, megafans and large-scale avulsive systems are formed by unstable rivers. Megafans exhibit alluvial radial channel patterns (active or abandoned) diverging from an apex, while large alluvial avulsive systems are characterized by long belts of avulsion but their paleochannels do not exhibit a radiating pattern from an apex.

Channel patterns on megafans frequently change downstream from braided at the apexes to transitional wandering, meandering patterns, and anabranching patterns. The avulsive rivers are usually slightly confined or unconfined, and, in some cases, the pattern can also be distributive, meaning with ramifications downstream, although it is not the norm. The change of channel patterns is not abrupt. It can coincide with a progressive but not exacerbated reduction of channel width as channel planform adjusts to changes in bed load caliber, total load, decreasing slope, and even, in some cases, discharge reduction, mainly when distributive patterns are present. As aggradational landforms, the slope surface of megafans and plains of large avulsive systems are very smooth, and local smooth relief created by the fluvial landforms plays an essential local role in concentrating or impeding surface flow. The megafan's alluvial plain surface is imprinted by paleochannels of different ages and local depressions formed by flooded paleochannels, lakes, swamps on the hyper-flat area, creating a mosaic of permanent, seasonal, or episodic wetlands.

Because megafans and avulsive rivers are megaforms widespread in large areas, they hold many of the most extensive wetlands on Earth. Some of the largest megafans are in the Chaco plain, the Pantanal of Mato Grosso, the Indo- Gangetic Plain, and in Africa, like the Okavango.

For far, the largest area of the world with megafans in the Chaco is also one of the most important wetland regions in South America. The major Chaco fluvial basins have their headwaters in the Andean mountains of Bolivia and Argentina, and several rivers debouch into the Chaco plain generating gigantic megafans. They are from north to south (from Bolivia to Argentina) the Grande, Parapeti, Pilcomayo, Bermejo, Salado-Juramento, and Dulce megafans, covering an area of approximately 520,000 km^2 (Iriondo, 1993; Latrubesse, 2015). The whole Chaco plain is a mosaic of permanent and seasonal wetlands related to relict fluvial landforms, widespread swamps and water bodies on the plain's flat surfaces, and areas that suffer the direct influence of river floods and water table saturation. At total, ~306,000 km^2 or 48% of the total surface of the megafans are seasonally flooded. When comparing megafans, the largest wet areas belong to the Pilcomayo and Juramento-Salado. However, when analyzing the ratio between wetland and total megafan area, Dulce has the most significant ratio (~64%) while the Bermejo has the smallest one (~32%). Several extensive Chaco wetlands are currently declared Ramsar sites or protected as Biosphere Reserves, Natural, Provincial Reserves, and National and Provincial Parks.

With a depositional area of ~200,000 km^2, the Pilcomayo is the largest megafan on Earth (Fig. 4). Two main mechanisms control the flood dynamics and shifting of the Pilcomayo River. The first one is the sequence of paleochannels that compose the old Quaternary megafan and the recent lobe. Downstream the river lacks entrenchment in the megafan surface, and becomes perched a couple of meters above the megafan surface. During floods, the water flows toward paleobelts 1.7–3 km in width on the megafan's surface. The fan slopes can be one magnitude bigger than the channel slope. In addition, lateral migration can capture and reactivate old morphologies, revitalizing the inactive landforms during floods. Both situations favor the development of splays, concentrated runoff on the paleofan surface, and potential avulsions. The second central mechanism triggering avulsion is the high accumulation in the channel of fine sediments and woody debris, which blocks the water flow, starts water spills over the megafan surface feeds with sediments extensive marshes and wetlands (esteros and bañados) and paleochannels on the plain become occupied by underfit streams.

The Mato Grosso's Pantanal in Brazil is the second-largest area with fluvial megafans. This tectonic subsidence basin holds a ~150,000 km^2 wetland formed by 11 megafans, sourced by fluvial basins draining the surrounding tablelands and lowlands catchments (Assine et al., 2015). The most extensive and unstable system is the Taquari River megafan, with an area of ~50,000 km^2 that accounts for about 37% of the Pantanal Basin area (Zani et al., 2012).

Although of smaller dimensions, megafans in other regions of the world are also relevant wetlands. In the Indo-Gangetic plain is the very active Kosi River megafan, which has repeatedly shifted in historical times (Sinha, 2014). Although the area is hazardous for floods, the intense land use and occupation prevent the presence of widespread natural wetlands on its surface. Different from other megafans in the Indo-Gangetic plain, the largest wetlands concentrate on interfan regions, such as the Buri Gandak-Ganga rivers interfluve and the Kaabar Tal wetlands in the Baghmati-Kosi interfan area (Sinha et al., 2017).

The large cratonic megafans store a slight amount of sediment but sustain huge wetlands. In Okavango, the flooded area seasonally ranges from ~2450 km^2 to ~11,400km^2 (McCarthy et al., 2003). In the Pantanal, the long-term inundation area is ~34,880km^2, but it can be ~130,000 km^2 during large floods (Hamilton et al., 2002).

Avulsive rivers with related remarkable wetlands are recorded in every continent, but also the most impressive are located in South America.

An almost unknown area, the Bananal, is the largest intracratonic Quaternary South American sedimentary basin. It is located at the Cerrado-Amazon ecotone in Central Brazil and is part of the Araguaia River basin. The Bananal sedimentary basin was filled-up by avulsive belts of the Araguaia river during the Pleistocene and Holocene (Valente and Latrubesse, 2012). Currently, this flat area is a large tropical plain with paleochannels and underfit river systems, swampy areas, and lakes, covering ~106,000 km^2. The plain is flooded by rainfall and water table saturation, and it can be classified as a seasonal wetland (Valente et al., 2013). The area includes a gigantic island called Bananal Island, and the inundation area can reach 58,550 km^2, although the long-term estimated coverage is 13,110 km^2 (Hamilton et al., 2002; Valente et al., 2013).

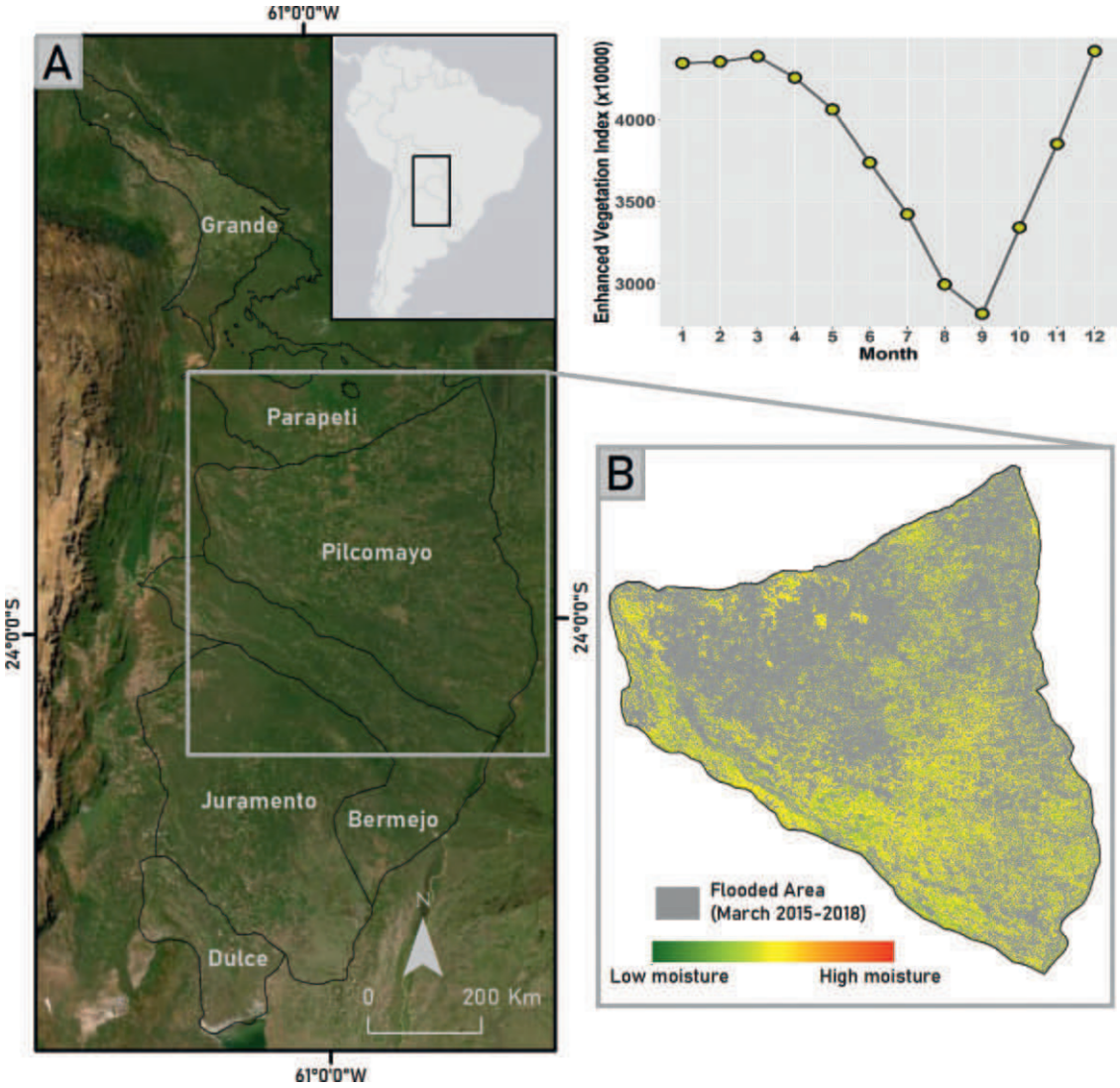

Fig. 4 (A) Chaco megafans (Image source: ESRI Basemaps). (B) Average flooded area (grey pixel) of the Pilcomayo megafans in March between 2015 and 2018, assessed by MODIS EVI. EVI is used to map both the open water (<0.36) and flooded vegetation (>0.47). Inset graph shows the inter-annual average (2015–2018) monthly EVI values for the three largest fans of the Chaco: Pilcomayo, Bermejo, and Juramento-Salado. The highest EVI is attained during March for the three fans, which is the month shown on the map. MODIS-Terra MOD13Q1 product (version 6) supplied from the Land Processes Distributed Active Archive Centre (LPDAAC).

The Yangtze River, one of the top 10 largest rivers in water discharge, also forms extensive wetlands by avulsion of meandering-anabranching belts when it crosses a tectonically active basin from Chijiang to Ouchi (Wang et al., 2011). The river gains some sinuosity and generates a complex set of secondary anabranching avulsive channels, transferring water flows and sediment toward Dongting Lake. This vast area covered by channels and paleochannels exceeds 20,000 km^2.

Another extensive area of wetlands formed by avulsive rivers is the subsiding Ucamara depression in the Peruvian Andean forelands, which is located immediately upstream of the confluence of the Marañon and Ucayali rivers. Very rich in biodiversity, the area is protected by the Pacaya-Samiria National Reserve. The wetlands were formed by multiple avulsion of the rivers Marañon and Ucayali during the Holocene. A complex network of paleochannels covers the very flat tectonic subsiding area of 33,0000 km^2, with floodplain channels, underfit channels, and permanent and semi-permanent swamps and lakes.

The unstable Beni River in Bolivia, which debouches from the Andes into the Moxos-Beni plain sequence of successive avulsed meandering belts in the Holocene now occupied by underfit rivers (Yakuma, Tapado, Bata, and Negro rivers) (Dumont, 1996). The whole plains are flooded by river water, rainwater, and water table saturation. It was estimated that the maximum flooded area is ~92,000 km^2 (Hamilton et al., 2002).

The anabranching Magdalena River in Colombia forms ~25,000 km^2 large wetlands in the Momposina depression tectonic basins where ~21 Mt. y^{-1} of sediment is trapped (Restrepo et al., 2006). The wetland is a geomorphic palimpsest of swamps, lakes, splays, and paleochannels abandoned by avulsion.

River inflows maintain moderate to extensive wetlands in drylands in combination with other factors that serve to impede drainage or reduce infiltration, including faulting, rock outcrops, swelling soils, and ponding by tributary or aeolian sediments (Tooth and McCarthy, 2007). In Asia, the Brahmaputra and the Indus (both dominantly anabranching systems) are rivers known for rapid migration and avulsions recorded since the XVIII century (Sinha and Tandon, 2014; Best et al., 2007). However, wetlands in those systems are relatively small because of the regulation by barrages and dams, the floodplain's land use, the highly seasonal monsoonal regime, and their fluvial geomorphic style.

Smaller but regionally relevant wetlands in avulsive rivers are the Murray-Darling basin in Australia and meandering rivers in southern Africa (Lisenby et al., 2019).

Fluvial wetlands like hydrosedimentary sinks

Wetlands are natural areas that act as sinks, storing water, sediment, and nutrients (Phillips, 1989). In the case of river wetlands, storage happens in both axial rivers, floodplains, and megafans-avulsive systems. A review of the most oversized active fluvial sediment sinks is provided by Latrubesse (2015). Both large axial rivers, as well as megafans and avulsive rivers, can store massive amounts of sediments. Although megafans and wetlands in axial rivers are found in every continent, South America is a land of superlatives because it is the home to both the most extensive axial fluvial wetlands and the largest megafans on Earth.

Sediment and water storage can be found at any spatial scale in axial rivers, from small to large rivers. Still, in large axial rivers, Holocene floodplains can be composed of huge complex areas of impounded water that spread over thousands of kilometers in length and tens of kilometers in width. The floodplains of some of the largest large rivers that transport abundant sedimentary loads, such as the Amazon and Paraná, are still acting as sediment sinks (incomplete floodplains). The 1200 km long stretch of the lower Amazon River wetland is a huge sediment sink that annually stores at least 140 Mt. y^{-1} of muddy sediments through channel-floodplain interactions (Park and Latrubesse, 2019) (Fig. 3), while the Middle Paraná in Argentina stores 17–60 Mt. y^{-1} of suspended sediments in the floodplain (Amsler, 2006; Latrubesse, 2015) through migration of meandering branches, floodplain deltas, and overbank deposits (Fig. 5). In the Colombian forelands, the anabranching Magdalena River stores in the Momposina depression tectonic basins ~21 Mt. y^{-1} of sediment (Restrepo et al., 2006).

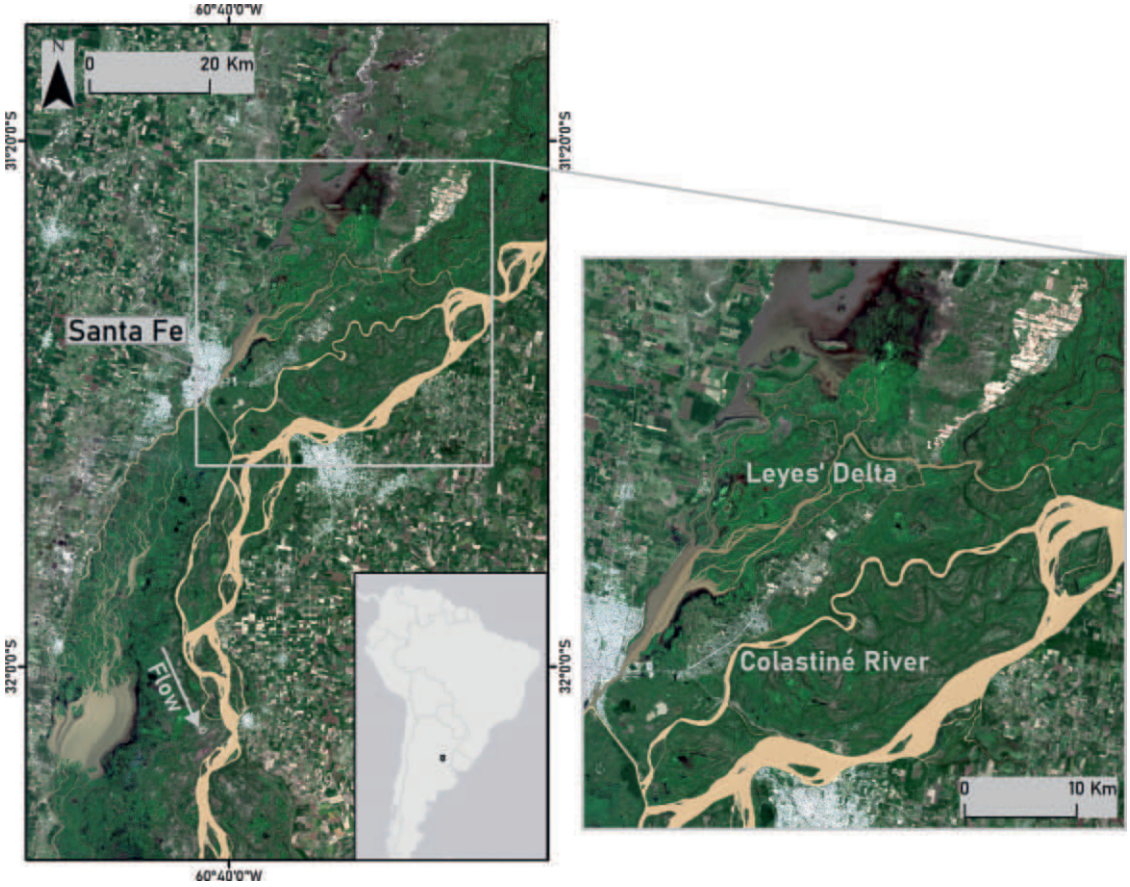

Fig. 5 The complex morphology of the middle Parana River wetlands at Santa Fe, Argentina. The main channel is anabranching with well-developed and large vegetated islands. The meandering Colastiné River branch shifts across the floodplain forming scrolled-plain morphologies. A connection from the main channel with the floodplain through the Leyes floodplain creek, creates the impressive fluvial-lacustrine Leye's Delta, which prograde on the Setubal floodplain lake. Background Sentinel-2 image (07 March 2021) downloaded from GEE platform.

Other rivers with headwaters in the mountains experienced high rates of sedimentation in the Holocene, such as the Brahmaputra and Ganges, or even the upper Amazon (Solimões), while its large Andean tributaries, have "complete floodplains" in the lowlands. Consequently, they have small to null space accommodation to sink sediments and export their sediment load downstream toward the Ocean. Those "complete floodplain" rivers are dynamic and shift laterally or can even suffer avulsion in historical times, such as the lower Brahmaputra. Still, the rates of erosion-depositions are in equilibrium or much closer to equilibrium regarding sediment fluxes than rivers with incomplete floodplains. An example of a fluvial wetland in a complete floodplain is the middle-upper Brahmaputra, one of the world's largest water and sediment discharge rivers. Despite its high discharge, the anabranching Brahmaputra River does not exhibit extensive alluvial wetlands compared to other large anabranching counterparts in South America and Siberia. Other significant rivers with complete floodplains, such as the Mekong, flow mainly into narrow geologically controlled valleys, so their floodplains are constrained to the lowermost reaches and delta.

Rivers draining cratonic old terrains of crystalline and metamorphic rocks have low sediment yields and suspended sediment load. In the Amazon basin, flooded areas of rivers draining the Paleozoic and Precambrian shields of Guyana and Central Brazil cover an area of approximately 200,000 km^2. The largest clear water rivers are the Xingu, Tapajós, and Trombetas, whose floodplains cover approximately 67,000 km^2 (Wittmann et al., 2010). With a mean annual discharge of about 32,000 $m^3\ s^{-1}$ and a drainage area of 600,000 km^2, the Negro River is the second largest tributary in water discharge of the Amazon. The Negro River is the typical black-water river of the Amazon basin, with olive-brown to coffee-brown colored water and transparencies from 1.3 to 2.3 m because of dissolved humic substances (Sioli, 1984). The Negro River transports 8 Mt. $year^{-1}$ of suspended sediment to the Amazon (Filizola, 1999), an insignificant quantity of suspended load in relation to the huge water discharge. Its basin's wetlands cover 118,000 km^2 (Melack and Hess, 2010), and the Negro holds the biggest fluvial archipelagos in a fluvial system that support the largest black-water inundation forest in the world, regionally called "igapó" (Montero, 2011; Montero and Latrubesse, 2013).

All these cratonic rivers described above are characterized by incomplete floodplains in the middle-lower reaches and their enormous valleys act as water reservoirs with low velocity flows because they are partially (Negro) or strongly blocked (Tapajós, Xingu) by the trunk-collector system, the Amazon.

Because these large cratonic anabranching rivers transport a minimum amount of suspended load, the wetlands on the large islands and other floodplain units that they exhibit are relict landforms in disequilibrium with the present morpho-dynamic conditions of the river. The most extreme case on the planet is the Negro River where the largest and most complex fluvial archipelagos developed and the islands are covered by tropical flooded forest (Latrubesse and Franzinelli, 2005; Latrubesse and Stevaux, 2015).

Located in active sedimentary basins (foreland and intracratonic basins), megafans are among the most effective sediment traps of the planet. The Chaco catchments draining the central Andes in the subtropical belt (~15°–30° S), have small discharges (>360 $m^3\ s^{-1}$), high discharge variability (Latrubesse et al., 2005), high sediment yields, and relatively low values of specific runoff. The sediment production of the central Andean rivers in the Chaco is one of the highest in the world, up to two orders of magnitude greater than high runoff rivers draining the northern Caribbean and Pacific Andes, and many times bigger than other orogenic mountain belts of the world, such as the Alps, while comparable or even higher than several fluvial basins in the Himalayas (Latrubesse and Restrepo, 2014). The sedimentary load is unproportioned when compared to the relatively small discharge of these rivers. From a total amount of ~475 Mt. y^{-1} sediments exported to the Andean piedmont through the main fluvial Chaco systems, ~68% (~327 Mt. y^{-1}) is trapped and stored in the Chaco plain by the six megafans, instead of being transferred to the Ocean through the Paraná or the Amazon basins. Thus, the Chaco plain and its megafans are one of the (and perhaps the most) largest active continental sedimentary basins of the planet.

Another area with high sediment load rivers and megafans is the Indo-Gangetic plain, in the Himalayan foreland. However, the Indo-Gangetic megafans have limited capacity of sediment trapping in the depositional area, exporting a significant part of their sediment load to the collector Ganga River (Sinha and Friend, 1994).

In cratonic basins, large megafans such as the Pantanal and Okavango sustain large wetlands but although they are important inland sediment sinks at a regional scale, the formative rivers have low sediment yields and suspended sediment loads, and the amount of trapped sediments is low when compared to the highly loaded megafans draining orogenic belts.

Fluvial connectivity-flood pulse and others

Several important concepts highlight the relevance of hydrogeomorphologic processes to identify, delimitate, classify and study fluvial wetland's functioning.

The concepts of river continuum (RCC) (Vannote et al., 1980), hydrological connectivity, and the flood pulse concept (Junk et al., 1989) have been paramount paradigms in the ecological studies of wetlands.

Hydrological connectivity for ecologists focuses on the relationship between flood pulses (as a dominant explanatory variable) and the ecological variables, as it has been conceptualized in terms of water volume and the rate of water transfer from the mainstream (and branches if present) to the floodplain. It has been extensively utilized as a central idea in ecohydrology, especially following the development of the flood pulse concept (Junk et al., 1989; Neiff, 1996; Neiff et al., 2003; Pringle, 2003; Tockner et al., 2000). Therefore, for floodplain ecologists, lateral connectivity and distance from the channel/s and the wet-flooded areas of the floodplain have been considered an essential factor in characterizing river-floodplain hydrological connectivity (Amoros and Bornette, 2002; Heiler et al., 1995).

But riparian and wetland landscapes are shaped, and genetically and functionally dependent on hydrological and geomorphic processes. Thus, wetlands are not just hydrological systems but also geomorphologic systems (Phillips, 1989). The plants that form vegetation types and the animals that use those spaces as habitat are influenced in their persistence and abundances by disturbance processes associated with a set of hydro-geomorphologic phenomena, such as channel morphodynamics, erosional-depositional landforms and processes, channel-floodplain interactions, floods, and many other processes and mechanisms that create and sustain complex environmental patterns and spatial geomorphic mosaics.

Consequently, understanding the connectivity between the channel and the floodplains is fundamental for incorporating morphodynamics and a broader time scale that allows assessing changes of functionality and connection through specific periods. Therefore, considering hydro-geomorphic changes under a particular time scale is crucial because rivers are dynamic systems, and both hydrogeomorphic and biogeochemical functioning and alterations in floodplain wetlands occur through these interactions.

Since the 1980s, multiple models strongly based on stage-discharge relationships and the statistic of hydrological series have been developed to assess connectivity (Junk et al., 1989; Poff and Ward, 1989). However, they only partially explain the diverse mechanisms of hydro-sedimentary transferences from the river toward the floodplain (and into the floodplain). The denominated Aquatic Terrestrial Transition Zone (ATTZ) (Junk et al., 1989; Junk and Wantzen, 2006) is far from a single terrestrial-flooded terrain relation but a complex response that depends on the spatiotemporal interrelations of hydroecological and hydrosedimentological connectivity among the different geomorphic units. Even more, connectivity processes over different geomorphic units are not necessarily correlated with their minimum distance (shortest lines) from the river. Distance has to be considered simply as another factor in analyzing hydrological channel-floodplain connectivity processes.

Beyond water stage variability as a primary factor, connectivity processes are affected by the complexity of the floodplain geomorphic mosaic, local hydrological inputs, and intricate paths and mechanisms of flow transferences that depends not only on the hydrological regime but on the channels pattern's types and the complex morphology and evolutive history of the floodplains mosaic. Some specific cases are discussed as follows.

As observed in floodplains of meandering rivers (Drago et al., 2008; Hudson et al., 2012; Phillips, 2013), each unit's geographic location (proximity to the River) does not necessarily directly relate to the sequential flooding. River-recharge connections and floodplain water residence time did not simply correlate with the ordinary distance (shortest straight line) from the river.

In the case of large anabranching rivers, there is no direct simple correlation between the floodplain flooding and the proximity to the main channel (Mertes, 1997; Neiff et al., 2003; Latrubesse, 2012; Dunne and Aalto, 2013; Marchetti et al., 2013; Stevaux et al., 2013; Lininger and Latrubesse, 2016; Park and Latrubesse, 2017, 2019). For example, Park and Latrubesse (2017) demonstrated that the connectivity processes in a reach of the middle Amazon are related to 12 geomorphic sub-units of the floodplain that are interconnected at different stage thresholds through channelized and overbank flow paths, while lakes act as reservoirs for flood waters, local rainfall, and water table saturation-seepage (Fig. 3). A large proportion of the middle Amazon River floodplain lakes are fully connected, reach their maximum areal development, and the floodplain is spatially water-saturated when the river reaches lower stages than bankfull, before overbank diffusive processes start to happen. Thus, a major recommendation to understand connectivity in certain detail is to develop specific studies at reach scales, calibrating individual thresholds of hydrological connection-disconnection levels and flood routing paths as they are dependent on the internal geomorphic variability of the floodplain. The heterogeneous flood thresholds and flood duration times for different floodplain units, as assessed by Park and Latrubesse (2017), are central for floodplain ecology because suspended sediments (mostly silt and clay) and colloidal particles source nutrients that sustain a broad range of floodplain ecological communities (Tockner et al., 2000), and hydrological stress (duration of drought or floods) is a main ecological factor (Junk and Piedade, 1997). As highlighted by some ecologists, the role of low water levels in the hydrological connectivity is also important for floodplain ecology because during the dry season, the plants suffer stress, ceasing the rowing and absorption of the leaves (Neiff and Poi de Neiff, 1990), and there is more limited space and lower habitat quality for the fauna of the floodplain (Neiff and Malvarez, 2004).

Another important concept on riverine wetlands is that of vegetation successions and the vegetational mosaics of the floodplain. Vegetation and water bodies are the main environmental components that easily reflect to the observer the environmental internal diversity and complexity of the fluvial wetlands. Linking the hydrogeomorphologic mosaic, the hydrology of the system, the morphodynamic processes, and the physiognomy of the vegetation offers a more holistic perspective about the functionality and evolutionary landscape stages of the wetland mosaic. Vegetation areas that occupy a specific location in a geomorphologic unit represent a particular environmental mosaic that in some order differs floristically, pedologically and topographically from neighboring morphosedimentary units. Thus, integrating geomorphology with vegetation maps produces functional geospatial morpho-vegetational units, and other relevant factors such as intensity and duration of floods, types of soils/catenas, and other parameters can be easily integrated into wetland qualificatives.

Early studies on fluvial dynamics and vegetation successions have concentrated on shifting meandering rivers in the Northern Hemisphere (e.g., Everitt, 1968; Nanson and Beach, 1977; among others). In the tropics, studies on meandering rivers from Peruvian Amazon related primary vegetation succession, large-scale forest disturbance, and forest regeneration as produced by the migration of meandering rivers (Salo et al., 1986; Puhakka et al., 1992).

However, the understanding of vegetation successions in anabranching rivers is still incipient, largely because of the different geomorphic styles and floodplain hydro-geodiversity they exhibit worldwide. Vegetation successions were documented in the Solimões and Japurá rivers by using recent channel migration rates, a simplified description of floodplain and terraces units (low and high várzea), and some physical variables such as local sedimentation rates and soils texture (Wittmann et al., 2004, 2010; Peixoto et al., 2009).

The relationships between morphosedimentary units, multitemporal geomorphic mapping of river changes, and vegetation successions, were also studied in the middle Araguaia River, a very dynamic anabranching sandy-loaded river of Central Brazil (Morais et al., 2008). Three floodplain geomorphic units of the floodplain named hindered floodplain, paleomeanders and present meanders, and accreted bars and islands correlated to five physiognomic vegetation units (pioneer herbaceous, shrub-arboreal, arboreal, anthropized areas), and lakes. The connectivity with the paleomeanders units is established before the river reaches bankfull stage. At the overbank stage, the floodplain becomes in average covered by floods only ~5% of the time (~18 days). During the last four decades, the river has been destroying older and more stable vegetation successions of the paleomeanders units and hindered floodplain units, while generating younger and more herbaceous successions on the accreted bars and islands unit. While in meandering rivers the continued vegetation renovation response to erosion is in equilibrium by creating similar repetitive successions on the accretion zones, in the Araguaia, the current anabraching morphodynamics is not balanced. The geomorphic processes are triggering the partial replacement of more diverse (in species and habitats) vegetation by removing arboreal and shrub-arboreal communities of the paleomeanders-meanders and hindered floodpain units, which are replaced by less complex and biodiverse herbaceous and pioneer shrub-arboreal vegetation along the channel dominated floodplain (islands and accreted bars).

The dynamic of the vegetational mosaic and vegetation successions of the riverine forest was also studied in the Paraná River in Argentina, on islands, floodplain deltas, scroll morphologies, swamps, and levees (e.g., Neiff et al., 2014; Marchetti et al., 2013; Marchetti et al., 2020) (Fig. 5). The hydro-sedimentological dynamics of the Paraná River floodplain are regulated by its geomorphological architecture. Hence, the annual dynamics of vegetation activity are influenced by the geomorphologic unit's level, rather than by the short duration modelling processes (i.e., hydrological cycles or drought-flood pulses) (Marchetti et al., 2013) (Fig. 5).

Thus, the development and distribution of the vegetation and aquatic environments follow the variability imposed by the geomorphologic environments of the floodplain and are subject to hydrogeomorphologic perturbations (state and transformation variables) by the channel style and dynamics. The hydrological, erosional, and depositional processes modulate the generation and renovation of vegetation successions and the time evolution/response of the fluvial mosaic.

Fluvial wetlands and their relationships with other geomorphic systems

Fluvial systems interact with other geomorphic systems where processes and landforms can coexist, creating a mixed hydro-geomorphologic mosaic. Both geomorphic systems can be simultaneously functional and interactive, but relict aeolian landforms on the landscape can also impose controls on the hydrogeomorphology dynamics of the river wetlands.

Among extensive fluvial-aeolian wetlands with a dominant presence of non-active dunes (paleodunes) are the Niger inner wetlands and the Orinoco Llanos of Venezuela. The Orinoco Llanos are a large and very flat plain covered by avulsed paleochannels of the Apure-Meta-Arauca-Capanaparo rivers. Widespread aeolian-fluvial interactions occurred in the Llanos during the late Pleistocene, and large fields of parabolic dunes developed from deflation of the alluvial deposits (Latrubesse, 2003; Carr et al., 2016). The rivers have been flowing and shifting across the aeolian fields, and the fluvial-aeolian plain behaves as a wetland seasonally flooded by rivers, rainwaters, and water table saturation. The total area covered by floods (excluding temporary lakes and rivers) can reach more than 105,000 km^2 (Hamilton et al., 2004). The Inner Niger Delta, a Ramsar site since 2004, is a large inland wetland of 41,195 km^2 located in Mali, between the Markala dam (near Se'gou) and Timbuktu. Downstream of the wetland depression, the massive east-west non-active linear dunes of the Erg of Bara, 5–10 m high and transversely oriented to the regional river flow, represent an obstacle that imposes conditions on the hydrogeomorphological dynamic of the Niger River (Fig. 6). The available interdune space controls the flood processes. The anabranching pattern becomes ramified in multiple sinuous to low sinuosity channels, flowing through the interdunes and struggling to connect downstream. However, the system can recover and integrate into a more constrained and narrower multichannel pattern downstream near Timbuktu.

Permanent fluvial wetlands in drylands are rare, but episodic floods triggered by episodic extreme rainfall events can activate both, permanent and ephemeral wetlands. For example, in Australia, ephemeral wetlands and permanent waterholes can be found on extensive floodplains and floodouts and among aeolian dune fields (e.g., Knighton and Nanson, 1994, 2000; Tooth and McCarthy, 2007).

Wetlands in fluvial basins can also be related to large inland depressions with very gentle slopes, characterized by impeded water flow and even peat. For example, the Cuvette Centrale in the Congo basin is a massive inland tropical peatland-flooded forest wetland, spreading over 145,500 km^2, that could store 30.6 Pg of carbon (Dargie et al., 2017). The wetland is characterized by diffusive drainage and low suspended sediment concentrations in the fluvial systems, sediment trapping that influences the hydrology, the biogeochemistry of the Congo River due to diluting the suspended matter (SM), as well as the total dissolved solids (TDS), while increasing organic matter concentrations and lowering the pH of the water (N'Kaya et al., 2020). But perhaps the most extensive peat wetlands are those of the Amazonian interfluvial region, which could contain the largest tropical wetland area (800,720 km^2) (Gumbricht et al., 2017).

At higher latitude, several of the largest rivers in Siberia and North America drain toward the Arctic throughout periglacial environments with continuous permafrost. Alluvial and periglacial processes can interact in the tundra and part of the taiga. Fluvial styles in periglacial zones are not of a particular style (braided, meandering, or anabranching). Still, climate imposes conditions on

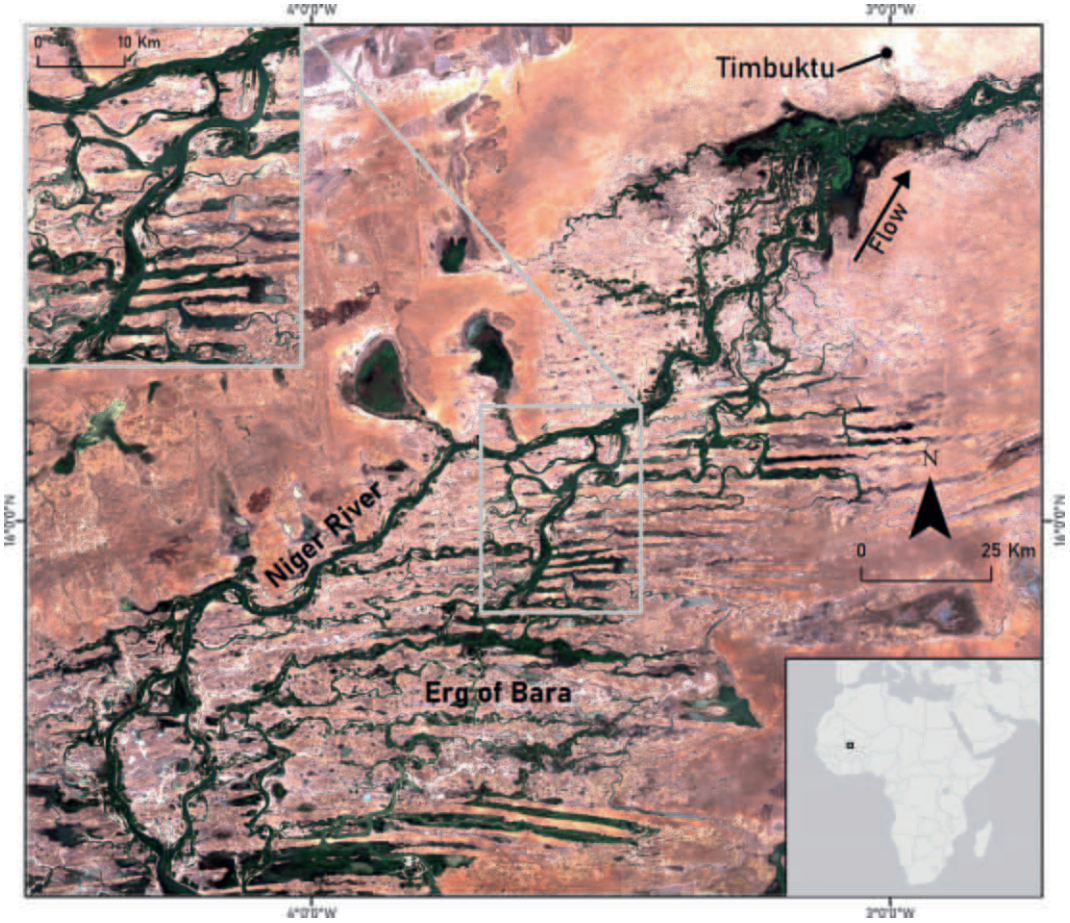

Fig. 6 The anabranching Niger River downstream the Inner Niger Delta. The linear paleodunes system of the Erg of Bara impose control over the river planform and the extensive wetlands. Background Sentinel-2 image (26–31 October 2020) downloaded from GEE platform.

the fluvial systems. It modulates the hydrology, the periglacial processes on the alluvial materials of the floodplain, and the channel becomes frozen in winter. The runoff concentrates in a few days or weeks during the melt period (30–90%) and ice jams can cause flooding (Vandenberghe and Woo, 2002).

The Lena River, one of the largest rivers of the world in terms of water discharge (~16,500 m^3 s^{-1}), has a relatively low suspended sediment load (20–49 Mt. y^{-1}) but still contributes ~15% of the total sediment input to the Arctic (Costard et al., 2007). Like the majority of the large rivers, the alluvial reaches of the Lena are anabranching (Fig. 7). The vast floodplains hold a variety of wetlands that are also dynamically related to the thermokarst process and river water recharge from the surrounding plains (Fig. 7). The combined thermal and mechanical erosion triggers thermo-erosive niches on the banks (Gautier et al., 2021). Before 1987 the river ice thickness near Yakutsk exceeded 1.5 m every 2 years, but since 1987, the river ice only exceeded that value four times (Costard et al., 2007). The permafrost causes low underground water input and rapid floods during breakups (Gautier et al., 2021). Permafrost also modifies the mechanical properties of frozen banks. During the break up periods (summer), the combined effect of the rising water and the stream temperature triggers thermal and mechanical erosion and high recession of the river banks (Costard et al., 2007; Gautier et al., 2003). Climate change consequences is resulting in an unprecedented increasing frequency of high floods and the disappearance of small floods (Gautier et al., 2018).

The alluvial islands of the anabranching reaches are dynamic. The island's area increased during the last 50 years, and the islands have high rates of migration (1967–2002). But since 2003, accretion has decreased, small young islands with seasonal permafrost are developing, and older islands with permanent permafrost are suffering erosion as the consequence of global warming and the floodplain permafrost degradation (Gautier et al., 2021).

The environmental struggle of fluvial wetlands

Most rivers are anthropogenically modified by land-use changes, river engineering, and river regulation that significantly impact and modify the river systems' hydrogeomorphology, sedimentology, connectivity, and fluxes. Anthropogenic stress results in long-lasting river morphology changes, reduction in water flows, altered sediment fluxes, loss of channel-floodplain connectivity,

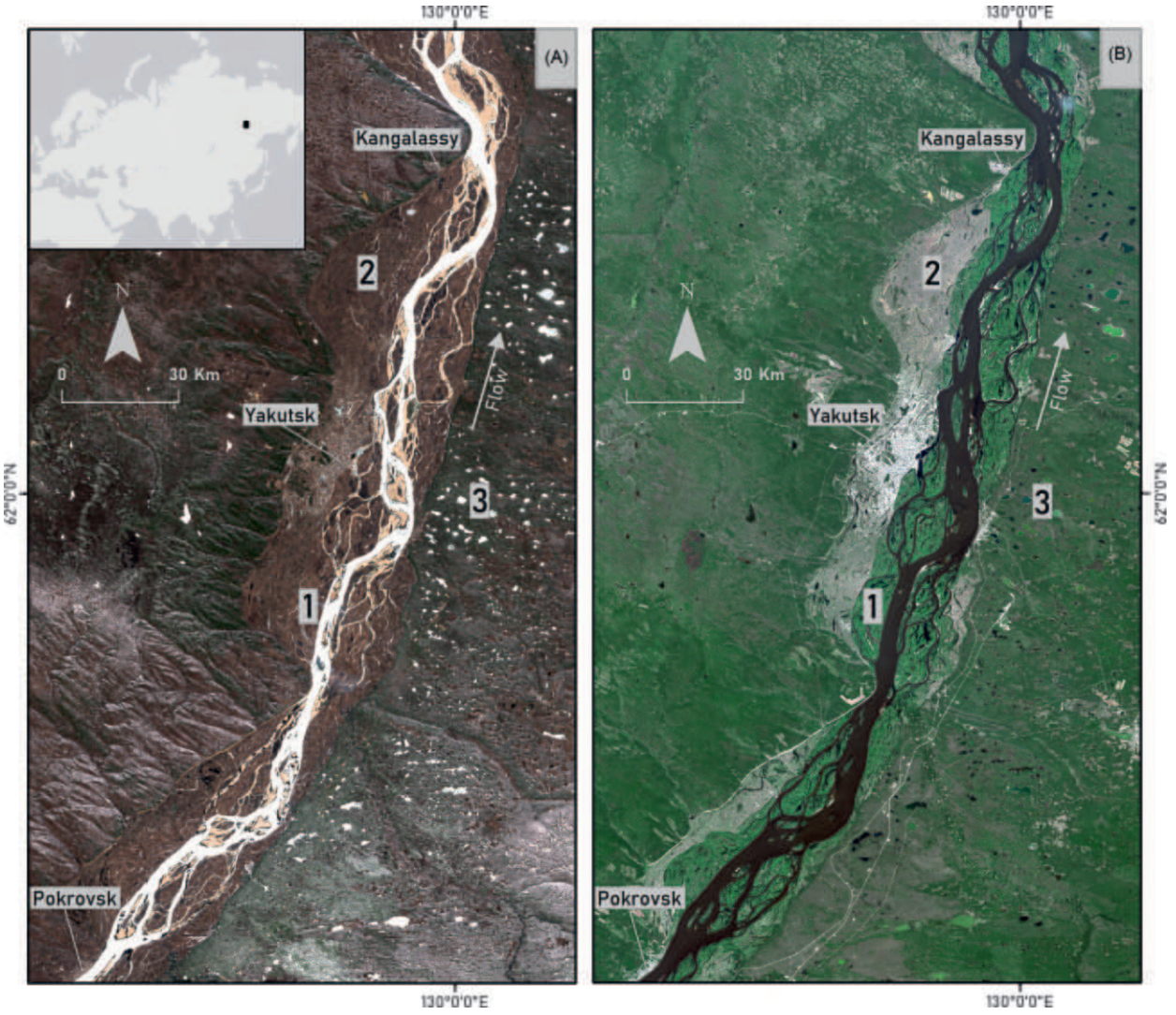

Fig. 7 Geomorphic diversity of wetlands on the anabranching Lena River and its valley. Background Sentinel-2 images from (A) 04 May 2020 and (B) 23 July 2020 A. 1. Lena River anabranching channel and floodplain. 2. River terrace. 3. Flat plain with thermokarst lakes. (A and B) differ in color due to the different spectral response of the Taiga forest in the transition between seasons. GEE platform.

damage and loss of floodplain wetlands, and alterations of the nutrient dynamics, among other factors. A substantial environmental impact is produced by dams that modify and regulate water flows and trap sediments in the reservoirs upstream of the barrages. It was estimated that dams reduced the global sediment yield to the world oceans by ~15% in the 20th century (Syvitski and Kettner, 2011). In some axial rives of east and southeast Asia, ~70% reduction in sediment flux from the major rivers to the Ocean has been documented in the last 1000 years (Wang et al., 2011), while in many large tropical African and South American rivers, water and sediment fluxes decreased because of recent human interventions (Latrubesse et al., 2021). In a few cases, sediment fluxes increased as a response to land-use changes (Latrubesse et al., 2021; Latrubesse and Sinha, 2021).

All these impacts are translated into loss and deterioration of fluvial wetlands worldwide. For example, in Central Europe, up to 95% of the floodplains have been restructured or destroyed (Werther et al., 2021). The situation is particularly critical in the tropics because tropical countries concentrated, during the last decades, the largest rates of deforestation and the maximum number of proposed dams to be constructed (Latrubesse et al., 2017; Latrubesse and Sinha, 2021).

Megafan wetlands are also being rapidly impacted and threatened. The Pantanal megafans and Okavango are natural world heritages and wildlife-protected sanctuaries, and the Chaco megafans also embrace multiple important wetlands, conservation areas, and Ramsar sites. However, all are under significant anthropogenic pressure, threatened by human settlements, cattle ranching, and agricultural activities that encroach and expand into the source basins and the megafans bodies, in addition to being impacted by waterways, channelization, and the multiplication of constructed and planned dams in their upper catchments. The upper catchments of the Pantanal, which source waters and sediments, are highly impacted by extensive soybean agriculture, while the megafan's depositional area supports cattle ranching. In the Chaco, deforestation accelerated in the recent decades

(Latrubesse, 2009). The native vegetation was replaced dominantly by soybean crops on extensive portions of the megafans. It negatively impacted the fluvial wetlands by artificial drainage, lack of connectivity, and desiccation.

But there is some hope, as society's perception on the relevance of fluvial wetlands for nature and environmental services is slightly changing across the world, and conservation and wetlands restoration are being promoted.

Final remarks

Fluvial wetlands enclose a variety of hydro-systems related to the geological and climatic settings of the rivers, their type of hydro-sedimentological conveyor (axial or megafans), channel patterns, and floodplains.

Braided rivers are restricted to medium-sized and small water discharge systems and do not create and sustain extensive wetlands. Their constrained plan-shape (channel-dominated corridor) and hydrogeomorphological characteristics (bedload dominant, high energy) are restraining factors in developing fluvial wetlands.

Meandering rivers are common on Earth, but only a small number of rivers with meandering patterns or sinuous branches (meandering-tendency to divide into branches) are part of the largest rivers in water discharge. Meandering rivers sustain mosaics of floodplains and related wetlands ecosystems and are a common planform at any scale.

However, for axial rivers, the most extended, widest, complex, most geodiverse, and most biodiverse fluvial wetlands on Earth belong to large anabranching alluvial rivers.

Megafans exhibit a variety of geomorphic types. The forming fluvial systems drain orogenic or cratonic lands, and the depositional fan areas spread on sedimentary basins and lowlands, holding a significant proportion of the global fluvial wetlands.

Fluvial systems are the main geomorphologic engine shaping the Earth, and fluvial wetlands in axial rivers and megafans are the main sediment continental sediment sinks of the planet. Although wetlands can be considered geomorphic systems, hydrogeomorphology has been relegated in the study and classification of river wetlands. We echo here the claim that understanding the genesis, functioning, and evolution of fluvial wetlands, incorporating hydrophysical processes, geospatial analysis, and geomorphologic time scales in wetland research and classification is not just desirable but a need. Fluvial wetlands are rampantly destroyed globally, and geomorphology is a fundamental tool for defining conservation areas, assessing impacts, and designing management and restoration plans in wetlands.

Acknowledgments

We thank Edward Park for his assistance in the processing of Fig. 3, Pilcomayo River megafan, and Florian Wittmann and Thomas Mehner for the constructive review.

See Also: Human pressures and management of Inland Waters: Hydromorphology: Overview and Assessment Methods; Physical Impacts of Sand Mining in Rivers and Floodplains; Structures and functions of Inland Waters - Groundwater: Groundwater – Global Abundance and Distribution; Structures and functions of Inland Waters - Rivers: Effects of Dams on Rivers; Hydrology and Classification of Rivers for Management; Structures and functions of Inland Waters - Wetlands: Mountain Rivers: A Global Overview of River Channel Forms, With a Focus on Braided Rivers; Patterns in Freshwater Fish Diversity; Wetland Plants: Adaptations, Classification, Ecology and Distribution; Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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The Landscape Role of River Wetlands

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Glossary

Alpha-diversity Species diversity at a local site.
Beta-diversity Or "absolute species turnover" (β), is the compositional differentiation among habitats.
Disjunct (species) distribution Two or more groups of related species that are considerably separated from each other geographically (i.e., through habitat fragmentation).
Gamma-diversity The total species diversity in a landscape.
Hypertrophied lenticels Loosely connected cells on the epidermis of different plant organs (stem, petiole, fruits) that always remain open and permit the exchange of gases (i.e., oxygen) between the environment and the internal tissue spaces of organs.
Invasive species Introduced organisms that become overpopulated, adversely affecting its new environment, causing ecological, environmental, or economic damage.
Pneumatophores Lateral (aerial) roots that extend out of the water surface and facilitate the exchange of oxygen and carbon dioxide with the atmosphere.
Trophic level The position an organism occupies in a food web.
Vicariance Fragmentation (splitting) of a landscape that divides a larger population into isolated subpopulations.

River wetland environments

Physically, riparian zones and river wetlands are distinguished environmentally from adjacent uplands in three important ways: (1) the episodic, seasonal or permanent presence of surface water and its interaction with ground water (2) the transport, deposition, and remobilization of alluvial substrate and nutrients and (3) the provision of special microclimates. Ecologically, linear watercourses are considered "open ecosystems," where any point along a water course is influenced by the environmental and biotic settings of upstream river sections, while these, in turn, influence rivers downstream. This longitudinal ecological connectivity and dependency over large geographic areas (i.e., river continuum concept, Vannote et al., 1980), combined with the transversal interactions with adjacent uplands (i.e., flood-pulse concept, Junk et al., 1989) result in a highly complex system where wetland organisms are influenced by multiple ecological gradients. Combined, the physical and ecological settings in river wetlands have strong controls on how biological communities are organized in time and space. In the following, the environmental settings of riparian areas and river wetlands are outlined, and examples on how they influence the landscape and biota are subsequently presented.

Water retention and hydrology

Wetlands cover approximately 12.1×10^6 km^2 of the global land surface (Davidson et al., 2018), emphasizing their importance for landscape ecology. As all life forms depend on water, it's presence on the land surface is an attracting force for many organisms, in particular where rainfall is permanently or seasonally limited. However, all surface waters undergo water-level fluctuations that can result in temporary flooding of larger areas, which results in considerable fine-scale wetland heterogeneity and consequently shapes the organization of biological communities.

River wetlands play an important role in regulating aquifers through groundwater-surface water exchange (Winter, 1999; Sophocleous, 2002; McLaughlin and Cohen, 2013). The groundwater recharges when surface waters are abundant and high, and river wetlands provide the base flow of streams and rivers in times of short rainfall. At low discharge, rivers flow in well-defined channels, while at high water levels, large floodplains maybe formed by lateral overflow and inundation. The ground water is important for a range of invertebrate communities inhabiting it (i.e., Boulton et al., 2008), but it is also a critical water source for many terrestrial plant species.

Water level fluctuations of rivers depend primarily on climate (mainly amount and variability in rainfall and temperature), geology and geomorphology (i.e., size of the catchment area, elevation, slope, permeability, pore volume of rocks and substrates), vegetation (transpiration, modification of infiltration), and anthropogenic alterations (water deviation, flow regulation, dams). Surface waters of streams maybe permanent, as in many temperate and tropical climates, or periodic, as in subtropical arid climates or in cold climates where the ice cover persists during parts of the year. Episodic inundation regimes prevail in desert and steppe climates with unpredictable rainfall events.

Stream order and basin size are important variables influencing water-level changes. Low order streams collect rainfall from small catchments and thus are mostly characterized by irregular food pattern. With increasing catchment area, local precipitation becomes less important in defining the hydrological regime (Junk et al., 1989). Rather, the regimes of lower courses of large rivers are determined by basin-wide climate that drives rainfall seasonality throughout its catchment. In tropical and subtropical latitudes (pluvial regimes), precipitation seasonality is often pronounced, and most tropical large rivers typically present a unimodal flood regime, with one high and one low water period during the year. Exceptions are rivers with catchment areas in the two hemispheres; these may present a bimodal flood pattern, such as the upper Negro, Magdalena and Zaire Rivers. In cold and temperate climates, stream and river hydrology is strongly influenced by the accumulation of water as snow or ice during winter and its melting during warm seasons (glacial or nival regimes), as well as by the timing of the vegetation period and evapotranspiration rates through the annual cycle. Flood regimes are mostly complex and polymodal, with several high and low water phases during the year, and, in regions that lack a clear climate seasonality, less predictable.

At the lower courses of large rivers, floodplains may extend to thousands of square kilometers. With increasing size of the floodplain, the rate of rising water levels is slow, but the period of inundation increases. The complex interaction of floods and terrestrial variables influencing the distribution of organisms and biological processes in large-river floodplains provide multiple environmental gradients that are difficult to disentangle. The timing of hydrological regimes with climate seasonality is crucial for the composition and productivity of plants and animals. For example, when local precipitation at low river water levels is comparatively high, floodplains are usually densely forested, such as in the tropical Amazon and Congo, and subtropical Mississippi. Conversely, when precipitation during low river water levels is low, floodplains are mostly dominated by herbaceous species while forests are restricted to the mesic environment of riparian areas and river wetlands, such as in many rivers in tropical and sub-tropical savanna climates (i.e., Paraguay, Paraná, Zambezi Rivers).

The ecotone of aquatic to terrestrial environments is named the aquatic-terrestrial transition zone (ATTZ, Junk et al., 1989). The ATTZ encompasses the transition from strictly aquatic to strictly terrestrial. The boundary between terrestrial and riparian ecosystems coincides with the lower elevation limit of terrestrial plants that do not tolerate inundation (Nilsson et al., 1993), while the boundary between riparian and aquatic ecosystems coincides with the upper elevation limit of strictly aquatic and semi-aquatic plant species (Nilsson et al., 1993; Naiman and Décamps, 1997). However, when water-level changes amount to several meters and seasonally inundate floodplains of hundreds of kilometers, such as in many tropical large-river floodplains, the aquatic-terrestrial ecotone might bridge entire landscape units or ecosystems (Junk et al., 2015).

As all surface waters undergo water-level fluctuations, the ATTZ is constantly subject to spatio-temporal movements across rivers, riparian areas and floodplains ("moving littoral" sensu Junk et al., 1989). Classical limnological or morphological features describing the typical habitats of shorelines become time-dependent, and this time-dependency is important because it affects the life-cycles and productivity of plants and animals. For example, increasing water levels expand the habitat for aquatic animals, but reduce habitat for terrestrial species intolerant to floods.

While terrestrial animals can move and therefore potentially avoid changing water levels, sessile plants cannot. The latter are therefore often better indicators of wetlands because they need to develop specific adaptations to changing hydrological environments. Numerous adaptations and functional life-history traits of plant species are specifically related to inundations and related disturbance. Adaptations to flooding include physiological, morphological and biochemical traits to avoid oxygen deficiency during the waterlogged period. Riparian and floodplain trees, for example, reduce their metabolism during flooded conditions, which results in decreased photosynthetic rates, and reduced wood and shoot growth (Worbes, 1986; Schöngart et al., 2002; Parolin et al., 2010). Further adaptations include partial or complete leaf shedding with the onset of flooding, the formation of adventitious roots and/or specialized roots such as pneumatophores, increased root biomass during flooding, the formation of hypertrophied lenticels on roots and stems, the formation of root aerenchyma, the induction of activity of fermentative enzymes under anaerobic conditions, as well as the production of elevated levels of anti-oxidant compounds (i.e., Wittmann and Parolin, 2005; Parolin, 2009; Kreuzwieser and Rennenberg, 2014). In addition, specific acclimations such as the timing of seed dispersal (Van Splunder et al., 1995), seed dispersal by river waters and aquatic dispersers, and enhanced germination rates of seeds in dependence of its contact with river waters are especially common in species subject to a regular flood pulse (i.e., Kubitzki and Ziburski, 1994; Oliveira Wittmann et al., 2007; Correa et al., 2015). Lastly, the degree of acclimations and adaptations in a riparian community defines the usually well-developed zonation of species along the gradient of flood frequency and duration, and thus directly influences on the composition and richness of communities (Wittmann et al., 2006, 2010).

Geomorphic disturbance

Geomorphic disturbance along streams and rivers is another phenomenon that importantly influences landscapes and vegetation communities mainly through alternating cycles of destruction, recolonization, vegetation succession, and floristic recombination. Slip-off and undercut slopes, swales and ridges, point bars and islands are important alluvial landscape patches of varying hydro-geomorphologic disturbance. Lateral river bed migration, in addition, creates abandoned secondary channels, lakes with varying connectivity to the main river channel, and fluvial terraces with varying connectivity to surface and ground waters. Locally varying hydraulic forces sort deposited grains by size and weight, influencing pore volumes, soil aeration, and the water retention potential of the substrate (i.e., Wittmann et al., 2010). The type and rate of geomorphic disturbance varies with a range of environmental factors, such as climate (mainly rainfall amount and seasonality), slope and hydraulic force, bedrock type, as well as sediment transport and cohesion, and importantly interacts with the vegetation cover and type along riparian areas and in floodplains. The notion of the integration of fluvial geomorphology and riparian plant ecology is the basis for important ecological concepts, where river ecological functioning is conceptualized in four dimensions: longitudinal, transverse, vertical, and temporal ("fluvial hydrosystem", Amoros et al., 1987; Ward, 1989). The "river continuum concept" (Vannote et al., 1980), the "flood-pulse concept" (Junk et al., 1989) and the concept of "aquatic-terrestrial ecotones" (Naiman and Décamps, 1997) also consider different aspects of interactions of hydro-geomorphic disturbance with longitudinal (i.e., from upper to lower river sections) and transversal (from rivers to floodplains) biotic processes.

When slopes are steep (i.e., mountain bedrock channels), hydraulic force combined with mass movements and very coarse substrates strongly limits plant establishment in the mostly small riparian zone. The geomorphic system is exclusively driven by interactions of flow regimes and sediment properties leading to the total destruction of previously established vegetation communities through fluvial landform remobilization (Corenblit et al., 2007). After catastrophic high water events, this "geomorphic phase" (Corenblit et al., 2007) in vegetative succession may lead to floristic recombination (Tabacchi, 1995). Notably, plants establishing in these dynamic riparian zones need to overcome several stressors, such as the complete absence of humus and soils, extreme shear stress through water flow and water-transported material (i.e., gravel), highly variable water levels, and, because of the lack of a close vegetation cover, full solar radiation (Fig. 1). In addition, low temperature and snow and ice cover at high elevations or high latitudes form additional stressors (i.e., Walker and Hudson, 2003).

Downstream, the riparian and floodplain vegetation increasingly influences stream and river geomorphology (i.e., Tabacchi et al., 2000; Wittmann and Parolin, 2005; Gurnell and Petts, 2006; Gurnell et al., 2012). Allogenic succession, which is solely controlled through abiotic factors, such as physical disturbance, increasingly shifts to autogenic pathways, where positive and negative interactions among plants prevail (Van Andel et al., 1993; Wittmann and Parolin, 2005). In this "biogeomorphic phase" (Corenblit et al., 2007), flexible (i.e., herbaceous species) and stiff vegetation (i.e., tree species) promote flow resistance and favor the deposition of transported material, organic matter, and nutrients. By modulating matter and energy fluxes, riparian plants

Fig. 1 Lech River, Austria. Braided gravel-bed rivers in mountain areas may undergo catastrophic river bed changes during a single high-water event and destroy previously established vegetation communities. Plants establishing in these dynamic riparian zones need to overcome several stressors, such as highly variable water levels, the absence of humus, extreme shear stress through water flow and water-transported material, full solar radiation, and seasonal snow and ice cover.

Fig. 2 Two examples of vegetative succession along river banks. Above: Amazon River, central Brazilian Amazon, with the macrophyte species *Paspalum fasciculatum* (front) and the tree species *Salix martiana* (back). Below: Danube Delta, Romania, with the macrophyte species *Phragmites australis* (front) and the tree species *Salix alba* (back). Following the differential influence of frequency, height, and duration of annual floods and associated geomorphic variables, such as fluvial erosion, sedimentation rate, and deposited grain sizes, sharply delimited successional pioneer stages establish. These trap further sediment, locally increase the accumulation of organic material and modify further environmental parameters, such as flood duration, solar irradiance, and water retention capacity of alluvial soils, facilitating the establishment of secondary species, which in turn are replaced through late-successional species.

impact fluvial landform dynamics (Gurnell et al., 2012; Gurnell, 2014). Riparian plants also modify physical and chemical substrate properties by means of roots, interaction with bacteria (i.e., Doty et al., 2005) and mycorrhizal fungi (i.e., Beauchamp et al., 2006), as well as nutrient uptake and the release of organic matter and exudates (Corenblit et al., 2015). In addition, they strongly influence local microclimates, including humidity, light regimes and temperature in the river-floodplain system (i.e., Tabacchi et al., 2000; Wittmann and Junk, 2003) (Fig. 2).

Adaptations to geomorphic disturbance are usually those that enable plants to withstand mechanical stress, excavation and burial (Gurnell, 2014). The first colonizers on bare substrates exhibit a range of traits related to reproduction, germination and growth. Seeds are usually small and light and dispersed by wind and water, and the time of dispersal is mostly attuned to river high flows (i.e., during winter and spring in temperate regions) and the presence of bare moist substrates for establishment after water-levels decrease (i.e., Guilloy et al., 2011). Many pioneers also combine sexual with asexual reproduction by means of resprouting from plant segments (i.e., branches, roots). Adaptations to flow regimes and shear stress are flexible stems, extensive below- and aboveground root systems, and the capacity to develop new secondary root layers close to the surface in areas prone to sediment burial (i.e., Wittmann and Parolin, 2005) (Fig. 3).

Sediment and nutrients

Because water courses transport bedload and suspended material over long distances, their riparian zones and floodplains often create "azonal" edaphic conditions that contrast soils developed in situ from local bedrock (Wittmann et al., 2017). Best examples are rivers that originate from tectonically uplifted regions, such as the mountain ranges of the Alps, Andes, Hindukush, Himalaya and Rocky Mountains. Rivers originating from relatively young orogeny may introduce fertile sediment with relatively un-weathered clay minerals of high ion exchange capacity into older geological formations where local weathering processes have decomposed and lixiviated underlying rocks. Even low-order rivers that develop on the same geological basement as surrounding terrestrial landscapes promote this azonal environment to a certain degree because the erosive material laterally introduced through denudation (wash load) derives from the entire catchment and thus concentrates a wider geographic range of sediment and nutrients in the linear discharge and transported alluvium.

Organic matter, either in its particulate form (POM), or dissolved (DOM) originating from the riparian zone is a further important nourishment for both, aquatic and semi-aquatic organisms (Vannote et al., 1980; Naiman and Décamps, 1997). While POM mainly derives from litter fall and—to a smaller degree—from lateral transport of litter to streams, DOM originates either from direct litter fall, lateral movements, groundwater base flow or seepage from fringing wetlands (McClain and Richey, 1996; Naiman and Décamps, 1997). Litter decomposition releases important nutrients to soils during the growing seasons. The sediment trapping through plants has an important effect on the accumulation of nutrients in riparian zones and floodplains. Plant uptake results in a short-term accumulation of nutrients in non-woody biomass and a long-term accumulation in woody biomass (Naiman and Décamps, 1997). Nutrient uptake may be enhanced in many wetland plants under low-oxygen conditions, and particularly N and P uptake might be several fold higher in wetland than in strictly terrestrial plant species (i.e., Hosner et al., 1965; Peterjohn and Correll, 1984; Cooper, 1990). Most riparian areas and wetlands, in particular those with organic soils, also show exceptional rates of either nitrification (i.e., Kern and Darwich, 1997; Kern et al., 2010) or denitrification (i.e., Alldred and Baines, 2016).

Fig. 3 Burial of trees by sediment is a common stressor in sediment-rich floodplains to which trees adapt through the formation of secondary root layers near the surface (i.e., Wittmann and Parolin, 2005). When the alluvium is composed of fine grains, topsoils crack during the low-water phases providing aditional stressors by the rupture of fine roots.

Elevated fertility in river floodplains may be one of the most important ecosystem services for humans, as it is widely held to be associated with the rise of human civilization along the Nile, Euphrates, Tigris, and Indus Rivers (Hammerton, 1972; Boulé, 1994), allowing for intense agriculture (Gopal, 2013) and the domestication of animals (Junk, 2002). High fertility also translates into fast plant growth and the comparatively high primary productivity of many nutrient-rich wetlands, which are among the most productive ecosystems on the globe. In Amazonian várzea floodplains, net primary productivity—the total amount of carbon (i.e., wood biomass increment + litter fall) fixed from the atmosphere for the biochemical construction of new aboveground organic matter per time unit (Chambers et al., 2001)—is extraordinarily high. In várzea forests, aboveground net primary productivity (ANPP, dry mass) ranges from 31.8 Mg ha^{-1} $year^{-1}$ in a 50-year-old secondary stage to 13.3 Mg ha^{-1} $year^{-1}$ in a 240-year-old late-successional stage (Schöngart et al., 2010), which is about 2–3 times higher than ANPP in surrounding upland forests and one of the highest reported ANPP on Earth. In herbaceous areas, however, primary productivity is even higher, measuring 70–100 Mg ha^{-1} $year^{-1}$ for the grasses *Paspalum fasciculatum* and *Echinochloa polystachya* (Piedade et al., 1991).

Microclimate

Wetlands importantly regulate local and regional temperatures because of the groundwater-surface water exchange, which buffers surface waters from high or low temperatures, and the effect of evapotranspiration and latent heat exchange from water and wetland plants. Mainly, the transformation of water from aqueous to gaseous phases resulting from evaporation of surface waters or transpiration from leaf surfaces releases energy, and cools the local surrounding. In any landscape, wetlands therefore provide a microclimate-regulation service (McLaughlin and Cohen, 2013) alleviating heat island effects through water availability, often linked to dense riparian or floodplain vegetation (Drexler et al., 2004) and the advection of sensible heat (Spronken-Smith et al., 2000). Besides being a significant factor in a wetland's water budget (i.e., Gilman et al., 1998; Gardner, 1991), high evapotranspiration rates of wetlands thus provide a cooling effect, which is especially pronounced in forested wetlands, where transpiration dominates evapotranspiration fluxes (Law et al., 2002).

Implications for landscape ecology

Corridor function

Rivers and their riparian zones and wetlands represent important ecological corridors for a wide range of organisms. Aquatic and wetland plants generally disperse both up and down riparian corridors (Naiman and Décamps, 1997) through the dispersal of diaspores or vegetative fragments. Because rivers flow from high to low elevation, and in addition connect different catchment areas, diaspore dispersal may cover large distances and different climate zones (Naiman et al., 1993) in relatively short time. Surface waters provide connectivity over large geographic ranges and many wetland plants make use of dispersal through water (hydrochory) or aquatic dispersers (i.e., ichthyochory). In Amazonian floodplains, the fruiting phenology of many tree species is timed to the annual flood cycle with many tree species maturing and shedding fruits at high water (Kubitzki and Ziburski, 1994). After dropping into the water, seeds may float during periods of up to 2 months. Seed buoyancy or submergence increase the distance of dispersal by river waters and enhance the probability of dispersal by fish and other aquatic organisms (Goulding, 1980). Moreover, seed dormancy is broken by exposure to river water (i.e., Oliveira Wittmann et al., 2007), thus seeds germinate as soon they land on substrates as water-levels recede.

The consumption of fruits and seeds by fish has been documented in approximately 200 freshwater fish species and more than 800 plant taxa (Correa et al., 2007), mostly occurring in—but not restricted to—tropical regions (i.e., Amazon, Congo, Mekong, Niger, Chad and Nile Rivers). Fish interactions with flowering plants are likely as old as 70 million years in some tropical regions, pre-dating most modern bird-fruit and mammal-fruit interactions, and contributing to long-distance seed dispersal and the radiation of early angiosperms (Correa et al., 2015).

Rivers that cross different climate zones are particularly important as migration corridors for many wetland and drought-sensitive terrestrial organisms and thus exert a fundamental role in landscape ecology and maintenance of biodiversity by sustaining biogeographic connections across humid biomes separated by otherwise inhospitable dry climates (i.e., Oliveira-Filho and Ratter, 1995; Wittmann et al., 2017). For example, many drought-sensitive tree species from Amazonian wetlands are able to track favorable wetland microclimates and expand their distribution ranges into tropical savannas (i.e., Cerrado and Caatinga), particularly along N-S oriented rivers, such as the Xingu and Araguaia (Wittmann et al., 2017). Similar biogeographic exchanges were reported for tree species of the Brazilian Atlantic rainforest that extend their distribution ranges towards the South American Cerrado, and the subtropical Pampas through riparian corridors (i.e., Oliveira-Filho et al., 2015).

Because many terrestrial animals depend on surface waters, the corridor function of rivers is not restricted to aquatic and wetland organisms. Many terrestrial vertebrate species strongly depend on habitat and resources from wetlands, which provide refuges from annual droughts, or seasonal low temperature at high latitudes and altitudes. For example, plant zonation along flood frequency and duration gradients across tropical Africa provide a temporal resource heterogeneity for herbivores, which graze on floodplain peripheries in the early dry season, but migrate to deeper floodplains and swamps during the late dry season and during droughts (Fynn et al., 2015). Many water and shore birds migrate annually between breeding grounds and wintering areas, and tropical/subtropical rivers that cross different climate zones are particularly important as corridors along which they are able to migrate (Sparks, 1995).

Species and habitat diversity

River wetlands host among the highest numbers of taxa in many animals, including planktonic and benthic communities, aquatic and terrestrial invertebrates, and aquatic and terrestrial vertebrates that live in or are highly dependent on rivers and wetlands. For benthic invertebrates, habitat diversity is especially high along the upper river courses, where river bed geomorphology is most diverse. Most invertebrates of river wetlands have relatively short life cycles, which allows their rapid occupation of the new sites provided by fluctuating water levels and river dynamics (Irmler, 1981). Many invertebrates also migrate or drift in the water to new sites (Junk and Robertson, 1997). In seasonal wetlands, life cycles of most invertebrates are tightly coupled to the hydrological cycle, with examples from Mediterranean climates (i.e., Cañedo-Argüelles and Rieradevall, 2011), semiarid climates of the United States (i.e., Hall et al., 2004), Amazon floodplains (Adis and Messner 1997; Adis and Junk, 2002) and the Brazilian Pantanal (Wantzen et al., 2016).

Globally, the freshwaters of rivers, floodplains and lakes harbor approximately one third of all vertebrates and nearly half of all fish species (Balian et al., 2007; Vega and Wiens, 2012). In addition, river wetlands also provide food and habitat for a range of terrestrial, deep water and bird species, including those that migrate to spawning and feeding areas (i.e., fishes), escape from seasonal drought (i.e., herbivores in savanna regions) or escape from low temperatures at high latitudes (i.e., migratory birds) (Welcomme, 1985; Sparks, 1995; Junk, 2007; Fynn et al., 2015). In all examples, water-level changes of wetlands are likely to influence the diversification of habitat specialists, either directly through the availability of water, or through the provision of habitat and high primary productivity of their vegetation cover.

Hydrological cycles in wetlands as well spur the evolution of plant species. Many wetland plants, for example, time their reproductive cycles to the flood pulse, and it is likely that over time this leads to speciation. In the Amazon basin, where flood pulses are high and prevalent since at least the Paleocene, many endemic tree species evolved in large-river floodplains (Wittmann et al., 2010, 2013). Endemic tree species in other wetlands are scarce, because climate changes during the past led to repeated drought or wet cycles that interrupted the formation of flood-specific adaptations and species. However, many wetlands of the globe host endemic herbaceous species, that are more likely to evolve over relatively shorter time scales because generation cycles are faster (Sculthorpe, 1985).

From riparian areas to large-river wetlands, the attraction of organisms to mesic environments increases with increasing drought (Wittmann et al., 2017). Therefore, river wetlands are the most species-rich environments in many arid climate zones, including tropical and subtropical savannas, but also continental boreal and subarctic steppes. In subtropical and tropical regions, riparian areas represent forest refuges within landscapes dominated by open savannas (Meave et al., 1991). Ground water availability in riparian areas contrasts the soil water deficiency that characterizes most of the savanna landscape. Impacts of seasonal drought and fire frequency are reduced (i.e., Felfili, 1995; Kellman and Meave, 1997) (Fig. 4). In per-humid, tropical forested landscapes, wetlands might be poorer in species than ecosystems of adjacent uplands. Here, variable periods of waterlogging and inundation act as an important environmental filter (i.e., Householder et al., 2021), selecting for species with specific adaptations to seasonal or permanent hypoxic conditions.

Fig. 4 Lower Miranda River, Brazilian Pantanal. Riparian areas contrast the soil water deficiency of the surrounding savanna landscape and are less affected by seasonal drought and fire activity—therefore, they often represent the most species-rich communities in tropical and sub-tropical savannas.

Independent of the climate zone, hydro-geomorphic activity provides a myriad of ecological niches along the flood-level and geomorphic disturbance gradients (i.e., Peixoto et al., 2009; Junk et al., 2012) (Fig. 5). Together with changing topographies, alluvial landforms may change at small geographic scales. High habitat diversity translates into high beta-diversity. According to the degree of adaptations developed by organisms to the disturbance provided by the interaction of hydro-geomorphic gradients, sharply developed zones of biotic communities (i.e., successional stages) develop. It is this patchwork of biotic communities that increases beta-diversity and frequently leads to exceptional species richness of riparian zones and floodplains compared to terrestrial landscapes. In their worldwide review on the comparative species richness of different taxonomic groups between terrestrial and riparian habitats, Sabo et al. (2005) reported that riparian zones increase regional species richness by harboring different, not necessarily more, species. The authors conclude that riparian habitats increase regional gamma-diversity across the globe by more than 50% on average, and thus suggest that conservation planners can easily increase the number of species protected in a regional portfolio by simply including a river within terrestrial biodiversity reserves.

The contrasting fertility of the alluvium compared to terrestrial landscapes represents a further attractive force to many organisms, and increases beta-diversity at the landscape scale. Nutrient-rich alluvial soils may represent vectors of range expansion in otherwise adverse landscapes of poor nutrient conditions. White-water river floodplains (várzeas) of the Amazon, for example, contain large populations of tree species that are nearly absent elsewhere in the Amazon, but dominant upon nutrient-rich soils of the tropical Andes and central America (Wittmann et al., 2010; Fig. 6). The disjunct distribution of these species are an important floral component in the Amazon contributing to elevated gamma-diversity.

The resetting of vegetation succession and the varying response of plants to differences in flooding, shear stress, sediment texture, and soil development and age has important biotic effects. Vegetation resetting constantly provides habitats for early-successional (i.e., pioneer) species, which are inhibited from competitive exclusion through dominant, late-successional species (i.e., Sedell et al., 1990). Moreover, most rivers provide a patchwork of environmentally differentiated habitats for both, early-successional species (i.e., at slip-off slopes) and late-successional species (i.e., on opposing undercut slopes) at relatively small spatial scales, enabling their coexistence within the same landscape. These functional groups contrast in resource allocation for growth (early successional stages) and survival (late-successional stages) (i.e., Grime, 1977; Pickett and Cadenasso, 2005) and therefore also profoundly affect landscape spatial patterns of resource availability for all organisms at higher trophic levels.

Lastly, while adaptations to environmental stressors such as flooding can lead to speciation of wetland organisms, large rivers may also represent physical distribution barriers for strictly terrestrial species and thus directly influence the beta-diversity of landscapes. In the Amazon, large rivers are thought to be the divisors for a range of terrestrial species, such as primates (Wallace, 1852; Boubli et al., 2015), lowland birds (Haffer and Prance, 2001; Ribas et al., 2012), lizards (Ávila Pires, 1995), butterflies (Hall and Harvey, 2002), and terrestrial woody plant species (Prance, 1982). In fact, the several recognized areas or "districts of endemism" in the Amazon basin are sharply divided by major rivers, which might have favored vicariance in numerous terrestrial species groups (Silva et al., 2005).

Fig. 5 Mamirauá Sustainable Development Reserve, between the confluence of the Solimões and Japurá Rivers, western Brazilian Amazon. Sediment-rich large-river floodplains (várzeas) often create a large number of ecological niches and increase the habitat diversity of landscapes by the creation of fluvial landforms such as ridges, swales, secondary channels, slip-off and undercut slopes and lakes of varying hydrological connectivity, which have differential influence of floods, hydraulic energy, geomorphic dynamics, topsoil grain size distribution, and ecological connectivity to both wetlands and uplands.

Fig. 6 Fluvial island in the Japurá River, central Brazilian Amazon, during the low-water season. Freshly deposited substrates incur environmental constraints for plant colonization, such as high solar radiation, high soil temperature, and low water retention capacity of alluvial soils, providing edaphic drought for colonizing plant species. Nevertheless, these conditions attract pioneer species, such as annual grasses, perennial herbaceous and also specialized woody species that are poorly competitive in the adjacent, strictly terrestrial environment, which in this landscape is nutrient-poor and vegetated by dense rainforest. The pioneer species in Amazonian floodplains are adapted to the higher fertility of alluvial substrates and therefore often display disjunct distribution in non-forested biomes of higher fertility, such as the higher elevations of the Andes, central America, and tropical savannas.

Refugia

Refugia are areas in which a population can survive through an extended period of unfavorable conditions. The relatively high water availability, habitat diversity, fertility and the provision of special microclimates is widely held to have provided important refugia for numerous plant and animal species throughout Earth's evolutionary history. For example, the cooling effect is interpreted as a principal driver for the persistence of disjunct distributions of boreal/alpine species in temperate wetlands, leading some ecologists to refer temperate wetlands as "interglacial climate refugia" (Frederick, 1974; Nekola, 1999). Refugia experience buffered climates and support species preferring cooler environments than surrounding regions (Barnosky, 2008; Ashcroft, 2010; Raney et al., 2014). In another example, Amazonian peat swamps were found to harbor taxonomic compositions appearing to be 1050 $\pm$ 391 m above their actual elevations due to a high abundance and number of families with high elevation optima (Householder et al., 2015). Similar findings originate from Amazonian várzea forests, where up to 20% of flood-tolerant tree species of lowland Amazonia were reported to occur at elevations >3.000 m along the Andean slopes (unpublished data F. Wittmann). While all these examples suggest temperature as determinant of wetland refugia, high relative water availability in river wetlands is likely the most important factor for the persistence of species in refugia, especially in landscapes subject to adverse climates with seasonal or permanent water scarcity (McLaughlin and Cohen, 2013). For example, in the Amazon basin, large-river wetlands are interpreted as one of the most prominent forest refuges for rainforest tree species diversity during drier climates of past glacial periods—the large Amazonian rivers were too large to dry out, preventing drought-sensitive rainforest tree species from regional extinction (i.e., Wittmann et al., 2013, 2017). Water availability in mesic riparian habitats and river wetlands may be loosely coupled to rainfall and therefore buffered from climate change (McLaughlin and Cohen, 2013). Limiting conditions, including elevated temperatures, increased drought, and soil nutrient deficiency, are all less pronounced in river wetlands, emphasizing their function in the provision of species refugia in terrestrial landscapes.

Consequences of habitat destruction and fragmentation

While any human influence on the hydrological cycle affects the ecological integrity of wetlands, the most dramatic effects of wetland degradation on catchments and terrestrial landscapes originate from deforestation, water deviation and flow regulation through channel rectification and damming. These activities directly influence fluvial processes that sustain their landscape functions, and also affect groundwater levels and as such the capacity of wetlands in their retention and release of water to landscapes. A disturbed water balance and buffering capacity of a wetland reduces its capacity to mitigate climatic extremes, which increases the probability of more frequent and more intense catastrophic drought and inundation events.

Globally, riparian zones and floodplains of an increasing number of rivers are affected by flow alteration through land drainage, water deviation, channel rectification, river impoundment, and the construction of reservoirs. Lehner et al. (2011) estimate that 7.6% of the world's rivers with average discharge >1 m^3 s^{-1} are affected by dams, while this number increases to more than 46% in large rivers (discharge >1000 m^3 s^{-1}). The highest degrees of river regulation were reported for North-America (38% of all rivers), followed by Europe (30%), Australia, Africa and Asia (16–19%), and South America (approximately 9%). Only for European rivers, Belletti et al. (2020) reported approximately 1.2 million instream barriers in the rivers of 36 European countries.

Channel rectification is one of the most prominent reasons for floodplain loss and degradation in European rivers, and also has far-reaching effects for catchment areas. Formerly multi-branched or braided rivers were linearly confined. As a consequence, river channels dispose of higher water energy and tend to incise their channels. Channel incisions lead to lowered ground water levels, affecting moist-dependent plants and invertebrates, which are more and more replaced by strictly terrestrial species. In addition, floodplains along rectified channels are flooded less frequently, because inundations are mostly restricted to extreme high-water events. While coarser sediment, such as gravel and sand, is transported by high water velocities of confined channels, the sediment deposited in rectified channel-floodplains is mostly fine (silt and clay). This leads to silting up and homogenization of sediment and alluvial soil types in floodplains. Many plant and animal species that inhabit coarser sediment of dynamic floodplain environments are replaced by generalist species, leading to species losses and even regional extinction in numerous examples. Rectified channel floodplains also show modified gradients of lateral connectivity, negatively affecting many macroinvertebrates (i.e., Paillex et al., 2007), and consequently aquatic and terrestrial food webs. Rectified channel-floodplains are especially prone to the colonization by invasive species, which reduce local biodiversity through habitat occupation, the introduction of pathogens and diseases, and lead to genetic erosion (i.e., Aguiar et al., 2001; Bunn and Arthington, 2002; Stromberg et al., 2007).

The impact of dams, barriers, and impoundments is particularly dramatic in lowland rivers. Modified flood regimes, sediment and nutrient trapping, and the loss of hydro-ecological connectivity significantly affect the flora and fauna of dammed rivers well beyond the limits of the artificial reservoir. Floodplains located downstream of barriers usually experience higher low water levels and lowered high water levels compared to pre-dam conditions, which leads to dramatic plant species losses at both the highest and lowest floodplain topographies ("sandwich-effect" sensu Wittmann et al., 2019). Species losses may occur along river stretches up to hundreds of kilometers downstream from a dam, as shown for central Amazonia (Assahira et al., 2017; Schöngart et al., 2021), and the Paraná River (Junk et al., 2021). The loss of wetland-specific plant species influences the provision of habitats and food sources of numerous animal species, cascading down to fish communities and thus also affecting the food chain of terrestrial vertebrates. Agostinho et al. (2008) have shown, that the several dams established at the Paraná River in south-western Brazil affected more than 80% of all native fish fauna, leading to a replacement of ecologically specialized species through generalist species. Sediment and nutrient trapping through river dams in addition lead to the transformation of the physico-chemical water properties (i.e., water temperature, pH, electrical conductivity), with often dramatic consequences for invertebrate and vertebrate communities. Ultimately, these changes also affect marine biogeochemical processes, salinity levels, food webs, and consequently biodiversity (i.e., Krumins et al., 2013), in particular in estuaries, deltas, and other terrestrial-marine transition zones.

Combined, the cumulative impacts of flow regulation, damming, and water deviation of river wetlands is exacerbated through climate change. The relatively dry summers and autumns in Central Europe in 2018–2020 resulted in exceptional low water levels of rivers such as the Rhine, Danube and Elbe and caused unprecedented lowered groundwater levels, causing a mass mortality of tree species in southern Poland, Czechoslovakia, Germany and France, particularly of the native genera *Picea*, *Pinus*, *Fagus*, and *Quercus* (Petit-Cailleux et al., 2021). Streamflow lows are increasing in magnitude and frequency in central and southern Europe especially during the spring and summer months (Stahl et al., 2012), and many organisms that depend on high ground water levels are increasingly threatened by hydrological droughts. In another example, the Pantanal wetland in Brazil was heavily affected by fires in 2021 (i.e., Leal Filho et al., 2021), when the meteorological drought was reinforced by the flow regulation and lowered ground water levels in the upper basins of important tributaries of the upper Paraguay River, as shown by the increasing number of hydropower facilities (Ely et al., 2020). In south-eastern Brazil, water volumes of most reservoirs are at 10–20% of their capacity, causing shortage of drinking water and hydropower generation. In this situation, the 88-year historical drought of the Paraná River in 2021, caused immense damage to biodiversity and agricultural economy (i.e., Abriel et al., 2021).

The reduced water retention capacity of flow-regulated river floodplains also reinforces catastrophic inundations, in particular where the active floodplains are limited through artificial dikes for flood protection. In many regions on Earth, climate change leads to an increase in the frequency and intensity of heavy rainfall events. While wetland degradation is not the single cause of high water events, those are strongly reinforced by the increased discharge of rectified and diked river channels, as painfully experienced recently in the Ahr river valley in western Germany in July 2021, causing the loss of 130 lives and an unprecedented damage of homes and infrastructure (i.e., Schlömer et al., 2021). Catastrophic events like this will affect many regions on Earth with increasing severity and frequency with climate change.

Deforestation, inadequate resource use, and pollution through mining activities, wastewaters, and agricultural activities are further environmental threats for most river wetlands on Earth. Whenever affecting wetland species populations and biogeochemical cycles, the impacts are not restricted to aquatic environments but mostly extend to the entire catchment, and vice versa. Worldwide, rivers annually transport 43 MT of nitrates and 8.6 MT of phosphates to the oceans, mainly originating from agricultural fertilizers and wastewaters, leading to the eutrophication of more than 80% of the World's marine ecosystems (Sutton et al., 2013). In another example, Peterson et al. (2021) reported on elevated mercury concentrations in raccoons and skunks in seasonally impounded brackish marshes in California and concluded that other wildlife of similar and higher trophic positions may also bioaccumulate methylmercury. Similar results are reported for bat species of the Peruvian Amazon, where mercury is used in the

mostly illegal gold mining activities along low order rivers. As shown by Kumar and Divoll (2014), higher trophic bat levels (i.e., piscivores and insectivores) bioaccumulated more mercury than lower trophic levels (i.e., frugivores), demonstrating the negative effects of water pollution that often has strong capacity to permeate through aquatic and terrestrial food chains.

Conclusions

Riparian zones and river wetlands influence the water balance of landscapes and are crucial ecosystems for landscape ecology and biogeography in how they influence species evolution, species exchange, biodiversity, trophic chains, biochemical processes, and the mitigation of hydrological extremes as caused through climate change. River wetlands are interdependent with surrounding terrestrial catchments, thus any fragmentation or ecological degradation of riparian zones and wetlands has direct impacts on terrestrial landscapes, and vice versa. The longitudinal ecological connectivity and dependency over large geographic ranges combined with the transversal connectivity of adjacent uplands results in highly complex ecological interactions where wetland organisms depend on multiple ecological gradients. This notion implies that organisms inhabiting riparian zones and river wetlands are particularly vulnerable to human activities and land-use change. Because riparian zones and river wetlands belong to the most biodiverse ecosystems in many climate zones, and provide vital ecosystem services for humans in terms of the provisioning of water, the regulation of biogeochemical cycles, and the mitigation of climatic changes, they should receive special attention in conservation efforts.

Future research

- Comparative phylogenetic studies on wetland plant and animal species with their terrestrial and marine congeners are needed in order to better understand the role of wetlands in species distributions, evolution, diversification, and refugia.
- Hydro-climatic models should be combined with experimental studies on species vulnerability and resilience to confidentially predict impacts of hydrological climate change on the wetland-dependent biota.
- Wetland conservation and restoration should focus on the integrative protection of freshwater systems including their terrestrial and marine interactions, using a landscape approach.

See Also: Human pressures and management of Inland Waters: Hydromorphology: Overview and Assessment Methods; The Role of Wetlands in Mitigating Impacts From Diffuse Agricultural Loads; Social/societal values of Inland waters: Riparian Buffers and Land Cover Change; Societal Implications of Kenya's Inland and Marine Waters; Structures and functions of Inland Waters - Rivers: Macrosystem Ecology of Inland Waters; Riparian Zones; Stream Geomorphology; Succession in Streams; Structures and functions of Inland Waters - Wetlands: Restoring Riparian Peatlands for Inland Waters: A European Perspective; Riparian Vegetation of Gravel-bed Rivers - A Global Review

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Mountain Rivers: A Global Overview of River Channel Forms, With a Focus on Braided Rivers

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Alluvial river Self formed river in which the bed and banks are made up of mobile sediment.
Confined river River characterized by a straight channel and few bends.
Fluvial Processes and landforms created by the flowing water.
Geological age Describes the timing and relationships of events in geologic history.
Gravel-bed rivers Coarse-grained alluvial rivers which are particularly characterized by dynamic fluvial processes that constantly change and renew the surface and subsurface of the river's valley floor.
Last glacial maximum The LGM was the most recent time during the Last Glacial Period where the ice sheets were at their greatest extent.
Meandering river Strongly winding river course with a sinuosity greater than 1.5.
Morphodynamics Landscape changes due to erosion and sedimentation processes.
Multi-thread anabranching river River with braided to sinuous-meandering channels usually with vegetated islands.
Multi-thread bar-braided river Braided river with almost only unvegetated gravel bars within the active channel.
Multi-thread island-braided river Braided river with vegetated islands within the active channel.
Permafrost Soil, sediment or rock which has in varying thicknesses and depths below the earth's surface been continuously exposed to temperatures below freezing point for at least few years.
Pseudo-meandering river Straight or sinuous channel that display large, alternate bars at low flow.
Sinuosity Ratio of channel length to valley length.
Specific stream power Represents the amount of work that a river may do.
Transitional wandering river Transitional channel form between fully braided and oscillating/sinuous patterns.

Introduction

Globally, mountain ranges cover 22% of the overall land area and provide space to live for 915 million inhabitants (Romeo et al., 2015). Formed by ongoing or abandoned plate tectonics, they constitute impressive landscape regions, which occur in every continent. Closely associated with the orogeny, or mountain development, a multitude of smaller and larger fluvial systems originate from, or are entirely located within the mountainous terrain (Paixão and Kobiyama, 2019). The morphological variety of these mountain rivers reflects the diverse nature of the individual mountain ranges in terms of geological age, tectonic processes, lithology and climate (Wohl, 2010). Besides typical bedrock-confined or braided channels, the spectrum of alpine river channel types also includes sinuous, transitional or even meandering forms (Hohensinner et al., 2019).

As recognized by the FAO, mountain rivers are of great importance worldwide because half of the world's population obtains drinking water from mountain catchments (FAO, 2014; Huss et al., 2017). Additionally, they provide habitats for many specially adapted animal and plant species, thus providing important contributions to global biodiversity (Arscott et al., 2003; Gray and Harding, 2007). Mountain rivers support some of the most endangered ecosystems worldwide due to the human impacts to their hydrologic and sediment regimes by river dams and diversions for flood control, hydropower generation and water storage, and

river flow regulation for irrigation and other human demands (Bravard et al., 1986; Hauer et al., 2016; Hohensinner et al., 2021; Müller, 1995; Tockner and Stanford, 2002; Tockner et al., 2006). Another threat to the biodiversity is their vulnerability to invasion by alien, or non-native plant species because they provide barren sites for seedling colonization and the river flows serve as seed dispersal pathways (Liendo et al., 2015).

Against this background, this chapter reviews the worldwide distribution of common river channel types in mountain ranges and determines their characteristics on a global scale. Accompanying this overview, braided rivers are analyzed in more detail relative to the physical and habitat characteristics. Braided river channels occur primarily in mountains and their foothills, and thus represent distinctive aquatic ecosystems with a global distribution.

Braided rivers are characterized by mobile, multi-thread channels within gravel or sand-dominated fluvial corridors (Gray and Harding, 2007; Leopold and Wolman, 1957; Rinaldi et al., 2016). These braided channels are characterized by continuous change, in sharp contrast to the more stable surrounding landscapes. Mountainous braided rivers are determined by dynamic flow and sediment regimes, the hydrodynamics and morphodynamics, respectively. These especially occur with high, late spring and early summer flows caused by rapid snowmelt, when the melt coincides with periods of high rainfall, and rain-on-snow provides further runoff contributions (Bristow and Best, 1993; Bridge, 1993; Pomeroy et al., 2016; Tockner et al., 2006).

Another fundamental factor leading to the development of braided river channels is high sediment supply of coarse substrates which originate from the steep mountainous catchments with high erosion rates. This braided channel form often accompanies reduced sediment transport capacity due to a decline in the river gradient, often combined with valley widening (Ashworth et al., 2004; Hohensinner et al., 2021; Piégay et al., 2009). This leads to sediment deposition that chokes the channel, leading to relocation and often channel splitting, or bifurcation. With these repetitive processes, braided river channels are repeatedly reshaped by floods of annual or sub-annual frequency (Rinaldi et al., 2016). These dynamic processes and environmental parameters of braided rivers channels have been investigated for different spatial scales, from river sections to catchments and mountain regions, as well as for entire mountain ranges. The braided river channels are classified as wetlands in a broader sense in this chapter and their description includes characteristics of the aquatic zone as well as of the transition zone. The majority of research publications originate from northern temperate sites and the underlying processes may be similar in many other mountain regions (e.g. Hohensinner et al., 2021; Sambrook Smith et al., 2006; Surian and Fontana, 2017; Tockner et al., 2003, 2006).

Definition and classification of mountainous river channel types

The study area is based on map data of Natural Earth (2018) and ESRI (2016), and includes 204 major mountain ranges of the world. To provide global conclusions regarding the typical physical and habitat characteristics of different channel types, 120 representative reference catchments were selected based on stratified random sampling. Within these reference catchments, the morphological channel types were determined for all river reaches within the limits defined by the Natural Earth (2018) and ESRI (2016) data. These river reaches were analyzed with respect to their physical and habitat parameters and the properties refer to the entire categories.

The 204 mountain ranges of the world were classified in categories comprising two decisive aspects: geological age of mountain range and degree of glaciation of catchment area under current conditions or in the last glacial maximum (LGM; RGI Consortium, 2017; Ehlers et al., 2011) (Fig. 2). The age of mountain range is important because correlations were detected with elevation, stream gradient and soil erosion. Younger mountain ranges have higher erosive processes which increase sediment supply in river reaches, which subsequently favors the development of braided channel types (Hohensinner et al., 2021; Mueller and Pitlick, 2014; Piégay et al., 2009). In addition, the degree of glaciation also increases sediment supply by increasing soil erosion and seasonal floods (McKernen et al., 2018). This also lowers water temperature and provides cool air drainage, which impedes the establishment of plants, further fostering the evolution of braided channel patterns (Huss et al., 2017).

Bivariate categories were defined by the combination of four ice cover classes: (i) recent high (>10%); (ii) recent low (>0–10%); (iii) no current ice cover but in LGM; and (iv) never ice-covered. Three geological age classes were determined by literature research: (i) young, Cenozoic (<66 MYA, million years ago); (ii) medium, Mesozoic (66-252 MYA); and (iii) old, Paleozoic (>252 MYA). Categories were investigated according to the distribution of channel types and those with few results and lacking significant differences were combined, which lead to a classification of eight categories (see Fig. 2): (1) very high ice cover and young or medium age, (2) high ice cover and young age, (3) ice cover in the LGM and young age, (4) never ice-covered and young age, (5) high ice cover and moderate or old age, (6) ice cover and moderate or old age, (7) never ice-covered and moderate age, and (8) never ice-covered and old age.

Fifteen representative river catchments were randomly selected for each category, and these were globally distributed in 77 of the worldwide mountain ranges. The subsequent analyses were based on these 120 reference catchments (Fig. 2; Table 1).

Inside the catchments, all rivers which have been identified by Linke et al. (2019) were considered and calculations were based on river reaches with relatively homogeneous boundary conditions, consistent process-form interactions and with a new reach starting at the confluence of another water body (Gurnell et al., 2016). For the European Alps, historical river data were used due to the extensive human impacts on those rivers (Hohensinner et al., 2021).

Following Rinaldi et al. (2016) and Hohensinner et al. (2019), the classification of channel types was based on the number of river branches, sinuosity, and the proportion of vegetation versus open substrate within the active channel. Subsequently, channel types and their percentage per river reach were determined by interpretation in QGIS from Google maps, Bing maps and satellite

Table 1 Category number, continent, climate zone, age of mountain range (Age Mt.R.: Cenozoic (Cz), Mesozoic (Mz), Paleozoic (Pz)), ice coverage of catchment during last glacial maximum (IC LGM), ice coverage area under current conditions (IC C) and proportion (%) of the four common river types braided river (BR), transitional gravel-bed rivers (TR), single-thread confined rivers (CR) and meandering rivers (MR) for the 120 reference catchments.

No	*Category no*	*Mountain range*	*Continent*	*Climate zone*	*Age Mt.R*	*IC LGM %*	*IC C %*	*BR %*	*TR %*	*CR %*	*MR %*
1	1	Alaska Range	N. America	boreal arctic	Cz	74.0	18.5	92.1	4.1	3.1	0.7
2	1	Andes	S. America	subtropic	Cz	100.0	40.5	19.8	16.1	56.3	7.8
3	1	Chugach Mountains	N. America	boreal arctic	Cz	98.3	11.1	13.2	29.9	55.0	1.9
4	1	Saint Elias Range	N. America	boreal arctic	Cz	100.0	12.9	33.3	22.7	44.0	0.0
5	1	Himalayas	Asia	subtropic	Cz	45.4	20.8	22.8	23.8	50.8	2.7
6	1	Hindu Kush	Asia	subtropic	Cz	0.0	23.5	22.3	24.3	50.9	2.5
7	1	Karakoram Range	Asia	subtropic	Cz	26.3	52.2	20.5	25.8	51.5	2.2
8	1	Karakoram Range	Asia	subtropic	Cz	57.3	12.2	17.4	30.5	52.2	0.0
9	1	Kunlun Mountains	Asia	subtropic	Cz	98.1	27.9	7.6	35.1	57.3	0.0
10	1	Pamirs	Asia	temperate	Cz	0.0	17.8	19.2	29.4	49.8	1.6
11	1	Pamirs	Asia	temperate	Cz	0.0	19.3	19.3	27.0	52.2	1.5
12	1	Southern Alps	Oceania	subtropic	Cz	76.0	13.4	20.6	24.9	53.2	1.3
13	1	Vatnajökull	Europe	boreal arctic	Cz	100.0	41.1	79.8	15.9	4.3	0.0
14	1	Wrangell Mountains	N. America	boreal arctic	Cz	94.7	26.0	45.7	16.3	26.2	11.8
15	1	Coast Mountains	N. America	temperate	Mz	100.0	34.4	7.9	13.1	69.4	9.5
16	2	Aleutian Range	N. America	boreal arctic	Cz	68.1	2.1	5.9	21.1	44.9	28.1
17	2	Alps	Europe	temperate	Cz	88.2	1.2	12.4	27.3	21.8	38.5
18	2	Alps	Europe	subtropic	Cz	16.5	0.0	10.5	12.5	55.7	21.3
19	2	Andes	S. America	subtropic	Cz	95.3	0.0	0.6	9.9	60.5	29.0
20	2	Andes	S. America	subtropic	Cz	7.0	0.0	19.3	58.4	18.9	3.4
21	2	Andes	S. America	tropic	Cz	22.3	0.2	0.2	34.2	65.6	0.0
22	2	Chugach Mountains	N. America	boreal arctic	Cz	83.5	2.3	5.3	29.4	41.6	23.7
23	2	Himalayas	Asia	subtropic	Cz	3.5	1.2	4.5	32.6	56.1	6.7
24	2	Kunlun Mountains	Asia	subtropic	Cz	10.6	1.8	57.2	32.1	10.7	0.0
25	2	Pamirs	Asia	subtropic	Cz	0.0	4.6	12.4	10.7	76.9	0.0
26	2	Qilian Mountains	Asia	temperate	Cz	28.8	0.3	19.8	49.8	28.2	2.1
27	2	Sredinny Range	Asia	boreal arctic	Cz	79.6	0.7	2.4	17.6	51.2	28.7
28	2	Tian Shan	Asia	temperate	Cz	0.0	3.1	33.4	29.1	36.9	0.6
29	2	Tian Shan	Asia	temperate	Cz	0.0	4.0	13.4	27.4	48.6	10.7
30	2	Tian Shan	Asia	temperate	Cz	0.0	2.9	1.5	14.5	73.4	10.6
31	3	Adirondack Mountains	N. America	temperate	Cz	100.0	0.0	0.0	46.2	25.4	28.4
32	3	Alps	Europe	temperate	Cz	38.3	0.0	5.7	32.7	61.6	0.0
33	3	Alps	Europe	temperate	Cz	72.3	0.0	42.0	46.6	3.5	7.9
34	3	Andes	S. America	tropic	Cz	8.8	0.0	2.6	37.9	59.4	0.1
35	3	Andes	S. America	tropic	Cz	14.9	0.0	3.6	64.4	20.3	11.6
36	3	Cascade Range	N. America	temperate	Cz	91.5	0.0	0.2	40.1	59.7	0.0
37	3	Cascade Range	N. America	temperate	Cz	8.7	0.0	0.0	22.8	77.2	0.0
38	3	Cascade Range	N. America	subtropic	Cz	17.8	0.0	0.0	13.3	86.7	0.0
39	3	Andes	S. America	tropic	Cz	5.6	0.0	8.4	45.6	44.1	1.9
40	3	Chukotka Mountains	Asia	boreal arctic	Cz	22.1	0.0	34.1	55.6	10.3	0.0
41	3	Dinaric Alps	Europe	temperate	Cz	3.9	0.0	0.2	15.9	79.4	4.4
42	3	Saint Elias Range	N. America	boreal arctic	Cz	100.0	0.0	44.8	11.5	37.2	6.5
43	3	Jura Mountains	Europe	boreal arctic	Cz	57.5	0.0	28.7	62.5	8.7	0.1
44	3	Kjølen Mountains	Europe	tropic	Cz	2.5	0.0	0.0	2.7	63.2	34.1
45	3	Zagros Mountains	Europe	subtropic	Cz	45.0	0.0	0.0	25.3	36.8	37.9
46	4	Al Hajar Mountains	Europe	tropic	Cz	0.0	0.0	22.1	71.0	5.4	1.5
47	4	Altun Mountains	Asia	temperate	Cz	0.0	0.0	0.0	81.5	18.5	0.0
48	4	Andes	S. America	subtropic	Cz	0.0	0.0	0.0	79.5	20.5	0.0
49	4	Andes	S. America	subtropic	Cz	0.0	0.0	2.9	60.5	35.9	0.7
50	4	Andes	S. America	tropic	Cz	0.0	0.0	7.4	72.4	20.2	0.0
51	4	Atlas Mountains	Africa	subtropic	Cz	0.0	0.0	1.0	47.7	51.3	0.0
52	4	Caucasus Mountains	Europe	temperate	Cz	0.0	0.0	0.0	51.6	32.6	15.9
53	4	Drakensberg	Africa	subtropic	Cz	0.0	0.0	0.0	51.9	48.1	0.0
54	4	Drakensberg	Africa	subtropic	Cz	0.0	0.0	0.0	27.6	72.4	0.0
55	4	Drakensberg	Africa	tropic	Cz	0.0	0.0	0.0	35.8	64.2	0.0
56	4	Hadhramaut Mountains	Europe	tropic	Cz	0.0	0.0	19.7	67.8	12.5	0.0
57	4	Kirthar Mountains	Asia	subtropic	Cz	0.0	0.0	7.8	80.3	11.9	0.0
58	4	Sierra Madre Occidental	N. America	tropic	Cz	0.0	0.0	0.9	56.6	42.5	0.0

(*Continued*)

Table 1 (Continued)

No	Category no	Mountain range	Continent	Climate zone	Age Mt.R	IC LGM %	IC C %	BR %	TR %	CR %	MR %
59	4	Siwalik Hills	Asia	subtropic	Cz	0.0	0.0	4.7	24.2	60.3	10.7
60	4	Tuwayq Mountains	Europe	subtropic	Cz	0.0	0.0	0.0	100.0	0.0	0.0
61	5	Cassiar Mountains	N. America	temperate	Mz	100.0	0.2	5.1	13.2	24.8	56.8
62	5	Chersky Range	Asia	boreal arctic	Mz	15.7	0.0	30.4	56.5	12.8	0.3
63	5	Columbia Mountains	N. America	temperate	Mz	100.0	2.0	0.2	25.4	73.5	0.9
64	5	Mackenzie Mountains	N. America	boreal arctic	Mz	43.9	0.1	23.6	45.2	11.5	19.6
65	5	Interior Mountains	N. America	temperate	Mz	100.0	0.3	1.8	14.2	17.0	67.0
66	5	Interior Mountains	N. America	temperate	Mz	100.0	1.9	5.7	44.5	47.0	2.9
67	5	Canadian Rocky Mountains	N. America	temperate	Mz	100.0	2.0	3.4	47.3	46.3	3.0
68	5	American Rocky Mountains	N. America	temperate	Mz	100.0	0.0	0.0	32.6	67.4	0.0
69	5	American Rocky Mountains	N. America	temperate	Mz	100.0	0.0	1.7	63.0	35.3	0.0
70	5	American Rocky Mountains	N. America	subtropic	Mz	44.3	0.0	0.0	28.5	67.3	4.2
71	5	Tarbagatai Mountains	Asia	temperate	Mz	0.0	0.4	6.5	48.8	44.7	0.0
72	5	Torngat Mountains	N. America	boreal arctic	Mz	100.0	0.3	11.9	20.7	67.4	0.0
73	5	Altay Mountains	Asia	temperate	Pz	37.2	2.4	2.2	37.4	60.4	0.0
74	5	Altay Mountains	Asia	temperate	Pz	18.8	0.2	4.0	39.1	56.9	0.0
75	5	Salt Range	Asia	subtropic	Pz	0.0	0.3	4.2	35.9	56.3	3.6
76	6	Birch Mountains	N. America	temperate	Mz	100.0	0.0	0.0	76.7	12.9	10.4
77	6	Cherskiy Range	Asia	boreal arctic	Mz	91.7	0.0	16.6	47.5	34.9	1.0
78	6	Columbia Mountains	N. America	temperate	Mz	100.0	0.0	0.0	81.4	18.6	0.0
79	6	Eastern Sayan Mountains	Asia	temperate	Mz	41.0	0.0	0.0	64.8	16.7	18.5
80	6	Eastern Sayan Mountains	Asia	temperate	Mz	92.4	0.0	0.0	93.2	6.8	0.0
81	6	Kolyma Mountains	Asia	temperate	Mz	0.0	0.0	4.9	56.5	38.7	0.0
82	6	Lesser Caucasus	Europe	tropic	Mz	0.0	0.0	0.0	27.7	72.3	0.0
83	6	American Rocky Mountains	N. America	subtropic	Mz	0.0	0.0	0.0	5.9	94.1	0.0
84	6	Verkhoyansk Range	Asia	boreal arctic	Mz	0.0	0.0	10.6	69.3	20.1	0.0
85	6	Altay Mountains	Asia	temperate	Pz	2.4	0.0	1.6	16.4	81.4	0.7
86	6	Appalachian Mountains	N. America	temperate	Pz	100.0	0.0	0.0	47.2	52.6	0.2
87	6	Appalachian Mountains	N. America	temperate	Pz	100.0	0.0	0.0	53.2	46.3	0.5
88	6	Appalachian Mountains	N. America	temperate	Pz	100.0	0.0	0.0	39.3	59.2	1.5
89	6	Appalachian Mountains	N. America	temperate	Pz	100.0	0.0	0.0	42.0	58.0	0.0
90	6	Cambrian Mountains	Europe	temperate	Pz	100.0	0.0	0.0	27.4	72.1	0.5
91	7	Brooks Range	N. America	boreal arctic	Mz	0.0	0.0	0.1	66.9	30.8	2.2
92	7	Chaîne Annamitique	Asia	tropic	Mz	0.0	0.0	0.1	33.5	66.1	0.4
93	7	Chaîne Annamitique	Asia	tropic	Mz	0.0	0.0	0.0	7.2	91.0	1.8
94	7	Dalou Mountains	Asia	subtropic	Mz	0.0	0.0	0.0	26.5	67.5	6.1
95	7	Eastern Ghats	Asia	tropics	Mz	0.0	0.0	1.4	37.8	60.7	0.0
96	7	Eastern Sayan Mountains	Asia	temperate	Mz	0.0	0.0	4.9	56.5	38.7	0.0
97	7	Ethiopian Highlands	Africa	tropic	Mz	0.0	0.0	0.0	27.7	72.3	0.0
98	7	Great Dividing Range	Oceania	subtropic	Mz	0.0	0.0	0.0	5.9	94.1	0.0
99	7	Khangai Mountains	Asia	temperate	Mz	0.0	0.0	19.8	12.1	68.1	0.0
100	7	Khentii Mountains	Asia	temperate	Mz	0.0	0.0	0.0	33.7	66.3	0.0
101	7	Lesser Khingan Range	Asia	temperate	Mz	0.0	0.0	0.1	28.3	68.1	3.5
102	7	Mbang Mountains	Africa	tropic	Mz	0.0	0.0	0.0	26.0	74.0	0.0
103	7	American Rocky Mountains	N. America	temperate	Mz	0.0	0.0	0.0	50.1	48.1	1.8
104	7	Serra Geral	S. America	subtropic	Mz	0.0	0.0	0.0	20.0	75.0	5.0
105	7	Stanovoy Range	Asia	boreal arctic	Mz	0.0	0.0	8.1	46.5	44.5	0.9
106	8	Aravalli Range	Asia	subtropic	Pz	0.0	0.0	0.0	5.6	94.4	0.0
107	8	Altay Mountains	Asia	temperate	Pz	0.0	0.0	61.2	20.6	18.3	0.0
108	8	Appalachian Mountains	N. America	temperate	Pz	0.0	0.0	0.0	14.2	80.1	5.7
109	8	Appalachian Mountains	N. America	subtropic	Pz	0.0	0.0	0.0	11.0	83.9	5.1
110	8	Bohemian Forest	Europe	temperate	Pz	0.0	0.0	0.0	16.3	83.7	0.0
111	8	Crystal Mountains	Africa	tropic	Pz	0.0	0.0	0.0	9.3	89.6	1.1
112	8	Great Karas Mountains	Africa	subtropic	Pz	0.0	0.0	0.0	2.5	97.5	0.0
113	8	MacDonnell Ranges	Oceania	subtropic	Pz	0.0	0.0	15.8	83.6	0.6	0.0
114	8	Muchinga Mountains	Africa	tropic	Pz	0.0	0.0	0.0	40.4	59.6	0.0
115	8	Cachimbo Mountains	S. America	tropic	Pz	0.0	0.0	0.0	22.9	64.6	12.5
116	8	Serra dos Gradaús	S. America	tropic	Pz	0.0	0.0	0.0	60.4	31.3	8.2
117	8	Serra Dourada	S. America	tropic	Pz	0.0	0.0	0.0	13.1	83.6	3.2
118	8	Selwyn Range	Oceania	tropic	Pz	0.0	0.0	3.7	55.1	41.3	0.0
119	8	Espinhaço Mountains	S. America	tropic	Pz	0.0	0.0	0.0	25.4	65.7	8.9
120	8	Ural Mountains	Europe	temperate	Pz	0.0	0.0	0.0	27.5	66.0	6.5

images. Several channel types can occur for each river reach and were considered as subreaches when they exceeded 20% of the reach length. In that case, the proportional length of each channel type was calculated for each river reach.

In total, 11 different classes could be sequenced by form: confined, multi-thread bar-braided, multi-thread island-braided, multi-thread anabranching, transitional wandering, transitional pseudo-meandering, single-thread meandering, highly altered/modified reaches, glacier lakes and braided meltwater brooks, rivers in glacier areas, and unclassifiable river reaches due to incorrect positioning. The unclassifiable rivers represented 8.9% and were excluded, along with the sparse classes: rivers in glacial areas (4.9%), glacial lakes and brooks (3.0%) and the anabranching class that included anastomosed rivers (0.6%). There was subsequent grouping of related classes to provide four common, composite channel types, which represented 82.6% of the total river reaches. These predominant channel types were: (i) multi-thread braided rivers (BR), (ii) transitional gravel-bed rivers (TR) which include transitional wandering and pseudo-meandering rivers, (iii) single-thread confined rivers (CR), and (iv) meandering rivers (MR). Following this classification, in the 120 river catchments (total 511,839 km^2 catchment area) there are 13,537 river reaches with a mean length of 3.9 km (total length of 53,085 km). Within these reaches, a total of 18,279 subreaches of the four dominant channel types could be distinguished and were analyzed considering their geomorphological channel types, and physical and climate parameters (Global Drainage Basin of Masutomi et al., 2009; and HydroATLAS of Linke et al., 2019).

Channel type distribution and environmental factors

The most common channel types in the mountain areas are confined rivers with 49.3% and transitional gravel-bed rivers with 37.3%. Braided rivers account for 8.3%, whereas meandering rivers are less common, representing 5%.

Table 2 provides an overview of the key physical and habitat parameters of the analyzed channel types for the locations presented in Fig. 2. Braided rivers are characterized by high soil erosion and correspondingly high sediment supply. That exceeds the transport capacity of the river which leads to their characteristic sand and gravel bars between numerous, interwoven flow channels (Buffington and Tonina, 2009; Hohensinner et al., 2021; Montgomery et al., 1996; Piégay et al., 2009). Sediment supply is highest in catchments with glacier areas, while soil erosion is more pronounced than in areas that are not affected by glaciers. Thus, the study underlines the decisive role of sediment supply in determining the channel type (Mueller and Pitlick, 2013, 2014). Glacier cover and a climate of cold temperatures and low precipitation also inhibit the establishment of vegetation, which also contributes to increased soil erosion and high morphodynamics.

In the long term, the retreat of glaciers leads to reduced runoff and reduced erosion (Huss et al., 2017; Huss and Hock, 2018; O'Neel et al., 2014). There is subsequently a decrease in bedload and suspended sediment load (Fleming and Clarke, 2005; Milner et al., 2017; Singh et al., 2016), and decreasing sediment availability (Moore et al., 2009), transport capacity and stream power (McKernen et al., 2018; Raymond Pralong et al., 2015). Confined and transitional gravel-bed rivers differ substantially, and according to Cohen, 1992; see Table 2) the primary effect size is in the amount of bare areas relative to the braided rivers. Compared to braided rivers, transitional gravel-bed rivers have a slightly lower specific stream power, which provides a surrogate for transport capacity. However, they can transport the incoming bed load due to smaller volumes of sediment supply and the focussed single river arm. Alternately, confined rivers are primarily characterized by their high stream gradient, which prevents the deposition of sediments. Finally, meandering rivers occur in warmer and wetter regions that are characterized by less permafrost and smaller glaciers, which in turn lead to increasing proportions of artificial impacts and cultivated areas.

The reaches of the transitional gravel-bed rivers are characterized by reduced soil erosion and higher upland forest cover in the catchment, warmer temperatures, higher precipitation, and greater evaporation in the river reach, as compared to braided rivers. Glacier and snow cover and permafrost proportion are less extensive in the associated catchment areas for the transitional gravel-bed rivers. Also compared to braided rivers, the transitional gravel-bed rivers occur at lower altitudes and have shallower channel slopes, while the average runoff is comparable but less variable. The subsequent decline in morphodynamics facilitates the establishment of vegetation in the active riverbed and initiates the transition from multi-channel braided rivers to single-channel transitional gravel-bed rivers (Kondolf and Curry, 1984). This trend continues with further decrease in morphodynamics, so that succession occurs, and more floodplain forest can establish following the 'fluvial biogeomorphic succession concept' proposed by Corenblit et al. (2007).

Confined river reaches have comparatively less soil erosion and higher forest cover than braided river reaches. Precipitation, temperature and evaporation are also higher, and the catchment areas have limited snow cover and very low proportions of glaciers and permafrost. Confined rivers have the steepest gradient and the smallest catchment area above their river reaches. The reaches mainly occur in higher elevations but occasionally also in lower areas. Their discharge is generally low and less variable. They occur predominantly, but not always, in the upper reaches of river catchments.

Meandering rivers are characterized by lower stream gradients compared to other channel types. They show higher discharges than most of the other channel types, and with less variability. The reaches occur in warmer and more humid climates so that the vegetation can establish more easily.

The distribution of the channel types with respect to the three mountain age classes shows that the braided river proportion is higher in the young mountains from the Cenozoic era with 62%, intermediate in the medium old mountains from the Mesozoic era with 24%, and only 14% occur in the old mountains from the Paleozoic era. The meandering rivers also have a higher proportion in the younger mountains (young/medium/old: 48/31/21%). In contrast, the transitional gravel-bed rivers (35/33/33%) and the confined rivers (28/35/37%) have approximately equal distributions in all three mountain age classes.

Table 2 Physical and habitat parameters of all channel types (Md: median, M: arithmetic mean).

Parameter	*Unit*	*Scale*	*Braided rivers (BR)*	*Transitional gravel-bed rivers (TR)*	*Confined rivers (CR)*	*Meandering rivers (MR)*
Glacier Extent (M)	%	upland	7.68	1.54[a]	1.78[b]	0.70[a]
Snow Cover Extent (M)	%	upland	44.17	25.00[b]	24.27[b]	29.33[b]
Permafrost Extent (M)	%	upland	47.25	20.09[b]	14.56[b]	13.7[a]
Artifical and Cultivated Land (M)	%	upland	3.37	11.13[b]	11.06[b]	9.79[b]
Bare Land (M)	%	upland	21.46	6.77[a]	4.13[a]	0.71[c]
Forest Cover (M)	%	upland	7.94	29.19[b]	35.58[b]	33.21[a]
Soil Erosion (M)	kg/(ha*year)	upland	12,160	8578[b]	8617[b]	6416[b]
Upland Kilometers (Md)	km	river reach	24	16	8.6[b]	17.3
Average Altitude (Md)	m	river reach	1099	882[b]	1003[b]	780[a]
Stream Gradient (Md)	m/km	river reach	9.0	9.1	22.3[b]	7.6
Average Runoff (Md)	m^3/s	river reach	0.967	0.725	0.337	1.26[b]
Specific Stream Power (Md)	$kW/(m^{2}*km^{2})$	river reach	0.022	0.019	0.023	0.026
Average Temperature (Md)	°C	river reach	−1.4	7.4[b]	8[b]	8.5[a]
Minimum Temperature (Md)	°C	river reach	−16.7	0.5[b]	2[b]	1.9[a]
Maximum Temperature (Md)	°C	river reach	12.1	18[b]	17.4[b]	15.9[b]
Average Precipitation (Md)	mm/year	river reach	497	642[b]	1019[b]	1000[a]
Actual Evaporation (Md)	mm/year	river reach	320	472[b]	610[a]	619[c]

Percentage values are based on the dominant river type of the reach. Superscript numbers indicate significant differences of other channel types compared to braided rivers by Kruskal-Wallis-Test (Kruskal and Wallis, 1952) and Dunn's-Test (Dunn, 1961), with different effect sizes according to Cohen (1992).

[a]0.3–0.5, medium effect.

[b]0.1–0.3, weak effect.

[c]>0.5, strong effect.

On a global scale, braided rivers are mainly distributed in the young mountain ranges with high ice cover (see Fig. 3). In the Category 1 combination of young and moderate-aged ranges with very high ice cover, the braided rivers represent about 20%, followed by Category 2 with high ice cover with about 15%. Within Category 1 the reference catchment of Alaska mountains contains the highest percentage of braided rivers (92.1%), followed by Vatnjajökull, Iceland (79.8%). Categories 1 and 2 include parts of the Canadian and Alaskan mountain ranges on the west coast, parts of the Southern Andes and high proportions in the Central Asian mountain ranges such as the Himalayas and the Tian Shan (Central Asia), and there is a noticeable decline in the occurrence of braided rivers with declining ice cover. Even formerly glaciated young mountain ranges of Category 3 have rather low median river length of braided rivers, but the high upper quartile values of almost 20% show the considerable occurrence of braided rivers like the reference catchments of the Elias Range (Canada) at 44.8%, the European Alps (prior to the extensive river regulation in the mid 19th to early 20th century) at 42.0% and the Chukchi Range (Russia) at 34.1%. Young mountain ranges that were never glaciated (Category 4) had low proportions of braided rivers but with a few exceptions including the Arabian mountain range (reference catchment of Al Hajar Mountains at 22.1%). Older mountain ranges with elevated ice cover had some braided rivers (Category 5; reference catchment of Cherskiy Range (Russia) at 30.4% and of Mackenzie Mountains (Canada) at 23.6%). In the remaining categories 6 to 8 there are few braided rivers (see Table 1 for selected characteristics of all 120 reference catchments).

About two-thirds of the investigated braided rivers are located in cold and wetter climates (Fig. 4). One peak of occurrence lies in extremely cold and wet climates such as the North Saskatchewan River (Fig. 5), with another peak in extremely cold and mesic climate (White River and River Lech; Figs. 1 and 6). There are occurrences in cool and moist (Rio Petrohue; Fig. 7), warm and mesic (Vjosa; Fig. 8), and cool and dry climates (River Naryn; Fig. 9). Some occurrences are also found in hot to the extremely hot and xeric to arid climates like the wadis of the Arabian Peninsula (Rostam River; Fig. 10).

There were also other environmental influences on the distribution of braided rivers (Fig. 11). Water area at mean water discharge covers only small amounts of braided river reaches (1.6%, SD 7). On average almost 22% (SD 29) of the catchments of braided rivers are covered by bare bedrock, gravel and sand bars and even more by herbaceous vegetation (40%, SD 32). Later succession stages cover a lower percentage, with 6% (SD 14) for shrubs and 9% (SD 19) for trees. Since the main global distribution of braided rivers lies in cool climates, average snow and ice cover approximately 16%. Human impact is rather low for braided rivers and artificial and cultivated areas cover only approximately 3% of upstream catchment areas. These percentage values are based on the dominant river type of the reach but there is substantial variation within and across the watersheds for the braided rivers (Fig. 11).

The average temperature of braided rivers is just below freezing (0 °C; Table 2). This provides an important difference from the other river types that occur in substantially warmer regions. For the median minimum temperatures, even the upper quartile of braided rivers is below the freezing temperature (Fig. 11). Conversely, a few outliers are located in much warmer climates with average and minimum median temperatures of more than 20 °C. Climate is generally dry with three-quarters of catchments with less than 1000 mm of precipitation, but outliers extend up to about 4000 mm.

Fig. 1 The White River (Alaska) is one of the largest tributaries of the Yukon River. It is glacier-fed and characterized by enormous sediment loads, which form the valley-wide braided river channel. The climate zone is extremely cold (temperature class) and mesic (aridity class; see Fig. 4). Photo: G. Egger.

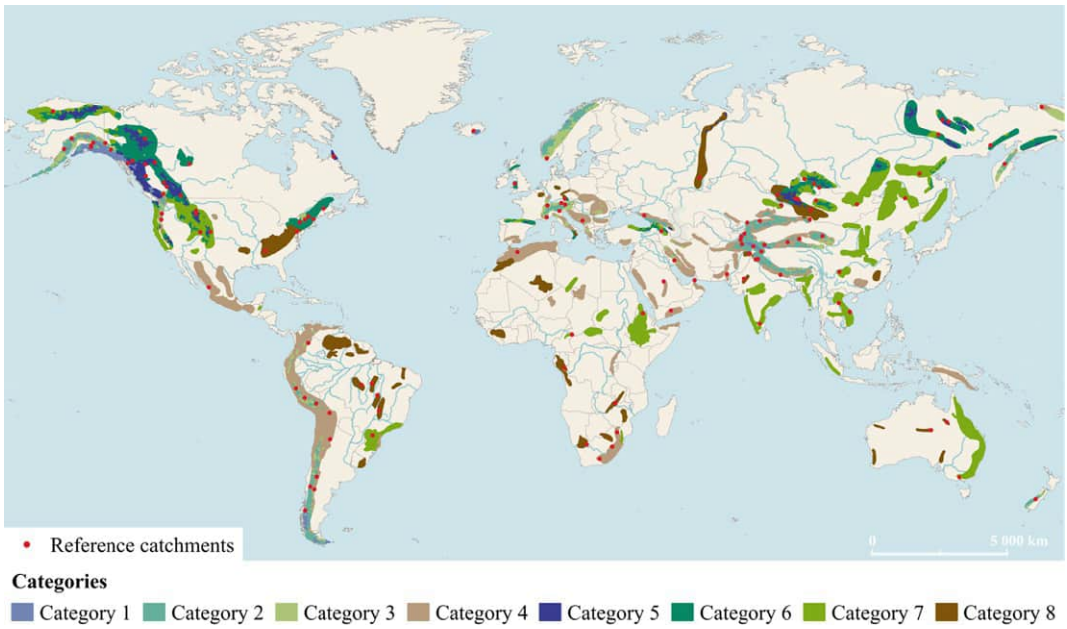

Fig. 2 Global distribution of the nine different bivariate categories of mountain ranges and locations of the 120 reference catchments (red dots - data sources: ESRI, 2010; ESRI, 2016; Natural Earth, 2018).

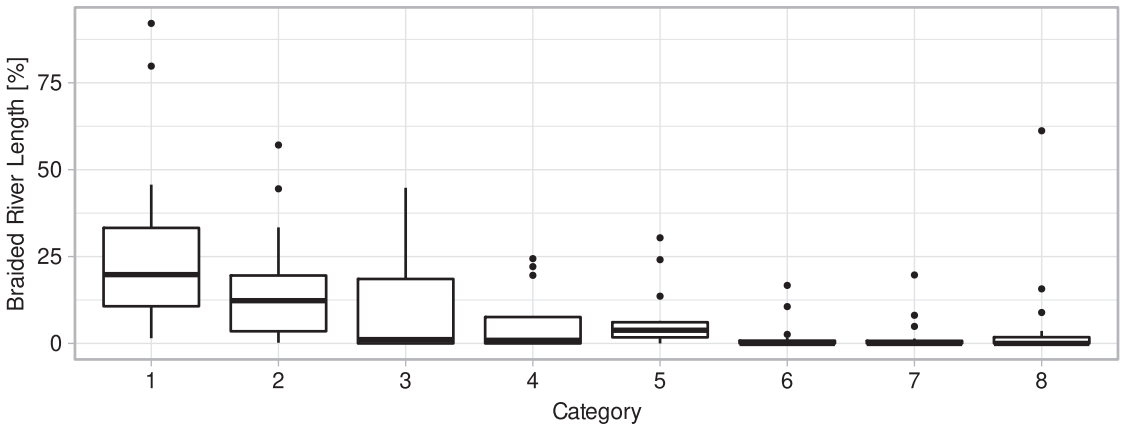

Fig. 3 Percentage of braided rivers by length of all rivers in the 15 reference catchments for each of the mountain categories (see Fig. 2).

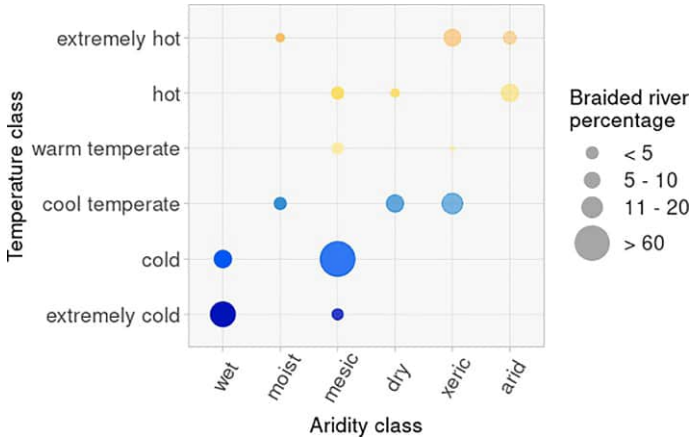

Fig. 4 Global occurrence of braided rivers in different climates categorized by temperature classes (growing degree-days on a 0 °C base (GDD), reflecting latitudinal and altitudinal temperature gradients; Metzger et al., 2013) and aridity classes (aridity index; Trabucco et al., 2008).

Fig. 5 The North Saskatchewan River in the Rocky Mountains in Banff, Canada, displaying the dynamic, braided channel form, with multiple shallow, interwoven channels and relatively barren islands. The climate zone is extremely cold and wet. Photo: S. Rood.

Fig. 6 The River Lech is one of the last near to natural braided rivers in the Eastern Alps (Austria). The climate zone is extremely cold and mesic. Photo: C. Damm.

Fig. 7 The Rio Petrohue nearby Chaiten is a typical island braided river of the Andes (Patagonia). It is characterized by largely natural forests in the catchment area, which have not become victims of the fire clearing. The climate zone is cool and moist. Photo: G. Egger.

Fig. 8 The Vjosa is the largest braided river in the Balkan region, which flows into the Adriatic Sea. It is characterized by natural morphodynamics. The riparian forests of the floodplain zone, on the other hand, have largely given way to farmland. The climate zone is warm and mesic. Photo: G. Egger.

The upstream river catchments of the braided rivers mainly have glacier extents below 10% of the area but some cases have with more ice cover. Snow cover is generally high, with half of the upstream areas ranging between 20% and 70%. Permafrost cover is substantial but variable in the braided rivers with a median of about 50% (Fig. 11).

For one quarter of the braided rivers, the catchment area is characterized by a higher proportion of unvegetated bare land. The amount of artificial/cultivated land as a surrogate of anthropogenic impact is rather low for braided rivers. Median forest extent is also very low with the upper quartiles reaching about 8% of upland areas. However, both indices have a broad distributions and outliers with values approaching 100% (Fig. 11).

Fig. 9 The Naryn is one of the biggest rivers in the Kyrgyz part of the Tian Shan Mountains and is overall the most water-rich river in the country. The climate zone is cool and dry. Photo: F. Betz.

Fig. 10 The Rostam River is located in the south of Iran and flows west of Bandar Abbas into the Persian Gulf. The climate is extremely hot and arid. Photo: G. Egger.

Conclusion and synthesis

Here, we present a global analysis of river channel types in mountain ranges. Globally, confined rivers and transitional gravel-bed rivers are the most common river types of mountain ranges, combining to represent 87% of rivers. A very small proportion of mountain rivers is represented by the meandering channel form (5%).

We emphasize the braided rivers that display a distinctive form with multiple, dynamic and interwoven channels, which is uncommon in other landscapes. The braided river form accounts for only a relatively small proportion of the total length within mountainous areas, with approximately 8%. However, there are large regional differences which reflect climate, historical and contemporary ice and snow cover and mountain age. The decisive parameters for the development of the geomorphological channel types are soil erosion, stream gradient, glacier cover and climate. Surprisingly, the local geology displayed limited influence on the expression of the channel types.

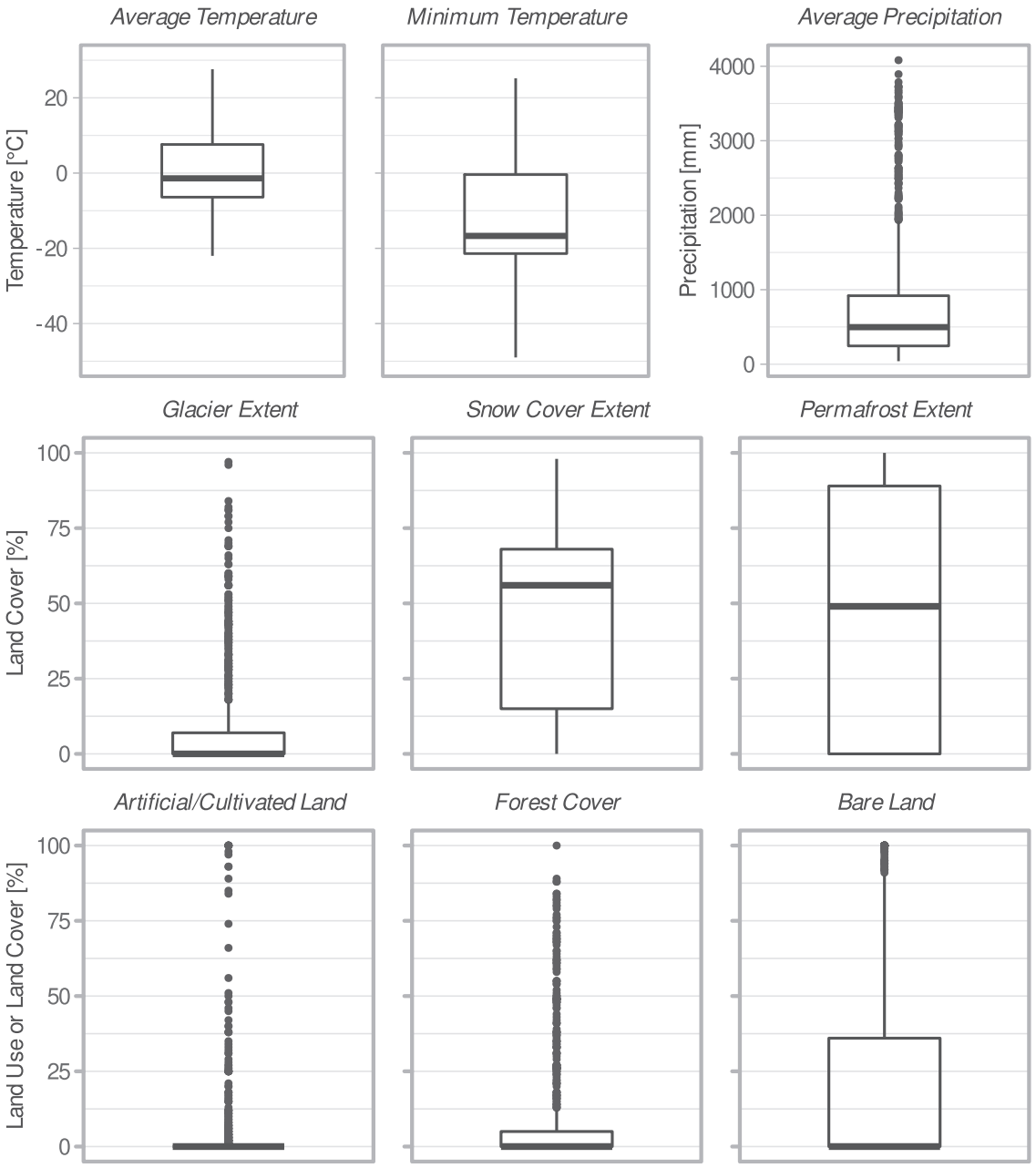

Fig. 11 Selected physical and habitat parameters of braided rivers.

Our study revealed that braided river reaches are characterized by extensive soil erosion, low temperatures, low precipitation and evaporation, and limited forest cover. The catchment areas are characterized by large snow and glacier cover extent and high permafrost percentage. The braided rivers generally occur in high altitudes and have comparatively steep stream gradients. Compared to other channel types, they commonly have lower but variable discharge regimes. The predominant proportion of braided rivers occurs in temperate to arctic boreal regions but a second, smaller distribution is in the dry-hot and vegetation-poor desert areas of the Middle East.

This study provides an initial overview of the physical and ecological relationships and effects of primary parameters on the characteristics of mountain river channel types on a global level.

Future research

However, there are still questions that need to be clarified. In particular, the effects of climate change in connection with the melting of glaciers, warmer temperatures and reduced runoff and sediment availability, must be examined and whether this could subsequently lead to a further decline of the proportion of the distinctive, braided river form.

Appendix: Supplementary material

Supplementary material related to this chapter can be found on the accompanying CD or online at https://doi.org/10.1016/B978-0-12-819166-8.00159-6.

See Also: Human pressures and management of Inland Waters: Physical Impacts of Sand Mining in Rivers and Floodplains; Structures and functions of Inland Waters - Groundwater: Groundwater and Surface Water Interaction; Structures and functions of Inland Waters - Rivers: Effects of Dams on Rivers; Hydrology and Classification of Rivers for Management; Stream Geomorphology; Structures and functions of Inland Waters - Wetlands: Boreal and Temperate River Wetlands

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Boreal and Temperate River Wetlands

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Eutrophic Nutrient-rich.
Geomorphology Study of Earth surface landforms and landform processes.
Hydrosere A typical sequence of organisms, particularly plants, that occur as water-bodies get shallower over time.
Hyporheic flow The flow of water through gravels normally in a river.
Limnophilic Fish that typically live in lakes.
Ombrotrophic mire Mire fed by only precipitation and usually domed above the local watertable.
Paludification Drowning by a rise in the water-table.
Rheotrophic Taking nutrients from flowing water.
Saproxylic Living on dead or decaying wood.

Introduction

River wetlands can be broadly defined as wetlands on river floodplains, and they can be classified in various ways; geomorphologically on their formation or genesis, hydrologically from their principal source(s) of water, and biologically on their ecology/hydroecology, particularly their vegetation. Together the geomorphology and hydrology form the abiotic template that conditions the biotic response, although other factors, most notably climate and land use change are clearly important. As can be seem from Fig. 1 these aspects are inter-related to a large degree, but any floodplain can have a mix partly dependent upon size, climate and history. The aims of this chapter are to summarize the past and present distribution of these systems and examine the interactions of the abiotic templates with ecological processes. This has relevance in conservation, management and restoration, and is a high priority because these ecosystems have been impacted, even before the Anthropocene, more than any other due to the high potential of floodplains for agriculture and human settlement (van Diggerlen et al., 2006). In a recent analysis of hydro-climatic changes of wetlands globally it was found that cold Temperate and Boreal wetlands had experienced the most warming and reduction in runoff in comparison with other biomes (Åhlén et al., 2021).

The distribution of river wetlands in both the Temperate and Boreal zones is closely associated with the distribution of lowland river and floodplains on the Earth's surface. In the Boreal zone nearly all floodplains have been glaciated and so rarely contain sediments or landforms that pre-date the last glacial period. Functioning wetlands (so excluding paleo-systems) are preferentially located along the lower sections of river valleys where the geomorphology is conducive to wetland formation (an exception to this are flow-through mires located above glacial sills in upland valleys). In the Temperate zone the same applies in areas that were glaciated but outside these areas wetlands can be of greater antiquity, especially where there is a tectonic component producing long-term subsidence. This applies to several riverine wetlands such as Padul in Southern Spain and the Lake Balaton wetlands in Hungary. The largest areas of riverine wetlands occur along deltaic river reaches across the freshwater—marine transitional zone,

Type	Formational processes	Typical size (km^2)	Connectivity	Comments
Headwater flow-through mires	Cirques, springs, infilled tarns	0.01-1	High	Sphagnum peat dominated
Valley-floor mires	Glacial or fluvial erosion	0.05-5	High-moderate	Sphagnum peat, also woodland (fens), reedbeds
Channel cut-offs (oxbow wetlands)	River channel change (avulsions)	0.01-0.1 (dep. upon river size)	Moderate-low	Open water to wet woodland
Glacial depressions	Formed on low terraces due to dead-ice or subglacial erosion (kames, kettles etc.)	0.001-0.05	Low	Open water to sphagnum mires, can go ombrotrophic
Undefined alluvial backswamps	Fluvial or glacial erosion	0.1-10	Moderate-low	Sphagnum mires, reedbeds, wet woodland, can go ombrotrophic
Tectonic depressions	Graben-type subsidence	1-10s	Low (internal drainage)	Sphagnum mires, reedbeds, wet woodland, can go ombrotrophic
Delta backswamps	Avulsions, levee formation, coastal processes	0.1-10s	Moderate	Sphagnum mires, reedbeds, wet woodland (drained), can go ombrotrophic

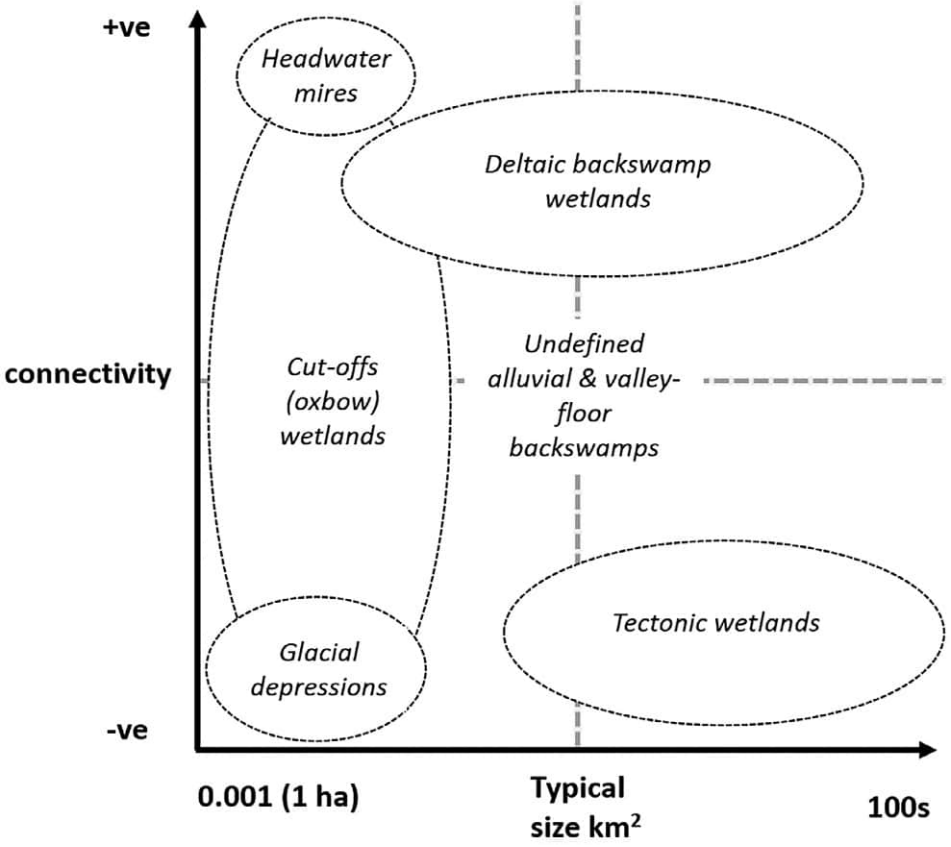

Fig. 1 A classification of temperate river wetlands with typical size and connectivity.

which would naturally make up much of the deltas of all the major rivers in the Temperate zone. However, most have been hugely impacted by channelization, drainage and agricultural improvement leaving only parts of a few such as the Rhone (Camargue), Loire (La Briere), Guadalquivir (Coto Doñana), Danube and Volga, with any functioning wetlands. These systems are also potentially liable to increased saline water-incursion with projected continuing sea level rise.

In glaciated areas there are three principal geomorphic features that produce wetlands; firstly, on-stream lakes that have partly or wholly terrestrialized, secondly back swamp areas with high water-tables but low rates of clastic (non-organic) sedimentation, and lastly cutoff river channels (paleo-channels or oxbow lakes/wetlands). The latter two types are a direct result of river behavior during this Interglacial, including whether the river system is multiple channel (anastomosing) or meandering, and the rates of channel change. An often overlooked mechanism for the development of organic deposits on floodplains is the development of river levees which form due to the rapid settling-out of suspended and saltating sediment from rivers when they flood. The other cause is permanent, or long-term, saturation by high groundwater-tables augmented by floods. Floodplains are normally located at the point at which the regional water-table intersects the land surface, and so springs are often found at the floodplain edge, with upwelling groundwater at topographic low points under artesian flow (pressurized flow). The wetland is also frequently connected at depth to the floodplain water-table and the river level (shallow groundwater).

Many studies have shown that it is the groundwater, and particularly this shallow (alluvial) groundwater, that maintains wetland water-tables and hence wetland biotic functions (Fig. 2). It follows that reductions in regional water-tables affect floodplain wetlands, and sensitive wetlands, where the water budget is finely balanced, are vulnerable to any change in water fluxes such as reduced precipitation. Since it is impossible for societies to control precipitation, and difficult to modify the river hydrograph, although not impossible (Lane, 2017), hydrological restoration of wetlands has therefore generally focused on the option of retaining water by reducing water losses. The fundamental driver of both floristic composition and biotic functions is the high water-table and its augmentation by both groundwater and nutrient inputs from the river. Isolated lakes or wetlands fed by non-calcareous groundwater progress through bryophytic succession to moss-carpets (sometimes forming floating mires) and then to raised or ombrotrophic (rain-fed) mires which rise to a dome above the floodplain surface. Although located on floodplains and draining into the river, these raised mires are not truly river wetlands as their inputs from the river and groundwater are minimal, or zero. However, where the groundwater is base-rich then fens form and since these cannot grow above the water-table (unless they become ombrotrophic) they tend to remain closely connected with the river system even if only in the largest floods. These are the most common river wetlands in the Temperate zone and include monocotyledon (grasses, sedges) dominated systems (e.g., reed-beds), shrublands and wet heaths, and forests in both North America, including Alaska (*Populus-Picea-Alnus-Salix*), and Europe (*Picea-Alnus-Salix*). Here nutrient cycling is controlled by both the groundwater input and also the quality and frequency of floodwater inputs from the river. All of these systems, including on-stream lakes, accumulate organic carbon largely from autochthonous (within lake) production.

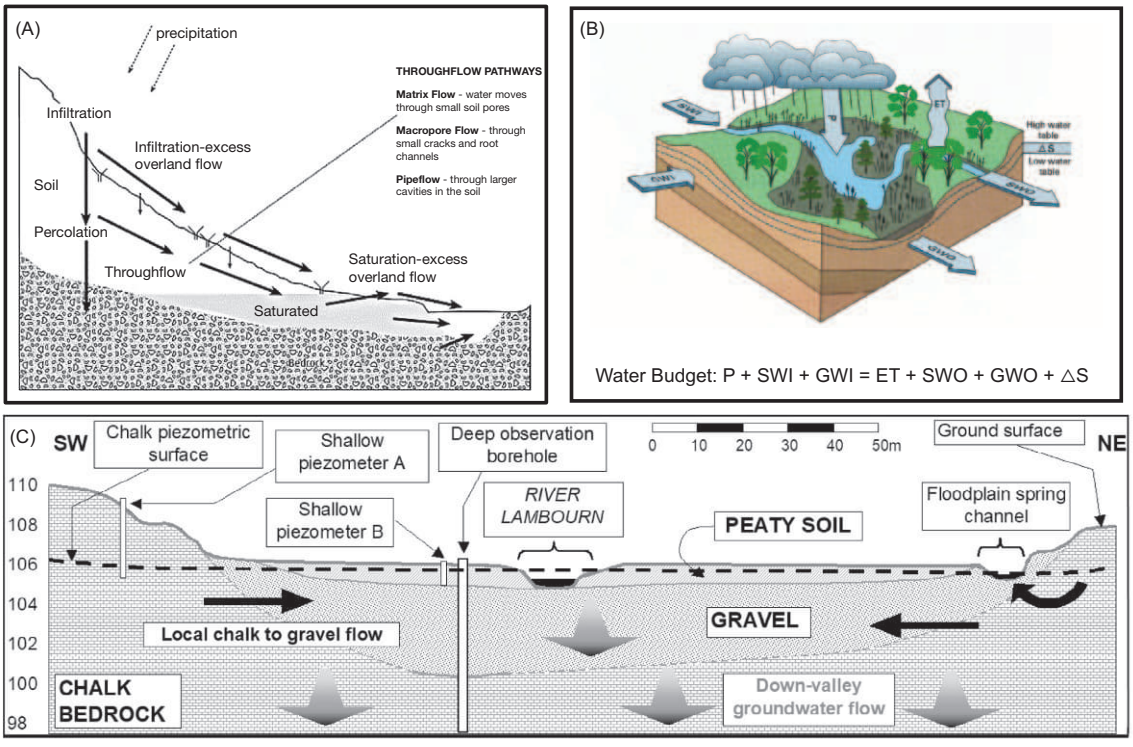

Fig. 2 Riverine wetland hydrology; (A) slope base river-marginal mire with throughflow pathways, (B) a riverine wetland water budget (Carter, 1996), (C) a conceptual model of the hydrological budget for a floodplain on pervious rocks from Grapes et al. (2006). In budget equation P = precipitation, SWI = surface water inputs, ET = evapotranspiration, GWO = groundwater outputs, △S is changes in storage. Permissions: (B) USGS, (C) *Journal of Hydrology*.

Riverine wetlands, carbon storage and ecosystem services

Carbon can accumulate and be stored in riverine wetlands because the annual addition of biomass from vegetation and other inputs exceeds the rate of decomposition and outputs. This is particularly common in the Boreal zone where for much of the year air and ground temperature are below 4 °C thus inhibiting decomposition, and even at higher temperatures soils are often water saturated and anoxic. However, for the rest of the year, and year-round in the Temperate zone, both aerobic and anaerobic decomposition occurs, so these wetlands can also be a source of C emitted to the air in the form of CH_4. It is therefore also possible that if the organic matter falls, or decomposition rates rise, then these wetlands can switch to becoming a C source rather than sink. There are few realistic estimates of the magnitude of C storage in floodplain wetlands but organic carbon (OC) accumulating in the floodplain generally has two sources, from in-situ biomass and from soil erosion upstream. River-borne OC can have three environmental fates: first it can be lost as CO_2 due to microbial activity within the channel system (Wohl, 2016); second, it can be transferred to the ocean bound to particulate matter or in dissolved form and; third, carbon can be stored in floodplains resulting in a long-term C fixation within alluvial wetlands. From a monitoring study of an on-stream boreal fen system Zhang et al. (2020) have shown how CH_4 emissions were lowest close to the stream and highest at intermediate distances.

A typical feature of pre-deforested Temperate floodplains and Boreal floodplains is the localized accumulation of peaty sediments in the form of rheotrophic-eutrophic fens. These peats are part of the sink term prior to disturbance that should be considered when assessing anthropogenic floodplain C, although they are often neglected (e.g., Stallard, 1998). These have about 40–80% organic matter (OM) whereas overbank silt clay deposits may have 2–4% OM on average. Typically, floodplain sediment profiles do not show systematic changes of past decomposition with profile depth, although organic-rich sediments can have a high sensitivity to compaction and humification and so mass accumulation rates should be adjusted for these effects (Ramade, 2003). Calculations from the River Frome, UK, suggest that OM storage in the upper inorganic unit amounts to 348 m^3 ha^{-1} (i.e., post-2700 BCE) whereas the underlying organic rich unit contains about 3500 m^3 ha^{-1} and although its date of initiation is not known it is unlikely to have been deposited over >4000 years ago (Brown et al., 2018). An approximation for a pre-deforestation temperate floodplain is a mosaic of wet woodland and open reed/sedge dominated fen (nutrients moderate to high). Alder (*Alnus*) leaves can contribute 5–10 t ha yr^{-1} and sedge fen and reed beds up to 20 t ha yr^{-1} (Lüscher et al., 2004). However, this is offset by carbon loss as methane (CH_4) and CO_2 outgassing associated with microbial metabolism which depends upon the morphology and connectivity with the main channel (Foster et al., 2012). Overall Ricker et al. (2013) have shown that riparian forest can sequester twice as much as upland plots primarily due to lower microbial respiration and CO_2 efflux.

Anaerobic conditions common on floodplains, particularly in the Boreal zone, are also conducive to methane (CH_4) and nitrous oxide (N_2O) production. In periodically inundated systems, such as floodplains, methane emissions can be highly variable. In a study of the carbon implications of floodplain restoration on a section of the river Danube, Welti et al. (2012) showed that the hydrology, and particularly length of water interchange period, regulated potential denitrification rates but that more efficient N and C cycling could produce an overall reduction in potential N_2O emissions.

A potential additional factor which may ultimately resolve the short vs. long-term dynamics question, is the discovery that anaerobic microbial decomposition is not just energy and mineral limited (reduction of N and S based compounds) but thermodynamically limited by microbes "ignoring" carbon compounds that do not provide enough energy to be worthwhile to degrade and so end up accumulating (Boye et al., 2017). From these results it would appear that in their entirety and in the short-term, floodplain wetlands may be either carbon sources or sinks, depending on their hydrological regime, and can switch between being carbon sinks to becoming net carbon sources at a variety of temporal scales. This switching can be a natural process due to seasonal or other factors or can be affected by human management (Wohl, 2016). Wetlands are also an important source of riverine carbon (e.g., Yukon—30% from wetlands) which can be characterized using fluorescence spectroscopy (e.g., Spencer et al., 2012) and Fourier transform infra-red (FTIR) absorbance spectroscopy and which can carry adsorbed pollutants (Gallé et al., 2004).

Carbon storage is just one of a number of ecosystem services that river wetlands can provide. One of the most fundamental is their potential to attenuate flood-peaks and it is the decoupling (or reduced connectivity) and drainage of alluvial wetlands that is partly responsible for increased flood peaks downstream (Wohl, 2016). The reconnection of large back swamp wetlands, and even river cutoffs, is therefore a practical and efficient way to reduce at least intermediate flood hazard (Acreman and Holden, 2013). A second ecosystem service is the stripping of nutrients and pollutants from river discharge. This is far more complex and less well understood, but data from constructed wetlands in the temperate zone suggest that they can be effective in trapping diffuse nutrients/pollutants, such as phosphorus, from agricultural land (Ockenden et al., 2012). This has implications for climate-driven changes in river channel behavior, such as an increase in bank erosion, which could result in increased remobilization of these stored nutrients into the fluvial system.

Concepts and models

There are four concepts that have increased our understanding of the ecology of river wetlands over the last 100 years.

1) *Terrestrialization and the hydrosere*—the infilling of floodplain waterbodies and the systematic trajectory of plants with decreasing water depth over time: as used by Dachnowski (1912) and Clements (1916) it remains fundamental to our understanding of wetland status and change (Mitsch and Gosselink, 2015), although, if there is a climax state at all, it is either wet-woodland or

sphagnum mire (Walker, 1970; Klinger, 1996). Wetlands may also expand into 'upland' forest through the rise in the water-table or paludification (Klinger, 1996). The vast majority of peatlands on floodplains in the Temperate zone have lake sediments under the peat revealing that they were formerly lakes. This is a function of our current interglacial state whereby biotic production and catchment erosion inputs sediment to fluvial systems. This can be shown now by new molecular techniques (see "Methods" Section).

2) *The river continuum concept and wetland trophic structure*—the systematic change in ecology, particularly feeding guilds and organic particulate matter downstream in rivers as first outlined by Vannote et al. (1980). Although only directly applicable to on-stream wetlands, and even then only partially, due to discontinuities (Ward and Stanford, 1983), the downstream changes it describes are important for the nature of the riparian and littoral zones and wetlands along a river system.
3) *The flood-pulse* concept explains how the hydrograph (flood and drought) controls the lateral exchange of water and nutrients from the river into the wetland (Junk et al., 1989). Its relevance is therefore directly proportional to the connectivity of a wetland to the river system. The input of sediment is also important especially in deltaic wetlands.
4) *Intermediate disturbance hypothesis* which states that levels of disturbance that are neither too rare, nor too frequent, promote high biodiversity due to the balance of competition to physical disturbance and limits to re-colonization. Although normally attributed to Connell (1978) its history goes back to studies of competition in herbaceous vegetation (Grime, 1973) if not earlier (Wilkinson, 1999). Again although not directly developed for wetlands this hypothesis appears to be particularly applicable to many systems with complex trophic structure and a strong abiotic element which is not constant. The work of beavers (*Castor fiber/canadensis*, see "Restoration" Section) are an obvious example, but the interaction of fluvial processes with wetland plants creates high inter-patch heterogeneity, short-lived niches and structural complexity, all of which help to maintain high biodiversity (Davis et al., 2007; Brown et al., 2021).

New methods

The methods available for both recording and investigating the distribution, extent and processes of floodplain wetlands have increased dramatically in recent years. In particular, our ability to map at high definition has increased due to the availability of high-resolution satellite imagery (sub-m with GeoEye-1) in multiple wavebands including near infra-red (NIR). This has been matched by a growth in even higher resolution airborne remote sensing and also Lidar (Light detection and ranging) which can produce cm-scale digital elevation models (DEMs). This potentially also allows automated estimation of biomass, although this is still challenging for structurally complex non-forested vegetation (Riegel et al., 2013) when terrestrial laser scanners (TLS) may be a better option (Owers et al., 2018). Important variables such as total N concentration can be measured from a variety of hyperspectral sensors (Luo et al., 2016) including the Sentinel platform for soil moisture (Dabrowska-Zielinska et al., 2018; Klinke et al., 2018). The full capabilities of these new technologies have yet to be realized, but they offer the potential of mapping vegetation type, or vegetation assemblages, and the estimation of vegetation cover, photosynthetic area and other physiological variables particularly through the use of NIR and hyperspectral sensors.

A second area of development has been in hydro-ecological instrumentation. Electronic miniaturization has now made it both possible, and affordable, to install multiple automatic weather stations, thermometers, tensiometers, water quality sensors and water-level recorders linked to cheap data-loggers. This potentially allows several sites to be measured, or for large sites enables intra-site variability to be quantified. One reason for this monitoring is to provide validation of remote sensing-based monitoring including synthetic aperture radar for surface temperatures and thermal dynamics (Kaplan et al., 2018).

The last area of method development has come from the explosion of molecular techniques and particularly environmental DNA (eDNA). It is now possible to use water, surface peat, or sediment samples to determine a large proportion of the species present on a site, including plants, invertebrates, fish and algae both today (Taberlet et al., 2018) and in the past (Capo et al., 2021). A major effort worldwide is taking place to maximize the efficacy of this methodology and there are various different strategies (shotgun sequencing, metabarcoding, capture-probes) but the aim is to record at least the presence of a very high proportion of the taxa present (Alsos et al., 2018), and even, as in the case of fish, some estimates of abundance or biomass. To-date these new techniques have still to be improved to assess the condition of river wetlands but the potential is there. A variant, sedimentary ancient DNA (sedaDNA) can even be used to record site history back in time (Capo et al., 2021). An example is the Holocene hydroseral record of a small infilled lake system in SW Scotland, United Kingdom shown in Fig. 3.

Restoration, rewilding and urban river wetlands

Although the ecosystem service and biodiversity value of riverine wetlands has been the driver for floodplain restoration for over 30 years (an early example being on the Upper Rhine (Moss and Monstadt, 2008)), there was relatively little progress in Europe until the adoption of the Water Framework Directive. Restoration, or rehabilitation, generally involves trying to reconnect the wetland with the river to recreate something approaching a natural inundation regime. Actions such as blocking drains, not clearing-out aquatic vegetation, scrub removal and mowing, have been shown to have potential climate-mitigating effects (Bereezowski et al., 2018). However, a major problem is that success varies depending upon the catchment hydrograph, sediment conveyance and water quality, which for transboundary rivers may not even be under national control. Some of the best known

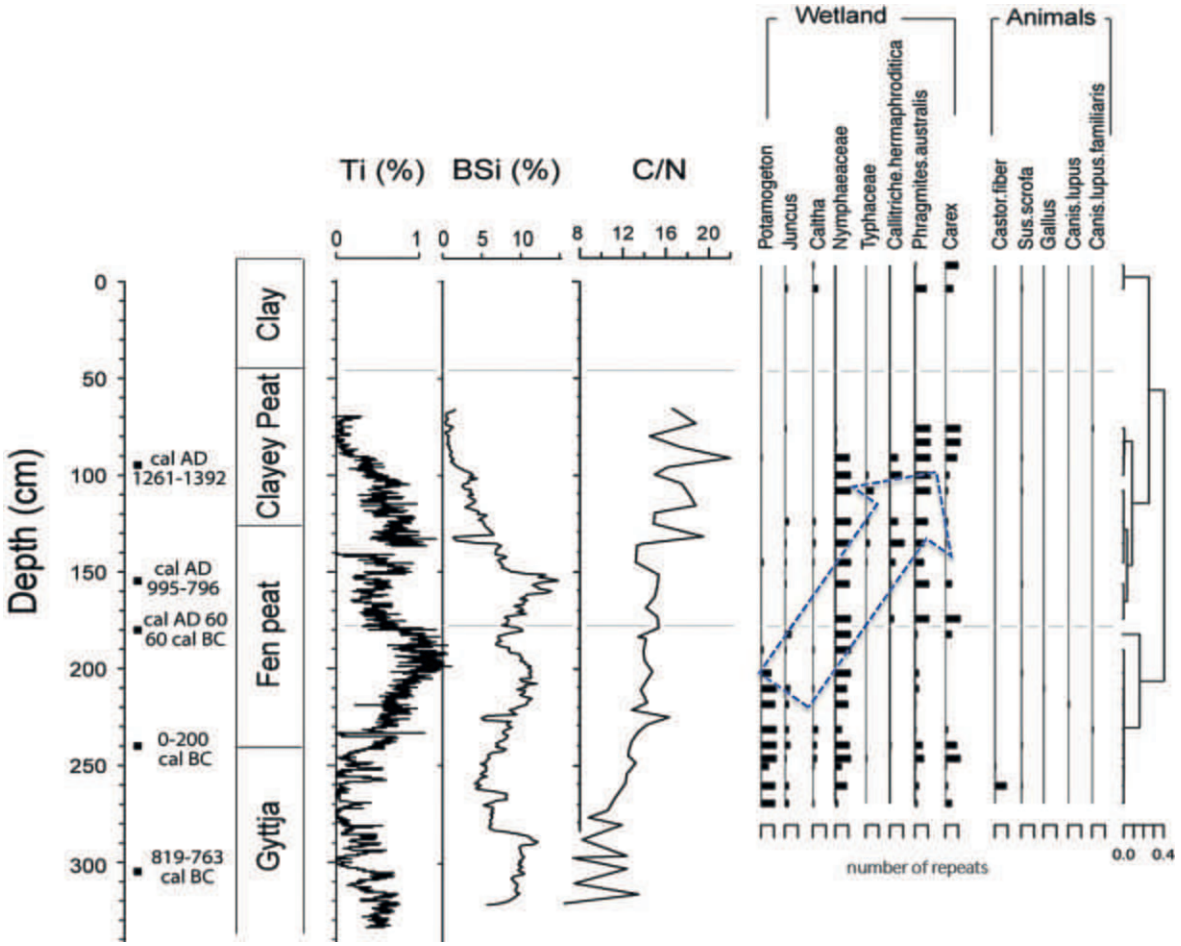

Fig. 3 The hydroseral succession signal of a terrestrialized on-stream lake-fen system form SW Scotland (Black Loch of Murton), United Kingdom determined using sedaDNA from metabarcoding. From van Hardenbroek Subm.

examples are attempts to reconnect wetlands with major rivers, such as reconnecting the Danube or the Rhine with more of its river corridor (e.g., van Alphen, 2019) and many smaller rivers in Europe (Gumiero et al., 2013; Brown et al., 2018). In some cases, this has also included attempts to restore biotic processes by re-introducing large herbivores such as ancestral (heck) cattle in the Netherlands and onto the Danube Delta (Stokstad, 2015). This is part of the growing fashion to 'rewild' wetland, or former wetland, areas. Whilst it can be argued that 'rewilding' is an inaccurate term, as these are still modified ecosystems, it can restore at least some biotic template functions. The best example is the recent fashion for beaver reintroduction across Europe (Vehkaoja, 2016; Brown et al., 2018). Re-introduction monitoring has shown that especially in headwaters, beavers increase dead wood and biodiversity in a range of organisms from beetles to bryophytes through paludification and increasing wetland area (Puttock et al., 2015; Brown et al., 2018).

Many cities in Europe were developed on or close to major wetlands (due their location as the lowest river-bridging point) and it follows that there is a huge potential for wetland restoration in these cities (Ehrenfeld, 2000). This also has been increased by the changing sewage treatment practices with the redundancy of so-called sewage farms and other large areas of effluent settling ponds. Cities with riverine wetland restoration schemes include London, United Kingdom (Barnes Elms reservoirs), Kristianstads, Sweden (Vattenrike), Amiens, France (Les Hortillonnages) and Bucharest, Bulgaria (Văcăreşti). This is part of the movement to create 'green' and resilient cities as recognized in the RAMSAR Wetlands Cities list.

Three examples

The three examples given here were selected to cover a range of spatial scales and river-wetland types. The first is typical of many, now isolated, wetlands on small temperate river floodplains, the second represents multiple small sites across the Boreal landscape, and the third typifies multiple wetlands in a large deltaic fluvial environment.

Small temperate floodplain wetland

Small wetlands on small-medium sized floodplains were extremely common up until the 18th–19th Century CE in both Europe and North America but were almost entirely drained for pasture, agriculture and development (Lewin, 2011). Small survivals occur including a 10 ha wetland on the river Soar in Central England (Narborough Bog; Lat. 52.575820 Long. –1.191096). The survival is so rare that local ecologists thought it had been created by the impeded-drainage following construction of a railway line in the 19th century CE. However, paleoecology and radiocarbon dating revealed that it had existed for the last 10,000 years accumulating at a slow rate of c. 0.1 mm year^{-1}. Pollen analysis has revealed that the site had a typical, but rarely preserved, vegetation history for lowland river wetland in the United Kingdom. It had been initiated about 10,000 years ago as a reed-bed in a wide-shallow cut-off channel, which was then colonized by birch (*Betula*), willows (*Salix* sp.) and finally alder (*Alnus*) surrounding areas of continued reed-bed. Whilst the wetland had this trajectory, the surrounding woodland changed its composition over time, and was cut-down and replaced by grassland and arable fields around 5000 years ago in the late Neolithic to early Bronze Age (Brown and Hatton, 2002).

From a management perspective, however, there was evidence that the reed-bed dominated by common reed (*Phragmites australis*) was drying out, and so the site was monitored from the early 1990s prior to modelling its water budget (Bradley, 1996, 2002). Using a three-dimensional groundwater model, coupled with monitoring, it was shown that the overall fluxes are highly sensitive to variations in hydraulic conductivity with depth and the water table configuration reflects the balance between horizontal and lateral water flow through the wetland complicating its relationship to stage. As Fig. 4B shows there are marked changes in the stratigraphy across the wetland that determines the 3D distribution of hydraulic conductivity. The modelling also enabled sub-surface flows from the wetland to the river Soar to be quantified, demonstrating the importance of sites like this in supporting river base-flow and probably flow through into the substrate (hyporheic flow).

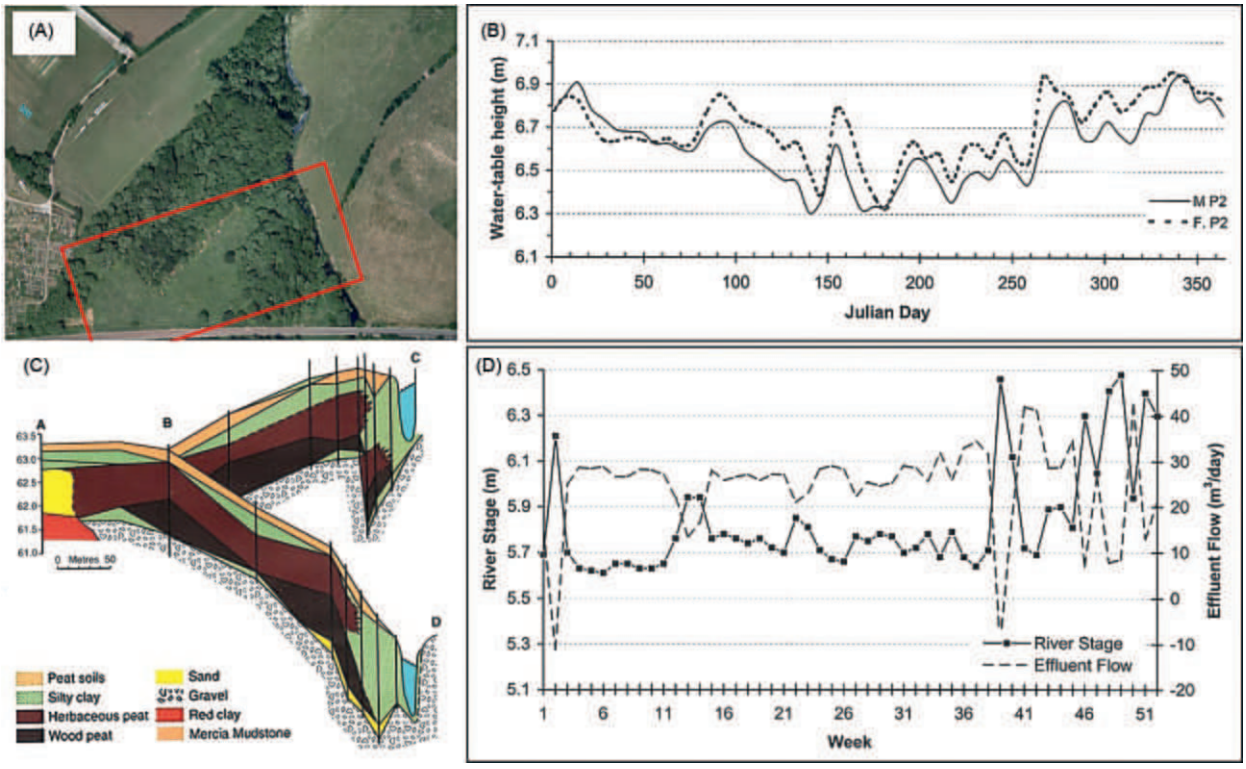

Fig. 4 Narborough Bog hydrological modelling. (A) aerial photography of the site with the modelled area (red box), (B) stratigraphy of the wetland, modelled (C) wetland water levels and d. effluent flow from the wetland to the river in 1992. Adapted from Bradley C (2002) Simulation of the annual water table dynamics of a floodplain wetland, Narborough Bog, UK. *Journal of Hydrology* **261**: 150–172.

Boreal swamp forests

Boreal swamp forests have been shown to be biodiversity hotspots in the relatively low biodiversity coniferous forests of Scandinavia. The rare surviving examples, which are dominated by old-growth Norway spruce (*Picea abies*), have particularly high bryophyte, lichen and fungal diversity (Hörnberg et al., 1998; Økland et al., 2001). Vegetation studies by Økland et al. (2003) have shown that approximately 20% of the enhanced biodiversity of vascular plants is due to the wetland conditions, but also that they show no biogeographical patterns related to local successional conditions. They are located at headwaters (i.e., first order streams) and are generally underlain by peat. An important aspect is the accumulation of dead wood and old trees and although they are affected by fires, it is at a lower frequency than the surrounding dry-land forest. Paleoecology (particularly pollen analysis) has suggested that at least some may have developed from birch-alder-pine (*Betula-Alnus-Pinus*) tall herb forest to spruce-bog moss (*Picea-Sphagnum*) swamp forest due to cultivation and grazing (Segerström et al., 1994). The conservation of this wetland type is largely dependent upon the cessation of logging in this region. However, a complication to both the history of these systems and their future is the presence, or absence, of beavers (*C. fiber*). Studies in Northern Finland have shown that beavers significantly increase both coarse and fine woody debris and create different saproxylic communities and increasing overall biodiversity (Thompson et al., 2016). The beaver today has a relatively restricted distribution in Scandinavia but was formerly much more widespread (Halley et al., 2012). In North America beaver is the major natural biotic engineer of Boreal and cool Temperate forest biodiversity damming both lakes and rivers (Martell et al., 2006; Naiman et al., 1988; Rosell et al., 2005). As many re-introductions across Europe have shown, the beaver's effects on all Temperate and Boreal landscapes is to increase the area of wetland through paludification, and so it is a critical biotic component of riverine landscapes both in the past and increasingly in the future as it offers a cost-effective method of ecological enhancement (Thompson et al., 2016; Brown et al., 2018).

Multiple wetlands in a large temperate deltaic system

The Danube Delta in Romania alone contains over 300 lakes, the ecology of which have been researched extensively due to the international importance of the system (RAMSAR site No. 521, 647,000 ha). Using a combination of remote sensing, hydrological and ecological monitoring, Coops et al. (2008) sub-divided these lake and wetlands into three types; (a) inflow lakes close to the river with a high flushing rate and high suspended sediment but low chlorophyll concentrations, (b) large relatively deep lakes with intermediate residence times and high pondweed (*Potamogeton*) cover that collapses during the summer and with high eurytopic fish, and, (c) smaller lakes a greater distance from the river with long residence times, in which water quality is strongly affected by large floating reed beds with a high vegetation cover of hornwort (*Ceratophyllum demersum*) and a stonewort (*Nitella obtuse*), and limnophilic fish population tolerant of low dissolved oxygen levels. From this and similar analyses (Tockner et al., 1999; Coops et al., 1999; Covaliov et al., 2003; Navodaru et al., 2002) the strongest driving factors are distance from the river and the interactions between seasonal plant growth and light conditions (Fig. 5). The persistence of high connectivity in the system means that there is still a high potential for large-scale restoration despite major hydro-geomorphological modification of the Delta and the three distributary channels of the Danube.

Although the history of the entire delta and the morpho-dynamics of its fluvial network are well-known (Giosan et al., 2005; Vespremeanu-Stroe et al., 2013) its vegetation history is rather poorly known as the first pollen diagram has only recently been completed (Hanganu pers. comm.). This shows that over the last 8000 years the aquatic ecology of the Somova-Parches wetland system (N45°12′23.54″; E28°39′40.51) has fluctuated in both structural and floristic composition in tandem with the lithology and connectivity with the Danube River. During periods of high connectivity, silt and clay is deposited and aquatics are low overall and dominated by cat-tail (*Sparganium*) and bulrush/reedmace (*Typha*), with water-lily (*Nuphar*) and *Myriophyllum* increasing as organic content has increased with reduced connectivity in the last 2000 years. Other aquatics, e.g., *Potamogeton* and water-starwort (*Callitriche*) appear and disappear more randomly. This also reflects increasing nutrient content in the system and is consistent with evidence from diatoms and dinoflagellates (Giosan et al., 2012), as well as the limited historical data that are available, and land use modelling (Pistocchi et al., 2015).

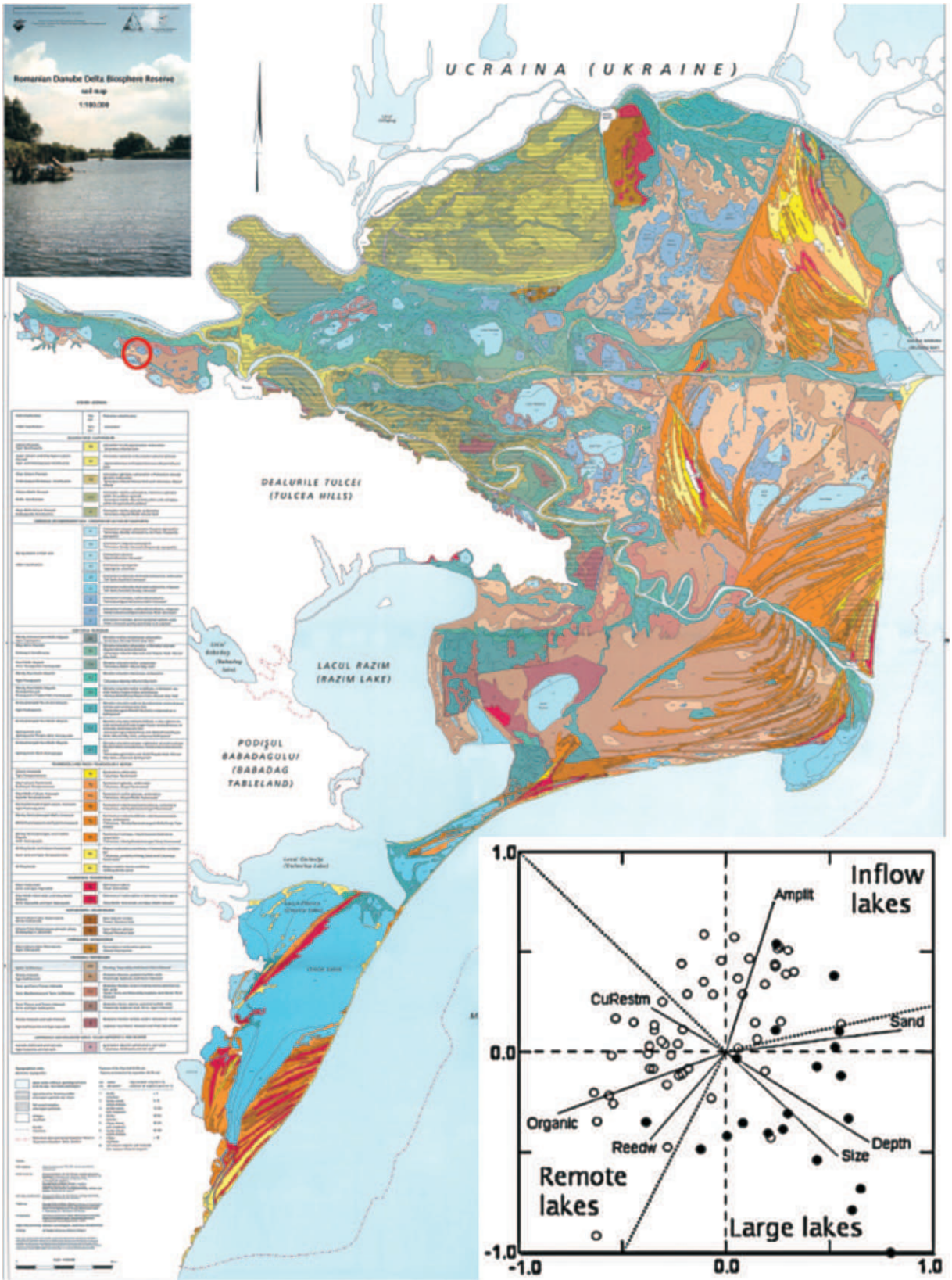

Fig. 5 Lakes and soils of the Danube Delta from Munteanu and Curelariu (1995), with Somova site (red circle) and inset lake PCA diagram using hydromorphological variables from Coops et al. (2008). Map reproduced by permission of Academy of Agricultural and Forest Services, Research Institute for Soil Science and Agrochemistry, Bucharest, Directorate General for Public Works and Water Management and Coops et al. (2008) from *River Research Applications* Wiley. From Munteanu I and Curelariu G (1995) *Romanian Danube Delta Biosphere Reserve soil map 1:100 000*. Academy of Agricultural and Forest Services, Research Institute for Soil Science and Agrochemistry, Bucharest, Directorate General for Public Works and Water Management.; Coops H, Buijse LL, Buijse AD, Constantinescu A, Covaliov S, Hanganu J, Ibelings BW, Menting G, Navodaru I, Oosterberg W, Staras M and Török L (2008) Trophic gradients in a large-river delta: Ecological structure determined by connectivity gradients in the Danube Delta (Romania). *River Research and Applications* **24**: 698–709.

Conclusion and synthesis

River wetlands in the Boreal and Temperate Zone are geomorphologically created, hydrologically maintained and biologically mediated ecosystems that can provide valuable ecosystem services. The examples presented here illustrate the hydrological importance of site stratigraphy and hence landscape history, the role of small wetlands in creating biodiversity hotspots in Boreal forest, and the interaction between wetland connectivity and long-term changes in sediment quality and quantity. Despite wider recognition of their value, attempts at large-scale restoration are limited by the continued human pressures on floodplains and the need to improve water quality and supply at the catchment scale. Several new techniques (remote sensing, instrumentation and molecular monitoring) provide us with potentially powerful tools to improve our understanding of the unseen aspects of their dynamics which may provide clever solutions to the problems of restoration. This will also be required in order to estimate the sensitivity of these systems to the changes in temperature and precipitation that are occurring at a rapid rate especially in the northern Boreal Zone.

Knowledge gaps

- Biotic effects on wetland resilience to climate and catchment change.
- Flood-wetland interactions for both discharge and nutrients.
- Groundwater contributions to wetland budgets.
- Effects of ecological management strategies on carbon sequestration.
- Potential costs and benefits of biotic re-introductions.
- Potential disease sensitivity of riverine wetlands.
- Remote sensing of wetland hydrological balance variables.

See Also: Human pressures and management of Inland Waters: Case Studies of (Semi)Constructed Wetlands Treating Point and Non-point Pollutant Loads to Protect Downstream Natural Ecosystems; Structures and functions of Inland Waters - Rivers: The River Continuum Concept; Structures and functions of Inland Waters - Wetlands: Mountain Rivers: A Global Overview of River Channel Forms, With a Focus on Braided Rivers; Riparian Vegetation of Gravel-bed Rivers - A Global Review

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Tropical Large River Wetlands

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Glossary

Anabranching River sections that divert from the main channel and rejoin the main channel downstream, often because of the formation of islands.
Catchment area Defined through water sheds, which are located upon the highest isolines (contour lines) of basins, the catchment area is the area of land from which water flows to the erosion base (river, lake, or depression).
Clay minerals Common ultrafine-grained weathering products, clay minerals are hydrous aluminum phyllosilicates with variable amounts of Fe, Mg, alkali metals, alkaline earths and further cations.
(Ecological) disturbance Temporary change in environmental conditions that causes a pronounced change in an ecosystem, including, for example, events such as fire, floods, storms, insect outbreaks, volcanism, or trampling.
(Ecological) succession Process of change in species structure of an ecological community over time.
Endemism Refers to species that are native and exclusive to a single defined geographic location (e.g. island, state, continent, or any other defined zone).
Flood pulse (concept) Explains how periodic inundation and drought (flood pulse) control the lateral exchange of water, nutrients, and organisms between the main river channel and the connected floodplain (Junk et al., 1989).
Hydrochory Dispersal of diaspores (fruits, seeds, spores) by water.
Ichthyochory Dispersal of diaspores (fruits, seeds, spores) by fish.
Macrophyte A plant that grows in or near water and is either rooted as emergent or submergent plant, or non-rooted (free-floating).
Net primary productivity Net carbon gain by plants, expresses the balance between the carbon gained by gross primary production (i.e., photosynthesis) and carbon released by plant respiration.
River terrace Bench or step that extends along the side of a valley and represents the former level of the valley surface—as a result of any hydrological or climatic shift that causes renewed down-cutting (incision).

Definition, distribution and extent of tropical large-river wetlands

Large rivers were first defined by Inman and Nordstrom (1971) and Potter (1978) by four main characteristics—they drain large basins, are very long, have high water discharge and transfer a considerable amount of sediment. There are several exceptions in one or more of Potter's characteristics of large rivers. The Nile River, for example, is the longest river on Earth, but is not included in the 50 largest rivers in regards to water and sediment discharge (Table 1). Likewise, the Negro River, an Amazon River tributary, ranks among the 10 largest rivers on Earth contributing approximately 35% of the immense total water discharge of the Amazon River, but carries less than 1% of the Amazon river system sediment discharge (Table 1). Here, we concentrate on tropical large rivers that rank among the largest rivers on Earth in either water or sediment discharge, or both combined.

Along their middle to lower courses, large river wetlands are mostly composed of fringing floodplains. These are defined as "low areas of land that are subject to inundation by lateral overflow waters from rivers or lakes with which they are associated"

Table 1 Selected tropical large rivers and associated floodplains of international importance.

	Mean annual discharge ($m^3 s^{-1}$)	*Drainage area ($10^3 km^2$)*	*Sediment discharge (Mt $year^{-1}$)*	*Countries within main drainage area*	*Associated wetlands*	*Sources (examples)*
South America						
Amazon	209,000	6100	1000	Ecuador, Bolivia, Peru, Colombia, Venezuela, Guyana, French Guyana, Surinam, Brazil	Large-river wetlands (várzea)	Junk et al. (2011, 2014)
Orinoco	35,000	950	150	Brazil, Colombia, Guyana, Venezuela	Llanos de Orinoco	Lewis et al. (2000) and Godoy et al. (1999)
Madeira	32,000	1360	450	Peru, Bolivia, Brazil	Llanos de Moxos	Hamilton et al. (2004)
Negro	28,400	696	8	Venezuela, Colombia, Brazil	Large-river wetlands (igapò), Roraima and Rupununi floodplains	Junk et al. (2015)
Japurá (Caquetá)	18,600	248	33	Colombia, Brazil	Large-river wetlands (várzea)	Duque et al. (2002) and Wittmann et al. (2004)
Paraná and Paraguay	18,000	2600	112	Bolivia, Brazil, Paraguay, Argentina	Pantanal	Damasceno et al. (2005), Nunes da Cunha and Junk (2011), and Junk et al. (2021)
Africa						
Congo	40,900	3700	32.8	Central African Republic, Cameroon, Gabon, D.R. Congo, Angola, R. Congo	Cuvette Centrale	Campbell (2005)
Niger	5589	2117	32	Guinea, Mali, Niger, Benin, Nigeria	Inner Niger Delta	Gupta (2011)
Zambezi	4200	1330	51	Zambia, Angola, Namibia, Botswana, Zimbabwe, Mozambique	Kariba lake, Cahora Bassa Lake	Moore et al. (2007)
Benue	3400	3380	No data	Nigeria, Cameroon, Chad	Lagdo Lake	Delphine et al. (2015)
Nile	2700	3255	160	Burundi, Ruanda, Tanzania, Uganda, South Sudan, Sudan, Egypt	Sudd	Rebelo et al. (2012) and Dumont (2009)
Senegal	650	337	2.2	Mali, Mauritania, Senegal	Ndiael wetlands	Isupova and Mikhailov (2008)
Asia						
Brahmaputra	20,000	610	520	China, India, Bhutan, Bangladesh		Islam (2016) and Kumar et al. (2019)
Mekong	15,000	795	145	China, Myanmar, Laos, Thailand, Cambodia, Vietnam	Tonle Sap	Wang et al. (2011)
Irrawaddy	13,000	414	364	China, Myanmar		Kravtsova et al. (2009)
Ganges	12,000	975	329	Nepal, India		Das et al. (2013)
Salween	6700	325	180	China, Myanmar, Thailand		Chen et al. (2019)

(Junk, 2002). This definition includes deltas (both coastal and inland) and estuaries (Tockner and Stanford, 2002). Following Brinson and Malvárez (2002), water sources contributing to inundation originate from lateral overflow, groundwater, upland sources, and direct precipitation. Besides floodplains that fringe river courses, several large tropical rivers also periodically inundate depressions during the rainy seasons mostly through backwaters which affect their tributaries or the main rivers during the high-water period, which creates large and important seasonal wetlands of international importance for biodiversity and ecosystem services. Examples in South America are the Pantanal (Paraguay River, Brazil-Bolivia-Paraguay) comprising 160,000 km^2, the Llanos de Moxos (Beni River, Bolivia) with 110,000 km^2, and the Brazilian Araguaia River wetlands (88,000 km^2, Irion et al., 2016) in the SW-Amazon. In Africa, most extensive wetlands associated to backwater effects are the Cuvette Centrale (Congo River, D.R. Congo, 145,000 km^2), and the Sudd (Nile River, South Sudan, 130,000 km^2). Smaller, but very important wetlands for biodiversity may also undergo huge seasonal changes in extension, such as the Okavango Delta, that increases from 3000 km^2 during the dry season to up to 16,000 km^2 during the rainy season (Mendelsohn et al., 2010). In Asia, freshwater marshes associated to rivers or lakes are the most common wetland type (Gopal, 2013), and most of them also expand several-fold during the flooding season. For example, the lake Tonle Sap in Cambodia shrinks and expands from 2500–15,000 km^2 as it gets flooded by the Mekong River (Campbell et al., 2006).

Global wetland estimates for the tropical and subtropical regions (excluding areas covered by open water) derived through remote-sensing range between 2.8 million km^2 (Cogley, 2003) to 4.8 million km^2 (GLWD-3 data, Lehner and Döll, 2004). A major problem in wetland mapping is the lack of classification systems that take into account specific hydrological conditions and plant communities (Junk et al., 2011, 2014). Most tropical large-river floodplains consist of a mosaic of habitat types, from year-round aquatic to entirely terrestrial, and in addition often include associated wetlands, such as internal deltas, river terraces, marshes and swamps, the latter often subject to inundation from local sources that drain through floodplains into the river system (Mertes, 2000; Hamilton, 2008). Therefore, permanently flooded habitats (i.e., swamps) and habitats with seasonally drying soils (i.e., marshes) are often not included as floodplains, although they may cover large areas in nearly all tropical large-river floodplains that are fed by rivers with seasonally oscillating water levels. Irrespective of the lack of a unified wetland classification system, the available global wetland data sets (Stillwell-Soller et al., 1995; Cogley, 2003; Lehner and Döll, 2004; Gumbricht et al., 2017) for tropical and subtropical regions agree that large-river wetlands are most extensive in South-America (approx. 1.6 million km^2), followed by Africa (1.3 million km^2), Asia (approx. 1.0 million km^2), North-and Central America (approx. 0.8 million km^2), and Australia and Oceania (0.3 million km^2). Out of these, large-river floodplains cover between 5% and 35%, depending on how floodplains are classified (i.e., if include associated swamps, marshes, and further wetland types).

Environment of large rivers

Flood regimes and inundation

Most tropical large rivers have highly seasonal discharges and their floodplains and associated wetlands are subject to predictable water-level fluctuations. Many experience a monomodal flooding pattern with one high-water and one low-water period during the course of the year. This pattern is driven by the annual shift of the Intertropical Convergence Zone and/or monsoonal climates that determine patterns of annual rainfall across a vast catchment area. Rivers that have catchments on both sides of the equator or that drain different (i.e., non-inner tropical) climate zones show slightly bimodal flood regimes, such as the Magdalena River in Colombia (Ricaurte et al., 2019) and the upper Negro River in the Amazon basin (Montero et al., 2014), or the Zaire River in Africa.

The magnitude of seasonal water-level changes along the mid- to lower courses of large tropical rivers may range up to 10–15 m, as in the Orinoco and Amazon rivers in South America, 6 m at the Niger and Benue Rivers and 2–3 m at the Congo River in Africa, 5–6 m at the Brahmaputra and Ganges Rivers, and up to 7–8 m in the Irrawaddy and Salween Rivers in Asia (Schwatke et al., 2015, Fig. 1). Variations in local flood regimes differ with geological and orographic framework of landscapes, the altitudinal ranges and slopes that rivers cross, channel widths and depths, the size of catchment areas, the presence of glaciers in their catchments, as well as the variability of water losses through evaporation and plant transpiration. The influence of anthropogenic activities in the catchment, such as water deviation, as well as the construction of dams, reservoirs and flow regulation of river channels strongly influence hydrology. Nevertheless, flood regimes of some tropical large-river wetlands tend to be stable over relatively long periods of time, a factor of particular importance for wetland organisms and communities, whose life histories and interactions are intricately linked to predictable annual variation in flood height and duration (Lewis et al., 2000).

Seasonal inundation regimes, or the flood pulse (Junk et al., 1989), provide the main environmental forcing factor for the biota in tropical large river wetlands. Organisms living in these floodplains not only tolerate, but require these water-level fluctuations for the long-term survival of their populations, including many fish and invertebrate species with spawning and feeding migrations between rivers and floodplains (i.e., Welcomme, 1979; Goulding, 1980; Lowe-McConnell, 1987; Adis and Junk, 2002; Correa et al., 2015). Many animal species synchronize their life cycles with the hydrological cycle, such as mammals, birds, reptiles and amphibians (i.e., Junk and da Silva, 1997; Tomas et al., 2011). Herbaceous and woody plant species have specific anatomical and physiological adaptations to overcome temporarily hypoxic conditions during the flooded periods, and reproductive strategies that are closely tied to the timing of floods. Many aquatic and semi-terrestrial herbaceous species are specialized to tropical and subtropical floodplains with numerous examples of wetland-specialized species and genera on each continent (Sculthorpe, 1985). In the Amazon basin, where seasonal water level oscillations are interpreted as relatively long lasting over evolutionary periods, a significant proportion of floodplain tree species are endemic to its floodplains (Wittmann et al., 2010, 2013, 2017).

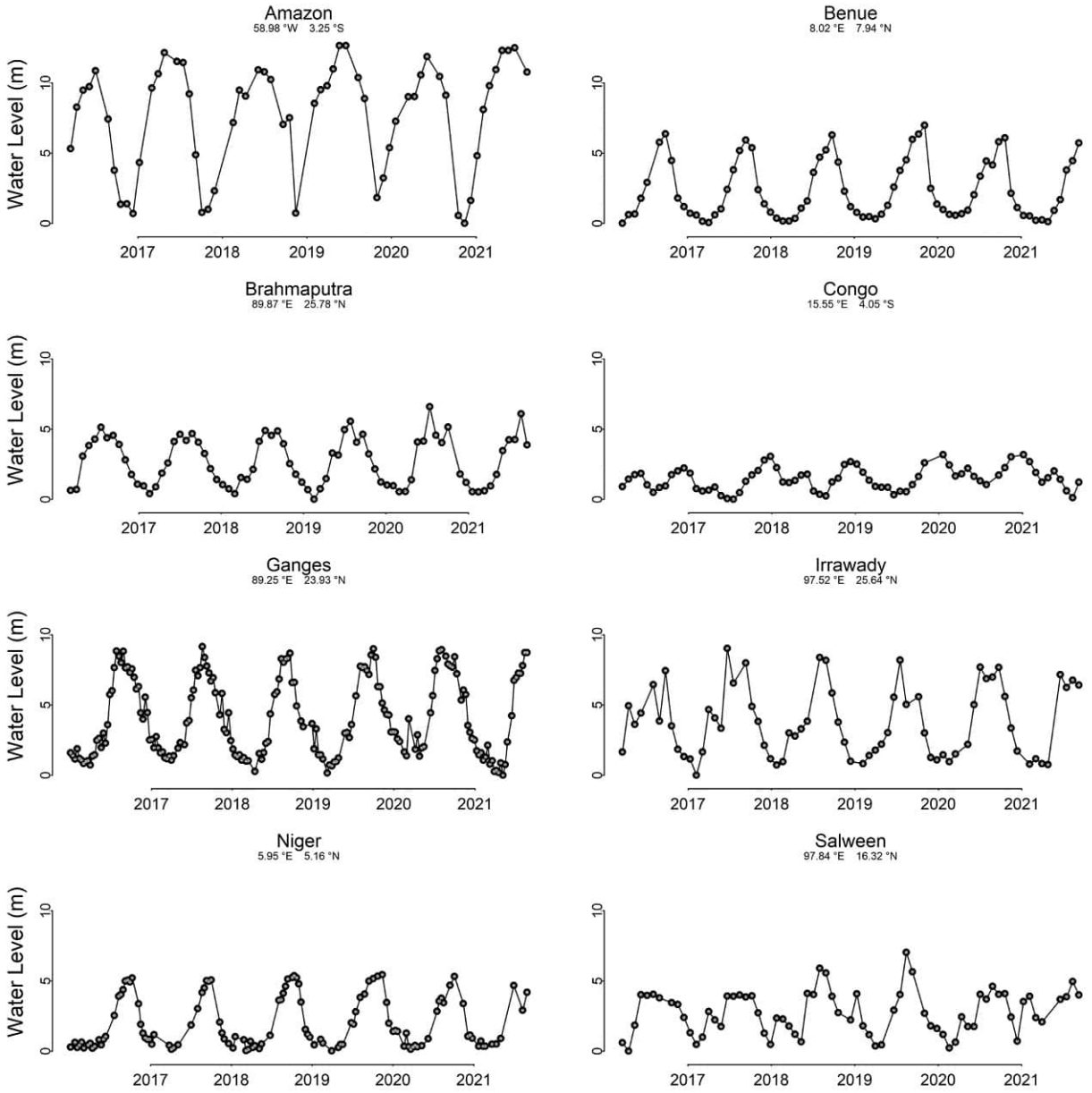

Fig. 1 Flood regimes of selected tropical large rivers, as recorded from water level time series from satellite altimetry in the Database for Hydrological Time Series of Inland Waters [DAHITI, Schwatke et al., 2015].

Geomorphology

Floodplains are formed by a complex interaction of fluvial processes (Nanson and Croke, 1992) where stream power on the one hand and sediment transport and deposition on the other, are the most important determinants of floodplain features and dynamics. Rivers are geomorphologically categorized as meandering, straight or braiding (Leopold and Wolman, 1957), and these channel patterns largely characterize floodplain development in tropical regions (Nanson and Croke, 1992; Latrubesse, 2008; Fig. 2). At their mid to lower courses, most large tropical rivers have anabranching channels with very low slopes and relatively fine-grained (medium- to fine-grained sand) bedload (Latrubesse, 2008). Large-tropical rivers with anabranching floodplains include the Amazon, Orinoco, Paraná, Congo and Brahmaputra (Latrubesse, 2008). Floodplains of anabranching channels are mostly formed by overbank deposition of fine-grained sediment that form islands with levees, backwater depressions, and lakes (Nanson and Croke, 1992). Occasionally, these rivers might also dispose of braided stretches, such as the Congo and Negro Rivers (Fig. 2). Lateral migration (i.e., meandering) floodplains with characteristic ridge and swale systems (scroll pattern) are also common tropical floodplain types. These rivers include, for example, the Mississippi, Purus, Juruá, and Paraguay (Fig. 2).

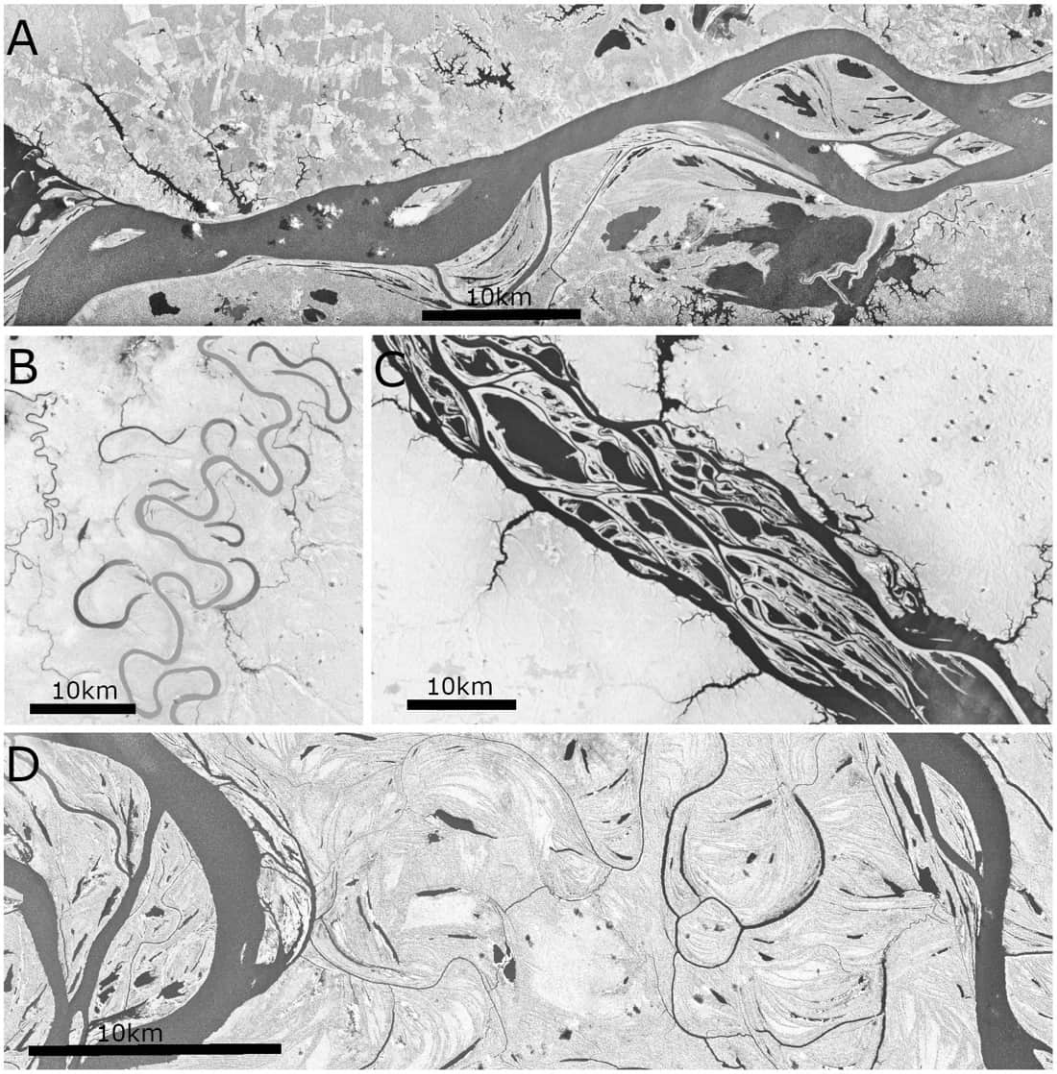

Fig. 2 Geomorphological styles of tropical large rivers and their floodplains: examples from the Amazon. (A) anabranching channel of the Solimões River with permanently connected, linear-shaped floodplain lakes and seasonally connected, dendritic shaped tributary lakes, central Brazilian Amazon. (B) Meandering channel of the lower Juruá River, with scroll lakes of varying hydrological connectivity and yazoo channels delimiting the active and paleo-floodplain, western Brazilian Amazon. (C) Braided system at the Anavilhanas arquipelago of the lower Negro River, with dendritic shaped tributaries, central Brazilian Amazon. (D) Mamirauá Sustainable Development Reserve, located between the Solimões (left) and Japurá (right) rivers. The linear shaped scroll lakes are seasonally flooded and part of the active floodplain, which is intermixed with mostly isolated lakes that are part of the paleo-floodplain, creating a complex system of geomorphic and hydrological gradients with high habitat diversity.

Because of their very low slope gradients (in the range of 1–50 cm km^{-1}), large-river channels and floodplains quickly change in response to environmental alterations that change flow and sediment regimes (Gregory and Lewin, 1987). Even slow tectonic movements or small changes in the base level propagate flow and sediment regimes to great distances upstream (Dunne and Aalto, 2013). For example, the last interglacial period affected the Amazon River system up to 2500 km upstream and largely defined the shape, geomorphology and fluvial styles of today's Amazon River and major tributaries (Irion et al., 1995). Over decades, centuries, or even millennia, only a small fraction of the total alluvium in a river valley is transported by the river, while the bulk is stored in contemporary floodplains or in ancient alluvial deposits (Nanson and Croke, 1992).

Hydraulic energy of flowing waters may be variable at small geographic scales, sorting deposited grains by size and weight. Thus, active floodplains are a complex mosaic of substrates of vastly different age and texture. Immense variation in substrate age, soil texture, and flooding is an important facet of habitat heterogeneity for flora and fauna and a principal driver of high beta-diversity, or species turnover, of large-river wetlands compared to terrestrial ecosystems (Wittmann and Junk, 2016).

In contrast to the linearly arranged active floodplains, the "geomorphological floodplain" may extend over large areas. Approximately one third of the area of the Amazon basin, or two million of km^2, is paleo-floodplain built up of Andean sediment, where geomorphological landforms, such as paleo-channels, slip-off and undercut slopes, levees, depressions, meander scars, and islands (i.e., Hudson, 2003; Peixoto et al., 2009) are clearly visible in the landscape (i.e., as river terraces) reflecting former flow regimes (Irion et al., 2010; Wittmann and Householder, 2017).

Substrates and soils

The amount and quality of dissolved and suspended solids determine primary and secondary productivity in wetlands (Junk, 2002) and, to some degree, also biodiversity. Wetlands of semi-arid and arid regions are usually richer in nutrients than their humid counterparts because of slowed weathering processes in their catchments, but also tend to eutrophication and salinization (Dumont, 1992). Wetlands of the humid tropics are generally characterized by relatively low nutrient status, as exemplified in the Amazonian black-water and clear-water floodplains (Junk et al., 2011) or the African Congo River floodplains. However, exceptions occur when rivers drain tectonically active regions and mountain ranges. Because rivers transport sediment long distances, the fertility of alluvial sediments can differ considerably from soils derived in situ on local material. Best examples are the nutrient-rich alluvial substrates in deeply weathered and nutrient-poor tropical landscapes, such as in large parts of tropical and subtropical South America, Africa, and India. Many large rivers flowing through these landscapes originate from uplifting mountain ranges, such as the Andes, Himalaya and Hindukush, or tectonically active regions, such as the East African rift-valley system, and deposit their suspension loads with high contents of relatively un-weathered and thus multi-layered clay minerals, such as illite, smectite, and montmorillonite, in the floodplains along their middle and lower courses. These clay minerals have high ion exchange capacities and release nutrients to alluvial substrates. For example, central Amazonian substrates of floodplains along white-water rivers draining the Andes have contents of Potassium, Magnesium, Calcium and Sodium that are 10- or even more-fold higher than the contents of these elements in non-flooded, ferralitic soils of the surrounding tertiary sediments that originated over millions of years from the Precambrian and Paleozoic basement (Irion et al., 2010). Consequently, plant and animal species with high fertility requirements can find refuge in alluvial settings where they would otherwise not survive local conditions. Those species often originate from biomes and ecosystems where climates and edaphic characteristics are different and thus form biogeographic disjunctions in river floodplains.

Arguably, human civilization arose along large-river wetlands characterized by high fertility, with examples from all continents. The Nile, Euphrates, Tigris and Indus Rivers were the economic basis for the high cultures of Egyptians, Sumerians, and Harappas, 5000 to 4000 years ago (Hammerton, 1972; Boulé, 1994). First records of agriculture originate from the Tigris-Euphrates and Indus floodplains, and rice paddy cultivation likely originated in the Ganges and Yanuma floodplains in India (Gopal, 2013). The fairly predictable inundation regimes combined with the periodical refreshment of soil nutrients from inundations favored the cultivation of productive aquatic macrophytes (i.e., rice, lotus, taro), lead to the domestication of animals (i.e., ducks, buffaloes), and allowed for the sustainable use of tropical floodplains by a dense human population (Fernando, 1980; Junk, 2002). In South America, Amerindian population density along sediment-laden rivers was about 10–20 times higher than in adjacent terrestrial ecosystems (Denevan, 1976). Indeed, the modern distribution of humans in the Amazon reflect similar patterns. Noteworthy is that the combination of high fertility with and high human density also favors the emergence and spread of many zoonotic diseases, which forced humans to create specific types of management for fertile substrates and floodplain resources. In the Amazon basin, most settlements and cities are located along river channels that still represent the only viable transport route for people. Most settlements are located along nutrient-poor black-water rivers, which reduces the exposition to mosquitoes and thus disease transmission, but still near white-water rivers (i.e., near river confluences or in distal parts of white-water floodplains) to ensure access to highly productive soils, and aquatic environments for fish and other natural resources from the fertile floodplains.

Biodiversity

Tropical large river wetlands are considered biodiversity hotspots (Gopal et al., 2000). Both, the adaption and speciation from regional species pools and ephemeral or migratory species that depend on wetland resources for the maintenance of their populations contribute to high biodiversity. Wetland habitats often account for an important fraction of regional habitat heterogeneity within biomes (Wittmann et al., 2015). While their relatively small coverage within larger biogeographic units means that wetlands are not necessarily richer in species at local scales than adjacent uplands, they do harbor mostly different species than surrounding uplands and thus significantly contribute to regional diversity (Sabo et al., 2005). Large-river wetlands are integrated into fluvial networks that provide wet dispersal corridors, these often crossing climatically different regions (Naiman et al., 1993). As such, rivers may be important vectors of range expansion for many semiaquatic and aquatic organisms. Wetland macro-habitats (sensu Junk et al., 2014) may also serve as local refuges (Kellmann and Meave, 1997). By mitigating environmental stressors in otherwise inhospitable regions, wetland occupation can allow organisms to tolerate larger temperature ranges as well as maintain more favorable edaphic and moisture conditions compared to adjacent, terrestrial habitats (Sculthorpe, 1985). In this sense, over evolutionary time, large-river wetlands are likely to have consisted of many habitats that have conveyed spatial and temporal resistance and/or resilience to populations of species living in constantly changing climatic contexts (Sedell et al., 1990). For example, in periods of reduced water availability during the Quaternary, wetlands, and especially those along large rivers, played crucial roles as refugia for drought-sensitive vascular plants and animals in both tropical and extratropical regions (Wittmann et al., 2015).

When rivers flow through semi-arid climate zones, soil moisture and the availability of near-surface ground waters provide important refuges for drought-sensitive plant and animal species. Floodplain and riparian areas in savanna climates are densely forested in contrast to adjacent uplands dominated by herbaceous species (Meave et al., 1991). Consequently, riparian habitats are usually the most species-rich ecosystems in savanna landscapes, where effects of seasonal drought, but also fire frequency are

comparatively low (Kellmann and Meave, 1997). In regions where rainfall seasonality is pronounced, the availability of surface waters in addition influences the migration behavior of many vertebrate species. For example, the African mega-fauna is highly dependent on water availability of seasonal wetlands. As soil moisture influences plant growth, plant zonation along flood frequency and duration gradients across tropical Africa provide a critical resource heterogeneity for herbivores, which graze on floodplain peripheries in the early dry season, but migrate to deeper floodplains and swamps during the late dry season and during droughts (Fynn et al., 2015). Similar patterns of species migrations along climate seasonality and spread out and shrinking of large river wetlands are known, for example, for crocodilians (Campos et al., 2006) and mammalian herbivores (Tomas et al., 2010) from the South-American Pantanal.

Higher vegetation

Tropical large-river wetlands are mainly forested in per-humid tropical climates, as for example in the Amazon and Congo floodplains. Highest tree species richness in large-river wetland forests was reported for the Amazonian nutrient-rich white-water floodplains (várzeas), where more than 1000 flood-tolerant tree species are reported to occur, and where tree species richness ($\geq$ 10 cm diameter at breast height—dbh) may account for up to 150 tree species ha^{-1} (Wittmann et al., 2006). Tree species richness in Amazonian black-water floodplain forests (igapó) account for approximately 70–80 species ha^{-1}, which is similar to the species richness reported for seasonally flooded forests in the northern Congo (Ifo et al., 2019). With increasing latitude, floodplain forests decrease in species richness, such as in the lower Mekong floodplains (some dozens of flood-tolerant tree species, Campbell et al., 2006), the Okavango Delta (approximately 10 flood-tolerant tree species, Ramberg et al., 2006) or northern Australian wetlands (approximately 5 flood-tolerant tree species, Finlayson, 2005). In climates with a distinct dry season, namely when the number of consecutive months with arid conditions increases to six or more, tree coverage is concentrated along moist riparian habitats, while macrophyte and herbaceous species of tree and shrub savannas become the dominant life form in floodplains, such as in the Llanos of Moxos, the Araguaia River wetlands and the Pantanal (South America), the Niger and Okavango Deltas (Africa), and the freshwater marshes of India and Mesopotamia (Gopal, 2013). If the number of arid months further increases, woody species may be either restricted to episodic riparian corridors, such as in the shrub savannas of the Caatinga (NE-Brazil), the woodlands of the Sahel zone (NE-Africa) or the Mara-Serengeti in Kenya and Tanzania (E-Africa), the Western Ghats in South-India (i.e., Johnsingh and Joshua, 1989), and the Kakadu region in Northern Australia (Finlayson, 2005), or are entirely replaced by macrophytes, namely emergent reeds (i.e., *Phragmites*), cattails (i.e., *Typha*), or sedges (i.e., *Cyperus*). Notably, herbaceous species richness is inversely related to tree coverage, reaching highest values in subtropical savanna regions. For example, species lists in the Okavango Delta report approximately 950 herbaceous taxa (Ramberg et al., 2006). Similar species numbers for herbaceous species are reported for the Pantanal (approximately 1150 species, Pott and Pott, 1994). Herbaceous species richness in tropical large river wetlands decreases both in direction to rainforest biomes, and also approaching extra-tropical regions. However, species numbers also strongly depend on habitat diversity, given that larger and geomorphological varied wetlands usually also present higher numbers of taxa (Junk et al., 2006).

Geomorphological landform, sediment and soil type, sediment turnover rates and the exposure to flood disturbance and light change at small geographic scales in tropical large-river floodplains and form complex environmental gradients that influence the occurrence and distribution of plant and, to some degree, also animal species (Hughes, 1997). Studies from many tropical floodplains show predictable patterns of plant species distributions along these gradients. Examples include Morison et al. (1948) on the Bahr el Ghazal floodplain in Sudan, Johnson and Little (1967) along the Mississippi (United States), Menalled and Adamoli (1995) on the Paraná (Argentina), Hughes (1988) on the Tana River (Kenya), Damasceno et al. (2005) on the Paraguay, Nunes da Cunha and Junk (2011) in the Pantanal, and Wittmann et al. (2004) on the Amazon River (Brazil). Most importantly, hydroperiod - defined through the location of plant species along the topographic gradient, is a powerful environmental filter because it impacts plant growth through reduced gas diffusion under waterlogged conditions that severely reduces soil oxygen availability for aerobic metabolism (i.e., Jackson and Colmer, 2005). In addition, if flood amplitudes are high, plants might be completely submerged and thus face reduced light conditions and even absence of light, which, combined with increased levels of CO_2, greatly hampers photosynthesis (Parolin, 2002, 2009). Depending on their location along the flood frequency and/or duration gradient, plant species need specific adaptations to overcome hypoxia during waterlogged periods. While the mechanisms of flood tolerance in plants are still not entirely understood, it is clear that most floodplain plants usually combine several adaptive strategies to withstand waterlogged periods (Parolin, 2009), and that these strategies likely developed numerous times in most phylogenetic groups. Adaptations can be morphological (i.e., aerenquimatic tissues, increase of root biomass, aboveground roots, pneumatophores; hypertrophied lenticels), biochemical (i.e., stimulation of fermentative pathways, accelerated glycolytic fluxes), or metabolic (i.e., leaf shedding, growth reductions, cambial dormancy) (i.e., Armstrong et al., 1994; Schöngart et al., 2002; Parolin, 2002; Jackson and Colmer, 2005; Kreuzwieser and Rennenberg, 2014). In addition, the reproductive phenology of many tropical floodplain species is linked to the seasonality of flooding, such as the timing of flowering, seed dispersal, germination and establishment (Voesenek et al., 2003), as well as the development or use of specific dispersal modes, such as hydrochory or ichthyochory (i.e., Correa et al., 2015).

While flood length and height are the dominant environmental filters for many tropical wetland plants and locally explain increasing species richness from long/high flooded to short/low flooded, it is important to state that inundation period is interlinked with multiple gradients that also include dry phases and drought, to which many organisms in tropical wetlands must be adapted (Parolin et al., 2010; Householder et al., 2021). Climatic droughts may be exacerbated by local edaphic conditions,

for example where coarse substrates (i.e., sand) desiccate more quickly relative to fine substrates (i.e., clay). The latter, however, may also limit oxygenation even in the absence of superficial flooding, and cracks formed during prolonged dry phases can damage fine roots of vulnerable seedlings. As such, the oscillating dry and wet phases provide very heterogeneous ecological niches that importantly shape local habitat diversity (Householder et al., 2021).

Along sediment-laden rivers, sedimentation and erosion processes constantly provide geomorphological disturbance. While alluvial sediments provide new habitats potentially available for new site colonization, they may also bury macrophyte and tree seedlings and thus act as another environmental filter. Pioneer plants colonizing these sites often have strategies to complete their life cycles within one terrestrial phase (i.e., annual macrophytes) or form new root layers (i.e., perennial plants such as trees) close to the surface in order to ensure water and nutrient uptake (Wittmann and Parolin, 2005). On the other hand, erosion along slip-off slopes destroys areas formerly covered by vegetation, and plant species maintain their populations at regional scales with effective strategies that allow new site colonization, including fast growth, long distance dispersal, and asexual reproduction (i.e., pioneer strategies).

Vegetation succession upon freshly deposited sediment follows the same ecological principles (i.e., allogenic versus autogenic successional pathways, Table 2) in tropical large-river floodplains as along rivers of extra-tropical climates. The first pioneer species to colonize newly deposited alluvial sediment are usually annual, followed by perennial grasses and herbaceous plants. This first group of colonizers may be extraordinarily productive, especially those with C_4-metabolism. From the Amazonian white-water floodplains, the net primary productivity of the grasses *Paspalum fasciculatum* and *Echinochloa polystachya* may amount to up to 70–100 Mg ha^{-1} year^{-1} (Piedade et al., 1991), twofold to threefold higher than the net primary productivity of fast-growing, early successional forests (Schöngart et al., 2010). If alluvial substrates are poor in nutrients, colonizing macrophytes are mainly low-productive sedges (Cyperaceae) (Junk et al., 2015). Pioneer species reduce water energy and trap further sediments, leading

Table 2 Relation of environmental and biotic factors during forest succession in Amazonian sediment- and nutrient-rich white-water floodplains (várzea), near the main river channel.

	Primary succession	*Early secondary succession*	*Late secondary succession*	*Late succession*
Environmental factors				
Hydraulic force	Very high	High	Intermediate	Low
Inundation height (m) and duration (days year^{-1})	8–12 (>300)	5–7 (230–270)	3–5 (50–100)	< 3 m (< 50)
Sedimentation rate	Very high	High	Intermediate	Low
Substrate grain size[a]	Coarse (i.e., sand)	Intermediate (i.e., fine sand)	Intermediate (i.e., silt)	Fine (i.e., clay)
Substrate compaction	Very low	Low	Intermediate	High
Relative photosynthetically active radiation (%)[b]	70–100	30–70	5–30	< 5
Substrate water retention capacity	Low	Very low	Intermediate	High
Litter and organic layer	Absent	Sparse	Intermediate	Thick
Biotic factors				
Vegetation type	Annual or perennial macrophytes	Shrubs	Trees	Trees
Tree density ha^{-1} (> 10 cm dbh)[a]	–	100–200	800–1000	400–600
Mean tree diameters (cm)[c]	–	10–15	15–30	> 30
Tree heights in the upper canopy (m)[a]	–	8–10	15–20	> 20
Stratification	–	Single	Double	Double or more
Max tree ages (years)[c]		10–15	35–100	> 100
Individual crown area (m^2)[d]	–	30–60	60–200	200–800
Aboveground root type[e]		Stilt roots	Stilt and tabular roots	Tabular roots
Wood density (g cm^{-3})[c]	–	Soft (< 0.4)	Intermediate	Hard (> 0.5)
Biomass (Mg ha^{-1})	70–100[f]	18 ± 3[c]	117 ± 9[c]	239 ± 11[c]
Net primary productivity (Mg ha^{-1} year^{-1})[c,f]	30–99[f]	11.25[c]	14.34[c]	6.46[c]
Biodiversity ha^{-1}	1–5 herb species	1–3 shrub species	10–25 tree species	> 80 tree species
Succession type	Allogenic	Mostly allogenic	Mostly autogenic	Autogenic

[a]Wittmann et al. (2004).
[b]Wittmann and Junk (2003).
[c]Schöngart et al. (2010).
[d]Wittmann et al. (2002).
[e]Wittmann and Parolin (2005).
[f]Piedade et al. (1991).

to the silting up and stabilization of local sites. In addition, they modify microclimates by shading. The modification of environmental site conditions facilitates the establishment of pioneer shrubs and trees, which usually establish a few years after the colonization of macrophytes. First colonizing pioneer trees usually form monospecific stands, but these are swiftly (during years to a decade) replaced by trees of early-secondary stages. These are, in turn, replaced by intrusion of late-successional or climax species (within decades or centuries) (Table 2). The successional sequence results in a continuous increase in species diversity but a decrease in stand densities. Succession is, moreover, characterized by a reduction in growth rate of woody species and an increase in mean wood density. Net primary productivity of stands is thus reduced as a consequence of the higher abundance of slow growing, long-living shade-tolerant species in late-successional forests (Wittmann and Junk, 2003; Table 2). This progression is often characterized as a transition from highly flooded "softwood" to low flooded "hardwood" forests (Ellenberg, 1963), which effectively captures how plant functional and life-history traits (i.e., growth rates, wood density, aboveground roots) and vegetation structure (i.e., canopy height, diameter distribution, biomass, diversity) are strongly linked to temporal shifts of local environmental site conditions (flood duration, hydraulic force, composition of grain sizes in alluvial substrates, and exposure to sun light). Exceptions in the progression may occur, when highly flooded forest patches are subject to relatively slow sediment deposition rates, as exemplified in the successional model provided by Wittmann et al. (2010). Worth mentioning is that successional processes might be highly variable in timing and duration, as they depend on the geomorphic dynamism of lowland rivers, in particular flow velocity and the amount of transported sediment and sediment turnover rates. For example, the entire successional sequence from first colonization of freshly deposited substrates through pioneer species until the development of late-successional forests may occur in a few hundreds of years where highly fertile floodplains are rapidly reworked by river dynamics, such as close to the Andes in the Peruvian Amazon (Salo et al., 1986; Kalliola et al., 1991). In contrast, where river dynamism is low, such as along the lower Negro River in the central Amazon basin, first pioneer tree species might show relatively slow growth rates and achieve ages of up to 100 years. Late-successional floodplain trees along these relatively stable rivers might achieve ages of up to 1000 years (Junk et al., 2015), demonstrating the comparatively slow successional processes in nutrient-poor and low-dynamic river floodplains.

Fauna

Tropical large-river wetlands range from permanent aquatic habitats in deep river channels to terrestrial habitats upon paleo-floodplains and represent complex functional units, where macro-habitats influence each other (Junk et al., 2014). They host among the highest numbers of taxa in many animals, including planktonic and benthic communities, aquatic and terrestrial invertebrates, and aquatic and terrestrial vertebrates that live in or are highly dependent on rivers and wetlands. Most species lists are far from being complete, and the rapid decline in global freshwater biodiversity likely means that many species will go extinct before their adequate taxonomic description. Invertebrates dominate the fauna of large river wetlands in terms of species diversity, abundance, and biomass (Williams, 2006). Because they are the link between primary production, detrital resources and the higher order consumers, aquatic invertebrates play an outstanding role in the food chain (Murkin and Blatt, 1987). Most invertebrates of tropical large-river wetlands have relatively short life cycles, which allows their rapid occupation of the new sites provided by fluctuating water levels and river dynamics (Irmler, 1981). Many invertebrates also migrate or drift in the water to new sites (Junk and Robertson, 1997). In large river wetlands, life cycles of most invertebrates are tightly coupled to the hydrological cycle, as, for example, shown for the Amazon floodplains (Adis and Messner, 1997; Adis and Junk, 2002) or the Brazilian Pantanal (Wantzen et al., 2016).

Globally, freshwaters of rivers, floodplains and lakes harbor approximately one third of all vertebrates and nearly half of all fish species (Balian et al., 2007; Vega and Wiens, 2012). Freshwater ecoregions with the highest fish diversity include Asia's Brahmaputra, Ganges and Yangtze basins, the lower sections of the Mekong, Chao Phraya (Thailand), Sittaung (Myanmar) and Irradwaddy, Africa's lower Guinea and Congo, and South America's Amazon, Orinoco, and Paraná (Abell et al., 2008). The Amazon basin alone likely hosts 2500–3000 fish species (Junk, 2013). About half of the total species number is estimated to occur in the large rivers and their floodplains and the other half in the headwater regions of smaller tributaries (Junk, 2007). Most of the former species have a large distribution area, whereas many species in the latter have a restricted distribution and are therefore much more vulnerable to extinction. Globally, fish species richness was shown to increase with drainage area, mean annual river discharge, temperature, and net terrestrial productivity within the basin, whereas historical climatic stability and geographic isolation had a minor effect (Oberdorff et al., 2011). Historical and biogeographic effects, however, strongly determine fish distribution ranges and species endemism. In global terms, the highest numbers of endemic fish species occur in the western Amazon and Magdalena rivers, east Brazilian São Francisco and smaller exoreic river basins, the lakes of the African rift-valley, and Asia's lower Mekong (Abell et al., 2008).

In an analysis of the geographical distribution range of more than 7000 freshwater animal species on the globe (including mammals, reptiles, amphibians, fishes, crabs and crayfish), Collen et al. (2014) state that absolute freshwater diversity is highest in the Amazon basin, which is particularly due to the high number of amphibians that accounted for more than 50% of the total of recorded freshwater species. Other outstanding regions for freshwater diversity include the south-eastern United States, the rift valley lakes in Africa, the Ganges and Mekong basins, as well as large parts of Malaysia and Indonesia. Local endemism is patchily distributed across the tropics, with hotspots in the rift-valley lakes, Thailand, Sri Lanka, and Papua New Guinea (Collen et al., 2014). In their global analysis, Brazil ranked highest in freshwater diversity (accounting for 12% of all investigated taxa), followed by United States, Colombia, and China (9–10% each). Megadiverse nations including tropical/subtropical climates with more than 50% of "political endemism" (Ceballos and Ehrlich, 2002) in freshwater species across the globe included Madagascar (96%), Australia (84%), United States (73%), Mexico (59%), China (55%), and Brazil (51%).

Worth mentioning is that many wetland-dependent vertebrate species (i.e., terrestrial, deep water and bird species) strongly depend on habitat and resources from tropical wetlands, which provide refuges from annual droughts or low temperatures during the winter at higher latitudes. Terrestrial animals migrate to the water, such as large herds of ungulates, which move between the Okavango Delta and the surrounding upland savannas, while aquatic animals migrate downstream to mainstem rivers when headwaters dry up or cool down (Sparks, 1995). Many water and shore birds migrate annually between breeding grounds and wintering areas, and tropical/subtropical rivers that cross different climate zones (i.e., N-S oriented, such as the Mississippi or Nile Rivers) are particularly important as long-distance migration corridors for water birds (e.g., ducks, swans, geese, herons, egrets), shorebirds (e.g., sandpipers), raptors (e.g., owls, hawks, eagles) and songbirds (e.g., warblers, finches) (Sparks, 1995). Fishes may undertake both longitudinal (i.e., along river channels) and lateral (i.e., from rivers to floodplains) migrations to spawning and feeding areas, because optimal conditions for both activities usually vary with the flood cycle and do not occur simultaneously in the same areas (Welcomme, 1985).

Lastly, tropical large-rivers also play a fundamental role in marine biogeochemical processes, salinity levels, food webs, and consequently biodiversity (i.e., Krumins et al., 2013), in particular in estuaries, deltas, and other terrestrial-marine transition zones. Global sediment input from rivers into the world oceans is estimated to account for more than 2×10^{10} t year^{-1} (Milliman and Meade, 1983). A few big tropical rivers including the Amazon, Yangtze, and Brahmaputra-Ganges drain tectonically active regions of uplifting, the erosion of which accounts for more than half of global river sediments supplied to the oceans (Williams, 2012). While the excess of river sediment through land use changes (e.g., deforestation) and intensified soil erosion including turbidity and increased levels of N and P as derived from pollution can have a detrimental effect on the biodiversity of marine and coastal ecosystems, such as coral reefs (i.e., Bartley et al., 2014) and mangroves (i.e., Ellison, 1999), tropical river sediments are crucial in providing nutrients that provide the trophic basis for a range of marine ecosystems, and here especially the sediment-associated biota (i.e., Levin et al., 2001). Damming large rivers considerably reduces down-river sediment transport which contributes to the destruction of river deltas, intensified coastal erosion, and loss of habitat and biodiversity (i.e., Vörösmarty et al., 2009), with numerous examples all over the globe (i.e., Yangtze, Mississippi, Mekong).

Threats

Tropical freshwater habitats are among the most threatened ecosystems globally. Extensive large-river floodplains have been lost due to regulation of rivers for flood control, irrigation, and hydropower generation. Meanwhile, inappropriate resource and land use, drainage, water deviation, channeling, damming, eutrophication, pollution, and climate change further fragment wetlands and threaten biodiversity. The degradation of tropical large-river floodplains is ongoing and even accelerating into the near future (He et al., 2019). Global water demand increased 10-fold during the 20th century (Biswas, 1998) and will increase in 50% by 2030. The decline in freshwater biodiversity during the last 50 years is estimated at approximately 80% (IUCN Water Knowledge Platform, 2021). Rapid growth of human population and economic development are tightly coupled with an increase in global energy demand and the use of renewable energy sources, namely hydropower. To date, almost half of all large-rivers on Earth are affected by dams (Nilsson et al., 2005; Lehner et al., 2011). This condition will increase as a result of an unprecedented global boom in dam construction since the 1990s (Zarfl et al., 2014), reinforced by the Paris Agreement for Climate Mitigation Strategies established in 2016 (Zarfl et al., 2019). Accelerating hydropower development is especially dramatic in highly diverse tropical river basins because it may cause the extinction of hundreds of freshwater species (Castello et al., 2013; Winemiller et al., 2016), and, in addition, also negatively affects marine biodiversity as previously described.

Because wetlands are often legally protected to some degree in most countries, a crucial legal problem for periodically flooded wetlands is the delimitation of their area. While conservation- and ecosystem-minded institutions may recognize the importance of a broad definition that encompasses varied flooded habitats (even those occasionally flooded) for the maintenance of biodiversity and services, economic institutions seeking to exploit wet areas usually favor more restricted definitions that limit borders to core wetland areas. In Brazil, for example, the delimitation of wetlands proposed by a group of scientists defines the wetland area as the area influenced during the mean maximum flood and includes permanent dry areas inside the wetlands as of vital importance for the maintenance of wetland integrity (Junk et al., 2014). This definition, however, is heavily contested by the Brazilian agroindustry. The latter accept the risk of losses in biodiversity but also of crops, live stocks and even human life during high floods. This problem will increase in the near future because of growing risks of extreme flood and drought events with climate change.

Deforestation and land-use change, in particular due to cattle ranching and agriculture, affects river wetlands in the short term because of locally altered hydrologic conditions, such as decreased rates of evapotranspiration, and increased runoff, water temperature, and stream discharge (Macedo et al., 2013). Long-term effects, however, include reduced precipitation regimes and alterations in rainfall seasonality, with increased frequency and intensity of extreme droughts and high-water events (Yin et al., 2014). It also increases soil erosion, sediment transport and changes water chemistry (Junk, 2013). Pollution through mining, agriculture, navigation, aquacultural activities and industrial and domestic wastewater affects many tropical rivers and floodplains. Mining activities also often alter stream and river morphology as a result of excavations that increase sediment loads (Wittmann and Junk, 2016). Large-scale mining also promotes deforestation, road, railway and pipeline constructions, as well as the construction of river dams and transmission lines for energy production.

River damming for hydropower generation is an increasing threat with perhaps the most disastrous consequences for the wetland biota at large scales, especially when it occurs along lowland rivers (Wittmann and Junk, 2016). Dams interrupt hydrological connectivity in multiple ways, lead to the alteration of hydrological cycles and flood pulses, trap sediments and nutrients, change water temperature, transparency, and chemistry in reservoirs and downriver, and act as dispersal barriers for fish and other aquatic organisms (Rosenberg et al., 1995; Nilsson and Berggren, 2000; Agostinho et al., 2008; Pelicice et al., 2014). While national policies still regard hydropower as a clean energy source, many dams and reservoirs are located far away from where energy consumption is needed and often operate significantly below initially designed energy outputs (Fearnside, 2006). In addition, greenhouse gas emissions from tropical hydropower plants may be as high or even higher than those emitted through fossil fuel burning (Kemenes et al., 2011; Fearnside, 2015), a fact still largely ignored by national governments. Although the construction of large dams in tropical regions is usually accompanied by studies of environmental impact, these concentrate on the floodable area of the reservoir and largely ignore environmental impacts far up- and downriver (Wittmann et al., 2015). The downriver impacts, however, including the death of floodplain trees and negative effects on floodplain food chains, may extend along river courses over hundreds of kilometers downstream of the dam, as shown for the Balbina dam in Amazonia (Schöngart et al., 2021) and the Engenheiro Sérgio Motta (Porto Primavera) reservoir at the Paraná River (Junk et al., 2021). In the latter case, after reservoir construction fish species composition changed more than 80% in 20 years, a nearly complete compositional turnover (Agostinho et al., 2008).

Most anthropogenic pressures on tropical large-river wetlands are reinforced through impacts caused by climate change. Global terrestrial water storage (TWS), which represents the sum of water stored in canopies, snow and ice, rivers, lakes and reservoirs, wetlands, and soil and groundwater, was recently modeled by Pokhrel et al. (2020) based on global climate models included in the Fifth Assessment Report of the IPCC, for the 21th century. Irrespective if moderate-to-severe or if extreme-to-exceptional climate models are applied, results indicate that climate change reduces TWS in many tropical regions, especially in the Southern Hemisphere, while increases in precipitation are most likely for Southern India, parts of SE-Asia, and northern Australia. Large part of South-America (with some exceptions in the western Amazon, eastern Brazilian Cerrado and along the Brazilian coast), and most parts of NW-, Central- and S-Africa and tropical Asia will be subjected to an increased frequency and intensity of droughts with varying severity. Along thousands of kilometers of river stretches, reduced precipitation combined with global sea-level rise will impact river discharge, dynamics, sediment balance, as well as habitat diversity that currently underpin this ecosystem's important function for biodiversity and human services, with so far mostly unknown consequences for human well-being.

Conservation

Many tropical countries have protected large wetland areas; however, increasing multiple pressures affect even the protected wetlands at the species, community and ecosystem levels. Local populations have managed many tropical wetlands sustainably for centuries or even millennia, but the rapidly growing population and globally-changing economic requirements have led to changes in political and economic strategies, new forms of land-use, new development priorities, and the rapid decline of traditional practices (Junk, 2002). While nature conservation globally is steadily increasing, only a few conservation efforts are effective for maintaining tropical freshwater biodiversity. Most protection is directed to the distribution of terrestrial taxa and therefore of limited use for the integrative conservation of freshwater systems (Peres and Terborgh, 1995; Abell et al., 2007). In addition, many protected areas of tropical wetlands are governed by laws that allow resource extraction, mining activities, hydropower generation and further economic activities affecting wetland ecosystem integrity.

While most tropical countries have established some form of environmental policy or have national programs that indirectly relate to wetlands—such as policies related to water resource management, biodiversity and genetic resources, forests, sustainable development, fisheries, water sanitation, etc.—only few countries (i.e., Australia), have specific policies regarding the integrative protection of wetlands at the national level (Wittmann et al., 2015). Most tropical countries signed the Ramsar Convention on Wetlands of International Importance, which targets the wise use, management and monitoring of important wetlands. While the number of Ramsar sites is continuously increasing (i.e., Ramsar, 2015), most signing countries are slow in meeting the requirements of the six major initial criteria of wetland conservation of international importance: (1) to provide a definition of wetlands, (2) to elaborate wetland classifications and delimitation, (3) to evaluate wetland conditions, (4) to implement the wise use of wetlands, (5) to implement national policies for wetland conservation, and (6) to manage wetlands and to monitor wetland characteristics. As an example, only a few tropical countries, (i.e., Australia, United States, Argentina, Brazil) have developed national wetland classification systems, while most of them lack specific wetland regulations, and have yet to complete national wetland inventories (Ramsar, 2015). Further exacerbating implementation is often limited financial and human resources, general lack of infrastructure, and limited monitoring capacity (Wittmann et al., 2015). In addition, many pressures on freshwater biodiversity, such as illegal fishing and hunting, aquacultural activities, poaching or the exploitation of bird and fish eggs continue in many wetlands in spite of protection measures.

Existing and newly emerging threats for freshwater biodiversity loss and ecosystem degradation of tropical large-river wetlands demands for urgent basin-wide, transnational or even worldwide solutions and efforts for effective conservation. The impoundment of large rivers flowing through different countries creates several trans-boundary water conflicts, which certainly will increase in the near future in a world of global climate change. However, while there are promising examples of transnational agreements on water security and the management of social water conflicts (i.e., Link et al., 2014), few efforts have been made regarding the transnational

conservation of freshwater biodiversity. Promising examples exist (i.e., Initiative for Conservation and Sustainable Use of Andean Wetlands, Initiative for the Conservation of Mangroves and Coral Reefs, Initiative of the La Plata basin, etc.), but much more efforts are required to protect system integrity and freshwater biodiversity of tropical large rivers and their wetlands, also considering both their terrestrial and marine interactions.

Future research

- Extend the wetland classification system of Brazilian wetlands (Junk et al., 2014) to tropical wetlands in Asia, Africa and Oceania to enable worldwide comparisons on biodiversity, wetland function, ecosystem services, and threats.
- Close knowledge gaps on habitat diversity, floristic and faunal composition, and ecosystem processes and functioning of African wetlands, particularly in the Congo basin.
- Investigate long-term effects of flow regulation, river dams and climate change on the tropical wetland biota, i.e., effects on ecological connectivity, species composition, diversity, and food webs, and extend investigations on impacts to coastal and marine ecosystems.
- Develop management options for the integrative protection and restoration of freshwater systems using a landscape approach, including cost-benefit analyses of traditional and modern land use, also extending to terrestrial and marine interactions.

See Also: Structures and functions of Inland Waters - Rivers: Dryland Rivers and Streams; Structures and functions of Inland Waters - Wetlands: Ecology and Conservation of Wetland Amphibians and Reptiles; Mangrove Forests: Structure, Diversity, Ecosystem Processes and Threats; Wetlands Under Global Change

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Tropical Peat Swamp Forests

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Alluvial Refers to sediments (clay, silt, sand, gravel) deposited by flowing water.
Carbon sink A reservoir that accumulates and stores carbon, thereby removing it from the atmosphere for long periods of time.
Carbon source A reservoir of stored carbon that releases more carbon to the atmosphere than it absorbs.
Fluvial Refers to physical features of the landscape shaped by erosional and depositional processes of streams and rivers.
Peat A type of soil derived largely from partially decomposed plant material under wet conditions, and thus characterized by its high organic, rather than mineral content.
Peat dome A convex-shaped peat deposit with greatest depths near its center, a condition driven by the maintenance of a higher ground water level in the center of an accumulating peat deposit.

Introduction

Swamp forests develop where topography results in poor drainage and permanent soil waterlogging. This unique hydrologic environment is not conducive to decomposition and plant debris tends to accumulate on the forest floor, the sustained buildup of which over long periods of time can lead to the formation of thick peat deposits (Blodau, 2002). As significant sinks or sources of carbon-based greenhouse gases, tropical peat swamps are increasingly linked to discussions of global climate change. In addition, as environmentally extreme habitats peat swamps make important contributions to tropical landscape heterogeneity and biodiversity. Here, we overview the environmental conditions that permit the development of peat swamp forests, from the local processes that allow peat accumulation, to the landscape and regional processes that determine their global extent and distribution. In doing so we also examine what is known about the amount of carbon stored in peat swamps, how it is measured, and which factors control its flux between soil and atmosphere. We then turn to assess the relevance of tropical peat swamps to biodiversity and the myriad ways in which local floras and faunas inhabit and interact with them.

Peat can be loosely described as a layer of soil composed mostly of partially decomposed organic material. Although working definitions vary among researchers, all are based on minimum thresholds of organic content (usually 50–65%) and the depth of the peat layer (30–40 cm) (Page et al., 2011). In the tropics, peat-forming swamps develop in a variety of conditions, but their greatest extents - and peat depths - are found at low elevations along fluvial valleys, over interfluvial divides, and fringing coastal areas (Cameron et al., 1989). Extensive peat swamps occur in tropical Africa, South America, and Southeast Asia (Gumbricht et al., 2017; Xu et al., 2018). Regardless of continent, however, these ecosystems have traditionally been regarded as biologically depauperate

and unproductive wastelands with little economic or scientific value. Scientific exploration has therefore lagged far behind that of other ecosystems, meaning that the biological, environmental, and societal significance of peat swamps has been habitually underappreciated. Consequently, management policies in many tropical countries have favored conversion to more productive agricultural uses, which have resulted in the wholesale deterioration of immense tracts of natural peat swamp area (Miettinen et al., 2012).

From relative disregard, tropical peat swamps have shifted to the fore of global scientific and societal discussion. This turn is largely the result of two lines of scientific inquiry over the past two decades. First, degrading peat swamps were found to be a considerable potential source of carbon to the atmosphere (van der Werf et al., 2009). In Indonesia, for example, estimates of carbon emitted to the atmosphere during dry season burning of peat swamps were of similar magnitude to the mean annual global carbon emissions from fossil fuels (Page et al., 2002). Second, vast areas of previously undocumented peat swamps were quantitatively described in both South America (Lähteenoja et al., 2009; Householder et al., 2012), and central Africa (Dargie et al., 2017), greatly increasing the known extent of peat swamps, as well as the tropical stock of peat carbon. These surprising revelations not only exposed severe knowledge gaps, but also anchored the discussion of tropical peat swamps to the foremost challenge of modern society - global warming.

A primary driver of global warming is the accumulation of carbon in the atmosphere resulting from human activities. The deep peats of many tropical swamps reflect a legacy of operating as a sink for atmospheric carbon, with a net cooling effect for the globe over millennia. Their large contact boundary with the atmosphere, however, also facilitates carbon effluxes from peat to atmosphere (Yu et al., 2010). Hence, large stocks of peat in carbon-rich swamps have tremendous potential to become a globally significant source of carbon to the atmosphere (Warren et al., 2017a; Wang et al., 2018). The magnitude of this potential carbon source and its possible negative or positive feedbacks on global climate is currently an active area of scientific research (Lawson et al., 2015).

Main topics/concepts

Local processes of peat formation

To more clearly understand the role of peat swamps as either carbon source or sink, awareness of the factors that regulate the carbon balance of peat-forming forests is a crucial starting point. Carbon enters a peat swamp system through biomass production of photosynthesizing vegetation, and leaves it via aerobic decay, anaerobic decay, and leaching (Fig. 1; Blodau, 2002). The rate of peat accumulation thus reflects the balance between carbon input and its removal, so that a peat deposit grows when plant primary production is high relative to its decomposition, and decreases when losses due to decomposition or transport become greater.

Various factors determine the relative balance of these processes, but among the most important is the position of the water table (Blodau, 2002; Wösten et al., 2008). Maintenance of the water level near the ground surface is a prerequisite for tropical peat accumulation as it results in anoxic conditions that considerably limit one of the main paths for carbon loss in soils - aerobic decomposition (Hirano et al., 2009). The activity of aerobic decomposers is generally high in warm and humid conditions of tropical environments. Thus, in well-aerated soils, organic material is rapidly oxidized, leaving little to accumulate as peat. A high water table restricts this process to a thin upper layer, while anaerobic decomposition predominates in the anoxic conditions that persist below the water level (Fig. 1). Because anaerobic decomposition is a much slower decay process, carbon effluxes are reduced and soil carbon accumulates in the form of peat. In addition, organic accumulation in the soil increases its water-holding capacity

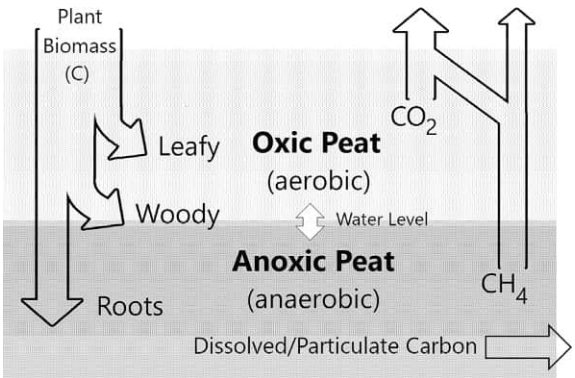

Fig. 1 A conceptual model of the carbon balance operating in a peat forming swamp. The level of the water table strongly mediates rates of both carbon input through plant productivity (left side) and carbon output (right side) that determine peat accumulation. Photosynthesizing plants incorporate atmospheric carbon into their biomass, which enters the peat carbon budget as separate litter fractions (left side) with differing rates of decay, determined primarily by the lignin content of the material and the level of anoxia where it is deposited. Carbon outputs (right side) occur primarily through gaseous fluxes mediated by soil microbes, as well as leaching, in the form of dissolved and particulate carbon. Carbon dioxide (CO_2) and methane (CH_4) are the principal carbon containing gases that result from microbial activity. Carbon dioxide is produced by aerobic decomposition in the oxic layer. Methane is the byproduct of decay processes in anoxic peat layers, a fraction of which is utilized by methanotrophs that are capable of oxidizing it to CO_2 (Jauhiainen et al., 2005).

and hydraulic conductivity, a condition that favors the upward capillary motion of soil water to further raise the water table, and thus soil anoxia, in a positive feedback. These processes can result in domed peat surfaces and deep peats to 20 m.

Another key factor influencing the balance of carbon in peat swamps is the nature of swamp vegetation, which in tropical peatlands is generally forested (Lawson et al., 2015). A diverse array of tropical swamp trees possesses effective morphological and physiological adaptations to sustain growth even in waterlogged conditions, which otherwise restrict growth of the vast majority of plant species (Draper et al. 2018; Householder and Wittmann, 2016; Page et al., 1999; Posa et al., 2011). Consequently, peat swamps often harbor multi-storied tree canopies that are able to support high levels of biomass production despite the locally harsh growing conditions. An important feature of this luxuriant growth in regards to peat accumulation is the production of different types of litter, ranging from fleshy leaves, woody debris such as branches and tree trunks, and underground roots. These various litter fractions all have different capacities for decay and therefore make different contributions to accumulating peat (Chimner and Ewel, 2005). Fleshy leaves contribute a high proportion of plant productivity, but their deposition on the soil surface leads to rapid, aerobic decay that yields little carbon for peat development (Yule and Gomez, 2009). Much of tropical peat is therefore derived from woody debris and roots. Woody debris from twigs and trunks of trees is deposited on the soil surface, but its higher lignin content and carbon:nitrogen ratios confer greater resistance to decomposition. Root systems of dominant peat swamp trees tend to be quite extensive, producing considerable biomass directly within anoxic layers of peat soils where their decomposition is strongly constrained (Chimner and Ewel, 2005).

The predominantly forested condition of tropical peat swamps contrasts with non-tropical peatlands dominated by *Sphagnum* mosses, which neither produce large amounts of recalcitrant wood nor root biomass. The forest vegetation is thus the principal component of tropical peat that determines its properties, rate of accumulation, and susceptibility to degradation (Könönen et al., 2016). Where peat swamp forest vegetation and its local hydrological environment are maintained over long periods of time, tropical swamps can accumulate peat rapidly, making them among the world's most effective terrestrial ecosystems for the long-term sequestration of atmospheric carbon (Dommain et al., 2011).

Regional and landscape processes of peat formation

While peat formation is the result of biogeochemical processes operating over small spatial and temporal scales, the unique hydrological conditions that enable these processes are determined by factors acting over the scale of the larger landscape. Three basic landscape requirements for peat swamp formation are (i) a local topographical depression, (ii) relatively stable water levels that persist over time, and (iii) a water source that carries limited sediment load. The first two sustain the waterlogged conditions that limit peat oxidation, while the latter prevents depressions from being plugged with mineral sediments at a faster rate than infilling of organic matter. These basic requirements are only satisfied under a combination of specific geomorphologic, geologic, and climatic contingencies.

Climate conditions are generally humid where peat swamps develop, with most concentrated in areas where yearly precipitation exceeds evapotranspiration. Strong rainfall seasonality can curtail long-term peat accumulation when prolonged dry periods lead to oxidative peat loss that exceeds organic accumulation. As such, the accumulation and maintenance of peat is sensitive to strong interannual climatic variability, such as El Niño-Southern Oscillation (ENSO). Long-term paleoecological records often report strong coupling of peat accumulation rates with climate variability over millennial time-scales, with expanding peats and rapid peat accumulation during wetter time intervals, and retraction with peat oxidation during drier intervals (Page et al., 2004; Dommain et al., 2011).

Although wet climates are favorable for peat swamp formation, the local conditions that actually sustain an appropriately wet environment are largely a function of the physical and geologic settings, which determine where and how water collects locally. In tropical lowlands, where the vast majority of peat swamps are located, topographic depressions are most commonly generated by dynamic fluvial processes. Indeed, most globally significant tropical peat areas occupy abandoned meander scars in river valleys (Householder et al., 2012; Lähteenoja et al., 2012), or alluvial terraces that have been subsequently bisected by river erosion (interfluves) (Dommain et al., 2011; Dargie et al., 2019). Although often embedded within fluvial settings, characteristics common to many tropical lowland rivers rarely favor peat swamp development. These include marked seasonal river level oscillations, large amounts of suspended sediment, or both (Latrubesse et al., 2005). Highly seasonal river-level fluctuations result in pronounced low water-table phases that expose peat to air and lead to rapid peat oxidation. During high river stages, on the other hand, organic accumulation on the surface can be carried away with currents. Overbank flow during floods can also bring in large amounts of suspended sediment, thus adding a significant mineral component onto accumulating organic material to create muck, rather than carbon-dense peat. In fluvial environments where rivers strongly regulate the hydrological setting, peats swamps are often associated with impermeable subsurface base layers such as clay strata or hard pans, which strongly modify the local hydrological setting. These subsurface layers inhibit drainage of rainfall, and often force groundwater laterally to cause local seepages. Hence, they establish favorable hydrological conditions for local peat accumulation by providing some level of hydrological independence from potentially fluctuating water table levels due to seasonal river discharge or rainfall (Dommain et al., 2011; Householder et al., 2012).

Global distribution and genesis of peat swamps

Tropical peat swamps have been documented on all major tropical land masses. Considerable uncertainty, however, still exists regarding their global distribution and extent. Indeed, scientific documentation of several large peat swamps has only recently begun. Despite significant knowledge gaps, it is clear that the geographic distribution of tropical peat swamps is noticeably unbalanced, with overwhelming concentration in only three large peat swamp complexes located in southeast Asia, northwest Amazonia, and central Africa (Fig. 2). This skewed distribution ultimately reflects the unique combination of regional climatic, geomorphologic, and geologic contingencies in these locations which have enabled peat accumulation over millennia.

Southeast Asia

In SE Asia, peat swamps are concentrated in the modern-day islands of Sumatra, Borneo, and parts of the Malay peninsula (Page et al., 2006). This island region is connected by the geologically stable and shallow continental Sunda Shelf, or "Sundaland," which has played an integral role in the genesis of the region's vast peat swamps (Dommain et al., 2011). During the last glaciation, shelf areas were exposed by lower sea levels, in which setting the eroding crystalline highlands formed extensive alluvial plains. It is in this flat alluvial setting where the majority of modern peat swamps have developed, primarily along river interfluves from coastal areas to over 200 km inland. Two regional developments during deglaciation were key for the initiation of these peat swamps. First, flooding of the Sunda Shelf in response to rising sea levels decreased the hydraulic gradient from river headwaters, impeding drainage on an already very flat landscape. Second, the climate became wetter, in part because of the newly formed regional evaporating area of the flooded shelf. Both developments led to increasing regional water tables that triggered the necessary waterlogging for peat initiation. The timing of peat initiation, however, varied along an elevation gradient from coastal to inland areas, a reflection of how the changing water table interacted locally with surface topography. In coastal areas at sea level, peat swamps arose only upon stabilization of sea levels in the mid-Holocene about 4000–7000 yrBP (Page et al., 2006). These relatively young peat swamps have depths from 1 to 3 m, forming over clayey substrates initially deposited under mangrove vegetation

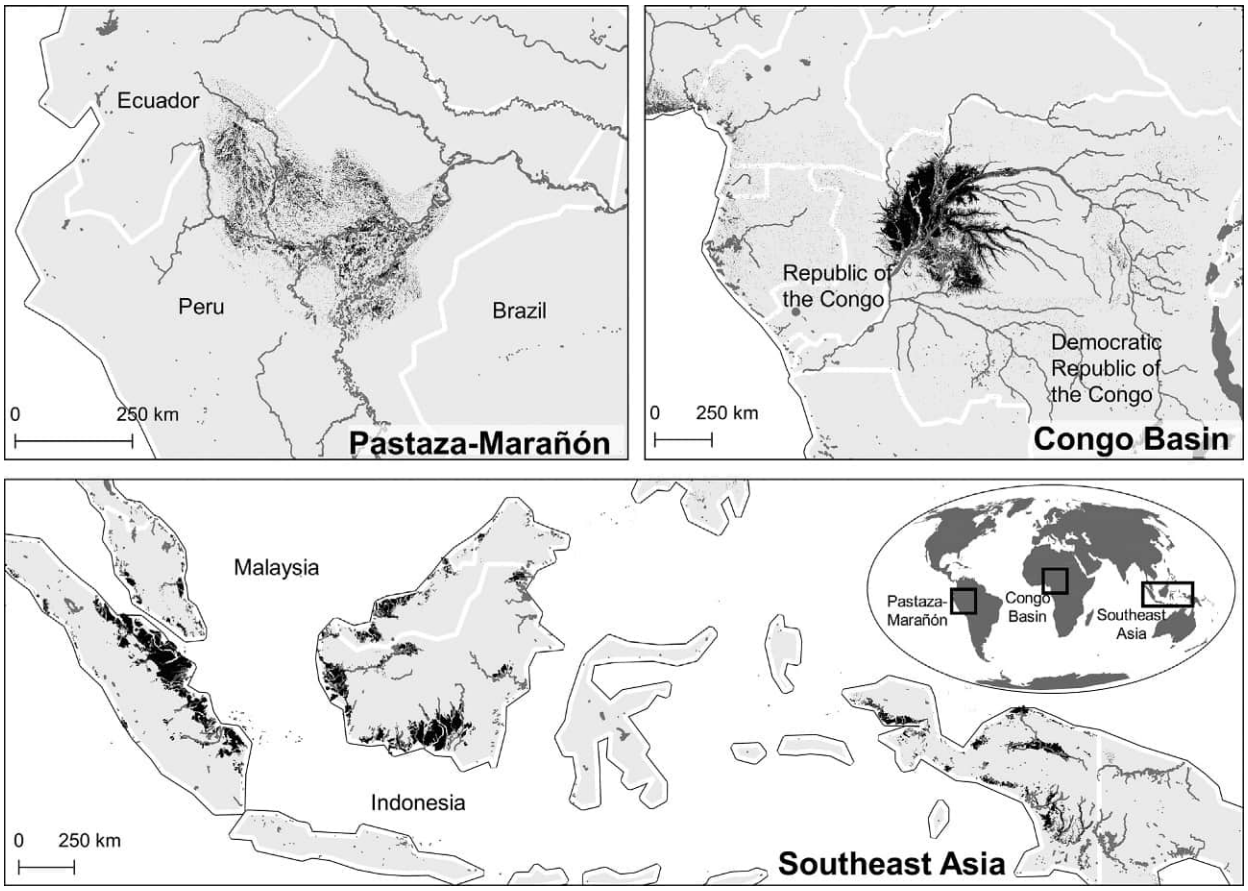

Fig. 2 Major regions of peat-forming swamps (black) in the tropics. Mapping is restricted to areas where large peat swamp complexes have been ground verified. Although permanent waterlogging drives peat accumulation in all regions through similar biogeochemical processes, the geomorphologic and geological contingencies that create and sustain the waterlogged conditions are quite different among regions. Peat swamp distribution data shown here are derived from remote sensing products obtained from publicly available datasets (consolidated by Xu et al., 2018, and in tropical regions largely based on Gumbricht et al., 2017 and Dargie et al., 2017).

(Cameron et al., 1989). Farther inland and at slightly higher elevation (5–15 m above sea level), peat swamps initiated slightly earlier (8000–9000 yrBP), in response to increasing sea levels and the rising water table. These domed peat swamps, up to 20 m deep, form in river interfluves, where water table mounds contribute to permanent waterlogging (Dommain et al., 2011) and natural levees limit floodwaters from adjacent rivers. The oldest peat swamps, initiating as early as 47,000 yrBP, are located at higher elevations to 30 m above sea level (Ruwaimana et al., 2020). The initiation of these older peats is too early to be explained by sea level rise associated with deglaciation. Many developed over podzolised sands with an impermeable hard pan in the substratum, a key feature defining the local hydrological setting in which peats well over 10 m have accumulated (Page et al., 1999, 2004). Others are the result of terrestrialization of lake basins.

Northwest Amazon

In tropical America, the most significant peat swamp complex is located in the northwestern Amazon (northeast Peru), which has developed within an actively subsiding foreland - the Pastanza-Marañon basin (Draper et al., 2014). The subsiding basin is linked to flexure of the continental lithosphere as a result of compressional tectonic forces and the uplifting of the Andes (Dumont, 1996). This ancient basin has formed a regional collecting point for rivers that drain an immense landmass with high and relatively aseasonal rainfall, thus establishing the waterlogged conditions appropriate for peat swamp development. Within this subsiding basin, fluvial sediments from Andean headwaters have built up several thousand meters of alluvial material (Räsänen et al., 1992) and it is in this highly depositional, and dynamic fluvial setting where peats up to 8 m in depth have accumulated, largely within river valley depressions formed by meander scars and abandoned arms of laterally migrating rivers (Lähteenoja et al., 2012). Peat formation generally commences in depressions only after overbank flood connections to sediment-laden rivers are minimized, which may happen as channels migrate away from developing peat swamps and sediment-free sources of rainfall and groundwater come to dominate local peat swamp hydrology (Householder et al., 2012; Lawson et al., 2014). Although suitable conditions for peat formation in the Pastaza-Marañon basin are likely to have persisted throughout the Quaternary, the basal peat ages that time stamp their initiation tend to be younger and more variable than their SE Asian counterparts. Whereas in SE Asia peat swamps initiated largely as a regional response to rising ocean levels after the last deglaciation, peat swamp initiation in the Amazon has tended to be a local response to river meandering (Householder et al., 2012; Lähteenoja et al., 2012). Meandering river channels not only generate local depressions for peat swamp development, but also cause the wholesale erosion of developing peat swamps, or alternatively, their burial under mineral sediments that are transported and deposited by river floods (Lähteenoja et al., 2012). As a result of this dynamism, individual peat swamps rarely exceed ages of 8000 years, and even within this short time span the constantly changing position of developing peat swamps with respect to the main river channel often brings about abrupt transitions and reversals of environmental conditions and vegetation succession (Roucoux et al., 2013; Kelly et al., 2017). The waxing and waning of fluvial influence over time is often reflected in complex peat stratigraphies, showing mineral layers (associated with river influence) intercalated with peat (Lähteenoja and Page, 2011). An important consequence of this fluvial dynamism is that peat can be buried under river sediments, thus forming a protective mineral cap that reduces peat to exposure and oxidation by drought, fire, and river erosion. The slow subsidence of this buried peat within the foreland basin is believed to be an efficient long-term carbon storage process that has presumably operated to remove atmospheric carbon throughout the Quaternary (Lähteenoja et al., 2012).

Congo Basin

Africa's largest complex of peat swamps has developed within the Congo Basin, also known as the Cuvette Centrale (Dargie et al., 2017). The Congo Basin is one of the least studied major river basins and considerable knowledge gaps exist regarding its geologic evolution. Its origins are most recently linked to extensional forces associated with continental rifting in eastern Africa, although its >800-million-year history is likely the result of varied (and still poorly understood) geological processes (Buiter et al., 2012). Reported sizes of the basin range from about 3.6 to 4.1 million km^2, and peat swamps are currently estimated to account for about 40% of its extensive wetland areas (Dargie et al., 2017). These peat swamps overlie river interfluves and show maximal peat depths of nearly 6 m at domed midpoints between bounding rivers. Basal peat ages between ~7000 to 10,000 years BP mark the initiation of conditions suitable for peat formation and coincide with increased precipitation of the African Humid period (Dargie et al., 2017). The current climate is slightly drier (between ~1100 mm yr^{-1} to 1900 mm yr^{-1} along an east-west trend), but swamps have nevertheless continued to accumulate peat since initiation. The hydro-geological scenario that generates the waterlogged conditions for peat swamp development is not yet well understood. Water levels on interfluves supporting peat are relatively stable and often a few meters higher than those of the immediately adjacent and more strongly fluctuating rivers (Alsdorf et al., 2016). Several other lines of evidence suggest that the interfluvial peatlands are primarily fed by rainwater, rendering them hydrologically independent of the fluctuating rivers that flank them (Dargie et al., 2017; Davenport et al., 2020). Under these circumstances interfluvial peat swamps remain inundated even during low-stage river levels and are unlikely to receive mineral input from overbank flooding.

Although far from an exhaustive account of the myriad settings in which tropical peat swamps can occur, what should be clear is that their formation reflects a unique set of climatic, geomorphologic, and geologic factors. These factors ultimately determine the local hydrological conditions that govern the distribution of peat swamps from landscape to global scales.

Carbon stock of tropical peat swamps and its measurement

Measurement of peat swamp carbon stocks at global scales has only begun within the last decade. Page et al. (2011) originally estimated tropical peat carbon stocks at 88.6 Gt C, a shocking amount equivalent to nearly 20% of the global peat carbon pool. Following emerging ground data from newly documented peat swamps in tropical America and Africa, carbon stock estimates of tropical peat have been significantly revised upwards to 104.7 Gt C (Dargie et al., 2017). This amount is equivalent to nearly half (45%) of carbon stored in living biomass of intact tropical forests (228 Gt C), but in only a fraction of the surface area (Pan et al., 2011; Dargie et al., 2017). Simultaneously, studies based largely on remote sensing of satellite imagery have suggested that large areas of tropical peat swamps with globally significant carbon pools may still remain unreported (particularly in the Amazon basin), although supporting field data continues to be lacking (Gumbricht et al., 2017; Xu et al., 2018; Riberio et al., 2021).

Considerable uncertainties still underlie all estimates of peat swamp carbon stocks (Lawson et al., 2015). Carbon stock is calculated as the multiplication of a peat swamp's aerial extent (m^2), peat thickness (m), dry bulk density of peat (kg m^{-3}), and peat carbon concentration. A first step in this calculation is often to map the aerial extent of peat swamps using a combination of ground reference data and satellite imagery. A wide variety of remote sensing satellite products reveal distinctive features of peat swamp vegetation, hydrology, and geomorphology, thus providing means of extrapolating ground reference points and identifying peat swamp habitat across larger areas. Underground peat properties (thickness, bulk density and carbon concentration) are most often addressed through field measurements using down-core sampling. Peat thickness can vary tremendously at small spatial scales because of complex subsurface geometries (Householder et al., 2012). Likewise, other underground peat properties such as bulk density and carbon concentration vary both vertically and horizontally within a peat swamp. As such, values of underground peat properties are often subject to a high level of uncertainty, particularly since they are often based on small sample sizes. These uncertainties are compounded when average values are extrapolated over broader peat swamp areas to estimate carbon stocks (Lähteenoja et al., 2012; Warren et al., 2017b). One promising approach to reduce the uncertainty of these extrapolations is to develop local relationships between underground peat properties and spectral properties derived from remotely sensed data. By taking into account the spatial variation of peat properties, these local relationships can be used to improve predictions at unmeasured locations and thus reduce uncertainty in carbon stock estimates (Draper et al., 2014).

Biological diversity

Globally, biological diversity peaks in tropical regions within lush and contiguous forest habitat growing on mineral soils. These forests have therefore been the traditional target of most scientific inquiry aimed at answering enduring questions of tropical biodiversity. Peat swamps, on the other hand, are relatively species-poor in most taxonomic groups, patchily distributed, and environmentally extreme. They are a striking departure from the diverse tropical forests that surround them, and therefore often perceived as anomalous exceptions that bear little relevance to questions of tropical biodiversity. This perception, combined with their remoteness and challenging working conditions, have contributed to a considerable lack of biodiversity information for peat swamp habitat.

It is increasingly recognized, however, that peat swamps form an important component of landscape environmental heterogeneity that contributes to regional biological diversity in important ways. The unique habitat often harbors a distinct set of species (Posa et al., 2011), novel species assemblages (Householder et al., 2016) or provides unique resources that are otherwise unavailable or rare outside of peat swamp habitat (Householder et al., 2010; Tobler et al., 2010). In addition, populations of species that encounter or inhabit peat swamps may undergo behavioral, morphological, or physiological change in response to the unique ecological setting, which itself underpins trait evolution and species diversification (Thornton et al., 2018). Far from anomalous exceptions to high tropical biodiversity, peat swamps provide a marked example of the importance of environmental heterogeneity in its maintenance and generation.

Flora

For the vast majority of vascular plants, year-round waterlogging is a significant environmental adversity because it greatly decreases the availability of soil oxygen for plant respiration. Local tree diversity thus often ranks low relative to the more diverse forests that grow on surrounding, well-drained, mineral substrate (Fig. 3; Draper et al., 2018; Giesen et al., 2018). In their oxygen-starved soils, plants require anatomical, physiological, or metabolic adaptations to obtain oxygen from above the soil surface or negotiate its scarcity in the substrate. Traits such as pneumatophores, lenticels and buttressed roots include some of the most outwardly visible manifestations of tree adaptation to a waterlogged environment. For the vast majority of plants, however, the suite of attributes that permit successful growth and regeneration in peat swamp habitat remain poorly understood.

In addition to complete water saturation, the peat swamp plant community responds strongly to local changes in nutrient availability, flooding depth and water chemistry, so that local vegetation is often markedly zoned along multiple environmental gradients (Page et al., 1999). It is not uncommon, for example, for closed forest to transition to an open herbaceous community within a matter of a few dozen meters. Strong variability in plant community composition among individual peat swamps is also commonly reported, reflecting differences among peat swamps in age, successional stage, disturbance history, abiotic conditions, as well as large dispersal distances between swamps that limit floristic exchange (Anderson, 1963; Posa et al., 2011; Householder et al., 2012, 2016).

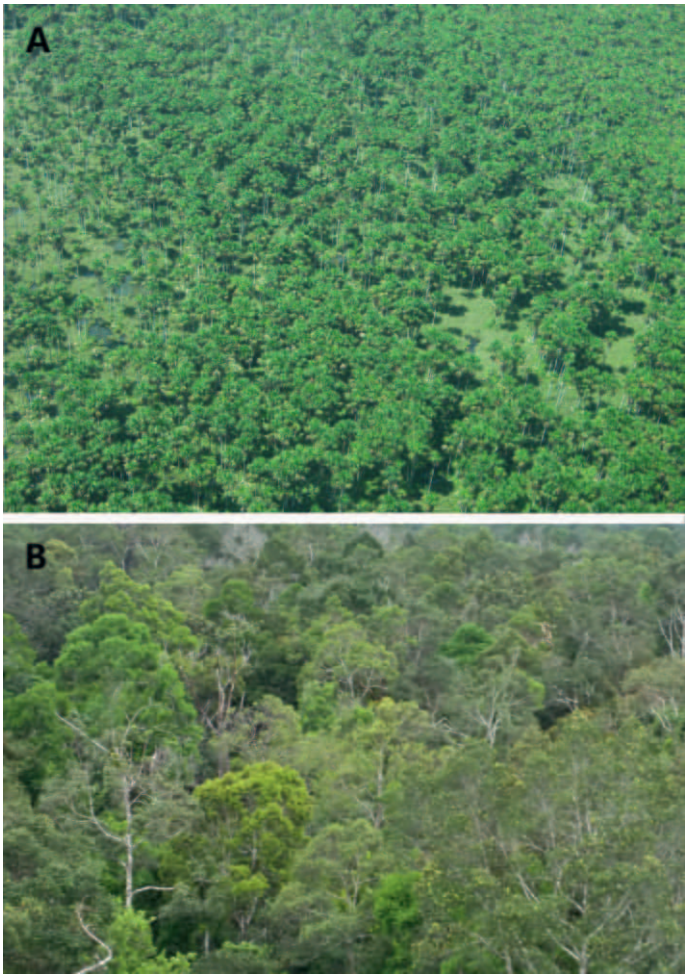

Fig. 3 Views over peat forest canopies in the (A) Peruvian Amazon, and (B) and Indonesian Sumatra. Peat swamp canopies in the Amazon region are dominated by a single species of arborescent palm (*Mauritia flexuosa*), which commonly achieves high densities of approximately 300 individuals per hectare. In this monodominant canopy, the largest fraction of floristic diversity is in the understory, which is often rich in shrubs, herbs, and epiphytes. Indonesian peat swamps, in contrast, have a much richer diversity of canopy species, ranging between 30 and 120 species per hectare (Giesen et al., 2018). Photo credits: M. Tobler (A), S.E. Page (B).

Peat swamp plant communities have long been regarded as highly unique and specialized to the novel environmental conditions that prevail in peat swamps (Anderson, 1963). Strict ecological specialization, however, tends to be rare among plants. A significant fraction of peat swamp floristic diversity, if not the largest, is composed of species that are also commonly found in forests of well-drained mineral soil, implying that many plant species of peat swamp habitat are broadly tolerant to a wide variety of soil conditions (Pitman et al., 2014; Giesen et al., 2018). Floristic ties to other environmentally extreme habitats are also prevalent, such as those on nutrient impoverished podzols, high elevation mountain forests, or seasonally inundated floodplains (Householder et al., 2015; Giesen et al., 2018). In such habitats where growth is similarly limited by abiotic extremes, plant traits required for survival and regeneration are also likely to be similar, thus facilitating floristic exchange among them (Householder et al., 2016). Although few plant species are strictly restricted to peat swamp habitat, it seems clear that peat swamps maintain large and biologically important populations of many species that are otherwise locally rare outside the habitat (Posa et al., 2011; Draper et al., 2018; Giesen et al., 2018).

Fauna

Information regarding faunal diversity in peat swamps is geographically unbalanced, most emerging from Southeast Asian swamps that have enjoyed a longer legacy of scientific exploration. It is also taxonomically biased, largely restricted to more conspicuous vertebrate members, and in particular large mammals and fish. Other groups such as insects, amphibians, reptiles, and small mammals have received scant attention. Few, if any, terrestrial vertebrate species are biologically dependent on peat swamp habitat. Rather, peat swamps tend to be one part of the larger ecological mosaic that local animal populations may utilize in a variety of important ways. In Amazonia, for example, fruits of the canopy dominant of peat forests (*Mauritia flexuosa*) are a valuable temporary food resource for large terrestrial mammals such as the lowland tapir (*Tapirus terrestris*) and peccaries (*Tayassu pecari*

and *Pecari tajacu*) (Tobler et al., 2010). Also, the dead, standing trunks of *Mauritia flexuosa* serve as a main nesting site for the blue-and-yellow macaw (*Ara ararauna*) (Brightsmith and Bravo, 2006). In SE Asia, peat swamp forests are an important refuge for some of the largest populations of a number of threatened animals, including orangutans (*Pongo* spp.), Bornean gibbons (*Hylobates albibarbis*), the false gharial (*Tomistoma schlegelii*), Storm's stork (*Ciconia stormi*) and the white-winged wood duck (*Asarcornis scutulata*) (Posa et al., 2011). Likewise, central African peat swamps are an important sanctuary for species whose habitats have been altered as a result of human land use, supporting considerable numbers of lowland gorilla (*Gorilla gorilla gorilla*), forest elephant (*Loxodonta cyclotis*), chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*) (Dargie et al., 2019). In contrast to terrestrial fauna, fish have been reported to exhibit higher levels of specificity to aquatic environments associated with peat swamp habitat, although most information regarding this group is still restricted to SE Asia (Ng et al., 1994). The aquatic habitats in peat swamp forest are characterized by their high acidity, high content of dissolved organic matter, low nutrient content, and often low levels of dissolved oxygen. This suite of conditions typically differs from nearby aquatic environments outside peat forest, offering habitat to unique assemblages of fish species that often exhibit high levels endemism (Ng et al., 1994). Posa et al. (2011), for example, estimated that about one third of the 219 fish species encountered in peat swamps could be endemics specialized to the habitat.

Threats

Tropical peat swamps face a variety of local and regional threats (Fig. 4). One of the most widespread and persistent is agricultural expansion into peat swamp habitat. Transformation to agricultural production initially involves both logging of the original forest and lowering of the water table by means of drainage ditches. These land use changes dramatically alter the carbon balance of peat

Fig. 4 A selection of images illustrating some of the major land use threats to peat swamp forests. (A) Peat fire in Indonesian Borneo. (B) Smallholder farming activity on peat in Indonesian Borneo. (C) Aftermath of recent peat fire in eastern Amazonia near cattle pasture from where the fire spread. Only the fire-tolerant *Mauritia flexuosa* persists. The dark bases of trunks are charred pneumatophores and adventitious roots. Their visibility high above the peat surface reflects a rapid lowering of peat by about one meter, likely a consequence of smoldering fires and drainage. (D) Felling of *Mauritia flexuosa* for fruits in Western Amazonia, driven by market demand of nearby urban centers. (E) Gold mining in a peat swamp in southwest Amazonia. Gold is concentrated in old meander scars where peat swamps also form. Miners have excavated a large area to create a deep black water pond where swamp forest with deep peat once stood. Photo credits: Borneo Nature Foundation (A), S.E. Page (B), J.E. Householder (C,D, E).

swamps by simultaneously reducing carbon input from plant productivity and increasing carbon output by stimulating aerobic decomposition and leaching. Changes to forest structure and composition under agricultural use can also drive carbon losses through direct harvest of plant biomass and changes in litter quality or soil compaction that impact rates of decomposition (van Lent et al., 2019). Under such conversions, peat does not accumulate, and peat swamps switch from primarily functioning as sinks of atmospheric carbon, to substantial sources (Murdiyarso et al., 2010). Indonesian peat swamps have suffered the largest losses to agricultural conversion (Fig. 4), largely through oil palm and pulp wood production, and only about 6% of peat swamps in Indonesia remain undisturbed (Miettinen et al., 2016). While peat swamps in tropical America and Africa are still relatively intact, encroachment is likely to increase in the near future. A wide variety of exploitative uses are arising from growing market demands, whether that be for non-timber forest products for consumption in local urban centers or commodities traded in global markets, such as gold and oil that are associated with peat deposits (Butler and Laurence, 2009; Householder et al., 2012; Draper et al., 2014; Dargie et al., 2019).

Change in precipitation with ongoing climate alteration is another significant concern, which will impact peat swamps through its influence on the water table and rainfall inputs. Although competing climate models disagree about future precipitation patterns in regions where extensive peat swamps occur, the majority predict either annual rainfall reductions or greater interannual variability, neither of which are conducive to sustaining peat swamp habitat and function (Li et al., 2007). Predicted drier or more seasonal climates are expected to greatly amplify degradation already initiated by land use change. This amplification is most dramatically played out through increased fire risk. Human activity provides ample opportunity for ignition, and under drought conditions superficial peat is highly combustible. Peat fires can smolder for months in subsurface layers, even under moist conditions (Fig. 4A). These fires rapidly consume peats that have accumulated over millennia and can have significant impacts on global levels of atmospheric carbon. During 1997–98, fires in Indonesia, for example, are estimated to have burned an amount of peat equivalent to 13–40% of the mean annual global carbon emissions from fossil fuels, contributing to the largest recorded annual increase in atmospheric CO_2 concentration in modern history (Page et al., 2002).

Conclusions and outlook

Tropical peat swamps are carbon-rich ecosystems that additionally support populations of valued plant and animal species. As such, they bear considerable importance in both global climate and biodiversity crises. They are also highly vulnerable and unable to absorb the increasing human activity that is often concentrated upon them by demand from local, regional and global markets. Current market mechanisms incentivize unsustainable land uses because short-term profits are captured by few, while the costs of degraded peat swamp are broadly distributed among many and overtime. While carbon credit–offset schemes such as REDD+ (reducing emissions from deforestation and forest degradation) offer market mechanisms and monetary incentives to protect remaining tropical peat swamps or restore degraded ones, it still remains unclear whether this is sufficient (Murdiyarso et al., 2010). Most peat swamps are located in regions of pronounced social inequality. Hence, a critical area of research should also focus on gaining a more complete understanding of how the health of peat swamp habitat interfaces with that of the livelihoods of local peoples (Dargie et al., 2019). In the end, the outlook for tropical peat swamps hinges on whether or not novel market mechanisms as well as future societal norms can successfully recognize (or monetize) both the true value of the habitat and the costs of its degradation.

Knowledge gaps

- What is the current surface area covered by peat swamp forest in the tropics?
- What factors determine the distribution of peat swamps forest?
- What is the current carbon stock of tropical peat swamps?
- How will carbon stocks in tropical peat swamps change in the future?
- What factors determine soil-atmosphere fluxes and how will these fluxes change with land use and climate alteration?
- What is the significance of tropical peat swamps for biodiversity?
- How should peat swamp forests be managed for carbon storage, biodiversity and human well-being?

See Also: Structures and functions of Inland Waters - Rivers: Hydrology and Classification of Rivers for Management; Structures and functions of Inland Waters - Wetlands: Prehistoric Wetlands; Restoring Riparian Peatlands for Inland Waters: A European Perspective; Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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Mangrove Forests: Structure, Diversity, Ecosystem Processes and Threats

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Blue carbon Carbon that is derived from carbon sequestration, i.e., the removal of CO_2 from the atmosphere, and stored in oceanic and coastal marine ecosystems. Mangrove forests, saltmarshes, seagrass beds and algal (kelp) forests, and other coastal wetlands, are considered the major players. While this implicitly refers blue carbon to organic carbon, recent debates pledge for including inorganic carbon, thus rendering reefs built by corals or other calcifying organisms blue carbon ecosystems, too.

Ecosystem process Physical, chemical or biological activity or reaction that links organisms and their environment, such as production, decomposition, or organic matter-turnover, nutrient-cycling and energy fluxes. Ecosystem processes are driven by organisms and their interactions, and underlie ecosystem services.

Ecosystem service Benefits people obtain from ecosystems; commonly categorized as *provisioning* (e.g., food- or water-supply), *regulating* (e.g., regulation of floods or droughts), *supporting* (e.g., soil formation or blue carbon-sequestration and -storage), or *cultural services* (e.g., offer of recreation, spiritual, religious or other nonmaterial benefits).

Ecosystem engineer Species that create, modify or maintain a physical habitat for themselves and other species by significantly changing abiotic environmental conditions.

Foundation species Dominant species of a biological community that, through their mere abundance and biomass, have a strong effect on other species, by creating conditions and stabilizing fundamental ecosystem processes, and thus community composition.

Keystone species Species that have a strong effect on other species, and thus community composition, upon strongly interacting with, or posing indirect effects on, other species, despite their low abundance; other than foundation species, keystone species are rare.

Sediment Mineral material deposited, off its site of formation upon weathering and erosion of a mother rock, through transportation by the action of wind, water, ice or by gravity. Sediments can become enriched in organic material of various allochthonous or autochthonous origins. The appearance of the stable and organic matter-rich forest floor of a mangrove growing high in the intertidal may render the sediment resembling a soil, but the allochthonous origin of the mineral portion determines this still as a sediment. By contrast, soil is the result of simultaneous weathering of the bed rock (from below) and biotic activity that incorporates organic matter (from above). The distinction from sediments is that the mineral compartment of a soil is autochthonous in origin and remains in place.

Introduction

Mangroves are trees and shrubs that grow on soft sediments in the upper intertidal zone of tropical and subtropical coasts. They can form dense and extensive forests (Fig. 1) of either monospecific stands or multi-species assemblages along sheltered coastlines, bays and lagoons, or estuaries. The global distribution of mangrove forests roughly coincides with the 20 °C-isotherm of the coastal oceans' surface water. Thus, they range from ca 30°N to ca 30°S (and further south in Australia), except for the west coasts of southern Africa and South America where the cold Benguela and Humboldt currents, respectively, hit the coasts. Close to the northern and southern distribution limit, as well as under otherwise unfavorable conditions, such as aridity or high sediment salinity, mangrove plants remain stunted and often form only sparse stands (Fig. 2).

While mangroves accumulate small sediment particles upon slowing down water movement (see below), they essentially depend on soft sediment environments for their settlement and establishment. Hence, mangrove forest mostly develop and dwell along coastlines that are protected from strong wave action, and thus, are rich in fine sediments. However, numerous cases are known where individual seedlings settle and establish in crevices of rocky shores or consolidated beach platforms, among

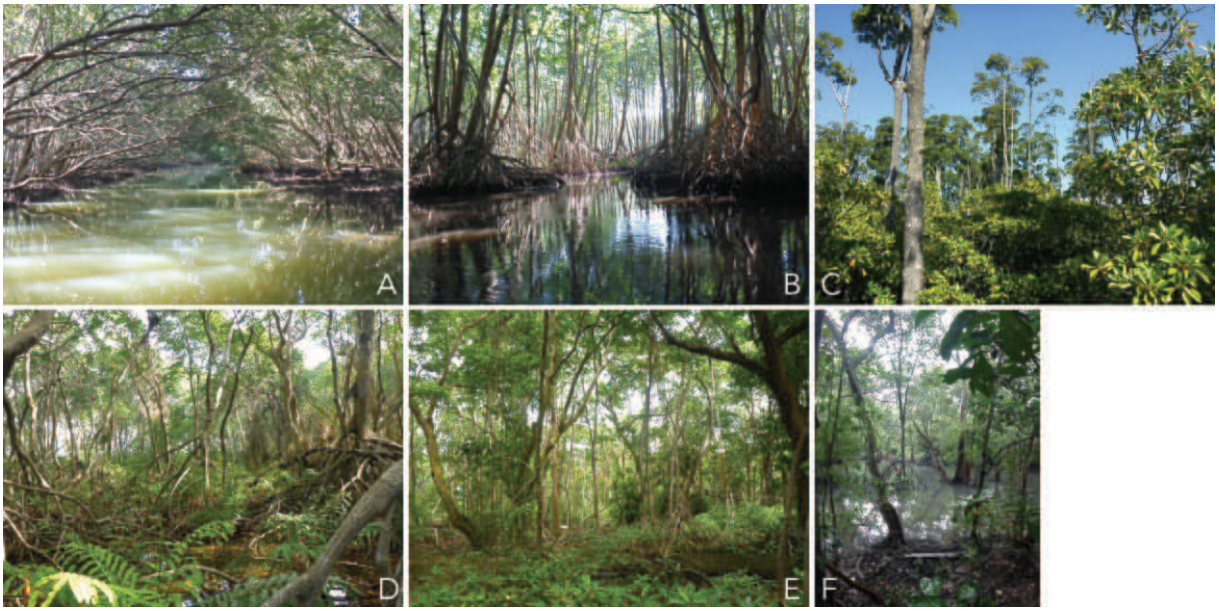

Fig. 1 Dense monospecific riverine stands of *Avicennia marina* (South Africa) (A) and *Rhizophora mangle* (El Salvador) (B); stand of sparse tall and dense young *Bruguiera gymnorhiza* in a protected bay (South Africa) (C); tall *R. mangle* with dense understory (e.g., *Acrostichum aureum*) (D) and mixed stand of *A. germinans* and *R. mangle* (E) on San Andrés Island (Colombia); species-rich, dense mangrove patch in Singapore (F).

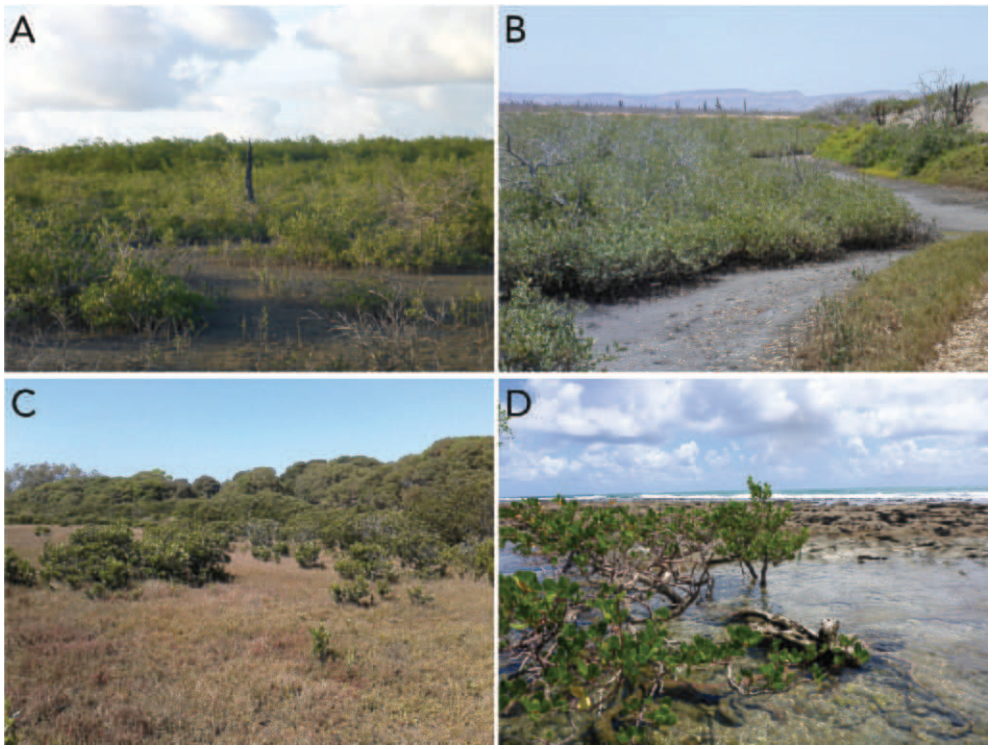

Fig. 2 Stunted *Avicennia germinans* on a hypersaline saltflat near Bragança, PA, (Brazil) (A); stunted *A. germinans*, next to desert vegetation, in an arid region near La Paz (Mexico) (B); sparse stand of stunted *Avicennia marina* in a mangrove-saltmarsh ecotone near Melbourne (Australia) (C); stunted *Laguncularia racemosa* on a degraded reef platform near Tamanadaré, PE (Brazil) (D).

boulders or on top of (partly protected) backreefs (Fig. 3). Such isolated trees may accumulate soft sediments and become cores of mangrove establishment, and eventually provide protection from wave action to the coastline and human settlements on the coast.

The attenuation of wave action, leading to sediment deposition and stabilization, thus contributing to coastal shoreline protection and prevention of coastal erosion, is among the manifold ecosystem services that mangroves provide to local societies and their wellbeing and livelihood, as well as to humankind worldwide. Mangrove forests are home to a rich and diverse fauna (Fig. 4) of both terrestrial and marine origin. Many of these species, along with other natural resources, form the basis for food and

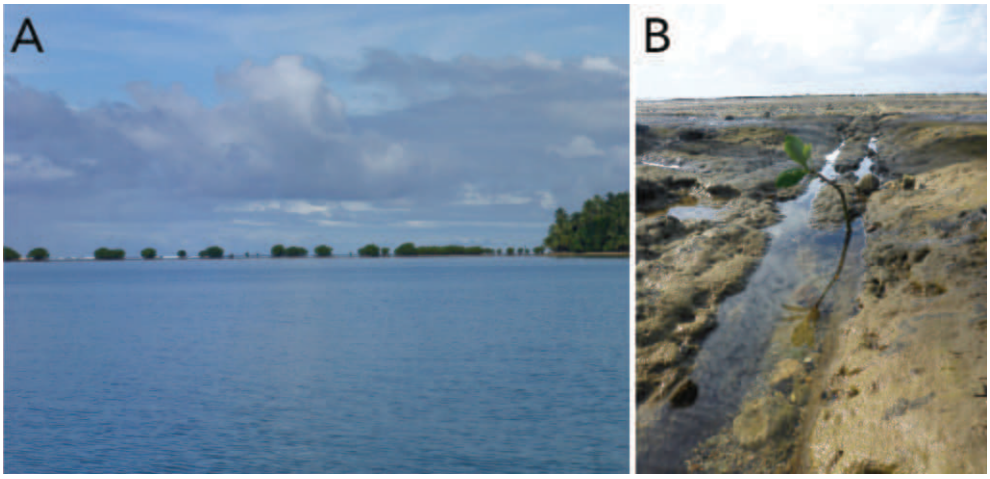

Fig. 3 Sparse *Rhizophora stylosa* trees on a backreef plateau (A) and recently established seedling of *R. stylosa* in crevice of a consolidated beach platform (B) of the main island (Viti Levu) of Fiji.

Fig. 4 Examples of mangrove fauna: tree-climbing *Episesarma versicolor* in Singapore (A; courtesy of Véronique Helfer, ZMT); *Goniopsis pulchra* (B), and dense population of fiddler crabs (C) in arid mangroves of Baja California (Mexico); mangrove (upside-down) jellyfish in a mangrove channel of San Andrés Island (Colombia) (D); epibionts on prop roots of *Rhizophora mangle* in Caribbean Colombia (San Andrés: E) and Senegal (F); barnacles on prop roots of *Rhizophora* sp. in Singapore (G); iguana (H) and crocodile (I) in the mangroves of Barra de Santiago (El Salvador); monitor lizard in Singapore (K); mudskipper (L) and mangrove snails (Cerithidea decollata) on *Avicennia marina* stem (M) in South Africa.

income for local stakeholders (Fig. 5). Mangrove crabs are collected and either used as food by the families themselves or sold on nearby markets, either as they are or upon processing by female family members. Consortia of women collect various shellfish species from the extensive root systems of mangroves or in sediments of nearby shallow waters. Mangrove forests act as nurseries –habitat, shelter and feeding ground– for juveniles of numerous fish and shrimp species that spend their adult lives in adjacent ecosystems (e.g., seagrass beds or coral reefs) or in the open sea, thus providing both rich fishing grounds for local fisher people and feeding areas for predators. Mangrove leaves, fruits and flowers are used for the production of fodder, teas and (alcoholic) beverages, food, honey and medicine. The wood of many mangrove species is not only dense and hard, rendering it an excellent construction material, particular for the use in seawater, but has high caloric values and is, thus, used as firewood or for charcoal production. Mangroves store vast amounts of organic carbon, derived from carbon dioxide (CO_2), and derivatives of other greenhouse gases in their above- and belowground biomass and, predominantly, in the sediment that is colonized by mangrove forests. Detrital organic

Fig. 5 Crab (*Ucides cordatus*) collector of Ajuruteua Peninsula (PA, Brazil) (A); crab fisherman deploying crab traps near Tamandaré (PE, Brazil) (B); fish trap (*coral*) (C) and net-fishing (D) in the Jaguaripe River (BA, Brazil); traditional cooking of shellfish (E) and air-drying of fish (F) in the Sine Saloum region of Senegal. E, F: courtesy of Véronique Helfer, ZMT.

matter from inside the forest (mostly leaf litter but also fallen wood, rotting fruits etc.) and from the nearby ocean (drifting seagrass and algal wrack, deposited by the tides and retained by the complex three-dimensional architecture of root structures) is incorporated into the sediment, either by burrowing crabs or by sediment-moving wave action and sediment deposition. In the saline and anoxic environment of the mangrove sediment, the sequestered organic matter forms organic carbon (and nitrogen) stocks that are stable over centuries and millennia rather than being deposited into the atmosphere as greenhouse gases (CO_2, N_2O, CH_4) upon decay and decomposition.

Irrespective of the invaluable relevance of mangrove forests for local societies and the growing acknowledgement of their value worldwide, mangrove area has been, and is still being, lost at alarming rates. Over less than 20 years from the 1980s to the early 21st century, mangrove forests encountered a loss of about one quarter of their global area. Even though current loss rates are, on a worldwide average, well below 0.5% (Friess et al., 2020), we are still losing some 50 ha of mangroves every day. The major threats to mangrove forests encompass habitat degradation and clear-felling. Slow degradation is driven by either pollution from nearby settlements or industries, or eutrophication from agriculture in the hinterland or through untreated sewage.

Clear-felling is brought about by different agents, first and foremost forestry (Fig. 6). Selective felling of individual trees or small groups of trees for harvesting firewood or wood for constructing houses, boat piers or jetties, or fish cages, has been traditional for centuries. Such small-scale activities are commonly considered sustainable and appear to not harm the forest or its integrity. However, over the last decades, the use of mangrove wood for various purposes developed into large-scale industries in many places. Only few of them are, or try to be, sustainable, and mangrove forestry contributes significantly to the global area loss.

The second major driver of mangrove area loss is clear-felling for giving space to aquaculture ponds (Richards and Friess, 2016). Over decades, mangrove forests had been transferred into large-scale aquaculture areas in many regions of the world. While the ponds are usually abandoned after a decade or so, because of decreasing productivity and increasing risk of diseases, the changes in topography and hydrodynamics upon constructing the ponds render the area essentially inaccessible to natural recolonization by mangroves. In recent years, novel concepts try to avoid, or compensate for, large-scale area losses through implementing, for instance, Integrated Mangrove Aquaculture (IMA).

The construction of infrastructure for harbors, industry, settlements or even tourism has added to the pressure on mangroves, either directly through clear-felling or indirectly (see above). Further, roads or dykes near, or even inside, mangrove stands can change hydrodynamics and water regimes drastically (Fig. 2A). The same applies to dams built nearby or in the hinterland of mangroves, affecting freshwater inflow and sedimentation patterns. The results can be immediate, but more often negative effects do only become obvious slowly and over years or decades. Thus, drying, salinization or sediment depletion lead to reduced growth and productivity of individual trees and the entire forest, impoverished species composition, stunted growth forms of surviving (or recolonizing: Fig. 2A) trees and long-term degradation. Recovery is often only possible upon removing the drivers of change and reinstating suitable conditions, and usually takes years and decades for ameliorating environmental conditions and allowing for (natural or assisted) recolonization by mangroves.

Mangrove diversity

Growing in a dynamic soft-sediment environment that is driven by hydrodynamics and frequently and regularly changing water flows and tidal regimes, mangrove trees act as ecosystem engineers and foundation species by changing their environment and providing habitat for organisms that require a hard substratum. Both their aerial roots and their stems slow down currents and attenuate waves, thus releasing stress (and disturbance) from the benthic and epibiotic fauna. Their aerial roots are used as substratum by various sessile marine organisms (e.g., mussels, oysters, barnacles, sponges, algae) and offer shelter and feeding ground during high tide for motile marine organisms (e.g., fish, shrimps), many of which being of relevance as food and income for

Fig. 6 Large-scale forestry of *Rhizophora apiculata* in the Matang Mangrove Forest Reserve (Malaysia), considered sustainable through intensively monitored reforestation of clear-felled areas (A); small-scale cutting of *Laguncularia racemosa* stems for building fish traps in the extractive reserve of the Ajuruteua Peninsula (PA, Brazil) (B).

local societies. Birds nest, rest and roost in the canopy of the forest and find their food there or in the nearby coastal waters. Terrestrial mammalian grazers and browsers use mangroves as feeding ground during low tide.

On a smaller spatial scale, mangrove roots aerate an otherwise anoxic sediment and enrich the dissolved organic matter of the porewater with their exudates and, thus, nourish the sediment microbiota. Particulate organic matter of autochthonous (leaf litter, flowers and fruits, woody debris) and allochthonous (algal and seagrass drift) origin are retained inside the forest upon being entangled among the complex three-dimensional architecture of the aerial roots. This detritus becomes incorporated into the sediment, either as particulate or leached-off dissolved organic matter, and contributes to the organic matter stock of the mangrove sediment.

Mangrove trees themselves show a small-scale spatial distribution across the forest that depends on local geomorphological and ecological environmental conditions. Often, species-specific zones along, and parallel to, coastlines, tidal channel or river banks appear, suggesting zonation across the tidal gradient (Bunt, 1996; Satyanarayana et al., 2002; Snedaker, 1982). Such a zonation, however, is not a universal pattern. Many species-rich mangrove stands in areas with complex topography exhibit heavy species-mixing on small spatial scales (Fig. 1F), i.e., at similar tidal elevations (Leong et al., 2018). Hence, the concept of mangrove zonation has been challenged recently. Zonation patterns can be (1) very different regionally and do not always exhibit the same order of species; and (2) the result of succession of colonizing species upon horizontal sediment accretion and mangrove extension. Thus, long-term observations in Northern Brazil demonstrate that freshly deposited sediments along the non-eroding side of meandering tide channels are first colonized (and stabilized) by the saltmarsh species *Spartina alterniflora*. Entangled propagules of the pioneer species *Laguncularia racemosa* (White mangrove) soon form dense stands in which *Avicennia germinans* (Black mangrove) establishes and outcompetes the White mangrove. During later succession, the Red mangrove (*Rhizophora mangle*), being shade-resistant, takes over and replaces the Black mangrove in the long run (U. Mehlig, pers. comm.; c.f. Mehlig et al., 2010). Along the gradient of shoreline progression, this process in time leads to a spatial pattern that resembles a pattern of spatial zonation.

Nevertheless, the spatial distribution of trees of different species in mixed mangrove stands is driven by small-scale variation in tidal elevation (Leong et al., 2018). Based on a comprehensive review of trait information available from the literature, Quadros et al. (2021), however, concluded that many functional traits of mangrove species did not evolve according to the species' position along the intertidal gradient but bear a strong phylogenetic signal, i.e., are driven by the evolutionary origin of the species. Yet, some traits of mangrove trees render them similar to other wetland plants, while, according to other traits, mangrove trees are similar to sclerophyllous plants from dry environments, probably because the saline environment renders the intertidal a "physiologically arid" environment (Quadros et al., 2021).

Mangrove forests are home to a rich and diverse fauna of decapod crustaceans. Many of these crabs dig burrows in the soft sediment, often in close association with mangrove trees and their roots (Robertson and Daniel, 1989; Gillis et al., 2019), possibly because of their stabilizing of a mobile fine-grained soft sediment (c.f. Lim and Heng, 2007). Other crab species do not burrow themselves but use the burrows of other species, either upon abandonment or as co-inhabitants. Yet other crab species do not reside inside burrows but live on mangrove trees or shelter among roots, in leaf axles (of the mangrove palm *Nypa*) or below the bark of mangrove trees.

Burrowing crabs are ecosystem engineers themselves. Their burrows drastically increase the area of the oxygenated/aerated surface of the sediment, thus affecting the community-wide metabolism of the sediment microbiota (Gillis et al., 2019), and providing a larger habitat volume for the aerobic sediment infauna. The burrows themselves serve as space, shelter and protection from adverse environmental conditions or predators to other species that do not construct their own burrows. Through vertically translocating (anoxic) deeper sediment layers onto the oxic surface (and potentially vice versa) of the forest floor (bioturbation), burrowing crabs affect the physico-chemsitry of the sediment and drive changes and variation in (aerobic vs. anaerobic) sediment processes (Lohrer et al., 2004; Stahl et al., 2014; Xiao et al., 2019).

Many of these ecosystem-engineering activities and their magnitude depend on the crab species. While some species build very simple and shallow I-, J-, or L-shaped burrows (e.g., fiddler crabs of the family Ocypodidae: e.g., Qureshi and Saher, 2012), other species (e.g., of the family Sesarmidae) dig burrow of several meters depth and complex architecture (e.g., Thongtham and Kristensen, 2003). Many of the latter are leaf litter-feeders and pull freshly fallen mangrove leaves into their burrows (for discussion: Forgeron et al., 2021), thus preventing them from being washed out by the tides and contributing to the organic matter stock of the mangrove sediment. Often, these complex crab burrows are interconnected with other burrows and exhibit high temporal and spatial dynamics (Egawa et al., 2021).

While mangroves and mangrove forests occur throughout the tropical (and subtropical) belt worldwide, mangrove floristics distinguishes two biogeographic realms with clearly separate mangrove floras that share only a single species, the Golden mangrove fern, *Acrostichum aureum*. The Indo-West Pacific (IWP), from the east coast of Africa to South East Asia and Oceania, hosts the majority of the total of some 80 mangrove species (there is an ongoing dispute about some species whether or not to be "true mangroves": e.g., Quadros et al., 2021) from 32 genera of 15 families. The IWP originates from the east coasts of the former Tethys sea where the majority of mangrove species evolved during the late Cretaceous (some 66–145 Mio years ago) (Ellison et al., 1999). The Atlantic-East Pacific (AEP), covering the Atlantic coasts of Africa and the Americas, as well as the west coast of the Americas, is derived from the former (north-)western shores of the Tethys, and harbors a mere 14 species (of 12 genera and 9 families), of which only a handful can be considered common and abundant. Notwithstanding the much higher species richness of the IWP mangrove flora, some mangrove forests of the AEP exhibit similarly high productivity and biomass stocks (Giri et al., 2011; Hutchison et al., 2014). Indeed, the tallest mangrove trees worldwide (of the most tall-growing species *Avicennia germinans* and *Rhizophora mangle*: Quadros and Zimmer, 2017) reach heights of up to 60 m along the Central African west coast (Chen and Twilley, 1998). Hence, the

major driver of mangrove productivity, growth and carbon sequestration does not seem to be taxonomic biodiversity (species richness) but rather the functional dispersion of the tree community, i.e., the trait distinctiveness of the coexisting species (Rahman et al., 2021; Quadros et al., 2021).

Much less is known about the species richness or diversity of other mangrove components, flora, fauna and microbiota, or their geographical distribution. Overall, the number of mangrove tree species in a given area correlates positively with the number of mangrove crab species of that same region (Lee, 2008), but both underlying mechanisms or reasons and ecological, ecosystemic or societal consequences of this pattern remain largely unknown.

An important, albeit often overlooked, floristic component of mangrove forests is their understory and their epiphytes. While it had been accepted (and not questioned) for long time that mangrove forests throughout the world largely lack such understory flora (assuming a lack of species that adapted to the peculiar environmental conditions of intertidal forests: Janzen, 1985), we now understand that weeds, shrubs, vines or epiphytes can make up an ecologically essential part of the mangrove vegetation. The understory flora seems to be particularly well developed and rich in mangrove areas of high precipitation rates, such as along the Pacific coast of Colombia.

Mangrove ecosystem processes

The species composition of an ecological community drives processes of the hosting ecosystem. The global distribution of the majority of mangrove species is well recorded, and regional species compositions of particular mangrove forests are well known. Conspicuous or enigmatic faunal elements of mangroves, such as mammals, birds, fish or crabs have been studied faunistically in much detail. Much less is known about the majority of the remaining invertebrate fauna of mangroves, despite extensive local knowledge about the distribution of oysters and mussels, barnacles or sponges, colonizing aboveground mangrove roots, or clams and crustaceans in the nearby sediments.

However, our understanding of which species of a given mangrove ecosystem, or their interactions, drive which ecosystem processes under which environmental conditions, and how these processes translate into the manifold ecosystem services of mangrove forests, is still in its infancy. In particular the sediment infauna and the sediment microbiota (Allard et al., 2020) of mangroves are essentially black boxes, not even to mention resulting processes and details of their contribution to ecosystem services. However, even species-specific contributions of the mangrove flora to ecosystem services of global relevance, such as the sequestration and storage of greenhouse gases into the vast stocks of blue carbon, are only recently being tackled and understood.

For instance, the prop roots of *Rhizophora* spp. are much more efficient in retaining freshly fallen mangrove leaf litter inside the system by preventing them from being washed out with the ebb tide than are the finger-shaped pneumatophores of *Avicennia* spp., as long as the leaves drift on the water surface (Gillis et al., 2016). As soon as the litter ages and loses buoyancy, leaf-retention reaches the same efficiency in *Avicennia* roots as in *Rhizophora* roots. Over successional change of neotropical mangrove forests from *Avicennia*- to *Rhizophora*-dominated stands, the amount of organic matter-input to the forest floor through litter fall increases, but litter quality decreases (Quadros et al., 2019), and thus organic matter turnover and sequestration into the sediment decreases. Fast-growing *Avicennia* spp. store larger amounts of carbon in their sediments than *Rhizophora* spp. in young (restored) mangrove stands (Kathiresan et al., 2013). Along a similar line, the leaf litter of young trees of the species *Rhizophora apiculata* decays remarkably faster than those of mature trees of the same species in Malaysian mangrove forests (Pradisty et al., 2021). Hence, mangrove stands with distinct species compositions, as well as those growing in different regions under different environmental conditions, differ from each other in the size of their blue carbon stocks and the stability of the sediment organic matter against degradation (for discussion: Zimmer and Helfer, 2020). The major driver of these differences seems to be the distinctiveness of co-occurring mangrove species regarding their traits rather than their taxonomic diversity (Rahman et al., 2021).

Often, the productivity (i.e., biomass production rate) of plant communities is viewed as a function of their (taxonomic or functional) biodiversity. However, species-poor mangrove forests of the AEP can develop almost the same standing stocks of aboveground biomass as species-rich forests of the IWP (Giri et al., 2011; Hutchison et al., 2014). Following the same line of argument as Rahman et al. (2021), Quadros et al. (2021) conclude that the productivity and standing stocks of mangrove forests are potentially driven by the trait distinctiveness of their mangrove species. The relationship between biodiversity and ecosystem processes in mangrove forests remains unclear. In this context, the observation that different mangrove crab species of the same family exhibit similar trait expressions adds to the conundrum. Functional redundancy of coexisting crab species of the same family (e.g., burrowing detritivorous sesarmids) will not add to the rate of ecosystem processes, but may increase the tolerance of a mangrove forest to (anthropogenic) disturbance that reduces species richness (Cannicci et al., 2021). The corresponding ecological equivalence of related species, on the other hand, may be the reason that mangrove forests in different regions of the world, hosting entirely different communities of crabs (and other faunal or floral elements), provide similar ecosystem services.

The differential effects of genus-specific root structures on wave attenuation and, thus, coastal protection have been studied (reviewed in Koch et al., 2009) and modelled (reviewed in Le Minor et al., 2021) in some detail. Thus, *Sonneratia* spp., developing finger-shaped pneumatophores above an extended sediment surface area, reduces wave height about twice as efficiently as *Kandelia candel* with buttress roots next to the stem (discussed by Koch et al., 2009). Further, the mechanisms of wave attenuation may differ among different root types, and thus, the period of the tidal cycle at which root structures mostly contribute to wave attenuation may be species-specific. Thus, we might hypothesize that a mangrove stand with distinct root types (i.e., with high functional distinctiveness of species, such as for *Avicennia* and *Rhizophora*) is more efficient in protecting the coastline against waves and storm surges than one with several species of the same genus that all bear the same type of roots.

Mangrove conservation and afforestation

During the two decades from the 1980s to the early 2000s, we lost some 25% of the global mangrove area. Considering the previous three decades or so, the loss probably sums up to 40–50%. During the past decade, the global average annual loss rate has dropped to way below 0.5% (Friess et al., 2020). However, we are still losing some 50 ha of mangrove forests worldwide every day. Effective mangrove protection and conservation is, thus, pivotal for sustaining their numerous services to local communities and humankind worldwide, and should be given highest priority. When and where mangrove forests are degraded or lost, their re-establishment aims at re-instating ecosystems that provide these services.

Among the many causes for mangrove degradation and area loss (see above), climate change and its direct consequences are most controversially debated. On a global scale, mangroves might benefit from the extension of (sub-)tropical conditions toward the poles through expanding their distribution range polewards (Saintilan et al., 2014). Within the tropical belt, increases in water and air temperature may exert negative effects on mangrove trees or entire stands (Jennerjahn et al., 2017). However, surface-near air temperatures are overall predicted to increase more rapidly and to a larger extent in high latitude regions than inside the tropical belt (Collins et al., 2013; Kirtman et al., 2013). Thus, indirect effects of atmospheric warming, such as regionally differing changes in precipitation patterns, and thus freshwater supply from the hinterland, or altered circulation patterns of the coastal ocean, affecting the distribution of mangrove propagules (Duke, 2017), will possibly affect tropical mangrove forests and their inhabitants –positively or negatively– more strongly (Jennerjahn et al., 2017).

Mangrove forests, besides their vast potential of sequestering greenhouse gases into their biomass and sediments, are more and more valued as mitigators of consequences of sea level-rise for coastal and lowland communities. At the same time, they face the issue of a spatial shift of their intertidal habitat upon sea level-rise themselves. While it is widely accepted that mangrove forests, in the long run, can respond to sea level-rise by adjusting their distribution along the intertidal zone that is transitioning upwards, this potential response will depend upon a range of hydrological, sedimentological and ecological factors (e.g., Rogers, 2021). The width of this adaptive response to spatial shifts of the suitable habitat is determined by the "accommodation space", defined as the space where sediments accumulate in the intertidal by Jervey (1988). By sharpening this definition to '*the thickness of a space which will have been filled with sediment*,' Muto and Steel (2000) stress the vertical dimension of the accommodation space. The translation of this vertical dimension into the change in the '*potential vertical range*' (Rogers, 2021) of mangrove distribution is the basis for spatial predictions of the future mangrove distribution and range perpendicular to the coastline. While this vertical range is expected to shift as the sea level rises, potentially opening areas for future mangrove colonization, many current mangrove areas worldwide are restricted by limitations to moving landwards. Either changed hydrodynamics do not support mangrove recruitment and sediment accumulation in future tidal zones, or landward structures, such as infrastructural constructions, buildings or roads, prevent a landward extension or shift of habitats suitable for mangroves. Further, numerous indirect consequences of sea level rise that affect mangrove processes and dynamics indirectly mediate sea level-rise effects (c.f. Jennerjahn et al., 2017).

This showcase exemplifies the relevance of providing a suitable habitat for mangroves in the future of a changing world as one of the major challenges of mangrove conservation, rehabilitation or afforestation. The choice of areas for protection versus (sustainable) use (Spatial Conservation Prioritization: Helfer and Zimmer, 2018) should consider both the present situation and integrity of ecosystems and projections, predictions and scenarios of their future distribution, extension and status (e.g., Ragavan et al., 2020). Will a current mangrove habitat still host a mangrove stand upon environmental change (see above: pollution, land-use change, sea level-rise)? Is it worth protecting this habitat for the sake of mangrove conservation? Are rehabilitation efforts reasonable in an area that will potentially become unsuitable for mangroves in the near future, or should afforestation in recent non-mangrove areas that are predicted to become suitable be a preference?

According to the Traffic Light Concept (Helfer and Zimmer, 2018), mangrove forests can be assigned as currently valuable (regarding the provisioning of non-extractive ecosystem services) but highly delicate and sensitive to disturbance through anthropogenic pressure or human activities. Such "red" areas need full protection from human use and further pressure. "Green" areas, on the other extreme, are currently degraded and/or predicted to be unsuitable as habitat for mangrove stands in the near future; investing in their conservation does not seem to promise much gain. Mangrove forests that are considered and predicted to be resistant (or tolerant) against disturbance and environmental change and consistently provide ecosystem services are flagged as "yellow" areas that should be managed under the umbrella of sustainable use of their natural resources. This, or similar approaches, will prove invaluable for finding the balance between the protection and use of mangrove forests for the sake of their conservation and sustainable management (e.g., Ragavan et al., 2020).

Conservation cannot be pursued against human needs, and any reasonable protection measure has to take into account requirements for the (sustainable) use of natural resources by local communities. Ecosystem-Based Management (EBM) considers site-specific information for ensuring the persistence of mangroves in a given area (Ragavan et al., 2020). Recognizing previous failures of management of marine ecosystems, EBM aims at combining conservation, sustainable utilization and fair allocation of benefits from natural resources (Cowan et al., 2012). Among 15 key principles of EBM, Long et al. (2015) identified the most important ones as Ecosystem Connection, Appropriate Spatial and Temporal Scales, Adaptive and Integrated Management, Stakeholder Involvement, and Use of Scientific Knowledge. Thus, EBM obviously requires in-depth and accurate information about the ecosystem to be managed. While it is still a long road to this aim from where we are, regarding mangrove forests, the urgency of the situation warrants that we accept "informed guesswork" where our knowledge and understanding are still incomplete, in concert with efforts to fill the corresponding knowledge gaps.

An alternative to the free use of degraded mangrove habitats of the "green" category according to the Traffic Light Concept is their rehabilitation or restoration (Fig. 7). While rehabilitation aims at re-establishing a degraded habitat for initiating a trajectory toward recovery of mangrove ecosystems, restoration encompasses actions of reinstating mangrove forests in a state that is similar to the lost forest. Alternative approaches to the (re-)establishment of mangrove forests range from facilitating natural recolonization of restored habitats to the active planting of a selected set of species that provide those ecosystem services that are mostly urgently needed in a given area.

The former approach is exemplified by Community-Based Ecological Mangrove Restoration (CBEMR) (MAP, 2021). Based on the concept of Ecological Mangrove Rehabilitation (Lewis and Brown, 2014), CBEMR acts on mitigating mangrove stressors and facilitating natural regeneration through re-instating pre-disturbance conditions of, e.g., topography and hydrodynamics. A focal aspect of Ecological Mangrove Rehabilitation (EMR) is the engagement of local communities and sincere consideration of social, economic and ecological factors before undertaking any action, and the monitoring of the success of all actions.

While usually avoided by EMR and CBEMR, assisted recolonization of degraded mangrove areas through plantation might prove necessary, when, e.g., hydrodynamics cannot be restored or propagule supply from nearby systems is limited. In these cases, many reforestation efforts over the past decades have been failures with little to no establishment success of the mangrove seedlings. Reasons for this are manifold (e.g., Kodikara et al., 2017; Worthington and Spalding, 2018). The major critique of such unsuccessful efforts stresses the attempt of planting monocultures of the wrong species in an unsuitable area, be it along the intertidal gradient or with respect to hydrodynamics and sediment supply. A recent White Paper of the IUCN Mangrove Specialist Group (MSG, 2020) pledges for thorough consideration of strategies and alternatives before investing in, and wasting efforts on, planting hundreds and thousands of mangrove seedlings in vain. While resulting in low biodiversity of reforested mangrove stands, commonly being criticized as a weakness of this approach, it might be advisable to keep the number of replanted species low (c.f. Rahman et al., 2021; see below). The approach of mangrove reforestation has become well perceived in society, possibly based on (successful) reforestation activities of terrestrial forests. The many advertisements for diverse commercial products that promise the planting of trees upon purchase are more and more including references to mangrove reforestation. As recent reports in the media illustrate, however, some of these offers are unserious or even used as opportunities for scam. The lack of command over actual actions and their success by the consumers or investors from the private sector warrants the development of control mechanisms and certificates.

A special case of mangrove restoration is the establishment of Integrated Mangrove Aquaculture (IMA; also referred to as "silvo-aquaculture"), aiming at finding an optimized compromise between the economic gain of aquaculture and the socio-ecological benefit of maintaining, or re-implementing, mangrove cover around and inside aquaculture ponds. While mostly considered as compensation for mangrove area loss in the context of blue carbon-storage and climate change-mitigation (e.g., Ahmed et al., 2017), the other beneficial effects of mangrove cover (see above), such as protection of the coastline and nearby infrastructure from damage through wave action or storm surges or provisioning of natural resources, should not be disregarded in the argumentation. Further, mangrove stands can be used for the treatment of nutrient-enriched aquaculture effluents before discharging the wastewater into the adjacent coastal water (see below: Ecosystem Design): planted mangrove trees stabilize the pH value, reduce the nutrient load and increase the oxygen concentration of the water (e.g., Peng et al., 2009). It remains unclear whether the reduced risk of shrimp diseases in IMA ponds are an indirect effect of improved water quality or might be driven by antibiotic properties of leaf leachates or root exudates.

Other than the above reforestation, afforestation refers to planting and establishment of mangroves in areas that were not covered by mangrove forests in the recent past. Such new areas might be the result of recent events of sediment deposition, opening space that is not occupied by other vegetation for mangroves, a consequence of ongoing sea level-rise, or the outcome of coastal land-reclamation. Yet, planting mangroves in "non-mangrove areas" has repeatedly been criticized by various organizations and practitioners, on one hand because of the often limited success, as "mangroves cannot grow where mangroves don't grow," on the other hand, because these actions often destroy other valuable coastal ecosystems. The Global Mangrove Alliance (GMA, 2021) has explicitly included newly established potential mangrove habitats in the updated formulation of their goals. A prerequisite for such

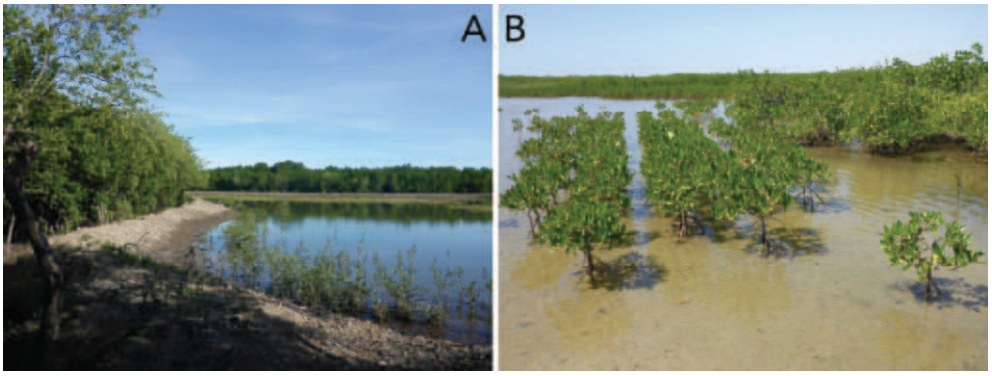

Fig. 7 Mangrove saplings established on the border of an aquaculture pond in Honduras (A); plantation of *Rhizophora mangle* in the Sine Saloum delta (Senegal) (B).

activities being justified and both socio-ecologically and environmentally reasonable is, however, that the environmental conditions in the to-be-established area are suitable for mangroves, any existing ecosystems are disturbed as little as possible, and the implemented species are regionally native (and propagules stem from the region).

While high biodiversity and near-to-natural ecosystem structure are at the very heart of most mangrove restoration and rehabilitation efforts, a recent approach focuses on the provisioning of ecosystem services according to human needs and demands: Ecosystem Design (Zimmer, 2018) aims at (re-)implementing those (simple) communities that most efficiently provide (a set of) ecosystem services of high human demand. In contrast to traditional restoration that focuses on the ecosystem, ecosystem design centers around the use of ecosystem benefits by local communities. Thus, designed ecosystems do not (necessarily) aim at high biodiversity but rather restrict the community to a number of species that, in concert and interaction, are most efficient in driving those ecosystem processes that underlie the required ecosystem service(s). As for EBM, Ecosystem Design requires detailed understanding of species-specific environmental requirements and ecophysiology, as well as of interspecific interactions – in many cases of mangrove trees and other mangrove inhabitants, we do not yet have this in-depth knowledge. Hence, for the time being, Ecosystem Design –just as EBM: see above– may have to rely on "informed guesswork". Accordingly, Ellison et al. (2020) consider the anthropocentric and high-intervention approach of "building with nature" through Ecosystem Design –as opposed to, e.g., the ecocentric "bringing nature back"-approach of EMR– a strategy of the future. At the same time, similar approaches had been implemented already (Cheong et al., 2013; Nengshi et al., 2018), and monitoring the success of deliberately implemented communities and designed ecosystems in driving the desired ecosystem processes and providing ecosystem services, thus considering Ecosystem Design a long-term experiment on mangrove restoration, will provide detailed ecological insight into how ecosystems and their processes are controlled and deepened understanding that is needed for sustainably managing them.

Synthesis

Mangroves form intertidal forests on soft-sediment coasts throughout the tropical belt. These forests provide numerous ecosystem services to local human societies and to humankind worldwide. According to their species richness and composition, they are split in two biogeographical realms, the species-rich Indo-West Pacific (IWP) and the species-poor Atlantic-East Pacific (AEP). Despite this marked difference in taxonomic diversity, mangrove forests in the AEP can be as productive as those of the IWP. The benthic fauna of mangrove forests seems to follow a similar pattern of biodiversity distribution. As ecosystem processes in different mangrove regions, however, seem to resemble each other, strong ecological equivalence of different species can be assumed.

Despite their ecological and societal relevance, mangroves are under anthropogenic pressure, and their conservation, also taking into account management and sustainable use, is of utmost importance. Degraded mangrove areas have been –more or less successfully– attempted to restore or rehabilitate over the last years and decades. These efforts reach from natural and assisted recolonization to active planting and afforestation. Specific-specific contributions of mangrove species to ecosystem processes and resulting ecosystem services could be the basis for designing ecosystems with simple communities that provide the most urgently required services most efficiently.

Knowledge gaps

- spatial distribution of species (e.g., within AEP vs. IWP) vs. traits (also across realms)
- taxonomic versus functional diversity of mangrove plants and other mangrove inhabitants
- drivers of ecosystem processes and services derived therefrom
- changes in species distribution, and consequences for ecosystem processes, upon climate or land-use change or other environmental changes
- response of mangrove forests (including all their inhabitants) and the distribution of individual species to (relative) sea level-rise and consequences for organic matter stocks (climate change-mitigation) or coastal protection (climate change-adaptation)

See Also: Structures and functions of Inland Waters - Wetlands: Tropical Large River Wetlands

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https://mangroveactionproject.org/—Mangrove Action Project MAP.
https://www.mangrovealliance.org/—Global Mangrove Alliance GMA.
https://www.wwfca.org/en/species_and_places/mangroves/—World Wildlife Fund for Nature WWF.
https://www.iucn.org/commissions/ssc-groups/plants-fungi/plants/plants-h-z/mangrove—Mangrove Specialist Group of the Species Survival Commission of the International Union for the Conservation of Nature IUCN.
https://nam11.safelinks.protection.outlook.com/?url=http%3A%2F%2Fmangrovewatch.org.au%2F&data=04%7C01%7CMRW-INW2%40elsevier.com%7C92407edcc1934e23863d08d9ac42a7f4%7C9274ee3f94254109a27f9fb15c10675d%7C0%7C0%7C637730224563930610%7CUnknown%7CTWFpbGZsb3d8eyJWIjoiMC4wLjAwMDAiLCJQIjoiV2luMzliLCJBTiI6Ik1haWwiLCJXVCI6Mn0%3D%7C3000&sdata=P2Gyqs4AYxaR0C%2BtDzUGb6ofkqdtLEaYoPf6BuEI9iI%3D&reserved=0.

Wetlands in Karst

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This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Aquiclude A hydrogeologic unit of impermeable material bounding an aquifer.
Carbonate Rock A rock that consists of one or more carbonate minerals.
Doline Simple closed circular depression with subterranean drainage, and commonly funnel shaped.
Estavelle An intermittent spring, active only in wet seasons. Typically, it acts alternatively as a swallow hole and as a rising according to ground-water conditions.
Hydroperiod The period in which a soil area is waterlogged.
Karst Landscape in soluble rock where solution rather than erosion is the primary geomorphic agent, typically with caves, sinkholes, and springs.
Marl Unconsolidated sedimentary rock consisting largely of calcium carbonate and clay.
Polje A large, spring-fed karst depression with a flat floor commonly associated with river sediment.
Stygobiont Obligate, permanent resident of aquatic subterranean habitats.
Uvala A multi-coned closed depression.

Introduction

In a karst landscape, the forces of solution (chemical weathering) are an important agent in molding the landscape. In non-karst landscapes, chemical weathering is unimportant and erosion (mechanical transport) predominates. The word karst is a Germanized form of the Slovenian name (*kras*) for a carbonate plateau situated just north of the Adriatic Sea immediately north of Trieste, Italy (Jones and White, 2019). Nearly all aspects of the landscape are the result of the dissolution of the underlying bedrock, and erosion is little in evidence. In general the dissolution of bedrock depends on the action of carbonic acid (itself the result of the dissolution of CO_2 in water) on limestone ($CaCO_3$) and related bedrock types. A variety of unique landforms occur on karst-karren, dissolutional pavements, closed depressions (dolines and sinkholes), cones and towers, poljes, large springs, and blind valleys. Other landforms are absent or rare—streams, lakes, and wetlands, though there is also an underground landscape in karst—that of caves.

If we define karst as a landscape of exposed carbonate (limestone and dolomite) or gypsum rocks (Jones and White, 2019), then it covers about 15% of the earth's surface. Many karst regions are also modified by the presence of non-carbonate rocks (fluviokarst), strong physical transport such as occurs in alpine karst, or by the action of glaciation (glaciokarst). However, all have frequent rapid vertical movement of water into and through bedrock of sufficient purity for dissolution.

Globally, the occurrence of major wetland areas is nearly the opposite of the distribution of karst areas (Fig. 1; Balász, 1977). Wetlands are commonest at far northern latitudes (50°–70° N) and near the equator; regions with poor soil drainage resulting in hydric soils. In contrast, karst regions are concentrated at intermediate northern latitudes (30°–50° N). Of 65 major world wetlands (Mitsch and Gosselink, 2015), only three are unequivocally in karst areas. One of these is the Hudson Bay lowlands in Canada, among the most extensive wetlands in the world, but it is the relatively low relief and Pleistocene glaciations that define this

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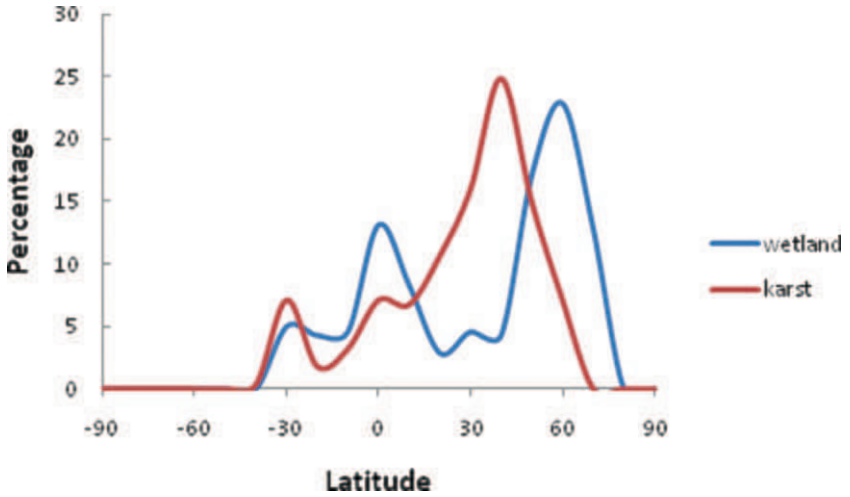

Fig. 1 Qualitative view of the distribution of wetlands and karst areas with respect to latitude. Data for wetlands from Mitsch WJ and Gosselink JG (2015) *Wetlands*, 5th edn. Wiley: New York, data for karst areas from Balász D (1977) The geographical distribution of karst areas. In: *Proceedings of the seventh international congress of speleology Sheffield*, vol. 1, 13–15.

wetland, not the underlying karst topography (Abraham and Keddy, 2005). Cuatro Ciénagas in Mexico, a 1500 km^2 wetland, is formed in a valley by more than 200 springs and home to a number of endemic obligate aquatic subterranean invertebrates (Minckley and Jackson, 2007). But this is a boundary karst wetland, i.e., forming as a result of exit water from karst (see below), and not an interior karst wetland. The Big Cypress Swamp, part of the Everglades wetlands, is a karst area with numerous sinkholes (Quintero and Cohen, 2019).

Overview of wetlands in karst

Hydrologically, the most striking aspect of karst landscapes is that the drainage is predominantly internal. In this case of extreme karstification, the only places where surface wetlands can occur is at the exit of the water, or where water sinks, both often at the boundaries between carbonate and non-carbonate rocks.

Downstream of a karst area, water emerges in springs of many sizes and morphologies (Ford and Williams, 2007; Kresic, 2010). Some, if not all, are wetlands as they have permanently or seasonally moisture-saturated soil and support vegetation typical of saturated soils. These include marl wetlands (Bartgis and Lang, 1984) and any situation where carbonate rocks are underlain by, or intersect with, impermeable layers. By their nature, springs are at the discharge end of the wetlands continuum (Euliss et al., 2004).

At the upstream end of a karst area, water may be slowed as it sinks at the carbonate/non-carbonate contact (or at contact of two carbonate rocks of different solubilities), perhaps at swallets. Only one case where the movement of water into the subsurface is impeded to the extent that wetlands form is known: the rather enigmatic disappearance of the Santa Fe River in Florida and it re-emergence in the Suwanee River. The region around the swirling input periodically floods and the sink of the Santa Fe has some characteristic wetland vegetation (Tan and Judd, 1995), such as bald cypress (*Taxodium distichum*). It is enigmatic because there is so little vertical relief in this region of Florida that is difficult to understand how hydraulic gradients develop.

Interior karst wetlands are perhaps more interesting from a karst science perspective, and are not karst boundary wetlands or subterranean wetlands, but wetlands surrounded by karst.

Focus and scope of the review

The overall goal of this review is to place interior karst wetlands in a wetlands context, and to indicate their major features and unique characteristics. After an overview of the distribution and types of interior karst wetlands, we provide detailed descriptions of three wetlands in Slovenia, one of the most extensive and well developed karst regions anywhere:

1. Cerkniško jezero/polje
2. Planinsko polje
3. Pivka intermittent lakes

We focus on several questions in these descriptions:

1. What is the role of karst and karst processes in the formation and functioning of these wetlands?
2. What is the connection with groundwater and what is the effect on hydroperiod?
3. What is the overall regional role of karst wetlands?
4. Are there any biological features shared by karst wetlands?

Characteristics of interior karst wetlands

One of the defining features of karst regions is the presence of closed depressions, the most common and familiar of which are sinkholes or dolines. Sauro (2019) divides closed depressions into five types, based on size:

1. Rain pits or rain craters (1–3 cm in diameter).
2. Solution pans and karst pans (cm to m in diameter).
3. Dolines (sinkholes) (a few m to over 1 km in diameter).
4. Compound depressions (hundreds of meters to a few kilometers).
5. Poljes (reaching up to tens of kilometers).

The last three have been extensively studied by hydrogeologists and geologists, because of their connection to water supply and their potential as geohazards (Waltham et al., 2010).

Rain pits are surface solutional features in carbonate bedrock, more generally known as karren, but are too small to be of interest in a wetlands context.

Solution pans and karst pans are small closed depressions in the karst landscape that are relatively isolated from the groundwater system and typically lack internal drains, such as the Tennessee Barrens (United States) (Wolfe, 1996). It is not entirely clear whether the closed depressions given the name "karst pans" by different authors are the same (O'Driscoll and Parizek, 2003, 2008; Wolfe, 1996), or whether they are all solutional features of bedrock rather than the overlying soil. Karst pans apparently form as a consequence of percolating water creating solution chambers in bedrock with the concomitant slumping of the overlying soil. Though these wetlands are very small, they are often the only wetlands where they occur and frequently harbor a distinct flora (Wolfe, 1996).

The most common closed depressions are sinkholes (dolines),[1] typically with a circular or sub-circular plan and a bowl- or funnel-shaped concave profile (Sauro, 2019). Given the relatively few shapes sinkholes can have (Cvijic, 1895), it is perhaps surprising that they form in a variety of ways (Gutiérrez et al., 2014; Parise, 2019). While they may form by solution, subsidence by collapse, sagging or suffusion as well, the frequency is increased by groundwater drawdown. Though karst wetlands are almost entirely closed depressions, most (nearly all) closed depressions are dry, as the connections with the surface are too open and there is usually no impermeable clay layer at the bottom. In areas of low relief with the water table close to the surface, many sinkholes form small ponds and lakes, as is the case in many sites in Florida (Upchurch et al., 2019).

Hydrostatic pressure, which is mediated by estavelles (Fig. 2; Vineyard and Feder, 1982) also keeps sinkholes (and compound depressions, see below) filled with water. At low flow, estavelles act as swallow holes; at high flow they act as springs. Many karst wetlands are connected to groundwater via estavelles (see section on "Pivka intermittent lakes" below).

As sinkholes age, they tend to get deeper and wider, and may coalesce to form multiple sinkholes, sometimes called uvalas. Closed depressions in karst may have irregular shapes due to these karst processes or other morphogenetic ones (e.g., tectonic, fluvial, glacial). Many turloughs, the seasonally flooded wetlands of Ireland (Sheehy Skeffington et al., 2006) and perhaps elsewhere (Sheehy Skeffington and Scott, 2008), may qualify as compound sinkholes.

Poljes are the largest closed depressions observed in karst terrains. The original definition of "a large karst depression, with a wide, flat and nearly horizontal floor, completely enclosed between steep slopes" (Cvijic, 1895) does not adequately distinguish poljes in practice or explain their genesis (Sauro, 2019). The flat floors may be tens of kilometers long. Their formation cannot be explained solely through karst processes. The main environmental peculiarity of poljes is the absence of a permanent lake, but with an ephemeral lake, the draining of which occurs solely through subterranean flow, typically through estavelles. Flooding is controlled by several parameters, e.g., recharge conditions, drainage capacity of ponors and presence of estavelles, and characteristics of aquifer draining the polje (Mayaud et al., 2019).

Most poljes occur in tectonic depressions and, although first described from the Dinaric karst, they occur in other karst regions in both temperate and tropical zones. They are the dominant wetland type throughout the Dinaric karst (from Italy and Slovenia to Albania), and comprise about 4% of the land surface. Upchurch et al. (2019) use the term polje to describe a wetland type in Florida, but it is in a radically different geological setting, and developed in different way.

[1]The term doline is used in somewhat different ways. In North American usage it is synonymous with sinkhole, but in English/European usage, it tends to refer only to steep sided sinkholes.

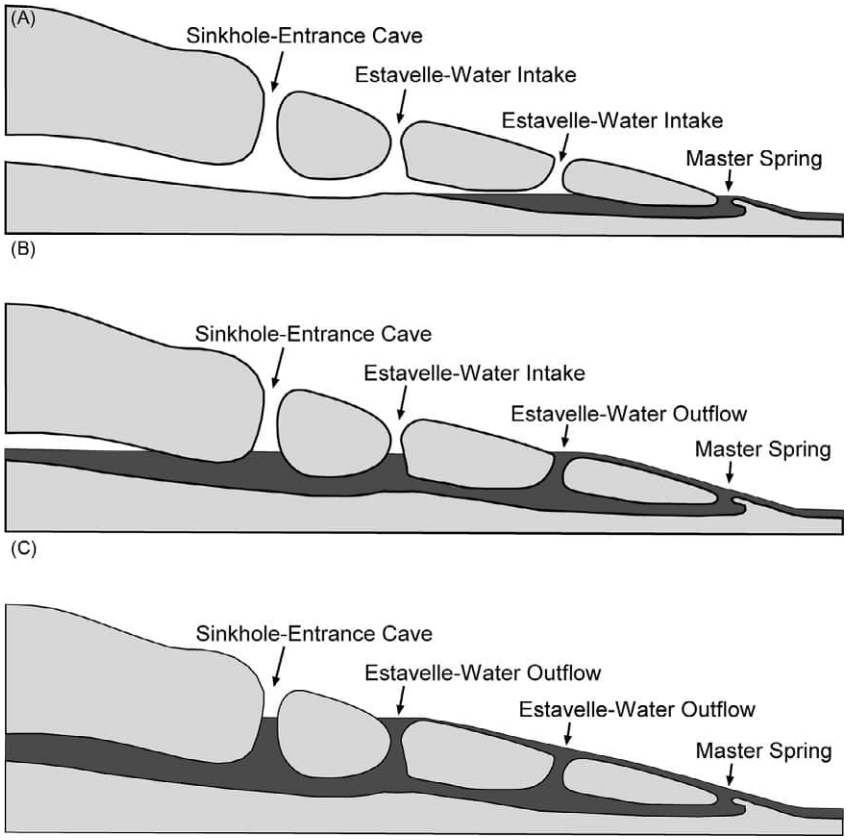

Fig. 2 Hypothetical stream profile showing sequential reversal of flow in estavelles. (A) Low flow, only lower section of karst drainage system is flooded and the estavelles act as swallow holes. (B) Medium flow, headward flooding of the system and the lowest estavelle acts as a spring. (C) High flow, storage capacity of karst system exceeded and all estavelles become springs. From Vineyard JD and Feder GL (1982) *Springs of Missouri*. Missouri Department of Natural Resources, Division of Geology and Land Survey: Columbia, MO.

Representative karst wetlands

Cerkniško jezero/polje

Cerkniško jezero (= lake) is an intermittent lake appearing at the bottom of the depression Cerkniško polje (549 m a.s.l.). The polje is about 11 km long and 4–6 km wide, covering a surface area of 41.7 km^2 (Smrekar, 2002). It is located in the heart of Notranjska region between the Dinaric Mountains and the Alps, one of the many poljes in the depression along the Idrija fault (Kranjc, 2002a).

The "vanishing" lake has inspired the imagination of local people and visitors for centuries, attracting numerous researchers who tried to decipher the mystery of the lake. The first detailed written information dates back to 1679, when the Slovenian polymath J. V. Valvasor, published an essay on the lake with a map of the area (Rupel, 1951), and a hypothetical diagram of the subterranean drainage.

Cerkniško polje (Fig. 3) is influenced by Mediterranean and continental temperate climates. Relatively high annual precipitation (from 1700 to 1800 mm) (Zupančič, 2002) significantly contributes to the hydrological regime. The bottom of the polje consists of carbonate bedrock, i.e., Triassic and Jurassic dolomite, and Jurassic and Cretaceous limestone (Kranjc, 2002b). The bedrock is covered by young Pleistocene and Holocene alluvial sediments up to 16 m deep (Gospodarič and Habič, 1978). The polje is a floodplain of the Stržen stream, which is one of seven streams that make up the Ljubljanica river. The Stržen stream meanders through the polje, cutting its river bed through alluvial deposits (Fig. 4; Skoberne, 2004). Water level fluctuations influence sediment deposition and erosion (which currently prevails), shaping the lake bottom (Kranjc, 2002b).

The catchment area of Cerkniško jezero extends over 475 km^2 (Kranjc, 1986, 2002b). The polje is characterized by extreme water level fluctuations, due to the high local precipitation, an extensive karst watershed and water runoff into an extensive underground drainage system in carbonate rocks (Gams, 1994). The hydrologic regime is characterized by spring and autumn floods coinciding with the highest monthly average precipitation (200 mm in November, Zupančič, 2002) and summer droughts, when water only remains in the Stržen stream bed and its tributaries. During "normal" floods, the water covers an area of 20.3 km^2 (Smrekar, 2002).

Water coming from the subsurface accounts for 80% of the lake water. The only significant surface tributary is the Cerkniščica stream. In the distant past, the input to Cerkniško polje was completely karstic and only in the last glacial period (the middle Würm) did the Cerkniščica stream turn toward Cerkniško polje (Šušteršič and Šušteršič, 2003). During rainy periods, water flows from the

Fig. 3 Cerkniško jezero (A) when it is flooded on the south and dry Cerkniško polje (B) at the eastern side. Photographs by S. Polak, used with permission.

springs at the E and SE edge and from estavelles in the bottom of the polje (Kranjc, 2002b), collecting in the wide Stržen stream bed which gradually increases in level. Usually it takes only a few days to flood the whole area (Fig. 5). There is no surface outflow and the drop in water level depends on the drainage of water underground, mainly to the vertical ponors (sinkholes, Fig. 6) and ponor caves at the N and NW part of the polje. A significant amount of water is also lost by evapotranspiration. On average it takes 3 to 4 weeks for the lake to dry out (Kranjc, 2002b).

Cerkniško jezero is a very complex, biodiverse ecosystem (Dolinar et al., 2010a). The plant communities depend on the water regime and soil properties (Gaberščik et al., 2003). Aquatic plant communities (e.g., *Myriophyllo-Nupharetum*, *Charetea fragilis*, *Rorippa amphibia-Eleocharitetum acicularis*) develop in tributaries, the main Stržen stream and in the polje depressions, while wetland communities (e.g., *Phragmitetum australis*, *Scirpetum lacustris*, *Caricetum elatae*) at the areas where regular floods of at least 6 months duration prevent further succession, and water does not exceed 1–2 m of depth (Martinčič and Leskovar, 2002). The edge of inundation zone is colonized by fen and wet grassland communities.

The water level fluctuations result in intermittent exchanges of oxic and anoxic conditions in the sediment that accelerate organic matter decomposition and nutrient release (Boulton and Brock, 1999; Urbanc-Berčič and Gaberščik, 2001, 2004). The dense swamp vegetation also functions as a sink for nutrients discharging into the lake (Gaberščik et al., 1994, 2003).

The more or less regular changes with a long aquatic phase (9–10 months) in the cooler part of the year are favorable to ecosystem resilience. However, in recent decades, flood and drought events have become more irregular, altering processes and conditions for many species. Many studies have demonstrated the effects of changing water regime on plant diversity and

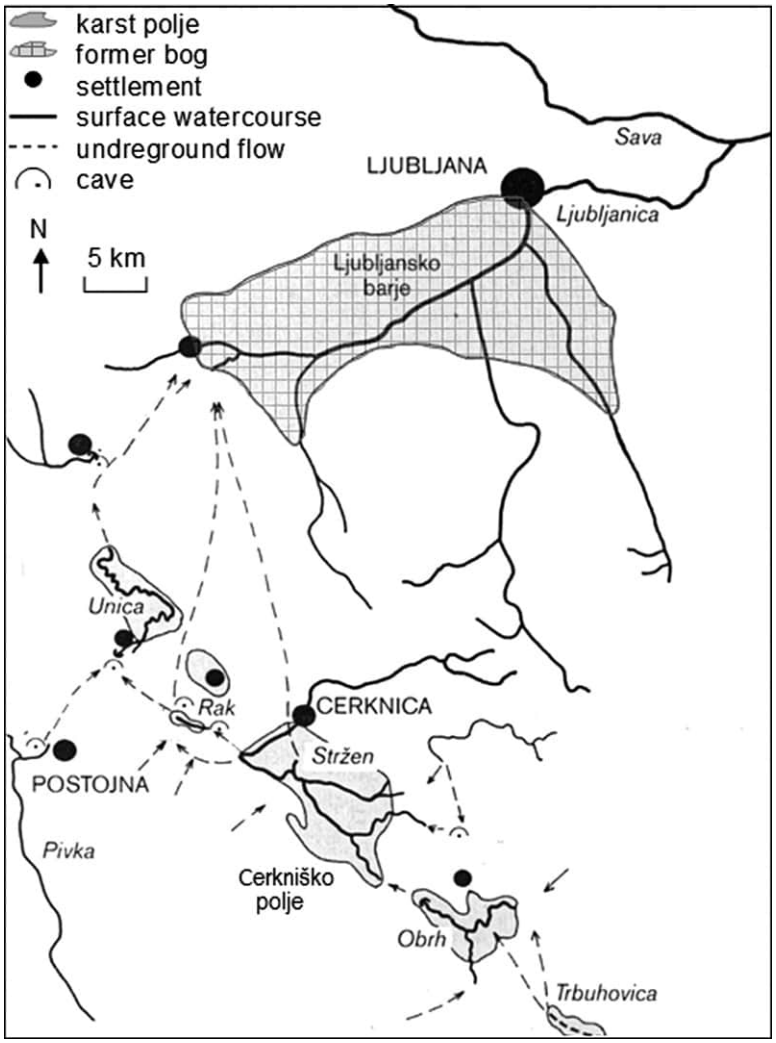

Fig. 4 The figure presents the sequence of poljes (Cerkniško polje with the stream Stržen and Planinsko polje with the stream Unica), the surface watercourses (solid lines), and the directions of underground flows (dashed arrows). From Skoberne P (2004) *Ljubljanica Od Izvira Do Izliva*. Mladinska knjiga: Ljubljana.

succession, their production, transpiration rate and fungal colonization of roots (Dolinar et al., 2010a; Dolinar and Gaberščik, 2010), on organic matter turn-over (Dinka et al., 2008; Dolinar et al., 2010b; Urbanc-Berčič et al., 2005) as well as on fish (Povž, 2002) and bird populations (Trontelj, 2001; Bordjan and Bordjan, 2014).

Planinsko polje

Planinsko polje is the second most studied polje. In comparison to Cerkniško jezero/polje, it is much drier, and the period of flooding is much shorter. During the 1954–2014 period, high waters on the polje occurred on average 38 days per year, the longest period in 1 year was 137 days. High water levels usually occur after mid-autumn rainfall peaks, winter rains and snow melting, and the flooded area can reach 10.3 km^2 (Ravbar et al., 2019).

It is typically referred to as a polje, not a jezero (lake). The geological setting for Planinsko polje and poljes in general is quite complex, typically aligned along tectonic axes, and covered with alluvium. Two main springs drain into Planinsko polje (Fig. 7) from the Javornik and Snežnik massifs, a string of poljes including Cerkniško polje, and from the Pivka River basin (Petrič, 2010). One of the springs, Unica, drains the large Postojna Planina Cave system. Unica river flows across Planinsko polje and plunges underground in a series of ponors at the eastern and northern end of the polje.

Since the polje is dry for most of the year, it is an important terrestrial habitat for mammals such as the wildcat, *Felix sylvestris*, many birds, butterflies and beetles. Postojna Planina Cave System, whose waters exit at Unica spring, is the richest cave in the world in terms of number of obligate cave-dwelling species. Especially during high water, the cave salamander *Proteus anguinus* washes out of the cave and can be found in the surface part of the Unica River.

Fig. 5 During snow melting and heavy rains in spring, water floods Cerkniško polje within a week. Polje is surrounded by hills; the NE part is closed by Slivnica (1114 m a.s.l.; in the background), while the SW part by high karst formations of Javorniki (1269 m a.s.l.). Photo courtesy of Archive of Notranjska Regional Park.

Fig. 6 Vertical ponors in the bottom of Cerkniško jezero. Photo courtesy of Archive of Notranjska Regional Park.

Fig. 7 Flooded Planinsko polje (January 2014). Photograph by F. Drole, used with permission.

Since there is a permanent stream across the polje, there is a persistent zonation of plants, from terrestrial to aquatic. Much of the land is used for grazing and some crops. Its position at the junction of Dinaric and Alpine regions accounts in part for the high floristic diversity. A species of hyacinth, *Scilla litardierei*, is limited to Dinaric karst wetlands and is common in Planinsko polje. Other species characteristic of Planinsko polje are *Gladiolus illyricus*, *Iris sibirica*, *Iris pseudacorus*, and *Ophioglossum vulgatum*.

Pivka intermittent lakes

The upper part of the Pivka River basin, southwest Slovenia, is formed on well karstified Cretaceous limestone. The river is dry during low waters and the water table is close below the surface in a relatively shallow karst aquifer underlain by Eocene flysch rocks of very low permeability. After more intensive or long-lasting precipitation the water table rises and water emerges through intermittent karst springs along the river-bed and recharge the Pivka River (Petrič and Kogovšek, 2005). Karst depressions, mostly on the slopes of the Javorniki and Snežnik mountains fill with water and up to 17 Pivka intermittent lakes are formed (Fig. 8). Depending on their altitude, morphology, karstification, and bottom sediments they differ significantly in size and duration. The biggest is Palško jezero, and the lowest in altitude is Petelinjsko jezero (lake bottom at 532 m a.s.l.), which has the longest flooding duration.

At the Pivka spring the water table is approximately 10 m below the surface during low waters and near Prestranek, more than 20 m below the surface (Fig. 8). The water table in wells and caves near the lakes oscillates several tens of meters, the highest measured being 50 m in the cave Matijeva jama at the edge of lake Palško jezero (Kovačič and Habič, 2005). The cave acts as estavelles. The other lakes also fill and empty through several karst fissures and channels.

Hydrological data describing the extent of the lakes are rare. The biggest floods were recorded in November 2000 when all 17 lakes were active after many decades (Kovačič and Habič, 2005). The surface of Palško jezero reached almost 2 km^2 and the water volume 23×10^6 m^3 (1 km^2 and 7×10^6 m^3 during average flooding).

More detailed observations from November 2006 to December 2007 (Kirn, 2016) were compared with meteorological data and discharges of the Pivka River (Fig. 9) (Daily Precipitation, 2013; Archive Hydrological Data, 2013). Petelinjsko jezero had the longest duration (84 days observed, but probably filled for additional 10 days in the beginning of January 2007 when the lakes were not observed) in a relatively dry hydrological year 2006/07 (11 Dec. 2006–30 Sep. 2007). Its occurrence is in close correlation with the discharges of the Pivka River at Prestranek—the lake is active when the discharge exceeds 1 m^3 s^{-1} (Kirn, 2016).

According to this assessment, Petelinjsko jezero is active 26–56% of a year (3–7 months per year respectively). Usually it is filled with water, typically intermittently, from November to February, and less likely from October to June. The duration of other lakes is shorter, and some of them are not active each year, but only at extreme hydrological conditions. The largest lake, Palško jezero, was active 46 days and 16% of hydrological year 2006/07—approximately from 1 to 3 months per year. At least five lakes that flood every year, most closely resemble turloughs, though the hydroperiod is shorter and more likely to be intermittent (Sheehy Skeffington and Scott, 2008).

The seasonal flooding of the Pivka intermittent lakes creates special growing conditions for interesting plant species as the floods last from some days to, in extreme circumstances, even more than half a year. Typically, the Pivka lakes have a thin and rocky soil on the lake margins, becoming deeper toward the center, making it more suitable for agriculture. In general, open meadow-like flooded areas and dry meadows at the margin of the lakes are important plant habitats (Tome, 2000). In the areas that are flooded for longer periods, purple willow (*Salix purpurea*) overgrows meadows and pastures in the absence of cultivation or grazing, though it is absent

Fig. 8 Hydrogeological map of the area of Pivka intermittent lakes. Legend: (1) karst aquifer; (2) porous aquifer; (3) rock of very low permeability; (4) permanent surface flow; (5) intermittent surface flow; (6) intermittent karst lake; (7) intermittent karst spring; (8) precipitation station; (9) main direction of groundwater flow; (10) direction of groundwater flow at high waters.

from Petelijnsko jezero, which has a flood duration of up to 6 months. Although a major part of the Pivka lakes is floristically poorly examined, more than 180 species of plants are recorded (Tome, 2000; Sheehy Skeffington and Scott, 2008). As with the turloughs and Cerkniško jezero, there is a zonation in the lake basin, related to flood duration.

Among endangered and rare species that grow in the Pivka intermittent lakes are the mouse garlic *Allium angulosum*, Siberian iris *Iris sibirica*, wild gladiolus *Gladiolus illyricus*, and solitary clematis *C. integrifolia* (Mulec et al., 2005). Rare plant communities include the wild gladiolus—purple moor grass (*Gladiolo-Molinietum*), and tufted hairgrass—tall plantain (*Deschampsio-Plantaginetum altissimae*) communities.

While the species list is very incomplete and excludes insects, it comprises stygobionts, species adapted to temporary waters and generalist species (Pipan, 2005). One copepod (*Diacyclops charon*) and one isopod subspecies (*A. aquaticus cavernicolus*) are stygobionts. The European cave salamander *Proteus anguinus* can also be found in the lakes as a result of washing out from springs and estavelles (Pipan and Culver, 2019).

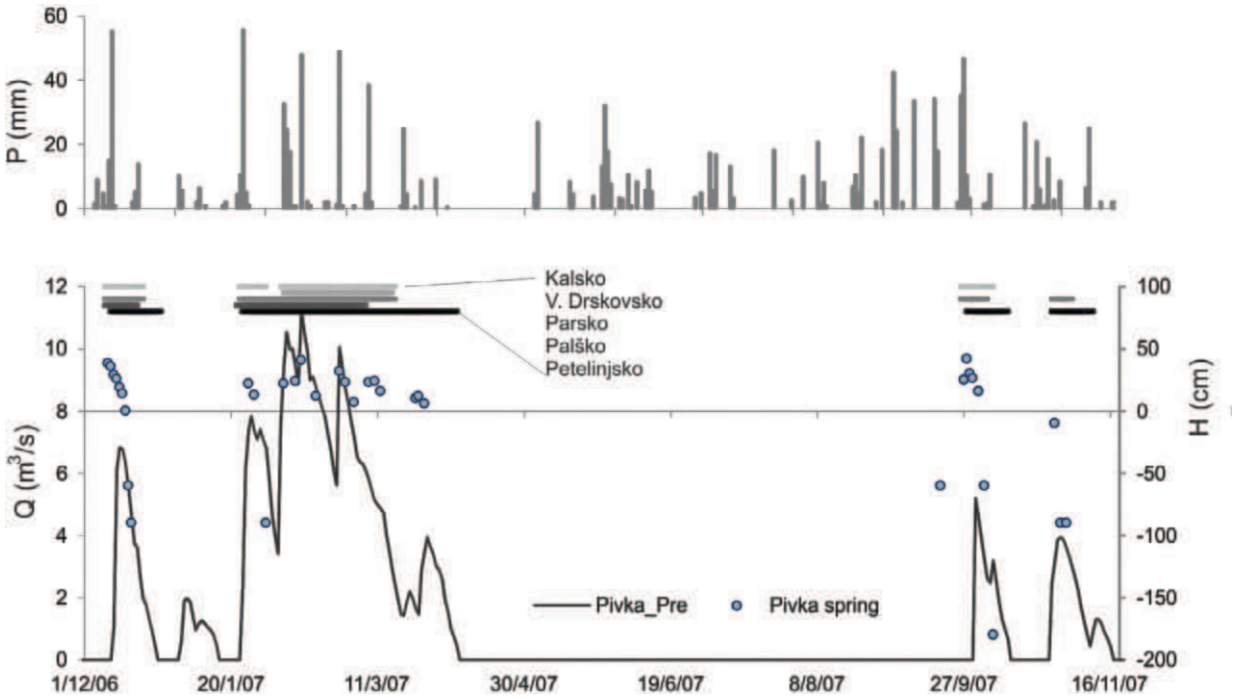

Fig. 9 Comparison of duration of selected Pivka intermittent lakes (duration marked with horizontal lines) with daily precipitation, water levels in the well at the Pivka spring and discharges of Pivka River.

Petelinjsko jezero is populated by an endemic species of karstic fairy shrimp *C. croaticus*. The population was probably destroyed in its type locality, a small lake in southern Croatia, as was a small population near Cerkniško jezero in south-central Slovenia. Petelinjsko jezero is now the only documented location for *C. croaticus* in Slovenia, where its population is apparently permanent and appears each year (Brancelj and Gorjanc, 1999), though recently a permanent population of the species has been found in lake Jeredovce (S. Polak pers. comm., see Fig. 8). It is threatened by the destruction of natural habitats and pollution, including fertilization of meadows.

Conservation and protection issues

The basic physical and biogeochemical processes in karst wetlands are similar to those in fluctuating water level ecosystems and temporary water bodies (Odum, 1971), where ecosystem structure and function depend on the timing of the aquatic or terrestrial phase as well as on frequency, extent and duration of flooding (Boulton and Brock, 1999). As disturbances, water level fluctuations also interfere with the process of succession, maintaining the ecosystem in an early, relatively productive stage of development (Odum, 1971). Regular water level fluctuations may support ecosystem stability, since they enable the community to adapt to the changing environment.

Because karst wetlands are uncommon, they play at least two key roles. One is as stopovers for migratory waterfowl, in regions where lakes are rare. In the Dinaric karst region, regularly flooded poljes cover 1500 km^2 in the 130,000 km^2 region and are key resting sites for the Western Siberian/Black Sea-Mediterranean populations of ducks, geese and swans (Stumberger, 2010). Second, karst wetlands, mostly due to their intermittent flooding, typically contain plant and animal communities not found elsewhere in the region even in the very small Tennessee karst pans.

There are a variety of country- or region-specific laws that are important in wetlands protection, such as the European Union's Habitat Directive and the United States' Clean Water Act. Internationally, the most important structure is the Ramsar Convention on Wetlands, adopted in 1971. Utilizing a broad definition of wetlands and a process by which individual countries nominate a site, over 2301 freshwater and marine wetlands have been designated as of February 2018 (https://rsis.ramsar.org). One of the wetland types is "karst and other subterranean hydrological systems." A total of 130 sites are included in this designation (Fig. 10), Cerkniško jezero being one of them. The designation of Ramsar karst wetlands has been utilized to varying degrees by different countries. Mexico has the most Ramsar karst wetlands, with 32, nine of which are in the state of Quintana Roo in the Yucatan Peninsula. By contrast, the United States has only three Ramsar karst wetlands and Canada has none (Fig. 10). The focus on Quintana Roo is especially timely because of the growing threats from development along the coast.

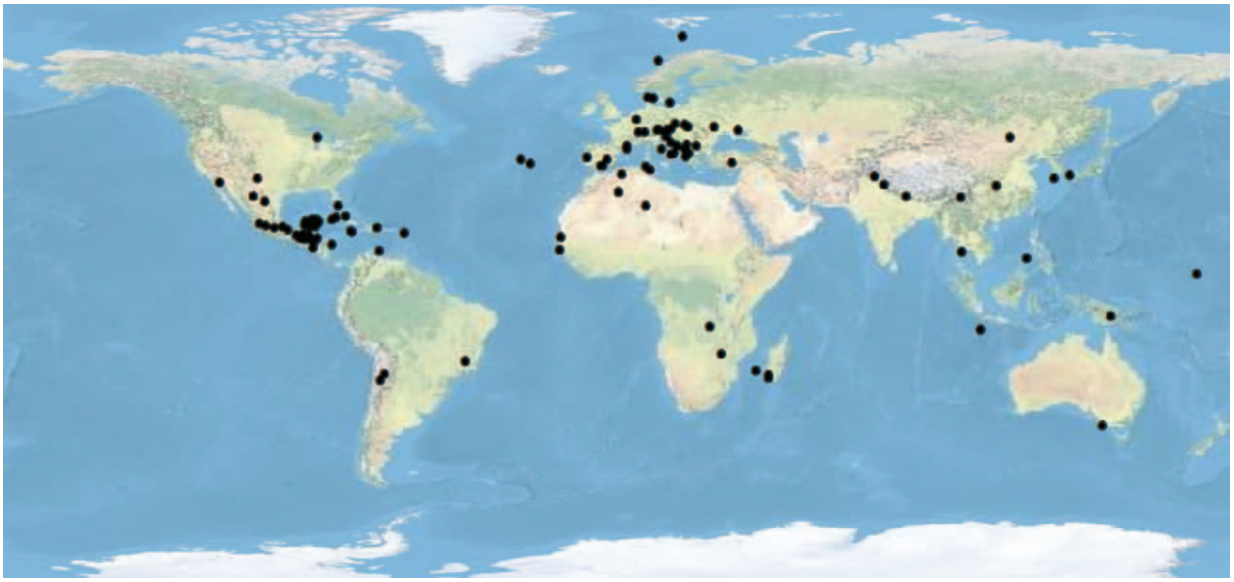

Fig. 10 Distribution of Ramsar karst wetlands. From https://rsis.Ramsar.org (accessed 15 February, 2018).

Discussion and overview

Although we know of no quantitative data on the density of wetlands in karst compared to non-karst areas, aside from Fig. 1, it seems likely that at least interior karst wetlands are much less common than wetlands in non-karst areas, especially in temperate zones. By contrast, closed depressions (e.g., sinkholes) are much more common in karst areas, and are a dominant feature of many karst landscapes. However, most of these closed depressions rarely, if ever, hold water. After all, limestone and other carbonate rocks typically have high primary and especially secondary porosity. Three conditions seem to promote water retention and an increase in hydroperiod in karst depressions: (1) proximity to the water table (e.g., Pivka intermittent lakes); (2) close subsurface connections via estavelles (Fig. 2) or a combination of ponors and springs (Cerkniško jezero); (3) presence of clay and other aquicludes (e.g., karst pans). Although beyond the scope of this review, it seems likely that permanent lakes in karst regions are even more uncommon, largely for the same reasons.

The existence of most karst wetlands does depend on karst processes, especially the formation of closed depressions. All of the karst wetlands reviewed here depend wholly or in part on the formation of closed depressions, along with dissolution of the underlying carbonate rock. Tectonic forces may also be involved in the formation of poljes. There are other processes on karst that may increase or decrease the likelihood of wetland formation in these depressions. These include the presence of clays and other sediments that act as aquicludes. Glaciation of karst areas would certainly increase the amount of sediment, and in some glaciated wetlands, like the Hudson Bay Lowlands, it is difficult to ascribe any role to karst processes. Wetland formation is also more likely if there is a close connection to groundwater, which in turn is relatively close to the surface.

It seems unlikely that any generalizations are possible concerning the hydroperiod of karst wetlands compared to non-karst wetlands. Nowhere is this more apparent than in Slovenia, where some wetlands flood every year with relatively long hydroperiods (e.g., Cerkniško jezero/polje and Planinsko polje), and some of the Pivka intermittent lakes rarely flood at all. Poljes in the Dinaric region include some that are almost always dry and others that are typically water-filled all year, although this last is rare (Stumberger, 2010). The reason for these disparate hydroperiods in regions of nearly identical climate is due to the local geological setting, especially distance and connection to groundwater.

A very small number of karst wetlands have been studied, and a greater range of types than reviewed here need to be examined. Perhaps most important is that wetland scientists recognize the unique features of karst and karst scientists recognize the unique features of wetlands.

See Also: Structures and functions of Inland Waters - Groundwater: Epikarst: An Important Aquatic and Terrestrial Habitat; From Groundwater to Drinking Water—Microbiology of Karstic Water Resources; Karst Groundwater Dependent Ecosystems—Typology, Vulnerability and Protection; The Ecology of Aquatic Cave Environments

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Salt Lakes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Arheic Areas without streams.
Athalassic Inland waters with no contact with the ocean.
Dimixis Lake stratifies twice per year, in winter and in summer.
DW m^{-2} y^{-1} Dry weight per meter squared per year.
Endorheic Internal drainage basin within a land mass.
Euhypersaline Very saline, generally >200 g L^{-1}.
Exorheic Drainage basin opening to the ocean.
Graben A lowland caused by downfaulting on both sides.
Halobionts Salt loving organisms, usually defined in the range 10–50 g L^{-1}.
Halophiles Salt loving organisms, usually defined in the range 50 to greater than 100 g L^{-1}.
Hypersaline Concentrated salty water, usually defined as greater than 50 g L^{-1}.
Hypolimnion The bottom part of a stratified lake.
Hyposaline Salt water usually defined within the range 3–20 g L^{-1}.
Meromixis/meromictic A stratified lake with a permanently stratified bottom layer but with upper layer either dimictic or monomictic.
Mesosaline Salt water usually defined in the range 20–50 g L^{-1}.
Monimolimnion Refers to the permanently stratified bottom layer of a meromictic lake.
Monomictic/monomixis Lakes stratify once a year in summer.
mS cm^{-1} Millisiemens per centimeter.
Playa Large shallow lake, often holding water temporarily.
Polymixis Lake stratifies many times a year, sometimes daily or for a few days.
Thalassic Lake of sea water or in contact with sea water.

Introduction

Saline lakes are distinct from fresh waters by having a salt content greater than about 3 g L^{-1} (Williams, 1964). For more details of salinity measurements, see "Measurement" section. Additionally, they commonly occur in closed endorheic basins where evaporation is greater than precipitation plus inflow and their organisms are almost entirely of freshwater affinities (e.g., Bayly and Boxshall, 2009). This later feature notably separates them from marine relict waters. Although most common in arid and semiarid regions, salt lakes occur worldwide (Fig. 1) and indeed combined contain almost as much water as freshwater lakes (Shiklomanov, 1990).

Some saline lakes are large, deep and permanent e.g., Dead Sea in the Middle East, while many are shallow and ephemeral, e.g., Australia's Lake Eyre. Although these waters share many characteristics with ordinary lakes such as geomorphic processes and

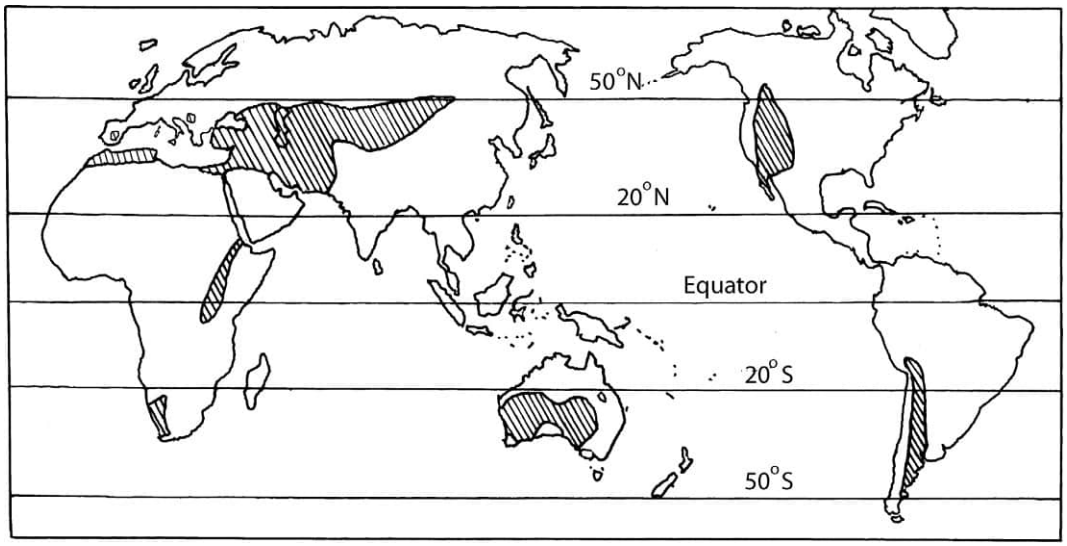

Fig. 1 Geographical distribution of major areas with saline lakes. Note that some occur outside these areas and on Antarctica. Modified from Williams WD (2002) Environmental threats to salt lakes and the likely status of inland saline systems in 2025. *Environmental Conservation* 29: 154-167.

thermal relationships, it is their restricted unique fauna according to salt concentrations which places them apart and drive ecological differences from fresh waters. Besides thus needing separate study, their decreased diversity permits easier ecosystem analysis.

Origins of salt lakes

Endorheic basins

Salty lakes are a result of climatic influences across endorheic basins. Most occur in semiarid and subhumid climates with their intermediate rates of evaporation and precipitation (Fig. 2). In arid and hyper-arid climates (e.g., Sahara), evaporation is too high and precipitation generally too low. By contrast, in humid climates, e.g., in almost all of Europe, a land of many freshwater lakes, high precipitation and low evaporation result in large river flows and exorheic basins and flushing of any salts.

It is in endorheic basins where there may be sufficient water flow but closed surface hydrology so that water is ponded to form lakes and salts can accumulate in them. Such basins are most common in the middle latitudes (20°–50°), and aided by conducive climates, the greatest world concentration of saline lakes occur there (Fig. 1).

Arheic regions

In some arid and hyper-arid climates rare local rainfall landing directly on the surface of a salt flat or similar can create a shallow lake. It may be wetted long enough to be inhabited by a distinctive fauna. There is a myriad of such lakes in the western half of Australia filling perhaps once per 20 or many more years and inhabited when wet by a variety of brine shrimps (Timms and Hudson, 2009). World distribution is unknown, as is their relationship to salt flats (see later); remoteness and short human timescales vis-a-vis the rare fillings of these lakes limit knowledge.

Modes of origin

Physically, the dominant modes of origin are tectonic in upland regions often resulting in large deep lakes and deflation on the plains which foster smaller shallow lakes. Less common are the influence of volcanism and glaciations and many are remnants of larger basins in Pleistocene pluvial times.

Specific tectonic mechanisms and examples (Table 1) include block faulting in western United States to form Walker Lake with Great Salt Lake lying in sedimented grabens within the once huge Lake Lahontan, many east African lakes lying in the grabens of the Great Rift Valley which extends to the Dead Sea in Israel-Jordan, and the Tertiary uplifted and subsequent local faulting to produce the salinas and salares (see later) of the Altiplano in South America. Volcanism has formed lakes in numerous ways, including crater lakes (Red Rock group in Victoria), maars (Zuni Salt Lake and Big Soda Lake in western United States, Bishoftu "Craters" of Ethiopia), and by damming and collapse (Lake Corangamite). Pleistocene continental glaciations are responsible for many shallower lakes across North America, including many the Canadian prairies such as in kettles, many in former glacial channels

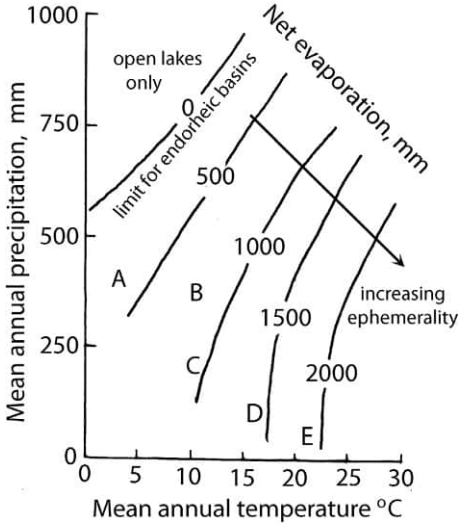

Fig. 2 Influence of climatic factors on endorheic basin lakes: interaction of mean annual temperature (°C), precipitation (mm) and net annual evaporation (mm). A = saline lakes of Saskatchewan, B = Great Salt Lake, C = Mono Lake California; D = Dead Sea Israel/Jorden, E = Lake Eyre Australia. Adapted from Cole GA (1968) Desert limnology. in: Brown GW. Jr. (ed.) *Desert Biology*, pp. 423-486. New York: Academic Press, and Williams WD (2002) Environmental threats to salt lakes and the likely status of inland saline systems in 2025. Environmental Conservation 29: 154-167.

Table 1 Location of the lakes mentioned in the text.

Abert, Oregon, 42°35′N, 120°15′W	Magadi, Kenya, 1°50′S, 36°18′E
Arenguade, Ethiopia, 8°41′N, 38°58′E	Manitou, Saskatchewan, 52°46′N, 109°40′W
Aral Sea, Kazakhstan, 45°N, 60°E	Mar Chiquita, Argentina,30°34′S, 62°32′W
Balkhash, Kazakhstan, 46°30′N, 75°00′E	Mariotic (Mariet), Egypt, 31°04′N, 29°57′E
Basin, Saskatchewan, 52°36′N, 105°15′W	Mono, California, 38°00′N, 119°00′W
Beachport-Robe, South Aust., 37°28′S, 140°00′E	Moses, Washington, 47°08′N, 119°21W
Big Soda, Nevada, 39°31′N, 118°52′W	Nakaru, Kenya, 0°12′S, 36°08′E
Bishoftu Craters, Ethiopia, 8°45′N, 38°59′E	Owens, California, 36°26′N, 117°59′W
Bonneville Salt Flats, Utah, 40°48′N, 114°02′W	Pink, Victoria, 38°04′S, 143°39′E
Borax, California, 39°06′N, 122°50′W	Pyramid, Nevada, 40°10′N, 119°35′W
Caspian Sea, Russia etc., 42°N, 50′E	Quill, Saskatchewan, 51°55′N, 104°22′W
Chad, Chad-Nigeria, 13°20′N, 14°00′E	Qinghai, China, Qinghai Prov., 36°54′N,100°09′E
Chilwa, Malawi-Mozambique, 15°13′S, 35°42′E	Red Rock Lakes, Victoria, 38°15′S, 143°30′E
Clifton, Western Australia, 32°48′S, 115°40′E	Red Rock Tarn, Victoria, 38°15′10″S, 143°30′14″E
Corangamite, Victoria, 38°10′S, 143°24′E	Salinaland, Western Aust., 24–29°S, 117–124°E
Coragulac, Victoria, 38°15′S, 143°41′E	Sambhar, Rajasthan, India, 26°54′N, 75°33′E
Dead Sea, Israel-Jorden, 31°30′N, 35°00′E	Sogo Nur, China, Gansu, 42°18′N, 101°13′E
Deep, Antarctica, 78°11′S, 68°34′E	Thetis, Western Australia, 30°30′S, 115°04′E
Eyre, South Australia, SA, 29°20′S, 137°20′E	Torrens, South Australia, 31°38′S, 137°59′E
Gnotuk, Victoria, 38°13′S, 143°06′E	Tswaing, Gauteng South Africa, 25°24′S, 28°04′E
Hamelin Pool, Western Aust., 26°12′S, 113°46′E	Tuz, Bozan, Turkey, 38°59′N, 33°19′E
Humboldt, Saskatchewan, 52°08′N, 109°40′W	Waldsea, Saskatchewan, 52°15′N, 105°14′W
Issyk-kul, Kazakhstan, 42°20′N, 77°00′E	Walker, Nevada, 38°45′N, 118°40′W
Karakul, Tajikistan, 39°00′N, 73°30′E	Werowrap, Victoria, 38°15′12″S, 143°29′57″E
La Alberca, Mexico, Guanajuato, 20°23′N, 101°12′E	Wyara. Victoria Queensland, 28°42′, 144°14′E
Lahontian, northwest United States, 38–43°N, 117–121°W	Yenyening, Western Australia, 32°14′S, 117°12′E
Little Manitou, Saskatchewan, 51°43′N, 105°29′W	Zuni Salt, New Mexico, 34°27′N, 108°46′W
Lop Nur, China, Xinjiang, 40°43′N, 90°34′E	

(e.g., Manitou and Humboldt), some by scouring (Quill Lakes), a few by damming by moraines (Basin Lake). All are relatively shallow though the local subhumid climate means almost all are permanent.

Wind action forming saline lake basins is important in semiarid regions with many examples containing water but temporarily. Small pans and bigger playas are common in many places including Australia, Texas, north and southern Africa, the Pannonian Plain centered in Hungary, the steppes of Russia, northern China, with a few in India (Sambar Lake) (Cole, 1968). There are impressive arrays of playas along former draining channels in inland Western Australia, whether on the large scale of "Salinaland" (Van de Graaf et al., 1977) or a local scale of the Yenyening lakes (Davies and Carling, 2012). Blocking dunes can be important in places (e.g., Moses Lake in Washington, United States; the lakes of the Nebraska sand dunes).

Of unusual origins, the Beachport-Robe lakes in South Australia formed between coastal dunes and originally marine, but dried. Similarly, Lake Mariotic in Egypt has been isolated from the Mediterranean and lost its thalassic character.

Details on origins are available in Hammer (1986), Timms (1992) and Touchart (2000).

Physical features of salt lakes

Amounts of water

Some saline lakes are among the world's largest. Excluding the Ponto-Caspian region, the fifth deepest is Kazakhstan's Issyk-Kul with a maximum depth of 702 m, an area of 6200 km^2, and volume of 1985 km^3. Also exceptionally large (in order) are Van in Turkey, Dead Sea (Israel, Jordan), Balkash (Kazakhstan), Qinghai (China), and Karakul (Tajikistan), all of tectonic origin. Of the shallower lakes, Lake Eyre when rarely full is the largest at 8806 km^2, volume 32 km^3 and up to 6 m deep (Kotwicki, 1986). Laguna Mar Chiquita of Argentina is 5770 km^2 in area, volume 21.4 km^3 and 3.7 m deep (Bayly, 1995).

Because most saline lakes occupy terminal basins, lake surface levels fluctuate. This is minimal in large deep lakes such as Issyk-Kul, but in very shallow lakes relatively obvious by large changes in surface area (caused by just a few meters change in depth) and also noticeable in many lakes of moderate area and depth like Nevada's Lake Walker with a drop of 55 m from 1882 to 2016 (Wurtsbaugh et al., 2017). Such big changes drastically affect salinity and ecological function.

Some saline lakes dry occasionally and those in arheic regions are dry most of the time. For instance Lake Chilwa (Malawi) has dried five times in the last 100 years (Hammer, 1986). A few are episodic, filling and drying cyclically over years, such as Lake Wyara (Queensland) filling in La Niña years and drying in El Niño years on an approximate 10–11 year cycle (Timms, 1998). Many are seasonal, mainly in Mediterranean climates. At the other extreme others rarely fill—Lake Eyre gets a minor inflow every few years, but major inundations are many decades apart (Kotwicki, 1986). Nearby Lake Torrens has filled only twice in 200 years (Williams et al., 1998).

Transparency

As in freshwater lakes, transparency ranges from turbid to crystal clear but the tendency in salinas is for light to penetrate deeper as the abundant ions in salinas usually cause clays and organics to settle. Acting against this is attenuation due to much phytoplankton in highly productive lakes and/or wind disturbance of bottom materials in shallow lakes. The spectral quality of light may vary more than in fresh waters and between lakes, due to different salinities, layering of phytoplankton, and ionic composition. These same factors influence color so that a great range is possible. Blooms of *Dunaliella* (Order Volvocales, Class Chlorophyaceae) produce color and severely limit the penetration of light.

Thermal characteristics

On average, saline waters heat a little more than fresh waters but more marked is the depression of the freezing point (e.g., –4.1 °C in Little Manitou Lake Saskatchewan at 120 g L^{-1} and Na_2SO_4/Cl waters). Hypersaline and monomictic Deep Lake in the Vestfold Hills, Antarctica, rarely freezes because the freezing point depression is about –20 °C (Ferris and Burton 1988). The normal spectrum of polymixis, monomixis and dimixis is encountered governed largely, in sequence, by shallow depths, maritime climates, continental climates, modified by altitude and latitude. Meromixis is more common than many texts admit; this is probably a function of the remoteness and hence poor monitoring of saline lakes, and of greater water stability promoted by salinity. An example is West Basin Lake in Victoria (Fig. 3) hidden in a small volcanic crater and persisting despite early calculations predicting its soon demise (Timms, 1972).

Oxygen

Dissolved oxygen is of critical importance in lakes, particularly those that stratify. Saline lakes present extra problems due to the reduced solubility of oxygen with increasing salinity. As in freshwater lakes, oxygen concentrations in saline waters vary with photosynthesis, organic decomposition, temperature and wind action. Deoxygenated hypolimnions in summer stratifications in deeper lakes, can be more severe in saline lakes due to lower solubilities and hence fish can be more affected. Shallow lakes can experience wide variations from supersaturation to deoxygenation (e.g., Tswaing Crater Lake (=Pretoria Salt Pan) has recorded values from 415% to 12% (Ashton and Shoeman, 1983)). The monimolimnions of meromictic lakes are permanently devoid of oxygen, and have much H_2S and high bacterial populations (Fig. 3).

Salts

Measurement

There are various methods of measurements of salt content of saline waters. Most thorough is the concentration of all the ionic constituents present, but this is the most time consuming to achieve. It can be simplified a little by analyzing for just the major ions, Na, K, Ca, Mg, Cl, $HCO_3/C0_3$ and $S0_4$. Results are usually expressed as g L^{-1} but there are many other measures. A quicker rougher measure is to determine the Total Dissolved Solids (=total filterable residue) by gravimetry. An even quicker method is measure conductivity, but there are some constraints on this method but it can work well for a defined series of lakes. Results are expressed in mS cm^{-1} at a specified temperature (often 18 °C or 25 °C).

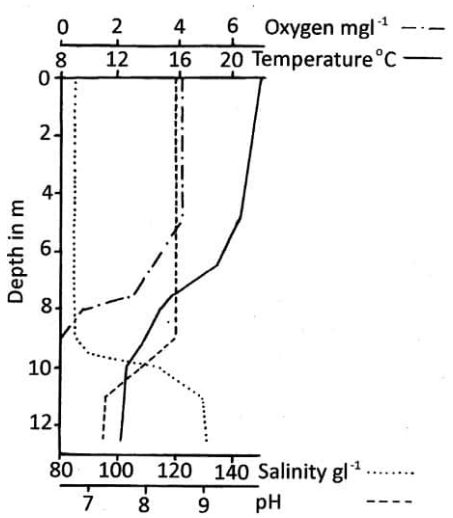

Fig. 3 Summer depth profiles in the meromictic lake, West Basin, Victoria. Modified from Timms BV (1972) A meromictic lake in Australia. *Limnology and Oceanography* 17: 918–922.

Variation

Large deep saline lakes vary little in salinity temporarily or seasonally, but shallow lakes do, both with season and secularly (Fig. 4). It is all a matter of the balance between gains and losses tempered by different lake volumes (Bayly and Williams, 1966). All waters are athalassic and can be characterized by their salinities as hyposaline 3–20 g L^{-1}, mesosaline 20-ca. 50 g L^{-1}, and hypersaline >50 g L^{-1}, based largely on salinity tolerances of component organisms (though other terms and salinity ranges may be used for specific groups of lakes) (Hammer, 1986). The term "brackish" is not applicable as this applies strictly to dilute seawater only. In most lakes salinities are increasing over time (Wurtsbaugh et al., 2017), due at least in part to climate change (see later).

Origin of salts

The salts in saline lakes originate (a) by weathering of soils and rocks in the catchment, and/or (b) via the atmosphere ultimately from marine sources and/or (c) underground from lake evaporates formed from (a) or (b) above. Controversy can rage over the proportion from each source, none more so than in Australia where atmospheric (or "cyclic") salts are important in southern lakes. Salt is lost by deflation in lakes that dry or perhaps by precipitation from the water column and/or burial by sediments.

Types of salts

The types of salts vary considerably between lakes, though there is regional similarity (Hammer, 1986). Considering anions first, there are carbonate, chloride or sulfate waters. Carbonate waters occur particularly in East Africa, Lake Chad in Africa and in Europe (Hungary) with some in North America. Most are hyposaline. Chloride waters are the most common and dominate particularly in Australia and South America and notably also include the Great Salt Lake of Utah and the Dead Sea. Sulfate waters are common in North America and Asia. All types of intermediates occur. Classification by cation dominance is even less distinct although among the nine types listed by Hammer (1986), sodium lakes are the most common, with magnesium lakes second.

Ionic ratios change as salts accumulate. Geochemical evolution is a popular study first promoted by Clarke (1924) with many later authors contributing (e.g., Kilham and Cloke, 1990; Svartsev et al., 2014). Sequences are complex and variable depending on ions present, but a broad precipitation sequence with increasing salinity is calcium carbonate, magnesium carbonate, calcium sulfate, sodium carbonate, sodium chloride, and magnesium chloride.

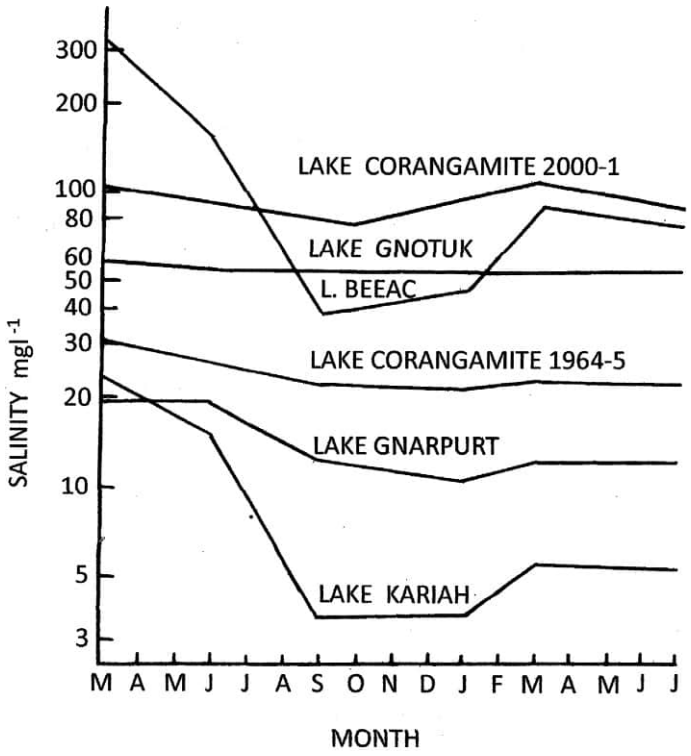

Fig. 4 Seasonal variation in salinity in six lakes in western Victoria. Variability is largely related to lake volume, Lakes Gnotuk and Corangamite (1964-5) have the largest volume and lakes Beeac and Kariah the smallest. Adapted from Bayly IAE and Williams WD (1966) Chemical and biological studies on some saline lakes of south-East Australia. *Australian Journal of Marine and Freshwater Research* 17: 177–228, with addition of Corangamite 2000-1.

Nutrients

Nutrients such as phosphorus, nitrogen and silicon can be high, which is not surprising given the endorheic status of most saline lakes (Hammer, 1986). Phosphorus (as orthoP) is greater than 100 mg L^{-1} in some and generally greater than 1 mg L^{-1} which in most cases mean saline lakes are very productive, if not hypereutrophic. Total nitrogen is very variable seasonally but values up to 30 mg L^{-1} are known, but usually much less and sometimes in amounts limiting to production. Ammonia and nitrite N can be important in reducing situations and gaseous N is fixed by some bacteria and cyanobacteria in some lakes thus overcoming shortages for high productivity. Silica can be limiting for diatom growth in freshwater lakes, but in saline lakes it can be abundant (to 730 mg L^{-1}) particularly in African and Asian waters. However low values (< 0.1 mg L^{-1}) are just as common (e.g., in Australian salinas) and perhaps limiting. Unusually high concentrations of other generally less important elements are known, such as boron and lithium and exploited commercially.

pH

The pH of saline lakes tends to be basic ca. 8, but to 11 in alkaline waters (e.g., in East African soda lakes) (Schagerl, 2016), Hungarian soda pans (Boris et al., 2014) but even lakes with more neutral pH may reach 9.5 during strong photosynthesis. Values may decrease with depth often associated with hydrogen sulfide accumulation, as in meromictic waters. Throughout southern Western Australia and in limited areas in elsewhere in the world, groundwaters tend to be acid and when exposed in playas these can be as low as pH 3 (Timms, 2009). Origins of such water are complex and are due basically to ferrolysis and/or reduction of sulfates (Lillicrap and George, 2010).

Diversity of life

Factors driving diversity

Species richness/alpha- and beta-diversity in saline lakes decrease with increasing salinity till few, if any, macroinvertebrates and algae are present beyond ca. 250 g L^{-1}. This relationship is often expressed linearly and the slope may change with drought conditions which affect insects far more than crustaceans (Fig. 5). In reality, once halophiles dominate, the decrease beyond 50 g L^{-1} is appreciably less in the mesosaline and particularly the hyposaline range (Williams et al., 1990).

While salinity per se is the major influencing factor (Timms, 1997), acidity adversely affects diversity in many mesosaline lakes in southern Western Australia (Timms, 2009), so that only one to two species are present at pH 3, just as in euhypersaline conditions (salinity >250 g L^{-1}). Another factor is heterogeneity of shores—in inland Australia beta-diversity is promoted by many small lakes

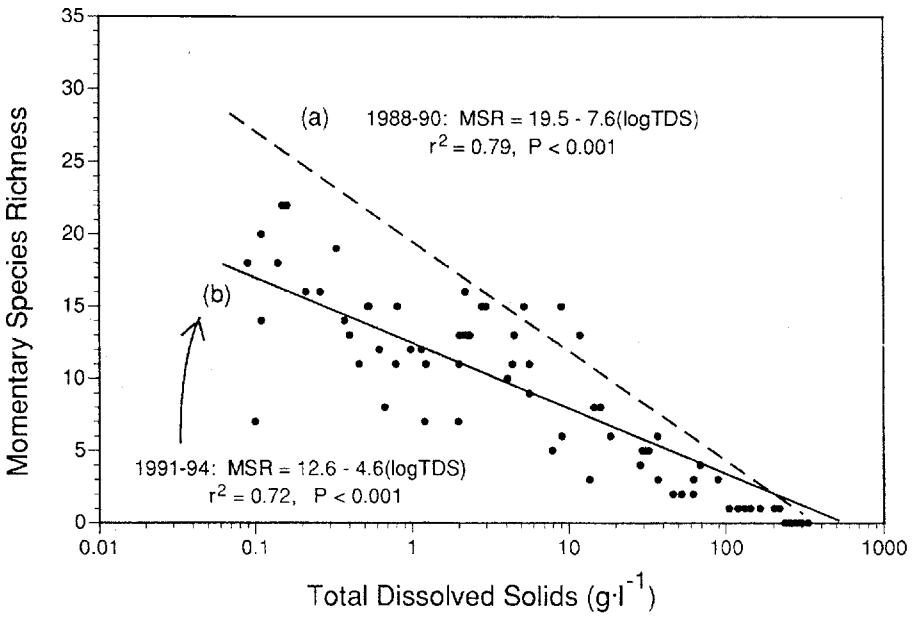

Fig. 5 Momentary species richness (alpha diversity) as a function of salinity in saline lakes in the Paroo, New South Wales in (A) 1988–90, the "wet" years and (B) 1991–94, the "dry" years. Original in Timms BV (1997) Further studies on the saline lakes of the eastern Paroo, inland New South Wales, Australia. *Hydrobiologia* 381: 31–42.

vis-a-vis large windswept lakes like Lake Eyre (Timms, 2021). This effect can be counterbalanced in deep vs. shallow lakes due to the addition of a distinct benthic community in the former. Diversity can be influenced by season as seen in lakes with irregular filling regimes, for insects are adversely affected in winter fills verses summer inundations (Timms, 2018). Another complication is provided by relict species of ultimate marine origin that may inflate species richness at higher salinities as in the coastal lakes in Crimea (Anufriineva and Shadrin, 2018). Details are given in Timms (2021).

Flora

Life cycles and ecological relationships of flora in salt lakes are usually similar to those in fresh waters, so no attempt will be made to highlight these in saline lakes. Instead attention will be given to the groups of organisms likely to be found in saline waters and their salinity tolerances (Hammer, 1986). Among microscopic organisms, there is a large variety of protists in saline waters, with a bewildering variety possible in hypersaline situations. Diatoms are extremely diverse in hyposaline waters decreasing linearly but still many in hypersaline lakes. Most have characteristic salinity ranges, and given their good preservation in bottom sediments, studies of bottom cores can be used to reconstruct past conditions in lakes. Much the same applies to the diversity of green algae and cyanobacteria, though many do not preserve as well in sediments. Most of these species are cosmopolitan, thus aiding in universal schemes for modeling. Among charophytes there are only a few hyposaline and mesosaline species with just *Lamprothamnium papulosum* penetrating into hypersaline waters. A few hundred angiosperms live at least in hyposaline waters with many of limited world distribution and only two genera, *Lepileana* and *Ruppia* in hypersaline sites.

Invertebrates

Overall, across the world there is surprising diversity of invertebrates in hyposaline waters with most freshwater higher taxa represented in at least moderately saline waters (10–15 g L^{-1}) in many/most salt lake districts (e.g., Hart et al., 1991). About the only exceptions for this restriction are cnidarians, platyhelminthes, polychaetes, hirudineans, bivalves, syncarids, ephemeropterans, and plecopterans all of which have only rare examples in waters beyond 3 g L^{-1}. Diversity across the world is much less in mesosaline waters with various crustacean groups well represented (branchiopods, copepods, ostracods, amphipods, but hardly any isopods and decapods) and the most likely insects are odonates, corixids, coleopterans and dipterans, though lepidopterans and trichopterans are occasionally represented. Also the gastropod *Coxiell*a occurs abundantly in mesosaline waters in Australia. Hyposaline and mesosaline waters also support diverse arrays of rotifers. It is in hypersaline waters that diversity is restricted mainly to brine shrimp (*Artemia, Paratemia*), rotifers (*Brachionus, Filinia*) and dipterans such as ceratopogonids (*Dasyhelea*) chironomids (*Chironomis, Tanytarsus*, culicids (Aedes), ephydrids (*Ephydra*) and a few other minor families and perhaps ostracods and copepods. Euhypersaline waters (>200 g L^{-1}) are almost the exclusive domain of brine shrimps. Only a few species of invertebrates are cosmopolitan (e.g., *Artemia franciscana, Brachionus plicatilis* sensu strictus) though many genera are shared across at least a few continents.

Fish

Fish are not diverse in saline waters due to many problems including osmoregulation, access, and impermanence (Hammer, 1986). Species present are of different phylogenetic origins in each continent, rarely penetrate beyond middle hyposaline range and then only to upper mesosaline with just a few, usually species of marine origin, surviving in hypersaline waters (e.g., the cyprinodont *Aphanius dispar* in Mediterranean coastal marshes to 145 g L^{-1}). Other examples of remarkable salinity tolerance include the cichlid *Alcolapia grahami* living in hot springs in Kenya and Tanzania and *Craterocephalus eyresi* in Lake Eyre. Fish do better in sodium chloride waters then in sulfate and especially alkaline waters, and if they do survive, reproduction may be suppressed.

Waterbirds

Representatives of flamingos, grebes, ducks, geese, swans, pelicans, cormorants, herons, egrets, cranes, waders, gulls, terns and phalaropes are variously prominent in salt lakes. The great majority of these are tolerant freshwater species; the difference is in how they use the richer resources of salt lakes. Representative of salt lakes particularly attractive to water birds include the Great Salt Lake, Utah (Jehl, 1994; Frank, 2016), Lake Albert, Oregon, (Senner et al., 2018), Lake Nakuru, Africa (Bennum and Nasirwa, 2000), Mar Chiquita, Argentina (Castro and Torres, 2014), Lakes Eyre and Wyara, Australia (Kingsford and Porter, 1993, 1994).

Suitable lakes with abundant invertebrates as a feeding resource lie between 10 and 150 g L^{-1}, but often narrower (30–80 g L^{-1}, Herbst, 2006). Sometimes high salinities can be physiologically limiting to the birds. Numbers per lake can exceed 250,000 (>5000 ha^{-1} in places), but fluctuate greatly seasonally/secularly (Roshier et al., 2002; Bennum and Nasirwa, 2000). In many cases, particularly among the migrating waterbirds of North America, lake phenology and bird life cycles are closely matched, (e.g., Wilson's Phalarope, Jehr, 1988) whereas in Australia with its unpredictable episodic flooding/filling regimes waterbirds move enigmatically to the Outback salinas, breed and then disperse outwards again (e.g., Banded Stilt, Burbridge and Fuller, 1987). Without doubt the ecologically most interesting waterbirds are the flamingos with their adaptations for living in highly saline waters and niche separation when species co-inhabit (Castro and Torres, 2014).

Regionalization

Although some hypersaline species occur across the world, in general each continent's saline flora and fauna is distinct. The greatest similarly occurs across the Nearctic and Palaearctic both formally extensively glaciated and their saline systems established in the Holocene. African and South American saline systems are somewhat older and unique, but it is in isolated and old Australia that the fauna of saline lakes is the most distinctive. This is contributed to by *Parartemia* instead of *Artemia*, an abundance of ostracods, the prominence of the snail *Coxiella*, the presence of the isopod *Haloniscus* (to name a few outstanding invertebrate genera) and also an adaptation to higher salinities in general (Williams, 1972, 1978). Copepods are more prominent in saline lakes in Europe than elsewhere (Hammer, 1986).

Saline biogeography in Australia is further distinguished by regionalization much more so than elsewhere—the faunas of each of southern WA, Eyre Peninsula SA, the southeast of SA, eastern and central Inland and southern Victoria plus Tasmania are distinct. Contributing to this is isolation, evolutionary history and separate climates (Williams, 1984).

Productivity

Introduction

Some saline lakes are thought of as being more productive, others less productive, than fresh waters. This ambiguity has encouraged many studies to quantify production in inland saline waters, particularly of the basic step, primary production of the phytoplankton. There are many methods, none perfect, and even the most widely used, incorporation of ^{14}C into algal tissue, can underestimate or overestimate production (e.g., Pierson, 2012). Besides method inaccuracies, the use of different units in reporting is confusing.

Production by phytoplankton

Many saline lakes across the world have now been studied ranging from small to large, and many chemical types (mainly carbonate, halite, sulfates, and borax lakes). Results vary widely, but in general hyposaline lakes exhibit the highest primary production and hypersaline lakes the least (Table 1). Carbonates seem to be advantageous to production, none more so than the Victorian examples, and borates could be depressive. The world's most productive salina is the small shallow Red Rock Tarn in Victoria. Conversion efficiencies of sunlight and biomass are in general higher by 2–8 times the average 1% expected in many ecosystems, but those in hypersaline lakes are significantly lower. As in most freshwater lakes, production occurs in the upper few meters, but in saline lakes this can be restricted to the uppermost meter or less by light attenuation due to dense algal crops. Sometimes production is inhibited very near the lake surface by high light intensities. While production usually tracks the daily flux in total radiation and is much higher in summer than in winter, inexplicable fluctuations are common particularly in shallow lakes where the environment can be quite unstable. For instance, Pink Lake in Victoria can have high rates for a very limited time, but almost nothing for days on end (Table 2). Winds and resultant high turbidities contribute to this problem. Readers are referred to Hammer (1986) for an analysis on primary production in saline lakes across the world and to the peculiarities in Pink Lake.

Production by macrophytes

In saline lakes there have been far fewer studies on macrophyte primary production and even fewer of the attached periphyton community. From these it seems production can be significant and add 20–50% to the whole lake primary production. Factors such as extensive shallow water, low turbidities and moderate salinities are positives (Wetzel, 1964).

Limnetic secondary production

Studies on secondary production often deal with one species or those of a particular habitat, with major variation between lakes (Hammer, 1986). Starting with rotifers which can be particularly common in hypo- and mesosaline lakes, production in Lake Werowrap has varied from 29 to 1909 g DW m^{-2} $year^{-1}$ which was 0.7% of phytoplankton production. A figure for Nakuru was an order of magnitude greater. Brine shrimp are usually efficient convertors of algal production into shrimp flesh with figures of 208 g $m^{-2}day^{-1}$ reported in cultures, but rarely in nature. Even so in Great Salt Lake a conversion efficiency was once recorded at 25%, similar to that for *Parartemia zietziana* (23%) in Pink Lake, but the latter could have got some energy from windblown detritus. Respiration can account for 60–80% of assimilation, leaving insufficient for life, resulting in mass deaths. While many cladocerans occur in salt lakes and life cycles have been studied, no information is available on productivity. Copepods are even more diverse in saline lakes and much is known of their life cycles and salinity tolerances. Two production studies yielded very different productivities—259 to 385 mg DW m^{-2} day^{-1} for *Lovenula africanus* in Lake Nakuru at 15–25% conversion efficiency and 7 mg C m^{-2} day^{-1} for *Diaptomus connexus* in Saskatchewan's Waldsea Lake at 7% of annual phytoplankton production. Ostracods are usually small and benthic, but in Australia many are large and planktonic, and while data are available on salinity tolerances, production is unstudied.

Table 2 Values for primary production in selected lakes arranged from least to most saline.

Lake	*Country*	*Daily P (mg C m^{-2} day^{-1})*	*Max P* (mg C h^{-1})*	*Efficiency (%)*
Hyposaline				
Mariiotic	Egypt	9611	–	–
Humboldt	Saskatchewan	7968	2.20	3.80
Pyramid	Nevada	2780	–	–
Arenguade	Ethiopia	–	6.00	3.34
Coragulac	Victoria	2921	13.20	1.31
Nakuru	Kenya	7067	6.33	2.60
Mesosaline				
Manito	Saskatchewan	2620	1.86	5.49
Big Soda	Washington	2800	–	–
Red Rock Tarn	Victoria	17,531	38.88	8.04
Werowrap	Victoria	7683	–	–
Corangamite	Victoria	4425	8.10	1.82
Borax	California	525	–	–
Hypersaline				
Gnotuk	Victoria	246	–	–
Little Manitou	Saskatchewan	1188	5.30	0.46
Great Salt	Utah	6147	–	–
Pink	Victoria	184	3.70	0.32

P = production.

Based on Table 7.14 in Hammer UT (1986) *Saline Lake Ecosystems of the World*. Dordrecht: Junk.

Benthic production

The benthos of many salt lakes have been studied and many standing crop figures are available. As in freshwater lakes, diversity and biomass decrease with depth, with generally higher figures in hyposaline lakes but little or no macroscopic benthos in hypersaline lakes. This relationship is best seen in a series of lakes as in Victoria where average biomasses decrease with increasing salinity, perhaps with a peak in the lower hyposaline range no doubt related to their higher primary productivity/nutrient load (Timms, 1983) (Fig. 6).

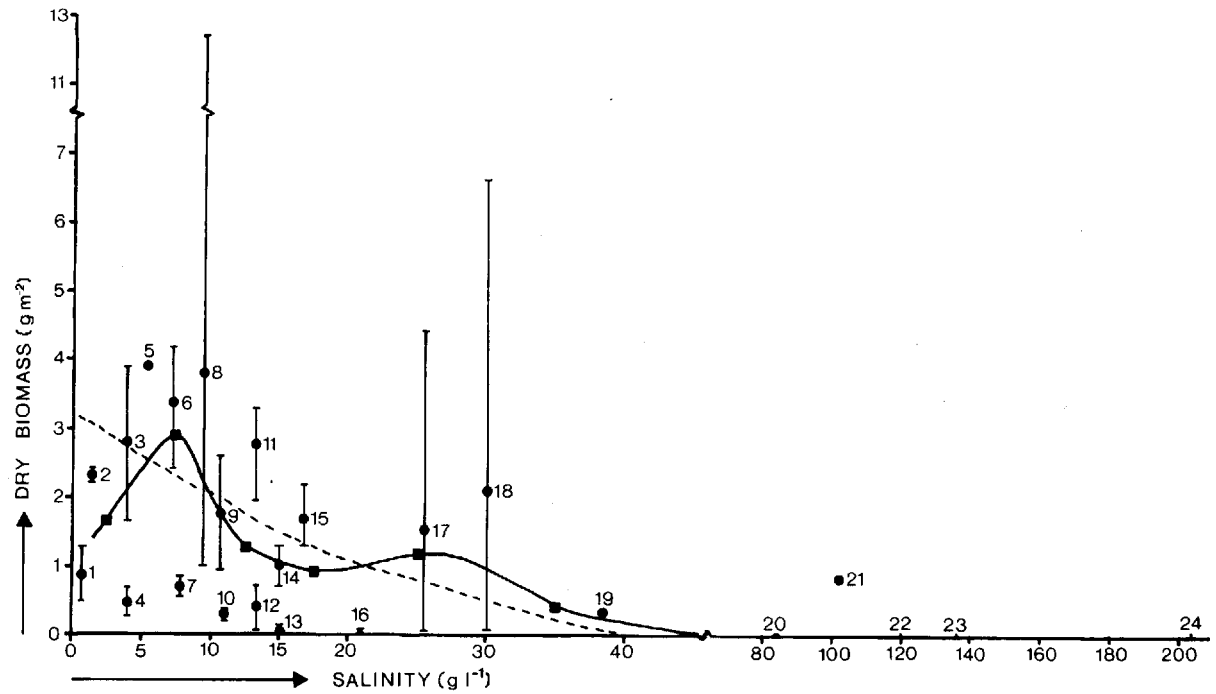

Fig. 6 Relationship between benthic biomass and salinity in 24 shallow saline lakes in Victoria. The solid circles indicate the mean value for each lake, and the bars the range of values. The solid heavy line shows an approximate relationship between the two parameters in that it connects six points (as squares) marking average biomass values for lakes within four (0–20 g^{-2}) and two (>20 g^{-2}) g m^{-2} intervals. The dashed line represents a mathematical solution for the relationship expressed by the equation x –g e^{hy} where g = 51.184 and h = 0.135. Note the scale changes on both axes. Original in Timms BV (1983) A study of benthic communities of shallow saline lakes of western Victoria, Australia. *Hydrobiologia* 105: 165–77.

Production figures are available for some lakes (Table 2). Lake Werowrap is the most productive of all lakes, due to its moderate salinity, shallowness, high primary production, and growth of 8 generations of chironomids per year (Paterson and Walker, 1974). Nukuru is next; it is also shallow and has 10 generations of chironomids per year (Vareschi and Jacobs, 1984). The reason for Soap Lake's productivity is claimed to be its high primary productivity and lack of fish to prey on the chironomids (Lauer, 1963). The long winter of no growth and hence only one generation of chironomids per year is negative for Soap and Waldsea and an extra depressive factor for Waldsea is possibly the ill effects of magnesium ions (Swanson and Hammer, 1983).

Ecophysiology of organisms

Introduction

This has been a favorite topic for investigators over the years. While the essence is known (Bayly, 1972), some aspects have yet to be elucidated. Central is how halophilic and halobiont organisms survive the salty environment.

Crustaceans

The most powerful osmotic regulators are anostracans *Artemia "salina," Parartemia zietziana* and by taxonomic affinity, all species in these genera. In mesosaline and hypersaline waters these brine shrimp (Fig. 7) maintain their body fluids at 350 mOsm L^{-1}, which can be as low as 10% of the environment. They do this by active regulation, swallowing the medium, removing Na and Cl across the gut wall and secreting these ions through the gills. This requires energy, which can exceed metabolic gain at extreme salinities and result in death. Australia has an unusual crustacean in its saline lakes, an oniscoid isopod *Haloniscus searli* of terrestrial origins. It can osmoregulate to 160 g L^{-1} (Fig. 7).

Many lower crustaceans in saline waters (branchiopods, copepods, amphipods) osmocomform in hyposaline and even mesosaline conditions. Perhaps in some cases, like those in hypersaline waters, survival is by ionic regulation. The situation is just not known.

Insects

Some mosquito larvae (e.g., *Aedes detritus*) survive in waters to 100 g L^{-1} by a similar process to that in brine shrimps, but removal of ions is by the malpighian tubules. Ephydrids (brine flies) are also strong osmotic regulators. *Ephydra cinerea* in Great Salt Lake can live in 300 g L^{-1} NaCl waters helped by an impermeable cuticle but in Mono Lake *E. hians* is adapted to alkaline waters and survives only to 200 g L^{-1}, with any chloride water above 200 g L^{-1} antagonistic to its survival. Some chironomids (e.g., *Ch. salinarius*) are weak hypo-osmotic regulators. Many corixids have some ability to osmoregulate, as do some beetles (e.g., *Hygrotus salinarius* in Saskatchewan), but it is unknown how many beetles regularly survive in waters greater than 50 g L^{-1}. Surely an impermeable cuticle helps.

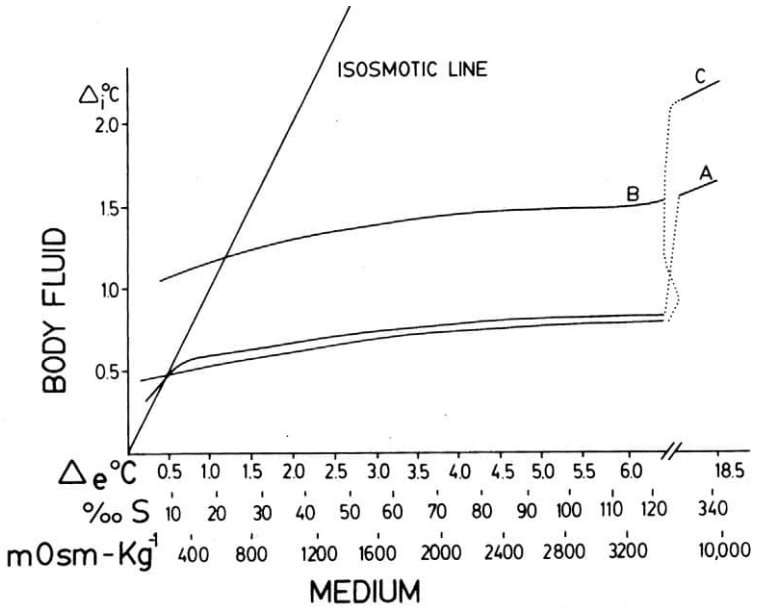

Fig. 7 Osmotic response curves for crustaceans in athalassic saline waters. (A) *Artemia "salina"* at 21° ± 3 °C (Croghan, 1958); (B) *Parartemia zietziana* at 18 °C (Geddes, 1975); (C) *Haloniscus searli* at 20 °C (Bayly and Ellis, 1969). Modified from Hammer UT (1986) *Saline Lake Ecosystems of the World*. Dordrecht: Junk.

Plants

The mechanism for survival of algae and angiosperms in saline waters are well known. Algae such as *Dunaliella* uses glycerol to maintain intracellular osmotic balance (Borowitzka and Brown, 1974). Some diatoms and some charophytes can regulate internal osmotic pressure by controlling KCl concentrations. Angiosperms use a variety of mechanisms, from selective salt uptake, salt exclusion by roots, increase in succulence and salt extrusion. Some use organic molecules such as proline. Similar use of organics by animals has hardly been investigated.

Adaptations for acid waters

Of similar interest to survival in mesosaline waters is living in acid salinas wherein below pH 6.2 no free CO_2 is available. However at least one brine shrimp in Western Australia, *Parartemia contracta*, is able to use respiratory CO_2 in its ATP to run its sodium pump for osmoregulation (Conte and Geddes, 1988). It is not known whether other brine shrimp such as *Parartemia acidiphila* which lives down to pH 3 uses the same mechanism or some novel method.

Microbial ecology

Introduction

Microbes are everywhere but they are arguably more noticeable, important and unusual in saline lakes, salares and salterns (Oren, 2002). What is more is that this is an active area of research bringing great rewards as new species are found, genome sequences compiled, metabolic diversity realized and biotechnological uses explored. Major discoveries have been made in the Dead Sea, Mono Lake, Great Salt Lake, alkaline soda lakes of Kenya such as Lake Magadi, and solar salterns especially those in Spain. In Deep Lake, Antarctica, two strains of a *Halobacterium* survive in one of the most extreme aquatic environments on Earth (salinity close to 350 g L^{-1} and temperatures approaching −20 °C) (Ferris and Burton, 1988).

Taxonomic diversity

Phylogenetically, halophilic and halotolerant microorganisms occur in all three life domains: Archaea, Bacteria and Eucarya. Archaeans are the most halophilic and they often comprise the greatest biomass in many highly saline sites. The Halobacteriales are a prominent group. The Bacteria include many types of halophilic and halotolerant microbes with a majority in moderate rather than extreme habitats. The Eucarya are in general the least tolerant and common, but the alga *Dunaliella* is an exception, being an important component in many moderate salinas and some strains even in extreme environments.

Osmotic solutions

There are two strategies to deal with the high environmental osmotic pressures. In the first and most common is to accumulate organic solutes to provide osmotic balance. A wide variety of such compounds are known and include glycerol, ectoine and glycine betaine. A second strategy is to accumulate K^+ and Cl^- ions at the expense of Na^+ to maintain osmotic balance. This is used by the Halobacteriales and some true bacteria and is less energetically demanding.

Metabolic activities

These microbes display a huge range of metabolic activities (Oren et al., 2009), many important ecologically such as photosynthesis, denitrification, sulfate reduction and other functions specific to certain species and situations, e.g., methane formation from acetate, or autotrophic ammonia reduction. Some activities release little energy, others much, and some occur at high salt concentrations, others have much lower limits. Many are important in mineral recycling and in the food chain of saline lakes, though exactly the processes and organisms responsible are not well known in most lakes (Fig. 8). In food chains, there are a range of protozoa that consume bacteria and it is probable that ubiquitous *Artemia* may help regulate bacterial densities too. However, at extreme salinities, bacteriophages seem more important in regulating prokaryote densities than protozoans.

Microbialites: Benthic microbial mats

Benthic microbial mats occur in many situations across the world (Prieto-Barajas et al., 2018) and can be photosynthetic or heterotrophic. They are made by an array of cyanobacteria, diatoms and other eukaryotic algae plus bacteria and can be mucilaginous films easily broken up or persistent due to lithification by carbonates. Originating over 3 billion years ago, such microbialites contributed to oxygenating the atmosphere. These days microbial mats in salt lakes are one of the alternate regime states in their ecology, favored by higher salinities, low nutrient status and wet-dry hydrology (Sim et al., 2006).

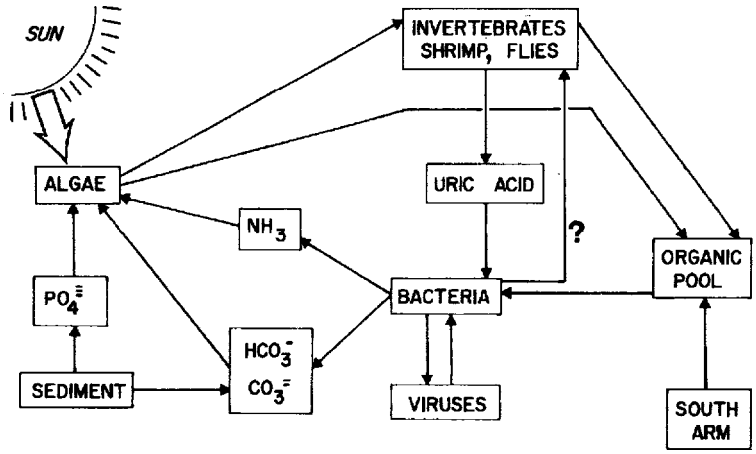

Fig. 8 Model showing the central role of bacteria in the ecology of Great Salt Lake, Utah. Original in Post FJ (1981) Microbiology of the Great Salt Lake, north arm. *Hydrobiology* 81: 59–69.

Microbialites: Stromatolites and thrombolites

Akin and far less common are stromatolites and thrombolites in which sediments are incorporated too and the structure is likely to grow into a dome or column. In stromatolites the sediment is in layers, while in thrombolites the sediment is spongy. The world's best modern examples occur at Hamelin Pool (thalassic), and Lakes Thetis and Clifton (athalassic) in coastal Western Australia.

Salares, salterns and salt flats

Salares

Salares, *sensu stricto*, are paleolake remnants, sometimes with shallow saline water but often with no water over a salt base or just pools and springs, and located mainly in the altiplanos of South America and in Tibet. They are subject to daily/seasonal/episodic extremes of climate including temperatures of –10 to +25 °C, precipitation of 50–300 mm annually and salinity range of fresh water to crystallizing brine. Adding to the tough physicochemical conditions is high solar radiation and generally negative water balance.

Their waters can sometimes support macroinvertebrates at lower salinities but it is the rich endemic microbial diversity that is characteristic particularly at higher salinities. Recent discoveries using molecular analyzes of 16S rRNA gene sequences have revealed exciting diversity in the Chilean Altiplano (Dorador et al., 2013). Up to 275 species, 32 phenotypes and 94 clones have been discovered in individual sites and what is more, adjacent pools can have very different microbes. Bacterial communities are dominated by Bacteroidetes and Proteobacteria while archaeal diversity is much lower and dominated by the Euryarchaeota. Just what each species does chemically is largely unknown, but possibilities for useful biotechnical applications are endless.

Salterns and salt flats

Salterns, salt flats, salt pans and salinas are much simpler systems, but still with harsh environmental parameters. They occur worldwide, salterns being the final stage in salt production, either from a marine or continental base; life in them is dominated by *Artemia*, *Dunaliella* or various bacteria including *Halobacterium*. Salt flats/pans are simply salty expanses that rarely contain water, and when they do they may support a limited hypersaline fauna and microbes. Their formation needs a closed basin, an arid climate and in most cases they are the remnants of paleolakes (as for Salares). However, the numerous pans/salinas of inland Western Australia are due to ponding along relict rivers and subsequent enlargement by wind action (Davies and Carling, 2012). The famous Bonneville Salt Flats of Utah rarely contain water and fauna, but those in inland Western Australia are episodically filled from cyclonic rainfall and their fauna is typical of a local meso- to hypersaline lake. The exact relationship of these to rainwater filled salt flats (see earlier) needs elucidation.

Management issues

Denial of water inflow

While there is some commonality in management between fresh and saline lakes, the fact most saline lakes lie in endorheic basins in arid/semiarid lands, leads to unique problems with water inputs (Jellison et al., 2008). Surface inflows are often diverted for irrigation or groundwater levels are lowered for the same reason resulting in increased salinities and/or reduced lake volumes or even drying the lake, despite their generally large size. There are a plethora of examples across the Middle East, central Asia, northern China and North America (Wurtsbaugh et al., 2017) such as the Dead Sea (Israel-Jordan), Tuz Lake (Turkey), Urmia (Iran), the Aral

Sea (Uzbekistan, Kazakhstan), Lop Nur and Sogo Nur (China), Lakes Walker, Owens ad Mono (western USA), and La Alberca (Mexico). Mexican lakes are particularly impacted by groundwater pumping. Fewer examples occur in South America (Mar Chiquita), Africa and Australia. The situation in Australia's Lake Corangamite is a little different as the main inflow has been diverted to prevent flooding and maintenance of the status quo of valuable nearshore land (Williams, 1995). Even more upsetting is the drying of the nearby unique Red Rock crater lakes (Red Rock Tarn holds the record for the highest primary production and Lake Werowrap for the greatest secondary production) due to completely unplanned groundwater pumping (Timms, 2005). Adding to the woes in most cases is global climate change, though increased temperatures do not necessarily mean greater water evaporation as increasing cloud cover and aerosol concentrations are reducing pan evaporation (Roderick and Farquhar, 2002). In some instances, long term climate change has resulted in fluctuating water levels, such as in Lake Van (Turkey) and Great Salt Lake (USA). Interestingly most of the affected lakes are Ramsar sites indicating their value in landscape ecology.

Other management issues

Other generally smaller salinas are affected by secondary salinization, particularly in southern Australia. In these, changing land use has mobilized salts dissolved in groundwater thus bringing them to the surface resulting in salinization of the land and any nearby lake. Also of significant but of localized impact is mining of evaporites in or near salt lakes. For instance, mining for halite and lithium has destroyed or scarred many salt lakes in inland China. In some places mineral deposits such as gold in Western Australia occur within the floor of salt lakes and their extraction results in damage, but these days limited by government control. Then in some lakes there are problems due to pollution or overfishing or invasion by exotic organisms (e.g., Caspian Sea for all three); these problems are shared with freshwater lakes, and though not as common, are ecologically similar. Also similar to freshwater sites, shallow ephemeral salinas can be subject to deflation with lunette formation and/or sedimentation, particularly in northern China, Texas, southwest South Africa and inland Australia.

Conclusion

The prognosis for most salt lakes is indeed bleak, due, in approximate order, to denial of water, secondary salinization, mining, organic pollution, overfishing, and invasion by exotic organisms (Jellison et al., 2008; Timms, 2005; Williams, 2002; Wurtsbaugh et al., 2017).

A case study

Lake Werowrap is a small (21.6 ha), shallow (1.4 m), saline lake (23–56 g L^{-1}) in a scoria cone ca. 140 km southwest of Melbourne, Australia. (Fig. 9 Photo). Its simple ecosystem epitomizers the value of saline lakes in ecosystem studies. Also it tended to be highly

Fig. 9 Red Rock Crater, Victoria. Foreground Lake Werowrap, right background, crater containing Red Rock Tarn (lake hidden). Picture taken 1971.

Table 3 Comparison of benthic production by dominant chironomids in four lakes.

Lake and country	*Salinity g L^{-1}*	*Chironomid species*	*Production g m^{-2} $year^{-1}$ DW*	*Efficiency (%)*
Nakuru, Kenya	12	*Leptochironomus deribae*	14.6	6.3
Soap, Washington	19	*Tanypus nubifer*	11.3	16
Waldsea, Saskatchewan	16	*Cricotopus ornatus*	0.08	6.3
Werowrap, Victoria	35–56	*Tanytarsus bartitarsus*	73.4	7.9

productive but variable, two common traits of salt lakes and what is more it has suffered from water denial, in fact complete drying, the fate of many lakes. It was studied during 1968–70 mainly by Walker (1973). The lake has now dried permanently due to nearby groundwater pumping (see earlier).

Volume and lake salinity was explained by rainfall/evaporation balance, but influenced by groundwater seepage. Water was of the chlorocarbonate type with a high pH of 9.8. There was rapid light attenuation due to dissolved organic matter and dense plankton populations, and nutrient levels were high partly due to nesting gulls, though inorganic nitrogen was depleted at times.

During 1968–70 the lake supported few species; three in the phytoplankton *(Anabaena spiroides, Gymnodinium aeruginosum, Chroococcus* sp.), four in the zooplankton (*Brachionus plicatilis, Hexarthra jenkinae* and two ciliates), one main littoral organism (beetle *Nectersoma penicillatum*) but a few more when salinity was lower early in the study and one benthic species (chironomid *Tanytarsus barbitarsus*). Phytoplankton production was high (Table 2), the main influencing factors being radiation and temperature. There was considerable "dark" ^{14}C assimilation indicating important bacterial activity. Secondary production by the rotifers was low but very high for the benthic chironomid (see "Productivity" section). It is possible that there was significant periphyton production in 1968 but not later when salinities were higher (Table 3).

When the lake was fresher (<20 g L^{-1}) in pre 1968 and 1982 it had the tolerant freshwater copepod *Boeckella triarticulata* and the predatory chironomid *Procladius paludicola* and more littoral beetles and dipterans. A bottom core had *P. paludicola* at depth and the tolerant freshwater chironomid *Chironomus duplex* near its base. These are indicators that the fauna of this lake changes with salinity, as is typical of shallow salinas. What was seen in 1968–70 was just a brief window in its existence.

Acknowledgments

I sincerely thank Ian Bayly for his insightful comments on the manuscript.

See Also: Structures and functions of Inland Waters - Lakes: pH of Inland Waters; Saline Lakes

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Wetland Soils: Physical and Chemical Properties and Biogeochemical Processes

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This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Gleization Soil-forming process that occurs under anaerobic conditions and involves the reduction of ferric iron and leaching of ferrous iron, resulting in the formation of grey or greenish-blue soils, or gley soils.

Hydric soils Soils formed under conditions of saturation, flooding or ponding long enough during the growing season to develop anaerobic conditions in the upper part (United States Department of Agriculture, Natural Resources Conservation Service, 2018).

Paludification The accumulation of organic matter in poorly drained soils that can result in the formation of histosols (organic soils) over time.

Pedogenesis Complex phenomenon leading to soil formation from mineral and organic parent material through factors including climate, parent material, topography, organisms, and time, and processes such as additions, losses, translocations, and transformations.

Redoximorphic features Features formed by the reduction, translocation, and/or oxidation of iron and manganese oxides (Vepraskas, 1995).

Introduction

Inland wetlands consist of freshwater marshes, prairie potholes, peatlands, and freshwater-forested wetlands. Each of these wetland types have unique soil characteristics based on their hydrology and physical and chemical properties of the soils. Wetland soils are a critical part of wetland functioning. It is where biogeochemical processes take place that are responsible for functions such as carbon sequestration and removal of nutrients. Due to their anaerobic conditions that slow the rate of decomposition, wetland soils, per unit area, store more organic matter than terrestrial soils and can serve as a sink for carbon (C) and nutrients (nitrogen (N) and phosphorus (P)). Microbial communities, vegetation, and organisms interact within wetland soils to facilitate these processes. Plants add organic matter to the soil, whereas microbes catalyze reducing reactions such as denitrification that enhance water quality and methane (CH_4) production (methanogenesis), a greenhouse gas.

Soil definition

Soils are defined as "a natural body comprised of solids (mineral and organic matter), liquid, and gases that occur on the land surface, occupies space, and is characterized by one or both of the following: horizons, or layers, that are distinguishable from the initial material as a result of additions, losses, transfers, and transformations of energy and matter *or* the ability to support rooted plants in a natural environment" (United States Department of Agriculture, Natural Resources Conservation Service, Soil Survey Staff, 1999, pp. 9).

Wetland soils are hydric soils, which are defined as "soils that formed under conditions of saturation, flooding or ponding long enough during the growing season to develop anaerobic conditions in the upper part" (United States Department of Agriculture, Natural Resources Conservation Service, 2018, pp. 1). Wetland soils can be either mineral or organic (discussed in more detail in Section "Mineral vs. organic soils") and support hydrophytic vegetation, which are plants that are adapted to growing in low-oxygen or anaerobic environments. Hydric soils have distinct characteristics from non-hydric, or upland, soils including color, formation of soil horizons, and biogeochemical processes, which will be discussed throughout the chapter.

Soil formation

Soils form through geochemical and pedochemical weathering. Geochemical weathering involves inorganic (non-biological) processes and includes oxidation, reduction, solution, hydrolysis, and hydration. Pedochemical weathering depends on biologic processes and involves oxidation-reduction cycles. Pedogenic, or soil-forming, processes are also important in soil formation and include additions (alluvial, colluvial and eolian deposition, leaf litter), losses (erosion and leaching), translocations (pedoturbation, melanization), and transformations (decomposition, mineralization, gleization, paludification) of materials.

Soil formation is driven by five factors: parent material, climate, topography, organisms, and time (Jenny, 1941). For mineral soils, "parent material" consists of rock or rock-weathered material including sedimentary, siliceous crystalline and mafic rock. Parent material is also material that has migrated from other areas, such as material brought in from wind (eolian deposition) or water (alluvial deposition). Organic soil parent material is of biologic origin (plant debris), such as in peats soils.

"Climate" includes temperature, precipitation, and microclimate. Temperature and precipitation are important global factors in controlling rates of chemical reactions and weathering, soil wetness, soil temperature, and vegetation.

"Topography" depends on landscape or geomorphic position and slope. Topography is important because slope affects erosion, deposition, and movement of water through the soils. Topography can also affect soil temperature, reactivity, wetness, color, and organic content.

"Organisms" consist of plants, fauna, and microorganisms. Plants add organic matter to the soil while fauna are important in mixing the soil and in the physical breakdown of leaf litter. Microorganisms are critical for decomposition of organic matter and mineralization of nutrients.

Finally, the degree of soil formation is a function of "time." Sufficient time is needed for the five factors in tandem with pedogenic, or soil forming, processes (below) to produce soils with unique characteristics.

Soil-forming processes include additions of mineral material and organic matter, losses from erosion and leaching, translocation of material downward from leaching and upward from bioturbation, and transformations such as decomposition of organic matter. Over time, soil-forming processes interact as new materials are being formed and added, lost, translocated and transformed resulting in the development of soil layers, or horizons, that are approximately parallel to the soil surface. In soils that are well drained (upland soils), soil horizons consist of (Fig. 1A):

- "O horizon" (usually a thin layer of organic material, plant litter and partially decomposed plant tissue).
- "A horizon" (mineral layer; mineral soil darkened by additions of organic matter).
- "E horizon" (mineral layer; zone of eluviation, leaching of clay, iron, aluminum, and organic matter).
- "B horizon" (mineral layer; zone of illuviation, accumulation of clay, iron and aluminum oxides, some organic matter).
- "C horizon" (mineral layer; not strongly affected by pedogenic processes; very little biological activity occurring).
- "R horizon" (mineral layer; bedrock).

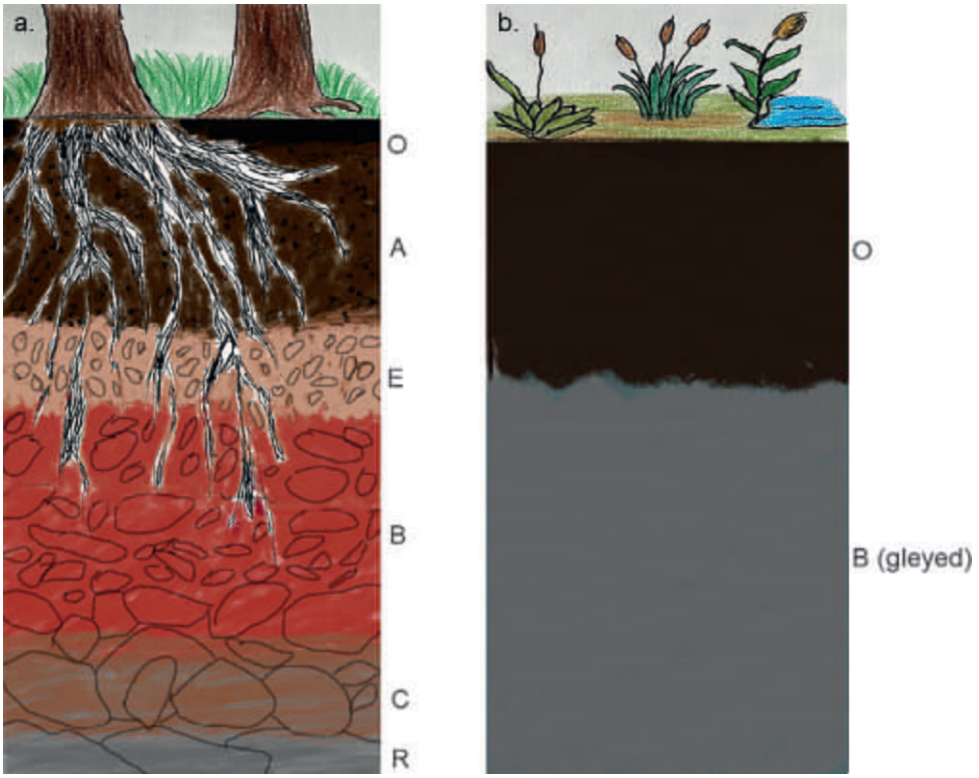

Fig. 1 (A) Typical profiles of an (A) upland and (B) wetland soil.

Wetland soils, however, differ from upland soil profiles in that the soil forming processes of gleization (reduction and leaching of soluble ferrous iron resulting in grey or greenish-blue soils, or gley soils) and paludification (accumulation of organic matter in poorly drained soils) predominate. Since wetland soils are saturated or inundated much of the time, downward translocations that occur in upland soils are less important, leading to the formation of fewer horizons (Fig. 1B). Wetland soils tend to have thicker O horizons than upland soils due to slow decomposition rates, and, in poorly drained soils that dry out periodically, a mottled B horizon below the O horizon where iron reduction occurs. In wetland soils that are very poorly drained and experience continuous anaerobic conditions, the soil may consist of only an O horizon followed by a uniform grey or black gleyed B horizon.

Mineral vs. organic soils

Hydric soils can be either mineral or organic. Organic soils, also known as "Histosols," are formed primarily from deposition and accumulation of plant material. The anaerobic conditions of wetland soils slow decomposition of organic matter leading to accumulation of above- and below-ground plant material. To be classified as a histosol, soils must contain at least 12–18% organic carbon (20–30% organic matter), depending on the clay content. They must also have an organic layer that is at least 40 cm thick (United States Department of Agriculture, Natural Resources Conservation Service, 2018). Soils that do not meet these requirements are classified as mineral soils.

Histosols can be further classified into suborders based on the degree of decomposition of the plant material. In fibric Histosols or "Fibrists," plant fibers compose more than 2/3 of the mass. The organic matter produced by peat mosses such as *Sphagnum* typically are classified as Fibrists. In hemic Histosols ("Hemists") plant material is more decomposed and fibers compose 1/3–2/3 of the mass, such as peat soils. "Saprists" (Fig. 2) are the most highly decomposed and fibers compose less than 1/3 of the mass. Muck is an example of a saprist. Hemists and Saprists usually form from herbaceous or even woody vegetation. Histosols form only in wetlands and under continuous inundation or soil saturation.

In contrast to organic soils where paludification is the dominant soil forming process, mineral soils of wetlands produce distinct changes in soil chemistry and color in response to inundation and saturation. These changes produce redoximorphic features that form through the reduction, translocation, and/or oxidation of iron and manganese oxides (Vepraskas, 1995). Microbial processes are responsible for the formation of redoximorphic features, which include redox depletions, redox concentrations, and reduced matrices and can be identified by soil color characteristics that are discussed in more detail in Section "Color".

Mineral and organic soils also differ in other properties besides the amount of organic matter and carbon content: bulk density and porosity, hydraulic conductivity, nutrient availability, and cation exchange capacity (Craft et al., 1991, Table 1).

Fig. 2 Peat soil (Saprist) produced by inputs and incomplete decomposition of wetland vegetation. Photo by Chris Craft.

Table 1 Physical and chemical properties of organic versus mineral wetland soils.

	Organic Soil[a]	*Mineral Soil*
Bulk density (g cm^{-3})	0.2	1.4
Particle density (g cm^{-3})	1.5	2.6
Porosity (%)	86.7	48.8
Hydraulic conductivity (cm h^{-1})	15.1	1.0
Texture		
Organic matter (%)	45.5	0.6
Sand (%)	–	84.5
Silt (%)	–	9.1
Clay (%)	–	6.4
Organic C (%)	23.4	0.3
Organic N (%)	1.5	<0.1
Atomic C:N (wt: wt)	15.1	20.1
Exchangeable NH_4-N (μg g^{-1})	74.0	6.1
Exchangeable NO_3-N (μg g^{-1})	4.7	0.3
Total P (μg g^{-1})	910	110
Extractable P (μg g^{-1})	25.8	4.6
Eh (10 cm)	268	238
Eh (30 cm)	–68	154
pH	4.5	4.2

[a]Mineral fraction was not characterized and will vary depending on the organic soil type.
Table modified from Craft CB, Seneca ED and Broome SW (1991) Porewater chemistry of natural and created marsh soils. *Journal of Experimental Marine Biology and Ecology* **152**: 187–200.

Physical properties

Physical characteristics of wetland soils include texture, bulk density, porosity, and color. Bulk density, texture, and porosity of soils are particularly important because they directly affect soil processes such as water holding capacity and hydraulic conductivity.

Texture

Soil texture is the relative percentages of sand, silt, and clay particles that make up the mineral (inorganic) fraction of soil (Fig. 3). Sand particles are the largest and range from 2.0 to 0.05 mm in diameter. Silt particles are smaller, ranging from 0.05 to 0.002 mm. Clay particles are smaller than 0.002 mm. Texture affects other soil properties such as bulk density, water holding capacity, permeability, and porosity. For example, soils that primarily consist of sand particles have high permeability and low water holding capacity compared to soils with higher silt and clay content.

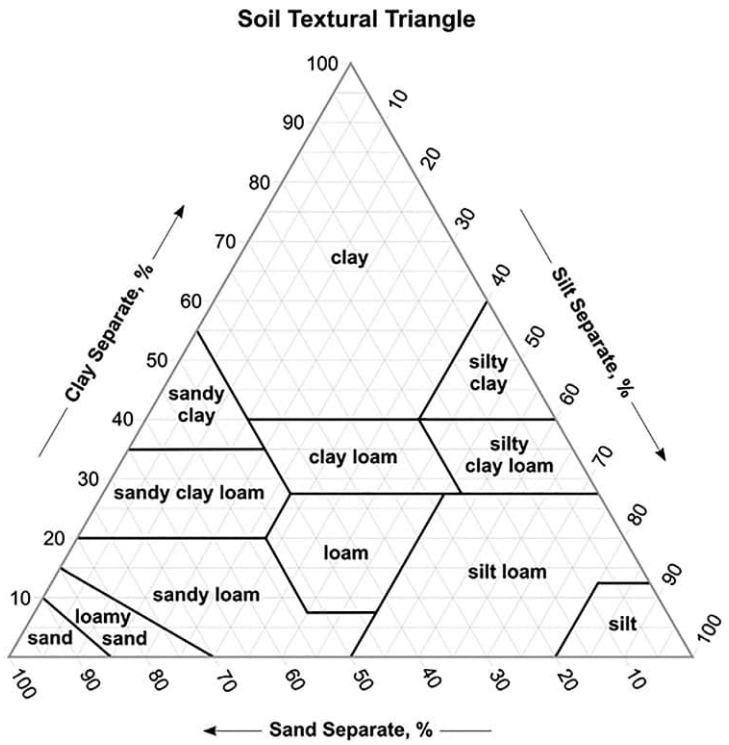

Fig. 3 Textural triangle describing the relative proportion of sand-, silt- and clay-sized particles.

Bulk density and porosity

Bulk density is the mass of dry soil per unit volume, typically expressed as g cm^{-3}. The proportion of mineral versus organic particles, to a large extent, determine bulk density. Organic soils have much lower bulk density compared to mineral soils (Table 1). In organic soils, bulk density ranges from about 0.1 g cm^{-3} for Fibrists to 0.2–0.3 g cm^{-3} for Hemists and Saprists. In wetland mineral soils, bulk density ranges from 0.5–1.5 g cm^{-3}.

Porosity is the volume of soil that is filled with either water or air. It is inversely related to bulk density; as bulk density increases, porosity decreases. Soil texture is an important determinant of porosity. Porosity of mineral soils is often around 50% for both sandy and clayey soils. However, the pores of sandy soils are large (macropores) whereas clayey soils have smaller pores (micropores). The macropores of sands promote air and water movement but limits their water holding capacity. Clays, because of their micropores, have excellent water holding capacity but poor air and water movement and, hence poor drainage. Organic soils, because of their low bulk density, tend to have much higher porosity compared to mineral soils (Table 1). The pore space of wetland soils is often filled with water, in contrast to upland soils where the pores are filled with air most of the time.

Color

Soil color is an indicator of the hydrology (wet or dry) in soils and is classified based on (1) hue, (2) value, and (3) chroma using the Munsell color chart (Munsell Color, 2010). Hue is the overall color of the soil, such as red or yellow. Value is the lightness or darkness of the soil color and chroma is the intensity or greyness of color. Hydric soils typically have a chroma of 2 or less, which indicates anaerobic conditions and long-term inundation or saturation. Iron (Fe) and manganese (Mn) play important roles in the color of wetland soils and the formation of redoximorphic features (redox depletions, redox concentrations, and reduced matrices, discussed below).

Redox depletions occur when the soil has a chroma of 2 or less, a value of 4 or higher, and iron and manganese oxides have been solubilized and leached from the soil. When the soil is continuously flooded or saturated, it may appear grey, black, greenish-grey, or blue-grey in color (Fig. 4). This process is known as gleization and results from the reduction of iron and manganese (see Section "Iron (Fe) and Manganese (Mn) Reduction"), producing what is known as "gleyed" soil. When a soil is flooded seasonally or for only a portion of the year, it takes on a mottled color (Fig. 5) of redox depletions, the grey-colored areas, and redox concentrations (discussed below). In their oxidized forms, iron and manganese give soils a red, orange or yellow color (Fig. 6). When soils become saturated and oxygen is depleted, ferric iron (Fe^{3+}) is reduced to ferrous iron (Fe^{2+}), which is a soluble form with a consequent change in color to grey. Manganese is also reduced to its soluble form (Mn^{2+}) under saturated conditions.

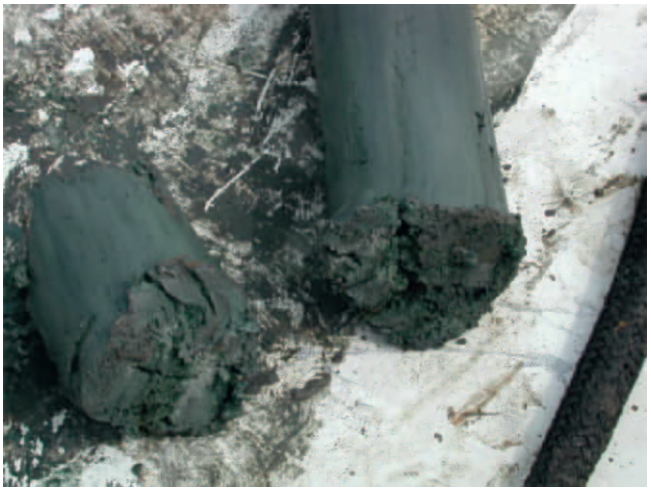

Fig. 4 Gleyed soils. Note the bluish-greenish color produced by continuous (year-round) flooding and anaerobic conditions. Photo by Chris Craft.

Fig. 5 Mottled soils containing redox depletions (grey areas of Fe^{2+}) and redox concentrations (red areas of Fe^{3+}). Soils such as this indicate periodic or seasonal flooding and dry-down. Photo by Chris Craft.

Redox concentrations are areas of iron and manganese oxide accumulations that are evident in mottled soils (Fig. 5). Redox concentrations appear as areas of yellow or reddish color where the iron is in its oxidized (Fe^{3+}) state. Oxidized rhizospheres, which are red and orange areas adjacent to roots where oxygen leaks out of plant roots, are also an example of redox concentrations.

Dark black or brown surface soils with a low value on the Munsell color chart indicate organic matter enrichment. The dark color results from the decomposition of organic matter and the formation of humus, which is black or dark brown in color.

Chemical properties

pH

Soil pH is a measure of H^+ ion activity and is an important chemical property that affects vegetation growth, microbial activity, decomposition rates, and nutrient availability (nitrogen, phosphorus, calcium). In particular, acidic (low pH) soils may be toxic to vegetation and microbes, reducing inputs of organic matter to the soil and slowing decomposition and other microbial processes. Soil pH depends on concentration of acidic and non-acidic-forming cations. H^+ and Al^{3+} are acid-forming while elements such as Ca^{2+}, Na^+, and K^+ are base-forming (Jackson et al., 2014). Soil pH is influenced by parent material of the soil, oxidation-reduction reduction (redox) reactions, and the dominant water source. For example, wetlands that are primarily fed by precipitation, such as bogs, generally are more acidic while wetlands such as fens that are fed by groundwater tend to be more neutral (Jackson et al., 2014).

Fig. 6 Upland soils with their well oxidized yellow and red color produced by oxidized (Fe^{3+}) iron. Photo by Daniel Markewitz.

Table 2 The sequence of microbially driven reducing reactions that occur when a soil is flooded.

Redox Reaction	Reactants		Products	Approximate *Eh*
Aerobic respiration:	CH_2O (C^{4+} + H_2O + $4e^-$) + O_2	→	CO_2 + H_2O + energy	>300 mV
Denitrification:	CH_2O + $2\mathbf{NO_3^-}$ + $6e^-$ + $8H^+$	→	CO_2 + $\mathbf{N_2}$ + $5H_2O$	~ +200 mV
Nitrate reduction:	CH_2O + $\mathbf{NO_3^-}$ + $2H^+$	→	$2CO_2$ + $\mathbf{NH_4^+}$ + H_2O	~ +125 mV
Manganese reduction:	CH_2O + $\mathbf{Mn^{4+}}$ (MnO_2) + $3e^-$ + $4H^+$	→	CO_2 + $\mathbf{Mn^{2+}}$ + $3H_2O$	~ +125 mV
Iron reduction:	CH_2O + $\mathbf{Fe^{3+}}$ (FeOOH) + e^- + $3H^+$	→	CO_2 + $\mathbf{Fe^{2+}}$ + H_2O	~ +50 mV
Fermentation:	$2CH_2O$ + H_2O	→	$HCOO^-$ + CH_3OH + H^+	~ 0 mV
Sulfate reduction:	CH_2O + $\mathbf{SO_4^{2-}}$ + $4e^-$ + $6H^+$	→	CO_2 + $\mathbf{H_2S}$ + $3H_2O$	~ -100 mV
Methanogenesis:	CH_3OH + $\mathbf{CO_2}$ + $12e^-$ + $10H^+$	→	$\mathbf{2CH_4}$ + $3H_2O$	< -200 mV

Decreasing Energy Yield ↓

All reactions require an electron donor, organic matter (CH_2O) and acceptor (O_2, NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-}). For some reactions (fermentation), organic matter can serve as both an electron donor and acceptor.

Soil pH also changes as the soils become reduced and pH generally shifts towards neutrality; pH in acidic soils tends to increase while pH in alkaline soils tends to decrease. The changes in pH largely depend on iron and organic matter content. For example, acidic soils with high organic matter and oxidized iron will see an increase in pH as Fe^{3+} is reduced to Fe^{2+}, a reaction that consumes hydrogen (see Table 2). In alkaline soils, organic acids and CO_2 are produced as a result of reducing reactions, which lowers soil pH (Ponnamperuma, 1972).

Redox potential (*Eh*)

Redox potential is the tendency of a chemical species to either be reduced by accepting electrons or oxidized by donating electrons (Reddy et al., 2000). Oxidation-reduction involves the transfer of electrons from one ion or molecule to another. Oxidation is the donation of electrons to other substances and reduction is the acceptance of electrons from other substances. Redox potential indicates how oxidized or reduced (anaerobic) the soil is as well as the electron availability in the soils. Redox potential of upland soils is greater than +300 mV whereas, in wetland soils, redox potential is less than +300 mV and may decline to −100 to −200 mV. When soils are flooded or inundated, redox potential decreases as the oxygen is consumed by microbes and plant roots to support respiration. Lower redox values indicate more anaerobic and reduced conditions while higher values indicate aerobic or less extreme anaerobic conditions.

Redox potential generally decreases with depth in wetland soils that are beneath the thin, oxidized surface layer. This oxidized surface layer is a result of oxygen diffusion from the overlying water, but the diffusion rate is slow enough that the oxygen is consumed in this zone and does not diffuse to the subsurface layers (Craft, 2000). Redox potential controls oxidation-reduction reactions, or redox reactions (see Fig. 7), which are critical in wetland nutrient and biogeochemical cycles (discussed in detail in Section "Biogeochemical processes").

Cation exchange capacity

Cation exchange capacity (CEC) is the ability of soils to hold (sorb) cations and is affected by clay and organic matter content and soil pH. Clays and organic matter possess a negative charge that sorb cations such as hydrogen and base cations, calcium, magnesium, potassium, and sodium. Cation exchange capacity is higher in clays than in sandy or silty soils. Organic matter also contributes to CEC and CEC increases as organic content increases.

Biogeochemical processes

Redox reactions

Microbially driven reducing reactions play a critical role in wetland nutrient cycling and decomposition and, in some cases, in global biogeochemical cycles. In most wetlands, a thin transitional zone exists between the oxygen-rich air, or water, above and the anoxic reduced soil below. This is known as the "reducing zone" and is where many redox reactions take place. As important metabolic processes, redox reactions control such processes as greenhouse gas emissions and water quality benefits through removal of nutrients (N and P).

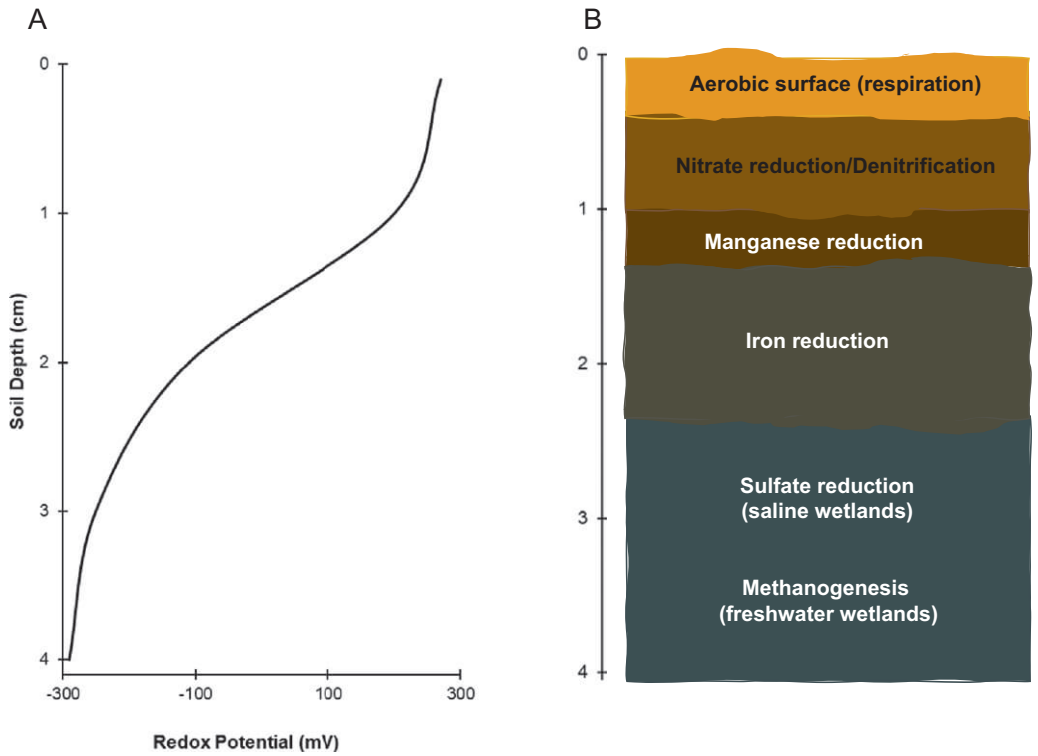

Fig. 7 (A) Redox potential (*Eh*) variation with depth and (B) nitrate, manganese, iron, sulfate and methane redox reactions as they vary with depth and redox potential.

Oxygen is the strongest electron acceptor and yields the most energy. When soils become flooded, vegetation, fauna, and aerobic microorganisms will quickly consume oxygen to support respiration. When oxygen is used up, facultative anaerobic microbes can use secondary electron acceptors as a source of energy for respiration, though these secondary acceptors yield less energy. These secondary electron acceptors include nitrate, oxidized forms of manganese and iron, organic matter (humic substances), sulfate, and carbon dioxide. As soils become flooded and oxygen is depleted, the sequence of reduction generally is as follows (in order from greatest to least energy yield): denitrification, nitrate reduction, manganese reduction, iron reduction, fermentation, sulfate reduction, and finally methanogenesis (Table 2, Fig. 7). All of these reactions require organic matter (carbon) as an electron donor. Terminal electron acceptors and a source of organic matter, which typically is abundant in wetlands soils, are both are needed to fuel these reactions. Redox reactions vary with depth and redox potential and this sequence of reactions can also be observed within the soil profile of hydric soils (Fig. 7).

Many of these redox reactions also involve the consumption of hydrogen ions, which raises the pH of soils and makes them less acidic. Several of these redox reactions are particularly important in global nitrogen (denitrification), phosphorus (iron reduction), sulfur (sulfate reduction), and carbon (methanogenesis) biogeochemical cycles.

Denitrification and nitrate reduction

Once oxygen is depleted in the soils, denitrification is the next reducing reaction that takes place as denitrifying bacteria can use nitrate as a source of energy. Denitrification is the reduction of nitrate (NO_3^-) to atmospheric N_2 and N_2O and the availability of nitrate is generally the limiting factor for denitrification in wetlands. Since nitrate is considered a water pollutant that can lead to eutrophication of aquatic ecosystems, especially estuarine and coastal waters, denitrification helps improve water quality. Some studies suggest that under less anaerobic conditions (such as on the edge of aerobic/anaerobic zones) incomplete denitrification results in higher production of nitrous oxide (N_2O), a potent greenhouse gas, rather than dinitrogen gas (N_2) (Hernandez and Mitsch, 2007). This is due to the fact that the enzyme involved in N_2 production is diminished by the presence of oxygen to a greater extent than the enzymes involved in N_2O production (Wrage et al., 2001).

Another form of nitrate removal is dissimilatory nitrate reduction to ammonium (DNRA), which is also carried out by microbes. Instead of being converted to gaseous nitrogen forms, nitrate is converted to ammonium (NH_4^+), which is also a form that can be taken up and used by vegetation and organisms.

Iron (Fe) and manganese (Mn) reduction

Iron reducing microbes can utilize Fe as an energy source, reducing ferric iron (Fe^{3+}) to ferrous iron (Fe^{2+}), leading to changes in soil color. The reduction of ferric to ferrous iron produces grey soil color, including mottles and gleying, as the ferrous iron is solubilized and leached from the soil (discussed in Section "Color"). Iron reduction also leads to the dissolution of iron-bound phosphorus (Fe-P) compounds, releasing soluble phosphorus, which can cause eutrophication of aquatic ecosystems, especially freshwater systems.

Manganese reducing microbes utilize Mn as an energy source and reduce Mn^{4+} to Mn^{2+}. Similar to iron, manganese significantly affects soil color and becomes soluble in its reduced state. Manganese is responsible for black color in soils in its oxidized state but can leach out of soils once it is reduced, resulting in gley soils (see Section "Color").

Fermentation

Fermentation occurs when organic matter, such as sugars or organic acids, serves as both the terminal electron acceptor and the electron donor. External electron acceptors are not needed for fermentation, which is carried out by obligate or facultative anaerobic bacteria. The end products of fermentation can include hydrogen, organic acids and carbon dioxide, which can serve as substrates for other microorganisms such as methanogens.

Sulfate reduction

Sulfate reducing bacteria (SRB) use sulfate (SO_4^{2-}) as an energy source and hydrogen sulfide (H_2S) is produced which can be toxic to vegetation and organisms. Hydrogen sulfide is also responsible for the distinct "rotten egg" smell in wetland soils, especially saline wetlands which have more sulfate than freshwater wetlands.

Methanogenesis

Methanogenesis, which yields the least amount of energy, takes place in the most extreme (reduced) anaerobic conditions. Methanogens carry out methanogenesis which produces methane (CH_4), a potent greenhouse gas. There are three pathways for methanogenesis to occur: acetoclastic methanogenesis, methylotrophic methanogenesis, and hydrogenotrophic methanogenesis. "Acetoclastic" methanogens use acetate as an electron acceptor while "methylotrophic" methanogens use methanol or methylamines. "Hydrogenotrophic" methanogens use H_2 and CO_2 to carry out methanogenesis. Hydrogenotrophic and acetoclastic methanogenesis are the most common pathways in freshwater systems (Fenchel et al., 2012). Further, studies have shown that bogs are typically dominated by hydrogenotrophic methanogenesis in contrast to fens, where the acetoclastic pathway tends to be dominant (Bridgham et al., 2013).

Wetland soils as nutrient and carbon sinks and sources

Wetlands can act as sinks, sources, or transformers for carbon, nitrogen, phosphorus, and sulfur. Organic matter accumulation leads to the storage of nitrogen and organic carbon while sedimentation and sorption to mineral soil particles leads to storage of phosphorus.

Carbon

Wetlands play a major role in global carbon cycling and, per unit area, wetland soils store much more organic carbon than upland soils. The stored carbon provides an energy source for microbial processes and accumulation of carbon depends on the balance between productivity and decomposition of organic matter. Due to the anaerobic conditions of wetland soils, carbon losses from decomposition are much less than inputs from primary productivity, allowing these systems to accumulate organic matter. Recent estimates suggest that in the top 1-m alone, wetland soils store up to 158 Pg of soil organic carbon, or nearly12% of the 1325 Pg of soil organic carbon stored in soils globally within the top 1-m (Kochy et al., 2015). However, wetlands can also be sources of greenhouse gases, especially methane. Total global methane emission estimates range from 500 to 700 Tg CH_4 $year^{-1}$ (Dlugokencky et al., 2011; Kirschke et al., 2013), with wetland emissions ranging from 80 to 280 Tg CH_4 $year^{-1}$ (mean of 166 Tg CH_4 $year^{-1}$) (Bridgham et al., 2013).

Nitrogen

Soils generally make up the largest nitrogen pool in wetlands and these pools include particulate and dissolved organic nitrogen, nitrogen in microbial biomass, inorganic forms such as NH_4^+ and NO_3^-, and gaseous end products. Organic nitrogen makes up the largest pool and accounts for about 95% of the total nitrogen (Craft, 1996). Forms of organic nitrogen in the soils include living forms such as in microbial biomass and other fauna and non-living forms such as peat and plant detritus (Reddy and DeLaune, 2008).

Nitrogen in wetland soils can undergo different transformations including nitrification, denitrification, dissimilatory nitrate reduction to ammonium (DNRA), and anaerobic ammonium oxidation (anammox). These processes are driven by microorganisms and, with the exception of nitrification, occur under anaerobic conditions. Denitrification (Section "Denitrification and nitrate reduction") is the major pathway of nitrogen removal from wetlands.

Anaerobic ammonium oxidation (anammox) is another microbially mediated mechanism for nitrogen removal from wetlands. Anammox is the oxidation of ammonium coupled with reduction of nitrite to produce nitrogen gas (N_2) and is carried out by a unique group of bacteria in the phylum *Planctomycetes* (Mulder et al., 1995; Strous et al., 1999). Estimates of the contribution of anammox to nitrogen removal from wetlands vary. Recent studies estimate that anammox is responsible for anywhere from ~2% to 20% of nitrogen gas (N_2) produced from wetland soils (Hou et al., 2015; Shen et al., 2016; Zhang et al., 2020).

Phosphorus

Unlike nitrogen and carbon, the phosphorus (P) cycle does not have a gaseous phase and so wetlands can act as phosphorus sinks through sediment deposition, sorption and precipitation to particles, as well as through uptake by plants (macrophytes, algae).

Soil phosphorus exists in organic and inorganic forms. Inorganic forms include phosphorus bound to iron, aluminum, and calcium while organic forms are associated with soil organic matter, detritus, vegetation, animals, and microorganisms. In wetlands with organic soils, organic phosphorus makes up a higher percentage (50–90%) of the total phosphorus compared to organic phosphorus in mineral soils (10–50%) (Reddy and DeLaune, 2008). In mineral soils iron and aluminum play a major role in the ability of mineral soils to retain phosphorus.

Adsorption and precipitation are two processes that retain inorganic phosphorus. Adsorption occurs when soluble inorganic phosphorus moves from the soil porewater to the (solid phase) sediments where it can adsorb to aluminum and iron oxides or hydroxides and accumulate in the sediment. Adsorption capacity is affected by soil texture and increases with increasing clay and mineral content. Adsorption occurs rapidly at first and then rates decrease as it reaches equilibrium with phosphorus concentrations in the porewater. Over time, the sorption sites become saturated. Precipitation occurs when phosphate reacts with metal cations such as iron, aluminum, calcium, or magnesium to form phosphate precipitates. Precipitation with Al and Fe predominates in acidic soils whereas precipitation with Ca occurs in circumneutral and basic soils (Reddy and DeLaune, 2008). Both processes are important for long-term retention of P. However, in soils with high iron-bound P, flooding leads to reduction of Fe^{3+} to Fe^{2+} (Section "Iron (Fe) and manganese (Mn) reduction") with consequent release of P into the water.

Sulfur

Sulfur enters wetland systems through atmospheric deposition, surface- and tidal-water exchange and, like C and N, sulfur transformations are mediated by microorganisms. Sulfur cycling is well studied in saline wetlands (salt marshes) due to the abundance of sulfate in marine systems (up to 2700 mg L^{-1}) compared to freshwater systems (~10 mg L^{-1}) (Mitsch and Gosselink, 2015). Major sulfur pools in wetlands include soil and soil organic matter. Sulfur can go through several transformations in wetlands including sulfate reduction, sulfide oxidation, and sulfur oxidation. In wetland soils, sulfate (SO_4^{2-}), which is used as a terminal electron acceptor in sulfate reduction under anaerobic conditions, is particularly important in the sulfur cycle. Sulfate reduction is the dominant sulfur transformation, especially in salt marshes and estuarine wetlands (Reddy and DeLaune, 2008). Recent studies, however, suggest that sulfate reduction may be more prevalent in freshwater wetlands and plays a larger role in

carbon cycling than previously thought due to the rapid recycling of sulfide to sulfate (Pester et al., 2012; Martins et al., 2017). Some studies estimate that sulfate reduction can account for up to 50% of organic carbon mineralization in freshwater systems as a result of the rapid recycling of reduced sulfur to sulfate (Pester et al., 2012). Additionally, sulfate reduction leads to the production of hydrogen sulfide (H_2S) which can be toxic to plants and animals. Many wetlands are sources of H_2S to the atmosphere, though typically salt marshes and estuarine wetlands have higher H_2S emissions (up to 79 μg S m^{-2} h^{-1}) compared to freshwater wetlands (~0.30 μg S m^{-2} h^{-1}) (Reddy et al., 2002).

Conclusion

Wetland soils are unique, with patterns and processes characteristic of both upland (oxidized) soils and aquatic (reduced) sediments that vary spatially and temporally. Periodic to continuous inundation and saturation drives a number of aerobic and anaerobic microbial processes that provide critical ecosystem functions and services, including water quality improvement through denitrification and cycling of carbon and greenhouse gases, CO_2 and CH_4. Because of their often high plant productivity and slow rate of decomposition, wetland soils are an important global sink for carbon. The variable physical (texture, bulk density) and chemical (pH, redox potential) properties of wetland soils affect the ability of wetlands to perform these ecosystem services and act as carbon and nutrient sinks.

Knowledge gaps

- How does the balance between plant production and decomposition, the opposing processes that build soil organic matter (SOM), vary with the duration and frequency of inundation and soil saturation?
- What is the long-term (centuries to millennium) rate of C storage and how does decomposition of (older) organic matter vary over these time scales?
- What is the contribution/importance of alternative microbial processes (DNRA, Anammox) that convert NO_3^- to N_2?
- How will climate change-induced changes in wetland hydrology affect soil-based functions such as carbon storage and denitrification?

See Also: Human pressures and management of Inland Waters: Agricultural Pressures on Inland Waters; Structures and functions of Inland Waters - Groundwater: Epikarst: An Important Aquatic and Terrestrial Habitat; Structures and functions of Inland Waters - Wetlands: Carbon Dynamics in Wetlands; Mountain Rivers: A Global Overview of River Channel Forms, With a Focus on Braided Rivers; Structure and Function of Inland Waters-Wetlands: Classification Systems of Wetlands; Tropical Large River Wetlands; Tropical Peat Swamp Forests

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Carbon Dynamics in Wetlands

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Biogeochemical cycle Exchange processes or pathways of essential elements of living matter through biotic and abiotic compartments of Earth. Net storage sites are called sinks or pools, net release sites are called sources, mostly however, both processes occur simultaneously at different rates. Here it is mainly referred to carbon exchange processes between the atmosphere and the wetlands within their surrounding ecosystems. The term biogeochemical emphasizes interdisciplinarity and suggests that biological, geological, and chemical elements of each cycle have to be considered.

Carbon sequestration The process of gathering carbon and storing it in a carbon pool.

Carbon storage The process of keeping carbon from cycling between the different ecosystem compartments or spheres of earth. In the case of wetlands, the carbon content often increases due to conditions inhibiting the complete mineralization of organic matter to carbon dioxide or methane.

Decomposition, Organic Matter Processing, Mineralization The stepwise breakdown of complex organic matter (mostly, dead plant parts) into less complex organic and inorganic compounds. Plant parts are often comminuted by detritivorous animals (shredders) or by physical impact (leaching, bleaching, erosion), while enzymatic activities of microbes (bacteria and fungi) continue the processing and transformation of organic matter on the molecular level. The "mineralized" end products are dissolved salts or gasses like carbon dioxide and methane (CO_2 and CH_4). A large part of the OM, however, becomes stored or, together with the decomposers, integrated into the detritus-based food chain. Therefore, the term Organic Matter Processing is more commonly used.

Greenhouse gasses Gaseous constituents of the atmosphere, both natural and anthropogenic, that absorb and emit radiation at specific wavelengths within the spectrum of terrestrial radiation emitted by the Earth's surface, the atmosphere itself, and by clouds. This property causes the greenhouse effect. Water vapor (H_2O), carbon dioxide (CO_2), nitrous oxide (N_2O), methane (CH_4) and ozone (O_3) are the primary GHGs in the Earth's atmosphere (see also Shukla et al., 2019).

Mineral associated organic matter (MAOM) Organic matter that is protected from decomposition or cycling by its binding to mineral matter. Minerals can prevent microbial access to organic matter and therefore hinder or slow decomposition.

Organic matter (OM) Matter that originates from the biomass of organisms (plants, animals microorganisms), mostly a mixture of decaying plant material and decomposing organisms. Important source of organic compounds (mainly

hydrocarbons). Abbreviations: DOM, dissolved OM; POM, particulate OM, similar abbreviations for carbon forms (DOC, POC); Soil organic carbon (SOC), the carbon part of organic matter in the soil, and volatile organic compounds (VOCs).
Radiative forcing The change in the net, downward minus upward, radiative flux (expressed in W m^{-2}) at the tropopause or top of atmosphere due to a change in a driver of climate change, such as a change in the concentration of carbon dioxide (CO_2). It is the scientific basis for the greenhouse effect on planets, and plays an important role in computational models of Earth's energy balance and climate, see Shukla et al. (2019).
Recalcitrance Chemical properties that makes organic matter intrinsically resistant to decomposition (Kleber, 2010), such as high concentrations of shredder-repellent substances (e.g., plant polyphenolics Haase and Wantzen, 2008) or inadequate ratio of compounds concerning the ecological stoichiometry of the consumers (e.g., C/N ratio).
Units Carbon storage is indicated as mass per size unit, often as g m^{-2} for localized studies, t ha^{-1} (1 ton = 1000 kg = 1,000,000 g = one mega gram (Mg), 1 ha (ha) = 10,000 m^2 = one hundredth of a square kilometer) for interbiome comparisons and Pg (petagram, which is identical to Gt (Gigaton) = a unit of mass equal to 10^{15} g) for global comparisons. In spite that ton and Gt are no SI units, they are commonly used. The conversion factor from g m^{-2} to t ha^{-1} is 0.01.

Introduction

Wetlands are highly diverse, varying in size, inundation period and geography. They occur as small, water-filled holes to huge ecosystems and as permanent bogs in the tundra or sporadic wetlands in deserts (Mitsch and Gosselink, 2015). Wetlands typically develop in topographic depressions and therefore accumulate substances, including organic matter (OM) and water. Low oxygen levels are characteristic, as oxygen is used for decomposition but the supply is hampered as its diffusion rate is 10^4 times lower in water than in air. Oxygen limitation hampers the process of OM breakdown. Consequently, despite the small proportion of land covered by wetlands, they store a disproportionally large amount of carbon (20–30% of the global soil carbon, Kayranli et al., 2010) while having a huge potential for carbon sequestration (Lal et al., 2018). Wetlands are still underestimated in global carbon budgets (Bastviken et al., 2011). Moreover, the assessment of the size of wetlands is difficult, especially if they are small sized or seasonally variable. The global estimation of land covered by wetlands (6–8%, Mitsch and Gosselink (2015) is contested by regional studies, e.g., 20% of South America (Junk, 2013) and 22% of the boreal zone by permafrost soils alone (Obu et al., 2019). In addition, linear-fringing wetlands may escape classical airborne habitat assessments (Guo et al., 2017). The uncertainty of wetland sizes translates into a large source of uncertainty of the contribution of wetlands to the global carbon cycle, for example important for the quantification of continental wide methane budgets (Grunwald et al., 2012). Certainly in geological time scales, wetlands can be seen as a sink for atmospheric carbon having accumulated biomass transformed into coal and petrol now released as fossil fuels.

Their variable character adds to the great importance of wetlands in global biogeochemical cycles. Carbon is stored and released at the same time, making wetlands both sink and source for atmospheric carbon. Depending on external forces the net flux rapidly switches between these two functions (Vega et al., 2014). For developing models and carbon budgets, it is necessary to understand the relationship between the main biotic processes at play, namely primary production and organic matter processing (decomposition or mineralization of organic matter). The environmental parameters driving these biotic processes mainly relate to climate (precipitation, temperature, solar irradiance) and soil properties (nutrient content, texture, drainage), which control water and oxygen dynamics. Moreover, wetlands are connected to other ecosystems, so that carbon may be imported or exported. Despite an obvious control of climate on wetland occurrence and functioning, most wetland types occur in any climatic region. This article deals with inland wetlands leaving out coastal and marine wetlands, such as mangroves, salt marshes and other mudflats despite their importance to the global carbon cycle (see, e.g., Ouyang and Lee (2020) for a review).

The interdependences of the above-mentioned basic elements of the carbon cycle of inland wetlands are in the focus of this article, while elucidating the conditions that may provoke switches from the processes of carbon storage to carbon release. This is done using a functional typology of wetlands concerning the carbon cycle and their specific sets of environmental parameters. Furthermore, historical and current impacts of Climate Change and Land Use Changes on wetland carbon budgets are discussed, and recommendations to maintain carbon-relevant ecosystem functions and ecosystem services by wetlands are presented.

Main topics

Parameters steering carbon storage and release in wetlands

Wetlands receive carbon as organic matter (OM), which is partially taken up by consumers but sooner or much later inevitable mineralized by microorganisms to CH_4 or CO_2.The delay depends on the cycling in microbial loops, being it the adsorption to minerals or the export to other ecosystems. The interrelations between the individual processes are manifold (Fig. 1). In simple words, carbon storage occurs if the input is higher than OM decomposition and carbon export.

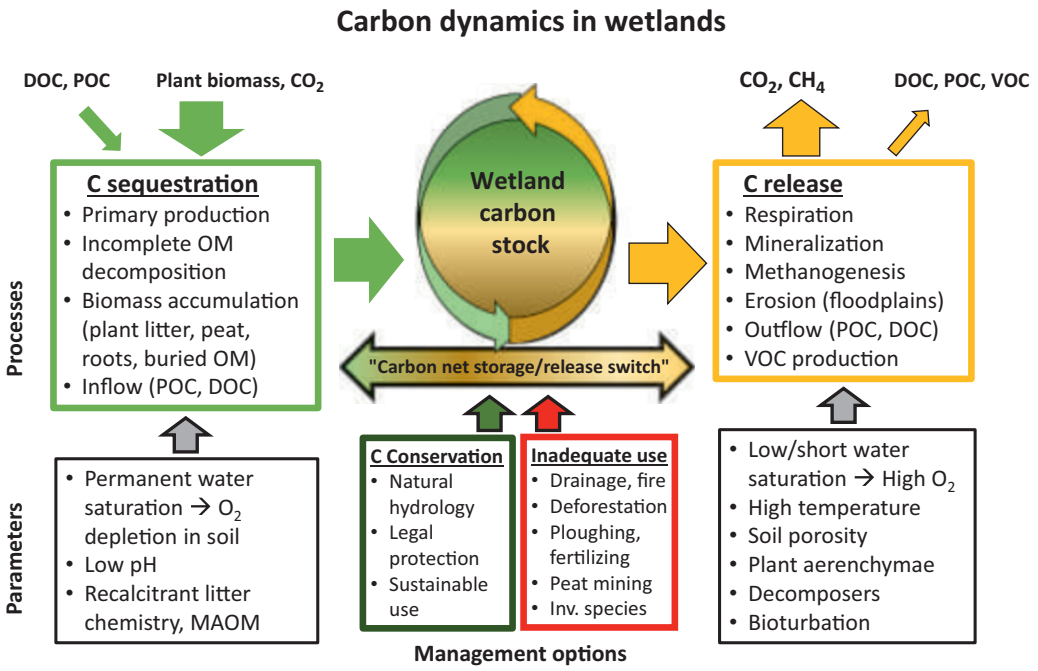

Fig. 1 Processes, parameters, and management options that favor carbon sequestration (left) or carbon release (right) in wetlands. See Glossary for abbreviations.

Microbial respiratory processes and coverage with stagnant water or water-logged soils result in anoxia, which, along with leachates from the OM (e.g., phenolic substances or organic acids), slow down decomposition processes. Favorable conditions for decomposition and mineralization such as high temperatures and oxygen concentrations transform organic matter into gasses (mostly CO_2 and CH_4) released to the atmosphere. Transport processes are generally mediated by water flow and sediment dynamics. Solid particles and dissolved forms of OM can be removed, carried and deposited along with sediments during flood events, and gas release triggered by hydrostatic pressure differences (e.g., during receding floods). However, OM can also be physically fixed by chemical processes such as the calcite precipitation in karstic springs (on mosses) or in lakes (on planktonic algae or macrophytes), or by clay particles and pedogenic metals (see below).

To measure the patterns and processes of wetland carbon budgets several methods exist. Sample collection depends on the physical state of the samples. Gaseous forms become collected with sampling chambers tightly exposed over the wetland surface, dissolved forms can be stored in water bottles, and solid samples are directly cut from the vegetation or retrieved from soils using specific soil corers. For the sampling of liquid sludge, corers that can be locked are used. The main problems consist (a) in adequate sample treatment (e.g., to avoid mineralization processes during sample storage) and (b) in setting up sampling strategies that correspond to the most important turnover processes. Along aquatic-terrestrial gradients, these often occur in spatially and temporally discontinuous patterns referred to as biogeochemical and biotic hot spots and hot moments (McClain et al., 2003; Wantzen and Junk, 2006). Carbon analysis is generally based on the attenuation of infrared light; for solid samples, total carbon analyzers exist, while gaseous samples (e.g., methane) are analyzed gaschromatographically by flame ionization detection (e.g., Mitsch et al. (2013)). For a review on methods, see, i.e., Villa and Bernal (2018).

A simple carbon budget can be established if stocks, net input and output fluxes are known or estimable. Mechanistic modeling based on the quantification of individual processes and their interactions can help to predict changes in fluxes and stocks due to changing environmental conditions, such as climate change.

Biomass contribution to wetlands

Organic biomass generally results from autotrophic CO_2 fixation by plants or microbes. Plants or animals supply soils with OM either directly belowground via roots (litter, or rhizodeposition) or indirectly from above by litter fall, death, or excretion. In most cases, plants growing directly in the wetland (algae, mosses, macrophytes, trees) deliver the bulk of the biomass, the *autochthonous* OM. In stream and river floodplains (and partially in lakes), carbon fixation processes may have occurred in neighboring terrestrial ecosystems (e.g., forests) all over the catchment. These OM types, i.e., litter fall of leaves, twigs, fruits etc. can be imported as *allochthonous* OM by wind and water (Wantzen et al., 2008c). Liquid contribution (leachates, dissolved OM) may be inconspicuous in mass but trigger important microbial consortia influencing the carbon stocks. Moreover, soil carbon that has been accumulated in earlier periods in the catchment (e.g., during interglacial warm phases in temperate zones) may become eroded and transported

downstream and accumulate in riparian wetlands. The analysis of tracers using chemical methods (lignin compounds, stable isotope analysis) or microscopy (phytoliths, pollen, fibers) may help to identify the origin of the organic matter in different layers of a sediment core and inform about land use changes (Behling and Hooghiemstra, 2000; Denham et al., 2003). Carbon sequestration is generally estimated by soil dating methods such as with cesium and lead (^{137}Cs and ^{210}Pb) isotopes (Mitsch and Mander, 2018).

Primary production depends on light, temperature, water, and nutrient conditions, as well as plant growth type. Due to permanent waterlogging and nutrient availability, some wetlands with grass-like vegetation are among the most productive ecosystems worldwide, e.g., Amazonian floodplain meadows (dry biomass up to 576 kg m^{-2} in communities of the perennial species *Paspalum fasciculatum*, Junk and Piedade (1993)), and lacustrine *Papyrus* swamps have a net primary production (NPP) of dry biomass of 2.51–3.09 kg m^{-2} year^{-1} (Saunders et al., 2014). Woody plants may contribute various types of OM, from nutrient-rich fruits to roots with high lignin content that may take decades to decompose. In Amazonia, their living belowground biomass (roots) varies from 7.5–40 ton ha^{-1} in whitewater floodplain and an aboveground coarse woody biomass (AGWB) of 15–307 ton ha^{-1} in whitewater and 68–324 ton ha^{-1} in blackwater floodplains (Schöngart et al., 2010). In a boreal forest (Bonanza Creek near Fairbanks Alaska, covered with *Populus* and *Alnus* bestanden, Gower et al. (2001) report AGWB of 4.8 g ton ha^{-1} (see both papers for further data). Care should be taken when comparing data between sites, due to natural variations within the studied areas, and to the different methods applied (e.g., exact below-ground biomass measurements require that trees become uprooted and weighed). Studies often consider either living biomass and net primary production or soil organic matter, but rarely both.

In peat bogs, wetness coupled to anoxia, nutrient poor water supply originating from rainfall and acidic soil may lead to very low GPP rates of ca. 0.8 kg m^{-2} year^{-1} (Drollinger et al., 2019). Bacteria may produce large organic mats when groundwater seeps to the surface. With the exception of termites and ants, animals contribute little to the direct biomass budget (e.g., carcasses of fish dying in drying wetlands, earth worms being killed during flooding, shells of invasive *Dreissena* mussels e.g., in the Great Lakes), but due to their migratory behavior, they may transport large amounts of nutrients against landscape gradients within short time (e.g., salmon run, migratory birds and their feces, mass emergence of insects). The foodwebs based on these migrations and the resulting allochthonous nutrient inputs may foster primary production in wetlands (Hocking and Reimchen, 2009). Moreover, the movements of animals in sediments (bioturbation), ranging from small midge larvae to large, digging crocodiles (Schmitz et al., 2014; Bezerra et al., 2020) strongly influence oxygen concentrations. The nutrient contribution to wetlands by the water inflow varies strongly between different origins of the water, e.g., rain water and deep groundwater (generally low), river water (medium to high), surface runoff and surface-near groundwater (high nutrient contents). Hence, the three-dimensional, annual and multi-annual flow conditions should be considered when assessing organic matter budgets (Junk and Wantzen, 2004; Wantzen et al., 2005; Keizer et al., 2014).

Organic matter processing

The proportion of the primary production that finally builds up the huge carbon stocks of wetland soils depends on biomass processing (Wantzen et al., 2008b; Baerlocher et al., 2020). The living plant biomass is partly consumed by animals entering the decomposer foodweb as feces but plant litter is the bulk contribution. Fungi and bacteria colonize live plant parts and activate as soon as antimicrobial defense mechanisms of the plants weaken. When plant litter falls from emerging plants into the water, a continuum of terrestrial to aquatic, microbial consortia becomes active. Under acidic conditions, this attack is predominantly carried out by fungi as bacteria require a higher pH to thrive (Rousk et al., 2010). The microbial biomass makes OM more attractive for decomposing invertebrates. These so-called shredders break up the structure into smaller pieces, allowing further microbial decomposers to act more efficiently. In riparian zones, where wet-and-dry conditions alternate, both, aquatic and terrestrial species can consume the plant parts, and the resulting plant detritus can be moved between both zones, resulting in faster decomposition (Wantzen et al., 2008b). Once the organic matter is exposed to anoxia, decomposition is slowed or stopped.

Organic matter persistence: Chemical quality vs. lack of access

Different plant parts become mineralized at different velocities due to their chemical quality. Environmental conditions like temperature and nutrient availability influence the processing dynamics. Plant secondary compounds, especially phenolics, and fibers (lignin and celluloses) in leaves and wood, but also silicates in grasses may additionally slow down both, the microbial and invertebrate decomposition processes, whereas energy-rich compounds, such as sugars and proteins, accelerate decomposition. Some plant associations have developed specific capacities to modify the soil/water phase to slow down decomposition, e.g., trees of Asian peat swamp forests (Lim et al., 2009) or many herbs in mires (Fukao et al., 2019) (see below). Analyzing the chemical compounds of OM helps to understand if plant parts are recalcitrant, or quickly decomposable (Baerlocher et al., 2020). The presence of microbial biomass may favor decomposition of OM ("conditioning") by shredders (Wallace and Webster, 1996), and the coverage by algae can directly or indirectly favor decomposition (Rier et al., 2014). The priming effect, i.e., the increase in soil organic matter (SOM) decomposition rate after fresh organic matter input to soil is supposed to result from the competition for energy and nutrient acquisition between the microorganisms specialized in the decomposition of fresh organic matter and those feeding on polymerized soil organic matter(SOM) (Fontaine et al., 2003).

Moreover, if decomposers lack access to OM, its decomposition can be hampered or even stopped. This can happen when mineral-associated OM (MAOM) is formed, for example, by complexes with clay minerals or surface bindings to pedogenic iron or aluminum oxide surfaces (Córdova et al., 2018). Thus, the lack of access for decomposing microbes may interfere with the positive or negative effects of plant chemical compounds on OM processing. These processes and their interferences need to be better understood for wetlands in order to improve wetland biogeochemical modeling.

Microbial processes: Carbon release to the atmosphere

Microbes mineralize OM to greenhouse gasses (GHG) like carbon dioxide (CO_2) and methane (CH_4). Natural wetlands are natural sources of GHG (Dušek et al., 2020), however the release rate is strongly influenced by human activities. Methanogenesis is a strictly anoxic process that may follow the previous release of CO_2 from decomposing OM (Conrad et al., 2010). As long as surface water and sediment layers of wetlands are well oxidized, bacteria transform most of the CH_4 back to CO_2, and their biomass can represent an important food source to the ecosystem (Jones and Grey, 2011). Therefore, CH_4 becomes released to the atmosphere only under specific circumstances (Saarnio et al., 2009). These include ebullition (release of large bubbles, e.g., when depressurizing a dam lake during drawdown), synchronous release of large amounts of methane (e.g., during drainage of mires and peat swamp forests, thawing of permafrost soils Schuur et al., 2015), or bypassing through aerenchyma (e.g., in rice paddies and locations of other plants having aerenchyma, Aulakh et al., 2000; Dušek et al., 2020). Stable isotope analysis and experiments with substances inhibiting methanogenesis can be used to reveal the balances between CH_4 vs. CO_2 pathways (Conrad et al., 2010). The release of greenhouse gasses from wetlands to the atmosphere can be assessed using gas chambers with a defined surface, or by eddy covariance. Long-term annual budgets have evidenced that inland wetlands can be significant sources of CH_4 and hydroperiods are the major determinants of the emission rates (Mitsch and Mander, 2018). Volatile organic compounds (VOCs, Keefe et al. (2004)) are rarely studied in wetlands. These short-chained C_2-C_{10} hydrocarbons (VOCs) and halogenated hydrocarbons (VHOCs) are released in small amounts compared to the gasses mentioned above (Hellén et al., 2006), but they are relevant as GHG.

The influence of wetting and drying of wetland soils

As anoxic conditions slow down the mineralization process, the highest carbon storage can be expected in soils of permanently anoxic systems (peatlands). On the other hand, drying up inverts the situation, as oxygen can penetrate deeply into the soils and sediments (Paranaíba et al., 2020). This process already begins when the water level approaches the sediment surface, due to increased surface temperatures (due to lacking transpiration cooling and heat absorbance by the water), increased evapotranspiration by plants, bioturbation due to smaller (invertebrates) and larger animals (e.g., wild boars searching for food). Especially in clayey soils, shrinking and cracking results in deep penetration of oxygen into the ground, resulting in fast OM decomposition but also in release of carbon dioxide.

Alternating wet and dry wetlands, e.g., river floodplains or savanna wetlands, undergo cyclic phases of OM accumulation and carbon release, whereby the duration of the inundation phase acts as a switch between sink and source function of the wetland (Vega et al., 2014). Climatic variations may cause multi-year periods of wetter and drier years with substantial effects on the carbon stored from macrophyte production (Wantzen et al., 2005). High release of GHG occurs during changes, i.e., either if wetlands that have been waterlogged for long periods become dried up for the first time, as it happens when peatlands are drained for land use purposes (see below), or when drained or dry-fallen wetlands are re-wetted (Hiraishi et al., 2014; Krüger et al., 2014). Rewetting of peatlands after drainage is an long-term strategy for environmental restoration and an important tool for carbon sequestration (see below), even if short-termed GHG release may occur just (Günther et al., 2020).

Major group types of wetlands according to their carbon dynamics

There is large variety of wetland types and typologies (Finlayson, 2003; Keddy, 2010; Junk et al., 2014; Mitsch and Gosselink, 2015). Here we use a strongly simplified typology explaining the major phenomena in their carbon dynamics, which is mostly based on the directions of carbon fluxes.

Permanently wetted wetlands with low vegetation cover: Bogs, fens and mires

In some wetland systems, persistent water saturation up to the topsoil and resulting anoxia slow down OM processing so that partially decomposed plant biomass becomes a major component of the soil. The resulting material (with $\geq$15% C content) is called *peat*, landscapes made up by a superficial peat layer of at least 30 cm thickness are called *peatlands* in soil science terminology, and under peat forming conditions, they are called *mires*, even if the superficial peat cover is <30 cm. *Bogs* are rain-fed (ombrotrophic) and *fens* groundwater-fed (minerotrophic); *transitional mires* represent a mixture of both types. Different plant structures may form peat, including fine roots (radicels), larger roots, rhizomes, leaves of herbs, and woody tissue. Macroscopic determination of formerly peat forming vegetation is often possible even after millennia of its formation, provided that pH and nutrient concentrations are low. In the case of bogs and some fens, a very low pH of 3–4 may occur if the ground- and/or rainwater is nutrient- and cation-poor. *Sphagnum* mosses are the most prominent ecosystem engineers in peatlands (except in tropical lowland regions); they actively acidify their habitat by ion exchange, release of organic acids, and maintain humidity so that bacterial activity

becomes suppressed and peat accumulated (van Breemen, 1995; Harpenslager et al., 2015). *Sphagnum* species occur mainly in the Northern Hemisphere in peat bogs, conifer forests, and moist tundra areas, but also in Chile, Argentina, New Zealand and Tasmania, and in sub-alpine zones of the tropics and sub-tropics.

In all mires, anoxia promotes carbon degradation processes to require alternative electron acceptors as nitrate, iron or sulfate, and at final stages acetate and recalcitrant peat itself. At these final stages, carbon dioxide as well as methane are resulting end products. These processes make mires CO_2 sinks, but also sources of CH_4 (Nilsson and Öquist, 2009). Moreover, the acidification may release CO_2 from carboniferous bedrock (Harpenslager et al., 2015). When drained, peat becomes aerated and the resulting aerobic microbial pathways make such sites CO_2 sources of global significance, contributing at least 5% to the annual anthropogenic CO_2 emission, despite covering only about 0.45% of the global land surface (Leifeld and Menichetti, 2018). It is therefore imperative to keep peatlands wet and to rewet drained peatlands in order to preserve their important carbon storage.

Peat swamp forests

Tree species that survive in permanently water logged soils have developed adaptive traits such as lenticels and pressurized aeration of their root systems (Graffmann et al., 2008) allowing them to survive soil anoxia and permanent attack by microbes. Peat swamp forests are highly diverse, especially in SE Asia (Posa et al., 2011). Antimicrobial substances in fallen tree leaves (Jackson et al., 2009; Lim et al., 2014) may have an additional effect to the above-mentioned parameters that slow down decomposition, resulting in extremely slow decomposition rates in spite of high concentrations of dissolved oxygen in the water covering the organic layers. From small tropical stream valleys (Wantzen et al., 2012), to huge forests of Amazonia (150,000 km^2) and Indonesia (200,728 km^2) (Lähteenoja et al., 2009), or in the Congo basin (145,500 km^2) (Dargie et al., 2017), peat swamp forests may accumulate enormous carbon stocks in peat layers reaching depths of 18 m (in Amazonia: 5.9 m, Lähteenoja et al. (2009), 12 m, Householder et al., 2012).

Like in all wetlands, hydrology is key for the maintenance of the carbon storage, and the increasing drainage for encroachment for land use like ranching, farming or oil palm and *Acacia* plantations (Charters et al., 2019) has detrimental effects for the atmospheric carbon (CH_4, CO_2) budgets. In SE Asia, only 36% of the historical peat swamp forest area remains, with only 9% currently in designated protected areas (Posa et al., 2011).

Alluvial floodplain wetlands

Alluvial wetlands are the floodplain zones accompanying the depositional zones of rivers. They can occur along the entire river continuum like "beads on a string," but they generally become more contiguous, wider, and longer and more predictably flooded in the lower sections of the rivers (Tockner and Stanford, 2002; Junk and Wantzen, 2004). The landscape gradient and hydromorphological dynamics play a crucial role for determining the duration of the inundation and organic matter accumulation. Especially in stream wetlands, there may be a large heterogeneity on small scales (Wantzen et al., 2008c). Flooding often acts as a fertilizing event, as nutrients become imported from the catchment during floods. Consumers of living and dead organic matter profit by the phase change, e.g., fish consume fruit falling from trees during high water, and scavengers consume stranded fish during the low water phase in reciprocal subsidies (Wantzen et al., 2002; see Fig. 2). Thus, wet-and-dry cycles mobilize nutrients, which often

Fig. 2 Wet and dry cycle in seasonal wetlands, (A) flood phase, (B) low water phases. Graph modified after Wantzen KM, Machado FD, Voss M, Boriss H, and Junk WJ (2002) Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. *Aquatic Sciences* 64: 239–251.

results in luxurious growth of vegetation (Junk and Piedade, 1993) and secondary production (Bayley, 1991). Floods (understood as overbank flow) transport sediments into the floodplain, which may cover organic layers, resulting in carbon "burial" (D'Elia et al., 2017). Alluvial wetlands may or may not develop peat soils, depending on the interplay between aerobic and anoxic conditions described above. Mineral alluvial soils (fluvisols according to FAO's World Reference Base, WRB) become logged by variable proportions of groundwater or overbank flow, resulting in different chemical settings and carbon transport pathways. The OM compounds in the soils derive from many autochthonous and allochthonous sources, yet most carbon is accumulated by litter accumulation and rhizodeposition. Especially during floods, alluvial minerals (clay) may become deposited in close contact with organic particles, so that they form MAOM associations that restrict microbial accessibility to carbon resources. Mechanisms that mobilize carbon from floodplains are transport by water (drifting of organic particles, including entire plant associations such as large macrophyte mats Wantzen et al., 2005 or tree logs, or washout of dissolved organic matter), and the above-mentioned decomposition pathways, which can be accelerated by wet-and-dry cycles (Wantzen et al., 2008c). Releases of gaseous carbon forms can be accelerated by plant structures such as aerenchyma and lenticels (lens-shaped openings on stems for the aeration of the rhizosphere Pangala et al., 2017).

Lake littoral wetlands

In a lake (lentic) setting, wetlands are usually riparian zones where macrophytes (as reed or cattail) rooted in the soil emerge through the water column. Like lotic wetland settings, lakeshore wetlands may experience water level fluctuations, sedimentation or resuspension of suspended solids and an import of export of matter (as carbon) by moving water or organisms (Wantzen et al., 2008a). Lake morphology is crucial for the determination of the relationship between littoral wetlands to permanently flooded, limnetic lake areas. In shallow lakes, macrophyte growth and increased organic matter storage can occur on the entire surface, revealing similar carbon uptake and release features as those described for river floodplains. Lakes, especially their deltas (Scott and Wohl, 2017), act as important sinks for carbon originating from their terrestrial catchment (Cole et al., 2007). The amount of carbon and nutrient stripping in lake littorals from terrestrial sources via aerial pathways (pollen deposition, wind-blown leaf litter) or of algal biomass from the limnetic zone depends very much on the wind exposure and the surrounding vegetation. Reeds can skim out floating organic particles and produce large amounts of biomass themselves that contribute to the carbon budget (Brix et al., 2001; Li et al., 2009). Sediments of the profundal zones accumulate carbon deriving from the phytoplankton-based food chain. Consumption by zooplankton and fish, and selective uptake of compounds by bacteria (lake snow, Grossart and Simon, 1998) result in a continuous degradation of the organic particles on their way to the (mostly anoxic) lake sediments. High temperatures in shallow lakes may produce optimum conditions for methanogenesis. Bioturbation, e.g., by tubificid worms, chironomids, or *Chaoborus* larvae may oxygenate the sediment surface (resulting in an improved oxidation of methane), but also help to "pump" methane bubbles into the water column (Bezerra et al., 2020). Degassing of sediments also occurs spontaneously (Langenegger et al., 2019).

In arid zones, lakes may become saline when evapotranspiration exceeds lake water recharge, resulting in an accumulation of salts in the sediments. In such a setting, production and decomposition of carbon may be controlled by salinity, as increased salinity decreases both processes. Although some salt-affected sediments have a high OM content, studies in freshwater ecosystems affected by marine intrusion have shown that increased salinity will promote carbon decomposition by a shift to sulfate reducing conditions and increased mineralization of organic matter (Weston et al., 2011).

Seasonal wetlands

In seasonal wetlands, poorly drained plains situated become alternatingly wet and dry due seasonal water availability, e.g., due to monsoon rainfall or snowmelt. They may connect to lakes or river floodplains, or are interspersed with more or less permanently wetted mires (for example, North American prairie wetlands and potholes Euliss et al., 2006). Their vegetation includes woody and herbaceous growth forms. The turnover of the biologically fixed carbon between the dry and wet seasons is even more expressed than in river floodplains. Especially the non-woody plant cover becomes largely decomposed or consumed when the phases change between wet and dry. Aquatic macrophytes decay quickly even before they become stranded (Fellerhoff et al., 2003). The lowermost areas concentrate the remaining water-bound nutrients and biomass during the falling waters. Before the soils fall completely dry, there is a vivid growth of annual plants in the first weeks, followed by a kind of "mummification" (conservation by drought) of the biomass during the peak of the dry season. Intensive solar radiation and high soil surface temperatures during drought also result in mineralization of the soil organic matter in the topsoil. Terrestrial grasses may remain longer, and continuous years of shallow or absent flooding may result in accumulation of biomass and increased fire risk. Fires may occur naturally and mineralize a large part of the above-ground biomass. The first rainfalls may then "strip out" the dissolved carbon of the terrestrial plant biomass, even before the water levels rise (Hamilton et al., 1995; Hamilton et al., 1997). With increasing water levels, a luxurious growth of algae and macrophytes sets in, as long as the nutrients from the mineralized terrestrial biomass are available (Loverde-Oliveira et al., 2011).

The carbon that escapes from this annual cycling is either stored in woody biomass (living or dead trees and their roots), or in the wetter layers or areas of the wetland. Studies in Neotropical seasonal wetlands have revealed a critical wetting time of about 250 days per year as a threshold between carbon storage or carbon depletion of the topmost 20 cm of soils (representing a "carbon switch," Vega et al., 2014). This sensitive balance makes seasonal wetlands specifically vulnerable to climate change and land use change. On the other hand, wise wetland management is an important tool for the mitigation of climate change effects, as most of the carbon retention by wetlands occurs in tropical/subtropical zones (Mitsch et al., 2013).

Global review on carbon storage in wetlands

Most carbon in wetlands is stored in the soils. Soil carbon stocks may exceed the amount of carbon that is sequestered in above-ground biomass by the factors 10–18.5 (Jaenicke et al., 2008; Silva et al., 2013). Soil carbon concentrations and stocks differ strongly between the different wetland types and climatic regions (Table 1). Long-term carbon sequestration is highest in permanent wet peatlands due to permanent anoxic soil conditions (Page et al., 2004; Cole et al., 2007; Leifeld and Menichetti, 2018). Thus, they play a key role (Lorenz and Lal, 2018) by storing 600–644 Gt soil organic carbon globally (Lorenz and Lal, 2018), representing the major soil carbon stock of wetlands and more than one quarter of the global soil carbon stocks on only 3% of the land surface (Yu et al., 2010; Page et al., 2011; Leifeld and Menichetti, 2018). Tropical Peat Swamp Forests alone may store more than 100 Gt carbon with highest carbon densities of all ecosystems of 1280–3500 t C ha^{-1} (Filoso and Palmer, 2011; Dargie et al., 2017) (see Table 1). Northern peatland average carbon stocks range between approx. 1100 and 1470 t C ha^{-1} (Gorham, 1991; Immirzi et al., 1992). The second largest long-term carbon stock, although often not included in global carbon balances, are terrestrial lake sediments with estimates between 400 and 800 Gt carbon accumulated during the Holocene (Cole et al., 2007). Mineral wetland soils are reported to store between 50 and 230 t C ha^{-1} (Mazurczyk and Brooks, 2018). Among those, seasonal pothole wetlands in the US may accumulate 44–66 t C ha^{-1} (Tangen and Bansal, 2020). Despite these numbers it is clear that the role of freshwater wetlands in the global carbon cycle is still not sufficiently understood on the global and regional scale. The knowledge base on C stock and C sequestration rates in wetlands remains small given the diversity of wetland types world-wide, and the diverging methods and reference units (especially soil depth). All presented numbers can only be approximate, and especially for the Tropics there are many uncertainties (Sjogersten et al., 2014).

Even though most of the carbon that enters wetlands is lost either through decomposition or aquatic export (Bade et al., 2007; Nahlik and Fennessy, 2016), up to 0.83 Gt C per year net may be sequestered by wetlands globally. This represents approximately 12% of the carbon annually released from fossil fuel combustion. Annual net C sequestration rates (the positive total C balance) in peatlands remain comparably low showing higher rates in tropical Peat Swamp Forests (0.46–0.88 t C ha^{-1} $year^{-1}$, (Page et al., 2010)) due to higher net productivity than in northern herbaceous peatlands (0.1–0.4 t C ha^{-1} $year^{-1}$ Frolking et al., 2011). The weighted average sequestration rate for wetlands is 1.18 t C ha^{-1} $year^{-1}$ (Mitsch et al., 2013). Variations range from 0.02 to greater than 6 t C ha^{-1} $year^{-1}$ depending on wetland type, location, and primary C source (see Tangen and Bansal, 2020 for a detailed review).

Wetlands are net C and radiative sinks despite being natural sources of CH_4 emissions of 0.45 Gt per year (see Table 1 for different wetland types). Radiative forcing of CH_4 is lower than CO_2 over time horizons of hundred and more years, reducing the negative effect of CH_4 emissions on global warming compared to the amount of CO_2 sequestered by wetlands (Mitsch et al., 2013; Günther et al., 2020).

Human impacts on carbon stocks and carbon dynamics of wetlands

Human activities interfere with all processes of carbon dynamics occurring in wetlands (Mitsch and Gosselink, 2015). The most critical ones concern the acceleration of carbon release (mostly by drainage and conversion towards cropping or blocking of freshwater access), the reduction of carbon inputs (e.g., due to deforestation or man-made fires) and the complete removal or transformation of wetlands, turning them from net sinks into net sources of carbon. The direct use of carbon stored in peatlands as

Table 1 Selection of carbon dynamics in wetlands worldwide.

Wetland type (name, country)	*Carbon storage (t C ha^{-1})*	*Net carbon sequestration (t C ha^{-1} $year^{-1}$)*	*CH_4 emissions (t C ha^{-1} $year^{-1}$)*	*Citations*
Tropical/subtropical wetlands		1.94	1.19	Mitsch et al. (2013)
Tropical Peat Swamp forest, Indonesia	Up to 3160	0.56	0.09–10.8	Parish et al. (2008), Lähteenoja et al. (2009), Page et al. (2010), Sakabe et al. (2018), and Wong et al. (2018)
Rio Negro floodplain, Brazil			0.098–0.394	Belger et al. (2011)
Riparian Forest and Vereda wetland, Cerrado, Brazil	206 (max 360) 142 (max. 202)	1.1		Wantzen et al. (2012)
Alluvial floodplain wetlands, Central Brazil	150–1500	1.2		Silva et al. (2013)
Papyrus wetland, Africa	728	0.48	0.30	Saunders et al. (2014)
Temperate wetlands		2.78	0.58	Mitsch et al. (2013)
Peatland, northern	1100–1470	0.34	0.12–0.29	Mitsch et al. (2013), Abdalla et al. (2016), and Hugelius et al. (2020)
Phragmites swamp, Denmark		0.55	0.48	Brix et al. (2001)
Seasonal wetland potholes, United States	44–66 (upper 120 cm)	3	0.24–1.07	Euliss et al. (2006), Bansal et al. (2016), and Tangen and Bansal (2020)

fuel has a long history in the northern temperate and boreal zones (Holmgren et al., 2008), while the degradation of peat swamp forest and other wetlands, e.g., in Asia is relatively recent (Nguyen et al., 2016; Page and Baird, 2016; Dohong et al., 2017; Hu et al., 2017; Meng et al., 2017).

As the ecosystem services of wetlands have been underestimated or even neglected too long time, their transformation into land use by humans has progressed without hesitation, e.g., agricultural use or just as dumping sites. Up to 89% of the SOC in a wetland can be lost by conversion to cropland (see Xu et al., 2019 and citations therein). Resulting changes in soil texture and related reduced water retention capacity, reduced plant organic matter inputs, increased erosion and higher temperatures determine higher SOC decomposition (Knops and Tilman, 2000). Case studies have indicated average losses of SOC of 10.1 t ha^{-1} on over 16 million ha of wetlands in North America (Euliss et al., 2006), and of 0.24 Gt carbon in north-eastern China (Xu et al., 2019). Degrading peatlands emit 1.3 Gt CO_2 $year^{-1}$, equivalent to 5% of the anthropogenic annual GHG emissions, from only 0.45% of the global land surface (Hiraishi et al., 2014).

Most urban wetlands have vanished in the Global North during the Industrial Age, whereas fast urban development in the Global South eliminates them very recently (Wantzen et al., 2019). All megacities are endorheic zones, i.e., they absorb much more water than the area they cover receives from precipitation, therefore the falling groundwater levels in the vicinity of cities cause dry falling of wetlands. Similarly, agriculture is increasingly tapping water from nearby wetlands, e.g., the illegal oblique water mining in the surroundings of the world-famous Spanish Cota Donana wetland (Zorrilla-Miras et al., 2014). Drainage or erosion by agriculture can quickly deteriorate wetland ecosystems that have stored carbon for millennia (Wantzen et al., 2012). Another impact on the carbon storage in this context is the spread of (native, and non-native) invasive plants that may result in a transformation of peat into mineral soils (Gogo et al., 2011).

All these trends are aggravated by current Climate Change, which often results in less predictable, shorter rainfall periods and more pronounced, hot droughts. Increasing temperatures and reduced water availability increase the decomposition of organic matter in wetlands leading to increasing C losses from wetlands as GHG emissions. The thawing of the permafrost of the sub-arctic wetlands for example is considered one of the tipping points of global warming leading to potentially very high SOC losses to the atmosphere as methane (Hugelius et al., 2020). Temperature is generally a critical parameter in land (and wetland) degradation and SOC losses (Joosten, 2014).

Conservation of wetlands and their ecosystem services concerning the carbon cycle

Conservation of wetlands and their many Ecosystem Services becomes more and more important, given the fact that more than one third is lost mainly due to human impacts (Hu et al., 2017). Important wetland ecosystem services are the shelter of biodiversity, their carbon storage, the provision of clean water, food and fodder and even cooling of the local climate (Mitsch et al., 2015). Moreover, wetlands fulfill many social and cultural ecosystem services (McInnes et al., 2017). International frameworks such as the Ramsar Convention, the SDGs, the UNFCCC and others explicitly or implicitly address wetland conservation. The latter implies countries to assess and report on the impact of human activities on wetland carbon budgets (Hiraishi et al., 2014), which since the Paris Climate Agreement implies a complete stop of wetland conversion until 2050.

Besides the conservation of wetlands, the increasing importance of their restoration is acknowledged by the UN Decade of Ecosystem Restoration (UN, 2019) and the EU sustainability objectives (Tanneberger et al., 2021). This is underlined by a recent modeling study which predicts that the land system would turn into a global net carbon sink by 2100, as projected by current mitigation pathways, if about 60% of present-day degraded peatlands were rewetted in the coming decades, next to the protection of intact peatlands (Humpenöder et al., 2020).

The re-establishment of natural hydrology and revegetation (active or passive) are key elements of wetland restoration (Keddy and Fraser, 2000; Keddy, 2010; Mitsch and Gosselink, 2015). Removal of dams that are retaining flood water and sediments worldwide (Grill et al., 2019) and thereby drain or disconnect floodplain wetlands is an important step especially considering that in Europe alone 10% of the 1.2 million barriers are obsolete (Belletti et al., 2020). Since wetland hydrology is closely linked to the whole catchment, effective conservation should address issues on a catchment scale. Wetland restoration has two implications for their carbon budget: (1) carbon losses due to degradation are reduced or stopped. Rewetting peatlands for example would avoid emissions between 25 and 60 tons $CO_{2\text{-eq}}$ ha^{-1} $year^{-1}$ in Central Europe (Couwenberg et al., 2011) and between 70 and 117 tons $CO_{2\text{-eq}}$ ha^{-1} $year^{-1}$ in Southeast Asia (Cooper et al., 2020). (2) Wetland restoration has the potential to re-stimulate C sequestration, with potentially 0.38 Gt of organic carbon that could be stored over a 10-year period (Euliss et al., 2006). Additionally, constructed wetlands are estimated to provide high C sequestration rates (Lal et al., 2018). To make use of wetlands as carbon sinks with efficient climate mitigation potential they need to be restored and maintained for long time periods (Günther et al., 2020).

Concepts of sustainable use of wetlands can be a way of preserving or restoring important wetland ecosystem service and simultaneously allowing production, as for example, paludiculture for peatlands (Biancalani and Avagyan, 2014; Wichtmann et al., 2016). Rural participatory appraisal of wetland ecosystem services (Ricaurte et al., 2014) can help to identify the cultural relationships to the nature of wetland and deliver both motivation and traditional ecological knowledge about sustainable use of wetlands (Wantzen et al., 2016).

Conclusion/Synthesis

Size does not matter to address relevancy adequately. Wetlands are prominent examples, as they cover only a small proportion of the Earth's terrestrial surface but perform outstanding functions in the water and carbon dynamics. They offer a wide range of ecosystem services, due to their simple function to collect water, organic material and mineral sediments. This holds true despite the great variety (diversity) of freshwater wetlands. Great storage is the result of higher input than output fluxes. Even if a dynamic equilibrium is reached (usually inputs to wetlands are higher than outputs) are these continuous biotic, physical and chemical processes determined by climate, topography, soil and time. External stress can easily tip this dynamic state from atmospheric carbon sinks towards sources of greenhouse gasses to the atmosphere. In the Anthropocene we are living in, the external stress is usually caused by humans. Indirect stress would be climate change that could increase feedback processes by increased temperatures and declining precipitation and additionally threaten wetlands. Draining wetlands for agriculture etc. (see Fig. 1) would be a direct impact leading to the loss of their carbon sink function. Their outstanding role for climate protection has been widely accepted, but clear actions to protect or even restore wetlands are still scarce. Effective wetland protection and restoration need to be further integrated in political frameworks on all levels and implemented in land use planning and management. Those need scientific guidance and despite the great knowledge already gained, more is needed to properly manage these fragile ecosystems. It will help to develop alternative uses of wetlands that allow or favor natural wetland processes after restoration of degraded wetlands.

Knowledge gaps

In spite of an increasing scientific interest in wetland ecology in the past decades, many important lacunae persist, i.e.,:

- Identify the carbon storage/release switches in different types of wetlands.
- Compensatory effects of decomposition-favoring (priming by labile, energy-rich, or stochiometrically rare substances) vs. decomposition-hindering processes ("recalcitrance" caused by plant secondary compounds, or "capping" of OM by MAOM, mineral associate organic matter).
- Effects of global warming on microbial soil organic matter decomposition and oxidation—temperature sensitivity of SOM decomposition.
- Sustainable Land use practices, that allow economic use of restored wetlands while maintaining ecological functions and biodiversity (e.g., Paludiculture on peatlands).
- Improve social awareness and valuing of wetlands and their ecosystem services (including cultural values) to achieve better political support for restoration and conservation measures.

Further reading

All citation details are found in the bibliography below.

Text books: (Keddy, 2010; Mitsch and Gosselink, 2015).
Reports: (Parish et al., 2008; Hiraishi et al., 2014; Pachauri et al., 2014; Shukla et al., 2019).
Reviews on carbon storage in wetlands: (Kayranli et al., 2010; Tangen and Bansal, 2020).
Soil organic carbon storage and potential: (Gaiser and Stahr, 2013; Lal et al., 2018; Lorenz and Lal, 2018).
Review on sequestration and methods (Villa and Bernal, 2018).
Impact analysis: Peatlands (Crump, 2017), SE Asian peat swamp forests (Page and Baird, 2016).
Peatland Restoration and Ecosystem Services: (Bonn et al., 2016).

See Also: **Fundamental concepts and theories**: Chemosynthesis; **Human pressures and management of Inland Waters**: Effects of Hydrocarbon Extraction on Freshwaters; Effects of Mining on Surface Water; **Social/societal values of Inland waters**: Societal Implications of Kenya's Inland and Marine Waters; **Structures and functions of Inland Waters - Groundwater**: Biogeochemical Cycling of Carbon and Nitrogen in Groundwater—Key Processes and Microbial Drivers; **Structures and functions of Inland Waters - Lakes**: The Carbon Cycle in Lakes: A Biogeochemical Perspective; **Structures and functions of Inland Waters - Rivers**: Ecological stoichiometry in streams; **Structures and functions of Inland Waters - Wetlands**: Restoring Riparian Peatlands for Inland Waters: A European Perspective; Tropical Large River Wetlands; Tropical Peat Swamp Forests; Wetland Soils: Physical and Chemical Properties and Biogeochemical Processes; Wetlands Under Global Change; Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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Relevant websites

https://www.iucn-uk-peatlandprogramme.org/—IUCN UK Peatland Programme.
https://www.wetlands.org/—Wetlands International.
https://www.ipcc.ch/—The Intergovernmental Panel on Climate Change.

Riparian Vegetation of Gravel-bed Rivers—A Global Review

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Alluvial river Self formed river in which the bed and banks are made up of mobile sediment.
Azonal vegetation Plant communities that depend on local extraordinary habitat characteristics e.g., microclimate, inundation, see also zonal vegetation.
Boreal zone Regions of the northern hemisphere with cold temperatures approximately between 50° to 70°N latitude.
Braided rivers Rivers characterized by mobile, multi-thread channels within gravel or sand-dominated fluvial corridors.
Ecological niche The match of a species to a specific environmental condition.
Endemic The state of a species being native to a single defined geographic location.
Floodplain Flat land area adjacent to a stream which is within the influence of the hydromorphodynamics of the river.
Fluvial Processes and landforms created by the flowing water.
Glacier fore-fields The region between the current front of the glacier and the moraines of the latest maximum.
Gravel-bed rivers Coarse-grained alluvial rivers which are particularly characterized by dynamic fluvial processes that constantly change and renew the surface and subsurface of the river's valley floor.
Last glacial maximum The LGM was the most recent time during the Last Glacial Period where the ice sheets were at their greatest extent.
Phreatophytes Deep-rooted plants that obtain a significant portion of the water that it needs from the phreatic zone (zone of saturation) or the capillary fringe above the phreatic zone.
Riparian vegetation Plant communities of floodplains (synonym floodplain vegetation).
Riverine Processes, landforms or species relating to or produced by a river.
Shear stress The external force acting on an object or surface parallel to the slope.
Taiga The boreal forest throughout the high northern latitudes, between the tundra and the temperate forest, from about 50°N to 70°N.
Trait Any morphological, physiological or phenological feature measurable at the individual level of a species.
Tundra Open, treeless landscape (mostly) over permafrost soils of the subpolar climate zone.
Wetland ecosystems Comprise areas that transition between terrestrial (land) areas and aquatic (water) areas.
Zonal vegetation Plant communities that depend on the large-scale habitat characteristics of the macro climate—see also azonal vegetation.

 https://doi.org/10.1016/B978-0-12-819166-8.00173-0

Introduction

Gravel-bed rivers and particularly braided rivers represent extraordinary wetland ecosystems due to their high disturbance regimes (Bornette and Amoros, 1996; Müller, 1998; Plachter and Reich, 1998). In contrast to groundwater- and flood-dominated wetlands, the main ecological factor is the geomorphological dynamics (Piégay et al., 2006). Their disturbance-adapted characteristic plant species create distinctive azonal vegetation types, contrary to the large-scale zonal vegetation in the surrounding areas (Fig. 1). Consequently, under natural conditions they contribute significantly to global biodiversity (Tockner et al., 2006).

However, due to the worldwide human impacts in the hydrological and sediment regimes by dams, diversions, flood control and river regulation (Hauer et al., 2016; Hohensinner et al., 2021) their characteristic native species have become extirpated along many river corridors (e.g., Müller, 1995; Tockner et al., 2008). Another threat to their biodiversity is their vulnerability to invasion of non-native plant species because the braided river floodplains provide regularly open sites for seedling colonization and the rivers serve as seed dispersal pathways (Liendo et al., 2015).

There have been many case studies of riparian vegetation existing in single mountain ranges (e.g., for Asia, Africa, Europe, Asia), but overviews of larger mountain regions similar to the analyses of the European Alps (Egger et al., 2019a,b; Kalníková et al., 2021) are lacking.

With this chapter we provide a global review of the riparian vegetation of gravel-bed rivers in mountain ranges, focusing on two questions:

- Which native plants are characteristic and abundant in the different successional phases of the riparian vegetation?
- Which invasive non-native plants are frequent within the riparian vegetation communities?

Mountain ranges

Mountain ranges of similar climatic conditions with frequent occurrences of gravel-bed rivers and including a high proportion of braided rivers were grouped into nine reference regions using data of ESRI (2010, 2016) and Natural Earth (2018) (Figs. 2 and 3).

Based on the data of Maier et al. (2022) the reference regions were selected to cover a wide range of abiotic factors. This includes their location on different continents of both hemispheres, different altitudes of mountain ranges, and varying percentage of current

Fig. 1 Gravel-bed rivers are shaped by high morphodynamics, drought and periodic flooding and are therefore colonized by adapted pioneer plants. This applies in particular to braided rivers like the shown Bush River that drains from the Columbia Icefields of the Canadian Rocky Mountains west. (Photo: S. Rood).

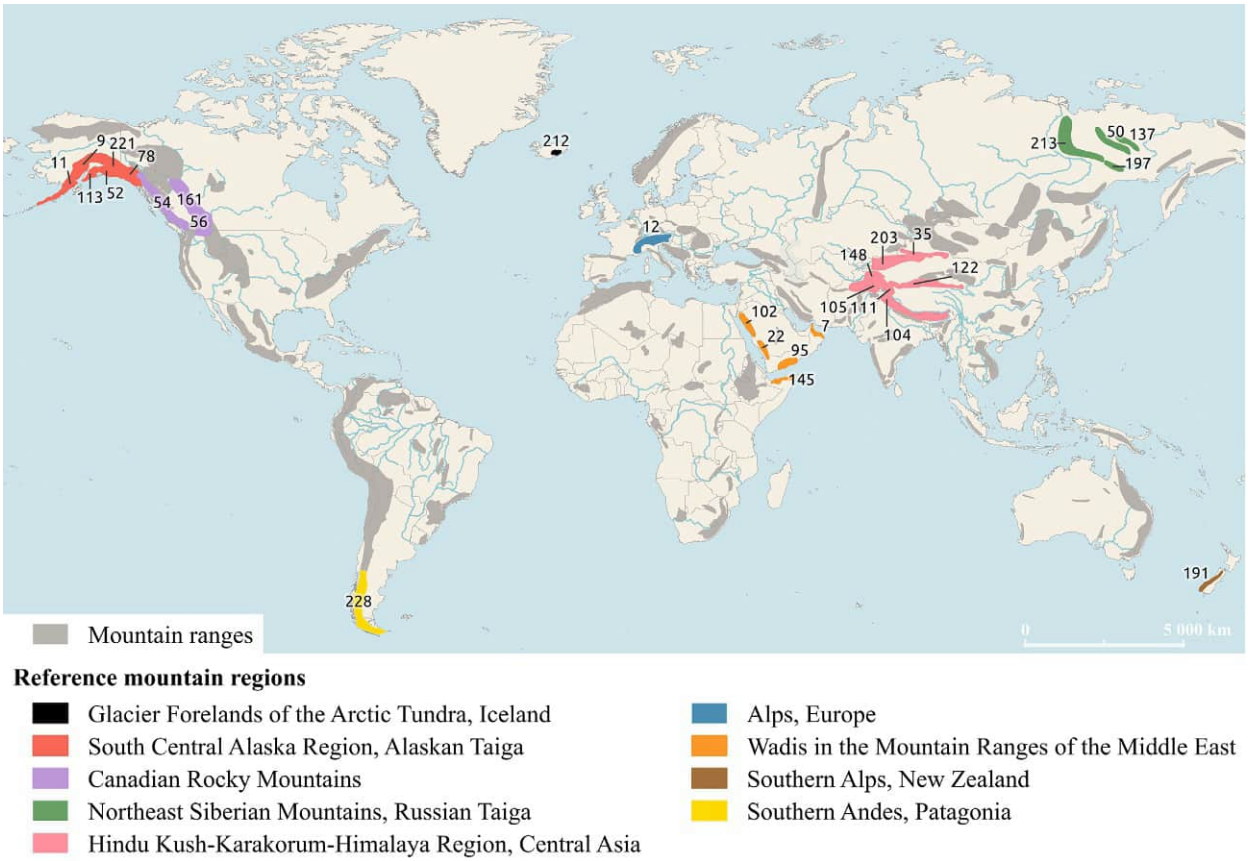

Fig. 2 Main global mountain ranges (grey) and reference regions with high proportions of braided rivers (described in chapters 4–12).

and historical glaciation. Climatic factors range from tropical to boreal and arctic climates, resulting in different floristic regions that influence riparian vegetation communities. Additionally, different extents of human impacts and land use intensities were considered. The reference regions include different numbers of regional mountain ranges, ranging from one main range such as the Patagonian Andes to several mountain ranges that occur in Central Asia. Each region is considered as representative of the associated mountain range for analyses of the riparian vegetation characteristics.

Reference regions and their riparian vegetation

The description of the nine reference regions and of their riparian vegetation, including their native and invasive non-native plant species, is based on published reports and was undertaken in close collaboration with regional experts. Invasive non-native plants (or 'invasive exotic species') indicates non-native species which have harmful effects on native biodiversity (CBD, 2010; Richardson et al., 2000). Plant species names were assigned according to Taxonomic Name Resolution Service (Boyle et al., 2013).

Commencing each subchapter, a short geographical introduction is provided using data from Linke et al. (2019), Masutomi et al. (2009), and RGI Consortium (2017). The subsequent description of the riparian vegetation is focused on the characteristic and frequent native and invasive non-native plants. Selected species of the nine reference mountain regions are provided in Table 1, with information about frequency, endemic status, occurrence of main habitat types and succession phase.

For the categorization of the riparian vegetation we used the 'fluvial biogeomorphic succession concept' proposed by Corenblit et al. (2007, 2011, 2015). Following this concept, river corridors worldwide are characterized by four consecutive succession phases. The concept starts with the initial 'geomorphic phase' with large areas of vegetation-free gravel sites, e.g., after total destruction of a site by a flood event. The areas are mainly shaped by the flow regime and the sediment properties (Corenblit et al., 2007). The open sand and gravel bars offer many sites for plant germination, but colonization is aggravated by the strong morphodynamics especially in braided river systems. Pioneer plants can only establish during a suitable window of opportunity (Balke et al., 2014) in the 'pioneer phase.' These pioneer plants are still particularly influenced by the hydrogeomorphic processes and require a set of functional traits to cope with the frequent disturbances and stressors in river corridors (Gurnell et al., 2016). In general, key traits relate to plant reproduction, growth and survival (Violle et al., 2007) with adaptive traits along braided rivers to resist strong shear stress, sediment deposition and uprooting (Bornette et al., 2008). Through these specialized adaptations and response traits

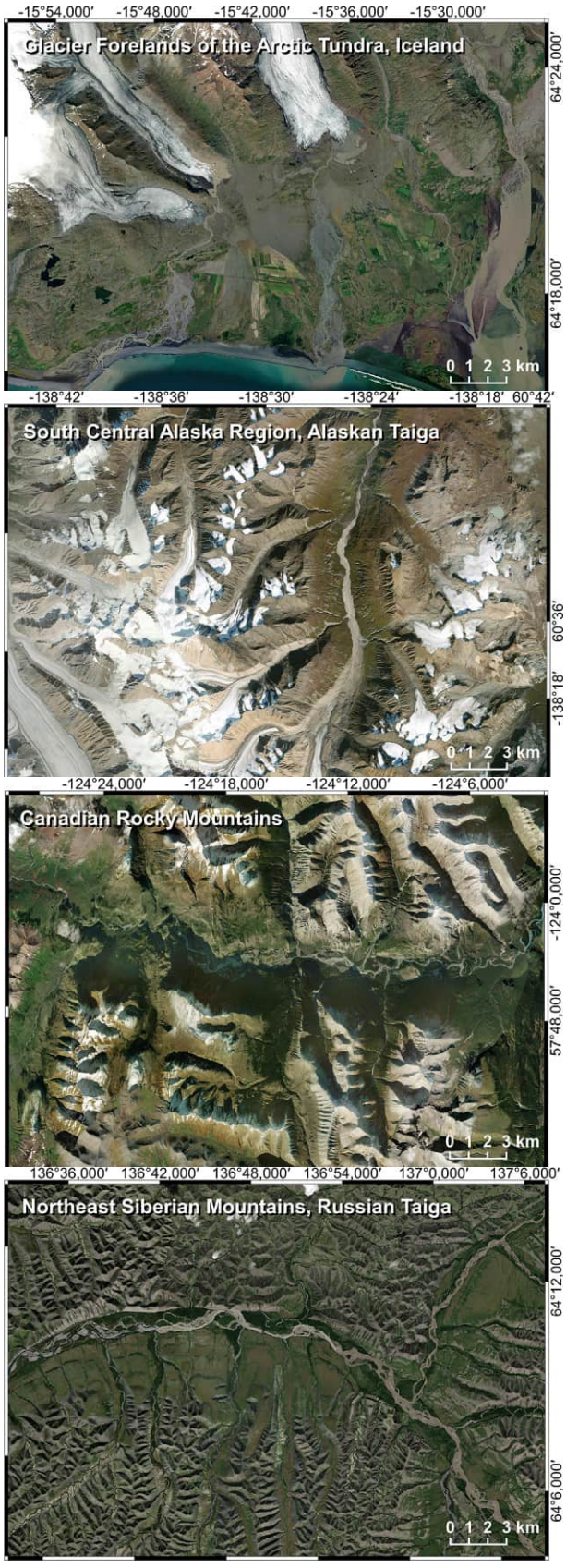

Fig. 3 Exemplary sites of the nine reference mountain ranges with frequent occurrences of braided rivers on the scale of 1:100.000 (ESRI Satellite).


75°48,000′
75°54,000′
76°0,000′
Hindu Kusch-Karakorum-Himalaya-Region, Central Asia
35°48,000′
35°42,000′
0 1 2 3 km
12°48,000′
12°54,000′
13°0,000′
13°6,000′
Alps, Europe
46°18,000′
46°12,000′
0 1 2 3 km
48°12,000′
48°18,000′
Wadis in the Mountain Ranges of the Middle East
15°54,000′
0 1 2 3 km
170°0,000′
170°6,000′
170°12,000′
Southern Alps, New Zealand
-43°48,000′
0 1 2 3 km

Fig.3—Cont'd

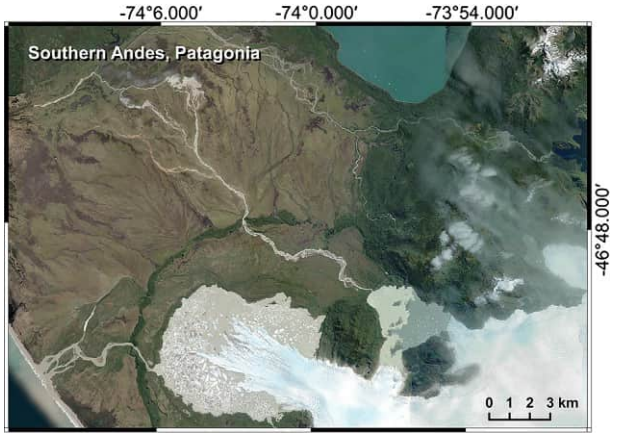

Fig.3—Cont'd

(Violle et al., 2007), plants increase their resistance ('maintaining structure') and resilience ('restoring structure') to disturbances (Holling, 1973) and also generate biogeomorphic feedback that reduces morphodynamics. The aboveground biomass modifies the flow field, increases roughness (Bennett et al., 2008; Gurnell, 2014; Gurnell et al., 2016; Liu et al., 2010) and retains sediment (Zong and Nepf, 2010), while the underground biomass reduces the erosion capacity of the land surface and thereby contributes to its stabilization (Gurnell, 2014). These interactions set the 'biogeomorphic phase' of succession in motion. Especially colonized sites by ecosystem engineers (Jones et al., 1994) are more resistant to disturbances and destruction due to their enormous effects on the morphodynamics. The final 'ecologic phase' is characterized by more stable habitats and autogenic ecological processes. Vegetation is less influenced by the river, succession processes continue and long-lived plant communities begin to establish (Bazzaz, 1979). In the presence of reduced fluvial processes, the late-successional stages transition into the surrounding zonal vegetation. We expanded the 'ecologic phase' into an 'early' and a 'late successional phase'. Characteristic trees of the 'early successional ecologic phase' establish on open bars, grow rapidly, are shade intolerant, and are well adapted to high hydro-morphodynamics. In contrast, trees of the 'late successional ecologic phase' establish on stable sites, are more shade tolerant and grow more slowly (Egger et al., 2019a).

Glacier Forelands of the Arctic Tundra, Iceland

The reference mountain region of the Arctic Tundra is located in the Vatnajökull mountain range (No. 212; Fig. 2) in south-eastern Iceland. The area is dominated by the Vatnajökull Glacier which currently covers over 80% of the mountain range. The glacier covers almost 7800 km^2 and is the largest ice cap of Iceland and outside of the Arctic. About 30 outlet glaciers flow from the ice cap, which reaches over 2000 m in altitude, and end in an extensive moraine landscape in the lowlands and highlands to the north of the glacier. These are closely interwoven with a number of fens of braided rivers, some several km wide, along with alluvial outwash terraces. Numerous large and small glacial rivers fall from the glaciers and the rivers flowing out of the mountain range to the South are mainly sparsely vegetated along their courses (Fig. 4). In general, the mountain range is scarcely forested and anthropogenic impact is very low with a population density of only 0.01 person per km^2. The median annual temperature is 0.9 °C and precipitation 1.380 mm.

The vegetation colonization of the braided river corridors in the glacier fore-fields is determined by a complex interaction of several environmental factors and succession is generally slower in the cooler Artic than in temperate climate regions (Glausen and Tanner, 2019; Vilmundardóttir et al., 2014). Following the glacier's maximum extent in the last Little Ice Age at the end of the 19th century, the glaciers of Vatnajökull have been continuously receding. The ice-free moraine fields vary in length and are gradually colonized by vegetation during different succession phases. In the area of braided river corridors, primary succession is additionally dominated by the alluvial hydro- and morphodynamics of the glacial streams (Vilmundardóttir et al., 2014).

The young alluvial soils are wet to dry, nutrient poor, and characterized by low carbon content. Most areas of these highly dynamic rivers are un-vegetated or sparsely vegetated. Common plants of the 'pioneer phase' are *Agrostis stolonifera*, *Festuca richardsonii* and sporadically *Arabidopsis petraea*, *Armeria maritima*, *Carex maritima*, *Cerastium fontanum*, *Equisetum arvense*, *E. variegatum*, *Juncus arcticus*, *Rumex acetosella*, *Silene uniflora* and *S. acaulis*. In addition, there are moss species such as *Racomitrium ericoides*, which form the largest cover, as well as *Drepanocladus aduncus* and *Philonotis fontana* (Magnússon et al., 2016; Vilmundardóttir et al., 2015) (Fig. 5).

Flat, sandy floodplains with organic soils are dominated by *Juncus arcticus* meadows. In addition, *Carex nigra*, *Empetrum nigrum*, *Salix arctica* and *S. lanata* are predominant (Fig. 6). Further characteristic plants are grasses like *Agrostis stolonifera*, *A. vinealis*, *Calamagrostis neglecta*, *Festuca vivipara*, *Luzula multiflora*, *Trisetum spicatum* and herbs including *Bistorta vivipara*, *Cardamine hirsuta*, *Epilobium palustre*, *Equisetum arvense*, *E. variegatum*, *Filipendula ulmaria*, *Galium normanii*, *G. verum*, *Leontodon autumnalis*, *Parnassia palustris*, *Platanthera hyperborea* and *Rhinanthus minor* (Magnússon et al., 2016).

Table 1 Selected characteristic native plants (light green = sparse; dark green = abundant) and non-native plants (yellow = sparse; orange = abundant) with information about succession phase (SP: PioPh = Pioneer phase; BiogeoPh = Biogeomorphic phase; ESEPh = Early successional ecologic phase; LSEPh = Late successional ecologic phase); endemic status in the reference regions (ED) and occurrence (OC) of main habitat types (RIP = restricted to riparian habitats; FAC = facultative, in riparian and terrestrial habitats).

Plant name	SP	ED	OC	IL	AT	CA	RT	AS	AL	ME	NZ	PA
Aquilegia parviflora Ledeb.	PioPh	-	FAC									
Eclipta prostrata (L.) L.	PioPh	-	FAC									
Impatiens glandulifera Royle	PioPh	-	FAC									
Lachnagrostis filiformis (G. Forst.) Trin.	PioPh	-	FAC									
Acaena magellanica Vahl	PioPh	-	FAC									
Agrostis inconspicua Kunze ex E. Desv.	PioPh	-	FAC									
Agrostis stolonifera L.	PioPh	-	FAC									
Arundo donax L.	PioPh	-	RIP									
Bacopa monnieri (L.) Wettst.	PioPh	-	FAC									
Calamagrostis pseudophragmites (Haller f.) Koeler	PioPh	-	RIP									
Delphinium cheilanthum Fisch. ex DC.	PioPh	-	FAC									
Echium vulgare L.	PioPh	-	FAC									
Epilobium angustifolium subsp. *angustifolium*	PioPh	-	FAC									
Epilobium brunnescens (Cockayne) P.H. Raven & Engelhorn	PioPh	NZ	RIP									
Epilobium dodonaei Vill.	PioPh	-	RIP									
Equisetum arvense L.	PioPh	-	FAC									
Fallopia japonica (Houtt.) Ronse Decr.	PioPh	-	FAC									
Festuca richardsonii Hook.	PioPh	-	FAC									
Gunnera magellanica Lam.	PioPh	-	FAC									
Imperata cylindrica (L.) Raeusch.	PioPh	-	FAC									
Juncus scheuchzerioides Gaudich.	PioPh	-	FAC									
Lachnagrostis lyallii (Hook. f.) Zotov	PioPh	NZ	FAC									
Lupinus nootkatensis Donn ex Sims	PioPh	-	FAC									
Lupinus polyphyllus Lindl	PioPh	-	RIP									
Melilotus albus (Medik.)	PioPh	-	FAC									
Phalaris arundinacea L.	PioPh	-	RIP									
Phragmites australis (Cav.) Trin. ex Steud.	PioPh	-	FAC									
Poa novae-zelandiae Hack.	PioPh	NZ	FAC									
Rytidosperma setifolium (Hook. f.) Connor & Edgar	PioPh	NZ	FAC									
Saccharum spontaneum L.	PioPh	-	FAC									
Saxifraga aizoides L.	PioPh	-	RIP									
Solidago canadensis L.	PioPh	-	FAC									
Sonchus arvensis L.	PioPh	-	FAC									
Tanacetum vulgare L.	PioPh	-	FAC									
Alnus alnobetula (Ehrh.) K. Koch	BiogeoPh	-	FAC									
Berberis microphylla F. Dietr.	BiogeoPh	PA	FAC									
Buddleja davidii Franch.	BiogeoPh	-	FAC									
Carmichaelia grandiflora (Benth.) Hook.f.	BiogeoPh	NZ	FAC									
Carmichaelia nigrans G.Simpson	BiogeoPh	NZ	FAC									
Coprosma acerosa A. Cunn.	BiogeoPh	NZ	FAC									
Cornus sericea L.	BiogeoPh	-	FAC									
Discaria toumatou Raoul	BiogeoPh	NZ	FAC									
Empetrum nigrum L.	BiogeoPh	-	FAC									
Escallonia virgata (Ruiz & Pav.) Pers.	BiogeoPh	PA	FAC									
Helichrysum depressum (Hook.f.) Benth. & Hook.f.	BiogeoPh	NZ	RIP									
Muehlenbeckia axillaris (Hook. f.) Endl.	BiogeoPh	-	FAC									
Myricaria germanica (L.) Desv.	BiogeoPh	-	RIP									
Myricaria pulcherrima Batalin	BiogeoPh	AS	RIP									
Salix alaxensis (Andersson) Coville	BiogeoPh	-	FAC									
Salix arctica Pall.	BiogeoPh	-	FAC									
Salix arctophila Cockerell ex A. Heller	BiogeoPh	-	FAC									
Salix bebbiana Sarg.	BiogeoPh	-	RIP									
Salix brachycarpa Nutt.	BiogeoPh	-	FAC									

Plant name	SP	ED	OC	IL	AT	CA	RT	AS	AL	ME	NZ	PA
Salix daphnoides Vill.	BiogeoPh	-	RIP									
Salix drummondiana Barratt ex Hook.	BiogeoPh	-	FAC									
Salix eleagnos Scop.	BiogeoPh	-	RIP									
Salix exigua Nutt.	BiogeoPh	-	RIP									
Salix glauca L.	BiogeoPh	-	FAC									
Salix herbacea L.	BiogeoPh	-	FAC									
Salix lanata L.	BiogeoPh	-	FAC									
Salix lucida Muhl.	BiogeoPh	-	RIP									
Salix monticola Bebb	BiogeoPh	-	RIP									
Salix phylicifolia L.	BiogeoPh	-	FAC									
Salix planifolia Pursh	BiogeoPh	-	FAC									
Salix purpurea L.	BiogeoPh	-	RIP									
Tamarix hispida Willd.	BiogeoPh	AS	FAC									
Tamarix mascatensis Bunge	BiogeoPh	-	FAC									
Tamarix nilotica (Ehrenb.) Bunge	BiogeoPh	-	FAC									
Berberis empetrifolia Lam.	BiogeoPh	-	FAC									
Cytisus scoparius (L.) Link	BiogeoPh	-	FAC									
Elaeagnus angustifolia L.	BiogeoPh	-	FAC									
Fuchsia magellanica Lam.	BiogeoPh	-	FAC									
Gaultheria mucronata (L. f.) Hook. & Arn.	BiogeoPh	PA	FAC									
Halostachys caspica C.A. Mey. ex Schrenk	BiogeoPh	AS	FAC									
Hippophae rhamnoides L.	BiogeoPh	-	FAC									
Jatropha pelargoniifolia Courbai	BiogeoPh	ME	FAC									
Nerium oleander L	BiogeoPh	-	FAC									
Pinus pumila (Pall.) Regel	BiogeoPh	-	FAC									
Rhazya stricta Decne.	BiogeoPh	-	FAC									
Rosa rubiginosa L.	BiogeoPh	-	FAC									
Tamarix ramosissima Ledeb.	BiogeoPh	-	FAC									
Ulex europaeus L.	BiogeoPh	-	FAC									
Betula nana L.	ESEPh	-	FAC									
Alnus incana (L.) Moench	ESEPh	-	RIP									
Betula pubescens Ehrh.	ESEPh	-	FAC									
Chosenia arbutifolia (Pall.) A.K. Skvortsov	ESEPh	-	RIP									
Populus alba L.	ESEPh	-	RIP									
Populus balsamifera L.	ESEPh	-	RIP									
Populus balsamifera ssp. *trichocarpa* (Torr. & A. Gray ex Hook.) Brayshaw	ESEPh	-	RIP									
Populus deltoides W. Bartram ex Marshall	ESEPh	-	RIP									
Populus euphratica Olivier	ESEPh	-	FAC									
Populus nigra L.	ESEPh	-	RIP									
Populus pruinosa Schrenk	ESEPh	AS	FAC									
Populus suaveolens Fisch	ESEPh	-	RIP									
Populus tremula L.	ESEPh	-	FAC									
Salix alba L.	ESEPh	-	RIP									
Salix fragilis L.	ESEPh	-	RIP									
Salix humboldtiana Willd.	ESEPh	-	RIP									
Salix rorida Lacksch.	ESEPh	-	FAC									
Sorbus aucuparia L.	ESEPh	-	FAC									
Salix babylonica L.	ESEPh	-	RIP									
Acacia ehrenbergiana Hayne	LSEPh	-	FAC									
Acer glabrum Pursh	LSEPh	-	FAC									
Betula pendula Roth	LSEPh	-	FAC									
Dacrycarpus dacrydioides (A. Rich.) de Laub.	LSEPh	-	FAC									
Ficus cordata subsp. *salicifolia* (Vahl) C.C. Berg	LSEPh	-	FAC									
Ficus vasta Forssk.	LSEPh	ME	FAC									
Fraxinus excelsior L.	LSEPh	-	FAC									
Larix cajanderi Mayr	LSEPh	RT	FAC									

Plant name	SP	ED	OC	IL	AT	CA	RT	AS	AL	ME	NZ	PA
Larix gmelinii (Rupr.) Kuzen.	LSEPh	-	FAC									
Nothofagus antarctica (G. Forst.) Oerst.	LSEPh	PA	FAC									
Nothofagus betuloides (Mirb.) Oerst.	LSEPh	PA	FAC									
Nothofagus menziesii (Hook. f.) Oerst	LSEPh	NZ	FAC									
Nothofagus pumilio (Poepp. & Endl.) Krasser	LSEPh	PA	FAC									
Quercus robur (Ten.) A. DC.	LSEPh	-	FAC									
Robinia pseudoacacia L.	LSEPh	-	FAC									
Salix schwerinii E.L. Wolf	LSEPh	-	RIP									
Ulmus laevis Pall.	LSEPh	-	RIP									
Tamarix aphylla (L.) H. Karst.	LSEPh	-	RIP									
Dacrydium cupressinum Sol. ex G.Forst	LSEPh	NZ	RIP									
Dicksonia squarrosa (G. Forst.) Sw.	LSEPh	NZ	FAC									
Luma apiculata (DC.) Burret	LSEPh	PA	RIP									
Picea abies (L.) Karst.	LSEPh	-	FAC									
Picea glauca (Moench) Voss	LSEPh	-	FAC									
Picea mariana (Mill.) Britton, Sterns & Poggenb	LSEPh	-	FAC									
Picea obovata Ledeb.	LSEPh	-	FAC									
Pinus sylvestris L.	LSEPh	-	FAC									
Podocarpus nubigenus Lindl.	LSEPh	PA	FAC									
Prumnopitys ferruginea (G.Benn. ex D.Don) de Laub.	LSEPh	NZ	FAC									
Thuja plicata Donn ex D. Don	LSEPh	-	FAC									
Leiospermum racemosum (L. f.) D. Don	LSEPh	NZ	FAC									
Ziziphus spina-christi (L.) Desf.	LSEPh	-	FAC									

The nine reference mountain regions include: IL = Iceland, Glacier Forelands of the Arctic Tundra; AT = Alaskan Taiga, South Central Alaskan; CA = Canadian Rocky Mountains; RT = Russian Taiga, Northeast Siberian Mountains; AS = Central Asia, Hindu-Kusch-Karakorum-Himalaya-Regions; AL = Alps, Europe; ME = Middle East, Wadis; NZ = New Zealand, Southern Alps; and PA = Patagonia, Southern Andes.

Fig. 4 A braided river fed by glacial meltwater in the extensive glacier forelands in the south-western region of Vatnajökull. (Photo: G. Egger).

Fig. 5 Vatnajökull dry gravel foreland, approximately 30 to 50 years old, dominated by *Racometrium ericoides* mossheath with *Empetrum nigrum* and *Thymus praecox* and several other vascular plants. (Photo: S. Metúsalemsson).

Fig. 6 A moist sandy floodplain at Vatnajökull. The *Juncus arcticus* meadow includes *Carex nigra, Calamagrostis neglecta, Salix lanata, S. phylicifolia* and numerous other vascular species and provides a habitat rich in bird life. (Photo: S. Metúsalemsson).

On more stable habitats—the 'biogeomorphic phase'—young successional dwarf shrubs occur, such as the spreading *Empetrum nigrum* and *Calluna vulgaris*. In addition to the listed species of the pioneer phase, *Thymus praecox* ssp. *arcticus*, *Alchemilla alpina*, *Botrychium lunaria*, *Campanula rotundifolia*, *Cerastium alpinum*, *Erigeron borealis*, *Luzula spicata*, *Minuartia rubella*, *Poa glauca*, *Saxifraga oppositifolia*, *Silene suecica* also establish here (Magnússon et al., 2016). Further, low-growing willow species such as *Salix lanata*, *S. phylicifolia* and *S. herbacea* and *Betula pubescens* are also present (Aradottir and Eysteinsson, 2005; Vilmundardóttir et al., 2015). As succession progresses, habitats become increasingly species-rich and a number of further mosses, such as *Racomitrium lanuginosum*, *Pogonatum urnigerum*, *Ceratodon purpureus*, *Lecanora polytropa*, *Placopsis gelida*, *Tremolecia atrata*, *Cetraria muricata*, *Cladonia borealis* and *Stereocaulon alpinum* are present in addition to *Racomitrium ericoides*.

On undisturbed moraine sites that have been ice-free for 60–120 years, mosses and lichens became more dominant in the 'early successional ecologic phase'. On sites more heavily grazed by sheep, these transition to the widespread *Vaccinium-Empetrum-Racomitrium* heaths in the lowlands of Iceland (Magnússon et al., 2016). Also, on the oldest sites with moderate sheep grazing, dense and species-rich willow scrubland and birch woodlands occur with *Betula nana*, *B. pubescens* and *Sorbus aucuparia* and in the understory *Salix lanata*, *S. arctica* and dwarf shrubs such as *Vaccinium uliginosum*, *Vaccinium myrtillus*, *Calluna vulgaris*, *Arctostaphylos uva-ursi* and *Empetrum nigrum* are present as well as grasses, tall forbs, and *Equisetum* spp. (Aradottir and Eysteinsson, 2005; Glausen and Tanner, 2019; Magnússon et al., 2016).

Despite the fact that nearly 336 alien plant species have been recorded in Iceland from 1840 to 2012, with about three new taxa added annually, only *Lupinus nootkatensis* and *Anthriscus sylvestris* can be currently classified as invasive non-natives along the rivers (Wasowicz et al., 2013). Originally from Alaska, *L. nootkatensis* occurs mainly in the 'pioneer phase' and is also common in the lowland areas of the moraines around Vatnajökull, where it is expected to spread extensively in the near future (Guðjohnsen and Magnússon, 2019).

South Central Alaska Region, Alaskan Taiga

This reference region covers the mountain ranges of southern Alaska and includes the Alaska Range (no. 9), Aleutian Range (no. 11), Chugach Mountains (no. 52), Elias Range (no. 78), Kenai Mountains (no. 113) and Wrangell Mountains (no. 221) (Fig. 2). These geologically relatively young, Cenozoic mountain ranges lie in the boreal climate region and have median elevations between 520 and 1200 m with the highest peak being Mount Logan (5959 m) in the Elias Range. Conversely, the Aleutian Range in the far west of Alaska has lower altitudes, lower precipitation and warmer temperatures.

The Aleutian Range and Alaska Range in the southwest currently have small areas covered by ice (below 8%). In the other mountain ranges the area covered by glaciers ranges from 16% to 31%. In the last glacial maximum these were almost completely glaciated. Current vegetation cover across these mountain ranges varies between 54% and 84%. The tree line drops to 500 m near the Gulf of Alaska which is relatively low compared to other reference regions and peaks in the Wrangell Mountains with around 1300 m.

The largest rivers of the south-central Alaskan region are the Copper, White, and Kenai Rivers and the headwaters of the Tanana River, such as the Delta, Nenana and Chisana River.

The braided rivers of this study region are generally characterized by extensive areas of gravel (geomorphic phase) (Figs. 7 and 8). The subsequent 'pioneer phase' on these floodplains of the bare alluvium include colonization of herbs common in the Alaskan taiga such as *Saxifraga aizoides*, forbs like *Lupinus polyphyllus*, *Solidago canadensis*, and grasses like *Phalaris arundinacea*.

Fig. 7 Susitna River in the south of Denali National Park (Alaska Range). (Photo: G. Egger).

Fig. 8 Riverbed of the Delta River, a tributary of the Tanana River, with large amounts of dead wood (large woody debris). (Photo: G. Egger).

This system progresses in the 'biogeomorphical phase' through stands dominated by *Salix alaxensis,* one of the most common and widespread pioneer willow species of the mountain regions of south central Alaska (Fig. 9). One of the most common pioneer trees of the 'early successional ecologic phase' is *Populus balsamifera,* which is abundant in the boreal regions across Canada. This fast-growing and generally short lived tree grows trans- continentally on upland and floodplain sites, where it has the best growing

Fig. 9 An early successional woodland with dense willow shrubs dominated by *Salix alaxensis* and young *Populus balsamifera* trees along the East Fork Chulitna River, Alaska. (Photo: G. Egger).

conditions. Along Pacific drainages, the closely related *Populus trichocarpa* (syn. *Populus balsamifera* ssp. *trichocarpa*), the largest of the American poplars, forms extensive groves at low elevations. *Alnus incana* is an abundant, large shrub on wetter sites on sand and gravel bars, in glacial and riparian shrublands and wet uplands from central to southern Alaska (Larson, 1994). Widely distributed along streams, rivers and in swamps and moist alluvial bottomlands from Alaska to the South of California and south-eastwards across North America, *Salix lucida* is a fast growing, deciduous large shrub or small tree.

In addition, a number of other representatives of early successional willows are found such as *S. arctica*, the northernmost woody plant in the world (Woodward, 2014), and *Salix glauca*. Both are very common willows in shrubby riparian and tundra habitat. Other willows are less common such as *Salix lanata*, *S. arctophila*, *S. pseudomyrsinites*, *S. interior*, *S. pseudomyrsinites*, and *S. brachycarpa* ssp. *niphoclada*. *Salix exigua*, a widely-distributed species occurs on finer sediments of floodplains and lower elevations to lower montane habitats across western North America. Other willows and willow hybrids also occur including *Salix arbusculoides*, which is widespread along river banks from central Alaska to Hudson Bay, colonizing fresh alluvial deposits and glacial outwash.

When initial trees of the "early successional phase of the forest" reach their maximum age and die, the dominant tree of the subsequent mid to 'late successional ecologic phase' is *Picea glauca*. This shade tolerant tree dominates the extensive boreal forests of Alaska and Canada. It occurs in all stages of boreal forest succession and also on recently disturbed sites. At poorly drained back swamps *Picea glauca* is replaced by *Picea mariana*.

In the largely remote and relative pristine regions, there are relatively few invasive plant species along the braided rivers in the Alaskan taiga, including *Sorbus aucuparia*, *Sonchus arvensis* and *Tanacetum vulgare*.

Canadian Rocky Mountains

This region comprises the mainly boreal Coast Mountains (no. 54), Columbia Mountains (no. 56) and the Canadian Rocky Mountains (no. 161) (Fig. 2). Compared to the Alaskan region, the mountain ranges of this region are older (Mesozoic), current ice cover is lower and vegetation cover is higher (82–97%). The highest peak is Mount Waddington in the Coast Mountains and the largest rivers are the Yukon, Fraser, Columbia and Kootenay Rivers.

The Canadian, or northern Rocky Mountains display braided, multi-thread river channels of three types. First, and similar to some other mountain regions on the Globe, as the mountain rivers drop down to shallower gradients, glacial scour and alluvial sediments are deposited, choking channels and leading to channel deflection and bifurcation. This generates very dynamic braided segments with sparse vegetation. The gravel bars of the 'pioneer phase' (Fig. 10) are commonly colonized by pioneers such as *Dryas drummondii*, which supports symbiotic actinorrhizal nitrogen fixation that is beneficial in an environment of nutrient-deficient mineral surfaces. Disturbance responsive plants like *Epilobium angustifolium* ssp. *angustifolium* create by aggradation slightly higher and more stable areas on which willows (listed below) and eventually *Pinus contorta* forests establish. As rivers flow downstream,

Fig. 10 Pioneer phase with *Dryas drummondii* at the Sunwapta River in Alberta, Canada. (Photo: S. Rood).

there are commonly progressive transitions from braided to meandering forms. These support arcuate bands or vegetation patches that result in a shifting mosaic of riparian community types. On the lower elevations the wet meadow zones that are commonly inundated, include the sedges *Carex aperta*, *C. aquatilis*, *C. lenticularis* and horsetails (*E. arvense*, *Equisetum fluviatile*). The willows include *Salix bebbiana*, *S. boothii*, *S. brachycarpa*, *S. drummondiana*, *S. eriocephala*, *S. geyeriana*, *S. monticola*, *S. planifolia*, *and S. wolfii*, with complexities in classification due to hybridization and introgression. *Cornus sericea* occurs on slightly higher surfaces of the 'biogeomorphic phase' contributing to the riparian shrublands. These blend into the slightly higher 'early successional ecologic phase' with riparian forests composed of *Populus balsamifera* along eastern drainages and *P. trichocarpa* (Fig. 11) along Pacific drainages. *Alnus incana* is common, and sometimes birches (*Betula occidentalis*, *B. glandulosa*) and *Acer glabrum*. *Picea glauca* and hybrids co-occur or follow with forest succession that may lead to the 'late successional ecologic phase', with *Thuja plicata* in wetter zones (Egger et al., 2015) (Fig. 12).

Fig. 11 Colonization of black cottonwoods (*Populus trichocarpa*) following a flood of the Elk River in British Columbia, Canada. (Photo: S. Rood).

Fig. 12 White spruce (*Picea glauca*) forest (late successional ecologic phase) with a few black cottonwoods (*Populus trichocarpa*; center of picture) representing a remnant from the previous early successional ecologic phase at the Elk River in British Columbia, Canada. (Photo: G. Egger).

The second type of regional river braiding, anastomosed channels, are very different relative to dynamics and vegetation distribution (Makaske et al., 2002). These occur in the broad and very shallow gradient glacial valleys, where post-glacial sediment deposition produces wide and flat floodplains with an interwoven complex of braided channels, wetlands and ponds. The complex braiding has been somewhat stabilized and natural levees flank the larger channels, following overbank sediment deposition. This inverts the elevational profile, with the higher surfaces adjacent to the river channel. Similar plants occur along the anastomosed channels but with opposing distribution. The black cottonwood (*Populus trichocarpa*) bands are directly along the channel on the elevated levees, and then sloping downward away from the channel to shrublands occur with willows (*Salix* spp.) and dogwood (*Cornus sericea*), and then lower surfaces with wet meadows and wetland ponds.

A third type of river channel braiding occurs as rivers flow into natural lakes or artificial reservoirs. Sediment deposition creates the river delta with shallow topographies and distributaries form as the channels are choked and redirected. The same riparian vegetation communities form as along the other regional channel types, with the same spatial transitions with increasing elevation and correspondingly reduced inundation: from wet meadow, upwards to riparian shrubland, riparian forest and then the transition to upland, coniferous forest. In addition, with lower zones or with sediment lenses that limit drainage, there may be wetland zones with perennial ponding that support bulrushes and other emergent aquatic plants.

Across these different braided and meandering channels and delta zones, a common invasive plant is *Phalaris arundinacea* (Spyreas et al., 2010). This plant is regionally native but vigorous hybrids have been developed and distributed as forage crops and these have invaded natural areas. A number of knapweeds (*Centaurea diffusa*; *C. maculosa*) and leafy spurge (*Euphorbia esula*) are also invasive in the riparian zones, especially in drier regions (Sheley et al., 1998).

Northeast Siberian Mountains, Russian Taiga

Northeast Siberia's mountains east of Lena River, Verkhoyansk Range (no. 213 including Suntar-Khayata Range (no. 197)) and Cherskiy Range (no. 50 including Momskiy Mountains (no. 137) (Fig. 2) stretch for approximately 1000 km from north to south, and cover nearly the same distance in a longitudinal direction. Median elevations are 510–1380 m (max. 3003 m a.s.l.). The largest rivers are the Indigirka River (Fig. 13), Yana River, and Kolyma River. Despite the boreal climate with low mean annual temperatures of about 16 °C and limited precipitation of below 300–420 mm, there are very few current glaciers. In contrast, at the last glacial maximum 20–84% of the mountain ranges were covered by ice.

The vast area of Siberia, along with complex geomorphology, determines the diversity of vegetation patterns there. In the highlands, belts developed along the slopes according to the Verkhoyansk-Kolyma altitudinal zonation type (Ogureeva et al., 1999): mountain taiga, subalpine shrubs, mountain tundra, epilithic lichens belt, and the high mountains above snow line ("nival belt"). Along with that ecosystem diversity, narrow and deeply incised river valleys support specific vegetation complexes that include forests and shrubs intermixed with meadows, bogs and aquatic vegetation.

The mountain taiga belt is limited to 600 m a.s.l. in the north and 1300 m in the south and is represented by the northern taiga of *Larix gmelinii* (Isaev et al., 2010). Valley complexes are most developed within this belt. Riparian forests of the 'late successional

Fig. 13 View into the valley of a tributary to the Indigirka river in its middle reaches in the Cherskiy Range with icing. (Photo: E. Troeva).

ecologic phase' with *Larix gmelinii, Alnus alnobetula* ssp. *fruticosa* and *Rosa acicularis* in the understory are more productive than the upslope communities. Along with larch, the late-successional forest stages in the Verkhoyansk Range features *Picea obovata* (Nikolin, 2014). At the lower floodplain levels, rapidly growing pioneer woodlands of the 'early successional ecologic phase' (*Populus suaveolens, Chosenia arbutifolia, Betula pendula, B. pubescens*) establish (Nikolin, 2012, 2013). *Chosenia arbutifolia* is a characteristic riparian species adapted to mountain rivers' high hydro- and morphodynamics. It germinates and establishes upon open gravel and sand banks along the active channel. After 12–25 years it can also dominate the 'biogeomorphic phase', growing up into deciduous forests approximately 25–30 m high. These floodplain forests can subsequently get ages of 60–120 years (Moskalyuk, 2016; Fig. 14).

In the border areas along the active channels, arborescent willow stands (*Salix schwerinii*, *Sapromyza rorida*, *Salix viminalis*, etc.) form intermixed with forb and grass meadows. Within the subalpine shrub belt (*Pinus pumila, Betula divaricata*, ca. 1000 m a.s.l.), low shrubs (*Betula nana* subsp. *exilis*, *Salix pulchra*, *S. saxatilis*) separate slope communities, and riparian willows (*Salix alaxensis, S. boganidensis*, *S. dshugdshurica*, *S. pseudopentandra*) grow along the active channels. Occasionally, *P. pumila* extends downslope down to the river. Shrubs alternate with bogs (*Carex* spp., *Eriophorum* spp.) and small patches of meadow (*Carex* spp., *Kobresia* spp.) (Nikolin, 2014).

Open gravel alluvium is a substrate for the 'pioneer phase' with communities of *Equisetum arvense*. Further silt accumulation provides habitat conditions for *Chamerion latifolium* (Fig. 15) and graminoid meadows (*Bromus* spp., *Leymus* spp., *Calamagrostis* spp.).

When considering the Northeast Mountains' river corridors, it is necessary to recognize the unique phenomenon of aufeis, or icing (Fig. 13). Sheet-like masses of aufeis form from successive flows of groundwater during freezing temperatures. Melting icings are surrounded by communities of *Equisetum variegatum*, which is a valuable forage plant for horses and for native ungulates and other herbivores. Towards the edges of gravel-bed rivers, these are replaced by meadows of *Calamagrostis neglecta*, *Carex* spp., *Pedicularis* spp., *Primula* spp., *Ranunculus* spp. and other plants (Efimova et al., 2010).

The river valleys are less systematically developed within the mountain tundra belt (1110–1500 m a.s.l.). Complex tundra communities (*Ledum palustre*, *Arctous alpina*, *Koenigia tripterocarpa*, *Andromeda polifolia*, *Empetrum nigrum*) with sparse shrubs of *B. nana* subsp. *exilis* represent a transition between upslope and riparian vegetation. On sandy-gravel alluvia, mesic meadows (*Leymus interior*, *Bromus pumpellianus* s.l.) develop. Ribbon-like thickets of low-growing willows (*Salix alaxensis, S. lanata, S. glauca, S. pulchra*, etc.) with sporadic *Calamagrostis purpurea* communities are confined to stream banks (Efimova et al., 2010; Nikolin, 2014). There are no serious invasive non-native plants in these riparian zones.

Fig. 14 The biogeomorphic succession phase with *Salix* spp. and *Chosenia arbutifolia* along the East Khandyga River bank (Verkhoyansk Range). (Photo: E. Troeva).

Fig. 15 *Chamerion latifolium* is a characteristic species of the pioneer phase of river corridors in the mountains of northeast Siberia. (Photo: E. Troeva).

Hindu Kusch-Karakorum-Himalaya-Region, Central Asia

The very high mountains of this region are heterogeneous in terms of global climatic types. These range from the monsoon-shaped subtropical south-eastern part of the Himalayas (no. 104) with extremely high tree lines up to 4000 m m.a.s.l. to the Eurasian winter humid subtropics in the Hindu Kush (no. 105) and the western Karakoram (no. 111), and to the north-western slope of the Hindu Kush Pamirs (no. 148) characterized by the winter humid continental dry climate. These also include the temperate climate of the Kunlun Shan (no. 122), the cold continental climate of Tian Shan (no. 203) on the Tarim Basin's edge, and the Borohoro Mountains (no. 35) (Fig. 2). The global climatic zones are strongly dominated by altitude and determine vegetation structure to a large extent (Schultz, 2005). Thus, the mountain ranges of Central Asia differ substantially from the other selected mountain regions of the arctic and temperate boreal zones of the northern and southern hemispheres, or the wadis of the Middle East. With exception of the Borohoro Mountains, these mountain ranges have maximum elevations of more than 7.150 m m.a.s.l. and comprise the highest peaks of the world. As a consequence, runoff from snow and glacier melt is very important for the rivers especially in the arid part of this region, even though the current ice cover ranges only from 2.7% to 14.5%. Several large rivers have their sources in these mountains, notably the Ganges, Indus, Brahmaputra, Yarkand and Ili Rivers.

In addition to the regional climatic complexity, vegetation spreads over several floristic provinces providing additional complexity for a comprehensive overview (Grubov, 2010). Information on these region's floodplain ecosystems is scarce and consequently we focus on the rivers of the Tian Shan, where scientific studies have been undertaken (Betz, 2021; Kamelin, 1973).

One distinctive riparian vegetation type in Central Asia is the Tugai floodplain forest. It extends far beyond the mountainous regions and is centered in the continental, cold winter deserts. These floodplain forests stretch from the middle reaches of rivers in the mountains to the lower reaches of the major inland rivers in Uzbekistan, Kazakhstan, Tajikistan (Fig. 16) and Turkmenistan. Major rivers include the Amu Darya and Syr Darya in the Aral Sea Basin. Tugai forests also occur along the Chu and Ili Rivers in Kyrgyzstan and Kazakhstan. Tugai forests have also been described in the eastern Tian Shan region along the Tarim River as well as in the Gobi Desert of Western Mongolia (Schulz and Kleinschmit, 2019; Tesch and Thevs, 2020; Treshkin et al., 1998). The key species of Tugai forests along the middle and lower reaches of the rivers are *Populus pruinosa* and *P. euphratica* (Aishan et al., 2015; Thevs et al., 2008, 2012). In the 'early successional ecologic phase', these poplars occur in association with *Elaeagnus angustifolia*, *Tamarix ramosissima*, *T. hispida*, *T. elongate*, *Halostachys caspica*, *Halimodendron halodendron*, *Alhagi sparsifolia* and *Myricaria pulcherrima* (Aishan et al., 2015; Thevs et al., 2008; Treshkin et al., 1998). In some cases, *Salix songarica* and *S. wilhelmsiana* also occur (Rüger et al., 2005; Treshkin et al., 1998). However, these species and *Populus pruinosa* were severely disturbed due to anthropogenic impacts to the river regime (Halik et al., 2019; Rüger et al., 2005). In the frequently inundated zone closer to the river, the 'biogeomorphic phase' is composed of a mosaic of *Populus euphratica* shrubs, *Phragmites australis* and *Calamagrostis pseudophragmites* (Thevs et al., 2008).

Tugai forests dominated by *Populus euphratica* stretch along the lower reaches of the Central Asian rivers and differ significantly from the riparian forests along the upstream river reaches in the mountains. Betz (2021) has described the riparian plants along the Naryn River in Kyrgyzstan, a braided gravel-bed river along most of its course. For the 'pioneer phase', juvenile individuals of *Salix babylonica*, *Populus nigra*, *Tamarix chinensis* and *Hippophae rhamnoides* are typical (Betz, 2021).

Fig. 16 A braided river section of the Obikhingo River valley in Tajikistan. (Photo: N. Lashchinskiy).

The most frequent species of the 'biogeomorphic phase' are *Hippophae rhamnoides* (Fig. 17), *Salix babylonica* and *Populus nigra*. The last species becomes dominant in the 'early successional ecologic phase' (Fig. 18). In its understory, thickets of *Rosa* spp., *Berberis vulgaris, Elaeagnus angustifolia* and *Caragana spinosa* are accompanied by *Carex* spp., *Artemisia vulgaris* and *Phragmites australis*.

This species composition is consistent with the findings of Imanbardieva (2015), for floodplain vegetation along the At Bashe River, a tributary of the Naryn River. River terraces form the boundary of the floodplain forests along the Naryn River, whereas

Fig. 17 Sallow thorn (*Hippophae rhamnoides*) is a typical species in the pioneer and biogeomorphic phases along the Naryn River, Kyrgyzstan. (Photo: F. Betz).

Fig. 18 Poplar forest (*Populus nigra*) on the floodplain of the Naryn River, Kyrgyzstan. (Photo: F. Betz).

hardwood forests of the late-successional stage are unusual (Betz et al., 2020; Betz, 2021). The absence of late-successional forests is also characteristic for the Central Asian floodplains, where climatic conditions lead to a transition of the early successional woodlands directly into forest-steppe, steppe or desert forests (Pfadenhauer and Klötzli, 2014).

In the middle reaches of the Western Tian Shan and Pamir-Alay rivers, and especially in valleys open to the west, there are riparian forests composed of *Fraxinus* species in the tree layer or forest canopy and well-developed, species rich herbaceous layers providing the understory (Kamelin, 1973, 1990; Lashchinsky et al., 2019). The mild climate of these valleys preserves *Fraxinus* forests as late-successional stage vegetation (Fig. 19) and these forests could be considered as relicts of Paleogene subtropical floodplain forests (Kamelin, 1973).

Fig. 19 *Fraxinus* riparian forest in the western Tian Shan mountains. (Photo: N. Lashchinskiy).

In the upper reaches of Pamir, Tian Shan and Pamir-Alay regional rivers, riparian birch forests with *Betula tianschanica* and *B. procurva* are common on the floodplains (Kamelin, 1973; Safarov, 2003). *Salix fragilis* is another common woody species in the riparian forests of Central Asia (Pfadenhauer and Klötzli, 2014).

There are relatively few alien plant species in the riparian forests of Central Asia, with *Ailanthus altissima* as the most common invasive plant for the 'early successional ecologic phase' of riparian forests in the middle reaches of the Tian Shan rivers.

Alps, Europe

The Alps in Europe (no. 12) (Fig. 2) have a mean elevation of 840 m and their maximum peak of 4.810 m with Mont Blanc in France. The moderate to Mediterranean climate with a mean annual temperature of 7.4 °C, mean precipitation of 1.023 mm and only about 1.2% glaciation of the mountain range allows for the development of extensive vegetation cover over about two thirds of the Alps.

The early human influences on the alpine rivers through 19th century included bank stabilization and later increased hydraulic-engineering and river regulations enabled human land use and resulted in current population densities of almost 100 inhabitants/km^2. About one third of the alpine river catchments is covered by settlements or croplands and the largest rivers of the Alps include the Rhine, Sava, Inn, Drava, Rhône and Tagliamento Rivers (Fig. 20).

The most active channels of braided rivers in the European Alps are dominated by gravel bars without vegetation. Less frequently disturbed bars are sparsely vegetated with herbaceous plants and shrubs, often with only a few species.

Characteristic plant species restricted to braided river corridors in the 'pioneer phase' include *Calamagrostis pseudophragmites, Chondrilla chondrilloides, Epilobium fleischeri, E. dodonei, Scrophularia canina* and *Typha minima*. These are accompanied by common species from the surrounding vegetation (Egger et al., 2019a; Kalníková et al., 2021).

For the 'biogeomorphic phase', *Salix eleagnos* is often the most frequent species of river corridors in the Alps. Further characteristic species are *Salix purpurea*, *S. daphnoides*, *Myricaria germanica* (Fig. 21) and *Hippophae rhamnoides* subsp. *fluviatilis*.

Less disturbed but regularly inundated floodplain areas characterize the 'early successional ecologic phase' with riparian forests dominated by *Alnis incana*. These extend up to an altitude of about 1.400 m in the Eastern Alps and 1.900 m in the Western Alps. The lower limit is about 250 m a.s.l. in the Southern Alps (Italian Eastern Alps) and about 900 m a.s.l. in the French Western Alps. In lower altitudes of the Western Alps *A. incana* (Fig. 22) is replaced by *Populus nigra* and in the Mediterranean locations, and complemented by *Populus alba*. In the lower Alps and the alpine foreland, *Salix alba* often dominates the floodplain forests.

Common deciduous trees of the 'late successional ecologic phase' are *Quercus robur*, *Carpinus betulus*, *Ulmus laevis*, and *U. minor*. Today these forests have become rare due to the extensive human impacts on the river ecosystems since the 19th century. On dry

Fig. 20 The Tagliamento river in the Southern European Alps (Italy) is the longest and largest remaining unregulated braided river of the Alps. (Photo: B. Kaltenböck).

Fig. 21 *Myricaria germanica* is well adapted to the high morphodynamics that characterize braided rivers like at the Upper Isar in the Alps. (Photo: I. Becker).

Fig. 22 The grey alder (*Alnus incana*) floodplain forest is the most widespread woodland community along the rivers of the Alps. (Photo: G. Egger).

gravel bars that are no longer inundated, *Pinus sylvestris* forests can be found throughout the Alps. The riparian corridors of the montane to subalpine zones are often associated with *Alnus alnobetula* and in the late successional phase with *Picea abies*.

In the European Alps, a large number of invasive non-native species especially from North America and East Asia have spread along the corridors of the braided rivers. The introduced plants are especially frequent in floodplains where river dynamics have been altered by humans and/or in floodplains at lower and warmer elevations. Most invasive species can be found in the 'pioneer phase,' including *Ambrosia artemisiifolia*, *Bidens frondosa*, *Impatiens glandulifera*, *Oenothera biennis* agg. and *Xanthium strumarium*. In the shrub communities of the 'biogeomorphic phase', *Amorpha fruticosa*, *Buddleja davidii*, *Fallopia japonica* and *Solidago canadensis* are frequent. In the understory of floodplain forests of the 'early successional ecologic phase', *Solidago gigantea* often competes with the native species. In floodplain forests of the 'late successional ecologic phase' *Ailanthus altissima* and *Robinia pseudoacacia* are frequent throughout the Alps (Egger et al., 2019b; Müller and Okuda, 1998).

Wadis in the Mountain Ranges of the Middle East

A different kind of gravel-bed rivers occurs in the tropical climate present in this region. The rivers are located in the mountain ranges at the western and southern coastal regions of the Arabian Peninsula, named as the Al Hajar (no. 7), Asir (no. 22), Hadramaut (no. 95) and Hejaz Mountains (no. 102). The Ogo Mountains (no. 145) in Somalia at the Horn of Africa are also included in this type (Fig. 2). Deil and Al Gifri (1998) distinguish three major montane vegetation types for the Arabian Peninsula, the: (1) north-western Mediterranean vegetation type (majority of annual rainfall of 50–150 mm in winter and early spring), (2) south-western Afro-montane type (majority of 200–500 mm of rainfall in spring and to a lesser extent in summer) and (3) eastern Omano-Makranian type (150–300 mm of rainfall mostly in the winter and early spring, with an additional summer rainfall peak in some years). The regional mountains were not glaciated in the last glacial maximum and remain non-glaciated today.

Wadis (or the Arabic, 'Oued') are river beds in the Saharo-Arabian desert. Water flow can be seasonal as in sub-humid mountains with a rainy season, or after short, heavy rainfall, which is episodic or erratic with the arid climate. These river systems are accompanied by common, near-surface groundwater flow. Big wadis with large catchments can have permanent water channels along parts of their length, but no permanent river drains into the Red Sea or the Gulf of Oman. In broader river valleys with low gradients and nearly flat plain deserts, sudden but infrequent heavy rainfall causes flash floods (the Arabic, 'Sayl') and the erosion, re-deposition and accumulation of sediments. This leads to the formation of braided channel patterns of mixed gravels and sands.

Braided wadis concentrate in the transition zone from the mountains of the Musandam Peninsula to the foreland, and from the Southwest Arabian Escarpment to the Central Arabian Desert, the Rea Sea coastal plain ('Tihama'). For the latter area, a typical sequence of hydrological conditions including the riverbed gradient, frequency and intensity of water flow, groundwater level and characteristic riverine plant species is presented with the example of Wadi Mawr (Yemen; Fig. 23). It is an allochthonous wadi, with

Fig. 23 Wadi Mawr in the Basin of At Tur, Mountainous Tihama, Jemen. Gallery thickets with evergreen shrubs (*Tamarix nilotica*, *T. aphylla*, *Salvadora persica*) colonize the sandy terraces. Terraces in the foreground were cleared for millet cultivation. (Photo: U. Deil).

Fig. 24 The Wadi Labtah, Syria, with remnants of gallery forest with broadleaved species (*Combretum molle*, *Berchemia discolor*, Combretaceae) and raingreen umbrella-shaped trees (*Acacia johnwoodii*, *Tamarindus indica*, Fabaceae). (Photo: U. Deil).

water flow in the semi-arid Basin of At Tur and the arid coastal plain triggered by rainfall events in the sub-humid upper parts of the catchment area. The sequence starts in the higher Escarpment with riverine trees of the 'late successional ecologic phase' such as *Breonadia salicina*, *Ficus* spp. (*F. vasta*, *F. populifolia*, *F. sycomorus*, *F. cordata* ssp. *salicifolia*) and the palm, *Phoenix reclinata*. These are replaced in the lower Escarpment and Mountainous Tihama by the broad-leaved, freshwater phreatophytes of the 'early successional ecologic phase' such as *Combretum molle*, *Berchemia discolor* and *Trichilia emetica* (Fig. 24). Sandy riverside terraces are colonized and stabilized by the *Acacia ehrenbergiana-Jatropha curcas-Desmostachya bipinnata* community of the 'biogeomorphic phase'. The riverbeds in the arid coastal plain (Tihama) contribute to this phase and are colonized by salt-tolerant evergreen *Tamarix* shrubs (*Tamarix nilotica*, *T. aphylla*), *Salvadora persica*, the flash flood resistant tall bunchgrass, *Saccharum spontaneum*, and by the soft-wooded shrub, *Calotropis procera* (Fig. 25). Intermittently flooded low terraces along broad wadis and active channels with fine grained sediments are covered with a layer of creeping and rooting herbs of the 'pioneer phase', including *Bacopa monnieri*, *Eclipta alba*, *Fimbristylis* spp. and *Phyla nodiflora* (Deil and Müller-Hohenstein, 1985; Patzelt, 2015). A liana veil with *Cissus quadrangularis*, *Leptadenia arborea* and *Cocculus pendulus* may border the riverine thickets.

Relief, substrate texture (grain size), hydrology and morphodynamics (stream velocity) are the main differentiating factors across the wadis. The vegetation patterns, characteristic plant species and life forms of a small wadi with remnants of gallery forests are documented by transects and riverside catenae by Deil (1986), Deil and Al Gifri (1998) and Deil and Müller-Hohenstein (1985).

Common wadi species throughout the Arabian Peninsula are *Tamarix* shrubs (*T. nilotica* s. str., *T. senegalensis*, *T. mascatensis*, *T. aucheriana*, *T. aphylla*) and tall bunch grasses of the genus *Saccharum* (*S. spontaneum*, *S. kajkaiense*, *S. griffithii*, *S. ravennae*). Additionally, *Jatropha* species (*J. glauca*, *J. pelargoniifolia*) characterize alluvial plains in the frost-free tropical lowlands, *Rhazya stricta* is common in the wadis with extratropical climates of the Arabian Peninsula (Deil and Al Gifri, 1998). In less arid conditions, *Rhazya stricta* is replaced by *Nerium* species (*N. oleander*, *N. mascatense*). A *Saccharum griffithii-Nerium mascatense-Dyerophytum indicum*-community was described from United Arab Emirates (Deil and Müller-Hohenstein, 1996) and further wadi species on the Peninsula are *Retama raetam* in the northwest, *Pistacia atlantica* in the north, and the widely distributed phreatophytes, *Prosopis cineraria* and *Ziziphus spina-christi*.

Intermittent water flow through the braided river corridors from the sub-humid mountains to the arid coastal plains is used for agriculture by diverting flash floods into walled fields (Sayl irrigation). Alluvial groundwater is overexploited by pumping for irrigation and by plantations of the deep-rooting date palm (*Phoenix dactylifera*).

A noxious weed and aggressive invader of sandy terraces and irrigation runnels is *Imperata cylindrica*. This plant has wide native ranges from Africa to Asia but is non-native to the wadis of the Middle East.

Fig. 25 *Saccharum spontaneum* and *Calotropis procera* stabilizing fine sediments in Wadi al Kharid, in the Eastern Yemeni highlands. (Photo: U. Deil).

Southern Alps, New Zealand

The Southern Alps on the South Island of New Zealand (no. 191) (Fig. 2) are characterized by temperate rain forests in the west, partially glaciated summit regions (current ice cover 2.6% of mountain range) with extremely high precipitation of 3.000–4.000 mm/year or more in the central region, and progressively drier lowlands to the east. Here, a number of large, braided rivers such as the Rakaia, Rangitata and Waimakariri (Fig. 26), with riverbeds up to about 500 m wide, flow eastward from the Southern Alps.

Species of the genus *Raoulia* are the most frequent and characteristic plants in the 'pioneer phase' of the extensive braided river corridors. On dry gravel alluvia in the mountain valleys with moderate to high rainfall, the lichen species *Raoulia tenuicaulis, R. haastii, R. monroi, R. parkii* and *R. australis* are widespread. These are associated with *Epilobium* species such as *E. brunnescens, E. nummularifolium* subsp. *nerterioides, E. microphyllum, E. melanocaulon* and *E. glabellum* (Meurk and Williams, 1989; Wardle, 1991; Woolmore, 2011; Fig. 27). Additionally, there are common widespread grasses such as *Lachnagrostis lyallii* and *L. filiformis*, and along the subalpine and lower alpine gravel-bed rivers also *Rytidosperma setifolium* and *Poa novae-zelandiae* (Wardle, 1991).

The most widespread shrub of the sparsely vegetated 'biogeomorphic phase' is *Coprosma brunnea*. Further woody plants on stabilized alluvium include *Muehlenbeckia axillaris*, *Coprosma brunnea* and additionally *Helichrysum depressum*, *Carmichaelia nigricans*, *C. grandiflora, Discaria toumatou* and *Leptospermum scoparium*, along with the mosses, *Polytrichum juniperinum* and *Racomitrium* spp. (Wardle, 1991; Meurk and Williams, 1989; Müller et al., 2017).

In the western region of the South Island, there are still natural floodplain forests of the 'ecologic phase', as described by Miller (2004). The most common species in the canopy and sub-canopy of these 'late successional' communities are the conifers *Dacrycarpus dacrydioides, Dacrydium cupressinum, Prumnopitys ferruginea,* the evergreen tree *Leiospermum racemosum,* and *Nothofagus menziesii*, the most widely distributed beech taxon in New Zealand. In the upper shrub tier, the tree fern *Dicksonia squarrosa* is very common.

In contrast to the western slopes, the lowlands in the east had already been extensively cleared by the turn of the 20th century, and the natural riparian forests are highly fragmented.

Under natural conditions, the flora of New Zealand is characterized by about 80% endemic species (McGlone et al., 2001). Today, many river corridors are dominated by alien species, with abundances of up to 60% (Williams and Wiser, 2004). While the headwaters still tend to be dominated by native species, the lower river reaches are often dominated by alien, non-native plants (Woolmore, 2011). Additionally, alien species cover is higher in rivers with higher maximum flows, especially in areas with fine substrate textures and on higher terraces along the rivers (Brummer et al., 2016). Frequently, invasive non-native species from the

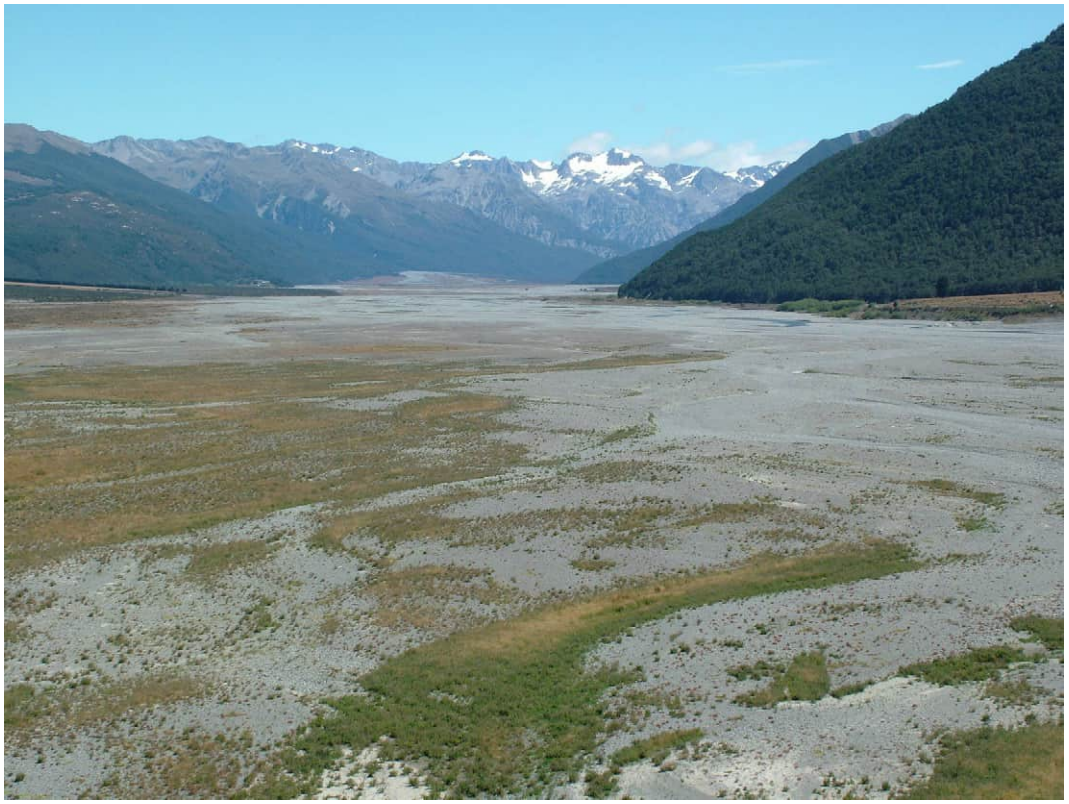

Fig. 26 The upper reach of the Waimakariri River near Arthur pass is typical of the braided rivers in the Southern Alps of New Zealand. (Photo: N. Müller).

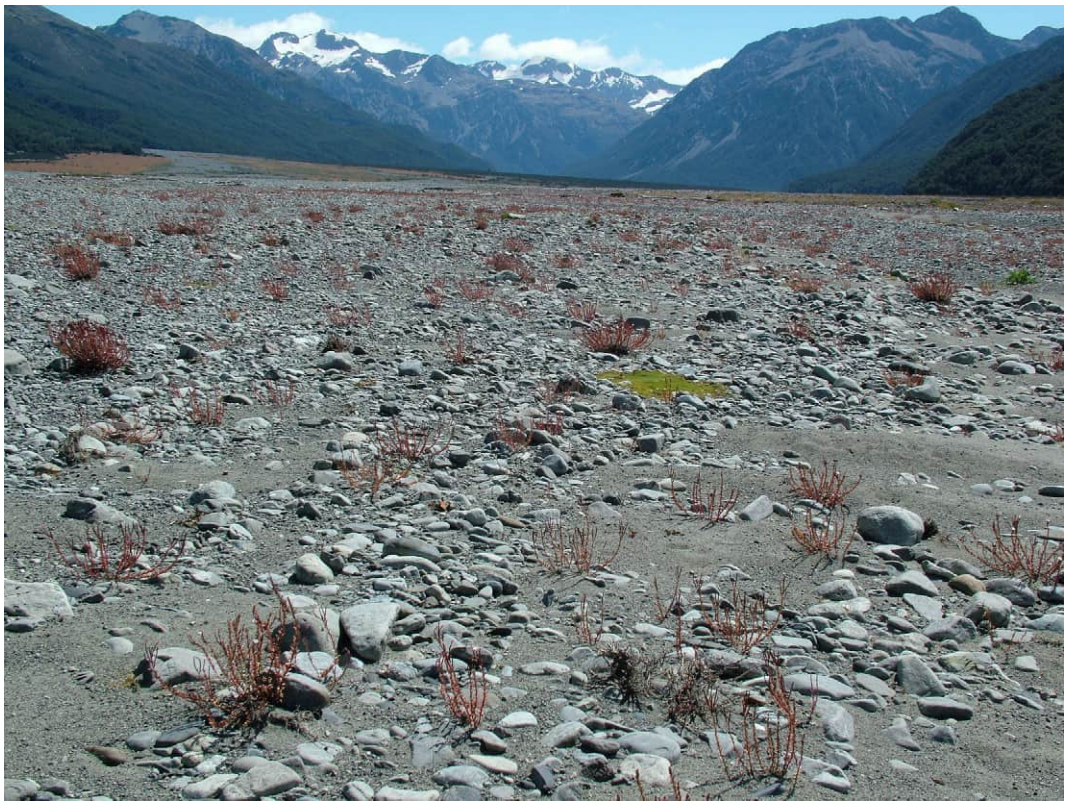

Fig. 27 In the headwater and upper reaches of rivers from the Southern Alps of New Zealand, native and endemic species (here, *Epilobium melanocaulon*) are typical for the pioneer phase. (Photo: N. Müller).

Fig. 28 Along the lower reaches of some New Zealand rivers, invasive non-native species (here *Cytisus scoparius* and *Lupinus polyphyllus* flowering) are dominating from the pioneer to the early successional ecologic phase. (Photo: N. Müller).

'pioneer phase' to the 'early successional ecologic phase' include the European grasses, *Agrostis capillaris*, *A. stolonifera*, *Anthoxanthum odoratum*, *Holcus lanatus*, *Festuca rubra* and *Dactylis glomerata*, the European herbs, *Crepis capillaris*, *Hypochaeris radicata*, *Lotus corniculatus*, *Plantago lanceolata*, *Trifolium repens*, *T. arvense*, *Rumex acetosella*, and *Sedum acre*, and the North American forbs, *Lupinus arboreus* and *L. polyphyllus* (Fig. 28). Widespread invasive shrubs include *Cytisus scoparius*, *Rosa rubiginosa*, *Salix* x *fragilis*, and *Ulex europaeus*—all originating from Europe (Müller et al., 2017; Williams and Wiser, 2004; Woolmore, 2011).

Southern Andes, Patagonia

The Andes in South America are considered as the Patagonian Andes (no. 228) (Fig. 2) south of Rio Bio Bio in Chile and Rio Colorado in Argentina. By moving from North to the South, climate changes from moderate to boreal arctic. Further, the Andes act as barrier for precipitation originating from the Pacific Ocean and consequently the Argentinean regions are much drier than those in Chile (Fig. 29). The tree line in the south is very low at about 400 to 600 m a.s.l., and rises in the north to about 1.000 to 1.700 m. Currently, glaciers cover almost 11% of the mountain range and in the last glacial maximum almost 75% was glaciated. The largest rivers are the Colorado, Negro, Chubut and Santa Cruz Rivers.

In Patagonia, the riparian zones are characterized by relatively low plant species richness as well as many other Patagonian ecosystems (Kellman, 1970). This is likely a result of the glaciation history (Mendelova et al., 2017), isolated location and restricted landmass of the Southern hemisphere, which limited colonization from other regions. The few specialized species of the floodplains (Lewerentz et al., 2019) are also distributed in areas with frequent and intense disturbance regimes like landslides and volcanic lahars. These areas of huge sediment loads are common in the vicinity of areas with volcanic activity (Iroumé et al., 2020) or glacial lake outburst floods (Ulloa et al., 2020).

The open gravel and sand bars provide the 'pioneer phase' of the gravel-bed rivers of Patagonia and are characterized by native pioneer plants such as *Agrostis inconspicua*, *Juncus scheuchzerioides*, *Gunnera magellanica* and *Acaena magellanica*, as well as non-native species such as *Plantago lanceolata*, *Prunella vulgaris*, *Trifolium repens*, *Holcus lanatus*, *Hypochaeris radicata* and *Agrostis stolonifera* (Fig. 30). In addition, there are native shrubs such as *Gaultheria mucronata*, *Berberis microphylla* and *Discaria chacaye*, while *Baccharis obovata* may be the most abundant. These species establish sporadic stands in the highly disturbed 'pioneer phase' along the active channel and form patchy to closed shrub layers in the later 'bio-geomorphological phase'. The taller native shrubs, *Escalonia virgata*, *Fuchsia magellanica* and *Berberis empetrifolia* and the non-native evergreen bamboo *Chusquea culeou*, are typical for the 'early

Fig. 29 The catchment area of the Rio Blanco is mainly located in the Parque Pumalín nature reserve near Chaitén, Chile and is characterized by an extensive and largely natural forest landscape. (Photo: G. Egger).

Fig. 30 Pioneer phase with buzzy burr (*Acaena magellanica*) at Rio de los Ñadis, Chile. (Photo: G. Egger).

successional ecologic phase' of the regional riparian forests (Harmel, 2020). The only willow species of the natural flora is *Salix humboldtiana*, which occurs sporadically in the floodplains of northern part of Patagonia (southern limit 38^{0} S).

In general, in the 'ecologic phase' for these riparian communities the shrubs display higher species diversity while there are fewer tree species. The trees are commonly represented by the deciduous *Nothofagus antarctica* in the south and evergreen *Nothofagus dombeyi* in the north and/or rainier climate zones. While *N. antarctica* stands are rare, these do occur both as early successional stands on open gravel bars and as mature forests in the inactive floodplain zones. Evergreen tree species usually predominate in the 'late successional ecologic phase' of the riparian forests. They are often associated with further characteristic trees of Valdivian temperate rain forests, including *Luma apiculata and Podocarpus nubigenus,* and of deciduous forests of the temperate zone in Chile, such as

Fig. 31 Species-rich floodplain forest (late successional ecologic phase) along the River Palena, Chile. (Photo: G. Egger).

Nothofagus pumilio, *N. betuloides*, *Pilgerodendron uviferum* (Gut, 2008; Vidal et al., 2011) and occasionally, *Amomyrtus luma* and *Embothrium coccineum* (Harmel, 2020) (Fig. 31). In contrast to the pioneer woody plants from the genera *Salix* and *Populus*, these species hardly germinate on the open gravel and sandy areas of the active channel, but establish on morphologically more stable substrates of the biogeomorphic and ecologic succession stages (Lewerentz et al., 2019).

Perhaps the most noteworthy aspect of Patagonian floodplains and riparian zones is the high abundance and sometimes complete dominance by alien plant species. Besides a potential vacant ecologic niche due to the lack of fast-growing early successional woody species and woodland phase, the invasion is facilitated by river regulation, road construction, a legacy of landscape scale wildfires, and clearing by logging and ranching activities. In this context, it is important to recognize the massive spread of the North American *Lupinus polyphyllus* in the 'pioneer phase' (Meier et al., 2013) and the European *S. fragilis* in the 'biogeomorphic' and 'early successional ecologic phase' (Harmel, 2020; Lewerentz et al., 2019; Fig. 32). In addition, a variety of alien woody species are common, including *Elaeagnus angustifolia*, *Rosa rubiginosa*, and *Cytisus scoparius* (Weber, 2017).

Fig. 32 *Salix fragilis* invades gravel bars at the Rio de los Ñadis, Chile. (Photo: G. Egger).

Conclusion and synthesis

The species composition of the riparian vegetation of gravel-bed rivers is differentiated according to the global floral regions. Thus, the global research indicates that only a few naturally occurring species or even only a few genera are more common at several reference mountain regions (see Table 1).

The majority of the investigated mountain regions with a high proportion of braided rivers are located in the boreal zone of the Northern Hemisphere such as the investigated mountain ranges of Alaskan Taiga, the Canadian Rocky Mountains, and the northeast Siberian Mountain ranges of the Russian Taiga (Maier et al., 2022). These boreal to sub-Arctic regions share common characteristics in climate and vegetation. Thus, the biogeomorphic phase is similarly occupied by a number of widespread, floodplain-typical ecologic pioneer tree and shrub species of the related genera *Salix* and *Populus* (Karrenberg et al., 2002). Further, native representatives of the genera *Myricaria* (Alps, Central Asia) and *Tamarix* (Central Asia) are also typical for the northern hemisphere. These species are characterized by prolific production of small, light seeds that are dispersed over wide areas by wind and water, the processes of anemochory and hydrochory, respectively. The obligate or facultative riparian plants also often display effective vegetative or clonal reproduction through root suckers or stump shoots. With typically vigorous growth, these ecological specialists are well adapted to the strong hydro-morphodynamics of the gravel-bed rivers.

Poplars (*Populus* spp.), willows (*Salix* spp.) and tamarisks (*Myricaria* spp., *Tamarix* spp.) are naturally absent along the braided river corridors of the Southern Hemisphere, where there are fewer woody pioneer species restricted to the riparian ecosystems or floodplain zones (Meier et al., 2013). This results in open niches that are available for colonization by the introduced Northern Hemisphere pioneer shrubs and trees, especially along the lower reaches of gravel-bed river corridors where agricultural and urban areas are increasing. This has resulted in severe invasions and serious alterations to the native biodiversity, as documented for the braided river corridors of the Southern Andes in Patagonia and for the Southern Alps in New Zealand (Budde et al., 2011; Caruso et al., 2013; Lewerentz et al., 2019; Harmel, 2020).

In contrast to the braided river corridors of the temperate zones, the Alps, Southern Andes and Rocky Mountains, the dominant tree species in established forests of the late successional ecologic phase differ in the Arctic zones, the Alaskan and Russian Taiga. In the Arctic taiga, conifers (*Picea* in North America or *Larix* in Eastern Russia/Siberia) that are adapted to the long, very cold winter months and very short vegetation period dominate the late successional ecologic phase. In contrast, in the temperate zones, flood-tolerant deciduous trees prevail, often from the genera *Quercus, Ulmus* or *Fraxinus* (Pfadenhauer and Klötzli, 2014).

An unusual case of the Arctic boreal zone is displayed with the very young riparian ecosystems of the glacier forelands of the Arctic tundra below the extensively glaciated mountains of Vatnjajökull (Iceland). Iceland was almost completely covered by ice during the last ice age (Hallsdóttir, 1995) and today there are very few endemic plant species. This is explained by a continuous long-distance influx of seeds and clonal vegetative fragments by ocean currents, winds or birds following the Holocene and even earlier (Rundgren and Ingólfsson, 1999). At present, most of the glacier forelands of the Arctic tundra are covered by young successional stages. Also, there are no native conifer trees in Iceland, which contrasts with comparable climatic areas within the boreal zones in Alaska, Canada and Russia. These trees of the late successional phase did not survive the ice ages in Iceland, and due to the isolated island location have not immigrated until recently (Hallsdóttir, 1995).

The continental floodplains of the inland rivers in Central Asia contrast to the riparian forests of the boreal and Arctic zones. In Central Asia, the early successional riparian forests of the ecologic phase tend to develop within a narrow corridor along the river channels and are often threatened by anthropogenic activities. Closed canopy, late successional riparian forests are mostly absent due to the arid climate.

The wadis of the Middle East represent very distinctive gravel-bed river corridors. Accompanying the hot and dry climates, the active channels are often intermittent and are predominantly characterized by sparse phreatophytic floodplain vegetation such as *Nerium* spp. and *Rhazya stricta* along with a number of species of the genus *Tamarix*.

It is notable that almost no endemic species occur in the river corridors of the reference regions in the Northern Hemisphere. The reason for this may be that the reference regions with a high proportion of braided rivers are mainly found in young (tectonic uplift) mountains and in most cases were covered by glaciers during the last glacial maximum. As a consequence, the time was too short and the environmental conditions too variable for the development of endemic species over the recent geological eras.

In contrast, the braided river corridors of the Southern Alps in New Zealand show a different pattern, with a flora dominated by endemic species in all succession phases. Most of those characteristic endemic species are woody plants, as reported by McGlone et al. (2001). These patterns originate in the long history of geographical and evolutionary isolation (McGlone et al., 2001).

Due to the biogeographic isolation by the surrounding oceans and the dry steppe to desert ecoregions in the east and north, the region of the Patagonian Andes is also characterized by a high proportion of endemic species (Rozzi et al., 2012). The endemic, riparian *Nothofagus* species also form the world's southernmost forests (Rozzi et al., 2012).

In addition to these riparian patterns, as revealed in Table 1, the majority of the selected characteristic plant species are not limited to floodplains, but are also present in adjacent, upland ecosystems. The plants are well-adapted to the local temperature regimes and display plant adaptations to the dynamic site conditions along the braided channels of the gravel-bed rivers. These life history requirements and ecophysiological adaptations also allow establishment in other regional sites with similar physical characteristics, such as with the rocky and stony habitats in the mountain regions, or in other disturbance-prone locations such as avalanche paths (Williams and Wiser, 2004).

See Also: Structures and functions of Inland Waters - Groundwater: The Ecology of Aquatic Cave Environments; Structures and functions of Inland Waters - Rivers: Riparian Zones; Stream Geomorphology

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Wetland Plants: Adaptations, Classification, Ecology and Distribution

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This is an update of J.K. Cronk, M.S. Fennessy, Wetland Plants, in Encyclopedia of Inland Waters, Edited by: Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00060-0.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Aquatic An aquatic organism lives in the water. If it is semi-aquatic or amphibious it can tolerate both a terrestrial and aquatic environment and inhabits the water only partially (Fig. 1).

Ecosystem services This term comprises different kinds of direct or indirect benefits people obtain from ecosystems such as provisioning services (e.g., natural resources, energy production), regulating services (e.g., climate, hydrology, erosion), supporting services (e.g., nutrient and biogeochemical cycles, soil formation, habitat provision) and cultural services (e.g., heritage, education, science, ecotourism).

Hydrophytes Plants which have vegetative parts submerged or floating at the water surface, but not emerging into the air, and which survive unfavorable seasons as submerged buds attached to the parent plant or lying free on the substrate. This excludes emergent herbaceous plants and woody species.

Macrophytes Aquatic macrophytes are plants that grow in water, in soil covered by water, or in soil that is usually saturated with water.

Neophytes Non-native plant species which has been introduced in recent history to a geographical region.
Sessile A sessile organism cannot move, it is permanently attached to a solid surface, such as the soil.
Submergence Complete submergence means that the whole plant is below the water line. Totally submerged plants have no direct contact with atmospheric oxygen, and sunlight is weak or extinguished.
Terrestrial A terrestrial organism lives only on land and not in water.
Waterlogging When the soil and root system is filled with water, plants are waterlogged. They may even have a part of their stems or crowns submerged, but much of the shoot remains above the water line. This way, the transpiring organs—the leaves—still have direct contact with atmospheric oxygen and sunlight.
Wetland Wetlands occur at the interface between aquatic and terrestrial environments and may be continental or coastal, natural or artificial, permanently or periodically inundated by shallow water or consist of waterlogged soils. Their waters may be fresh, or highly or mildly saline. Wetlands are home to specific plant and animal communities adapted to their hydrological dynamics.

Introduction

Inland waters are colonized by all sorts of plants which occur in all regions of the globe, from the hottest desert oases with temperatures that can reach 58 °C, to the coldest regions like parts of Antarctica without ice (Sculthorpe, 1985). They grow below or

Fig. 1 The strong roots of a tree that grows on solid rock in the middle of a small river bed (Brague river, Southern France; photo © Pia Parolin).

Fig. 2 Temperate riverside forest (Brague river, Southern France; photo © Pia Parolin).

above the water surface, may have roots in the submerged ground or may float, ranging from minuscular algae to huge trees (Fig. 2). Some wetland plants are specialized in life between a flooded and a dry period, others live constantly in the water.

All life forms, from small buoying macrophytes over long herbs, endless vines to huge woody stems can be found. They all have in common that, from a terrestrial life, the evolution led to adaptations for life in an aquatic environment with high tolerance to flooding or even submergence.

The aim of this chapter is to give an overview of what life of wetland plants is all about, show an overview of their most important adaptations and ecology and indicate which are critical constraints they face.

What is a wetland plant?

Wetland plants occur in or near lakes or rivers. Here, we deal with freshwater environments, and with plants which are flooded for some hours or days or even weeks and months. Some can cope with prolonged waterlogging over several years, and some can even withstand total submergence for several weeks. Others are totally dependent on a submerged life, but here we focus on those that grow at the interface between water and air and must cope with a flooded and a dry period. Algae, mosses and lichens have a huge diversity in wetlands, but our focus is on flowering plants which are highly evolved, i.e., grasses, shrubs, trees and vines.

There is a gradual transition from terrestrial to aquatic conditions and it is impossible to establish sharp distinctions between swamp-forests and forests on dry land. It is a continuum, with boundary zones at the limit between marshes and terrestrial habitats. Depending on flooding depth, plants may be floating or growing in soil which is covered by water. As a result of excessive water content of the soil, they are subjected to periodic deficiencies in oxygen supply to their roots.

Higher aquatic plants are basically terrestrial organisms which evolved back to a life in water. Some can merely withstand a flash flood; others maintain an active physiological rhythm despite the constraints that flooding brings. Their differing tolerance to water in the root zone is linked to specialized morphological structures and all kinds of adaptations which allow them to cope with flooding. Without specific adaptations, higher plants cannot grow in wetlands.

Flooding constraints

Flood effects have manifold implications for sessile organisms such as plants.

(a) High mechanical stress: the dynamics, current and erosion of the river system cause mechanical damage to plants and can inhibit the establishment of seedlings.
(b) Inhibition of gas exchange and photosynthesis due to water and hypoxia. Gas is less present in water than in air. The diffusion coefficient of oxygen in the water is much lower than in the atmosphere. Therefore, as soon as water covers the soil, hypoxic conditions appear in the rhizosphere. Decomposition and high sedimentation rates further increase the lack of oxygen for the roots, which in order to function properly, need gas exchange and the presence of oxygen for respiration.
(c) Soil flooding lowers the redox potential and leads to the formation of trace gases (N_2O and CH_4) as well as to the formation of phytotoxic compounds (Mn^{+2}, Fe^{+2}, H_2S). Increased solubility of mineral substances and drastic changes in nutrient bioavailability are linked to flooding and may cause problems for plant ecophysiology.
(d) High sedimentation rates in rivers cause mud layers on leaf surfaces and impair leaf photosynthesis under water by turbidity and deposition of sediment layers on leaf surfaces. Sedimentation may also bury roots near the soil surface (Wittmann and Parolin, 2005).
(e) Changes in water levels may occur very fast and do not leave time to adapt with a quick physiological or anatomical response.
(f) Not enough, in the low water period drought may severely affect plants which are highly specialized to withstand exceeding water quantities. Drought causes particularly heavy stress for wetland plants.

Waterlogging vs. submergence

The level of flooding matters: for plants it makes a huge difference whether the whole plant is submerged and no gas exchange is possible at all, or whether parts of the roots and stem are waterlogged but the leaves are at least partly above the water surface (Fig. 3). Flooding height therefore has a key role and determines the species composition along a flooding gradient.

Another key factor is the predictability of flooding. If flooding occurs at a regular and thus predictable rhythm, a bit like a cold winter season in the temperate regions, then the plants can develop specific adaptations which allow them to survive the flooded period.

As an example, in Central Amazonia the river levels rise as much as 9 m where forests grow. This has an extreme impact on all organisms living there. But since the periodicity is strictly rhythmic and repeated—we speak of a monomodal flood pulse—every year at the same time (Junk et al., 1989), flooding does not kill the plants but enhances the development of diversity and species richness. Slight differences in height and duration of floods occur in different years, but—at least prior to climate change (Barichivich et al., 2018)—the living conditions are regular and predictable. Floods and droughts still occur in the time of the year, but due to global climate change, the amplitude of the flood pulse changed, mainly due to the increasing frequency and magnitude of severe flood events.

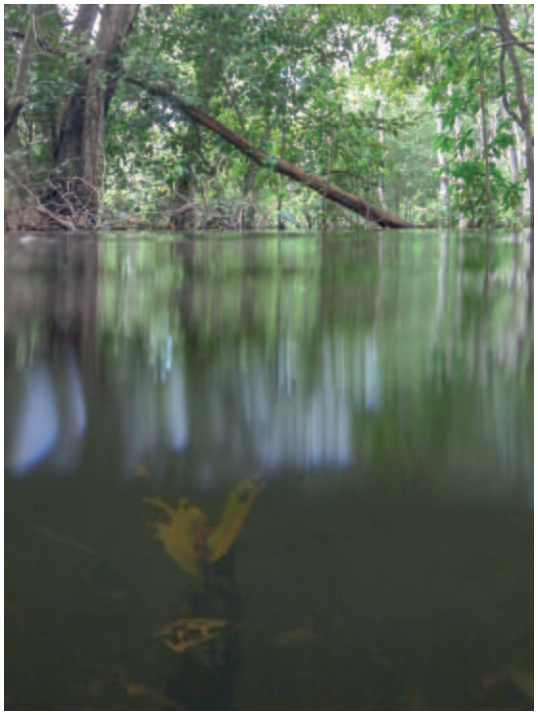

Fig. 3 Floodplain forest (Pantanal near Cuiabá, Brazil; photo © Pia Parolin).

In contrast, in temperate European floodplains such as those of the river Rhine, the periods of high water and flooding are short and unpredictable, which makes them much more difficult to withstand. Even so, trees that may survive flooded periods of up to 300 days per year, such as *Salix alba*, do also occur here.

Central Amazonia has some of the most extreme flooding conditions for plants and yet the floodplains are colonized by highly diverse forests (Fig. 4). Under these extreme conditions the natural limit for tree growth is where the annual flooding does not

Fig. 4 Central Amazonian black water floodplain forest near the Anavilhanas archipelago, Brazil (photo © Pia Parolin).

exceed 8 m of height. In the vicinity of Manaus, this corresponds to a flooded or submerged period of 300 days per year. The regularity of the flood pulse and mostly absence of salt and fires there allow for a highly diverse ecosystem. However, during extremely low water levels and dry periods, fire becomes an important problem for plant establishment and growth.

Tropical or temperate, does it make a difference?

The timing of flooding plays a crucial role. If a plant is dormant and without leaves, e.g., in a temperate winter, flooding of the roots is not deleterious to the whole plant. Physiological activities are downregulated.

However, if flooding occurs in a period when the plants grow—in a temperate summer, or in a tropical environment with high temperatures all year round, then flooding poses serious constraints.

Therefore, even in tropical environments trees may interrupt or lower their metabolism to survive with a decreased growth rate. The unfavorable growth conditions with inhibited water and nutrient absorption are tolerated until the plant takes on growing again, which is possible due to specific adaptations. In environments with a periodical regular flooding, trees may therefore form clear annual growth rings, superficially similar to those we find in temperate trees.

Concepts and their meaning for plant life

Flood pulse concept

The flood pulse concept (FPC; Junk et al., 1989) states that the regular alternation between a flooded and a non-flooded period is the driving force in a floodplain system. Where the periodic inundation and the dry phase occur at predictable intervals and alternate in foreseeable patterns, the plants and animals are able to adapt and follow the all-determining hydric rhythm. This concept is an integrative approach for studying highly diverse and complex ecological processes in floodplains.

Intermediate disturbance hypothesis

The "intermediate disturbance hypothesis" (Connell, 1978) states that disturbance may be a driving force for diversity. If we consider the high dynamics of an inland water system and flooding as a disturbance, in many ecosystems this disturbance will be an intermediate force which increases habitat diversity by erosion and sedimentation, or simply due to hydraulic stress. Flooding with freshwater represents a stressor which imposes only a low level of restrictions on the life of plants. This way, these forces lead to higher plant diversity.

The point of non-return hypothesis

The "point of non-return hypothesis" (Wittmann et al., 2010) states that part of the species adapted to the flood pulse may result from ecotypes originating from the pool of upland species associated with small streams, which gradually develop adaptations along the drainage systems. This allows them to tolerate gradually higher, prolonged, and predictable floods, as they migrate from small bodies of water to the large rivers. Finally, they acquire adaptations that no longer allow them to compete and colonize environments without large flood pulses. This hypothesis is valid for tropical regions with longstanding stable hydrological conditions, such as the Amazon, where plants adapted to regular flood pulses over evolutionary time scales.

Classification

All major groups of plants are represented in wetlands. They belong to families which are exclusively aquatic or to families with aquatic, palustric and/or terrestrial representatives (Junk, 2021).

Several classification systems exist for higher plants growing in wetlands. Here, we present one that Brazilian scientists elaborated for large floodplains. It splits the higher plants growing in wetlands into plants which grow in permanently terrestrial macrohabitats and into hydrophytes (according to the definition of wetland delimitation, Junk et al., 2014).

Those growing in permanently terrestrial environments include herbaceous and woody plants without specific adaptations to wet conditions which would harm them. Hydrophytes on the other hand are truly adapted and range from herbaceous free-floating or rooted species to woody species (Fig. 5).

Some herbaceous hydrophytes grow mainly during the aquatic phase (aquatic macrophytes *sensu strictu*), whereas others grow during the terrestrial phase. Among the former, the aquatic macrophytes *sensu strictu*, there are rooted herbaceous plants which can be emergent (e.g., *Typha, Echinochloa, Cyperus*), have floating leaves (e.g., *Nymphaea, Victoria*) or be submersed (e.g., *Utricularia foliosa, Cabomba*) (Figs. 6 and 7).

Free floating plants also include species which are almost fully emergent (e.g., *Eichhornia azurea*—Fig. 8, *Pistia stratiotes*) or where only the leaves float on the surface (e.g., *Lemna, Spirodela, Azolla, Limnobium*) or which are fully submersed (e.g., *Ceratophyllum, Wolffiella*).

Finally, woody plants are categorized depending on the influence of the flooding water (Fig. 9). Some can grow where the soils are permanently saturated with water or covered by a sheet of shallow water. Others grow in areas subjected to frequent predictable flood pulses of short duration. And yet others, namely riparian forests, grow in areas subjected to frequent unpredictable flood pulses of short duration or to predictable flood pulses of long duration. Interestingly, the absence of woody species in some habitats of savanna floodplains is not because of excess of water but because of drought stress during the dry period.

Fig. 5 Submerged *Apalanthe granatensis* (*Hydrocharitaceae*) in the Amazon river, with a matamata turtle (*Chelus fimbriatus*, right bottom corner; photo © Pia Parolin).

Fig. 6 Rooted herbaceous plants with floating leaves: *Victoria amazonica* in the floodplains near Manaus, Brazil (photo © Pia Parolin).

Fig. 7 Rooted grasses on the Amazon river (near Belém, Brazil; photo © Pia Parolin).

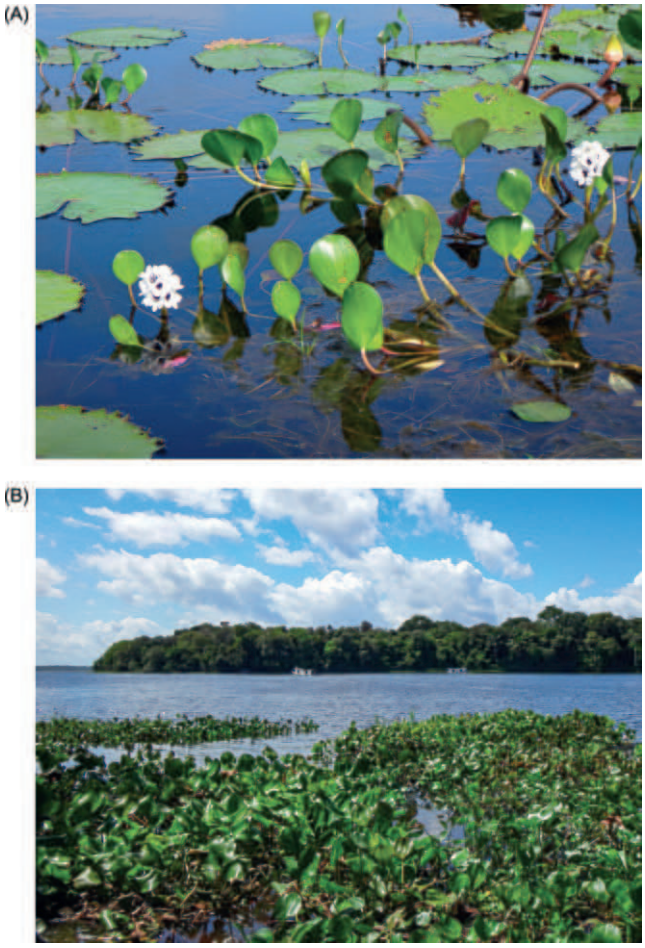

Fig. 8 Floating emergent herbaceous plants: *Eichhornia azurea* (left), in its natural environment with floodplain forests in the background on the Amazon river (right) (near Belém, Brazil; photos © Pia Parolin).

Fig. 9 Floodplain forest with a closed canopy subjected to predictable flood pulses of long duration in Amazonia, Brazil (photo © Pia Parolin).

Ecology

Adaptations

Plant life is not possible without adaptations to the specific constraints imposed by waterlogging and submergence (Hook, 1984). The adaptations are manifold, and different plant species may have evolved different amounts and combinations of responses (Goncalves et al., 2021; Householder et al., 2021). Many responses may have developed several times in certain orders, families, or genera. These enable them to colonize specific habitats within the wetlands, with more or less flooding durations and height.

Specific adaptations at the leaf level include anatomical and morphological structures which allow the leaves to perform photosynthetic activity. Xeromorphic leaves which are thicker than usual are an adaptation against lack of water. This is caused by the inhibited root function. Even if a plant is standing in the water, it can suffer from a shortage of water because the roots are less functional. Where flooding is very intense, plants may respond with leaf shedding and a reduction of their metabolism. Others are able to maintain their leaves below water for many weeks (Fig. 10).

At the stem level, typical adaptations include periodical growth reductions of stem increment, stem water storage, internal oxygen transport and pressure ventilation. Adventitious roots and hypertrophied lenticels are morpho-anatomical structures which are mainly formed by the stem.

The roots are adapted in that they can form lysigenous and shizogenous aerenchyma and produce increased intercellular spaces for gas diffusion. Suberization is frequently encountered as well as structures promoting the diffusion of oxygen and anaerobic metabolism. Roots are also able to switch to anaerobic metabolism (Fig. 11).

Water is an important means of dispersal in wetlands (Van der Pijl, 1982). Therefore, in many wetland species the peak of fruiting occurs at high water (Fig. 12). This way, the fruits or seeds drop into the water and are dispersed by hydrochory (Van der Pijl, 1982) or by fish (Goulding, 1983; Horn et al., 2011).

While in the majority of land plants seeds lose their viability if submerged, in wetlands many fruits and seeds float or sink and remain viable (Sculthorpe, 1985). Whether they float or sink, in general they do not germinate until the flood recedes and the conditions are favorable for seedling growth.

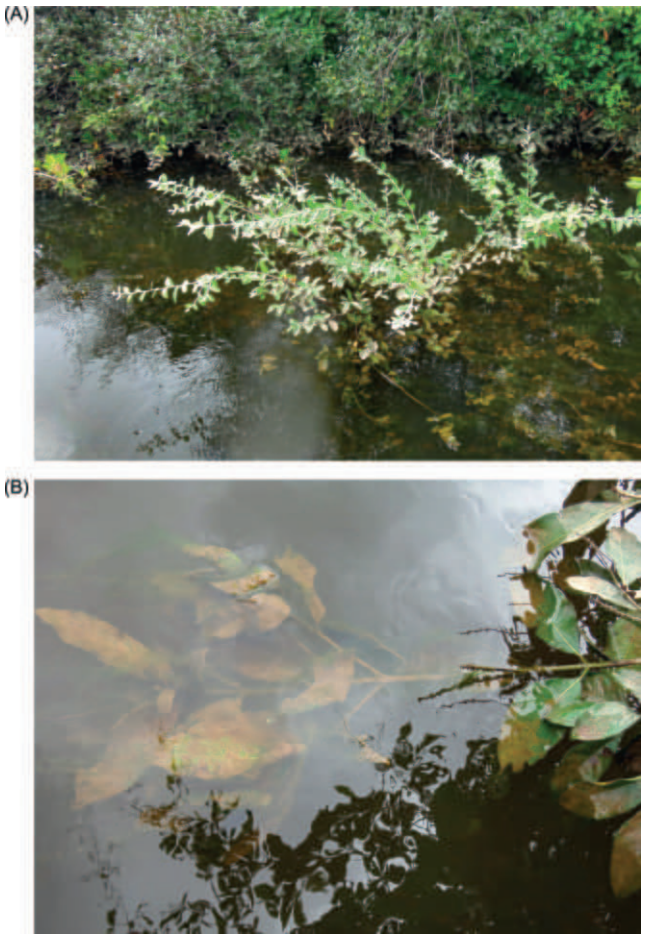

Fig. 10 Waterlogged shrubs (left) with submerged leaves (right) (Pantanal near Cuiabá, Brazil; photos © Pia Parolin).

Fig. 11 Aerial roots—pneumatophores—of the palm tree *Mauritia flexuosa* (Amazon river near Belém, Brazil; photo © Pia Parolin).

Fig. 12 Waterlogged tree flowering at high water, in the Amazon floodplains (photo © Pia Parolin).

As an example, in the swamps of the southern United States trees like *Taxodium distichum*, *Nyssa aquatica*, and *Nyssa sylvatica* do not germinate under water. The natural regeneration is limited to dry periods, when the soil surface is exposed (Hook, 1984). A fine-tuned mechanism of dormancy enables the diaspores to start germinating immediately after the retreat of the flood. As long as the seeds are in the water, they remain dormant and viable. Especially where the dry phase is very short, rapid and exactly timed seed germination is essential for the establishment and survival of the seedlings.

The diaspores—the units of dispersal of a plant—have adaptations to improve floatation, e.g., spongy tissues and air-filled spaces. Once the flooded period is over, germination starts. In a few cases, seeds may initiate germination while still floating. The emergence of a radicle was observed in the seeds of several tree species from Amazonia (Fig. 13). This is seen as a strategy to gain competitive advantages and may have ecological significance in specific environments (DuBarry, 1963; Oliveira-Wittmann et al., 2007).

The newly established seedlings will soon be exposed to the next flooded period. Therefore, in wetlands the species are highly adapted also in terms of tolerance of submergence and dormancy of the very young plants. They are too small to maintain a part of their stem and leaves above the water surface. But they will not succumb to submergence and withstand exceeding water levels (Fig. 14).

The combination of adaptations results in well-diversified species pools. Different tolerances to flooding result from specific structures of roots, stems and leaves. This leads to species-specific distributions and to zonations along the flood gradient (Fig. 15).

On the high levels in the flooding gradient, many adaptations are directed towards "escaping" submersion (Parolin, 2002). Since the water levels usually do not cover the whole plant, the responses are targeted towards obtaining oxygen and gas exchange. An increased stem and twig growth can be observed in the seedlings of many species. This rapid growth enables the protrusion of leaves above the water surface (Parolin, 2009).

Fig. 13 Seeds which germinated while floating on the Amazon river (near Belém, Brazil; photos © Pia Parolin).

Fig. 14 Sapling growing on a low level in the floodplain: when the water rises, it will most likely be fully submerged. This small plant can be several years old, it withstands prolonged submergence (photo © Pia Parolin).

Fig. 15 Natural distribution and zonation of plants in a forested wetland with rooted and floating macrophytes and grasses, a woody pioneer vegetation belt and the floodplain forest adjacent to upland forest (photo © Pia Parolin).

On very low levels in the flooding gradient, where a regularly recurring water column will be too high for this strategy, adaptations are more directed towards "tolerating" submersion. This includes that many species will lower their metabolism, have starch reserves and some are postulated to have photosynthetic activity under water.

Diversity

Despite the big changes of hydric conditions, a high diversity of species, life forms, adaptations are typical for plants in inland waters. The high diversity may be explained by several factors. Apparently, the stressors like flooding, submergence or drought only have a limited negative influence on plant growth. Favorable factors like stable temperature, light, water, nutrient supply, especially in tropical environments, and a high predictability of the flooded period enhance the evolution of adaptations.

Among the wetland plants there are specialists and generalists. In Amazonia, *Eschweilera tenuifolia* is an example for a specialist tree, extremely flooding tolerant and growing only on the lowest positions in the flooding gradient. It tolerates several years of uninterrupted waterlogging and is so specialized that it does not grow on other sites. On the other hand, the Kapok tree (*Ceiba pentandra*) is a generalist which occurs on the whole flooding gradient and also on the non-flooded uplands, and even on different continents.

One reason for the high diversity of species in Amazonia is the high age of the system. Changes of paleoclimatic conditions also caused changes of the vegetation (Prance, 1973; Ab'Saber, 1982; Haffer and Prance, 2001), but in Amazonia the river beds and their floodplains were always present and thus Amazonian floodplains are probably very old systems (Irion et al., 1997; Colinvaux et al., 2001) which may have represented refuges for the plants during drier periods, such as the ice-ages.

Interactions

Ecology is all about interactions. In wetlands, all the interactions that occur in uplands are also present, but additionally, the hydric element is present in a specific and dominant way. Food webs include plants and animals that live in the water, and which interact in very specific and close relationships. Animals feed along the edges of the water, or inside the wetlands, and they migrate between uplands and floodplains (Fig. 16). This way, there is connectivity of nutrients and species between uplands and wetlands. Overall, inland waters can be considered as highly complex and intertwined ecosystems.

Many fish species and aquatic mammals, birds and amphibians, need the plants for their development. Several animals reproduce in the dense stands of aquatic macrophytes or in trees of the flooded forests. These are the nurseries for the next generation, they provide shelter and food.

Also, the people who settle on the river or lake margins take profit of the sediment inputs and the nutritional values provided by the flooded ecosystems. The wetlands are therefore of fundamental importance for the local human river populations.

Utility of wetland plants

Plants of inland waters provide ecosystem services for the whole biological system and the human population. They provide all the services which plants as the main producers in the food chains supply, i.e., related to gas exchange and water cycles, cleaning the air and filtering, regulating diseases, pests, and climate. However, plants in inland waters have additional tasks which they naturally fulfil.

Fig. 16 Capuchin monkey feeding in the Amazon floodplains at high water (photo © Pia Parolin).

Sediment retention

Plants may be very efficient for sediment retention and thus enhance the natural nutrient input provided by the floods (Fig. 17). This way, biogeochemical cycles and food chains are strongly influenced by the plants which grow in the inland waters. Plants in inland waters provide regulating services which help to control floods and create environments which can act as sponges in the case of exceptional floods. Plants prevent riverbanks from erosion, and their roots may dispose deeper soil horizons to weathering by creating connectivity.

Human nutrition

Plants provide nourishment for all organisms linked to the inland waters. Animals feed on floating plant parts, or on fruits and seeds that fall into the water.

Many plant species of inland waters are of fundamental importance in the diet of the local human populations. Rice, taro, and other plants which need to grow in water assure the survival of millions of people worldwide (Fig. 18). Palm trees and local plants which are less known across the globe provide important quantities of fruits which are directly consumed or sold on the local markets. Macrophytes supply fodder for cattle and buffaloes.

Other uses

Wetland plants supply materials which the people need to construct their houses, boats, furniture, tools, and much more. Palm leaves are used for the roofs, local water resistant wood is employed for everything needed in the houses. Large perennial reed grasses (e.g., *Phragmites*) are used to cover the roofs of many houses in Germany.

Many tree species are important for timber and are thus traded on the markets. Plants supply fuel, fibers and medicines. Many diseases are linked to standing water and the presence and filtering activities of plants can decrease illnesses through a natural equilibrium of natural food webs.

The traits and morphology of wetland plants do not necessarily make the difference here, but the mere presence of specific plants in places where people tend to settle due to the need for constant water resources makes them highly valuable in inland waters. The nutrients in the alluvial soils spurred the colonization of wetlands by humans, as can be found on the Rhine, the Nile, the Amazon and many more rivers.

Fig. 17 Sediments are retained by the plant roots but also eroded by the river currents, making most wetlands highly dynamic ecosystems (Amazon river near Manaus; photo © Pia Parolin).

Fig. 18 Taro plantation in the Hanalei Valley on Kauai, Hawaii (photo © Pia Parolin).

The vegetation on the banks of rivers and interfluvial wetlands in the Amazon is currently recognized as landscapes managed by indigenous populations from the pre-Columbian period to the present day. However, knowledge about this sustainable use and management is gradually being lost by the increasing rural exodus leading to the forgetting of traditional knowledge (Ferreira et al., 2019). Less and less people know about the values of single plant species, be it for human nutrition, medication or related to complex food webs (Fig. 19).

Major problems of wetland plants

Contrary to upland ecosystems, in inland waters many plant species face problems which occur only under the influence of flooding and in linkage with wetlands.

Fig. 19 Local use of açai palms (Amazon river near Belém, Brazil; photo © Pia Parolin).

Problems for the plants in inland waters

Pollution

Problems for the plants include water pollution, e.g., through gold mining or oil search, the presence of herbicides or over-fertilization. Some species, like *Eichhornia crassipes*, have a high tolerance to pollutants and are used to clean polluted inland waters. However, the biomass accumulated by the species will retain the pollutants and may become a problem if well designed removal strategies and disposal are not used.

Alteration of hydric cycles

Altered hydric cycles arise with artificial water regulations where dams or river rectifications have been built. Dams and hydropower stations are being built all over, and their influence on the inland water networks is mostly disastrous. Changes which are linked to the presence of dams include the emergence of different flooding periodicities, which lead to disruptions of interactions and the asynchronicity of the plant life cycles and even change in species composition. Large-scale deforestation in catchment of rivers leads to changes in hydrological cycles and also alters hydrochemical parameters. In rectified rivers, such as all over Europe and N-America, many habitats along the river channels and wetlands were lost, and the concentration of hydraulic energy along a linear river channel increased bed erosion and consequently led to lowered groundwater levels. The results were fragmented river wetlands with reduced habitat and plant diversity, as well as the introduction of non-native invasive species (neophytes), which in turn endanger local species pools.

Changes of precipitation

Climatic changes lead to changed precipitations at a local and global level. Thus, the natural patterns of floods and droughts are undermined. Increased length and height of flooding has strong impacts on plant survival. Increased or less frequent floods and droughts can have devastating effects on plant life and species composition. Disruptions of networks and asynchronicity of life cycles are a consequence.

Fires following exceptional droughts are emerging ecological constraints. Since wetland plants of most inland water systems are usually not subjected nor adapted to fires, they may become a major concern in wetlands under climatic change scenarios.

Problems caused by the plants in inland waters

Plants also provoke problems. They can be invasive or simply grow too much once the natural equilibria are broken.

Invasive species

Many plants are invasive around the globe, and wetland species are particularly efficient as invaders. Wetland plants have been carried around voluntarily for ornamental purposes, or involuntarily with globalization. Fragmented (i.e., rectified, dammed) wetlands are most vulnerable to invasive species. Once arrived in a new ecosystem, some species are very efficient in forming monospecific stands because they have nearly unlimited resources in several wetlands: water and nutrients are often present in high quantities. And many wetland plant species appear to be good generalists which can easily cope with different inland waters. The only limiting factors are temperature and salinity.

Excessive biomass production

The very fast growth of floating macrophytes is a major problem in many circumstances. Once the natural network and equilibrium is broken, fast-growing plants will dominate an ecosystem. This often is counterproductive to what the human population needs, not to speak of the naturally occurring plants and animals.

Fast growth of few species fills the water surfaces and inhibits oxygen and light to penetrate the water. The large amount of biomass leads to increased decomposition and low oxygen rates in the water. This heavily affects fish and all other organisms.

Fast growing invasive species like the Amazonian water hyacinth (*Eichhornia crassipes*, Figure 20) currently occur in almost all freshwater lakes around the tropical regions of the globe and outcompete the local vegetation. Huge mats of floating plants choke waterways and the turbines of hydroelectric installations. This is an immense problem worldwide.

Conclusion/synthesis

This chapter shows that several adaptations and specific ecological features allow different wetland plants to grow under certain circumstances which otherwise are lethal for plants. They have different capacities to tolerate flooding or submergence, and to cope with the harsh conditions of standing water or strong currents. These not only determine their distribution, but also make them survivors in an otherwise often hostile environment.

Floodplain management should be based on conceptional considerations in order to avoid negative side effects as much as possible (Junk and Wantzen, 2004). The FPC predicts exchange of nutrients and energy between the aquatic and terrestrial phases. Human use of terrestrial resources will affect aquatic resources and vice versa. These impacts have to be considered when developing management concepts.

Wetland plants fulfil key roles for ecosystem services of inland waters. Their presence guarantees stability, favorable environments for the reproduction of several animal species including fish, crabs, molluscs, mammals and many more. Additional studies are needed to improve our knowledge about their optimal use and sustainable management, for regeneration projects of secondary forests and the rehabilitation of wetlands around the globe (Fig. 21).

We have to spread the understanding of inland water ecosystems which are a natural capital. Valuing the privilege of diversity instead of compromising the well-being of nature and humans is fundamental. And we must pay attention that diversity does not only mean a high number of species, but it also includes diversity of genetics, of adaptations, of macrohabitats, of social and cultural richness.

Knowledge gaps

- We need to understand adaptations and tolerance of aquatic plants: We only have a superficial knowledge of the ecophysiology of most species, and thus it is difficult to understand the reasons for their distribution in macrohabitats.
- There is a lack of basic knowledge for management, restoration, and replanting plans, for sustainable use and conservation of wetlands.

Fig. 20 Invasive *Eichhornia crassipes* in the city of Antananarivo, Madagascar (photo © Pia Parolin).

Fig. 21 Converted wetlands in Madagascar with varied agriculture (left), and rice cultivation (right) (photos © Pia Parolin).

- We need to better understand the role of salt and fire, two strong factors which more and more often appear in inland water ecosystems.
- Our understanding of food webs and interactions of animal species and plant species in different inland water ecosystems has to be enhanced.
- We need to better understand the spread of invasive species and how to control or use them if it applies.
- We need more research in order to understand the complexity and the interdependence of many processes. Research has to be focused on questions about recent, past and future climatic impacts, the importance of landscape connectivity and dynamics of flooding on biodiversity and biogeochemical cycles and how to include the results of floodplain research into sustainable management strategies (Junk and Wantzen, 2004).

See Also: **Emerging methods and topics**: Fatty Acid—Markers as Foodweb Tracers in Inland Waters; **Human pressures and management of Inland Waters**: Biological Invasions: Case Studies; Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment; **Structures and functions of Inland Waters - Lakes**: Benthic Algae in Lake Littoral Habitats; Macrophytes; **Structures and functions of Inland Waters - Rivers**: Energetics and Food Webs in Large Rivers; **Structures and functions of Inland Waters - Wetlands**: Riparian Vegetation of Gravel-bed Rivers - A Global Review; Structure and Function of Inland Waters-Wetlands: Classification Systems of Wetlands

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Benthic Invertebrates of Running and Stagnant Inland Waters

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This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Bioindicator Biological processes, species or communities that are used to assess the quality of the environment and its evolution over time.
Ecohydrology Interdisciplinary scientific field studying the interactions between water and ecological systems.
Functional feeding groups Classification of the trophic role of macroinvertebrates in hydrosystems based on mouthpart morphology, feeding behavior and stomach/stable isotope analysis.
Hyporheic/hypolacustric interstitial Transitional habitat of stream or lake sediment which is influenced by both, shallow groundwater and surface water.
Neobiota Animal plant and microbiota species that colonize areas where they did not occur previously, mostly due to human intervention (e.g., transport, release).
Nerites Common name for the family Neritidae, small to medium-sized freshwater and saltwater snails, which have a characteristic gill and operculum.
Patch dynamics Differential distribution of benthos due to temporal changes of their habitats.
Reciprocal subsidies Flow of matter and energy between ecosystems (here: at the aquatic-terrestrial interface).
Voltinism Number of generations per year (for insects).

Introduction

In aquatic ecosystems, the community of organisms living at the bottom is called benthic, and its habitat, benthos. The expression "benthic invertebrates" includes a very heterogeneous group both in terms of their species composition and their contributions to ecosystem processes. Their size can vary tremendously from single-celled protists to large crayfish or mussels weighing more than 1 kg, but the size of most species ranges from less than one to a few millimeters. The distinction between micro- and macro-zoobenthos is often defined by the catchiness of 500 μm-mesh size nets, however, early larval instars and many tropical insect larvae commonly attributed to "macro" zoobenthos would slip through this mesh.

Despite their relatively small body size, benthic invertebrates can travel far distances, either by flying themselves (the dragonfly *Pantala flavescens* is known to make migrations of several hundred kilometers), or by using other animals as means of transport. For example, water mites and gordiid worms use winged aquatic insects as aircraft, unionid mussel larvae stick to migratory fish. Others use the water flow to become dispersed. Some nereid snails, shrimps and crabs have marine ancestors and need to reproduce in the sea, and later their offspring migrates back into the coastal rivers (Blanco and Scatena, 2006). Some benthic invertebrates are even of clinical importance, as they can be vectors of water-borne diseases such as malaria, West Nile virus, dengue fever dispersed by midges, onchocerciasis by black flies, or schistosomiasis by snails (not discussed here).

With the exception of few purely marine or terrestrial groups, all known invertebrate taxa can be found in inland waters, including 13 orders of insects (larval midges of the dipteran family Chironomidae being the most common), sponges, mollusks, crustaceans and worms from different groups (mostly nematodes and oligochaetes). Due to their enormous diversity, the taxonomic composition of the communities cannot be dealt with here, and only in few long-term studies, the cumulative species curves have reached a saturation point, e.g., in the Breitenbach study (Wagner et al., 2011). A detailed description of the morphology of many species (especially insect larvae) is yet missing, and the life cycle, habitats and diets of their different life stages are only known from few species.

Considering the functional diversity even within a single species, combined with a high local species diversity due to the patchy distribution (especially in running waters, microhabitat-specific communities vary on few centimeters distance) and the temporal (annual, multi-annual) variability of species, one can imagine the enormous importance of benthic invertebrates in the flow of matter within, across and between inland water ecosystems. Invasive, filter-feeding mussels may literally clean out planktonic algae and bacteria from lakes and rivers and switch the pathways of biotic carbon flow from the planktonic to the benthic food web (Karatayev et al., 2005). Some species act as environmental engineers by changing the physical habitat structure. Many benthic invertebrates are very sensitive concerning environmental quality, making them excellent bioindicators for the chemical and physical quality of the ecosystems they live in Pander and Geist (2013).

This chapter synthesizes classical and current knowledge on freshwater benthic assemblages, with the following main topics: (i) technical aspects of field sampling, (ii) the general environmental (abiotic and biotic) controls over community structure and ecological concepts, (iii) functional ecology and ecological concepts, (iv) types of habitat and their respective communities and adaptive strategies (streams, rivers, floodplains and lakes, the hyporheic/hypolacustric zone, and extreme habitats), and (v) management and conservation aspects. Finally, it also warns about the dramatic biodiversity decline of this group of animals, which is so little known that many species disappear without ever being known to science.

Methods for the study of benthic communities in continental waters

Aquatic habitats and their specific invertebrate associations are very diverse. A wide range of literature references covers sampling methods and analysis of benthic macroinvertebrates. Environmental assessment monitoring is extensively addressed in the classic texts of Hynes (1960, 1970), Bartram and Balance (1996), or the frequently used protocols of the United States Environmental Protection Agency (USEPA, 2016) and the European Water Framework Directive (Hering et al., 2003). Global harmonization of bioindication methods is urgently needed (Buss et al., 2014). European and North-American textbooks such as Tachet et al. (2010), Thorp and Rogers (2015), or Merritt et al. (2019), provide keys for the identification of benthic biota including an extensive list of sampling equipment. For tropical aquatic biota, methods have been reviewed by Wantzen and Rueda-Delgado (2009) and local identification guides are given, e.g., by Yule and Yong (2004) for South-East Asia, and Domínguez and Fernández (2009), Damborenea et al. (2020), or the ABLA book series for Latin America (Adis et al., 2006–2009).

Prior to sampling, the distribution and coverage of the habitats should be known, and the strategies for sample storage and analysis, as well as the identification and data and sample management need to be set up. Stratified random sampling allows to compare individual microhabitat types in streams (Hauer and Lamberti, 1996) or depth zones in lakes. The sampling gear needs to be selected according to the substrate type, current and target organisms (Table 1; Fig. 1).

Sampling, even for conservation purposes, always represents an impact on the ecosystem and needs to be well planned, including the request of permits. Special care has to be taken concerning rare and protected species, e.g., unionid mussels, dragonflies or crayfish. All sampling material including boots needs to be cleaned, dried and possibly sterilized in order to avoid the transfer of invasive species or diseases such as the crayfish plague (*Aphanomyces astaci*) between sampling sites. The timing of the sampling needs to be adapted to the life cycle of the organisms and to hydrological variations. Recently flooded riverbanks, sediments freshly deposited after storms, or sites where a mass emergence of adult, winged aquatic insects has just taken place before sampling are not representative. Eggs and smaller instars of invertebrates are hardly visible and can rarely be identified by morphological characteristics. More and more, environmental DNA and metabarcoding are used for identification (Deiner and Altermatt, 2014) and bioindication (Hering et al., 2018), revealing however only the presence/absence of species (including rare, cryptic, or yet undetected invasive species). Whenever possible, living animals should be observed in their natural habitat (or when freshly sampled) to understand their species traits. Living samples need to be aerated and cooled and quickly analyzed to prevent predation or decay. Therefore, most studies are based on animals that were killed and analyzed in the laboratory. Conservation of specimens lacking an exoskeleton needs specific treatment, most arthropods and shell-bearing mollusks are generally preserved in alcohol.

The term “benthic invertebrates” usually describes animals living on and in the uppermost layers of the sediments, however, if present, animals plant parts protruding into the water (macrophytes, floating roots, wooden logs) should also be sampled with specific gears (i.e., nets that can be closed around the plant parts before lifting it to the surface). For the sampling of macroinvertebrates in streams, Surber with defined sampling areas or D-type nets are classical devices, which use the water current to catch animals from the stirred substrate. Some taxa, especially mayflies (Leptophlebiidae, Oligoneuridae) may sense nets and escape (Bretschko, 1990). In stagnant waters, Surber samplers can be coupled with air-lift current from SCUBA equipment (Baumgaertner et al., 2008). Small species (microbenthos) can be removed from substrate surfaces with scrubs or ultrasonic devices. If they occur in fine sediments, these can be sampled with corers or suction pumps. Fine to medium-sized sediments in lakes and rivers can be

Table 1 Types of benthic microhabitat in different continental aquatic ecosystems.

Ecosystem/habitat	*Streams (wadeable)*	*River channel and floodplain*	*Floodplains of rivers and lakes*	*Permanent marshes*	*Lakes*
Rocks	X	x			X
Boulders	X	x			X
Gravel (surface)	X	x	x		x
Gravels (intertidal)	X	x	x		x
Sand	x	X	x		x
Silt	x	x	x	x	X
Clay	x	X			x
Mud				x	X
Leaflitter	X	x			x
Stream (ritron, drift organisms)	x	x			x
Water surface (Pleuston, surface organisms)	x	x	x	x	x
(emergent aquatic insects)	X	x	x	x	x
Large woody debris	x	X	x	x	x
Floating tree roots	X	x			
Submerged shrubs, reed		X	x	x	x
Floating macrophytes	x	x	x		x
Submerged soft macrophytes	x				x
Macro algae			x		x
Rigid macrophytes	X	x			

Capital X denotes habitats to be included in the sampling (translated from Wantzen and Rueda-Delgado, 2009).

Fig. 1 Straight stretch of a river or stream ideal for sampling benthic macroinvertebrates. Blue arrow: direction of the current (sampling should be done against the current, to avoid drift losses), red arrow: lower end of the stretch (starting point), green arrow: path outside the bed to the sampling starting point. Yellow lines and blue diamonds: sampling path and microhabitats for sampling. (Photos: Barrick PVDC, with permission).

sampled with Ekman-type dredges or freeze-coring (Weigelhofer and Waringer, 2003). Emergence traps capture adult aquatic insects and deliver information about life-cycle duration (voltinism), they need to be regularly controlled to avoid predation by spiders (Freitag, 2004; Malison et al., 2010) (Fig. 2). Large mussels can be identified in situ using optical devices ("aquascopes", Prié et al., 2017). Standardized artificial substrates for colonization (Rosenberg and Resh, 1982) deliver an excellent baseline to compare faunal assemblages between different sites for biomonitoring; however, they are selective and not representative for the entire habitat diversity of a site.

In addition to sampling animals, key environmental parameters always need to be registered in the study of benthos. In faunistic studies, at least sample rarefaction tests, alpha and beta biodiversity analyses, and NMDS (Nonmetric MultiDimensional Scaling) inform about community composition and species distribution, multivariate analyses such as PCA and DCA (Principal and Detrended Component Analyses) help to interpret the influence of diverse environmental parameters on the distribution and composition of the species.

Fig. 2 Some classical methods for sampling benthic invertebrates. (A) Surber net, (B) D net, (C) Emergence trap and (D) Ekman dredge.

Abiotic and biotic controls over benthic assemblage structure

Among the most fascinating features in the study of benthic invertebrates are their spatial distribution and their species composition (Fig. 3). Both in rivers and lakes, specific assemblages can be found in specific zones of the respective ecosystem, with surprisingly similar patterns in different regions of the world, although they show biome-specific trends (Feio et al., 2018). These patterns are the result of a large number of biotic and abiotic conditions, which can be described in hierarchical scales (O'Neill et al., 1989) or as landscape filters (Poff, 1997). Next to general key controls of biodiversity such as evolution time and geographical dispersal potential, the structure of benthic communities is controlled in first place by hydraulics (Statzner et al., 1988). Water movement and the availability of the original bedrock material determine the physical habitat structure, with coarser sediments in wave impact zones of lakes and the mountainous sections of rivers and streams, and fine sand and silt in the depositional zones of both, lotic and lentic ecosystems. Coarser and medium-sized sediment particles provide surfaces to which larger invertebrate species may cling, and their larger porosity allows oxygenation of deeper zones that can be colonized by metazoans. On the other hand, fine sediments can be mobilized at lower flow velocity or wave impact, and their oxygen concentration quickly decreases with depth due to reduced exchange with the open water. Water movement also transports food particles and increases the oxygen solution at the water surface. This results in a fine-tuned distribution of benthic invertebrates, e.g., multi-species caddisfly larvae assemblages with different mesh sizes along the outlet of lakes.

In running water systems, life-cycle length of the organisms is coupled with the probable mobility of the sediments, resulting in habitats preferable for r- or K-strategists (Resh et al., 1988). This phenomenon results in a generally higher biodiversity, abundance and biomass of macro-zoobenthic species in gravellish substrata (Hynes, 1970; Allan et al., 2020) compared with lower values in fine substrata of lakes and the lower sections of rivers (but small specialist species may occur in high abundances, Wantzen et al., 2014). The introduction of solid substrates on soft lake sediments (e.g., shells from invasive mussels) may completely change the community structure (Werner and Rothhaupt, 2007). Tree logs may also interfere with soft-bottom habitats and create abundant,

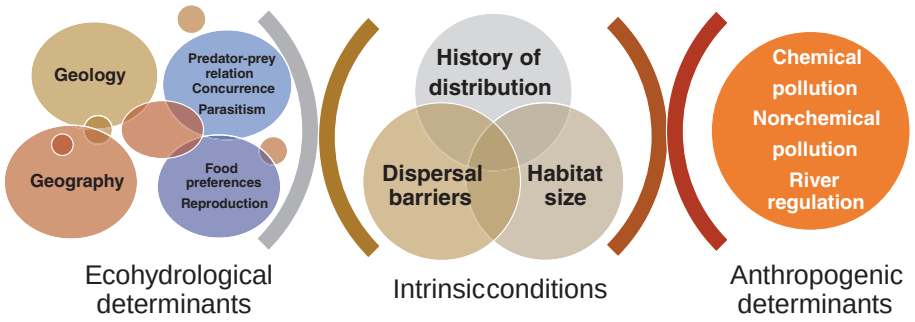

Fig. 3 Factors explaining the occurrence of benthic communities in inland waters. Modified from Braukmann, 1992.

Fig. 4 Tipuliid larvae (Diptera) dispose of a spiracular disc found on the end of the abdomen which is surrounded by hydrophobic lobes, which allow them to breathe atmospheric oxygen while the animal dwells in oxygen-poor environments. Photo: M. Schmidt, Mexico, with permission.

species-rich "biotic hot spots" in rivers and lakes (Wantzen and Junk, 2006). Moreover, flow and flood phenomena permanently modify this primary pattern in natural hydrosystems by erosion, transport and deposition of sediments, but also by expanding and reducing the wetted part of the floodplains, and by changing the relative contribution of water of different origins (surface, ground, and rain water). This results in a permanently changing spatial-temporal mosaic of differently old physical habitats, especially in river systems (Pringle et al., 1988; Ward, 1989; Junk and Wantzen, 2006; Tockner et al., 2010), but to some degree also in lakes (Wantzen et al., 2008).

Physical and chemical water quality (temperature, oxygen concentration, pH, dissolved salts and nutrients) exert the next level of control in the community composition, as they represent physiological limits for the survival of aquatic species. Diffusion speed of gases in water is 200 times slower than in air, and the amount of oxygen that can be solved in water decreases fast as temperature rises, therefore, many aquatic metazoans are limited by oxygen supply. Especially in fine, organic sediments, only the uppermost layer is oxidized, and only specialists pumping fresh water into the tubes they colonize by body movements ("bioturbation") may go deeper than that.

Benthic invertebrates have developed an impressive variability of respiratory organs. For small and flat animals (e.g., flatworms), the body surface may suffice for gas exchange. All aquatic insects and spiders have evolved from terrestrial ancestors, and some have maintained an air-filled, tracheal respiratory system. Some species directly breathe air at the water surface but their mobility is limited by the length of their respiratory organs, e.g., tipulids (Fig. 4). Water beetles and bugs (Heteroptera) carry tiny air bubbles under water or have developed a fixed-volume plastron for the exchange of gaseous oxygen (in the plastron and tracheae) and dissolved oxygen (in the water and in their body liquids). Other taxa have developed all kinds of internal (e.g., Odonata: Anisoptera) and external gills (e.g., Ephemeroptera, Trichoptera, Plecoptera). Some oligochaetes and chironomid larvae produce hemoglobin to survive in low-oxygen environments. Underwater respiration is connected to osmotic exchange with the water, which can become a physiological problem, if the water was much saltier or much less salty than the body liquid (see below: extreme habitats). Therefore, adaptive traits of respiration and osmoregulation are generally combined (Griffith, 2017).

Indirectly, the nutrient content triggering plant growth (and subsequent heterotrophic processes) also restricts the oxygen concentration, resulting in the absence of sensitive species in nutrient-rich waters. Most mollusks and crustaceans need calcium carbonate to produce their shells, therefore, their occurrence is restricted to waters with sufficiently high calcium content. In Amazonia, the apple snail *Pomacea papyracea* circumvents this problem by having a calcium-free shell of pure periostracum. Changes in the pH of the water (acidification as a consequence of air pollution) and/or presence of divalent heavy metal ions may severely interfere with shell growth (Boon et al., 2019).

Predator-prey relationships and competition are further, biotic, levels of control on the benthic biocoenosis. Their body size makes invertebrates a perfect prey for fish, which has cascading effects also on invertebrate predators (Diehl, 1992). Similar to planktonic invertebrates that can chemically sense the presence of predators and perform diel vertical movements in lakes, benthic invertebrates also adapt their daily behavioral patterns to reduce predation. In many lakes, mysid shrimps and phantom midge larvae (genus *Chaoborus*, Gosselin and Hare, 2003) switch between a nocturnal planktonic and a daytime benthic life. Displacement between microhabitats and drift behavior for dispersal in streams represent high predation risk for invertebrates. Ramírez and Pringle (2001) could show that above waterfalls that limit the access of predators, drift showed a diffuse pattern, but it was concentrated at the dusk and dawn periods (when fish cannot sense their prey) when vertebrate or crayfish predators were present below the waterfalls. Many other benthic invertebrates avoid fish predation by resting underneath stones at daytime and feeding at night (e.g., grazers, Fig. 5).

Fig. 5 Larvae of the cosmopolitan caddisfly family Helicopsychidae produce cases that look like snail shells. During daytime, they hide below stones, at night they graze algal films on stones. Photo: Karl M. Wantzen, Mexico, 2018.

Functional ecology of benthic invertebrates and ecological concepts

Benthic invertebrates play an important role in the dynamics of organic matter and nutrient processing of aquatic ecosystems, their floodplains and neighboring terrestrial ecosystems (Covich et al., 1999). Due to their body size, they can convey organic carbon from the microbial loop (i.e., the energy flow between bacteria, fungi, viruses and protists) and/or primary producers (algae, macrophytes, terrestrial plant debris) to larger invertebrate or vertebrate predators. They thereby connect the benthic with the pelagic food webs, the lentic (still-water) to the lotic (running water) foodwebs, or even the aquatic and terrestrial foodwebs. Emerging adult insects (e.g., adult mayflies, caddis flies, chironomids) or stranded aquatic invertebrates become a cornucopia for terrestrial spiders, beetles, birds and bats, whereas the feces or corpses of the latter become consumed by aquatic invertebrates. This phenomenon is known as "reciprocal subsidies" between foodwebs (Nakano and Murakami, 2001; Dahlin et al., 2021). Foodweb interactions do not occur in continuous processes, but rather in locally and temporally restricted "biotic hot spots and hot moments," e.g., when migratory, Polymitarcidae mayflies carry one ton of carbon upstream the Orinoco river (Wantzen and Junk, 2006), or when the fastest growing, last larval instars of the shredding caddisfly *Chaetopteryx villosa* litterally clean out leaf litter in temperate streams and even feed on terrestrial vegetation (Wantzen and Wagner, 2006). These phenomena may remain unperceived due to too long observation intervals.

During their life cycle, benthic invertebrates can act on different trophic levels. Net-spinning caddis flies, for example, feed on tiny organic particles during their early instars, are predators in larger larval stages, and winged adults may feed on nectar (or do not feed at all). Water mites are micropredators, then parasites on aquatic insects (Smith et al., 2010). Despite a high degree of specialization, omnivory is widely distributed, especially if high-energy food sources (e.g., pollen on water surfaces, honeydew from aphids) are shortly available. For benthic invertebrates, the classification in feeding guilds is commonly named "functional feeding groups" (FFGs, Merritt et al., 2019). The FFGs are the result of the morphological analysis of mouth parts and observation of feeding behavior, stomach content analyses or stable isotope analyses. The major functional feeding groups are (1) scrapers/grazers which consume algae and biofilms; (2) shredders, which consume leaf litter or other Coarse Particulate Organic Matter (CPOM), including wood; (3) gatherer-collectors, which collect Fine Particulate Organic Matter (FPOM) from the stream bottom; (4) filterer-collectors, which collect FPOM from the water column using a variety of filters; and (5) predators, which feed on other consumers. Sub-groups exist i.e., for the predators (e.g., engulfers, piercers). Identifying the composition and proportion of functional feeding groups may indicate the functioning and integrity of the ecosystem (Thorp and Rogers, 2015). FFGs can be combined with other characteristics such as mobility type (crawlers, clingers, swimmers, etc.), life span and reproduction type and period to sets of species traits, which allow a detailed functional analysis of the community and its sensitivity to environmental impacts (e.g., Hershkovitz et al., 2015).

In a general theory, the headwater zones of streams receive fresh leaf litter (CPOM), so that shredders prevail there, grazers prefer the intermediate stream parts where sunlight provides benthic algal growth, while gatherer and filterer-collectors increasingly dominate in the lower river sections that receive the CPOM, which has been comminuted to FPOM and where the residence time of the water is long enough to support the development of riverine plankton. This functional ecosystem model, known as the "River Continuum Concept" (Vannote et al., 1980), has dominated benthological research for decades, however it has overlooked important aspects, such as the primary production of and trophic interactions with floodplains, which may have a greater importance for the foodwebs than the food sources in the river main channel itself (Flood Pulse Concept, Junk et al., 1989; Junk and Wantzen, 2004), that headwater streams may depend on primary production rather than allochthonous litter input (Lau et al., 2009) and that leaf litter decomposition is subject to a number of geographical parameters, including the chemical quality of leaves (Graça et al., 2015; Rueda-Delgado et al., 2006). Moreover, the classical structural sequence of rivers from coarse-grained headwaters

to fine-grained lower sections (and their respective faunal assemblages) may be interrupted by natural or man-made structures (Serial Discontinuity Concept, Ward and Stanford, 1983). In synthesis (see, e.g., Thorp, 2009), the local hydromorphological and geochemical environmental conditions are decisive for the ecosystem functions in rivers. Functional concepts in lakes have a stronger focus on planktonic foodwebs, however, the importance of benthic assemblages (especially the benthic-pelagic coupling, see Karatayev et al., 2005) and flood effects (Wantzen et al., 2008) are increasingly acknowledged.

Specific benthic assemblages

Low to medium-order streams

In headwaters, aquatic and terrestrial ecosystems have a large contact zone. Hydrographs reflect the contributions of permanent groundwater inflow (with low temperatures allowing the presence of stenothermous species) and the flashy variations due to precipitation (flushing terrestrial organic matter into the stream). Densely arranged sediment patches of fine and coarse, mineral and organic particles allow the coexistence of highly diverse assemblages even in narrow stream sections (Pringle et al., 1988). Gravel and sand often form a "pool-and-riffle" structure that serves as a trap for FPOM and attracts gatherer-collectors, while shredders focus on debris dams. Many species show adaptations to the swift current, such as flattened body architecture, or an arrangement of external gills that avoids turbulences below the body (many may fly larvae). Biofilms reduce the adhesion to stones so that animals using suckers (e.g., Diptera: Blephariceridae) are only found in the uppermost stream sections where frequent spates remove slippery surfaces. Simuliid larvae clean surfaces, then glue a cushion of silk to cling themselves with their abdominal claws at the edges of boulders located in the current, where they filter particles with their antennae.

Habitat patches are quite dynamic, as frequent spates redefine the physical habitat structure (Matthaei et al., 1999). Life cycles of the invertebrates are generally short, often with highly polyvoltine species in the Tropics (possibly, an adaptation to the frequent sediment disturbance after rainstorms) and 1–2 year-long cycles in the temperate zones. Only few microhabitats in headwaters provide sufficiently stable conditions for the survival of long-living species such as true river mussels (Unionoida). In boreal streams, pearl mussels (*Margaritifera margaritifera*) belong to the longest-living animals on earth, attaining more than 200 years (Ziuganov et al., 2000). Along with the "EPT taxa" (Ephemeroptera: mayflies, Plecoptera: stoneflies, Trichoptera: caddisflies), they belong to the most pollution-sensitive taxonomic groups. If fish are absent, large invertebrate predators (decapods and larvae of stoneflies, dragonflies, dobsonflies) are the top predators. Many invertebrates drift down the stream to escape predation for dispersal, so that emerged adult aquatic insects fly against the air current above the waterline to compensate for this movement. In temperate zones, adult gammarids (amphipod crustaceans) migrate towards the springs that provide a thermal shelter. The terrestrial vegetation structure is very important for adult insects as mating sites.

Foodwebs are largely based on the diverse terrestrial inputs (leaf litter, but also fruits, flowers, terrestrial invertebrates) providing food sources for detritivorous or scavenging invertebrates (Graça et al., 2015; Wantzen and Wagner, 2006) but also on primary production by algae (Lau et al., 2009). In the middle to lower section of streams (or in wide high-mountain valleys), the stream bed widens and meanders or broadens, so that the bottom sediments are fully exposed to sunlight, and benthic green algae can develop well. Exclosure experiments with under-water electric fences (Pringle et al., 1999) show that grazing invertebrates (Fig. 5) remove the non-filamentous algae at night time, so that they are a rare sight in unpolluted streams.

Main channels of rivers

Downstream fining of sediments defines the physical habitat structure and—along with water quality—the benthic assemblages in larger rivers. The continuous gradient from coarse to fine substrata, known from textbooks, however, is often interrupted by inflowing streams or river sections crossing rocky outcrops that may "rejuvenate" both, sediment and community structure (see "Serial Discontinuity Concept" above). Some typical "rhithral" (stream) species may therefore occur locally in the "potamal" (river) sections of larger rivers, provided that the temperature and water quality requirements are met. Gravellish river sections, river banks and especially the channels connecting rivers to floodplain lakes, provide habitats for an abundant and diverse fauna, especially filter feeders and grazers that may use the organic particles brought by the water movement. On the other hand, mobile (often sandy) bed sediments, as they occur in the central channel strip of the lower section of rivers, are among the least densely colonized freshwater habitats (Marchese et al., 2005). In underwater sand dunes the fauna is often composed of Oligochaetes and other, worm-shaped taxa, which respond to the instability of the substrate, the quality of the water, and the organic matter accumulated on the bottom of these channels (see review in Wantzen et al., 2014).

Lakes and river floodplains

In lakes, the above-mentioned habitat dynamics are much slower, however, the relationships between substrate structure and faunal assemblages are similar to those of rivers. Lakes generally have a clear sequence of habitat zones, beginning with a fluctuating upper littoral zone inhabited by an invertebrate community of terrestrial and aquatic origin (Scheifhacken et al., 2007), a permanently wetted, lower littoral zone with different types of substrata and plant communities, and a profundal zone, which accumulates fine sediments and FPOM. The landscape topography is decisive for the lake morphology and the relative extension of the depth zones. In shallow lakes, light and wind-driven currents can influence even the deepest zones (Brauns et al., 2007).

While the wave actions in the upper littoral may provide comparable habitat conditions as the rhithral zones of streams (with some overlapping species), the community of the profundal zone of lakes is quite monotonous, adapted to the low oxygen concentrations typical of the bottom of these systems (O'Sullivan and Reynolds, 2004). In the macrophyte-covered lower littoral of lakes and in slow-flowing lowland rivers, the "true" benthic community (mostly nematodes, oligochaetes, chironomids) is usually less diverse than that associated with macrophytes. The latter include herbivores such as the aquatic butterfly *Acentria ephemerella* (Gross et al., 2002) but also many snail and caddis fly species. Macrophytes may play an important role as shelter against predators (Thomaz and Cunha, 2010; Hesselschwerdt and Wantzen, 2018).

Both in the upper littoral of lakes and in the floodplains of large rivers, water level fluctuations change life conditions in the sediments near or above the waterline (O'Leary and Wantzen, 2012). In this "Aquatic-Terrestrial Transition Zone", aquatic organisms need specific adaptations to survive drought (in some regions, even frost) and predation by terrestrial predators. These adaptations include resistant propagules such as eggs, diapausing life stages (e.g., *gemmulae* of freshwater sponges) or the migration into moister zones (see Wantzen et al., 2016 for a review).

The interstitial pore spaces in sediments of rivers (hyporheos) and lakes (hypolacustric zone)

The hyporheic interstitial zone is a specific ecotone between the shallow benthic zone and groundwater, colonized by specific epibenthic invertebrates (Brunke and Gonser, 1999; Thorp et al., 2006) and stygobionts (groundwater species, Danielopol and Griebler, 2008). Originally described for small streams (Orghidan, 1959; Schwoerbel, 1961), it is now known that coarse sediments of large rivers (Malard et al., 2002) and even lakes (O'Leary and Wantzen, 2012) have similar structures. Eggs, larvulae, larvae of aquatic insects and early instars of mollusks and crustaceans are often overlooked in benthos studies because they spend a part of their life hidden in the sediments. Interstitial invertebrates are either pre-adapted to live in the narrow pore-space by an elongate, worm-like shape and small size, or they display morphological adaptations (stretched body form in water mites, Schwoerbel, 1961) or the reduction of pigments and eyes (e.g., the amphipod genus *Niphargus*). This ecotone may extend far beyond the visible stream banks (Stanford and Ward, 1988) and the subterranean fauna of tributaries may expand into the interstitial of the main river. Presence of stygal species in the benthos of rivers can be seen as an indicator for groundwater upwelling. In spite of its great importance as habitat of all kinds of invertebrates and vertebrates (e.g., juvenile salmon and lampreys), the interstitial zone is still understudied (Marmonier et al., 2012), specifically in the Tropics.

Benthic invertebrates of extreme habitats

Benthic invertebrates are found in all types of water bodies, even tiny water bodies such as tree holes become colonized, and specialist species even survive in the digestive liquids of flesh-eating pitcher plants (Williams, 2000). In continental hypersaline habitats, they have to cope with salt concentrations up to tenfold that of the sea. Their fauna is often depauperate, however, it can be quite distinctive (Dejoux, 1993). Brine shrimps (*Artemia* spp.) have a remarkable osmoregulation and produce encysted eggs when the salt concentrations exceed their physiological limits (Gajardo and Beardmore, 2012). Survival in extremely ion-poor waters (conductivity $<<10$ µS/cm) also causes osmotic problems that is overcome by some species living in leaf packs or even inside fallen leaves (e.g., the chironomid genus *Stenochironomus*, Wantzen and Wagner, 2006). Drought resistance is known from many species (Williams, 2000; Wantzen et al., 2016). Dormant eggs of diverse notostracan crustaceans (e.g., the tadpole shrimp *Triops* sp.) can survive many years in dry sediments and hatched animals profit by the absence of fish predators in recently developed ponds.

Management and conservation of benthic biodiversity

Benthic invertebrate communities face classic problems related to water pollution and habitat loss, however, new threats arise (Reid et al., 2019). They all have in common that adaptive species traits that successfully evolved over millions of years are becoming obsolete due to the artificialization of the environment by humans. Light pollution, for example, attracts adult aquatic insects during their mating flights so that they end up at lamp posts rather than to reproduce and supplement terrestrial food webs (Perkin et al., 2014). Another new problem for the benthos is the effect of abundant plastic particles that are dispersed and maintained for decades in inland waters (Blettler et al., 2018) and affect the biodiversity and the functioning of aquatic communities (Redondo-Hasselerharm et al., 2018). Endocrine disruptors (hormone-like, artificial substances released to the environment) may have significant effects on the reproduction and the ontogeny of benthic invertebrates (Oehlmann et al., 2006). Inadequate agriculture and illegal gold mining release enormous amounts of sediments and toxic substances that have deleterious effects on benthic and fish communities in streams (Wantzen and Mol, 2013). More and more streams switch from perennial to intermittent discharge due to climate change, lacking conservation of headwaters, damming and water abstraction. This impoverishes the stream fauna (Larned et al., 2010). Due to river engineering (especially for navigation), the central channel strip of rivers is frequently dredged, and the habitats of the river banks have been transformed into concrete channel walls or rip-rap, which are less diverse but offer habitat for invasive species. Large benthic invertebrate species, such as the Giant River Pearl Mussel (*Pseudunio auricularius*, syn. *Margaritifera auricularia*) or the large potamal mayfly species have gone extinct in most of Europe and hardly return despite restoration efforts (Wantzen et al., 2014; Prié et al., 2017). Restoration efforts need to focus on the elimination of the known causes of species decline and on the reintroduction of a natural flow and sediment regime. Re-established floods below an alpine reservoir have successfully restored habitats for sensitive stonefly species (Jakob et al., 2004).

Modern river works connecting formerly separate river basins, increased shipping, sport fishing and the pet trade overcome biogeographic barriers and introduce new species around the world. Many benthic species have become invasive species. They affect ecosystem functioning and biodiversity but also human health, well-being and economy. Biofouling by byssus-fixed mussels such as *Dreissena* in North America (Hebert et al., 1989) and Europe (Bij de Vaate et al., 2002), or *Limnoperna* in Latin America (Darrigran, 2002) cause high economic costs associated with clogging strategic infrastructures such as aqueducts, pipelines or turbines. These and other filter-feeders like *Corbicula* mussels outcompete the native mussel fauna (Ferreira-Rodríguez et al., 2018; Karatayev et al., 2010). Golden snails (*Pomacea* sp.) are pests for rice culture in SE Asia. Invasive crustaceans are competitors, predators and disease vectors at the same time (Lodge et al., 2000). Diverse invasive species may facilitate each other, causing an "invasive meltdown" (Ricciardi, 2001). Global warming can break down thermal barriers of invaders in cooler regions (Hesselschwerdt and Wantzen, 2018). In all these cases, the structure and functioning of ecosystems become permanently disturbed. Once established, the control of invasive species is hardly possible. Locally, small barriers hinder upstream migration of invasive decapods and protect native decapods from crayfish disease. Species monitoring including eDNA analyses are needed to prioritize efforts to avoid the further establishment of these species, including the rigorous cleaning of sport boats (and angling devices) before transporting them to another water body, and the avoidance of canal constructions that connect distinct hydrographic basins.

Conclusions

Acting on many different trophic levels, benthic invertebrates hold a key position in all aquatic ecosystems. Their fascinating taxonomic, physiological and functional diversity has allowed them to colonize practically all types of habitats in inland water ecosystems. Detailed studies on their specific species traits allow us to use them as bioindicators for environmental impacts but also for the success of restoration projects, but there is a distinct bias concerning studies in the Global North and the Global South. More specifically, it is necessary to achieve a continuum from biodiversity analysis (along with environmental parameters and species traits), via the bioassessment of the environmental integrity of the ecosystems, to socio-ecological decision support for implementing adequate management/restoration actions and their subsequent effect monitoring. In this sense, it is urgent to join efforts and resources to create joint transnational and interdisciplinary programs that facilitate the exchange of taxonomic, biological and ecological knowledge and technical support to acknowledge the global value and better protect this wonderful world of aquatic biota.

Knowledge gaps

- Combined ecological and taxonomic studies, especially in the Tropics, linking genetic barcoding and morphology with species trait analysis and bioindicator value attribution.
- More detailed studies on "biotic hot spots and hot moments" (long-term, high-frequency studies).
- Effects of drought, microplastics, endocrine disruptors, and other novel threats (Reid et al., 2019).
- Effects of neobiota, including their role as vectors for diseases for other invertebrates (especially mussels and crayfish).

Further reading

- Integration of DNA-Based Approaches in Aquatic Ecological Assessment Using Benthic Macroinvertebrates (Duarte et al., 2021).
- Freshwater Biodiversity: Status, Threats and Conservation (Ecology, Biodiversity and Conservation) (Dudgeon, 2020).
- Invertebrates in Neotropical Floodplains (Wantzen et al., 2016).
- Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics (Bartels et al., 2012).

See Also: Structures and functions of Inland Waters - Lakes: Benthic Algae in Lake Littoral Habitats; Macrophytes; Structures and functions of Inland Waters - Rivers: Algae and Primary Production of Streams and Rivers Ecosystems

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Relevant websites

http://www.freshwaterplatform.eu/—Freshwater Information Platform.
https://www.freshwaterecology.info/—The taxa and autecology database for freshwater organism.
https://www.field-studies-council.org/biodiversity/freshwater-invertebrates-identification/—Freshwater Invertebrates Identification.
http://www.ephemeroptera-galactica.com/—The Ephemeropterists' Home Page.

Patterns in Freshwater Fish Diversity

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Allochthonous sources Externally produced, such as organic material from riparian forests.
Allopatry Originating in, or occupying, different geographical areas.
Autochthonous sources Internally produced, such as algae and aquatic plants.
Clade A group of species that are more closely related to one another phylogenetically than to other species, which represent a single branch of the Tree of Life composed of an ancestral species and all of its descendants.
Diversity Differences between species, or more inclusive (i.e. higher or supra-specific) taxa.
Floodplain Area of land adjacent to a stream or river which experiences flooding during periods of high discharge.
River capture A geomorphological process by which the flow of a river or stream is diverted from one outlet to another.
Speciation The evolutionary process by which populations evolve to become distinct species.
Species A fundamental unit of biodiversity, biogeography, evolution and ecology. Definition of species depending on species concept (e.g. the biological species concept or the genealogical species concept).
Sympatry Occupying the same or overlapping geographic areas.
Taxon (taxa, pl) A named group of organisms in biological systematics.
Variation Differences within a species, with trait values usually characterized by a normal frequency distribution.
Vicariance Speciation that occurs when biological populations become geographically isolated.

Introduction

Freshwaters are among the most biologically diverse habitats on Earth, with more than 140,000 species of macroscopic fungi, plants and animals representing about 12% of all described species on earth (Reid et al., 2019). Freshwater rivers, lakes, and wetlands include about 18,000 fish species, with hundreds of new species described each year (Fricke et al., 2020). Yet all of these distinct evolutionary lineages are compressed into a habitat less than 0.5% the total continental surface area, and only about 0.3% the volume of the hydrosphere (Shiklomanov, 1998; Lundberg et al., 2000).

These myriad species exhibit a bewildering range of physiological, morphological and behavioral adaptations, which allow them to inhabit almost all continental aquatic environments. Fish thrive in alpine lakes above 4000 m elevation, cascades and rapids of torrential mountain rivers, benthos of deep river channels (to >100 m deep) in meandering lowland rivers, seasonally desiccated swamps and ephemeral desert pools, karstic caverns and subterranean aquifers, moist forest leaf litter, and coastal estuaries, mudflats, and mangroves swamps. Riverine fishes in particular constitute the great majority of the species and exhibit the greatest range of functional adaptations.

Freshwater ecosystems and their biodiversity are increasingly threatened by human activities, including habitat alteration, water pollution, overfishing, exotic species introduction, river diversions, fragmentation and flow regulation, expansion of agricultural and urban landscapes, rising sea levels and altered precipitation regimes (Dudgeon, 2019; IPBES, 2019). For freshwater fish, the rate

of their decline is closely associated with the extent of riverine diversions and wetland loss (Albert et al., 2021). Freshwater vertebrates, especially fishes and amphibians, are currently the most threatened groups of vertebrates on our planet (Reid et al., 2019).

This chapter provides a brief overview of freshwater fish diversity, summarizes the main patterns and processes in freshwater fish ecology and evolution, and highlights role of aquatic-terrestrial linkages in maintaining healthy fish populations and diversity. The last section describes the main threats to the persistence of freshwater fish diversity in the 21st century.

Freshwater fish

Surprisingly, not all the fishes encountered in freshwaters are obligate freshwater species. Many freshwater fishes are **diadromous**, meaning they migrate between freshwater, defined as <500 ppm dissolved salts, and seawater to feed or reproduce. These migrations occur on time scales ranging from daily to annually or longer, and over distances ranging from a few meters to thousands of kilometers. The Bull shark (*Carcharhinus leucas*) for example, is mainly a marine species, but commonly enters freshwater rivers around the world, having been caught up the Amazon river as far as Iquitos (Peru), about 5000 km upstream from the Atlantic Ocean. Others fish groups, like salmons (Salmonidae) and sturgeons (Acipenseridae) are **anadromous**, hatching in freshwater but spending most of their lives feeding at sea before returning to their home rivers to spawn. Yet others fish groups like the true eels (Anguilidae) are **catadromous**, spawning in the sea but spending much of their lives in freshwater lakes and rivers.

To distinguish among species with varying affinities to continental waters, freshwater fishes worldwide may be classified into three categories based on their physiological tolerances to saltwater (Myers, 1949). **Primary** freshwater fishes are strictly confined to freshwater, and have little or no tolerance to salty or brackish waters. As a result, marine water is an important barrier to dispersal in primary freshwater fishes. **Secondary** freshwater fishes have somewhat greater tolerance to brackish waters, but normally occur in inland continental aquatic systems rather than coastal waters or the open sea. Secondary freshwater fishes are capable of occasionally crossing narrow marine barriers. **Peripheral** freshwater fishes are members of otherwise marine groups and exhibit high salt tolerance. Such fishes are more or less permanent residents in freshwater or spent part of their life cycle in freshwater and another part in marine habitats.

These different tolerances to saltwater strongly affect fish biogeographic distributions and evolutionary histories. For example, repeated sea-level fluctuations associated with global climate (i.e. ice age) cycles during the Pliocene (c. 5.3–2.6 Ma) and Pleistocene (2.6–0.01 Ma) resulted in multiple episodes of marine transgressions and regressions, alternately inundating and exposing low-lying coastal plains and the lower reaches of rivers around the world. Rising seas result in the geographic isolation of river mouths among coastal drainages, creating vicariance events for primary freshwater fish species, while representing semipermeable filter barriers for secondary and peripheral freshwater fishes (Leprieur et al., 2011; Abreu et al., 2020).

Differences in salt tolerance also help illuminate the origins of insular freshwater faunas. Continental islands like Trinidad or Britain, with a geological history of being connected to an adjacent landmass, usually share primary freshwater fishes with the mainland. Oceanic islands however, like Iceland or Hawaii which have never been connected to a continent, have no native primary freshwater fishes. The fish species of oceanic islands are usually secondary or peripheral species.

Global patterns in freshwater fish diversity

Freshwater fish diversity is highest in large tropical river and lake basins, such as the Amazon, Congo and Mekong, and large ancient lakes such as those in the Rift Valley of East Africa (Fig. 1). Islands commonly have lower freshwater fish diversity than continental areas of the same size, and a lower percentage of primary freshwater fishes (see "Freshwater fish" section). At the intercontinental scale, variability of riverine fish species richness has been related to three main factors: the total amount of aquatic habitat, spatial heterogeneity of aquatic habitats, and the stability of aquatic environments over evolutionary time scales. These factors are interrelated, and their relative contribution in a specific region is difficult to assess.

Habitat volume. The effects of river basin size and total amount of aquatic habitat is known as the species-discharge relationship (McGarvey and Terra, 2016; Rolls et al., 2018). Large river basins generally hold more species than smaller ones. All else being equal, larger drainage basins contain larger fish populations than smaller ones, which decreases the probability of an extinction after catastrophic disturbance events. Furthermore, larger river basins generally also have greater habitat diversity, and thus more potential niches that can be exploited, compared to smaller rivers.

Habitat heterogeneity. The number of fish species is positively correlated with measures of habitat variability and its spatial turnover (Heino, 2011; Dias et al., 2014; Craig et al., 2020). One main reason for the remarkable species richness in freshwaters is the heterogeneous distribution of freshwater habitats across biogeographic space and through evolutionary time (Albert et al., 2018). The unique geographic conditions of riverine and lacustrine environments allows fish populations many opportunities to disperse, thereby lowering their extinction risk (Miller and Román-Palacios, 2019), and to become geographically disconnected, thereby increasing the chance of speciation (Carrete Vega and Wiens, 2012; Bloom et al., 2013). By contrast, most marine environments are highly connected, and rates of lineage accumulation are generally lower in oceanic groups of organisms (Miller, 2020; Rabosky, 2020).

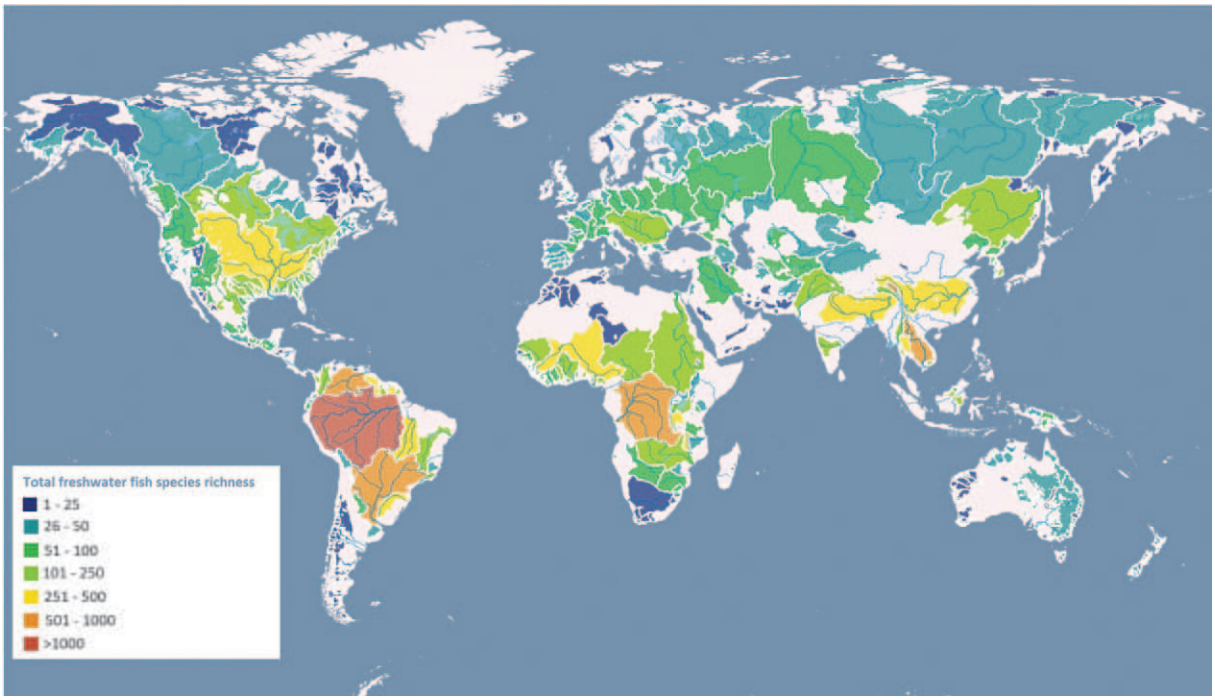

Fig. 1 Global freshwater fish richness patterns (rivers basins as spatial units). Map from Tedesco PA, Jézéquel C, and Oberdorff T (2013) *Global Freshwater Fish Species Richness*; accessed through the Global Freshwater Biodiversity Atlas (http://data.freshwaterbiodiversity.eu) on July 2020.

Habitat persistence and biome stability. Differences in species richness may also reflect the degree to which rivers have been recolonized since the last major climatic or tectonic disturbance event, and thus degree to which the ecosystems have reached an equilibrium level of species richness (Rabosky, 2009). Temperate and boreal rivers tend to have fewer species than tropical rivers of the same size, which can be understood in part by the more severe impacts of glacial intervals over the last 2.5 million years. Many rivers at high latitudes did not exist during the last glacial maximum (~20,000 years ago) and exhibit a relatively low diversity as they are still being colonized (Knouft and Page, 2003). By contrast, the large tropical river basins with the highest species richness have been the location of evolutionary diversification over millions of years (Oberdorff et al., 2019).

Freshwater fish biogeography

Biogeographical realms

Freshwater faunas of the world have been divided into seven main biogeographic realms based on similarities in species composition (Leroy et al., 2019). Each realm embraces a major continental landmass and is separated from the other realms by prominent dispersal barriers like oceans, mountain ranges, and deserts. The freshwater fishes realms are: (1) Neartic, including North America and Mexico north of the Isthmus of Tehuantepec; (2) Neotropical, including southern Central America and South America; (3) Palearctic, including Europe, and southwestern, northern, and northeastern Asia; (4) African or Ethiopian; (5) Sino-Oriental, including the Indian subcontinent, China, Southeast Asia and Sundaland; (6) Australian, including Australia, New Guinea and New Zealand; and the (7) Madagascan realm. Fig. 2 gives recent estimates of the freshwater fish diversity in each of these realms (Madagascar included in African realm here) and the distribution of species over the 15 fish orders that represent most of this diversity.

For freshwater fishes, each of the zoological realms may be further subdivided into freshwater ecoregions (Abell et al., 2008), whose boundaries generally, but not always, correspond with those of watersheds (i.e. drainage basins or catchments). Within an ecoregion there may be a turnover of species, such as when moving upstream or downstream within a river system (see "Within river patterns: From headwater to estuary" section), but taken as a whole, the ichthyofauna of a freshwater ecoregion has a distinct assemblage of species, although commonly overlapping with those of neighboring ecoregions. Interactive maps of these freshwater ecoregions, including descriptions of habitats and fishes, can be found on the webpage of the Freshwater Ecoregions of the World (https://www.feow.org/). Information and maps of the distributions of all freshwater fish families can be found in Berra (2007).

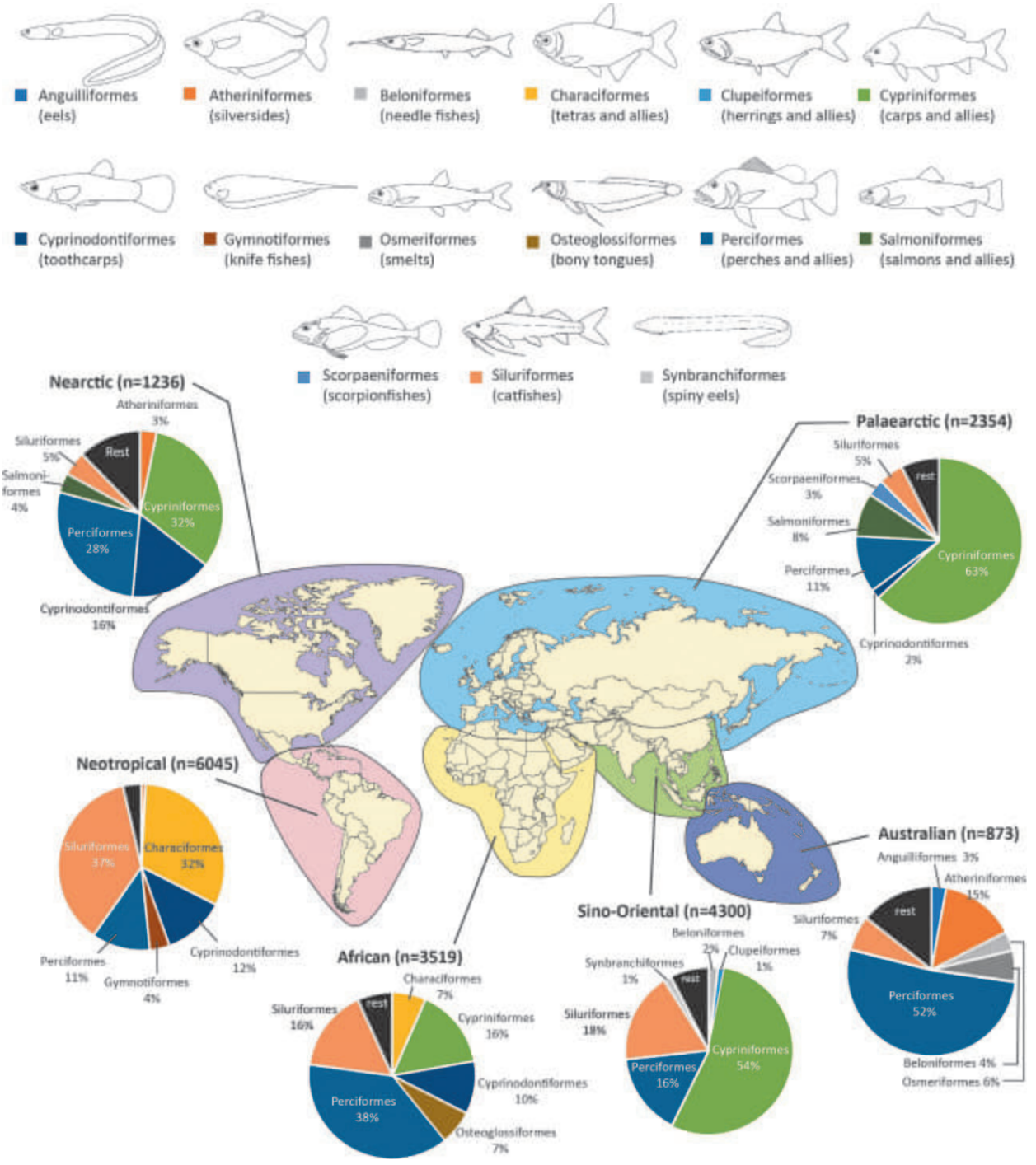

Fig. 2 Zoogeographical realms and the taxonomic composition of freshwater fish species. Number of species (*n*) in each realm and the contribution (as a percentage of the total diversity in each realm) of the six most dominant fish orders. Pie charts based on >15,000 freshwater fish species. Data from fishbase.org, accessed November 2019.

Dominant freshwater taxa

The reasons why certain fish orders dominate in some parts of the world and are absent in others (Fig. 2) is rooted in Earth's geological history and the breakup of the supercontinent Pangea (c. 250–100 Ma). The distinctiveness of continental fish faunas roughly reflects the amount of time that the organisms on those landmasses have been isolated from one another. Continents that have relatively high similarity, at least at a higher taxonomic level, were connected during the more recent parts of their geological histories. The very distinct floras and faunas of the Australian realm, on the other hand, reflect their long geographic isolation from any of the other major land masses. At lower taxonomic levels, distributional patterns of genera and species are further determined by interactions between (a)biotic conditions and species' functional traits (allowing them to thrive in some habitats, but not in others), as well as species' dispersal capacities (see "Taxonomic and functional disparities" section).

Remarkably, around 85% of the total global freshwater fish diversity belongs to just five taxonomic orders. Given their dominance, these groups are briefly described below.

Characiformes (tetras and relatives) are known from more than 2000 species, including tetras and piranhas. All are primary freshwater species. As a group, characiforms occur in tropical freshwater in Africa, Central and South America, with one species (*Astyanax mexicanus*) extending to the Texas border. Characiformes usually have an adipose fin, well-developed teeth in their oral jaws, a scaled body, and lack barbels. Most species grow to a relatively small adult body size (<5 cm SL), but some (e.g. *Hydrocynus goliath* in Africa and *Salminus franciscanus* in South America) can reach up to 1.3 m.

Cypriniformes (carps and relatives) are known from more than 4600 species, including goldfish, common carp, minnows and loaches. All are primary freshwater species, with the greatest diversity found in south-eastern Asia, and the group is absent from Australia and South America. Cypriniforms are characterized by a protrusible jaw in most species, having only a dorsal fin on their back (no adipose fin), and lacking teeth on the oral jaws, but possessing unique tooth plates in their throat (the pharyngeal jaws).

NOAA, obtained through Wikimedia Commons.

Cyprinodontiformes (toothcarps) are known from more than 1400 species, including guppies, mollies, swordtails and killifishes. They are secondary freshwater species, found mostly in freshwater and coastal marine areas, especially marshes, on all continents except Australia and Antarctica. Most species are small to medium-sized fish, with small mouths, large eyes, a single dorsal fin, a rounded or truncate caudal fin, a lateral line with pores on the head and pitted scales on the body, and pectoral fins usually set low on the body. Many species are livebearers (viviparous or ovoviviparous).

Perciformes (perches and relatives) are known from more than 10,000 species, both marine and freshwater species. Freshwater species include cichlids, freshwater sunfishes (centrarchids), and perches and North American darters (percids). They are secondary freshwater species found on all continents (except Antarctica) and in all oceans. Most, but not all species have spines present in the dorsal and anal fins, thoracic pelvic fins with one spine and five rays, ctenoid scales, two dorsal fins and no adipose fin.

Siluriformes (catfishes) are known from about 4000 species. Most catfishes are primary freshwater species, with two families of predominantly marine species. They occur on all continents except Antarctica, and are easily recognized by having up to four pairs of barbels around the mouth, lacking teeth, usually having an adipose fin, spine-like rays at the anterior dorsal and pectoral fins, and the body naked or covered by bony plates. Catfishes have an electroreceptive sense, and most species are nocturnal.

Within river patterns: From headwater to estuary

Despite idiosyncratic differences in taxonomic composition and evolutionary history of regional ichthyofaunas, many aspects of fish assemblage structure change predictably from headwaters to river mouth, a phenomenon known as the River Continuum Concept (Vannote et al., 1980; Fig. 3). Changes in river basin geomorphology and hydrology along the course of rivers reflect processes governing current speed, sediment load and organic matter decomposition, and allochthonous versus autochthonous production (Leopold, 1994). The taxonomic composition, phenotypic characters, and community structure of freshwater fishes in all regions of the world is strongly affected by longitudinal fluvial gradients (Matthews, 2012; Lujan et al., 2013).

Headwater streams are usually narrow and, when originating below the tree line, often over-shaded by marginal vegetation. Headwater streams generally also have cooler water temperature, because of the high elevation and the rapid flow rate down steep terrains. Consequently, in situ productivity is low and food chains relatively simple and short, depending strongly on allochthonous

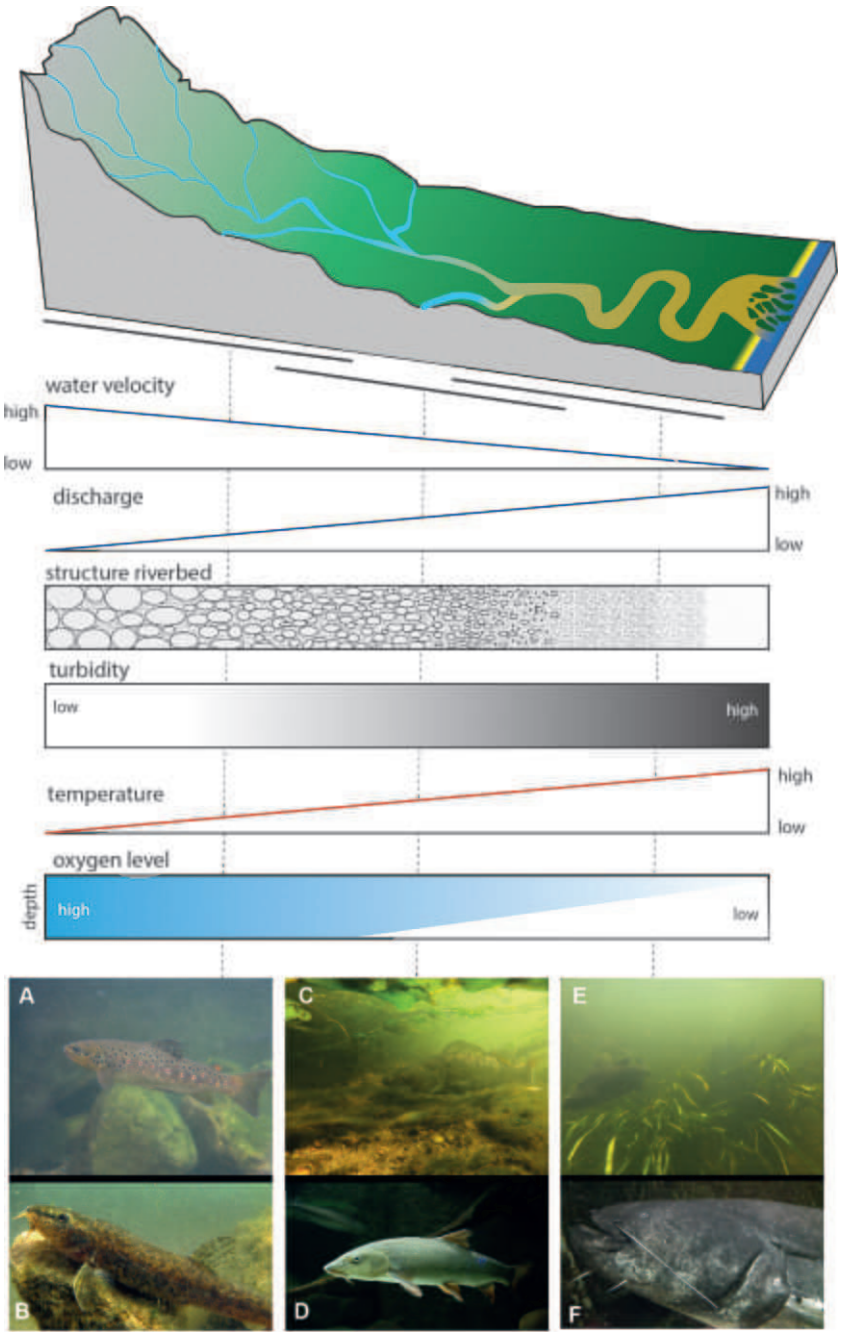

Fig. 3 Most rivers have a clear turn-over of fish assemblages (and dominant species) from headwaters to delta, reflecting changes in the physical environment as shown in a generalized form here. Some headwaters may originate in the lower sections of rivers (e.g. small forest creeks) and will not show pronounced changes in some of the physical properties illustrated here (e.g. temperature and structure of the riverbed). Some examples of indicator species for different river sections from the Rhine basin: (A) brown trout (*Salmo trutta*), (B) stone loach (*Barbatula barbatula*), (C) zander (*Sander lucioperca*), (D) common barbel (*Barbus barbus*), (E) common bream (*Abramis brama*), and (F) wels catfish (*Silurus glanis*).

inputs from terrestrial photosynthesis. In headwaters that lie above the tree line the predominant fishes are small-bodied algae-grazers.

Mountain-dwelling fishes usually exhibit morphological and ecophysiological specializations that facilitate life in high-elevation and torrential waters; i.e. rheophily. Rheophilic fish species commonly possess streamlined bodies or morphological structures that allow them to cling to bottom substrate, such as fin hooks, and mouths or fins shaped to form a sucker disk (Lujan and Conway, 2015). As headwaters are usually oxygen rich water, headwater specialist fishes have low tolerance to low oxygen levels such as can be found in lower sections of river.

Mountain and hill-stream fishes have evolved multiple times independently in each of the world's major mountainous regions (Albert et al., 2018). North American groups include the rainbow trout and relatives (*Oncorhynchus* with 10 species) in the mountains of western North America, and minnows and shiners (*Cyprinella* and *Notropis* with 64 species), and North American darters (*Etheostoma* and *Percina* with 132 species) in uplands of eastern North America. South American groups include the characiforms *Creagrutus* with at least 75 species and *Parodon* with 15 species, the catfishes *Astroblepus* with at least 80 species, *Chaetostoma* with at least 48 species, and *Trichomycterus* with at least 49 mountain species, and the killifishes *Orestias* with 45 species.

Eurasian groups include the snow minnows (Schizothoracinae) with at least 76 species in the Himalayas-Tibet region, the hillstream loaches (Balitoridae) with at least 102 species in the mountains of south and southeast Asia and Sundaland, the catfish families Akysidae with 57 known species and Sisoridae with at least 292 species. African mountain fishes include the cyprinid *Luciobarbus* with 38 species and the catfish family Amphiliidae with at least 102 species. There is also a curious group of fishes in their own family, Galaxiidae, with about 66 species that exhibit a circum-Antarctic distribution in high-altitude rivers of southern New Zealand, Australia, Africa and South America.

Middle sections have warmer water than headwaters and more autochthonous production (e.g. by algae) because of the nutrients that come down from headwater streams and because of increased light availability as rivers widen. Water flow is slower and food chains begin to lengthen. In West- and Central Europe, common fish species in middle sections are those of the genus *Barbus* (Fig. 3D), which depend on gravel beds for spawning.

Toward the mouth of the river, conditions start to resemble a slowly moving lake. Energy availability from both allochthonous and autochthonous production is high, as is energy input and dissolved organic matter from upstream reaches, leading to an increase of detritus- and plankton feeding species and mud as feeding ground. Turbidity is commonly also high and species that find food visually decrease in abundance. Oxygen levels are usually much lower compared to headwaters because of the combination of higher water temperature, lower flow rate and high decomposition of organic material. Brackish water, or occasional brackish conditions, in the lowest reaches of rivers can limit the occurrence of primary freshwater fishes, but fish diversity can be high due to the presence of secondary and peripheral freshwater fishes (see "Freshwater fish" section).

There may be many fish species that do not clearly conform to the river continuum concept, roaming from headwater to delta, but large rivers usually have a clear turn-over of fish assemblages along their course, at least among the species that dominate.

Importance of river floodplains for riverine fish diversity and abundance

Although the River Continuum Concept provides an important holistic view of river systems, it initially did not consider the role that lateral floodplains play in supporting aquatic productivity. Possibly, the importance of floodplains for fish was long misunderstood because nearly all large rivers in the temperate region were already heavily modified landscapes prior to scientific study (Opperman et al., 2017). It is now broadly recognized however that floodplains play a crucial role for fish abundance and diversity, with many studies across the world showing direct relationships between fish production and the extent of floodplain inundation (e.g. Welcomme, 1979; Risotto and Turner, 1985; Beechie et al., 1994; Agostinho et al., 2004; Pander et al., 2015). Consequently, the river continuum concept has been extended with the flood pulse concept (Junk et al., 1989), recognizing that floodplains are intimately connected to rivers (Fig. 4).

Floodplains are inundated seasonally (predictably) in most river systems, but irregularly (unpredictable) in others. The predictably, seasonality and duration of the flooding determine the extent to which fish fauna in a river system depend on, and have developed specific adaptations for, exploiting floodplains (King et al., 2003). When flooding is predictable (e.g. annual) and duration relatively long (e.g. several months), many fish will show adaptations to exploit the abundant food resources on floodplains and will use the floodplains as spawning and nursery areas. This is the case in most large tropical rivers, such as large parts of the Amazon, Congo and Mekong. Here, the flooding season usually represents the time of plenty during which fish built up fat reserves and use floodplains for spawning and rearing (e.g. van der Sleen and Albert, 2017). Predation rates are commonly low during the flooding season as fish are dispersed over large and vegetated areas. In the Amazon basin, the flooding period also coincides with the peak of the fruiting seasons of riparian trees. Many fish species feed on floodplain tree seeds and fruits, which form important nutritional items (e.g. Goulding, 1980; Fig. 4). In return, fish can be important (upstream) dispersal agents of tree seeds, a process known as ichthyochory. Access to this seasonal bonanza can be limited by extreme and persistent hypoxia in tropical floodplains, caused by decomposition of forest litter during the flood season. Fishes that exploit tropical floodplains therefore commonly possess a combination of morphological, physiological and behavioral adaptation for hypoxia.

The dry season can represent the opposite case, when fishes are restricted to the main river channels or oxbow lakes on the floodplain, food availability is low, and many fish species use fat reserves, built up during the floods, to survive. Predation rate and mortality can be very high during the dry season. These pronounced seasonal changes in food availability and predation risk may be an important mechanism for maintaining high levels of riverine fish diversity in tropical rivers (Lowe-McConnell, 1987). During the

Fig. 4 Example of floodplain forests (flooded forests) in the Amazon basin (middle Rio Negro, Brazil), during the low-water season (A; October to April in this part of the basin) and high-water season (B, May to September). Fishes and trees; a few examples of fish utilizing floodplains at high- and low latitudes: (C) a small pike (*Esox lucius*) hiding in the branches of a submerged willow tree, the Netherlands. (D) Common carp (*Cyprinus carpio*) spawn in areas of submerged vegetation in floodplains and lakes (photo from the Meuse basin, Belgium). Carp reproduction success is restricted to years when water levels start rising in May and when high temperatures and flooding of terrestrial vegetation last for a long period during May and June. (E) *Brycon hilarii* and *Piaractus mesopotaminus* swimming through an open area in the middle of submerged floodplain forest, Paraguay river, Brazil. (F) *Brycon pesu* in a submerged floodplain forest in the lower Tapajos River, Amazon basin, Brazil. Species of *Brycon*, *Piaractus* and carps are known to disperse seeds of floodplain plants, a process known as ichthyochory.

flooding season, food is abundant in such quantities that fish are not competing with each other, sharing the available resources. Any competitive advantage, and disproportional increases in population size, will be unset during the low water season, when predators likely prey on the more abundant species, and switch to other prey species with decreased abundance. As such, high predation during the low-water season may prevent any given species from becoming dominant and outcompeting others.

In temperate regions, water temperature will co-determine how much fishes can exploit floodplains. If floodplains are inundated in winter, fish may not be able to utilize the floods because of low metabolic rates and/or because of low primary productivity on the floodplains during winter. Fish in temperate region will therefore benefit most strongly from flooding in spring or summer. If that is the case, floodplains can be highly favorable habitats for juvenile fish, because of the slower water speed, usually warmer water (due to reduced flow rates), high food availability and low predation risk.

When flooding is unpredictable in timing and/or duration fish communities will lack specific adaptations for using floodplains. Nonetheless, fish will still benefit from the allochthonous energy input and use the floodplains more opportunistically. The importance of floodplain habitats for fish is difficult to overstate. Unfortunately, natural floodplains continue to be among the fastest disappearing habitats in the world.

Taxonomic diversity of freshwater fish

At a macroevolutionary scale, the species richness of a clade, such as a fish family or genus, is a balance between rates of speciation that increase diversity, and extinction, that reduce diversity. Rates of speciation in fishes have been hypothesized to be higher in lacustrine than riverine habitats (see "Lacustrine species flocks" section; Miller, 2020). Yet most freshwater fish diversity is thought to have arisen by allopatric speciation within the dendritic spatial geometry of continental river systems (Albert et al., 2011b, 2017; Miller, 2020). River basins have a much larger total habitat footprint than lakes, are often much older, and have a more complex history of rearrangements due to river capture and sea-level changes (Albert and Crampton, 2010; Albert et al., 2018).

Taxonomic and functional disparities

Diversity measures for freshwater fishes vary strongly among taxonomic groups. This may relate partly to the amount of research effort that has been dedicated to particular fish groups, but it is undeniable that diversity is not distributed equally across branches of the phylogeny of fishes (Alfaro et al., 2009). Among fishes, some higher taxa (e.g. families or genera) are exceptionally diverse, with hundreds of species exhibiting a wide range of functional traits, while others are represented by just one or a few species and little functional diversity. In fact, most of the higher taxa in fish, as in most groups of organisms, are species poor, while most species are members are a few species-rich groups (Albert et al., 2011a; Worm and Tittensor, 2018).

Many reasons have been proposed to explain these taxonomic and functional disparities. Some explanations focus on the role of so-called "key innovations," novel evolutionary traits that either spur speciation or reduce extinction (Seehausen, 2006; Siqueira et al., 2020). These traits can include any aspect of an organism's phenotype that allow many closely-related species to co-exist together in sympatry, including for example: small adult body size (Albert and Johnson, 2012), chromosomal and genomic reorganization (Volff, 2005), developmental canalization and modularity (Larouche et al., 2018), ecological specialization (Seehausen and Wagner, 2014), and specialized sexual communication systems (Crampton and Albert, 2006; Arnegard et al., 2010).

In addition, speciation rates can also relate to traits that impede dispersal, such as **philopatry** or the absence of dispersal-specialized developmental stages (Likens et al., 2009). For example, the loricariid catfishes (family Loricariidae) from South America attain relatively small adult body sizes and most species are highly territorial. As a consequence, the dispersal capacity of most loricariid species is low, which increases the chances for geographic isolation and speciation. Indeed, over 1000 loricariid species are known. In contrast, only 114 species are known in another catfish family occurring on the same continent, the Pimelodidae, which consists of large-bodied migratory catfishes, many of which are widely distributed. Reduced dispersal capacity has been suggested as an important factor underlying species richness in many fish families.

Other explanations for differential diversification focus on properties of the external environment, including the contributing roles of ecological opportunity (Roxo et al., 2017), total amount of evolutionary time and ecological incumbency (Albert et al., 2011a), and the vagaries of random diversification (Albert et al., 2020). Most higher taxa of freshwater fishes originated tens of millions of years ago, in the Late Cretaceous (c. 100–66 Ma) or Paleogene (c. 66–23 Ma). For example, the bowfin or choupique (*Amia calva*) of eastern temperate North America is the sole surviving lineage of the Amiiformes, a group that was once diverse and geographically widespread across much of the world during the Mesozoic period (250–66 Ma; Long, 1995; Arratia, 2013). Indeed, almost all of the early branches of bony fishes (Osteichthyes) are relicts of groups that were formerly diverse and widespread, and which only survive in the modern world with a few species in isolated freshwaters.

Regardless of the causes, the wide distribution of evolutionary ages among fish clades indicates that the formation of the modern biodiversity arose from interactions of landscape and biotic processes over an immense time span.

Lacustrine species flocks

Some fish groups exhibit a tremendous capacity to diversify rapidly. This capacity is well-illustrated by the phenomenon of "lacustrine species flocks," the accumulation of many closely-related species within the circumscribed area of a large lake basin (Echelle and Kornfield, 1984). Such rapid accumulations of many closely-related species, often differing from one another in traits related to feeding and habitat, have long been thought to represent classic examples of Darwin's hypothesis for the origin of species by means of natural selection (Goldschmidt, 1998; Foote, 2018; Richards et al., 2018).

Species flocks of lake-dwelling fishes have been described on all continents except Antarctica, concentrated in regions that were previously defaunated due to climatic or tectonic events (ice ages, vulcanism), or otherwise lacking an incumbent fauna of primary freshwater fishes (Cavin, 2017). Some of the more well-studied fish lacustrine species flocks include the cottoid sculpins of Lake Baikal, Russia (with 22 spp. in two genera), *Orestias* killifishes of the Lake Titicaca basin in the Andes of Bolivia and Peru (with 23 spp.), *Coregonus* ciscos or whitefish salmonids of the Great Lakes of North America (with 8 spp.), cypriniform barbs of Lake Tana,

Ethiopia (*Labeobarbus* 27 spp.) and Lake Lanao, Philippines (*Barbodes* 18 spp.), and Sailfin silversides (*Telmatherina* 10 spp.) in the Malili Lake system of Sulawesi, Indonesia.

Certainly the most spectacular of all of the fish species flocks are those of the haplochromine cichlids in the Great Lakes of the East African Rift Valley. These haplochromines have radiated into more than 3000 distinct phenotypes, each representing a putative species lineage, in only a few millions of years or less. Lake Victoria, with a flock of 500 morphotypes, is thought to have been a dry lake-bed perhaps as little as 14,000 years ago (Meier et al., 2017). There are also at least 241 cichlids representing several different clades in Lake Tanganyika (age 9–12 Ma) and about 400 species representing other additional clades in Lake Malawi (age 4.5–8.5 Ma). There are also well-studied cichlid species flocks in smaller lakes in volcanic calderas, for example in Cameroon (West Africa) and Nicaragua (Central America).

Cichlid fishes differentiated most rapidly in aspect of their head and mouth shape, structure of the teeth in the oral and pharyngeal jaws, and color patterns based on pigment cells called chromatophores. All these tissues are derived developmentally from a unique and exceptionally plastic vertebrate cell type called the neural crest (Bronner and LeDouarin, 2012; Powder and Albertson, 2016). These traits, associated primarily with feeding and sexual behaviors, allow species to occupy a wide variety of ecological roles in lacustrine ecosystems.

Species flocks have attracted much attention in the hope they would illustrate conditions in which adaptive divergence based on ecological specialization results in speciation. Yet in most cases where detailed population genetic and phylogenetic studies have been performed, the species that constitute a lake fauna have not been found to be monophyletic. Rather the species flock has been found to have accumulated through multiple rounds of dispersal and subsequent speciation, in and among the lake and tributary rivers of the regional watershed (Turgeon and Bernatchez, 2003; Lüssen et al., 2003; Martin et al., 2015). Many of the classic examples of sympatric speciation in lakes have been shown to involve complex histories of gene flow and dispersal into and out of the lake (Kontula et al., 2003; Fruciano et al., 2016; see review by Stroud and Losos, 2016). Lacustrine species flocks in general represent cases in which both ecological and geographic factors conspired to generate rapid adaptive diversification.

Threats to freshwater fish diversity

There are hardly any large rivers systems left on our planet in which fish do not face a multitude of threats (e.g. Dudgeon, 2019; Reid et al., 2019). Severe and persistent pollution continues to be a major problem in many rivers and includes pesticides and fertilizers running off from agricultural land, mercury from gold mining in headwaters, microplastics, and pollutants that affect the sex ratio in fish populations. Loss, or severe reduction, of river connectivity is another major threat. The construction of large hydrological dams for power plants is a growing concern for fish diversity in many tropical rivers (Winemiller et al., 2016). Hydropower dams modify habitat conditions in large areas upriver and down-river of the dam, retain sediments and nutrients in the reservoirs, and block fish migration routes. Fish passages (i.e. fish ladders) are often insufficient to fully mitigate the loss of connectivity and obstructions to fish migration routes (Brink et al., 2018).

Dams and other water diversion structures also strongly modifying the natural flood regime downriver (Timpe and Kaplan, 2017). These structures change the annual flood pulse to become highly intermittent, with important consequences for fish populations that depend on predictable access to floodplains for food, reproduction and rearing. In addition, floodplains have been severely modified throughout most of the world due to drainage and land-use change (e.g. deforestation for agriculture). In some parts of the world, the introduction of non-native (i.e. exotic) species is another major issue, causing (local) extinction of native species. The introduction of the Nile Perch (*Lates niloticus*) in Lake Victoria is a much studied example of the dramatic effects that alien species can have on an entire ecosystem (e.g. Goldschmidt, 1998). For other species, persistent overfishing led to the disappearance of larger individuals, with ramifications for the important ecological and demographic roles that larger individuals can play. On top of all this, climate change is becoming an increasing stress factor in many freshwater ecosystems, affecting species through warming water temperatures, shifting streamflow regimes, increasing extreme (e.g. flooding and drought) events, and facilitating species invasions.

Freshwater ecosystems and their associated riparian habitats are among the most biologically diverse on Earth, and have inestimable economic and cultural values. Yet human impacts to lakes, rivers, streams, wetlands and groundwater are dramatically reducing biodiversity and robbing critical natural resources and services from current and future generations. Freshwater biodiversity is declining rapidly on every continent and in every major river basin on Earth, and this degradation is occurring more rapidly than in terrestrial ecosystems (Albert et al., 2021). The abundances of freshwater fish populations have become dramatically reduced since 2000, at local scales in both temperate (Freyhof and Brooks, 2017) and tropical (Cohen et al., 2016; Pelicice et al., 2017) latitudes, and in different climate zones (Ngor et al., 2018). From 1970 to 2012 populations of freshwater fishes have declined by 88%, with mega-fishes (>30 kg) undergoing the largest declines (–94%, Carrizo et al., 2017; He et al., 2019).

Many freshwater fish have narrow distributional ranges or have small population sizes, making them intrinsically rare and sensitive to local disturbances. Data suggest that up to 40% the freshwater fishes in Europe and North America are at risk or already lost (Maitland, 1995; Jelks et al., 2008). Globally, it is estimated that 20% of all freshwater species have become extinct or face extinction in the decades to come, and this percentage will likely continue to increase in the future. The Yangtze basin is among the most impacted of any large river on Earth, with the recent extinction of the Yangtze paddlefish *Psephurus gladius* (Zhang et al., 2009). The Yangtze paddlefish was the last surviving species of a lineage that originated in the super-greenhouse world of the Mesozoic, with fossils from the Upper Cretaceous about 75 million years ago.

Effective management of freshwater resources and ecosystems must be ranked among humanity's highest priorities. The remedies - restrictions to the construction of dams, pollution control, restoration of wetlands areas, limits on harvests of vulnerable species, and restrictions on the translocation of non-native species—are well known, but modification and degradation of river systems still outpaces initiatives to mitigate the threats to freshwater diversity in most parts of the world. Freshwater faunas worldwide are imperiled and the future looks bleak for many freshwater fish species. Coordinated actions are urgently needed at the local, regional and international levels, in order to conserve freshwater habitats and species that have taken millions of years to evolve.

See Also: Emerging methods and topics: Electronic Tagging and Tracking of Animals in Inland Waters; Freshwater Ecoacoustics—A New Addition to the Limnologists' Methods Toolkit; Human pressures and management of Inland Waters: Biological Invasions: Case Studies; Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment; Implications of Climate Change for Freshwater Fisheries; Inland Fisheries Management - Case Studies of Inland Fish; Inland Fisheries Management - Exploitation and Livelihoods; Social/societal values of Inland waters: Societal Values of Inland Fishes; Structures and functions of Inland Waters - Lakes: Fish Populations; Structures and functions of Inland Waters - Rivers: Succession in Streams

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Relevant websites

http://atlas.freshwaterbiodiversity.eu/—Information on Global Freshwater Fish Diversity Patterns.
https://www.calacademy.org/scientists/projects/eschmeyers-catalog-of-fishes—Database and Reference Work on the Scientific Names of Fish Species.
https://www.feow.org/—Maps and Information on the Freshwater Ecoregions of the World.
https://www.fishbase.org/—Global Database on Fish Species (e.g. Taxonomy, Ecology, Distribution).

Ecology and Conservation of Wetland Amphibians and Reptiles

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Adaptation Heritable trait that fits an individual to its conditions of existence, leading to similarity among organisms that have similar lifestyles.
Amniotic egg Type of egg in which the embryo develops inside a protective membrane called amnion.
Anthropogenic impact Impact directly or indirectly caused by humans. Anthropogenic impacts in the environment include habitat degradation and climate change.
Body plan General morphological structure each organism assumes as it develops.
Cryptic diversity Defined as the occurrence of two or more distinct species erroneously classified as one species, often made up of morphologically similar but genetically distinct taxa and largely affected by biodiversity shortfalls and sampling gaps.
Embryonic development Process by which the embryo is formed and developed.
"Herps" or Herpetofauna Reptiles and amphibians of a particular region, habitat, or geological period. This is an artificial classification convenient for research purposes but does not reflect evolutionary relationships among these groups of vertebrates.
IUCN Red List The International Union for Conservation of Nature (IUCN) Red List of Threatened Species (also known as the IUCN Red List or Red Data List), is the world's most comprehensive inventory of the global conservation status of species.
Non-avian reptiles Cladistic term referring to all representatives of the class Reptilia, excluding birds (Aves).
Osmotic stress Physiological dysfunction caused by a sudden change in the concentration of solute around a cell, which causes a rapid change in the movement of water through its cell membrane.
Riparian environment Interface between land and a river or stream. Its geographical extension differs depending on the type of organism considered.
Semi-aquatic Organism that spends part of its life in an aquatic environment.

Introduction

Amphibians (frogs, salamanders and caecilians) and reptiles such as squamates (amphisbaenians, lizards and snakes), chelonians (turtles and tortoises) and crocodilians (alligators, caimans, crocodiles and gharials) have traditionally been recognized as "herpetofauna." Although such classification may be convenient for research purposes, it does not reflect evolutionary relationships among these animals, because amphibians and reptiles are distantly related in biological evolution. Furthermore, even though birds are closely related to crocodilians, they are not traditionally considered to be reptiles. Finally, the evolutionary origin of chelonians has been historically uncertain (Pyron et al., 2013; Shaffer et al., 2017; Zheng and Wiens, 2016).

Although all "herps" share the characteristic of being ectothermic animals, having body temperatures mainly varying according to the environmental conditions, they have a critical difference that influences their level of dependence to water: the amniotic egg. Amphibians lack an amniotic membrane during embryonic development, which imposes an aquatic phase at least during part of their development. However, many lineages conquered certain independence from water through development of the embryo on humid terrestrial habitats, or inside body pouches. Conversely, reptiles are amniotes, and their embryonic development is completed under protective membranes inside the egg. The origin of the amniotic egg, approximately 300 million years ago, was an important step in the evolution of vertebrates that allowed diversification of species without an aquatic larval stage (Pough et al., 2003).

More than 8500 amphibian and reptile species (43.4% of global diversity; Frost, 2020; Uetz et al., 2020) live in wetlands around the world, and therefore those ecosystems are extremely important for herpetofauna conservation (Junk and da Silva, 1997). While some species rarely leave permanent wetlands during their lifetimes, others temporarily occupy ephemeral swamps or seasonally flooded forests and grasslands, or just use wetlands as dispersal routes. Regardless of the time spent in wetlands, these ecosystems provide the resources necessary for herpetofauna to thrive. For instance, wetlands are bridges connecting terrestrial and aquatic habitats (Junk et al., 1989), so amphibians with aquatic larvae can complete the life cycle within these habitats, and reptiles can move freely between land and water to perform vital activities such as eating, thermoregulating and fleeing predators.

In this chapter, we introduce wetland amphibians and reptiles to the reader. We show some of their ecological and morphological adaptations that enable life at different degrees of association to these environments and discuss the overall threat status and challenges to promote species conservation. Finally, we argue on the importance of protecting these species-rich and threatened ecosystems. We based our species diversity and conservation assessments on the International Union for Conservation of Nature (IUCN) Red List. We further use more refined group-specific assessments when available for turtles (Rhodin et al., 2018) and for lizards and snakes (Meiri, 2018; Uetz et al., 2020).

Amazing forms, incredible diversity and conservation challenges

Amphibians

The term "amphibian" derives from the ancient Greek meaning "two kinds of life," and is allusive to the use of both terrestrial and aquatic environments. Modern amphibians (subclass Lissamphibia) are a monophyletic group comprising all frogs, toads, salamanders, newts, and caecilians, which are generally thought to be closely tied to wetlands because of general characteristics such as unshelled eggs (Fig. 1A) and permeable skin (Fig. 1B). Even though a few from the ca. 8300 species known to date (Frost, 2020) are able to tolerate high levels of salinity, amphibians have no marine representatives. The high rate of species discovery and the lack of knowledge on details about their natural history precludes us from obtaining an accurate estimate of the magnitude of the use of inland waters by amphibians. However, it was estimated that about three quarters of the extant amphibian species have a close relationship to freshwater environments at least during some part of their life cycles, usually during their larval, tadpole stage (Vences and Köhler, 2008).

Amphibian species can be categorized in four main groups depending on their relationship with water environments (Vences and Köhler, 2008): (a) aquatic: with at least part of their life cycle in or on the water; (b) water dependent: which do not live directly in the water but closely depend on it for resources such as habitat or food; (c) water related: aquatic plus water dependent species; and (d) non-water related: which are neither aquatic nor water dependent. The overwhelming majority of known amphibians are aquatic organisms that depend on water environments for egg deposition and tadpole development. However, just a few species can be considered water related (strictly aquatic) since most of them do not necessarily depend on water bodies during the post-metamorphic stage, which is rarely fully aquatic. Extreme association with aquatic environments occurs in some groups of caecilians (Fig. 1C) and salamanders, whose species usually share dorsolaterally flattened tails and large fins that facilitate swimming. As for anurans, two frog families can illustrate both extremes of the water dependency gradient: all species on the Pipidae family are closely tied to freshwater environments, as their entire life cycle occurs inside water (Fig. 1D). Members of this family show remarkable adaptations such as vocalization, mating, and egg deposition entirely underwater. Adults also show morphological traits such as presence of a lateral-line system for detection of movement and pressure gradients in the surrounding water and interdigital membranes for swimming. Conversely, Craugastoridae is a speciose non-water related family comprising terrestrial frogs whose males vocalize from territories established on the forest floor. Egg clutches are usually deposited in the soil under fallen leaves and depend on environmental humidity. Development to metamorphosis occurs within terrestrial eggs with the absence of an aquatic, free-living tadpole stage.

At a community level, the affinity with wetlands strongly influences the formation of amphibian assemblages. For example, distance from streams is the main factor influencing the occurrence and abundance of aquatic-breeding species in Amazonian forests (Menin et al., 2011). As a consequence, the distributions of amphibian species with aquatic reproduction are more related to environmental variables, whereas species with terrestrial reproduction show strong spatial patterns (Landeiro et al., 2014). Fine-scale distributional patterns of aquatic-breeding species such as *Atelopus hoogmoedi* and *Scinax ruberoculatus* are affected by subtle changes in limnological variables such as water pH and pond availability (Ferrão et al., 2018; Jorge et al., 2016). This reinforces the notion that aquatic-breeding amphibians are highly sensitive to environmental heterogeneity and must be regarded as powerful and reliable indicators of habitat alteration.

With regard to the conservation of amphibians in wetlands, hunting and illegal trade are worrying but represent relatively lesser threats when compared to emerging climate changes and diseases, as well as habitat degradation and loss (IUCN, 2020). For

Fig. 1 Important ecological and morphological adaptations of amphibians and reptiles that allow lifestyles linked to wetlands, exemplified by Neotropical species. **Amphibians**: A. Unshelled eggs, exemplified by a spawning in a puddle (*Osteocephalus taurinus*; Hylidae; Ph: LM); B. Permeable skin (*Hyalinobatrachium cappellei*; Centrolenidae; Ph: LM). C, D. Fully-aquatic species with sense organs and adaptations for swimming, as developed interdigital membranes or compressed bodies with fins (*Typhlonectes compressicauda*; Typhlonectidae; Ph: Adriano Maciel and *Pipa arrabali*; Pipidae; Ph: LM). **Lizards**: E. Long and laterally compressed tails. Tail and body with fins or strongly keeled scales and enlarged tubercles, helping with propulsion and stability during swimming behavior (*Potamites ecpleopus*; Gymnophthalmidae; Ph: LM); F. Dietary specialization, feeding on snails, fishes and arthropods (*Dracaena guianensis*; Teiidae; Ph: Paulo Bernarde); **Snakes**: G. Eyes and nostrils positioned in the upper region of the head to see and breathe in the water surface while avoiding overexposing the body (*Helicops leopardinus*; Dipsadidae; Ph: RF); H. Dietary specialization, feeding on fish, tadpoles and adult frogs (*Leptophis ahaetulla*; Colubridae; Ph: FV); I. Body thickness and color matching vegetation cover for efficient camouflage (*Thamnodynastes lanei*; Dipsadidae; Ph: RF); **Turtles**: J. Strong shell to avoid the predation by caimans (*Peltocephalus dumerilianus*; Podocnemididae; Ph: FV); K. Terrestrial species are able to swim considerably well (*Chelonoidis denticulatus;* Testudinidae; Ph: Thais Morcatty); **Crocodilians**: L. Laterally compressed tail (*Paleosuchus trigonatus*; Alligatoridae; Ph: William E. Magnusson); M. Flexible trunk (*Paleosuchus palpebrosus*; Alligatoridae; Ph: Boris Marioni); N. Four-chambered heart that allows complete submersion for long periods (*P. palpebrosus*; Alligatoridae; Ph: FV).

example, the waterborne disease-causing fungus *Batrachochytrium* sp. is linked to declines of hundreds of amphibian species around the world such as anurans with aquatic larvae and salamanders, and aquatic hosts are more exposed to disease during their ontogeny than species with terrestrial reproduction (Mesquita et al., 2017). Another key amphibian life-history aspect is breeding migration of individuals between suitable aquatic and terrestrial habitats, and disconnection between these systems negatively affects the richness of species with aquatic larvae (Becker et al., 2007). Although research has been carried out since amphibian declines were first detected in the 1990s, apart from some specific examples, little empirical progress on their conservation has been made (Grant et al., 2019), and currently amphibians constitute the tetrapod group most threatened with extinction (IUCN, 2020). Consequently, the viability of their populations in the Anthropocene depends on actions aiming to the integrity of aquatic environments, as well as their proper connectivity to suitable land, thus permitting the amphibious way of life of these highly sensitive organisms.

Lizards

Various squamate groups that began to diversify about 200 million years ago are collectively known as "lizards." Most of the extant lizards share a characteristic standard body plan, which also corresponds to the body plan of their extinct relatives and the first amniotes (Pough et al., 2003). Such a generalized body allows these highly adaptable vertebrates to explore the environment in a very efficient way, leading to high species diversity, currently occupying most of the distinct ecosystems on Earth (Pough et al., 2003). Throughout evolutionary history, lizards also diversified into alternative body plans, well adapted to different dietary preferences and habitats. One of the best known evolutionary changes in this group is the reduction or loss of limbs associated with body elongation (Wiens et al., 2006). This "serpentiform body plan" increases the efficiency in burrowing or crawling lifestyles and independently occurred several times during the evolution of fossorial, arboreal and terrestrial animals (Caldwell, 2003). Extreme examples of these changes in lizard evolutionary history include highly specialized groups, such as the diggers amphisbaenians and the hyperdiverse snakes (focus of the next section).

As a result of the evolutionary novelty provided by the amniotic egg, lizards have widely diversified at the terrestrial interface and strictly aquatic species are currently unknown (Bauer and Jackman, 2008). However, the spatial occurrence of lizards across the landscapes are largely controlled by humidity and temperature gradients, both in global and local scales (Bauer and Jackman, 2008; Faria et al., 2019). This is because species have largely variable requirements regarding optimal activity temperatures and resistance to dehydration (Diele-Viegas et al., 2018; Leal et al., 2002). Most lizard species periodically exploit the inland riparian environments, but for at least 132 species, those habitats are strictly necessary for their occurrence and survival, in such a way they can be considered as semi-aquatic (count updated from Bauer and Jackman, 2008; Meiri, 2018). The relative proportion of the global diversity of this lizard functional group varies widely. Diversification of semi-aquatic species are especially notable in the rainforests of the Americas and Southeast Asia (de Ávila-Pires, 1995; Bauer and Jackman, 2008; Vidan et al., 2019; Fig. 2). Most of these semi-aquatic lizards live at the terrestrial interface, but some are arboreal, commonly found perched above water, and especially diverse in the stratified forest environments around the globe (Meiri, 2018; Vidan et al., 2019; Fig. 2). Conversely, semi-aquatic lizards are not diverse in the other main tropical region (Afrotropical), and are absent in the Palearctic (Bauer and Jackman, 2008; Vidan et al., 2019; Fig. 2).

Lizards with higher levels of water dependence may present remarkable ecological and morphological adaptations that facilitate their life in this environment (Bauer and Jackman, 2008), especially regarding the improvement of swimming capacity. They often possess laterally flattened paddle-like compressed tails, with crests or fins, especially useful in aquatic environments as propellers and rudders (Bauer and Jackman, 2008; Uzzell, 1966; Fig. 1E). Many species also swim by undulating the body, and they usually share keeled scales, enlarged tubercles or crests, that increase the propulsive surface (Uzzell, 1966; Vitt and Ávila-Pires, 1998). The growing evidence on the evolutionary relationships among species has shown that such unique characteristics linked to this lifestyle (known as "caiman-like" morphology) have evolved independently in lizards not directly related (Marques-Souza et al., 2018).

Some lizards living in aquatic environments also use water bodies as antipredator escape routes and have longer hind limbs, occasionally complemented with lateral extensions of the fingers, allowing support and resistance in rapid bipedal runs over the water (Bauer and Jackman, 2008; Leal et al., 2002). Similarly, semi-aquatic Amazonian lizards sleep over water bodies, and when disturbed, promptly jump into them and escape using the same strategy (de Ávila-Pires, 1995; Bauer and Jackman, 2008). Semi-aquatic anoles are also able to dive when disturbed and stay several minutes underwater, possibly breathing using air pockets like scuba tanks (Swierk, 2019). There are also some dietary specializations considering the species most linked to wetlands, which actively forage submerged and feed on aquatic organisms as arthropods, snails and fishes (de Ávila-Pires, 1995; Bauer and Jackman, 2008; Leal et al., 2002; Martins, 2006; Fig. 1F). In Amazonian seasonally flooded forests, lizards explore the terrain and resources in synchronicity with flooding events (de Ávila-Pires, 1995; Martins, 2006; Mesquita et al., 2006), even leading to the prevalence of species with seasonal reproductive cycles with small clutch sizes in these environments (de Ávila-Pires, 1995; Dixon and Soini, 1986; Mesquita et al., 2006). However, it is interesting to note that despite these similarities among some subsets of species, the semi-aquatic lifestyle is not necessarily accompanied by general syndromes of morphological homogeneities in the lizards' body plan (Leal et al., 2002). This may be a result of the fact that semi-aquatic lizards exploit the riparian environments in a very heterogeneous way (Leal et al., 2002).

As a consequence of this greater dependence on wetlands for semi-aquatic lizards, and the great sensitivity of these environments to natural or human-induced changes, many species of this functional group are currently considered threatened (IUCN, 2020). In fact, considering only semi-aquatic lizards that until publication of this book had their conservation status properly evaluated, 17% are included in one of the extinction threat categories (IUCN, 2020; Fig. 2). The main threats to these organisms include changes in the dynamics of aquatic ecosystems and deforestation, and some larger species are hunted by humans for skin trade or to

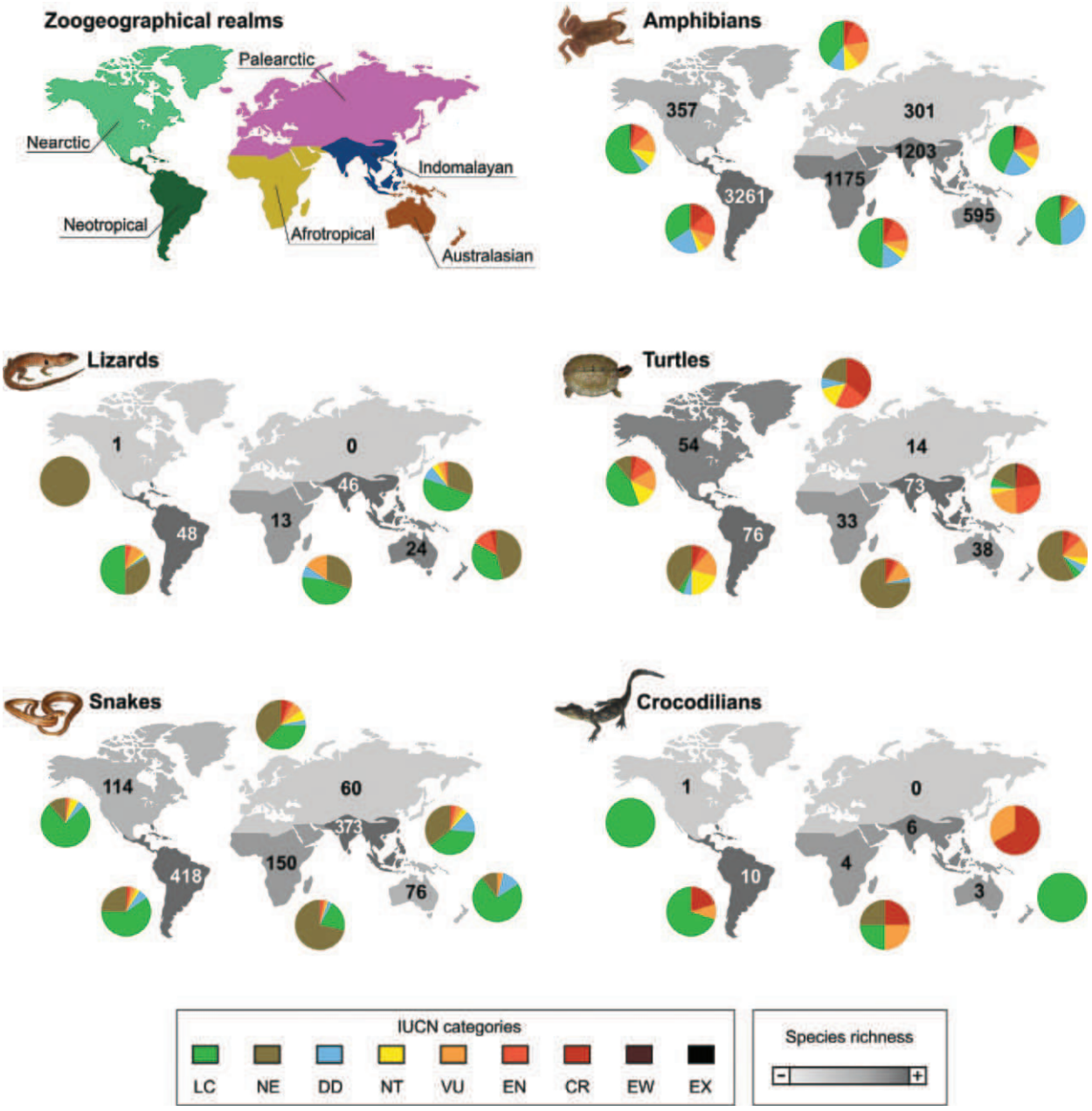

Fig. 2 Patterns of global diversity and conservation status of wetland amphibians and reptiles based on IUCN Red List assessments. Species lists are based on IUCN, with updates from Meiri (2018; lizards) and Uetz et al. (2020; snakes, crocodilians, turtles). Earth's land surface is divided in zoogeographical realms according to the IUCN classification (Oceanian and Antarctic realms omitted), with their respective species richness. IUCN categories are presented in relative percentages in pie charts using distinct colors: (LC) least concern; (NE) not evaluated; (DD) data deficient; (NT) near threatened; (VU) vulnerable; (EN) endangered; (CR) critically endangered; (EW) extinct in the wild; (EX) extinct.

be eaten (Bauer and Jackman, 2008). Although no climate-change vulnerability risk assessment has been conducted specifically for semi-aquatic lizard species, the group as a whole is considered under high extinction risk to global warming (Sinervo et al., 2010; Urban, 2015), and the wetland lizard fauna should be no exception.

Snakes

Snakes are limbless squamates closely related to lizards, which have been successful in colonizing almost the entire planet, thanks to their ability to occupy different habitats within ecosystems (O'Shea, 2018). While some species rarely emerge from underground holes, leave the water or descend from the canopy, others frequently cross through different habitats. Scientists may find clues about the habitat type more frequently used by a snake through its morphology (Cadle and Greene, 1993; Guyer and Donnelly, 1990).

Like many other animals, snakes that spend most of their time in the water often have eyes and nostrils in the upper region of the head, as this should generate some adaptive advantage to see and breathe in the water surface while avoiding overexposing the body (Fig. 1G). These snakes are commonly considered to be strictly aquatic, although the proportional area of wetlands they use may depend on their body size. Large aquatic snakes usually have a great dispersal capacity, so they are expected to explore large proportions of wetlands, or even use these environments as dispersal routes to reach adjacent habitats. For example, the giant South American Anaconda *Eunectes murinus* and the Australian Water Python *Liasis fuscus* can cross multiple wetlands connected by streams, lakes, or even dry lands (Pizzatto et al., 2009; Rivas et al., 2007). On the other hand, the smaller water snake *Nerodia sipedon sipedon* from North America rarely moves away from a single wetland. Interestingly, its closely related *Nerodia erythrogaster neglecta* has a greater ability to move across connected wetlands, even though it is not much larger than *N. s. sipedon* (Roe et al., 2003, 2004).

Snakes with similar body sizes have distinct abilities to cross wetlands, so body size is not the only factor determining the use of wetlands by snakes, but there are other factors likely to be related to local environmental conditions. Such conditions usually vary seasonally in response to climate, and snakes occupying wetlands must be prepared for changes in habitat quality (Roe et al., 2004; Seigel et al., 1995). Like all non-avian reptiles, snakes are ectotherms, and therefore have survival and reproduction largely affected by temperature. This is particularly critical in wetlands because heat is lost more quickly in the water. The temperature ranges at which a snake can maintain optimal physical and physiological activities vary widely among species, but if the tolerated water temperature range is relatively narrow for a species, it must have limited ability to cross wetlands during a cold winter (Roe et al., 2004). In addition, periods of high drought may lead to osmotic and heat stress, temporary scarcity of prey such as frogs and birds, and high exposure to predators. Therefore, during cold or dry seasons, snakes may aestivate, maintaining basal metabolic levels (just enough not to die), or they may migrate to less hostile habitats and return when conditions are more suitable (Vogrinc et al., 2018; Willson et al., 2006).

Instinctively, one could think that most snakes in wetlands are aquatic, which may be eventually true in some regions. However, a random sample of 130 species that occupy wetlands around the world reveals that most species are traditionally classified as terrestrial (Fig. 3) by the herpetological literature (see O'Shea, 2018). This classification is based on the fact that these species do not have eyes and nostrils in the upper region of the head and are more frequently found outside water. However, this does not mean that these snakes are unable to swim or move over the vegetation covering wetlands. One of the main reasons why non-aquatic snakes occupy wetlands is that these habitats are usually rich in prey such as fish and frogs (Fig. 1H). Additionally, hunting a snake in aquatic environments requires skills that are not common to most snake predators. Therefore, occupying wetlands simultaneously provides a source of food and protection for snakes (Roe et al., 2004). A good example is the semi-arboreal *Thamnodynastes lanei* (Dipsadidae), which is rarely found in the forests of eastern Amazonia, but it is the most frequently species found in the grasses covering wetlands. The diet of this species is mainly based on frogs, and its thin and light-brown colored body makes it very well camouflaged in the grass (Fig. 1I).

Investigating wetlands locally may reveal that snakes use these habitats at different levels of specificity. While some species may never leave a wetland in their lifetime, others migrate to adjacent habitats when conditions become inadequate at some time of the year, or even use wetlands only as temporary hunting sites or dispersal routes. The combination of species with different levels of specificity in the use of wetlands makes the snake diversity in these environments unique, which has led snake scientists to consider wetlands as ecologically distinct from adjacent habitats (de Fraga et al., 2011). This is relevant for conservation programs and policies, because differences in snake diversity between wetlands and adjacent habitats suggest that regional habitats are biologically complementary to each other. Therefore, wetlands should be protected at ecosystem level, although most conservation-status assessments have been conducted at species level. Looking at a comprehensive sample of 1191 snake species that occupy wetlands, most do not appear to be threatened according to the IUCN criteria (Fig. 2). However, a considerable percentage of these species (32.5%) have never been rigorously evaluated, especially in the Afrotropical realm, which is alarming in relation to the anthropogenic impacts that have affected the snake diversity of wetlands. Contamination of water and soil by heavy metals, pesticides and other pollutants is perhaps the greatest source of threat to wetlands, and there are studies showing that snakes absorb these pollutants in worrying concentrations (Campbell and Campbell, 2001; Hopkins et al., 2009). Considering that snakes are prey to a wide variety of mammals and avians, snakes contaminated by pollutants potentially harm the entire wetland ecosystem functioning.

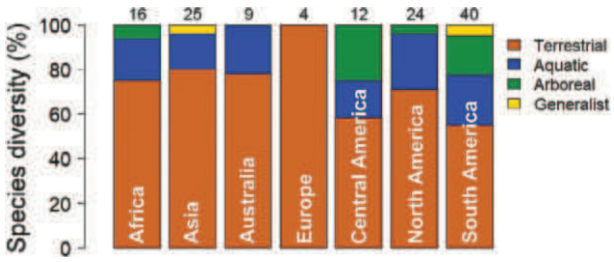

Fig. 3 Proportional species diversity of a random sample of 130 species that occupy wetlands in different regions of the world, classified by the most frequently used habitat type. The numbers above the columns indicate the number of species analyzed in each region.

Turtles

Turtles are one of the most distinctive animals on Earth that have essentially kept the same body plan for at least 220 million years (Stanford et al., 2020). The shell is their main characteristic (Lovich et al., 2018). Their lineage had millions of years of evolving adaptations that contributed to the success of this group in several ecosystems (terrestrial, freshwater, and marine). Turtles have developed morphological, ecological, and behavioral specializations that allowed them to feed and reproduce in different habitats (Moll and Moll, 2004).

Turtles show morphological adaptations to live in freshwater habitats that allow them to walk on the bottom, swim and dive. Their limbs have interdigital membranes that enable them to move in the water, and some species are able to travel long distances. Another adaptation that enhances a turtle's swimming ability is its streamlined shell (Renous et al., 2008). The shells of freshwater turtles are softer and flatter than those of terrestrial turtles, a trait that improves their hydrodynamics by decreasing drag. Also, the neck of freshwater turtles is fused to the body by a thick connective tissue, an adaptation that contributes to their ability to swim.

Wetland turtle species comprise specialized and generalized lineages whose behavior is adapted to spatial and temporal ecosystem fluctuations (Moll and Moll, 2004). Most species are influenced by the annual variation of the hydrological cycle in the various river systems where they occur, changing their densities and abundances in the geographic space accordingly. These cycles are coupled with natural flood and drought drainage regimes that alter the availability of environments used for feeding and reproduction (Bury, 1979; Junk and de Mello, 1990; Junk et al., 1989).

The Podocnemididae family in the Amazon is a good example of a lineage adapted to the hydrological cycles. All *Podocnemis* species have their feeding and reproductive cycles adapted to the dynamics of the river systems. During the annual flooding season, they stay in feeding areas, composed mostly of flooded forests, and when the water level drops, they migrate to large river waterbeds for nesting. *Podocnemis expansa*, the largest species of the genus, shows strong and extremely expanded hind limbs with well-developed interconnections between digits, that enable their migration for hundreds of kilometers (Vogt et al., 2015). Unlike other members of the genus, *Podocnemis unifilis* is a habitat generalist and has the ability to nest in different types of substrate to avoid predation; this plasticity may result in greater resilience of the populations to the ongoing climate change (Erickson et al., 2020). Another shared trait among *Podocnemis* species is the feeding behavior called neustophagia that occurs when the turtle opens its jaws slightly near the surface level to ingest food particles (Rhodin et al., 1981). On the other hand, some members of the group are less associated with deeper water levels and occur mostly in lakes and flooded forests. For instance, *Peltocephalus dumerilianus* (Fig. 1J) shell and limbs are not very well suited for swimming, but they allow an underwater walk in shallow waters in search of seeds, fruits, fish, and mollusks that are captured and chewed by strong beak and jaws. However, there are hungry predators wandering around, and it is interesting to note that the shell of *Peltocephalus dumerilianus* is strong enough to avoid predation by caimans (Vogt, 2008).

Some Chelidae species, such as *Phrynops geoffroanus*, *Mesoclemmys gibba*, and *Chelus fimbriatus*, nest at the beginning of the dry season, when it is easier to access the riverbanks (Ferrara et al., 2017). Hatchlings start to be ready at the beginning of the rainy season, when the availability of large water bodies and resources increase, and predation is reduced, since predators such as fish and caimans are more scattered in the landscape.

Among terrestrial species, *Chelonoidis denticulatus* (Fig. 1K) deserves mention for some behavioral adaptations to seasonally flooded habitats in the Amazon. Some populations that dwell in *várzea* forests and white-water rivers are able to swim considerably well, crossing rivers and large water bodies during the flooded season. Local people say that they are able to wander in the bottom of rivers for a few hours, and usually rest on floating tree trunks and branches. Unfortunately, under these circumstances they become more vulnerable to poaching (Morcatty and Valsecchi, 2015).

Presently, there are 360 chelonian species and about 80% dwell in freshwater ecosystems. A large proportion of these species (46%) are threatened at some degree, especially due to illegal consumption of their eggs and meat, and their cultural use in traditional medicine (Rhodin et al., 2018). Unfortunately, in the Amazon basin, this scenario is not different. One of the most remarkable Amazonian species, *P. expansa*, has a long history of exploitation. Turtles have been used for at least 200 years to produce oil and butter, and these unsustainable practices have resulted in depleted populations across the species range (Forero-Medina et al., 2019).

Podocnemis expansa is classified by the IUCN Tortoise and Freshwater Turtle Specialist Group (TFTSG) as a Critically Endangered species (Rhodin et al., 2018). However, a recent study indicates that although some populations are slightly declining, most populations are stable or increasing their numbers and *P. expansa* has been classified as Near Threatened in Brazil (Vogt et al., 2015). Nevertheless, as the cultural heritage in the Amazon basin values the turtles throughout the region, there is a widespread demand for meat and eggs. In 2017, Brazil took the first steps towards the turtle management with the creation of legal conditions that allow turtle community-based management initiatives for two of the most important species, *P. expansa* and *P. unifilis*. This step is very important for turtle conservation in Brazil, since it would be unfeasible to conserve species excluding the people that depend on the resource to survive. These initiatives can embrace sustainable practices if supported by useful information and technical support.

Crocodilians

Crocodilians (crocodiles, alligators, caimans and gharials) belong to a very ancient group that diversified little since they appeared some 250 million years ago (Brazaitis and Watanabe, 2011). Although earliest crocodilians were terrestrial and their original body plan evolved for life on land (Parrish, 1987), the evolution of a body plan much more efficient for swimming with a laterally

compressed tail (Fig. 1L) and a flexible trunk (Fig. 1M) facilitated aquatic lifestyles. Additionally, one of the most interesting adaptations that allowed crocodilians to fully explore aquatic environments is their four-chambered heart that allows submergence for long periods of time (reviewed in Grigg and Kirshner, 2015; Fig. 1N).

Today, all extant crocodilian species are semi-aquatic reptiles that thrive in freshwater habitats such as marshes, swamps, rivers, lakes, ponds, creeks, floodplains, artificial canals and agricultural lands throughout the tropics, subtropics, and some temperate regions (Grigg and Kirshner, 2015). Some species may even occupy estuaries and near-shore marine habitats (Nifong and Silliman, 2013; Rosenblatt and Heithaus, 2011). Some evidence suggests that habitat selects for different crocodilian species rather than the species selecting different habitats and many life history features such as reproduction, habitat use, feeding, genetic flow and social interactions have been shaped by the surrounding environment (reviewed in Somaweera et al., 2019).

In general, most crocodilians are habitat generalists. Some species such as the American alligator (*Alligator mississippiensis*) may occupy both coastal and inland habitats (Wilkinson, 1984). The freshwater crocodile (*Crocodylus johnstoni*) from northern Australia thrives in almost all freshwater habitats, including small and sometimes ephemeral headwater streams, and the downstream tidal reaches of large rivers (Webb et al., 1983). However, in places like the Amazon basin, four crocodilian species occupy the same geographical area with overlapping distributions, but avoid interspecific competition by occupying specific habitats and partitioning food resources (Villamarín et al., 2011, 2017). There, the black caiman (*Melanosuchus niger*) occurs predominantly in seasonally inundated floodplains, whereas the spectacled caiman (*Caiman crocodilus*) and the Cuvier's dwarf caiman (*Paleosuchus palpebrosus*; Fig. 1N) are somewhat more generalist occupying both floodplains and forest streams. Finally, the cryptic Schneider's dwarf caiman (*Paleosuchus trigonatus*; Fig. 1L) occupies almost exclusively non-flooded forest streams (Magnusson, 1985). Thus, even within the same landscape some crocodilian species may occupy wetland habitats more frequently than others. In fact, only *P. trigonatus* and the African dwarf crocodile *Osteolaemus* spp. inhabit almost exclusively small streams in closed canopy rainforests (Magnusson and Lima, 1991), whereas the great majority of crocodilian species inhabit -and modify- to some extent wetland habitats worldwide.

Crocodilians are known to physically alter the environments they inhabit and have been referred to as ecosystem engineers, especially in relation to the alteration of plant communities and the creation of different microhabitats (reviewed in Somaweera et al., 2020). It is not surprising then that crocodilians exert an important role in the modification of wetland habitats. Many species excavate and take refuge in holes, burrows and tunnels or create depressions along their regular pathways where water may store (Magnusson and Taylor, 1982). Also, the construction of mound nests implies the removal of vegetal material which can result in physical habitat modifications at specific locations (Campos, 1993; Hall and Johnson, 1987). Thus, crocodilians impose considerable physical modifications and may even influence landscape-level topography.

As large-bodied predators with the ability to feed at different trophic levels, crocodilians would potentially play a key role in food webs in the environments where they inhabit. However, a recent thorough review on this topic failed to find compelling evidence on this and suggests that there is uncertainty about whether crocodilians play a key role in ecosystems (Somaweera et al., 2020). Regardless of the documented scientific evidence, crocodilians are arguably an important group of semi-aquatic predators and declining populations of many species during most part of the 20th century brought extreme concern to environmentalists and the scientific community.

Until the late 1970s, uncontrolled commercial hunting of crocodilian species led to dire population declines worldwide. Crocodilian skins have been used mainly for the manufacture of exotic leather products and not long ago, most species were considered threatened by extinction. However, over the last 50 years, hunting restrictions and incentives for sustainable management both at national and international levels have been issued and many of the once-overexploited species have been successfully recovering (Thorbjarnarson, 1999).

These protective measures were put in place at the right time and no crocodilian species has become extinct as a result of overhunting. In fact, in places where habitat loss is not a serious problem, controls over illegal commercial hunting has led to population recovery of most species. Today, 52% of assessed species experience a low risk of extinction (Fig. 2). Nevertheless, in some places habitat loss has been a further contributing factor, and allied to commercial hunting or the culling of unwanted individuals, habitat degradation has led to critical situations for species especially in the Indomalayan biogeographical realm (Ross, 1998). Thus, allied to hunting restrictions and incentives for sustainable management, the protection of wetlands is an essential further measure to guarantee the conservation of crocodilian populations.

Conclusion/synthesis

Amphibians and reptiles are conveniently known as "herpetofauna" for research purposes, although they are not closely related in biological evolution. The main difference between amphibians and reptiles is the amniotic egg. The lack of this feature determines the dependence of amphibians to water (or environmental humidity) at least during part of their development. On the other hand, protective membranes in the egg provide reptiles more independence from water. In any case, numerous "herps" have evolved remarkable ecological and morphological adaptations to thrive in aquatic environments for at least some part of their lives.

Worldwide, around 43.4% (8500 species) of the global diversity of amphibians and reptiles thrive in wetlands and thus, the conservation of these threatened ecosystems is vital for these species. Although some of the threats currently faced by these animals are specific for certain groups, such as a waterborne disease-causing fungus affecting amphibians, broad patterns on the conservation status suggest that a great part of the world's wetland herpetofauna depends on habitat integrity and availability.

Knowledge gaps

- Updated assessments of conservation status for all amphibian and reptile species, refined according to taxonomic updates.
- Accurate estimates of species richness considering cryptic diversity and sampling gaps.
- Data on basic natural history aspects such as habitat use, reproductive mode and feeding habits for both described and undescribed taxa.
- Factors regulating species densities (number of individuals per area) and diversity estimates (numbers of species and differences in species composition among sites) in wetlands.
- Empirical assessment of the ecosystem importance of amphibian and reptile species.
- Impacts of climate change on the maintenance and viability of wetland herpetofauna.

See Also: Emerging methods and topics: Electronic Tagging and Tracking of Animals in Inland Waters; Structures and functions of Inland Waters - Wetlands: Benthic Invertebrates of Running and Stagnant Inland Waters

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Wetland Ecosystem Services

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Benefit Ecosystem benefits are material things (like timber) and services (like flood protection or water purification) that have value to human society.
Ecosystem Services (ESS) The benefits human populations derive, directly or indirectly, from ecosystem functions.
Function Ecosystem functions are the capacity of natural processes and components to provide goods and services that satisfy human needs, directly or indirectly. Whereas this definition focusses on the outcome, some authors define functions restricting it to the internal functioning of ecosystems and thus use it similar to the term 'process' (see above).
Goods Any material, mostly tangible product of an ecosystem that is or can be used by humans, thus serving a human demand and usually having an economic price.
Natural Capital The natural environment's limited living and non-living resources (like organisms, minerals, fossil fuels, air, water) and its functions and processes to persist (e.g. weathering, the water cycle, evolution, nutrient cycling, recruitment, and ecological interactions).
Process Ecosystem processes are the complex interactions (events, reactions or operations) among biotic and abiotic elements of ecosystems. The term is often synonymously used with "ecosystem function."
Valuation Attributing a value to an ecosystem service, which is needed to assess its benefits and thus be able to decide any action and compare the importance of different ecosystem services. It can be monetary (like the €-market value of fish) or non-monetary (like saved lives due to flood protection or spiritual and cultural values).

Introduction

Wetlands are among the most important natural features for humanity (Russi et al., 2013). The particular importance of wetlands for humanity arises from an extraordinarily large number of 'ecosystem services' (ESS) which they provide (Costanza et al., 1997; MEA, 2005b; De Groot et al., 2006, 2018; Mitsch and Gosselink, 2015). For thousands of years human existence has depended on natural resources tied to the existence of water (Hook, 1993; Finlayson, 2014). Human biology and culture rely on natural processes, functions and goods which are intricately connected to the presence of water. Coastal and inland waters and especially the (semi-)terrestrial environments adjacent and hydrologically connected to them have and still are providing the foundation of man's existence and the development of human civilization.

The multitude of benefits which man derives from wetlands is based on their particular position within the landscape at the land-water interface "as recipients, conduits, sources, and sinks of biotic and abiotic resources" (Clarkson et al., 2013). Wetlands receive, accumulate, store and convey water, sediments, nutrients and propagules from their catchment. These processes provide the basis for a great structural and functional variability: water is diverted from flood peaks, stored, purified and released, its energy creates morphological structures providing habitat, sediments are retained and soils are building up, nutrients are processed, pollutants neutralized and biomass is produced to name just a few of the processes, structures and functions which wetlands provide. Many of these natural functions are highly beneficial to human existence and have long been directly or indirectly used by man. Concepts and language to adequately evaluate and discuss these services, however, are relatively recent. The term 'natural capital' has been coined by E.F. Schumacher (1973) and was taken up by economists and ecologists alike (e.g. Costanza and Daly, 1992; Mace, 2019). Westman (1977) investigated the value of what he called "nature's services" as an objective basis for decision making when weighing the benefits of undeveloped nature against the benefits of resource development and consumption with subsequent damage to ecosystems. The term "ecosystem services" is attributed to Ehrlich and Ehrlich (1981) who used it in their elaboration on species extinction and biodiversity loss. The concept of ecosystem services greatly advanced after the publications by Daily (1997) and Costanza et al. (1997), the latter providing a first global monetary assessment of 'nature's contribution to human welfare,' attaching concrete USD-figures to a large number of ecosystem services. This courageous and highly disputed attempt was nevertheless an 'eye-opener,' creating worldwide awareness for the enormous values provided to human society by natural ecosystems. The worldwide growing awareness for the limits of natural resources, their depletion by human overexploitation and the need to act in order to safeguard the life supporting functions greatly promoted the development of the ecosystem service approach in science and beyond. Living in a globalized economic world requires the inclusion of natural resource use into economic accounting, an important basis for decision making processes on all scales (De Groot et al. 2012). Therefore, the ecosystem service concept was and still is being developed with the idea of a common methodology for the valuation of natural assets that contribute to human well-being. Defining and delineating the structures, processes and goods generated by ecosystems and their interrelations was and still is a main task of this development, as well as creating a common language among ecologists, economists and decision makers in order to implement efficient and sustainable policies.

Intentions of the Ecosystem Service-Concept:
- Raising appreciation for nature's benefits to human welfare
- Create accountability for human's use of natural resources within our economic framework
- Support resource-conscious, sustainable decision making

Today the concept of ecosystem services, despite it's still unsolved details, has long been accepted beyond the scientific community, thus providing a conceptual link between ecology and economy as well as a tool for environmental accounting to support decisions concerning sustainable use of natural resources (Wallace, 2007; TEEB, 2010; Seppelt et al., 2011).

Definition of ecosystem services

The Millennium Ecosystem Assessment defines ecosystem services as "the benefits that people obtain from ecosystems" (MEA, 2005a,b). Daily (1997) defines them as "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life." Similarly, the European TEEB-study (The Economics of Ecosystems and Biodiversity) views them as "the direct and indirect contributions of ecosystems to human well-being" (TEEB: Russi et al., 2013). Other analogous definitions exist (Boyd and Banzhaf, 2007), all commonly conveying the idea that ecosystem services are essential assets to human society and are thus socially valuable (Daily, 1997). Differences exist in ESS definitions regarding the treatment of natural structures, processes, functions, goods, benefits and services (Boyd and Banzhaf, 2007; Wallace, 2007; Fisher and Turner, 2008; TEEB, 2010). But how does an ecosystem generate a 'service' for humans to be used? The following cascading scheme shows the connection of the biophysical structure of ecosystems (e.g. a lake or river we see), their processes (e.g. primary production of growing plants), functions (e.g. production of biomass) and the final service provided (e.g. food). The final benefit for human wellbeing in this case is nutrition which can be translated into an economic value using common market prices for the goods or services provided (TEEB, 2010) (Fig. 1).

Classification of ecosystem services

The use of the ecosystem service concept in science, planning, politics and other fields requires a common understanding of terms and contents. Clear definitions, delineations and a consistent classification are required when ESS are to be quantified to allow for assessments, comparisons and trade-offs. Various systems have been proposed to classify Ecosystem Services. The UN-based Millennium Assessment (MEA 2005a), aiming at a global stock-taking of the consequences of ecosystem change to human

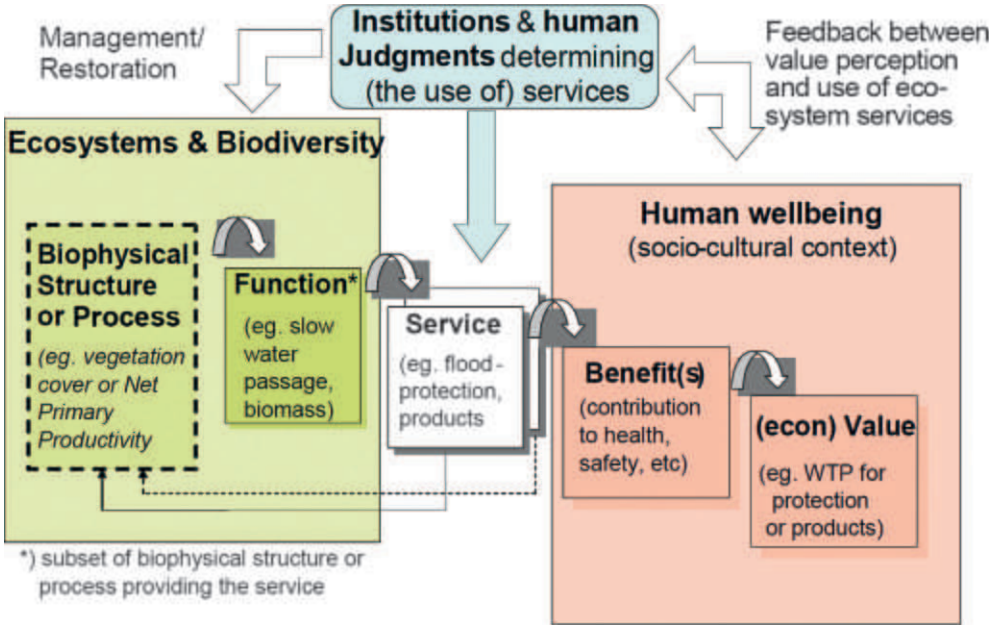

Fig. 1 Ecosystem Cascade-Model (TEEB, 2010). Adapted from Haines-Young R and Potschin M (2010) The links between biodiversity, ecosystem services and human well-being. In: Raffaelli, D. and C. Frid (Eds.): *Ecosystem Ecology: A New Synthesis. BES Ecological Reviews Series*, Cambridge University Press, Cambridge, ch 6, 31 pp and Maltby (ed.) (2009).

well-being, set a milestone in the application of the ecosystem service approach and proposed a most widely used classification. It differentiates four classes of services:

- *Provisioning services*: Material benefits (=goods) ecosystems provide like freshwater, food, raw material, medicinal resources, as well as cultivated plants and animals (genetic resources).
- *Regulating services*: The benefits obtained from natural processes which control the rates and states of physical and biotic systems like the regulation of climate, water flow, sediment flow, carbon sequestration, disease control and more.
- *Cultural services*: Non-material benefits ecosystems provide such as esthetic inspiration, cultural identity, sense of home, spiritual experience, science and education, physical and mental health are often related to the natural environment. Arts and design, tourism, recreation and many religious practices are also based on these services.
- *Supporting services*: The formation of fertile soil, the cycling of nutrients facilitated by microbial activity and the provision of habitat as living space for plants or animals as well as the dispersal of propagules like seeds are examples of '*supporting services*.' They relate to 'the underpinning natural structures and processes that ultimately give rise to final services' (Potschin and Haines-Young, 2016) thus are the basis of all ecosystems and their services.

Other classifications differ to a large or smaller degree from this categorization. Among the four classes given above the supporting services are the least accepted, mainly because they do not result in direct benefits to human welfare, but rather are basic ecosystem functions that support other ecosystem services which then generate the final uses for human society. E.g. the service to provide intact aquatic habitat for fish is not yet a use for humans, whereas the catching of a fish turns it into an economically important benefit as a 'final service.' Therefore, there is doubt about these 'intermediate services' as they are sometimes called as opposed to the final ecosystem services. Thus the 'Common International Classification of Ecosystem Services (CICES) e.g. originally excluded the supporting services from ecosystem services also in order to avoid inconsistencies (e.g. double counting) esp. in economic accounting of ESS (Potschin and Haines-Young, 2016; Haines-Young & Potschin 2018).

Numerous lists of ecosystem services have been published with smaller or larger differences in classification, delineation and number of ecosystem services. Being the most widely used ecosystem service classification, the Millennium Ecosystem Service Assessment provides the following list of Wetland Ecosystem Services (Table 1).

Other ecosystem components like abiotic energy (e.g. hydropower) and abiotic materials (e.g. sand, gravel, clay extraction) (van der Meulen et al., 2016) can be added to this list but again it is not undisputed whether they are "services" of an ecosystem or rather supporting functions (e.g. Haines-Young and Potschin, 2013).

Examples of wetland ecosystem services

So what is special about ESS of wetlands? Wetlands provide an extraordinarily large number of ecosystem services, with a higher cumulative value than most other ecosystems (Costanza et al., 2014; Russi et al., 2013). Some of them will be described briefly in the following section.

Table 1 Ecosystem Services provided by or derived from wetlands.

Services	*Comments and Examples*
Provisioning	
Food	production of fish, wild game, fruits, and grains
Fresh water	storage and retention of water for domestic, industrial, and agricultural use
Fiber and fuel	production of logs, fuelwood, peat, fodder
Biochemical	extraction of medicines and other materials from biota
Genetic materials	genes for resistance to plant pathogens, ornamental species, and so on
Regulating	
Climate regulation	source of and sink for greenhouse gases; influence local and regional temperature, precipitation, and other climatic processes
Water regulation (hydrological flows)	groundwater recharge/discharge
Water purification and waste treatment	retention, recovery, and removal of excess nutrients and other pollutants
Erosion regulation	retention of soils and sediments
Natural hazard regulation	flood control, storm protection
Pollination	habitat for pollinators
Cultural	
Spiritual and inspirational	source of inspiration; many religions attach spiritual and religious values to aspects of wetland ecosystems
Recreational	opportunities for recreational activities
Esthetic	many people find beauty or esthetic value in aspects of wetland ecosystems
Educational	opportunities for formal and informal education and training
Supporting	
Soil formation	sediment retention and accumulation of organic matter
Nutrient cycling	storage, recycling, processing, and acquisition of nutrients

Source: Millennium Ecosystem Assessment (2005b) *Ecosystems and Human Well-being: Wetlands and Water. Synthesis*. Washington, DC: World Resources Institute. 68 p.

Inland fisheries and aquaculture

The provision of food is one of the most easily understood ESS of wetlands. Fish, mussels and other aquatic organisms have always been an important resource to support human life. In 2017, 3.3 billion people received 20% of their average intake of animal protein from marine and freshwater fish. The global inland fishery capture in 2018 reported by FAO was 12 million tons which represents 12.6% of total global capture fishery production and excludes aquaculture which today accounts for half of the total global production. Asia contributes 66% to these figures with Africa adding another 25% (FAO, 2020). The reported global inland catch 2015 was estimated to be about USD 26 billion (Funge-Smith, 2018). These figures include FAO-reported capture only and are thus likely to be underestimated. Including this hidden component, as well as freshwater mollusks and crustaceans, the FAO estimated the total use value to be USD 43.5 billion (Funge-Smith, 2018). The non-market use value (NMUV) of the recreational fishing, 72% of which is estimated to stem from the US and Canada, is remarkably high. About 5.4% of global reported catch are attributed to recreational fishing. Increasing introduction and establishment of non-indigenous species to support recreational fishing has a considerable impact on ecosystem integrity. Whereas overexploitation of fish stocks is an increasing threat to marine systems, inland waters are more threatened by changes in species composition due to overexploitation, habitat change, pollution, non-native species introduction and interaction with hatchery-reared fish, the cumulative effect of which results in substantial losses of biodiversity and ecosystem services (Allan et al., 2005).

Inland fisheries globally provide an important source of protein to millions of people, particularly in low income countries (Fig. 2). At least 43% of the global inland capture comes from 50 low income nations with chronic food deficit problems (Funge-Smith, 2018). Inland fisheries are mostly rural and small-scale, large scale commercial inland fisheries being limited. Inland fisheries ecosystem service accounts for 2–6% of global agricultural workforce and thus contributes to poverty alleviation and nutrition security.

Raw biotic materials

Wetlands are among the most productive ecosystems in the world (Whittaker and Likens, 1973; Holland et al., 1990; Clarkson et al., 2013) comparable to rain forests and coral reefs (Dodds et al., 2019). They supply human societies with numerous natural materials, which are some of the most easily observed and direct ecosystem services (goods) that wetlands provide. In many parts of the world, wetlands do not only provide the most important food source, but rather provide building and fuel materials important to local economies, especially in poor countries (FAO, 2020). Floodplains in particular are highly productive sources for hardwood and softwood for timber as a building material, fuel for energy, and pulp for the production of paper, tissue and insulation materials. Similar uses can be applied to reeds, such as Common Reed (*Phragmites*) and papyrus (*Cyperus*) (Ye et al., 2016; Jones et al., 2018) cattail (*Typha*) and sugarcane. Energy crops for biogas production or direct combustion are an increasing

Fig. 2 Subsistence fishery is an important means to sustain livelihood in poor countries. Source: Wikimedia.org.

use of natural and artificial wetlands using woody species like Willow (*Salix*), Poplar (*Populus*), Alder (*Alnus*), Eucalyptus and non-woody species like the reeds already mentioned, Cattail (*Typha*), Rushes (*Scirpus*), Sedges (*Carex*) and many others. Another economically important wetland organic material is peat, which originates from organic debris (from sedges, rushes, mosses) accumulated under oxygen-deprived conditions over hundreds or thousands of years. Peat is commonly burned directly or used to generate electricity, to ameliorate soils (e.g. potting soil) and for other industrial uses. A large number of other uses of wetland species for direct consumption or as raw material for numerous uses exists.

Water related ecosystem services

Water is a principal feature of wetlands and is the basis for a number of provisioning and regulating ecosystem services.

Water for drinking and non-drinking purposes

The provision of water from wetlands for direct human consumption, to feed aquaculture, irrigate agriculture and other areas, for industrial utilization like cooling processes and other uses is a most obvious ecosystem service wetlands provide.

Water purification

Wetlands are embedded in the flows of global and local water cycles. They are a source of clean water – but also a sink and end point or transitional structure for polluted waters in the form of e.g. sewage, rainwater runoff loaded with sediments, fertilizers, agrochemicals and microplastic and pathogens from wastewater. They are often referred to as the 'earth's kidneys,' because they receive water and waste from both natural and human sources (Mitsch and Gosselink, 2015) and function as biologically active filters, absorbing pesticides and chemicals and removing harmful waste from water. Nevertheless it is important to note that the water purification function of wetlands is limited with overloads of nutrients and chemicals threatening the ecosystem's own integrity or e.g. providing additional risks for global warming (Verhoeven et al., 2006). With the global demand for clean water rising continuously, wetlands as water sources assume an increasingly important role for humanity.

Water purification in wetlands removes solid impurities, particulate or suspended matter as well as dissolved substances and enables access to cleaner water with reduced or even avoided costs for technical water purification, thus assuming substantial economic value. Water purification by wetlands can be described as the cumulative effect of three interrelated biogeochemical processes consists of

- Sediment retention, physically removing particulate or suspended matter e.g. from agricultural runoff (Venterink et al., 2006)
- Nutrient retention resulting in the removal of excess phosphorus and nitrogen (Fisher and Acreman, 2004), commonly associated with agricultural runoff and sewage effluents causing eutrophication, algal bloom with subsequent oxygen depletion and other negative impacts on ecosystems
- Reduction of contaminants by physical retention or active breakdown of harmful substances through microbial activity (detoxification)

Water purification occurs by more or less reversible absorption to superficial organic matter of plants or plant residue or on soil particles, with bacterial and fungal metabolic processes or detoxification. Aerobic and anaerobic processes in close proximity as well as a diversity of decomposers and decomposition processes in wetlands help to reduce the chemical load. High productivity and the built up of preserved organic matter (e.g. peat) can trap contaminants in wetlands (Mitsch and Gosselink, 2015). The quantification of the purification processes is difficult (Tockner et al., 1999).

As a "nature based solution," so called 'constructed wetlands' make use of the natural purification processes provided by vegetation, soils and microbes and are used in waste water treatment as a cost-efficient alternative or supplement to conventional technologies (Masi et al., 2017).

Water storage (surface and groundwater)

Within the global and local water cycle, wetlands have an important role in regulating water quantity in landscapes. Receiving discharge from their headwaters originating from rainfall or snowmelt, wetlands store water above ground in open waterbodies like lakes, ponds and rivers and temporarily on flooded areas. Below the soil surface, pore water (groundwater) in the saturated zone and soil moisture in the unsaturated zone contribute to water storage. Like natural tubs or sponges, wetlands take up water from their catchment area, fill their storage capacity and release it when incoming surplus falls below outgoing runoff. Thus changing discharges are buffered, prominently evidenced in the flattening of flood waves in rivers with intact lateral connectivity between river and floodplain. Water storage is essential for the development and maintenance of hydric soils, hydrophytic vegetation and their respective wildlife habitat. It supports the biogeochemical processes that occur in wetlands, such as the removal of nutrients and particulates, resulting in improved water quality. Water storage is the physical basis for other regulating ecosystem services like erosion control, flood retention, low water regulation, groundwater recharge and others.

Flood retention

Being based on wetland water storage, flood retention is commonly referred to as a separate ecosystem service, the final service or benefit being the reduced risk or avoided damage to human population and infrastructure caused by extreme flooding. When well connected to a rising river, wetlands enable excess water to spread out into the landscape, reducing its depth, its speed and causing a delayed discharge. More technically flood retention alters the form of a flood wave, reducing the flood peak, broadening the wave and slowing down its speed. The term flood retention mainly refers to the benefit of lowered risk of flooding, an effect that depending on the size of the wetland extends upstream and downstream. It helps to avoid damage caused by insufficient adaptation (e.g. unprotected settlements in a flood-prone area) or caused by failure of flood-protection infrastructure (e.g. dike breaching) or unusually high flood levels.

Low water regulation

Maintaining permanent surface waters during drought is another buffering function connected to water storage. The excess volume of water stored within the wetland is released slowly, supplying a base flow in outgoing water courses. Thus wetlands are of even increasing importance for water security and the maintenance of aquatic habitats in times of climate change with prolonged periods of drought and increasing flooding events.

Groundwater recharge

is another ecosystem service connected to water storage: water from periodic or permanent waterbodies like lakes or oversupplied, saturated soils permanently infiltrates into the ground supplying the groundwater reservoir (=aquifer). On the other hand, wetlands often have impermeable layers of sediment that also limit infiltration to ground water. The recharge function of a wetland is thus often limited to the edges, making wetlands with a relatively large perimeter/area ratio more important for this function (Mitsch and Gosselink, 2015). The quantification of groundwater recharge is quite difficult and not completely understood (Hunt et al., 1996). Nevertheless, the supply from wetlands for local and regional groundwater storage can be very important.

Erosion control

Erosion control and storm protection have so far mostly been investigated in marine and tidal wetlands but also present a highly valuable ESS in inland wetlands. Erosion control is provided by different processes that act on different spatial scales. At small spatial scales, the dense vegetative cover of wetlands on riverbanks, lake shores and runoff slopes builds an effective structure to prevent excessive erosion by the dissipation of wave and current energy. Furthermore, an interwoven layer of roots stabilizes the soil against erosion. Rough vegetation cover slows down water velocity and covers open soil, reducing the current's erosive force. This effect protects the wetland itself, stabilizes e.g. stream- and riverbanks, affects natural water course development and helps protect landscapes and man-made structures. At large spatial scale lateral connectivity reduces discharge and velocity which potentially reduces erosive effects on the river channel upstream and downstream.

Erosion control constitutes obvious benefits to human society and considerable economic value. The great potential of this ESS is depicted by the correction of the 1997-estimates of the monetary value of coastal wetlands by Costanza et al. who in 2014 ESS increased the value of tidal marshes and mangroves from 14,000 $/ha/year to 194,000 $/ha/year, largely influenced by new studies on storm protection, erosion control and waste treatment function of these systems (Costanza et al., 2014). In contrast to coastal

wetlands there is a lack of data on the monetary value of erosion control by inland wetlands (Russi et al., 2013). Nonetheless, given the large extent of floodplain wetlands along most rivers in the world, a considerable contribution of this ESS can be safely assumed.

Climate regulation: Climate mitigation

Natural wetlands are important climate stabilizers on a local and global scale (Neubauer & Verhoeven 2019), providing a regulating ecosystem service of increasing importance to human welfare. Cooling of local and regional climate results mainly from evapotranspiration, which is an energy consuming - thus cooling - process of wetland vegetation and other moist or wet land and water surfaces (Hesslerova et al., 2019). Urban regions in particular benefit greatly from this effect, being increasingly employed in the establishment of 'urban wetland parks.' The Ramsar Convention's "Urban Wetland Accreditation"-program encourages this trend to utilize ecosystem services for human welfare.

The large amounts of water in wetlands of the boreal climate zone have recently been considered important for climate regulation, absorbing solar energy in summer (cooling) and releasing it in winter (warming) regulating temperature on a regional scale (Wu et al., 2021). Besides temperature regulation, evapotranspiration sends vapor into the atmosphere, increasing humidity and even cloud formation which is easily observed in tropical rain forests. This affects precipitation and incoming radiation, thus temperature (Kleidon et al., 2000).

Climate regulation: Carbon sequestration

A separate climate regulating ESS of inland wetlands pertains to the plant-based reduction of atmospheric greenhouse gas (mostly carbon dioxide) into organic matter. The wet, waterlogged conditions of wetland soils slow down decomposition rates of decaying, carbon-rich plant litter which due to high biomass production results in large accumulation of organic matter, mostly as peat or other hydric soils with high carbon content (Mitsch and Gosselink, 2015). 20–30% of the estimated 1.5×10^{12} tons of global soil carbon are stored in wetlands which cover only 5–8% of earth's land surface (Nahlik and Fennessy, 2016). This process of incorporating atmospheric carbon into vegetation and a soil-bound long term storage is called carbon sequestration.

Rates of Wetland Carbon Accumulation per square meter and year (modified from Mitsch and Gosselink, 2015).

Northern peatlands	10–50 g-C m^{-2} $year^{-1}$
Temperate wetlands	140–504 g-C m^{-2} $year^{-1}$
(Sub-)Tropical freshwater wetlands	19–480 g-C m^{-2} $year^{-1}$

Estimates of Global Carbon Storage of Wetlands and other ecosystems (1 pg = 10^{15} g).

Wetlands	455–700
Tropical rain forest	450 (total released: 75)
Terrestrial ecosystems total	3000
Fossil fuels	5000–10,000 (total released: 375)
Oceans (0–75 m)	630
Oceans (>75 m)	38,000

(modified from Mitsch and Gosselink, 2015)

There is considerable concern about the decrease of carbon sequestration services, since human impact continues to destroy wetland area and degenerate its quality globally resulting in a reduced capacity to sequester carbon. Moreover, rising temperatures increase microbial biomass decomposition, releasing carbon dioxide from wetlands, thus turning them from a sink into a source of greenhouse gases. Furthermore, wetlands are known to emit methane, another and even more effective greenhouse gas, which could offset the positive climate function of wetland carbon sequestration. However, models suggest that the sequestration of intact wetlands will nevertheless continue to have a net positive effect on the reduction of greenhouse gases (Mitsch and Gosselink, 2015).

Habitat function and biodiversity

Any ecosystem service provided by organisms – the nutrient cycling realized by microorganisms, the growth of timber trees as well as the food provided by fish – requires in the first place the presence of a suitable living environment to exist. Quality habitat is needed for reproduction, growth and survival of individuals. Furthermore, an appropriate amount of space is needed to maintain populations, allowing for dispersal among patches that enable interaction and genetic exchange. Thus the ESS habitat provision is an underlying requirement supporting other ESS. This ecosystem service is dependent on habitat size (quantity) and its ecological intactness (quality). Reduction of both is endangering wetlands globally at an alarming pace (Ramsar, 2018).

Wetlands in particular provide a great diversity of habitats, based on their inherent combination of terrestrial and aquatic conditions, explicitly expressed in the term 'wet-land.' Wet and dry conditions can occur in close spatial proximity and are overlain by various patterns of temporal change in water level - or flooding regime. This temporal and spatial variability creates a diversity of sites with changing combinations of ecological conditions. In addition to high productivity it results in various species communities

and a high level of biodiversity locally as well as on a global scale (Bacon, 1997). Natural ecosystems have been called 'storehouses' of genetic information, their millions of species containing the information of environmental adaptations acquired over 3.5 billion years of evolution. To safeguard this genetic treasure, it is essential to maintain and restore the habitat of natural ecosystems (De Groot et al., 2002). The importance of the habitat function is also reflected in the disproportionately high percentage of endangered and threatened species: e.g. in the US, wetlands cover 3.5% of the land surface but 50% of threatened and endangered occur in this habitat (Mitsch and Gosselink, 2015) as well as about a third of all US-American plant species.

Cultural ESS

Swimming in a clear lake, canoeing through a jungle of reed, enjoying a hike in a bog, birdwatching in a marsh, learning about the water cycle on a small stream – what are all these activities worth? Wetlands provide many of these so called 'cultural ecosystem services.' They are sites of local identification and inspiration to indigenous and non-indigenous people, places of spiritual and religious significance. Their landscapes are appreciated for their special esthetic value that most of us can easily relate to. They are inspirational to artists, writers, painters and photographers. Swimming, boating, hiking, catch-and-release fishing, there are many kinds recreational uses of wetlands that many people appreciate and benefit from. Their complexity of structure and function makes wetlands excellent sites for research and a great place for environmental education. Thus wetlands provide a broad range of these 'non-consumptive use values' – uses that usually do not diminish the resource they are based on. Many of these cultural ecosystem services are not easily monetized. A number of indirect methods has nevertheless been developed to assign a monetary value to some of them like the willingness-to-pay method or travel cost analysis for recreational activities.

Outlook

The ecosystem service concept has experienced an exploding development over the past decades in policy and academics circles. The concept is increasingly being used to raise awareness for the growing impact of human activity on our life-sustaining resources from local to global scales. It has proven to be a practical tool for the assessment, comparison and valuation of the manifold goods and services nature provides to human well-being. Its capacity to communicate these benefits to citizens, experts and decision-makers alike provides a critical framework for wise use of natural resources. Wetlands in particular, whose ecosystem services continue to be negatively impacted by climate and land use change greatly benefit from the application of this concept.

Future efforts should communicate the inherent limitations of the approach as well as its well-proven opportunities to facilitate decisions regarding our shared natural capital and its management. Further efforts should focus on:

- increasing the practical application of the ESS-concept by providing user-oriented tools for ESS assessments (e.g. River Ecosystem Service Index RESI: http://www.resi-project.info)
- improving interdisciplinary and transnational cooperation by further harmonizing ESS definitions and classification
- studying the dynamics of trade-offs and off-site effects in ecosystem services
- the development of globally recognized methods and institutions for ESS valuation targeting at incentive policies supporting wise resource use (like REDD+ in forest management)

See Also: **Fundamental concepts and theories**: Regime Shifts and Tipping Points; **Human pressures and management of Inland Waters**: Case Studies of (Semi)Constructed Wetlands Treating Point and Non-point Pollutant Loads to Protect Downstream Natural Ecosystems; Constructed Wetlands for Urban Wastewater Treatment: An Overview; The Role of Wetlands in Mitigating Impacts From Diffuse Agricultural Loads; **Social/societal values of Inland waters**: Riparian Buffers and Land Cover Change; **Structures and functions of Inland Waters - Groundwater**: Ecology of the Hyporheic and Parafluvial Zone; Karst Groundwater Dependent Ecosystems—Typology, Vulnerability and Protection; **Structures and functions of Inland Waters - Rivers**: Biodiversity Conservation of Aquatic Ecosystems; Ecosystem Services of River Systems – Irreplaceable, Undervalued, and at Risk; Flood Plains of Large Rivers; Riparian Zones; River Resilience; **Structures and functions of Inland Waters - Wetlands**: Mangrove Forests: Structure, Diversity, Ecosystem Processes and Threats

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Restoring Riparian Peatlands for Inland Waters: A European Perspective

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Drainage Peatland drainage for agricultural purposes uses surface ditches, subsurface permeable pipes, or both, to lower the groundwater depth. Excess water from the plant root zone and underlaying soil layers can enter the pipes through perforations and flow away from the field to a ditch or another outlet.

Eutrophication A process of increasing generation of biomass in lakes or other water bodies caused by increasing concentrations of plant nutrients such as phosphate and nitrate.

Fen A common peatland ecosystem that typically develops at groundwater discharge sites. Fens are usually dominated by sedges or occasionally by reedbeds, shrubs, and trees. While the groundwater flow path is often the main water source, the hydrology can be much more complex than the simple lateral groundwater flow.

Helophytes Plants adapted to live in aquatic environments. Important representatives in rewetted peatlands are reed communities, specifically *Typha latifolia* (cattail) and *Phragmites australis* (common reed).

Mineralization Conversion of organic compounds into inorganic compounds through various decomposition processes.

Peat (Also known as turf) consists of decomposed and humified plant litter. The organic matter content is defined to be at least 30% of dry matter (DM) but may also be higher than 90% of DM.

Peatland Terrestrial wetland ecosystems, also named "mires", where waterlogged soil conditions prevent full decomposition of plant material. The thickness of the peat layer is defined to be at least 0.3 m, but this strict definition does not apply in all European countries.

Restoration Management measures that aim to recover the original form and function of peatland habitats to favorable conservation status.

Rewetting Measures to raise water levels back to the soil surface to recover anaerobic soil conditions that are important for the growth of natural peatland vegetation while simultaneously halting carbon emissions from oxidation. Due to subsidence, rewetting of soils by closing pumping stations and/or drain systems might also cause inundation.

Topsoil removal Removal of the upper degraded peat layer can be a suitable measure to avoid mobilization of phosphorus and carbon after rewetting. At the same time, unwanted seed banks may be removed, improving the water flow through the soil matrix.

Introduction

Peatlands have long been regarded as wastelands, and for several hundred years they have been drained to attain economic value (Schoock, 1658). Surprisingly, many people today have never heard about peatlands; yet, some might be familiar with the famous bog body the "Tollund Man", found in a Danish peatland (https://search.creativecommons.org/search?q=Tollund%20Man), or

associate these wetland ecosystems with a scene from "Lord of the Rings" where the hobbit Frodo has to walk through the dead marshes (https://lotr.fandom.com/wiki/Dead_Marshes). However, the increasing ecological challenges that we are facing presently, such as deterioration of water bodies due to high nutrient inputs from agriculture, has made it evident that there is an urgent need of vital peatlands. The eutrophication of inland waters because of land management creates major environmental challenges, and even though fundamental ecological knowledge is increasing, these challenges are exacerbating. An important reason for this is the pressure on agricultural land to meet the food, energy, and water demands of the world's increasing population (WWAP, 2015; Scanlon et al., 2017). Despite attempts in recent decades to control excess fertilizer application (Lam et al., 2011), diffuse pollution of watercourses remains sufficiently large to counteract the fulfillment of the environmental goals of European legislation and national environmental programs (Land et al., 2016). Among the mitigation measures targeting diffuse pollution, the restoration of riparian peatlands has been suggested as a tool to mitigate the deterioration of watercourses by non-point pollution (Zak et al., 2010). Rewetting has been proposed as a valid strategy to restore the unique biodiversity of peatlands, and in recent years focus has increasingly been directed at the recreation of the carbon (C) and nutrient sink functions of peatlands in order to lessen both the impacts of climate change and the eutrophication of water bodies (Kimmel and Mander, 2010). This approach is consistent with Target 12 of the 4th Strategic Plan of the Ramsar Convention, which advocates the restoration of degraded wetlands prioritizing biodiversity conservation, disaster risk reduction, livelihoods, and climate change mitigation and adaptation (Resolution XII.11, 2015). However, eutrophic shallow lakes (water depth mostly <1 m) may be formed after the rewetting of former agricultural peatlands because of historical land use and soil subsidence (Fig. 1), leading to nutrient mobilization, elevated methane emissions, and slow development towards the desired target vegetation (Zak et al., 2018). This chapter will inform about the ecological importance of peatlands, their loss and restoration, the biogeochemical processes as drivers of elevated nutrient mobilization, and interventions to mitigate negative side effects after the rewetting of long-term drained peatlands.

Fig. 1 Peatlands are often neighbors to lakes or rivers. Natural peatlands, as shown in the upper image from NW Poland, are only rarely found nowadays in Central Europe since most have been drained for agricultural usage. After rewetting of long-term-drained peatlands, shallow lakes often form. The lower image shows a site at the River Peene Valley (NE Germany), which for many decades was used as grassland for cattle farming.

Ecological importance of peatlands

Peatlands cover about 4.4×10^6 km^2, which equates ca. 3% of the total global land area (Yu et al., 2010). The formation of peatlands across wide parts of Europe commenced at the end of the last glaciation about 14,000 years ago. Depending on hydro-geological conditions, peatlands may form with a thickness of 10 m and more. The growth rate of peatlands in northern Europe is estimated to 0.2–0.9 mm/year (Gorham, 1991; Pontevedra-Pombal et al., 2019) and is thus rather low compared to, for example, sediment growth rates (0.6–7.5 mm/year, Baud et al., 2021). A prerequisite for peat growth is permanent waterlogging of the complete peat body. Under these conditions, senescent plant tissues, mainly roots, will only be partly decomposed. Carbon and nutrients can be stored over several thousands of years in non-disturbed peatlands. The great peat thickness (up to several meters) as well as the high organic matter content ($\geq$30%) are the reasons why they store more than 20% of the global terrestrial soil C stock or 40–60% of the atmospheric CO_2 content. Therefore, the conservation and protection of peatlands have global importance in the current climate debate (Tanneberger et al., 2021a). Natural peatlands also provide important habitat functions for many highly adapted endangered plant and animal species (Lamers et al., 2015). Most peatlands (ca. 80%) are found in the temperate regions of the northern hemisphere and in the tropical regions of South Asia (Joosten and Clarke, 2002). In Europe, Finland has the highest proportion of peatlands, which cover 30% of the land area (Fig. 2). There is a large array of different peatland types, and their classification therefore differs nationally or even locally (Davis and Anderson, 2001). In the following, groundwater-charged peatlands (=fens) are considered; however, their separation from rainwater-fed bogs may prove difficult due to obscure hydrology or water budgets at certain sites. The proportion of fens has been estimated to around 40% of the global peatland area and more than half of Europe's peatland area (Joosten et al., 2017). Since fens often appear at the interface between upland areas and surface waters, such as lakes, rivers, or coastal waters, they are supposed to play a significant role, not only for regulating the water balance in the landscape but also for cleaning inflowing ground- or surface water for nutrients (Fig. 3). This double function once earned them the name "kidneys of the landscape" and the currently common term "wetland buffer zones" (Walton et al., 2020). Accordingly, these specific ecosystems may also be valuable for reaching the environmental goals of WFD and other directives. It is important to note that besides their large-scale impacts, the water surplus of peatland systems favors a specific microclimate with higher air humidity and lower temperatures than the surrounding areas, making these sites attractive niches for certain species (Helbig et al., 2020).

Large-scale peatland drainage for land use

European peatlands have been subjected to drainage for many centuries. In the 1960s, drainage was intensified to convert peatlands to grassland and land for other arable crop production (Fig. 4). In some places, drainage practices led to a lowering of the water table by more than 1 m causing loss of almost all ecological functions and degradation of the peat (Holden et al., 2004). Nowadays, the proportion of drained peatlands accounts for 15% on a global scale and about 50% in Europe; in some countries the total proportion is >90% (e.g., Denmark, Germany, Luxembourg, the Netherlands, and Portugal; Tanneberger et al., 2021b). The consequences of peatland drainage for peat properties, as well linked matter fluxes, are well documented and are briefly summarized below (Lamers et al., 2015; Liu et al., 2020):

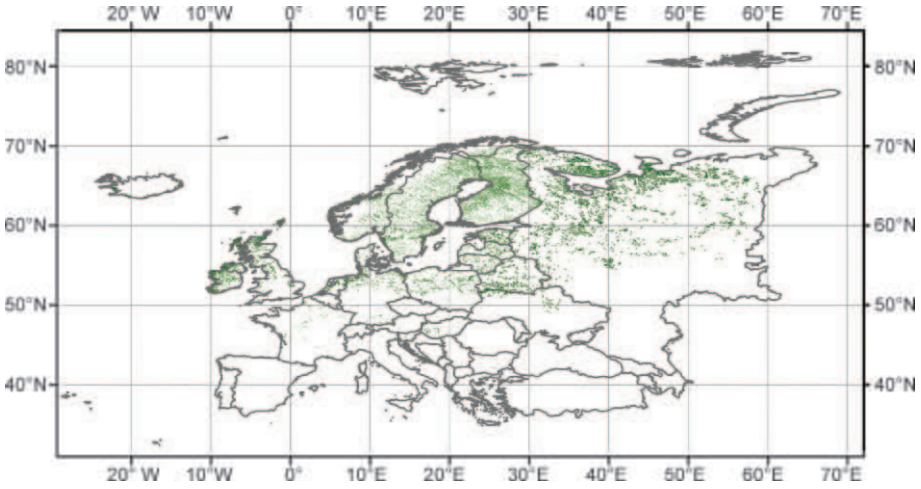

Fig. 2 Peatland map of Europe (Xu et al., 2018). The highest proportion of peatlands is found in the northern part of Europe, while the southern part is rather poor in peatlands.

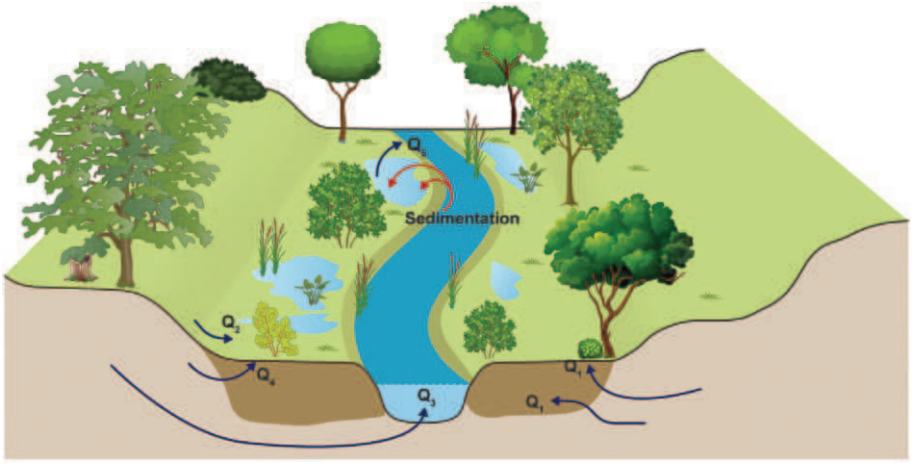

Fig. 3 Riparian peatlands as interface between mineral upland and watercourses retain water and nutrients from the catchment before the remaining water enters the downstream systems. Due to this double function, they are called the "kidneys of the landscape". Water flow paths occurring as sub-surface and surface flows (Q1–Q5, including flooding events) can be rather heterogeneous and variable in space and time, implying that the assessment of the nutrient filter function of riparian peatlands can be rather challenging (Walton et al., 2020).

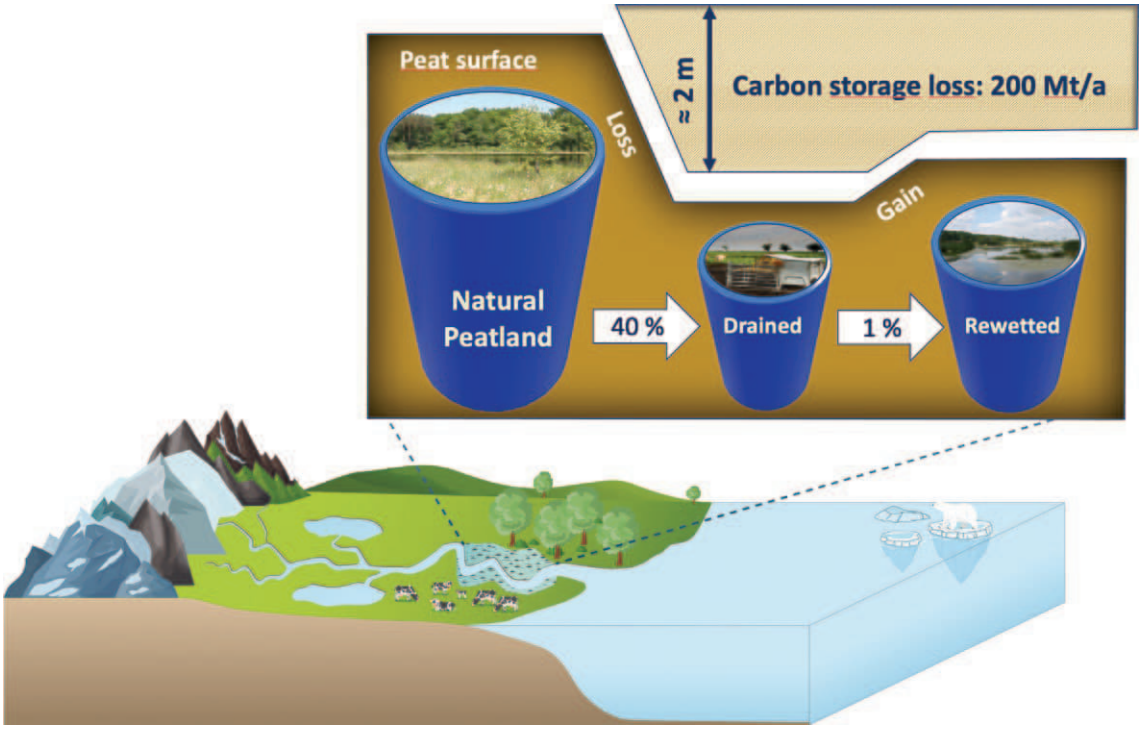

Fig. 4 Nowadays, a large proportion of European peatlands are drained—in some European countries more than 90%. Drained peatlands emit substantial amounts of carbon dioxide and have lost their important habitat function as well as their role as nutrient sinks and water storages. There is no information available about the global total carbon loss from drained peatlands but according to annual estimates the carbon loss in 2019 was about 200 Mt (Conchedda and Tubiello, 2020).

- Non-reversible loss of the oscillation capability and water storage capacity of drained soil layers due to peat mineralization, subsidence, and formation of highly decomposed peat characterized by high dry bulk densities, low water permeability, and hydro-phobicity.
- Elevated net emission of greenhouse gases (GHGs) such as carbon dioxide and partly of nitrous oxide with a high climate impact during wet-dry cycles. Drainage of peatlands has a significant effect on the anthropogenic release of GHGs, amounting to, for example, 4.5% even in industrial countries like Germany.
- Loading of downstream systems with nutrients due to both missing filter functions (bypass of ground water in ditches before it reaches the peat soils) and accelerated mineralization and release of nutrients accumulated over centuries in the peat matrix itself.

- Elevated washout of dissolved organic carbon from upper degraded peat layers during temporary rewetting after high precipitation or seasonal groundwater table increases.
- Acidification of low-carbonate soils by oxidation processes.
- Substantial loss or extinction of peatland-adapted flora and fauna, fragmentation, isolation, and thus endangerment of many species in the few remaining natural peatlands (genetic impoverishment).
- Increasing risk of peat fires as documented in the European part of Russia in 2010 and Indonesia in 2015.

Peatland rewetting to restore their ecosystem functioning

The UN Decade of Ecosystem Restoration starting just now is a critical period for meeting our commitments under the Paris Agreement regarding peat soils as well as for peatland science (Tanneberger et al., 2021a). During recent decades, substantial progress has been made in terms of analytical methods, linking of various research disciplines, and knowledge transfer, and at the same time awareness of the need to solve environmental problems and the challenges of global change has increased across all generations.

While it has been clearly demonstrated that it is better to protect and preserve existing peatlands in pre-disturbed conditions, restoration of damaged and severely degraded peatlands may still be a viable solution under certain circumstances. Good examples are available from all around the world of the restoration of peatlands to provide multi-functional benefits (Kimmel and Mander, 2010; Grand-Clement et al., 2013). Such benefits include recreation and amenity values, management and reduction of flood risks and storm surges, improvement of water quality, and the ever increasing need to store C and mitigate the impacts of climate change (Jabłońska et al., 2020). In Europe, the value of peatlands is acknowledged through a variety of policies such as the EU Biodiversity Strategy (European Commission, 2011), the Habitats Directive (European Union, 1992), the Water Framework Directive (European Union, 2000), and obligations under Resolution XII.11 of the Ramsar Convention on Wetlands (Resolution XII.11, 2015). However, peatland restoration is often opportunity driven and opportunities will vary. In the areas of Central and Eastern Europe where population densities and agricultural intensification rates are relatively low, opportunities arise to restore areas of former wetlands on sub-optimal farmland, such as in Northern Germany. However, in other areas of Europe, for example the United Kingdom and the Netherlands where the pressure on land is extreme due to high population densities and intensive agriculture, opportunities to restore wetlands are often smaller and piecemeal.

It should be noted that the term "restoration" has a rather broad definition in the literature and that it has provoked some controversy in different communities, mainly because the natural state might not be reached even after decades of land restoration. Thus, in the following, we apply the term "restoration" to all measures aiming to recover the ability of peat accumulation. This means that restored fens will act as long-term sinks for C and nutrients in the future again. Eventually, the resumption of this role would be just a question of time even without human intervention, but this contradicts common thinking that operates within legislative periods or project lengths of only a few years.

To recover the sink function of severely degraded peatlands, re-establishment of anoxic soil conditions is essential. This requires ground-water tables near the peat surface throughout the year (Evans et al., 2021). In the rewetting practice, such conditions can only be met if temporarily or permanently inundated conditions are established since (1) severely degraded fens have lost their capability to move the peat body up and down ("oscillation") to compensate for natural fluctuations of groundwater tables and (2) the peat surface level can vary by several decimeters over short distances, implying that water table depths will differ accordingly. Nowadays, it is well accepted that rewetting of degraded peatlands systems will not restore the hydrology to predominantly groundwater-percolated peatlands; rather it will create novel ecosystems (sensu Hobbs et al., 2009) fed by a mixture of groundwater, rainwater, and surface water (Wheeler and Proctor, 2000). High nutrient availability in the altered peat soils poses a risk of nutrient and C fluxes (as dissolved organic carbon, DOC) to surface waters post-rewetting (Zak et al., 2010). A long-term monitoring program in Denmark has emphasized that rewetted organic soils may act as P sources several years after restoration (Audet et al., 2020). The mobilization of nutrients and other substances due to changes in soil characteristics will be covered in the next section.

Biogeochemical controls of nutrient and carbon mobilization in rewetted peat soils

Overall, the processes and the driving factors controlling the mobilization of nutrients and C in inundated fens are well understood. Both seasonal and spatial aspects as well as the time of rewetting must be considered (Zak et al., 2010). For recently rewetted fens, the highest mobilization of matter is found in the highly degraded peat at the soil surface, while the underlaying less decomposed peat can be widely ignored for matter mobilization (Zak and Gelbrecht, 2007). However, after a few years, newly inundated fens can be found with a several centimeter-thick detritus mud layer that stores C and nutrients similar to those quantities reported for other wetland types (Cabezas et al., 2014). However, the muddy substrate becomes a hot spot of methane and phosphorus mobilization (Zak et al., 2018). This layer is mainly formed by dead plant litter. The litter breakdown at the end of the growing season is here termed the 'hot period' of matter mobilization, as also found for other freshwater ecosystems (Webster and Benfield, 1986). Litter decomposition by microorganisms is a key biogeochemical process that regulates nutrients and the C cycling in peatlands. Decomposing litter consists of a set of biopolymers like carbohydrates, lignin, and protein, which vary in stability and hence are

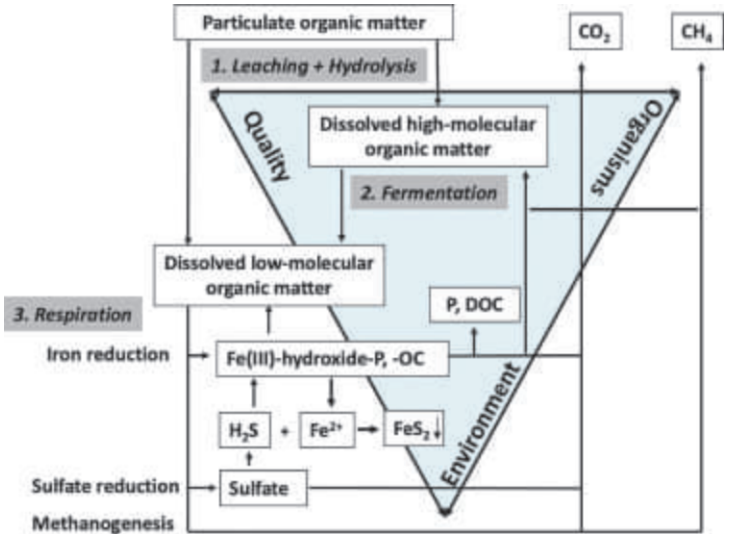

Fig. 5 The decomposition of particulate organic matter (e.g., plant litter) and the associated nutrient and carbon fluxes follow a distinct sequence that is controlled by the quality of organic matter, environmental conditions, and the presence or activity of certain water and soil organisms.

decomposed at different rates (Berg and McClaugherty, 2003). There is a distinct sequence of processes driving the recycling of nutrients and C from primary production back to the environment (Fig. 5). First, there is the "leaching stage" together with hydrolytic cleavage that occur after the die back of plants, causing high losses of plant nutrient stock (Aerts and De Caluwe, 1997), hydrolysable polyphenols, and other organic substances with low-molecular weight such as carbohydrates and amino acids (Maie et al., 2006). The second stage involves slow decomposition of submerged and settled plant litter at low-oxygen or even anaerobic conditions (Asaeda et al., 2002). Besides microbial-mediated redox-processes, like iron or sulfate reduction, abiotic processes such as ion-exchange reactions between the solid and aqueous phases, as well as mineral formation or dissolution, can have a significant impact on matter mobilization (Beltman et al., 2000; Zak et al., 2010). As for other systems, the interaction between different spheres -the atmosphere, the hydrosphere, and the pedosphere—must be considered to understand the turnover of matter and the associated fluxes. The interactions determining the growth of plants and microorganisms exert an important feedback on the interactions between the spheres and processes. The major challenge is the potentially high spatial and temporal variability of certain factors such as soil properties, hydrology, or microbiological control of the rates of the different biogeochemical processes and their complex interactions, creating high uncertainty of model predictions. The role of macroinvertebrates and higher levels of organisms is not well investigated in fens despite their potentially strong impact, as documented for other freshwater ecosystems (e.g., Webster and Benfield, 1986).

Phosphorus mobilization

Oxidation of peat during long-term drainage has been observed to lead to a substantial loss of organic C and, therefore, to an enrichment of phosphorus (P), iron (Fe), and aluminium (Al) with decreasing molar ratios of C:P and C:N in the upper soil layers (Zeitz and Velty, 2002). In addition, subsequent peat subsidence and peat compaction have been demonstrated to lower the porosity and increase the dry bulk density of the peat (Liu and Lennartz, 2019). Concurrently with this, refractory organic-bound P is transformed into more labile and mobile inorganic P forms (Fig. 6). Such P forms are inter alia sorped onto redox-sensitive Fe(III) hydroxides, formed by oxidation of Fe sulfides, or onto other reactive surfaces from metal oxides (Litaor et al., 2004). The sum of these processes explains the elevated P mobilization potential of highly decomposed peat compared to slightly decomposed peat in deeper undrained soil layers of drained fens and/or natural fens (Zak and Gelbrecht, 2007). Correspondingly, net P mobilization in inundated degraded peat soils has been found to be significantly higher than in less decomposed peat soils (Zak et al., 2010), even when determining the rates under water-stagnant conditions. In peat cores from different degraded fen peatlands (Zak et al., 2010), the level of P mobilization rates, i.e., the release from peat to soil water, was 0.1–52.3 mg P m^{-2} d^{-1}, and the rates were significantly correlated with in-situ P concentrations that ranged between 0.4 and 15.3 mg L^{-1}. This finding was rather unexpected. Apart from P mobilization, two other processes control P concentrations in peat soils—P uptake by plants or microorganisms and P resorption, which vary in importance according to the particular fen sites (Fig. 6). It is interesting to note that "internal P mobilization" (Smolders et al., 2006) and the corresponding P concentrations may vary by two orders of magnitude in rewetted fens; this has been explained by different soil properties, mainly the amount of P bound to redox-sensitive compounds and Fe/P ratios in peat (Zak et al., 2010). Overall, oxygen-free conditions were found to promote the reductive solution of redox-sensitive P compounds (Lamers et al., 2002). The dissolution of Fe(III)-P-binding forms can be caused either directly by microbially mediated iron

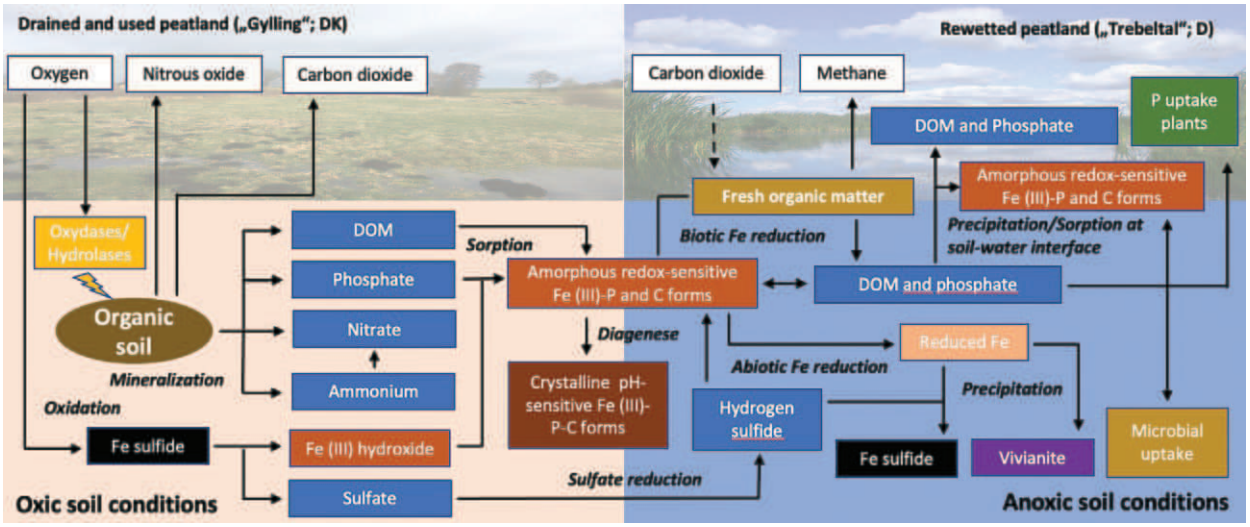

Fig. 6 The lowering of water tables by drainage measures results in peat mineralization and enhanced nutrient and carbon fluxes (left image). After rewetting, enhanced mobilization of phosphorus might occur due to biotic and abiotic process but mobilized phosphorus might also be recaptured by formation of phosphorus minerals or nutrient uptake by plants (right image).

reduction or indirectly by hydrosulfides formed during sulfate reduction (Fig. 6). Besides inorganic P forms, it has been estimated that the release of organic P from degraded peat due to ongoing decomposition of organic matter might account for at least 15% of total P release (Zak et al., 2010). Interestingly, despite comparatively high concentrations of dissolved organic matter (>100 mg DOC L^{-1}), only a low proportion of dissolved organic P was found in degraded peat soils, usually less than 5% of dissolved P, in a study by Zak et al. (2014). Microorganisms mediating organic matter decomposition and associated redox processes are extensively investigated in other systems, but only few studies on inundated peatlands have been conducted to unravel species distributions and abundances depending on varying soil conditions (Weil et al., 2020; Zak et al., 2015). A major part of dissolved P can be taken up by growing plants. Thus, the level of P uptake by dominant plants like *T. latifolia* and *P. australis* was found to be as high as P mobilization rates in degraded peat, ranging between 1.1 and 3.0 g m^{-2} during 150 days of the growing season, in a study by Zak et al. (2014). Likewise, P uptake by an increasing microbial biomass might partly buffer the high P mobilization in inundated peatlands; however, the quantitative importance of this process is not yet clear. As for plant uptake, microbial storage of P can be only short-term depending on seasonal changes in soil conditions (Turner and Haygarth, 2001). Lower acidic to circum-neutral soil pH conditions (3–7) support P sorption due to a positively charged surface of iron compounds. A positively charged surface can also be achieved under more alkaline conditions (pH >7) since calcium (Ca) occurs as a bivalent cation acting as "bridging ion" for P sorption (Bruland and Richardson, 2006). To sum up, peat soils enriched with metals like Fe, Al, and Ca compared to P will be characterized by lower net P mobilization than soils having lower metal/P ratios or lower P-binding capacities, respectively.

Nitrogen and dissolved organic matter mobilization

Processes and factors controlling the mobilization of P in inundated fens are tightly linked with nitrogen (N) and C mobilization, but the quantitative importance of some of the identical processes and above all the associated flux paths may differ substantially. Thus, gaseous fluxes account for a significant part of the N and C cycling but can be ignored for P since the volatile substance phosphine can be formed only at a very low redox potential and other conditions (Fu and Zhang, 2020) that are probably not fulfilled in inundated fens. Likewise, contrary to P, both C and N contents become lower during long-term drainage of peat, again because nitrate or carbonates other than phosphate can be easily leached from the soil matrix at fluctuating groundwater levels and water runoff (Gosch et al., 2019). Only ammonium and some dissolved organic matter fractions (some containing N) have a somewhat higher binding affinity to the soil matrix and can therefore accumulate. Binding partners can likewise be redox-sensitive iron-hydroxides or redox-stable aluminium compounds (Riedel et al., 2013).

Dissolved N occurs mainly in reduced form as both ammonium and dissolved organic N (DON) contrary to P, which is mainly present in its oxidized form as phosphate. Higher nitrate concentrations are only found in the surface water of inundated fens (Kieckbusch and Schrautzer, 2007). In contrast, nitrate concentrations are mostly lower than 0.01 mg N L^{-1} in soil water (Zak et al., 2014). Already during the first weeks of rewetting, nitrate becomes depleted by microbial heterotrophic respiration and biomass assimilation or oxidizes reduced iron or sulfur compounds (Burgin and Hamilton, 2007). In rewetting experiments with different degraded peat soils, it was found that ammonium concentrations rose immediately after rewetting, mainly in the highly decomposed peat but to some extent also in the underlying less decomposed peat (Zak and Gelbrecht, 2007). However, ammonium release rates were found to be almost 100-times higher in highly decomposed peat cores from degraded fens than in less decomposed peat samples from near-natural fens in an investigation by Zak et al. (2010). It is assumed that this ammonium

mainly derives from mineralization of organic matter accumulated in the peat matrix during the drainage phase; however, ongoing mineralization of organic matter in anaerobic peat soils cannot be excluded (Cabezas et al., 2012). After rewetting, washout of ammonium occurs either due to ion-exchange reactions or simply due to the establishment of a new chemical equilibrium between the aqueous and the solid phase. Average concentrations of ammonium in soil water of inundated peat soils can reach levels exceeding 10 mg N L^{-1}, which is two orders of magnitudes higher than in near-natural fens. Likewise, elevated DON concentrations up to almost 30 mg N L^{-1} were recorded over 5 years in the surface water outlet of an inundated rewetted peatland (Kieckbusch and Schrautzer, 2007).

During the last three decades, DOC concentrations have nearly doubled in many inland waters of Central Europe and North America (Monteith et al., 2007). This phenomenon has been proposed to be caused by a decrease of atmospheric sulfate deposition and the large-scale drainage and agricultural use of riparian peatlands (Worrall and Burt, 2007). The common dry-wet cycles in drained peatlands potentially causing high DOC pulses into adjacent surface waters are of critical importance (Brothers et al., 2014). There is some evidence that also the rewetting of degraded fen peatlands might be responsible for enhanced DOC export to lakes and streams in the long term. DOC concentrations of pore water near the soil surface were found to be higher than 200 mg L^{-1}, i.e. up to 10-fold higher in peatlands rewetted for more than 10 years compared to natural peatlands (<50 mg L^{-1}) in a study by Zak et al. (2010). A comparison of experimental net release rates of DOC, carbon dioxide, and methane suggested that DOC export may be an important pathway of carbon loss (Zak et al., 2018). However, other investigations strongly indicate that DOC is retained at the oxygenated soil surface, as corroborated by low in-situ DOC surface water concentrations found in inundated peatlands (Riedel et al., 2013). Interestingly, higher nitrate concentrations in rewetting water lowered the level of DOC mobilization (Cabezas et al., 2013). Overall, it can be expected that only a minor part of the DOC released within the peat soil will be exported to adjacent water courses, but the amount is probably still higher compared to natural peatlands.

Restoration measures moderating adverse effects of peatland rewetting

In recent decades, our understanding of biogeochemical processes in rewetted formerly degraded peatlands has increased substantially. Additional experience from the monitoring of peatland restoration projects has enabled us to establish some robust scientific principles for understanding the implications of actions and for optimizing restoration measures. Still, avoidance of predictable undesired side effects after rewetting of fens can require very cost-intensive operations (Fig. 7). Accordingly, some may argue that we should just follow "the beaver strategy" where large, drained areas are flooded and beaver introduced without preliminary research, without any technical debate, and without asking the landowners. However, beaver, once a cute, respected animal, has become increasingly unpopular among the land users, and also the conservation movement are skeptical towards the beaver strategy as the

Fig. 7 Rewetting of peatlands is often linked with further management such as water table control, topsoil removal, or plant harvesting using either special harvesters or water buffalos in order to (i) improve the restoration outcome, (ii) reduce high nutrient and carbon fluxes after rewetting of long-term drained peatlands, and (iii) gain an income to reduce restoration costs.

flooding has impacted the few remaining intact peatland habitats. The new knowledge we have may to some extent be theoretical but may nevertheless support water authorities, landscape managers, and decision-makers in making sound environmental choices. Eventually, other practical aspects such as economic and social issues, which may vary strongly even at local scale, and which restoration measures to implement must be considered when developing overall realistic management plans (Lamers et al., 2015).

Water management

The water regime has been shown to be the main driver of nutrient mobilization and GHG exchange in peatlands (Evans et al., 2021) and in many other wetland types as well (Kim et al., 2012). Previously, in the restoration of peatlands, adjustment of water tables to the surface or just below has been suggested to prevent, as far as possible, inundated conditions (Joosten et al., 2012). In fact, the highest mobilization of P and methane has been found at high water tables under inundated conditions (Tiemeyer et al., 2020). Therefore, more naturally fluctuating water levels have been recommended in order to improve the ecological quality of wetlands (Lucassen et al., 2005) as well as to avoid flooding of soils with high total P content and low Fe:P ratios (Cusell et al., 2013). Accordingly, it is not the water table that is the primary driver of the mobilization of matter, but other factors like soil properties and the quality of the rewetting water also determine the level of mobilization rates (Zak et al., 2010; Forsmann and Kjaergaard, 2014). Eventually, adjustment of the water table in a degraded peatland is a theoretical approach. Even seasonal changes of water tables might be partly buffered by maintaining the existing drainage infrastructure with pumps and weirs. A pronounced microtopography of long-term drained areas inevitably results in the formation of shallow lakes with water depths varying spatially from a few centimeters to several decimeters, even across short distances, which renders a uniform water depth unfeasible. If technical and financial means are available to manage the inflow and outflow of water to and from rewetted fens, surface water tables should preferably be kept at levels as low as possible to promote recolonization of peat-forming plants. A low water table favors certain species of sedges and brown mosses that are not able to grow under water or float as some sphagnum species in flooded bogs (Visser et al., 2000). Otherwise, submerged macrophytes with a high methane production potential like *Ceratophyllum demersum* might colonize and become dominant over time in open water bodies of inundated fens (Zak et al., 2015). Finally, it remains questionable if inflow of surface water from adjacent rivers should be avoided or if outflow of surface water from peatland should be minimized. If inundated peatlands are already affected by internal eutrophication, inflow of nutrient-enriched river water will support the sedimentation of particulate P compounds (Walton et al., 2020). However, in places where adjacent water courses are vulnerable to slightly increasing nutrient concentrations, maintenance of existing dams is recommended to reduce the water outflow from the peatland. In practice, pipes with non-return valves have proved useful for this purpose, although there is a risk that the valves may be blocked.

Removal of highly degraded peat prior to rewetting

Where peatlands have undergone extensive degradation over time, especially due to intensive drainage and agricultural use, it is usually not sufficient to simply rewet them to restore low DOC concentrations, low CH_4 emission, and oligotrophic-mesotrophic conditions during the first stage of their post-restorative development (1–100 years) (Pouliot et al., 2011). Removal of upper degraded peat soils, often less than 30 cm, before rewetting will minimize the nutrient availability for plants and also promote recolonization of plants adapted to more nutrient-poor conditions (Emsens et al., 2015). This so-called topsoil removal could potentially lower substantially the biomass production. Additionally, the chemical composition of plant material might change towards a more refractory character; this, however, needs further investigation. Topsoil removal might also force the development of even deeper shallow lakes upon rewetting. However, depending on the peatland topography and the restoration measures applied, rewetting does not necessarily lead to the formation of shallow lakes, as has been previously demonstrated (Zak et al., 2017). Brown moss-low sedge communities and low-nutrient conditions can develop within a few years following rewetting. Therefore, prior to undertaking topsoil removal, an evaluation of the restoration objectives and the potential risk of elevated fluxes of matter is recommended. This should include analysis of the state of the soil degradation, the hydrology, and the topography of the system (Zak et al., 2018). If water-saturated conditions in the top peat layer cannot be guaranteed, then the creation of bare substrate might delay the recolonization of peat-forming vegetation because of heat stress on the bare peat surface or enhanced germination of ruderal and competitive species (Klimkowska et al., 2007). An option to mitigate this problem might be mulching with straw material or combining this with the introduction of seeds to accelerate the re-establishment of fen communities (Klimkowska et al., 2007). However, both approaches may fail if the appropriate hydrological conditions are not established. Topsoil removal can be a rather expensive measure, and its carbon footprint needs to be carefully assessed, particularly if the objective of the peatland restoration is to mitigate climate change. The degraded surface peat might be a suitable material for some horticultural purposes and thus hold a commercial potential, and it may be a preferable source rather than extraction of peat from intact peatlands (Klimkowska et al., 2010). Such a commercial use may partly offset the high removal costs. The total carbon footprint needs to be evaluated for the cases when removed peat is used to dam the ditches or improve the surrounding mineral soils for agriculture. For this purpose, an estimation is needed of the mineralization rate of the remaining organic carbon under oxic conditions compared to the GHG potential of methane emission if the degraded peat layer is not removed. Finally, consideration should also be given to whether the C in the peat can be sequestered under oxic conditions, for example by hydrothermal carbonization technologies, i.e., biochar production.

Plant harvesting and removal

Rewetting of drained fen peatlands induces the establishment of tall, graminoid wetland plants (helophytisation) like *P. australis* and *T. latifolia* and these may become the dominant vegetation for several years to decades (Baumane et al., 2021; Kreyling et al., 2021). Due to high nutrient availability, these plants form dense stands with a high biomass, which results in rapid export of nutrients from the soil water (Zak et al., 2014). Harvesting of plant biomass in rewetted peatlands is thus an additional effective method of permanently removing N and P from the soil-water nutrient cycles. Harvested plant material needs to be removed; otherwise, a major part of the plant nutrients will be released during leaching (Zak et al., 2014). Nitrogen availability is initially growth limiting, but due to high levels of atmospheric N deposition common for intensively used agricultural landscapes and high P plant uptake and removal rates, P will eventually become limiting. Therefore, regular harvesting of plant biomass can be considered a longer-term method of restoring peatlands with high soil P, peatlands that exhibit a continual loss of phosphate, or in catchments with high P inputs from agriculture. As biomass harvesting can deplete the soil P pool, it can be an effective method for a return to nutrient-poor conditions. Harvesting can oppose to topsoil removal be considered a long-term mitigation method and requires special harvesting techniques (Fig. 7). Over time, harvesting will aid the re-establishment of plant assemblages better adapted to nutrient-poor conditions, such as bryophytes in fen communities. The various harvesting options show that apart from pollution management, N and P are potential resources to be restored for circular economy value chains such as for energy, construction, and fodder (Ziegler, 2019).

Conclusions and synthesis

There is clearly a need for strengthening the links between the restoration of ecological and biogeochemical functions of peatlands and the wider benefits that may thus be provided to society. Efforts are required to raise the awareness of the linkages between the restoration of severely degraded peatland systems and international commitments, such as the Nationally Determined Contributions under the Paris Climate Change Agreement or the Sustainable Development Goals (SDGs), especially those related to Goal 6 Clean Water and Sanitation, which calls for the protection and restoration of water-related ecosystems, including wetlands and lakes. Policymakers need to understand how peatland restoration can make a significant contribution to global initiatives; however, peatland scientists need to ensure that their knowledge is translated into a language that is understood within broader policy forums. In the long term, rewetted fens have the potential to fulfil multiple restoration goals, including those targeting climate, water, and species protection. Ultimately, the restoration of peatlands is a matter of societal choice, and it is essential that society understands the potential benefits that such restorations can bring to ensure that informed and intelligent choices are made.

Knowledge gaps

The current knowledge gaps concern:

- nutrient balances in both drained, natural, and rewetted peatlands.
- importance of hydrology, specifically of water fluxes and change of hydro-physical peat properties over time of rewetting.
- formation of P minerals like vivianite as stable P sinks changes in DOC quality and the export over time in rewetted fens.
- importance of nutrient status on recolonization with specific peat-forming plant species.
- new peat formation and the role of macrozoobenthos in nutrient recycling.
- long-term effects of harvesting management or topsoil removal on certain soil nutrient fractions like organic bound N and P, including legacy P and plant litter quality.
- pre- and post-rewetting microbial abundances along with changes in CH_4 emissions, plant communities, and peat geochemistry to better assess carbon and nutrient cycling over rewetting time.

Important case studies

Site name	*Country*	*Coordinates*	*Topic/Concept*	*Key reference*
River Peene Valley (riparian fen peatlands, both natural, drained, and rewetted)	Germany	53.8502° N; 13.6959° E	Restoration of ecosystem functioning of peatlands	Kreyling et al. (2021)
River Odense Valley (rewetted riparian peatlands and floodplains)	Denmark	55.3297° N; 10.3267° E	Restoration of ecosystem functioning of peatlands	Baumane et al. (2021)
Narew floodplains (riparian fen peatlands, sedge, and reed beds)	Poland	52.7558° N; 21.2154° E	Cost-benefit analysis of peatland restoration	Jabłońska et al. (2020)

See Also: Structures and functions of Inland Waters - Rivers: Hydrology and Classification of Rivers for Management; Structures and functions of Inland Waters - Wetlands: Prehistoric Wetlands; Tropical Large River Wetlands; Tropical Peat Swamp Forests; Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

Assisted migration Intentional transfer of a species beyond its current distribution, especially to move the species to a suitable habitat formerly outside of its range.
Dams (for hydroelectric, water storage) An obstruction impeding the downstream flow of water. Dams are often constructed by humans to generate electricity or store water for urban, agriculture, or industrial development.
Down-cutting Lowering of channel elevation due to hydrologic alteration of a river by damming or straightening.
Dredging Excavation to deepen a channel, typically to improve navigation or increase water flow.
Groundwater abstraction Extraction of water from subsurface layers or aquifers for urban, agriculture or industrial development.
Land drainage Dewatering of a wetland via ditches, tiles or other means for the purpose of urban, agriculture, or industrial development.
Land filling Artificially increasing the elevation of a low-lying area.
Land-use/climate change interaction The combined effects of both land-use and climate change on biota and their environment.
Levee An obstruction built for the purpose of preventing water flow from the channel or other parts of the watershed, which dewaters or impounds parts of a floodplain.
Protected area A legally protected tract of land, which is managed to conserve long-term ecosystem and cultural services (following Dudley, 2008).
Return water Water that is released after usage, often to a water body that is not its original water source.
Sea level rise Increase in elevation of sea water, which contributes to salinity intrusion in coastal wetlands.
Water diversion The redirection of water flow usually from one river to another, sometimes for the purpose of increasing sediment or freshwater supply to a damaged floodplain.

Introduction

This article will review global and regional trends in wetland loss and conservation, with the goal of evaluating best strategies for conservation and management to address future challenges to these important ecosystems.

Main topics/concepts

Global and regional trends of wetland loss

Humans have altered wetlands since ancient times, especially to store water by building dams and levees on floodplains. Wetlands also are dried through ditching, tiling and filling, and subsequently used for agricultural, forestry, urban or industrial development (Table 1) (Smith, 1971; Middleton, 1999). Levees and sea walls have been constructed to protect farms, industries and cities from flooding along rivers and coasts (Table 1). For example, levees were constructed along the Mississippi River after destructive

 https://doi.org/10.1016/B978-0-12-819166-8.00058-X

Table 1 Causes of wetland loss in world inland wetlands.

Human-related impacts	*Impact*	*Additional Citations*
Land drainage for agriculture, forestry, industry, urban development, mosquito control	Drying of wetland by ditching, tiles, pumping, and/or modification of landform by bulldozing	Middleton (1999)
Land filling, excavation or sediment addition for raising elevation of wetland for agriculture aquaculture, forestry, industry, waste disposal, urban development	Drying of localized portion of wetland, especially to create elevated mounds in forestry, or excavation of wetland for aquaculture or rice paddies	Dong et al. (2020)
Construction of levees (i.e., dikes, berms, bundhs, seawall) e.g., coastal and inland river flood and storm protection	Drying of wetland on one side, impoundment of water on the other side of levee; lack of flood pulsing	Junk et al. (1989)
Water diversion for agriculture, industry, urban usage	Water reduction and/or seasonally inappropriate water levels in the affected area	Middleton and Souter (2016)
Groundwater abstraction for agriculture, industry, or urban usage	Regional aquifer depletion; especially damaging to spring seepage wetlands	Middleton (1999)
Water return from usage (e.g., irrigation return water, sewer release, heavy metal, nutrients and other pollution	Water increase and discharge with agriculture, industrial and urban runoff	Dong et al. (2020)
Dredging for navigation	Deepening of channel and filling of wetlands	Middleton (1999)
Mining of peat, or underlying strata (e.g., gravel, sand)	Open water creation, vegetation change	Middleton (1999)
Logging or plant harvest	Vegetation loss	Middleton (1999)
Fire	While lightning strike fires are a natural process, fire can create holes in hydrologically-altered peatland	Middleton (1999)
Sediment diversion or application	Added sediment raises elevation of wetland	Craft et al. (2002)
Subsidence	Earthquakes, extraction of groundwater, oil, gas, minerals	Dokka (2006)
Sea level rise	Melting of ice caps and glaciers	Middleton and Souter (2016)
Drought	Natural drought cycles, but vegetation death exacerbated by water abstraction in waterways and any increase in salinity in arid inland wetlands	Middleton and Souter (2016)
Hurricanes and storms	Natural process, with suspected increases in occurrence due to climate change	Middleton and Souter (2016)
Down-cutting	River entrainment and other land-use changes	Middleton (1999)
Dams for hydroelectric and other purposes	Causes loss of vegetation upstream due to impoundment, and drying with seasonally unnatural water release downstream	Middleton (1999)
Land-use change/climate change interaction	Effects of land-use alteration may worsen if climate change drought/flooding/sea level rise/storm activity become more intense	Sirami et al. (2017)

flooding in 1927–1928 (Newling, 1990). Particularly near urban areas, wetlands are altered for mosquito control by ditching, tiling, pumping, vegetation management and pesticide spraying (Table 1) (Middleton, 1999).

These and other direct drivers of wetland loss and change have altered global wetlands (Table 1) including land drainage and filling; levee construction; channel deepening for floodplain dewatering and development (ag, urban, industrial); excavation for aquaculture and rice farming; navigation channel dredging, straightening, and stream channel entrainment; below-dam channel down-cutting and floodplain dewatering; above-dam impoundment; freshwater extraction from impoundments with polluted water return (agricultural, urban, industrial); mining of peat and underlying strata; oil and gas exploration; subsidence; and vegetation harvesting including logging (Middleton, 1999; Ramsar Convention on Wetlands, 2018). Climate change could interact with these land-use drivers to exacerbate the negative effects of drought, fire, hurricane intensity, and sea level rise (Middleton and Souter, 2016).

The alteration of wetlands can result in their ultimate destruction; estimates of global wetland loss following transformations by humans are as high as 87% of the Earth's total original wetlands (Fig. 1) (Davidson, 2014). On the average, region-wide wetland loss is 53.5% since 1700 (Davidson, 2014) (Table 2), with average loss higher in inland vs coastal wetlands (average loss = 60.8% vs. 46.4%, respectively). Regional wetland loss has been disproportionately greater in Europe and North America than elsewhere (Table 2) (Hu et al., 2017).

Without wetland alteration by humans, the world would have as much as 29.83 million km^2 of wetland area based on remote sensing coupled with the Precipitation Topographic Wetness Index, which assesses wetland status using global water table, topography, precipitation and basin boundary distributions (Hu et al., 2017). Using this approach, estimates of global wetland loss are 1.53–14.86 million km^2 (Table 1) or 33% of the original wetlands (Table 2) (Hu et al., 2017). While there is not a strong consensus among studies on the overall loss of world wetlands, these widely varying estimates are no doubt due to differences in methodology (Table 2). Geographical estimates of wetland loss might be improved by adding analyses of flood frequency based on water gauge information and local knowledge, but such an approach might still miss smaller wetlands below the detection size of the remote sensing technique (Allen, 2016).

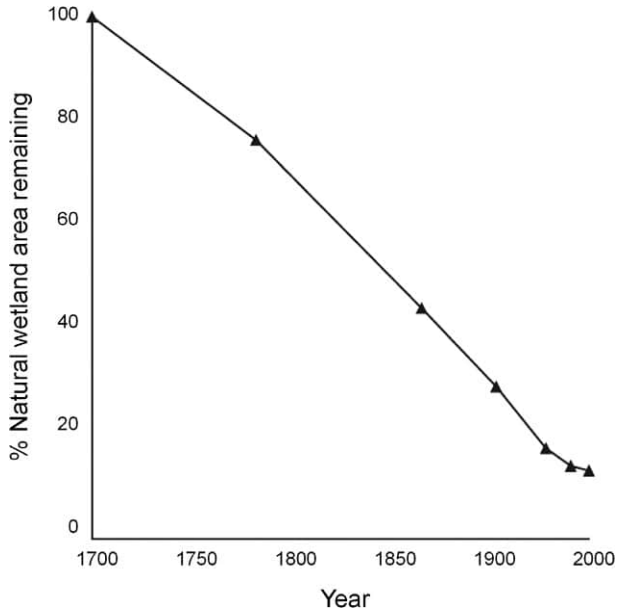

Fig. 1 Natural wetland loss from 1700 to 2000 based on rates of wetland loss based on published reports. From Davidson NC (2014) *How Much Wetland had the World Lost? How Much Wetland had the World Lost?*, with permission.

Table 2 Estimates of percentage area loss of wetlands on various continents.

Continent	*OECD (1996)*	*Davidson (2014)*	*Hu et al. (2017)*
Time period	Until 1985	Long term average	Until 2009
World	50%	54–57%	33%
Asia	27%	45%	27%
Africa	2%	4%	16%
Europe	56–65%	56%	45%
North America	–	56%	8%
South America	6%	–	32%
Oceania	–	44%	18%

From Hu S, Niu Z, Chen Y, Lifeng L and Zhang H (2017) Global wetlands: Potential distribution, wetland loss, and status. *Science of the Total Environment* **586**: 319–327.

Overall, wetland ecosystem types account for more than 6% of the land area on earth with varied percentages of wetland landmass remaining in some regions including South America (20%), North America and Russia (10% each), China and Africa (7% each), Europe (5%), as well as Australia, tropical Asia, and subtropical Asia (3% each) (Junk et al., 2013). In Brazil and other South American countries, wetlands may account for as much as 20% of the country's total land area. Following conservation efforts after the 1980s, loss in North America and Europe has slowed, but has remained high in Asia (Hu et al., 2017).

While the Ramsar Convention on Wetlands has designated 2410 wetland protected areas by Ramsar Convention on Wetlands (2020), it is unclear if the Ramsar Convention on Wetlands has stemmed the rate of regional wetland loss (Davidson, 2014) (Fig. 1; Table 3). For example, most countries in South America have been slow to define, delineate and classify wetlands, so that threats to Ramsar sites continue (Wittmann et al., 2015).

Currently, 89% of the world's wetlands are not protected (Reiss et al., 2017). Based on the Wetland Extent Trends Index, wetlands excluding man-made ones declined by 30% between 1970 and 2008 including 50% in Europe and 17% in Oceania (Dixon et al., 2016). Extensive areas of freshwater and coastal wetlands have been lost in the last 50 years in China (23.0% and 51.2%, respectively) (An et al., 2019). In North America, wetland loss has decreased substantially in recent years so that the current rate of loss is roughly equal to the amount of gain via restoration and creation (0.06% per year) (Kolka et al., 2018).

Wetland conservation

Natural area protection is an important approach in the conservation of wetlands, which included land designation by local, state, or federal entities, NGOs (e.g., Nature Conservancy), and the Ramsar Convention on Wetlands. Designated protected areas (irrespective of wetlands) cover 12.7% of lands, and have lower levels of human disturbance and habitat loss than surrounding areas (Geldmann et al., 2013). While protected area designation has been effective at preventing habitat loss, the practice has been less effective for preventing species decline (Geldmann et al., 2013). Even so, 89% of the world's inland wetlands are not in a

Table 3 Area and number of Ramsar sites by region.

Region	*Site number*	*Area (km^2)*
North America	185	227,002.8
Europe (excluding Russia)	936	153,981.9
Russia	35	103,237.7
China	37	31,685.4
South America	95	290,704.0
Africa (excluding islands)	277	823,967.0
Tropical Asia	163	97,476.3
Australia	64	75,101.8

From Junk W An J, Finlayson S et al. (2013) Current state of knowledge regarding the world's wetlands and their future under global climate change: A synthesis. *Aquatic Science* **75**: 151–167, based on Ramsar; http://www.ramsar.org/cda/en/ramsar-documentslist/main/ramsar/1-31-218_4000_0.

protected area status (Reiss et al., 2017). A high level of protection is important for wetlands given their importance in providing critical habitats for biota, and human services.

There are many inventories that describe regional wetland protection status and distribution around the world. Some of the best descriptions of wetland type, distribution and status come from the United States (U.S.) Fish and Wildlife Service wetland inventory, the Canadian wetland inventory, the Australian Wetland Database and Directory of Important Wetlands in Australia, and from European efforts including Annex I of the Habitats Directive [92/43/EC], the Manual of European Union Habitats-EU-27 (Reiss et al., 2017). Description, classification and status of various Brazilian wetland types are included in this volume (Junk, 2021). Ramsar protected wetlands are listed in reports and websites and represent worldwide cooperation to protect wetlands (Junk et al., 2013) (Table 3).

Protected area status does not always mean that a wetland is completely without land-use pressures. The Ramsar Convention reports that after designation, human influence may remain in wetlands particularly in Europe, Central America and Asia, with the lowest human pressure in designated wetlands in Oceania and North America (Ramsar Convention on Wetlands, 2014; Reiss et al., 2017). While the U.S. has fewer Ramsar-designated wetlands than some other regions, unlike some other countries, many U.S. wetlands are protected by federal, state, local and NGO designation (Beilfus, 2012).

Of the various wetland types, rivers and associated floodplains generally have the highest level of protection. Nevertheless, 70% of the world's river reaches have no protection in the upstream portion of their watersheds (Abell et al., 2017). While the Convention on Biological Diversity has targeted a 17% protection level for inland waters, only 11% of the world's rivers have integrated protection for the entire upstream to downstream river system (Abell et al., 2017).

The integrated protection of the entire river and its floodplain is important for many reasons. Downstream conservation threats often need to be remediated in the headwaters, and cannot be effectively addressed in only downstream reaches (Vörösmarty et al., 2010). In fact, an emphasis on downstream freshwater resources for humans could facilitate freshwater flow from upland wetlands and be a useful concept in floodplain conservation (Harrison et al., 2016), particularly from the perspective of maintaining biotic refugia during drought (Hamilton et al., 2005). Certain types of special river designation can provide such protection e.g. the U.S. National Wild and Scenic River Act of Oct 2, 1968. This act designates particularly remarkable rivers for their value (e.g., scenic, recreational, geological, biotic, cultural) and preserves them in a free-flowing state (United States Fish and Wildlife Service (USFWS), 2020).

Non-riverine peatlands have fewer national level designations to protect them; however, knowledge is emerging that peatlands and other wetlands store carbon that can be of value in reducing greenhouse gases in the atmosphere (Moomaw et al., 2018). Peat is conserved via carbon-based peat initiatives (REDD+, Green Climate Fund), and recognition of wetland carbon storage lends an important argument for conserving wetlands on public lands, particularly in peatlands (Richardson et al., 2014; Roucoux et al., 2017; Middleton, 2020).

Synthesis: Future conservation, management and emerging perspectives

This article has examined global and regional trends in wetland loss and conservation, and opened the conversation on future challenges in the protection of these ecosystems. Of particular concern for the future is the potential of ecosystem damage from the combined action of land-use and climate change (Sirami et al., 2017). Particularly in wetland protected areas, a number of strategies to counteract these threats may be useful.

Remediation of damage caused by land-use alteration can help wetland species and ecosystems maintain themselves. For example, freshwater remediation of hydrologically-altered floodplains can help species and ecosystems maintain themselves during drought, especially in salt-affected tidal freshwater wetlands (Souter et al., 2014; Middleton and Souter, 2016). Alternatively, during severe drought or dewatering of a wetland, refugia for aquatic species might be protected from development in permanently wet or low-lying areas (Table 4) (Middleton, 2009; Davis et al., 2013). In particular, seed banks may harbor species (Middleton, 1998), so that stream corridor vegetation may be regenerated after drought (Baron et al., 2002; Middleton and Souter, 2016).

A few landscape-level approaches have emerged including the idea of assisted migration, which is the intentional transfer of a species to a suitable habitat outside of its current range. While assisted migration is controversial, the procedure may be a way of

Table 4 Example protected areas designated for the conservation of wetland resources, with the year of first national level designation given (n.d. = not designated) (Ramsar Convention on Wetlands, 2020 and other sources).

Location	*Year*	*Resource*	*Area size (km^2)*	*Wetland type*	*Conservation threats*	*Designation status*
Keoladeo National Park, Rajasthan, India	1956	Diverse bird & emergent wetland	29	Monsoonal wetland	River water extraction for agricultural and urban development on upstream floodplains (Fig. 2; Table 4) (Middleton, 2009).	Maharajah's hunting reserve (<1763), Bird sanctuary (1976), Ramsar designation (1981), National park (1982)
Cypress Creek National Wildlife Refuge, IL, United States	1990	Upland and floodplain forests, archeological significance	243	River floodplain	Agricultural development on surrounding floodplain of river with land clearing, ag/urban chemicals, and surface erosion.	National Wildlife Refuge (1990), Ramsar designation (1994)
Danube Delta Biosphere Reserve, Romania	1991	Floodplain ecosystem	6264	River floodplain	Urban development, upstream dams	Ramsar site (1991), MAB Biosphere Reserve (1992)
Palo Verde National Park, Costa Rica	1978	Migratory bird stopover	184	River floodplain	Water pollution, salinity intrusion, *Typha* dominance	Wildlife refuge (1970s), National park (1978), Ramsar designation (1991)
Hunan West Dongting Lake National Nature Reserve, China	2013	Migratory bird stopover	300	Monsoonal wetland	Water pollution from agricultural, urban and industrial development including heavy metals (Dong et al., 2020)	Provincial nature reserve (1998), Ramsar designation (2002), National Nature Reserve (2013)
Hunan East Dongting Lake National Nature Reserve, China	1994	Migratory bird stopover	1900	Monsoonal wetland	Water pollution from agricultural, urban and industrial development including heavy metals (Dong et al., 2020)	Provincial nature reserve (1982), Ramsar designation (1992), National Nature Reserve (1994)
Hunan South Dongting Lake National Nature Reserve, China	n.d.	Migratory bird stopover	1680	Monsoonal wetland	Water pollution from agricultural, urban and industrial development including heavy metals (Dong et al., 2020)	Provincial nature reserve (1997), Ramsar designation (2002)
Hunan Henglinghu Provincial Nature Reserve, China	n.d.	Migratory bird stopover	430	Monsoonal wetland	Water pollution from agricultural, urban and industrial development including heavy metals (Dong et al., 2020)	Provincial nature reserve (2003)

reducing species extinction in a future with climate and/or land-use change (McLachlan et al., 2007). Wetland reserve design could be enhanced to support maximum biodiversity and ecosystem services with respect to connectivity, elevation variability, longitudinal and latitudinal floodplain connectivity, interconnection of the freshwater-terrestrial landscapes at different timescales, and the free flow of water to groundwater-fed wetlands (Reiss et al., 2017). Also, the intensity of local management (e.g., burning, cutting) might be reduced or softened during periods of stress to avoid damaging vegetation and ecosystem services (e.g., drought) (Middleton et al., 2017).

Conclusion/synthesis

This article reviews trends in global and regional wetland loss and conservation, and strategies for future conservation and management from the perspective of climate and land-use changes. Wetland loss assessments are not uniformly in agreement with estimates of global wetland loss, which are as high as 87% since 1700 CE as based on reports (Davidson, 2014), or as low as 33% as based on remote sensing (Hu et al., 2017). Estimates of wetland loss might be improved by refining both remote and local assessment techniques.

Conservation is essential given the biological importance of wetlands as critical habitats for biota and human services. Given the potential of the interaction of land-use and climate change to cause stress in wetland protected areas (Sirami et al., 2017), a number of management actions could improve the situation. These actions include the reversal of certain land-use changes through freshwater remediation of hydrologically-altered floodplains, improved wetland reserve design, assisted migration, and the softening of burning/cutting regimes during drought.

Knowledge gaps

- What is the minimum flow of freshwater that can maintain vegetation and ecosystem function during drought, especially in various types of hydrologically-altered wetlands?
- After human usage, can return water abstracted from ground and surface water be delivered to hydrologically-altered wetlands in a fashion that maintains ecosystem function?
- How important is the interaction of land-use and climate change in various world wetland types and situations?
- Are extreme environments the main extinction factor of wetland species i.e., do species become extinct during extreme drought or burning episodes?

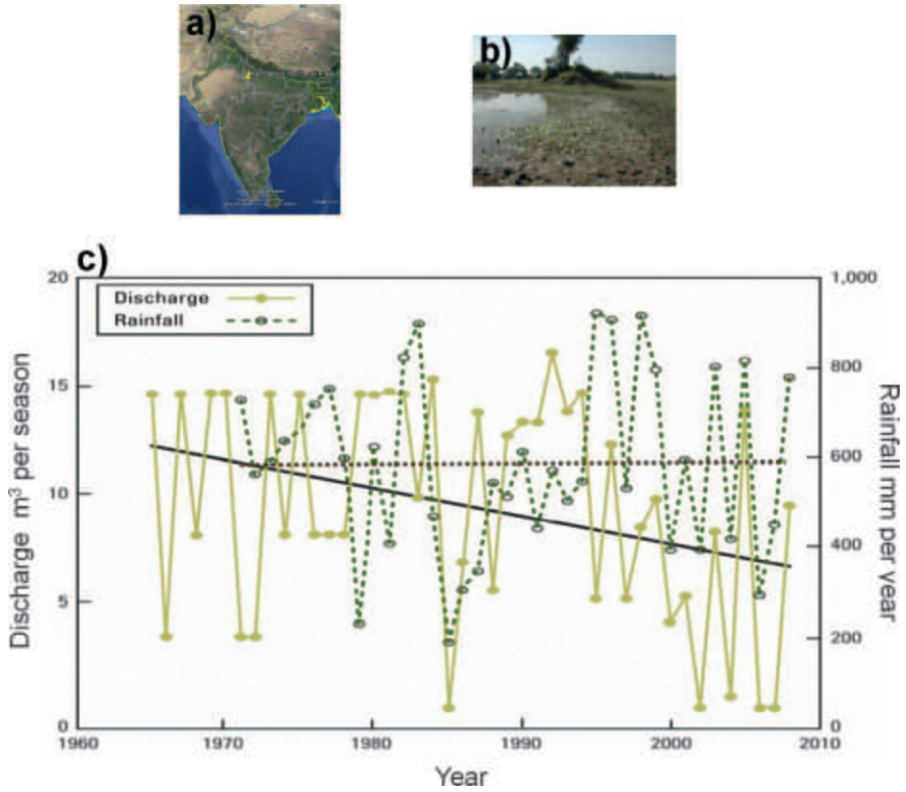

Fig. 2 (A) Location of the Keoladeo National Park, Bharatpur, Rajasthan along the Banganga River. (B) Increasing water extraction for development occurred in the 1990s. By the late 1990s, floating beds of aquatic species were mostly absent but reemerged in wet depressions after a large monsoon in 2009. An interbasin water transfer re-flooded the park for a period of time after 2010. (C) Precipitation (mm) and water discharge from the Ajunbund to the Keoladeo National Park, 1965 to 2008 (Middleton, 2009).

Important case studies (where appropriate)

Case Study: Keoladeo National Park, Rajasthan, India

Subtropical monsoonal wetlands in northern India (Fig. 2A) flood seasonally following the monsoon, and then dry down slowly during the winter season (October-March). In the Keoladeo National Park, during the flooded season, floating grasses such as *Paspalum distichum* floated in the water column, and then died back during the summer season drawdown (Fig. 1B; ~March-June). Aquatic plant regeneration is driven by seed banks during sporadic rains in (July–September) (Fig. 2B; Middleton, 1999). The Keoladeo National Park is a historic overwintering ground for waterfowl of the Asian flyway, and is of critical value for humans as well as biodiversity (Middleton, 1999).

Water diversion for agricultural irrigation and urban expansion along the Gambhir and Banganga Rivers affected the water supply to the Keoladeo National Park in the early 1990s (Fig. 2C; Middleton, 2009). Before the 1990s, water was discharged from the river into the park from Ajunbund from September through February. By 2009 following dewatering, the floating marshes of grasses had mostly disappeared in this protected area. The wetland vegetation partially returned following the monsoon of 2008, following an interbasin water transfer from another river after 2010. Certain aquatic plants reappeared in wet depressions of the flooded wetlands during 2008–09, most likely regenerating from the seed banks (Middleton, 1998, 2009). The national park demonstrates that certain types of wetland vegetation have some resilience to dewatering after hydrological alteration because some plant species are stored in the seed bank and can regenerate when water becomes available (Middleton, 2009).

See Also: Emerging methods and topics: Citizen Science, Crowdsourcing, and Social Media Advance Our Understanding and Conservation of Inland Watersaters; Environmental DNA Advancing Our Understanding and Conservation of Inland Waters; Human pressures and management of Inland Waters: The Best Management Practices in Agriculture for Protection of Inland Water Ecosystems; Social/societal values of Inland waters: The Gender Gap: Women as Authors and Leaders in International Publications in Fisheries Science; Structures and functions of Inland Waters - Groundwater: Karst Groundwater Dependent Ecosystems—Typology, Vulnerability and Protection; Structures and functions of Inland Waters - Rivers: Biodiversity Conservation of Aquatic Ecosystems; Riparian Zones; Structures and functions of Inland Waters - Wetlands: Ecology and Conservation of Wetland Amphibians and Reptiles; Patterns in Freshwater Fish Diversity; Riparian Vegetation of Gravel-bed Rivers - A Global Review; Wetland Plants: Adaptations, Classification, Ecology and Distribution

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Relevant Website

https://rsis.ramsar.org/ris/ - Ramsar Site Information Service.

Wetlands Under Global Change

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Wolfgang Junk and Florian Wittmann.

Glossary

'Blue' carbon Carbon sequestered by coastal ecosystems, including coastal wetlands. As opposed to 'green' carbon of terrestrial systems or 'teal' carbon sequestered by inland waters and associated ecosystems.

'Teal' carbon Carbon sequestered by inland waters and wetland ecosystems. As opposed to 'green' carbon of terrestrial systems or 'blue' carbon sequestered by coastal ecosystems.

C_3 plant C_3 plants are plants which utilize a metabolic pathway where the initial product of carbon dioxide assimilation is 3-phosphoglycerate. C_3 carbon fixation is the most common metabolic pathway for photosynthesis in modern plant species.

C_4 plant C_4 are plants which utilize a metabolic pathway where the initial product of carbon dioxide assimilation is four carbon oxaloacetic acid. C_4 carbon assimilation is an adaptation of the ancestral C_3 carbon assimilation pathway that reduces energy loss to photorespiration and water loss via transpiration.

Eutrophication Excessive concentration of nutrients in a body of water, often associated with human activities higher in the watershed, such as land clearing or fertilization. Eutrophication may result in large increases in phytoplankton populations (i.e., 'algal blooms').

Evapotranspiration Water transferred from an ecosystem to the atmosphere via evaporation from surfaces and transpiration of plants.

Invasive species A species that creates negative environmental, ecological or economic impacts through overpopulation. Invasive species are often introduced or exotic, though native species may be deemed invasive due to overpopulation as a result of human activities through alteration of environments, food webs or introduction of exotic genotypes.

Monoclonal stand A patch of vegetation occupied by a single genotype of a plant species, usually spread through vegetative reproduction, such as root or rhizome networks.

Particulates Microscopic particles of solids or liquids suspended in the air, also known as aerosol particles. Depending on size, some particulates may be injurious to human health, increasing risks of cancer, heart attacks and respiratory disease.

Peatland An ecosystem characterized by soil composed largely of partially decomposed organic matter. Different types of peatlands include bogs, fens, mires, muskegs and pocosins.

Radiative forcing A change in the Earth system energy balance, often in reference to a human impact to an ecosystem, such as wetland conversion or restoration. For detailed definitions and discussion regarding application to ecosystem processes, see Neubauer (2021).

Volatile organic compound An organic compound that has high vapor pressure at room temperature, low boiling point and high number of molecules in surrounding air (or volatility). Many volatile organic compounds can have negative human health and environmental effects, such as promoting the formation of tropospheric ozone and smog.

Introduction

Wetlands are among the ecosystem types most threatened by global change (Erwin, 2009), including both climate change and other anthropogenic factors such as sea level rise, urban development, deforestation, agricultural land use, drainage, levees, tidal flow restrictions, pollution, eutrophication, and fires. Wetlands also have a disproportionate influence on the global carbon cycle, containing approximately 20–30% of soil carbon despite accounting for only 6–8% of land area (Mitsch et al., 2013). Historically, wetlands have often been viewed as unproductive lands and were targets for drainage and conversion to other land uses (Kolka et al., 2018). For example, within the 48 conterminous states of the U.S. (CONUS), an estimated 53% of wetlands were drained or converted from 1790 to 1980 (Dahl, 1990). From 1990 to 2009, overall losses of wetland area in CONUS were not significantly different from zero; however, certain wetland types continued to be lost, particularly coastal saltwater wetlands (Dahl, 2011).

Indeed, wetland conversion and loss remain issues of global importance. Global losses of some coastal wetland types, such as salt marshes and mangroves, may be as high as 2% or 3% per year (Pendleton et al. 2012), though considerable disagreement exists about those rates and if they have changed in recent years (Feller et al., 2017). Considerable concern remains about coastal ecosystem losses, along with their potential for 'blue' carbon sequestration and storage (e.g., Windham-Myers et al., 2018), a term coined in contrast to the 'green' carbon accounted for in terrestrial ecosystems. Other authors have pointed to the importance of 'teal' carbon found in inland wetland systems and the relative lack of data concerning their global rate of loss (Nahlik and Fennessy, 2016; Middleton, 2020). While forecasting the impact of global change on any ecosystem is a complex problem, wetlands are particularly difficult due to their nature as biogeochemical hotspots that are variable in space and time. As it may be unclear whether wetlands should be treated as primarily terrestrial or aquatic due to their position at the terrestrial-aquatic interface, they have been historically neglected in global Earth system models (Bailey et al., 2017). This promises to be an area of active research in the coming decades.

In this chapter, we focus on the major global change factors affecting wetlands and the responses of different wetland types to those global change factors. We will not explicitly address the question of wetland impacts on Earth system processes and global climate. While some have argued that the climate impact of restoring some wetland ecosystems may be neutral or increase global temperature in the short term, due to relative contributions of CO_2 uptake and emissions of other greenhouse gases such as CH_4 (Bridgham et al., 2006), others have argued that most inland and coastal wetland restorations have a present net cooling effect (i.e., a negative radiative forcing) that is more readily apparent on longer time frames (Mitsch et al., 2013; Taillardat et al., 2020). The exact accounting of radiative forcing, greenhouse gas emissions and carbon sequestration is complex and dependent on both the timeframe and modeling approach used in such analyses; it is not a simple property of a given ecosystem (Neubauer, 2021). What is generally undisputed in scholarly literature is that the historical conversion of wetlands to other land uses-such as crops, production forestry, pastures and urban/suburban areas-have had the largest effects on global climate and that such transitions continue to release large amounts of greenhouse gases to the atmosphere when they occur.

Global change factors

The term 'global change' refers to many factors both inclusive of and extending beyond the usual definitions of 'climate change.' "Global change research" as defined by the U.S. National Academies of Sciences, Engineering, and Medicine (2017) is the "study, monitoring, assessment, prediction, and information management activities to describe and understand the interactive physical, chemical, and biological processes that regulate the total Earth system; the unique environment that the Earth provides for life; changes that are occurring in the Earth system; and the manner in which such system, environment, and changes are influenced by human actions." Thus, if we discuss global change affecting wetlands, we must include a wide array of factors. These include, but are not limited to:

Climate Change: Anthropogenic emissions of greenhouse gases, primarily CO_2 has been the major driver of widespread warming of the global climate and related changes to local climates, which have been documented since the 1950s (IPCC, 2013). Changes in the long-term distribution of global temperatures, humidity and precipitation could affect all types of wetlands. Climate not only regulates the supply of water to wetlands via precipitation and snow melt, but also the losses of water from the landscape via evapotranspiration to the atmosphere. The frequency and intensity of storm events play an important role in ecosystem disturbance regimes, especially in coastal areas. Climate change is also a major factor in fire risk for wetland ecosystems (Turetsky et al., 2015). Another consideration sometimes overlooked is that the CO_2 concentration of the atmosphere directly impacts ecosystems. As CO_2 is a substrate for photosynthesis by plants, it may be expected that increasing atmospheric CO_2 will impact plant productivity and growth directly, as opposed to indirectly through changing climate. Special attention is given to this question in the section *'Direct effects of CO_2 on wetland ecosystems'* below.

Hydrological Alterations: Human activities have had dramatic impacts on the hydrology of many areas, impacting the quantity, quality and timing of water flowing into and out of wetlands. Historically, wetland drainage often preceded conversion to other land uses, such as agriculture or production forestry, though other reasons, such as reducing the spread of malaria were used to promote wetland drainage (McCorvie and Lant, 1993). River dikes and levees reduce sediment and freshwater delivery to floodplains and alluvial deltas outside the levee system, while concentrating flow and increasing water depth between levees. Sea dikes, canals and spoil banks can greatly alter the delivery of sediments and saltwater to coastal saline wetlands (Day et al., 2008). Urbanization, with its concomitant increases in impermeable surface, storm drainage and reduction in organic inputs, can have large impacts on wetlands, even when they are not drained or converted directly (Faulkner, 2004; Lee et al., 2006).

Sea Level Rise: Sea level rise (SLR) can be measured either eustatically (relative to the center of the earth; ESLR) or relative to local land surfaces (RSLR). Tide gauge data suggest that ESLR is over 200 mm since 1880, while satellite data gives an ESLR rate on the order of 80 mm from 1995 to 2015 (Rovere et al., 2016). Wetlands, however, respond to RSLR, not ESLR directly. Other factors may contribute to make RSLR either greater or less than ESLR in a given area, such as tectonic activity, geological subsidence, subsurface fluid extraction, and sediment compaction (Day et al., 2008; Törnqvist et al., 2008; Giambastiani et al., 2020; Herrera-García et al., 2021). Sea level rise impacts are not limited to coastal saline wetlands. Indeed, RSLR impacts are expected to extend many kilometers inland along waterways to affect tidal freshwater wetlands (Doyle et al., 2010; Krauss et al., 2018) (Fig. 1).

Nutrient Loading and Pollutants: Runoff water from human-dominated landscapes such as urban and agricultural areas may carry chemicals that function as either toxic pollutants or nutrients. Through fertilization and the cultivation of crops, humans have

Fig. 1 A wetland forest impacted by sea level rise and increasing salinity in North Carolina. Such forests are often termed 'ghost forests' due to their prevalence of dead tree stems. Courtesy Melinda Martinez.

increased the bioavailability of many nutrients to ecosystems, which flow into adjacent natural areas including wetlands. Human activities now make bioavailable to terrestrial and wetland ecosystems more nitrogen, which is of the most essential nutrients to plant growth, than all natural processes combined (Vitousek et al., 1997). While nutrients are critical to plant growth and other ecosystem functions, an excess of nutrients in wetlands can lead to eutrophication of adjacent aquatic systems. Eutrophication may cause algal blooms, which can cause aquatic die-offs due to limited light penetration to littoral plants, changes in pH and subsequent depletion of dissolved oxygen when algae decompose (Chislock et al., 2013). Some algal blooms are categorized as harmful algal blooms (HABs), associated with release of noxious toxins that degrade water quality, pose risks to human health, and induce die offs of both aquatic and terrestrial animals. Impacts to commercially important fisheries are immediate, but effects may extend to terrestrial species that use such water supplies. Indeed, livestock losses were linked to HABs as early as the late 19th century (Francis, 1878).

Nutrient loading also impacts wetlands themselves, changing community structure of plant species and sometimes reducing overall biodiversity (e.g., Drexler and Bedford, 2002). While wetlands at the terrestrial-aquatic interface can be useful in removing nutrients and reducing aquatic eutrophication, loss of biodiversity, greenhouse gas emissions (e.g., nitrous oxide release from denitrification of nutrient inflows) and shifts in microbial and plant communities may all lead to undesirable changes in wetland structure and function (Verhoeven et al., 2006; Faulkner, 2004). Similar to nutrients, wetlands can serve an important function in the retention of potentially harmful pollutants such as lead, chromium, copper, nickel, and zinc, which could damage adjacent aquatic ecosystems and drinking water supplies. However, these same pollutants may damage wetland ecosystems themselves, including animal populations such as amphibians and migratory birds that depend on such ecosystems (Faulkner, 2004).

Biological Invasion: Wetlands are prone to invasive species, especially when disturbed by human activities such as hydrological alteration, nutrient loading and introduction of non-native species and genotypes (Bansal et al., 2019; Ciotir et al., 2013; Zedler and Kercher, 2004). Indeed, the number of highly invasive plants in wetlands worldwide seems disproportionate to their coverage on the landscape, perhaps due to their interconnectedness and position at the terrestrial-aquatic interface (Zedler and Kercher, 2004). Many invasive plants in wetlands are large-bodied, plants that produce large amounts of leaf litter in monoclonal stands. The removal of not just aboveground living biomass, but also belowground biomass and leaf litter may be necessary to restore lost biodiversity in invaded ecosystems in such situations (Lishawa et al., 2019). Invasive species not only can out-compete native species, but may alter nutrient cycling, microtopography, ecosystem structure, soil microbiomes and ecosystem food webs (Ehrenfeld, 2003; Windham and Meyerson, 2003; Zedler and Kercher, 2004). Invasive species in wetlands also include a variety of animals, including gastropods, insects, fish, reptiles, birds and amphibians, but the full impact of them is rarely fully understood (Swarth and Kiviat, 2009). The control of invasive animals that inhabit wetlands and adjacent waters has been the target of large public expenditures, ranging up to hundreds of millions of dollars in the U.S. for certain species (Jenkins, 2013).

Interactions among factors: Importantly, global change factors do not act in isolation. Ecosystem resilience to one type of change may be affected by the impacts of another global change factor (Day et al., 2008). For example, land-use conversions upslope may

limit migration of coastal ecosystems in response to sea-level rise (Borchert et al., 2018). Hydrological changes are almost invariably accompanied by changes in nutrient inputs in both coastal and inland systems (Day et al., 2008; Faulkner, 2004). Because of their hydrological connections and placement at the terrestrial-aquatic interface, the conservation of wetlands involves accounting for uncertainties related to interacting stressors, which has led some to advocate for a 'safe operating space' concept in their management (Green et al., 2017).

Wetlands responses to global change

Direct effects of CO_2 on wetland ecosystems

The long-term effects of elevated atmospheric CO_2 on ecosystem productivity of biomass and biomass allocation patterns remain research areas of great uncertainty. However, we do now have the benefit of a handful of long-term elevated CO_2 experiments in otherwise intact ecosystems or agroecosystems using free-air carbon dioxide enrichment (FACE) technology. A review of 15 such FACE studies suggests that indeed carbon uptake in C_3 plants is enhanced under elevated [CO_2], despite a mean decrease of ~10% in photosynthetic capacity (Leakey et al., 2009). This carbon uptake usually is accompanied by a decline in leaf and canopy-scale water use, as well as an increase in nitrogen-use efficiency. However, it is important to note that these effects are not equal in all ecosystems or agroecosystems. In particular, this same review found that productivity enhancement in C_4 plants only occurs under drought. It is unclear if the general response trends among plants holds true for wetland plants, but it does provide a good basis for testable hypotheses in wetland studies.

The longest running elevated CO_2 field study in an otherwise intact ecosystem employs open-top chamber technology rather than FACE and is located in a *Scirpus olneyi* tidal marsh in the Chesapeake Bay (Rasse et al., 2005). This experiment indicates that long-term gains in productivity are possible in such systems but interacting factors such as rising salinity could dampen these enhancements, as may species composition shifts associated with nutrient loading that favor C4 forbs over C3 graminoids (Langely and Megonigal, 2010). Thus, while there may be productivity gains in some systems associated directly with elevated atmospheric CO_2 concentrations, we cannot expect such responses to be universal in magnitude or direction across ecosystems, nor with other interacting global change factors. For example, freshwater marsh species germination and seedling growth responses to CO_2 are dependent on water level and salinity (Middleton and McKee, 2012).

Forest ecosystems may be of particular interest, due to their capacity for C storage in both the decadal scale as biomass and even longer timescales in the soil. Elevated CO_2 studies in wetland forests are limited, though notably a large-scale manipulation of whole ecosystem warming and elevated CO_2 is currently underway in a spruce-tamarack bog in northern Minnesota (Hanson et al., 2017). Initial results show little response to elevated CO_2 in overall carbon balance of the ecosystem (Hanson et al., 2020), though the response of individual species or groups, such as ericaceous shrubs (Ward et al., 2019) and conifers (Warren et al., 2021), have been noted. This suggests that the structure and composition of the ecosystem may respond directly to elevated CO_2 levels and these responses may interact with other drivers such as temperature, even if there is not an ecosystem level response in carbon exchange. Unfortunately, there are no studies using FACE technology in wetland forests, though the response of FACE studies in other forests may provide some guidance in what would be expected. Initial results from the first few years of operation suggested a very consistent (~23%) increase in biomass productivity across four forest FACE studies (Norby et al., 2005), but longer term results were dependent on nutrient status and species (McCarthy et al., 2010; Norby et al., 2010; Talhelm et al., 2014). In general, elevated CO_2 experiments in coniferous forests have suggested little to no impact on canopy scale water-use, whereas an effect is often observed in deciduous broadleaf forests (Medlyn et al., 2001; Leuzinger and Körner, 2007; De Kauwe et al., 2013; Hasper et al., 2016; Ward et al., 2018). Overall, it seems many types of plants react positively to elevated CO_2 concentrations, however, the exact impact on wetland ecosystem productivity and carbon assimilation depends on interactions among species (community shifts) and interactions of elevated CO_2 with other global change factors.

Global change responses of different wetland types

Wetlands can be categorized in various ways, but many begin with the hydrological, geographical or geological context of the wetland, such as the classifications of Cowardin et al. (1979), Brinson (1993), and the Ramsar Convention (Matthews, 1993). Of these the Ramsar classification scheme is the broadest, including marine, inland and man-made wetland ecosystems that may not meet all definitions of 'wetland' including coral reefs, rocky shores, salt pans, reservoirs, aquaculture ponds, lakes and rivers. The Cowardin et al. (1979) and Brinson (1993) classifications were made primarily with wetlands of the United States in mind and rely on substantial knowledge of a wetland to properly classify it, but these systems are applicable to a wide range of wetlands globally if such data are available. The Brinson classification scheme relies heavily on hydrogeomorphic setting and characteristics, with little reference to biota, though a category of peatlands was included that relies upon biogenic accretion of soil. Below we will refer mainly to categories from the Cowardin et al. (1979) system that relies on both hydrogeomorphic setting and biotic communities, because both of these may be important in the context of global change. A full accounting would be exceedingly long, but here we tackle some of the main contrasts between wetland types and what they mean for global change responses.

Riverine, estuarine, lacustrine, and palustrine wetlands: A common distinction made among wetlands is among major systems that describe their hydrologic, geomorphic, and biogeochemical setting or habitats (Cowardin et al., 1979). These include *riverine* (within a flowing water channel), *estuarine* (tidal habitats partially sheltered from open ocean), *lacustrine* (within a basin

characterized by open freshwater) and *palustrine* (freshwater wetlands without significant open water areas). Palustrine wetlands are often hardest to distinguish from the other systems and can border any of the other three, but are characterized by persistent vegetation, low salinity (<0.5 psu), shallow water depths and the lack of erosive action from open water. In such settings, global change may be expected to shift the transitions between different ecosystems. For example, rising sea levels and salinity intrusion may shift the boundaries between palustrine and estuarine systems, while human activity or climate change may change river flow, shifting boundaries of palustrine and riverine systems. Indeed, many or even most wetlands may transition to different ecosystems entirely in response to global change factors. Another way to view this is that ecosystems may 'migrate' as their respective communities respond to changes in hydrology, climate and other global change factors. Estuarine wetlands are expected to move landward and up slope, though their ability to do so may be severely limited by urbanization and flood control infrastructure in these areas (Enwright et al., 2016; Thorne et al., 2018). Sea level rise and salinity intrusion are likely to lead to migration of tidal riverine and adjacent palustrine systems upstream and upslope, but the degree to which this does and will occur remains uncertain (Ensign and Noe, 2018). Water levels in lacustrine and depressional palustrine systems may be impacted by changing water levels due to shifts in precipitation or evapotranspiration as a result of climate change. Some wetlands, such as peatlands, show a capacity to adjust to such water table changes (Bridgham et al., 2008), but again, the limits to such responses remain uncertain.

Dominant vegetation type: Another way of organizing wetlands is by dominant vegetation types and we may expect different types will respond to global change in different ways. The Cowardin et al. (1979) classification scheme defines these as vegetation 'classes' within the systems listed above. The most typical vegetation types in wetlands are forests, scrub/shrub and emergent marsh communities, though some would also include floating vegetation (rooted and unrooted), mudflats and shallow submerged vegetation in the general umbrella of wetlands, especially given that some vegetation is seasonally ephemeral, or shifts based on interannual variations in water availability. Some variation in response to global change factors may be assigned to these broad classes. For example, herbaceous vegetation may be more resilient than forest vegetation to disturbances such as storms, fires, floods, drought or sea-level rise; this may be due to differences in belowground or hydrological processes (Loiselle et al., 2021; Stagg et al., 2016; Zhang et al., 2019) as much as the differences in aboveground stature more obvious to a casual observer. As the range limits of one vegetation type may be set by one climatic factor while another by a different factor, it is important to not limit projections to a single factor or a single boundary. For example, future wetlands of the coast of the Gulf of Mexico are likely to change distribution in response to both less frequent freezing events leading to the expansion of mangroves in some areas, and increased aridity expanding the distribution of unvegetated mudflats and succulent marshes in others, both at the expense of emergent marshes (Osland et al., 2019). Trade-offs between succulent and emergent marshes in this last example also highlights the importance of studying differences within the major vegetation classes. Different species or communities within the forest, scrub/shrub and herbaceous classes may respond differently to global change factors, such as the differences in direct responses to CO_2 between conifer and broadleaved trees or C3 and C4 graminoids discussed in the section on elevated CO_2 impacts above.

Soil type and nutrient status Another set of divisions commonly made between wetlands is based on soil type and nutrient status. Mineral and organic soil wetlands are often considered separately, partly because of the large difference in carbon density of these types (Kolka et al., 2018; Nahlik and Fennessy, 2016). Historically, much of the conversion of wetlands to agriculture and commercial forestry has been in mineral soil wetlands, over 90% in Canada and the United States (Kolka et al., 2018); however, much of the remaining carbon stored in wetlands of this region is in organic soil. Quantifying the global extents of mineral versus organic soil wetlands is complicated by various definitions used to distinguish these types of wetlands and delineate wetlands from other ecosystems (Mitra et al., 2005). Within organic-soil wetlands (i.e., 'peatlands'), especially in boreal zones, differentiation is made between more acidic, nutrient-poor bogs that receive limited or no surface water inputs (i.e., 'ombrotrophic' peatlands) and fens, which receive surface water and nutrient inputs (i.e., 'minerotrophic' peatlands). However, global peatlands are diverse in structure and nutrient status, found in a variety of geomorphic contexts from alpine depressions to coastal lowland floodplains bordered by mangroves (Page and Baird, 2016). As peatlands generally form under high water table conditions that limit the incidence of fire, peatland drainage and drought can increase fire risk. These environments have important interactions that contribute to rapid carbon loss from increased fire risk (Turetsky et al., 2015; Page and Baird, 2016). Unlike vegetation fires typical in mineral soils, peatland fires smolder within the soil column and persist under low oxygen conditions, releasing a wide array of particulates and volatile organic compounds that lead to regional air quality problems (Page and Baird, 2016).

Boreal, temperate and tropical wetlands: Another major way of classifying wetlands is by climatic zones or biomes. While responses may vary somewhat by climate zone, it is important to emphasize that many of the same global change factors, such as hydrologic alteration, pollution, biological invasion, sea level rise and climate change, which must be considered across all climate zones (Mitsch and Hernandez, 2013). At the highest latitudes, it has long been recognized that a likely outcome of increasing global temperature is the expansion of some wetlands from permafrost melt and the loss of others due to increased evapotranspiration and geomorphological changes (Carpenter et al., 1992). Relative to wetlands in temperate and tropical regions, many northern peatlands remain relatively undisturbed. Because temperature changes are most pronounced at the highest latitudes, northern peatlands may face some of the largest impacts from climate change, and least in part because of the added impact of the accumulated impact of permafrost melting, fire and vegetation changes (Page and Baird, 2016). While climate change remains a factor to consider in temperate and tropical zones, anthropogenic land use change and hydrological alteration play a much larger role in these warmer climates. Historically, many peatlands were drained and converted to other uses in temperate regions of Europe and North America, much of which continues to be used for commercial forestry and agriculture (Kolka et al., 2018; Page and Baird, 2016). Peatland drainage for agriculture and commercial forestry use is also common in tropical areas, including at least 20% of lowland tropical peat forest in Indonesia and Malaysia (Miettinen et al., 2012). While wetland conversion for agriculture and tree

plantations in Southeast Asia is perhaps best documented in scholarly literature, it is an issue throughout the global tropics, including Amazonian várzea forests (Vijay et al., 2018) and African papyrus marshes (Saunders et al., 2012). One of the challenges of estimating global change impacts on tropical wetlands is that the basic extent of tropical wetlands is not well documented, but modeling based on hydrological and geomorphic factors suggest that extensive areas of peatlands in South America and Africa have not been mapped, much less studied in the context of global change (Gumbricht et al., 2017; Page and Baird, 2016).

Conclusions

Understanding wetland responses to global change is important to the human capacity to predict changes in future climate, as well as the cycling of carbon, water and nutrients in the Earth System. Wetlands not only store disproportionate amounts of carbon compared to other terrestrial ecosystems, but they lie at the terrestrial-aquatic interface crucial to understanding landscape and global scale biogeochemical cycles. While human management of wetland ecosystems is centuries or even millennia-old in many areas of the globe, current global change factors may present novel conditions such as permafrost thaw, elevated atmospheric CO_2, and sea level rise, which defy simple inference based on past experience. However, experiments addressing how global change factors effect wetland species and communities may provide some guidance in our predictions, such as experiments on direct plant responses to increases in atmospheric CO_2 and their interactions with other environmental factors such as temperature and hydrology. Responses of wetland ecosystems to global change factors are complex and may come down to subtleties between different dominant species found within the same vegetation classes. While the past decades have seen many important experimental and observational studies of wetland responses to such factors, large uncertainties remain.

Future research could be targeted to knowledge gaps in the diversity of wetlands outside of temperate (and some boreal) regions that are well studied, especially within tropical regions where even the basic extent of wetland ecosystems is not well documented. The interactive effects of multiple global change factors likewise form an area of interest to the global Earth system modeling community where knowledge gaps exist, especially in real-world management-relevant contexts. Wetlands are prime examples of ecosystems where not just conservation efforts, but also restoration efforts are often targeted, so practical approaches for such efforts in the context of global change factors is likely to be another area of active research in the coming decades.

See Also: **Fundamental concepts and theories**: Regime Shifts and Tipping Points; **Human pressures and management of Inland Waters**: Citizen Science for Co-monitoring and Co-managing Impact on Ecosystems and Inland Waters; Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment; Implications of Climate Change for Freshwater Fisheries; Inland Fisheries Management - Case Studies of Inland Fish; **Social/societal values of Inland waters**: Riparian Buffers and Land Cover Change; **Structures and functions of Inland Waters - Groundwater**: Anthropogenic Pressures on Groundwater; **Structures and functions of Inland Waters - Lakes**: Ecological Consequences of Climate Extremes for Lakes; Lakes as Recorders of Earth Surface Dynamics From Yearly to Plurimillennial Time-Scales; **Structures and functions of Inland Waters - Rivers**: Climate Change and Extreme Events in Shaping River Ecosystems; Inland Waters—Rivers: Land Use and Water Quality; Succession in Streams

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Section Introduction: Groundwater sciences in Limnology

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Groundwater is quantitatively the most important source of freshwater and sustains surface terrestrial and aquatic ecosystems and human beings across the globe. Groundwater has for millennia been used as a drinking water source, for recreation and therapy (e.g. thermal springs), as well as for irrigation. Scientific disciplines targeting abiotic aspects of groundwater (e.g. hydrology, hydrogeology, geology, geochemistry) have a long history. However, research on the biotic and ecological aspects of groundwater, particularly subterranean ecosystems started comparatively late, about 100 years ago, first looking into the biodiversity of fauna and later into microbial communities. By definition, groundwater of the terrestrial subsurface is inland water, making groundwater ecology a sub-discipline of limnology. Despite this, standard textbooks in limnology largely ignored groundwater and aquifers as limnic ecosystems (Welch, 1952; Ruttner, 1962; Lampert and Sommer, 2007; Schwoerbel, 1999; Wetzel, 2001). Only recently, limnology textbooks have paid attention to subsurface aquatic habitats (Schönborn, 2003; Schwoerbel and Brendelberger, 2013; Dodds and Whiles, 2020). There is a handful of books focusing on groundwater microbiology and biogeochemistry (e.g. Chapelle, 2000; Cullimore, 2007). The first book solely dedicated to groundwater ecology appeared in 1994 edited by Janine Gibert, Dan Danielopol, and Jack Stanford. This year (2022) a completely reworked 2nd edition will be released (Malard et al., 2022). While there are a few other books on groundwater fauna (Spandl, 1926; Chappuis, 1927; Botosaneanu, 1986) and subterranean ecosystems including caves (Vandel, 1965; Wilkens et al., 2000; Culver and Pipan, 2014), groundwater ecology textbooks have never been published, with the exception of the German textbook by Griebler and Mösslacher (2003).

The first edition of the 'Encyclopedia of Inland Waters' released in 2009 contained over 240 topic-related articles, of which less than ten dealt directly (Alley, 2009; LaBaugh, 2009; Pipan and Culver, 2009; Puri, 2009; Valett and Sheibley, 2009) or indirectly (De'camps et al., 2009; Glazier, 2009; Nimmo, 2009) with groundwater. In this 2nd edition, we have 26 chapters included in a groundwater-focused section, with content covering groundwater disciplines and habitats in an integrative and comprehensive manner.

The series of chapters starts with a review by Robert Reinecke on the global abundance and distribution of groundwater, pointing at the multiple factors that impact this valuable resource. The chapter discusses available data and identifies knowledge gaps and research needs in pursuit of exploring this hidden resource. The two chapters that follow introduce the typology of groundwater systems (Steffen Birk) and their hydrology (Andreas Hartmann). Besides the common hydro(geo)logical terminology, the chapters describe general aquifer properties including groundwater recharge, groundwater storage and groundwater discharge, and how these attributes vary with aquifer type and geology. Conceptual hydrogeological models are presented as valuable tools to combine the available information about these processes and their underlying physical structure into visual hypotheses of groundwater systems. Similar to the first edition, there is a chapter about the unsaturated (vadose) zones. This time, Christine Stumpp and Gerhard Kammerer complement the introduction into the hydrology of the subsurface. The chapter already hints at the importance of biological processes for seepage water quality as source of groundwater.

Grant Hose and coauthors introduce the different types of groundwater dependent ecosystems (GDEs) that occur across subsurface, terrestrial and aquatic realms. GDEs are natural systems that require access to groundwater to maintain their biodiversity and ecosystem processes. The limited knowledge of the degree and timing of groundwater dependency of most GDEs, and the pressures of climate change are challenges for the management and conservation of these valuable ecosystems. The discussion of GDEs is extended to the transition zones between surface and subsurface aquatic environments, which include the parafluvial-hyporheic zone. In consecutive chapters, Maurice Valett and Ann Marie Reinhold, and Ignacio Peralta-Maraver and Anne Robertson dig into groundwater-surface water (GW-SW) interactions within this interface between the surface water, the groundwater systems and the riparian habitats, which are characterized by the simultaneous occurrence of multiple physical, biological and chemical processes stimulated and originating from the three habitats. The interplay between sediment depth, redox potential and pore-space hydrodynamics determines both the shape and the size of the parafluvial-hyporheic biotope, the distribution of organisms within it, and the rate at which physical, biological and chemical processes occur. Without doubt, parafluvial-hyporheic zones are hot spots of biodiversity. A range of field methods to assess GW-SW interactions is introduced. Recent advances in computer modeling of stream systems allow the integration of ideas from hydrology, engineering, and ecology to increase understanding and predictive ability.

The next set of chapters introduces the smallest biological entities and organisms in groundwater ecosystems. Starting with natural groundwater viral communities, Schweichhart and coauthors for the first time compile existing knowledge on viruses in groundwater systems. Also for the first time, a chapter on fungal communities in groundwater ecosystems has been composed by Alice Retter and Ali Nawaz. Both chapters provide a condensed overview on the occurrence and potential roles of prokaryotic viruses

(phages) and fungi in groundwater ecosystems. While our knowledge of these fields is steadily growing, they are two topics that require much further research. These chapters provide a segue to those by Clemens Karwautz and Christian Griebler, as well as Martina Herrmann and Martin Taubert, which provide a comprehensive introduction into the microbial biodiversity in groundwater ecosystems and key processes as well as microbial drivers involved in biogeochemical cycling of carbon and nitrogen in aquifers. Microbial consortia in groundwater habitats ranging from shallow to deep environments, including karst and porous aquifers, as well as contaminated groundwater and drinking water are described in terms of their composition and functions. A focus is on processes of the nitrogen and carbon cycling in aquifers and its tight interconnection. Recent advances in "multi-omics" and isotope-based approaches are highlighted. With a specific focus on the ecology of microbial contaminant degradation in groundwater, Tillmann Lueders and András Táncsics point to the versatility of microbial communities to clean up organically polluted aquifers. Knowledge about opportunities and limitations of biodegradation can support societal efforts to protect and restore groundwater resources and habitats.

The following set of chapters is dedicated to groundwater habitats and their fauna. Starting with karstic systems, Tanja Pipan and Dave Culver introduce the epikarst, its hydrological functioning, physical structure, and organisms. Anton Brancelj and Fabio Stoch look deeper into karst systems, from epikarst to the vadose zone and from the epiphreatic to the phreatic zone of karstic cave systems. Key controls such as the local climate, particularly temperature, precipitation, and subsurface hydrology, along with vegetation are discussed. Living space and the amount of available organic material determine the community structure within a given karstic zone. The structure of stygofauna, both functional (body size, feeding habits) and compositional (species diversity), is closely related to the habitat structure and environmental conditions. Nataša Ravbar and Tanja Pipan further extend the characterization and classification of karst habitats including all types of karst groundwater dependent ecosystems (KGDEs) considering important driving processes and their vulnerability and opportunities for protection. Without doubt, KGDEs and their ecosystem services need greater understanding and improved predictions of how they will change and adapt under current pressures and global challenges, including climate, land use and societal changes. Due to their great importance for biodiversity, KGDEs are of considerable conservation value, and are crucial for the preservation of biota and for socio-economic development. A more general view on the diversity of groundwater fauna is provided by Florian Malard. Groundwater metazoans are typically hidden and still poorly known. In fact, they are an important, yet underestimated, contribution to global freshwater biodiversity. Documenting and understanding their compositional and functional diversity has revealed an enormous wealth of species new to science, but many parts of the world remain unexplored or poorly documented. Much of the progress achieved in understanding mechanisms shaping phenotypes, distribution patterns and organisms' function is yet to translate into policies that frame the management of groundwater ecosystems and protect the important services they deliver to humans.

Springs are another economically and ecologically important type of groundwater dependent ecosystem. Chapters by Marco Cantonati and Dudley Williams introduce into the typology of springs across disciplines and scales and highlight their unique properties and features. The chapter of Cantonati in addition offers an overview of the main groups of photoautotrophs in springs, while Williams does the same for invertebrates. Overall, broad and specific characteristics of spring communities, and the mechanisms of community assembly are examined together with the ecological controls that account for the differences observed between individual springs. The importance of springs in natural, global landscapes is emphasized alongside increasing anthropogenic pressures.

Trophic interactions and food web dynamics are covered in two further chapters. The first one by Schmidt and co-authors has a strong focus on interactions at the micro-scale, the playground of microbes in the pores of sediments. The authors outline how an increased understanding of micro-scale processes may lead to an improved appreciation of the range of ecosystems functions taking place at larger scales. An overview of existing concepts, methods, and findings is provided. Saccó and co-authors report the current knowledge of trophic dynamics in both aquatic and terrestrial subterranean communities including fauna. Substantial shortage of nutrients drives food web interactions and opportunities for adaptive opportunistic strategies in subterranean environments. Recent research contrasts the archetype of poorly structured food chains against convoluted mechanisms sustaining a range of biotic diversity and functional complexity. Novel analytical designs described in the chapter provide important new perspectives into the investigation of these key ecological dynamics.

The final set of chapters considers applied aspects of groundwater ecology. Robert Luetkemeier and colleagues start with an article on global anthropogenic pressures on groundwater. While groundwater is essential for drinking water supply, food production and ecosystem functioning, human-groundwater interactions often critically lead to overexploitation and quality degradation. In this chapter, the authors explore anthropogenic activities in the agricultural, domestic and industrial sectors and their direct consequences for quality and quantity of groundwater. In addition, indirect effects from anthropogenic activities in terms of the likely impacts of climate change on groundwater systems are considered. Two subsequent chapters report on drinking water production from groundwater and the aspects that need to be considered. Savio and co-authors give an overview of the available knowledge on the microbiology of karst aquifers, typical sources of microbiological pollution, and available management strategies for the protection of karst water resources used for drinking water production. In this context, a recently developed concept for the sustainable quality management of karst water resources based on a holistic analysis of fecal pollution and its sources is presented. While the chapter of Savio et al. focuses on karst systems, the chapter of Derx and colleagues deals with porous aquifers. In particular, they focus on river bank filtration for production of drinking water. The chapter summarizes the current approaches for evaluating pathogen fate and transport in the environment, their removal during subsurface transport in porous aquifers, and the protection needed to achieve safe drinking water. Modelling techniques for estimating the required pathogen reduction by riverbank filtration or subsequent disinfection steps are presented. The monitoring and modelling techniques include microbial source tracking, experimental tracer tests, analytical and numerical transport models and quantitative microbial risk assessment.

A case study by Erin Haacker summarizes the physical geography, hydrogeology, and management of the High Plains Aquifer, one of the most important aquifers in North America. The High Plains Aquifer is heavily utilized for irrigation of corn, soy, and cotton and is threatened by agricultural development, with much of the aquifer already depleted to the point of no longer

supporting efficient irrigation pumping. The remaining aquifer lifespan varies over space and is difficult to predict, with estimates ranging from less than a decade in some places, to several centuries in others.

Anne Jäger und Hans Jürgen Hahn provide a chapter on methods for sampling and monitoring groundwater fauna. Since groundwater ecosystems are among the least explored habitats in the world, it is timely that this chapter describes the methods, strategies, and challenges of accessing subterranean aquatic habitats. Common methods for collecting groundwater fauna are described including their accuracy and efficiency in collecting organisms, as well as to whether they allow for a representative, quantitative sampling of aquifers. Moreover, morphological and molecular approaches for species identification, and their use in biodiversity and community ecology research are discussed.

The section finishes with a chapter that summarizes important knowledge gaps, obstacles and research frontiers in groundwater microbial ecology. Griebler and colleagues compiled 10 hot topics that need consideration in future microbial ecological research. Among these are the quantitative assessment of the subsurface carbon cycle including the import and export of carbon, rates of organic matter transformation, and the role of chemoautotrophy. Furthermore, the link between microbial communities and their processes with the meio- and macrofauna is not understood at all, and groundwater fauna microbiome studies may constitute a promising starting point. Finally, ecological principles and laws determined for other terrestrial and aquatic ecosystems await testing to assess their validity in groundwater ecosystems.

In conclusion, the 26 groundwater-related chapters contained in the 2nd edition of the Encyclopedia of Inland Waters, provide readers with the most comprehensive compilation available to date. We hope that in a 3rd edition of the Encyclopedia of Inland Waters, this compilation will be further extended to include topics we could not envisage this time. The ecology of hot springs and the deep subsurface, a chapter on groundwater ecosystem services, and more case studies on the world's largest aquifers are examples. Nevertheless, we hope readers share our excitement about this groundwater section and make frequent use of the material in basic science, applied groundwater issues, and teaching.

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Groundwater – Global Abundance and Distribution

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This is an update of W.M. Alley, Ground Water, in Encyclopedia of Inland Waters, edited by Gene E. Likens, Elsevier Inc., 2009, https://doi.org/10.1016/B978-012370626-3.00015-6

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Aquifer A layer of (ground-) water carrying permeable materials.
Baseflow Streamflow that is sustained by groundwater inflow.
Grid cell Discretization of the spatial domain of a model into parts.
Groundwater depletion A shortage of groundwater supply.
Groundwater Water that exists beneath the earth's surface in saturated zones.
GWAAEs Groundwater-associated aquatic ecosystems.
GWDTEs Groundwater-dependent terrestrial ecosystems.
Karst Rocks of particular material where percolating water widens cracks and fissures.
Land subsidence Lowering of the ground due to a lack of support (e.g., due to missing water).
Permeability Ability of porous material to let fluids pass through.
Stomata Pores in the epidermis of plants that control the rate of gas exchange.
Transboundary aquifers Aquifer systems that extend across political boundaries.
Water table Boundary between saturated and unsaturated zones underground.

Introduction

Groundwater is the source of about 40% of all human water abstractions (Döll et al., 2014). It supplies water for human consumption, irrigation, and various industrial purposes. It is also an essential source of water and habitat for freshwater biota in rivers, lakes, and wetlands. These different water bodies can be connected to what is known as an aquifer, a layer of (ground-) water carrying permeable materials that can be hundreds of meters deep and extend for hundreds of kilometers, acting as a steady water supply to surface water bodies even in periods without rain. These aquifers are replenished by groundwater recharge, a complex process driven by precipitation and various other factors.

Billions of people rely on groundwater as an accessible source for drinking water and irrigation, especially during droughts. The importance of groundwater will likely increase with climate change, as surface water availability is related to changing precipitation patterns (Taylor et al., 2013). For example, rain events that occur less often but with higher intensity may lead to flood events followed by periods of drought and vice versa. During both floods and droughts, groundwater can be a reliable source of clean water. However, increased demand may limit the availability of groundwater for humans and biota alike (Kløve et al., 2014).

This chapter provides an overview of the current state of knowledge on the global abundance and distribution of groundwater. It provides information about the global availability of groundwater and the multiple factors that impact this valuable resource (Section "Global water availability and the role of groundwater as an accessible source of clean water"). Existing knowledge gaps are discussed alongside current research in pursuit of exploring this hidden resource, for example, with the use of global groundwater models (Section "Simulation of global groundwater"). Further, current information on global surface water-groundwater interactions and global coastal groundwater availability is presented and discussed in the context of a changing climate (Section "The importance of groundwater in a changing climate").

Groundwater - a resource under threat

In the last century, the global population has quadrupled and altered terrestrial water fluxes, with a lasting impact (Wada et al., 2012). Dams and other river regulations have led to changed flow regimes affecting downstream users and freshwater biota (Biemans et al., 2011; Grill et al., 2014). In addition, the use of groundwater for irrigation has increased the amount of water transpired by plants. Eventually, water used for irrigation ends up as excess water in streams and finally the ocean. It is likely that this additional water is contributing to rising sea levels (Wada et al., 2012).

Groundwater, a reliable source of freshwater throughout the year, has been heavily affected by human abstractions. Groundwater pumping has lowered water tables and even led to groundwater depletion (a shortage of groundwater supply due to continuous overuse; Döll et al., 2014; Scanlon et al., 2012; Wada et al., 2012; Konikow, 2015). Subsequently, lower water tables cause reduced base flow (the share of streamflow sustained by groundwater) to rivers and wetlands, deteriorating water quality and freshwater ecosystems. Additional effects of groundwater abstraction are land subsidence (lowering of the ground due to a lack of water support), increased pumping costs (deeper wells require deeper drilling, stronger pumps, and therefore more energy) and seawater intrusion (lower groundwater levels might lead to seawater inflow; see "Coastal groundwater"; Bierkens and Wada, 2019; Gleeson et al., 2016).

Groundwater is a central resource for global food security and the health of freshwater ecosystems worldwide (Kløve et al., 2014). For example, depleted aquifers that are no longer able to supply water in ecologically and economically critical periods, e.g., by providing water to surface water bodies, are a persistent threat to ecosystems as well as to humans. This threat has already led to unprecedented actions by legislators; in California, for example, following recent massive droughts, the Sustainable Groundwater Management Act (SGMA) was implemented. SGMA enforces the development of groundwater sustainability plans for all over-drafted basins in the state. Importantly, overuse of groundwater is not a local but a global issue, as demonstrated by international programs such as UNESCO's program for International Shared Aquifer Resource Management (ISARM, http://isarm.org (last access: 22.05.21)) and the Transboundary Waters Assessment Program (TWAP, UNESCO-IHP, 2012). In a globally connected world, with trade and consumption affecting remote water resources, it is crucial to understand the distribution and availability of groundwater as one of the planet's most vital resources.

Despite the importance of groundwater, there is a fundamental lack of data that hinders the assessment of its global distribution, availability, and quality. While the strategic importance of groundwater for worldwide water and food security will likely increase with climate change, we still lack the necessary data (e.g., on hydrogeology, water levels) to thoroughly assess groundwater on a global scale, but also on continental and even local scales.

Global water availability and the role of groundwater as an accessible source of clean water

Groundwater represents 97% of the available freshwater globally (excluding inaccessible frozen water at the poles and bound in glaciers; Guppy et al., 2018). As highlighted earlier, groundwater is often used in an unsustainable way; hence, an estimated 20% of the world's aquifers are currently overexploited (Gleeson et al., 2012). Unsustainable groundwater use has led to the deterioration of groundwater quality, especially in coastal aquifers affected by seawater intrusion. In light of these developments, the following section discusses groundwater in the context of the United Nations' (UN) Sustainability Development Goals (SDGs) and is followed by a section that provides deeper insights into the Global distribution of groundwater. The replenishment of groundwater resources is shown in section "Groundwater recharge," while the connection to the world's oceans is discussed in section "Coastal groundwater." Section "Global groundwater abstractions" summarizes the current knowledge about global groundwater use, and Section "Observation of groundwater on large scales" discusses available global datasets.

The sustainable development goals (SDGs) and their link to groundwater

The UN SDGs are a collection of global goals that the member states set out to pursue by 2030. While they do not explicitly feature groundwater, their goals, such as ending poverty and hunger, protecting the planet, and targeting peace and prosperity for all, depend on groundwater. Groundwater is pivotal for sustaining industrial and agricultural development; its sustainable use determines the future of groundwater-dependent ecosystems, too (GWAAEs, GWDTEs). On the other hand, aquifers may extend across political boundaries, called transboundary aquifers, and are thus a potential source of conflict (Puri, 2009). Therefore, the challenge is balancing the needs of nature and humans (industries, agriculture, sanitation, drinking water) in the context of a limited and pivotal resource shared across political boundaries. For sustaining and creating a liveable and peaceful planet, groundwater is

an important piece of the puzzle that needs to be considered. The following summarizes the interlinkages between the SDGs and groundwater because of the importance of the SDGs as a global political framework that decision-makers and stakeholders widely recognize.

A special connection between groundwater and the SDGs exists with respect to the availability of clean water and sanitation for all people (SDG 6), responsible consumption and production (SDG 12), and climate action (SDG 13) (Guppy et al., 2018). However, a connection does not mean that the goals, or sub-goals, may only positively affect groundwater; some goals may even contradict each other. For example, the goal of ensuring safe access to drinking water (SDG 6.1) can be compromised if groundwater is overused or if the groundwater is unsafe to drink, e.g., due to fecal contamination from increased agricultural use of the area implemented in order to reach SDG 2 (zero hunger). Lesser but visible connections can be drawn between groundwater and the eradication of poverty (SDG 1), the goal of zero hunger (SDG 2), industry, innovation, and infrastructure (SDG 9), and life on land (SDG 15) (Guppy et al., 2018).

Global distribution of groundwater

Our knowledge about the global distribution of groundwater is highly uncertain, as we still lack global datasets that allow for a more precise assessment. Current assessments conclude that while surface water adds up to about 100,000 km^3, groundwater accounts for almost 25 million km^3 (Fig. 1). The majority of this water is ancient and has been recharged over millennia (Gleeson et al., 2016).

Multiple computer models (Reinecke et al., 2019b; Fan et al., 2013; deGraaf et al., 2015) have estimated the distribution of that volume by applying numerical approaches (see Section "Simulation of global groundwater") to compute a map of global groundwater levels (Fig. 1). The map shown in Fig. 1 is based on a quasi-equilibrium (also called steady state) representing what the depth to groundwater would look like if climate and groundwater-surface water interactions could balance out over millions of years without any changes or abstractions by humans. The figure clearly shows the impact of the topography, as groundwater naturally follows gravitational gradients to the lowest points.[1]

Irrespective of the assumptions of a steady state, all current estimates of the global distribution of groundwater are very uncertain, mainly due to (1) a lack of global hydrogeological data (see also Section "Observing groundwater from space – GRACE"), (2) uncertainties regarding the amount of groundwater recharge (Reinecke et al., 2021; Section "Groundwater recharge") and interactions between surface water and groundwater (Reinecke et al., 2019b; Section "Groundwater-surface water interactions"), (3) and a coarse spatial resolution of the models used. Added to this list is a general lack of understanding around certain groundwater processes themselves, even on smaller scales, such as the flow in karst (rocks of particular material where percolating water widens cracks and fissures), fractured aquifers, capillary rise, or permafrost, all of which are currently not represented in global models.

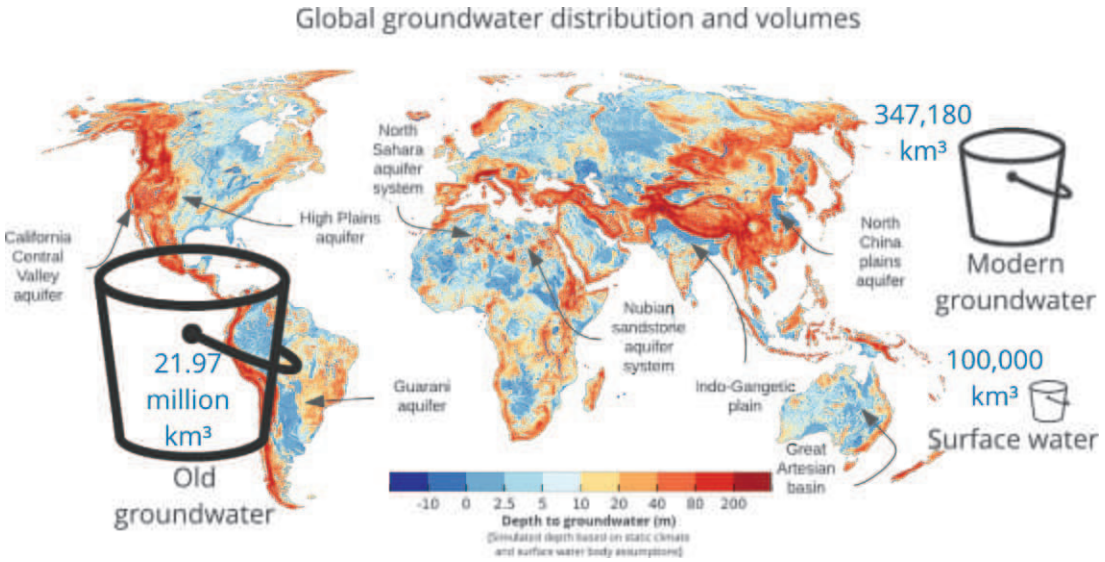

Fig. 1 Global groundwater abundance and distribution. Arrows mark the location of major aquifers. The depth to groundwater map is based on a steady-state simulation of Reinecke et al. (2019b). Volumes of groundwater and surface water are based on Gleeson et al. (2016), where modern groundwater is considered to be recharged over the past 50 years. Modified from Reinecke R, Foglia L, Mehl S; Trautmann T, Cáceres D, Döll P (2019b) Challenges in developing a global gradient-based groundwater model (G^{3}M v1.0) for the integration into a global hydrological model. *Geoscientific Model Development* 12(6): 2401–2418, https://doi.org/10.5194/gmd-12-2401-2019.

[1]Some of the blue areas in Fig. 1 are indeed much too wet for their location, e.g. the Sahara. These places exist due to the steady state assumption of that particular simulation, which also assumes the steadiness of wetlands in regions where they would typically only occur once every couple of years.

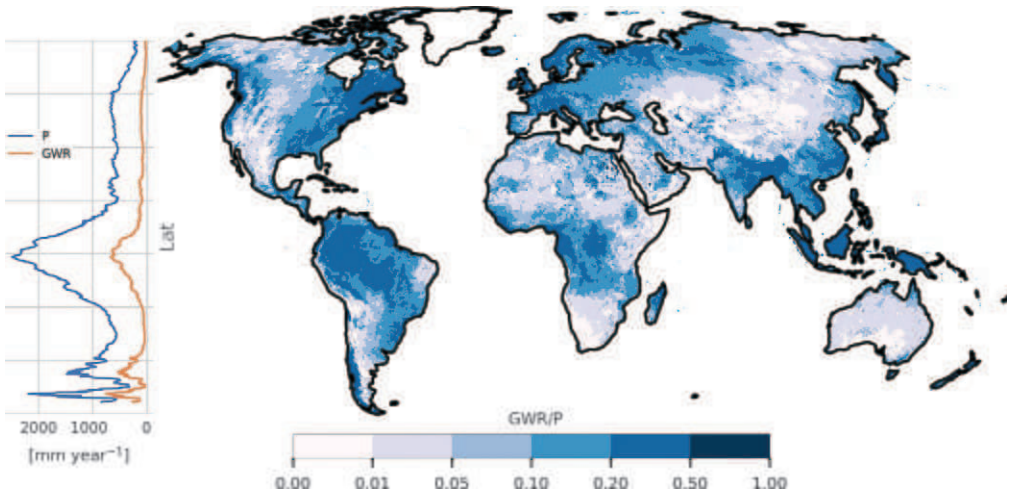

Fig. 2 Groundwater recharge ratio (diffuse groundwater recharge (GWR) relative to precipitation (P)) at preindustrial CO_2 concentrations based on an ensemble of eight global hydrological models (Reinecke et al., 2021).

Groundwater recharge

Aquifers are replenished by groundwater recharge, which can be conceptualized to occur mainly in two ways. (1) Diffuse recharge occurs over large areas as excess water from precipitation infiltrates into the soil and percolates downwards without being taken up by plant roots. (2) Focused recharge occurs when streams, rivers, and wetlands lose water to aquifers or when water flows through fractures, e.g., in karstic systems. This process is influenced by complex local conditions and is thus challenging to estimate for larger areas (Reinecke et al., 2021). Recharge is an important indicator for assessing the sustainable use of a groundwater body (Herbert and Döll, 2019). Only when less water is abstracted than replenished is sustainable use possible. Fig. 2 shows the global distribution of groundwater recharge according to an ensemble of eight global hydrological models. Diffuse recharge can account for up to 20% of the yearly precipitation in some regions.

Groundwater-surface water interactions

Groundwater and surface water bodies are connected. Continuous groundwater pumping can lead to declining river discharge (deGraaf et al., 2019) when groundwater flows recharge surface water. In the opposite direction, a large percentage of streams provide vital recharge to aquifers when the streambed is permeable enough (Jasechko et al., 2021; Reinecke et al., 2019b; Hare et al., 2021). However, due to a lack of global geological data, it is currently unclear how much water is transferred via that interface even though it is pivotal for understanding groundwater's global distribution and availability (Jasechko et al., 2021; Reinecke et al., 2019a).

Coastal groundwater

Particularly in coastal areas, people rely on groundwater as a source of drinking water. While groundwater is under pressure globally due to extensive water abstractions (e.g., Gleeson et al., 2012; Wada et al., 2010), proximity to coasts amplifies these pressures because of potential sea water intrusion (lowered groundwater levels and in addition higher sea levels may lead to reversed gradients and thus sea water flowing inland into the aquifer) that can endanger groundwater quality (van Camp et al., 2014). Future climate change and rising sea levels may additionally alter coastal groundwater dynamics (Befus et al., 2020) and thus threaten the water supply for a large percentage of the global population.

Global groundwater abstractions

In some places, groundwater has been accumulating over millennia and is only recharged slowly. When an aquifer is used unsustainably (abstraction exceeds recharge), it can be depleted, leading to dire consequences for humans and ecosystems. In Iran, for example, abstractions have already led to widespread groundwater depletion in around 77% of the land area (Ashraf et al., 2021). Globally, millions of wells could run dry if abstractions continue (Jasechko and Perrone, 2021). This is especially concerning, as the importance of groundwater for freshwater supply will likely increase with a changing climate (Taylor et al., 2013).

Reasons for continued abstractions are manifold; however, non-sustainable irrigation practices and the international food demand are likely the main drivers of this continuing trend (Dalin et al., 2017). These continuing abstractions may contribute to rising sea levels, as the ultimate sink for abstracted water is the ocean (Wada et al., 2012; Döll et al., 2014).

Observation of groundwater on large scales

Assessing the global abundance and distribution of groundwater is a challenge, as data sources are scarce. Three main reasons for this lack can be identified: (1) countries may not have the necessary resources to collect hydrogeological data and well observations on a large scale, (2) countries may not wish to make these data available to others, as it reveals insights about an increasingly strategic resource; this is exacerbated in regions with transboundary aquifers that provide conflict potential, (3) and compiling available data into global datasets is a challenging and time-consuming task. Even the global observations that have been published need to be regarded with care, as they are primarily available in regions where human influences on the natural system are most significant.

Observing groundwater from space – GRACE

The only current data source that is indeed a "global" dataset is the GRACE (Gravity Recovery and Climate Experiment; Table 1; NASA, 2007). The satellite mission started in 1997 and was succeeded by the GRACE-FO (Follow-On; NASA, 2018) in 2018. Two satellites measure gravitational anomalies that can be used to trace mass changes triggered by large-scale groundwater depletion. However, the spatial resolution of the data is very coarse (2°; about 222 km at the equator) and GRACE measures total variations in gravity, thus much pre-processing is necessary to assign gravity changes to a particular source in the water column, e.g., groundwater mass changes (Döll et al., 2014).

Table 1 Global datasets relevant to the distribution and availability of groundwater.

Name	*Data*	*Spatial extend/resolution*	*References*
GRACE	Gravity anomaly	Global, 2°–0.5° (depending on data product)	NASA (2007, 2018)
GLHYMPS	Permeability map	Global, variable resolution, 100 m depth	Gleeson et al. (2014)
GLHYMPS 2.0	Permeability map	Global, variable resolution, 100 m + depth to bedrock information	Huscroft et al. (2018)
WOKAM	Karst map	Global, variable resolution	Goldscheider et al. (2020)
GGIS	Groundwater levels	Global, point data	IGRAC (2004)
GEMStat	Groundwater quality data	Global, point data	ICWRGC (2014)
Groundwater Watch	Selected well data of the USGS	US, point data	USGS (2021)

Data centers and datasets

A key to assessing groundwater resources is adequate data on the subsurface permeability (the ability of porous material to let fluids pass through). Currently, only two global datasets, GLHYMPS (Gleeson et al., 2014) and its successor GLYMPS 2.0 (Huscroft et al., 2018), provide insights on the distribution of global permeability of the first 100 m vertically (Fig. 3; Table 1). Overall, the permeability from this dataset can be assumed to be underestimated (Reinecke et al., 2019a), and additional efforts are needed to improve the currently available data to allow for a more detailed representation of the hydrogeology, for example, its vertical heterogeneity.

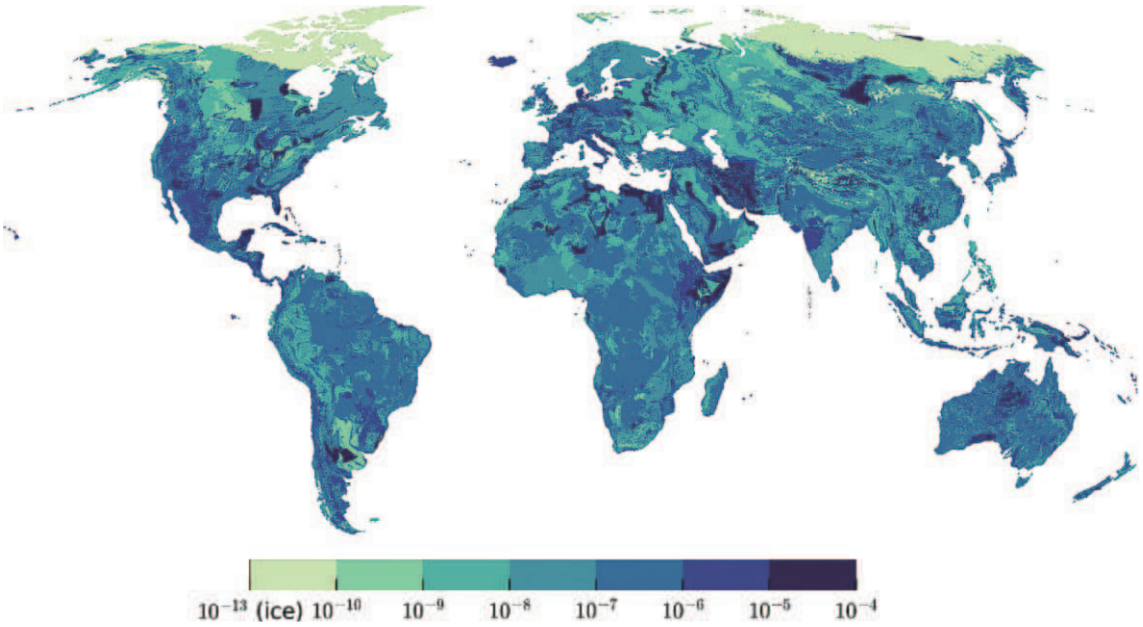

Fig. 3 Hydraulic conductivity [m s^{-1}] derived from Gleeson et al. (2014) scaled to 5 arc-minutes based on Fig. S3 from Reinecke et al. (2019b). Very low values in the northern hemisphere are due to permafrost conditions. From Reinecke R, Foglia L, Mehl S; Trautmann T, Cáceres D, Döll P (2019b) Challenges in developing a global gradient-based groundwater model (G^3M v1.0) for the integration into a global hydrological model. *Geoscientific Model Development* 12(6): 2401–2418, https://doi.org/10.5194/gmd-12-2401-2019.

A complimentary dataset is the World Karst Aquifer Map (WOKAM; Table 1; Goldscheider et al., 2020), showing the global distribution of karstifiable rocks (for example, carbonates and evaporites). Currently, no global modelling assessment includes this landscape characteristic, which is crucial for water availability in many regions of the world.

Global data on groundwater levels from well data can be retrieved from the supplemental material of Fan et al. (2013) and Jasechko and Perrone (2021); a unique dataset for the continental US is the Groundwater Watch data of the USGS (Table1; USGS, 2021).

An additional source for information is the UNESCO category 2 centers and their data center activities. IGRAC (International Groundwater Resources Assessment Centre) runs the openly accessible Global Groundwater Information System (GGIS; Table 1; IGRAC, 2004), an online platform that supports sharing of global groundwater data. Information about global groundwater quality data, on the other hand, can be found in the GEMStat database (Global Environment Monitoring System for Freshwater; Table 1; ICWRGC, 2014) hosted by the ICWRGC (International Centre for Water Resources and Global Change).

Data on groundwater recharge is still rare because estimates are very challenging to obtain and are often delineated from groundwater level changes. Two existing large-scale datasets are the global estimate of Mohan et al. (2018) and an Africa-wide dataset by MacDonald et al. (2021).

Simulation of global groundwater

In recent years, global groundwater models have emerged as a new modelling category, often coupled to existing global hydrological and land surface models to improve their representation of surface water-groundwater interactions and their simulation of evapotranspiration (Reinecke et al., 2019b; deGraaf et al., 2015; Fan et al., 2013). Still, these models are relatively new and present challenges for evaluation (Gleeson et al., 2021; Reinecke et al., 2020) due to their relatively coarse spatial resolution and the limited availability of hydrogeological data.

Fig. 4 shows both a conceptualization of reality (also called a perceptual model; Wagener et al., 2021) and a possible implementation in a global gradient-based groundwater model to convey the level of abstraction necessary for a global-scale

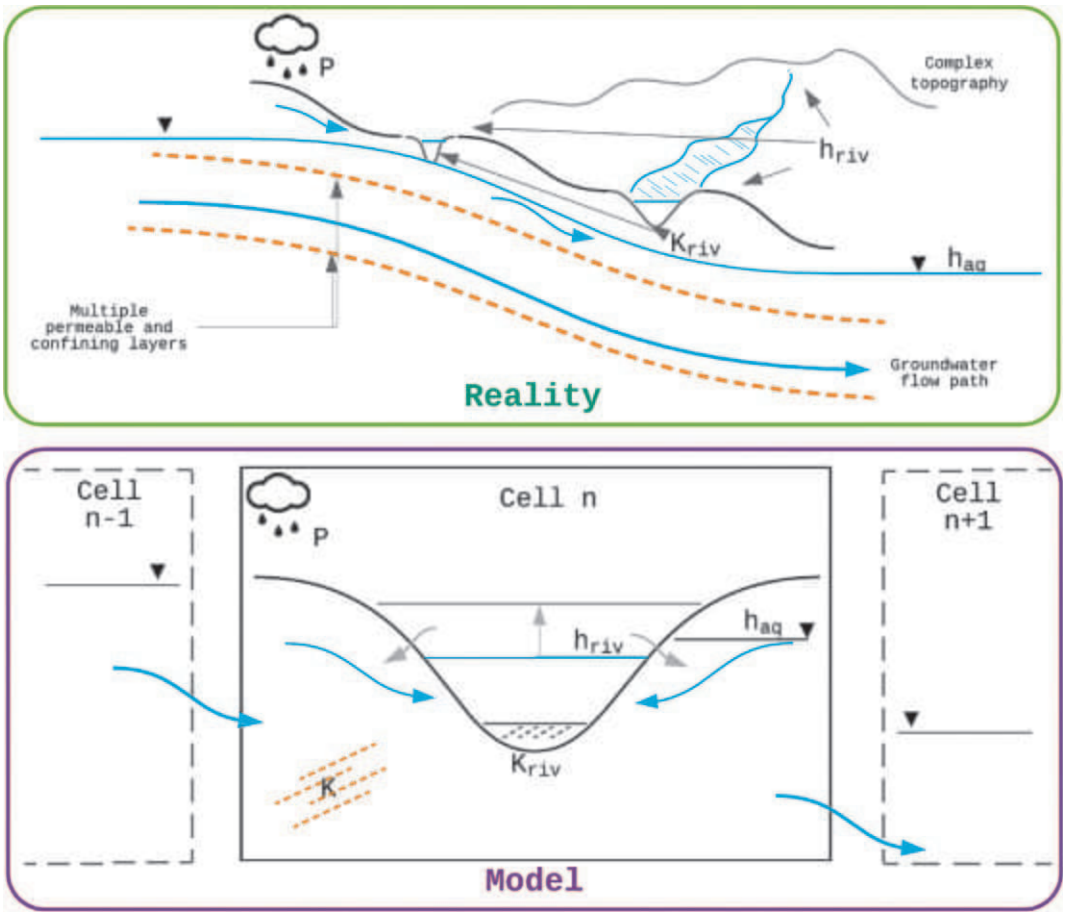

Fig. 4 Conceptual representation of reality (top) and simplified global gradient-based groundwater model representation (bottom). Blue lines in both boxes represent groundwater flow paths. Adapted with modifications from Reinecke R, Wachholz A, Mehl S, Foglia L, Niemann C, Döll P (2020) Importance of spatial resolution in global groundwater modeling. *Ground Water* 58(3): 363–376, doi: 10.1111/gwat.12996.

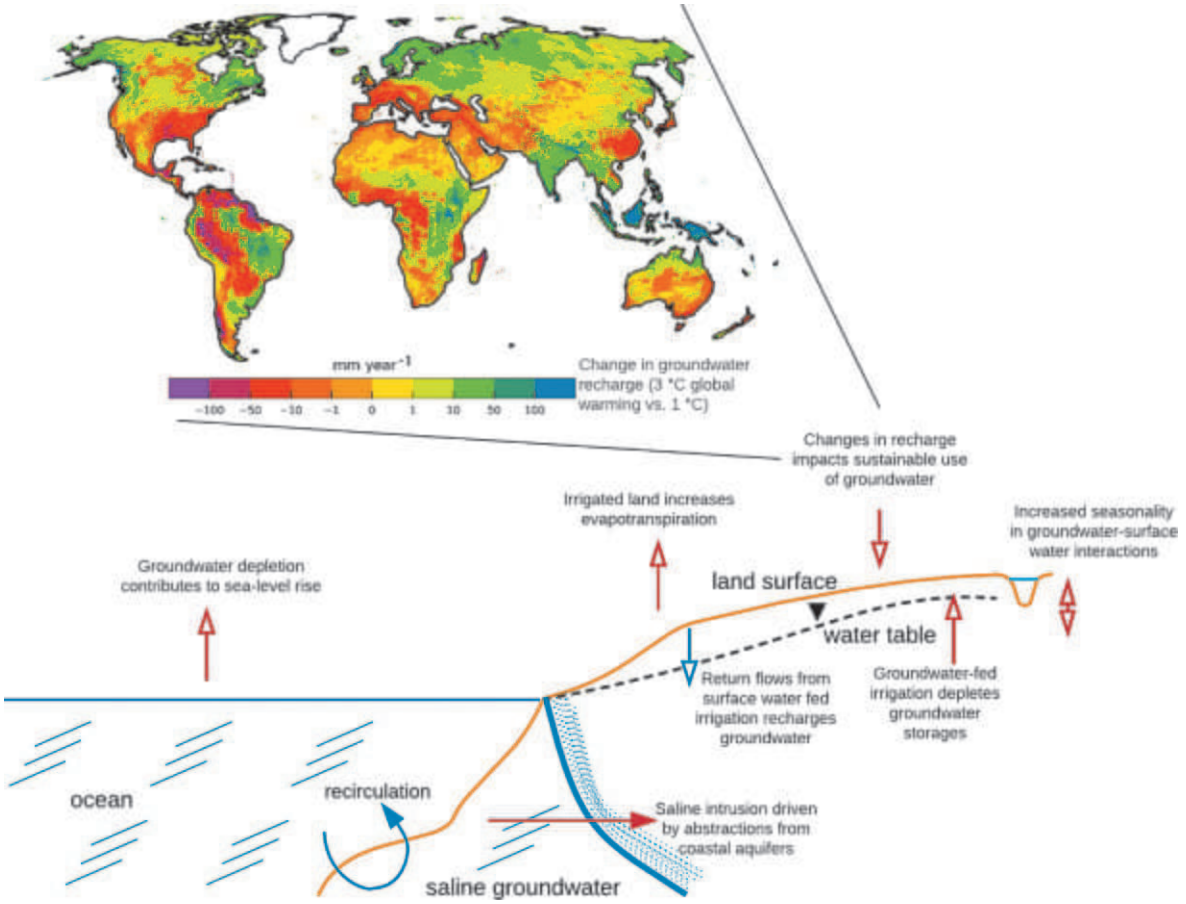

Fig. 5 Different impacts of climate change (red arrows) on groundwater based on Taylor et al. (2013). The map of simulated groundwater recharge changes is based on Reinecke et al. (2021). Modified from Reinecke R, Müller Schmied H, Trautmann T, Andersen LS, Burek P, Flörke, M, Gosling SN, Grillakis M, Hanasaki N, Koutroulis A, Pokhrel Y, Thiery W, Wada Y, Yusuke S, Döll P (2021). Uncertainty of simulated groundwater recharge at different global warming levels: a global-scale multi-model ensemble study. *Hydrology and Earth System Sciences* 25(2): 787–810, doi: 10.5194/hess-25-787-2021 and based on Taylor RG, Scanlon B, Döll P, Rodell M, van Beek R, Wada Y, Longuevergne L, Leblanc M, Famiglietti JS, Edmunds M, Konikow L, Green TR, Chen J, Taniguchi M, Bierkens MFP, MacDonald A, Fan Y, Maxwell RM, Yechieli Y, Gurdak, JJ, Allen, DM, Shamsudduha M, Hiscock K, Yeh, PJ-F, Holman I, Treidel H (2013) Ground water and climate change. *Nature Climate Change* 3(4): 322–329, doi: 10.1038/nclimate1744.

model. In reality, one might find multiple streams and rivers inside a 5 × 5 km area; however, these are often represented as only one major stream inside a model grid cell (models often discretize the spatial domain into parts, for example, 5 × 5 km lots, that are referred to as grid cells). This simplification might also be necessary for other parameters found in Fig. 5: the precipitation (P) and resulting recharge, the river height (h_{riv}), the conductance of the river (K_{riv}), the hydraulic head of the aquifer (h_{aq}), and the hydraulic conductivity (K). While it is clear that the reality is much more complex and one might, for example, find multiple layers of permeable and confining material that influence groundwater flow, global models are limited to simplified representations due to a lack of data and computational challenges (Reinecke et al., 2019b).

The importance of groundwater in a changing climate

The importance of groundwater for global water security will likely increase with the changing climate (Taylor et al., 2013). In a world with an increased frequency of extreme events like floods and droughts and a global shift in precipitation patterns, and thus also a changing availability of surface water, groundwater as a reliable resource will be vital for many communities. However, it is still unclear how the changing climate will impact groundwater availability and where sustainable use of this resource will be possible. Recent analyses suggest that even the slow-changing groundwater fluxes could adapt to the changing climate on human time scales (Cuthbert et al., 2019).

Groundwater is affected in multiple ways by climate change. Changes in precipitation may reduce groundwater recharge in parts of the world, while others may see increases in recharge (Map in Fig. 5). Additionally, a decrease in precipitation will likely also lead to increased groundwater pumping. However, it is difficult to determine whether increased pumping is only the result of decreases

in precipitation or surface water availability or simply a growing population. It is also unclear how rising CO_2 levels will affect plant water use and thus groundwater recharge: with rising CO_2, plants open their stomata less, which in turn reduces evapotranspiration and thus increases runoff; on the other hand, plants might grow better with increased CO_2, which will increase evapotranspiration (Reinecke et al., 2021).

Continuing or even increased abstractions from groundwater for irrigation will likely increase the contribution of groundwater depletion to rising sea levels (Wada et al., 2012; Fig. 5). If this water is taken from coastal aquifers, an increase in saline intrusion could result (Fig. 5). Additionally, the rising sea levels threaten these aquifers with saline intrusion through overwash (flow of seawater over the crest of a beach system; Befus et al., 2020). While the abstractions from groundwater deplete groundwater storage, they increase evapotranspiration (Fig. 5), and changes in precipitation patterns can change the interactions between surface water and groundwater bodies (Fig. 5).

Outlook

Groundwater is the largest available source of freshwater and is a key resource to ensure clean and available drinking water for humans and biota alike. While it is not explicitly mentioned in the UN's SDGs, it is a crucial resource for achieving them. Compared to surface water, groundwater by volume is 100 × larger, but its accessibility varies globally, and abstractions worldwide have led to widespread lowered water tables with dire consequences. Our knowledge about this hidden resource is still limited by data availability, mainly groundwater levels, and hydrogeology. While current modelling efforts provide initial insights into how groundwater is distributed globally and how it interacts with our other water resources, limited knowledge about processes like groundwater recharge call for further research. Especially since groundwater is such a vital resource when facing the challenges of a changing climate, knowledge about how it is affected and how it can be used sustainably on a global scale is imperative and of utmost relevance, especially in the context of transboundary aquifers. Currently, the global abundance and distribution of groundwater remain uncertain.

Knowledge gaps

- Global hydrogeology, especially vertical resolution
- Current and past distribution of groundwater (limited global data)
- Reliable estimates of groundwater recharge on large scales (challenging to measure and model)
- Large-scale understanding of groundwater-surface water interactions
- Long-term impacts of climate change on groundwater

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Groundwater Systems—A Hydrogeological Typology

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Aquifer Water-bearing units underground capable of yielding water to wells or springs.
Confined aquifer Aquifer where the groundwater is pressurized such that it rises above the bottom of an overlying confining unit when the aquifer is penetrated by a well.
Confining unit Geological units significantly less permeable than aquifers.
Consolidated rocks Rocks in which the individual minerals are firmly held together; includes sedimentary rocks where grains are cemented as well as igneous rocks (formed by crystallization from magma, e.g., basalt or granite) and metamorphic rocks (formed under high temperature and pressure, e.g., gneiss).
Groundwater Water occupying the pore spaces below the (subsurface) water table.
Piezometric surface Imaginary surface to which groundwater rises if a confined aquifer is penetrated by a well.
Primary porosity Pores created when the rock was originally formed.
Secondary porosity Porosity developed after the original formation of the rock; more narrowly defined, discontinuities (fractures) separating blocks of intact rock, which were created by mechanisms other than dissolution.
Tertiary porosity Conduit porosity developed where the dissolution of rock widened fractures.
Unconfined aquifer Aquifer where the water table is located within the water-bearing unit (water-table aquifer).
Unconsolidated rocks Sediments composed of loosely arranged particles or grains (not cemented).
Water table Surface where the water pressure is equal to the atmospheric pressure.

Introduction

Groundwater is a major water resource for the world population and sustains streams, lakes, and wetlands. Sustainable use and protection of groundwater must be based on a sound understanding of groundwater flow and storage. As part of the hydrological cycle, groundwater systems are dependent on hydrological processes controlling their recharge and discharge. Yet, regional and local assessments of groundwater systems also require knowledge of subsurface properties controlling groundwater flow and storage. The aim of this chapter is to introduce the basic terms and concepts needed to characterize and classify groundwater systems with regard to these hydrogeological properties and their effect on flow and storage.

The following section introduces basic definitions of different types of subsurface waters, in particular groundwater. Subsequently, different types of aquifers are distinguished based on the hydraulic conditions found in the subsurface. Then different types of porosity are considered, which correspond to a classification of aquifers based on the geological material. Building on this typology, aquifer properties controlling groundwater flow and storage are introduced and discussed with regard to the different aquifer types. Finally, chemical and thermal properties of groundwater and how they are interlinked with groundwater flow are discussed.

Basic definitions

After intense rainfall or snowmelt, the soil or rock at the ground surface may temporarily be saturated with water. Generally, however, the shallow subsurface contains both air and water and thus is termed the *unsaturated zone* (or vadose zone) (Fig. 1). Underneath the unsaturated zone follows the *saturated zone* (or phreatic zone), where all voids are filled with water. If observation wells are drilled into the saturated zone, the lower part of the well fills with water. The top of the water column in the well marks the *water table*. Water below the water table is termed *groundwater*. At the water table, the water pressure is equal to atmospheric pressure. Below the water table, the water pressure increases with increasing depth. Conversely, the pressure in the unsaturated zone is lower than atmospheric pressure. This is a result of the capillary forces within narrow pores spaces and leads to a *capillary fringe* where water is held above the water table.

Processes within the unsaturated zone and the capillary fringe, such as the infiltration and downward percolation of water, play an important role in replenishment of groundwater systems and in the fate of contaminants released at the ground surface or shallow subsurface. Yet, these processes are dealt with elsewhere. The remainder of this chapter focusses on the zone below the water table, i.e., groundwater.

Types of aquifers

Aquifers are water-bearing units capable of yielding water to wells or springs; the unsaturated zone of such a unit is understood as being part of the aquifer (Todd and Mays, 2005). Aquifers can be overlain or underlain by *confining units* that are significantly less permeable than the aquifer. Confining units can be further classified into aquicludes (containing but not transmitting water), aquifuges (neither containing nor transmitting water), and aquitards (transmitting less water than adjacent aquifers). Evidently, aquifer and confining unit are relative terms. A geological unit that yields only little water may be considered an aquifer if other units within the same region are even less productive, whereas the same geological unit may be classified as confining unit if overlain or underlain by rocks that yield more water. A quantitative measure of the capability to transmit water thus is needed and will be introduced in the section "Flow properties".

Based on the position of the water table different types of aquifers can be distinguished (Fig. 2). In an *unconfined aquifer* (or water-table aquifer) the water table is located within the water-bearing unit (upper aquifer in Fig. 2). This condition is often found where permeable rock crops out at the land surface. A *perched aquifer* is a special case of an unconfined aquifer that occurs if a local groundwater body develops on top of a discontinuous confining layer above the regionally extensive water table of a main groundwater body. Thus, the perched aquifer and the underlying groundwater body are separated by an unsaturated zone. The groundwater within a *confined aquifer* is pressurized such that it rises above the bottom of an overlying confining unit when the aquifer is penetrated by a well (lower aquifer in Fig. 2). The imaginary surface constructed from water levels of such wells is termed

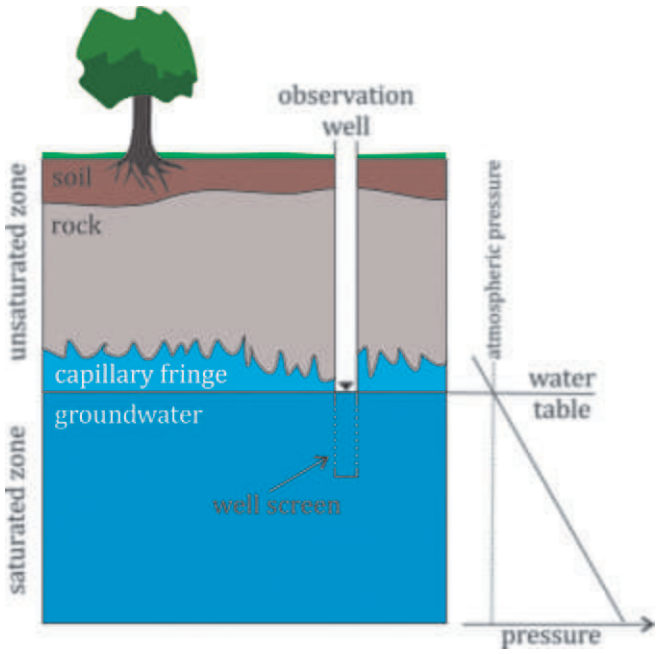

Fig. 1 Zonation of the subsurface and basic hydrogeological terms. Groundwater enters the well through the slotted part of the well casing termed well screen (dashed line). The water table observed in the well is marked by an inverted triangle.

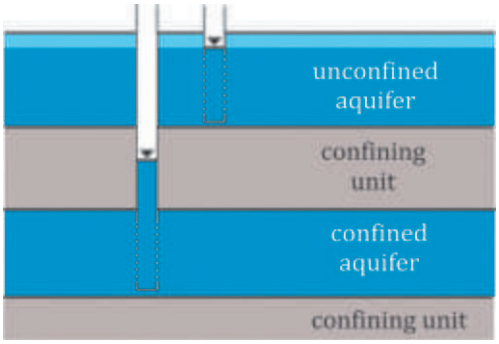

Fig. 2 Definition of unconfined and confined aquifers based on the relative position of the water table observed in the well.

piezometric surface (or potentiometric surface). If the pressure is sufficiently high to rise the water above ground level a flowing artesian well results. Confined or artesian aquifers may be found when a water-bearing unit crops out in a topographically elevated recharge area and dips into a basin where it is covered by a confining unit.

Distinguishing between unconfined and confined aquifers is important in several ways. From a practical point of view, it is vital to recognize confined conditions when drilling into the underground, as the rise of groundwater in the borehole might require technical measures that need to be planned in advance. Evidently, this particularly applies to artesian conditions where the water rises above ground level. Yet, also groundwater flow from a confined aquifer into an overlying unit generally results in undesired changes of hydraulic conditions and potentially adverse effects e.g., on water quality. A striking example is a case reported from Staufen, Germany, where confined groundwater had been allowed to rise in a borehole and caused swelling of the adjacent rock; the resulting uplift of the land surface caused severe damages to buildings (Sass and Burbaum, 2010). Confined and unconfined conditions also need to be distinguished from the more theoretical perspective of groundwater hydraulics. Although comprehensive treatment of groundwater hydraulics is beyond the scope of this chapter, fundamental differences in the storage properties of confined and unconfined aquifers are addressed below in the section "Storage properties".

Types of porosity

The occurrence of groundwater requires voids or pore spaces in the underground that can take up water. The percentage of pore spaces in a rock volume is termed (total) *porosity*. Different geological materials not only have different values of porosity; more importantly, also the size, shape, and connectivity of the pore spaces differ. The different nature of the pore spaces is closely related to their origin and thus to the type of geological material. Hence, hydrogeologists distinguish different types of porosity depending on when and how the pore spaces where formed.

Primary porosity denotes pores created when the rock was originally formed. This type of porosity is most relevant in unconsolidated sediments. Such sediments consist of grains that were transported and deposited by wind, water, or ice. The size distribution of these grains is one major factor controlling porosity. As a rule, total porosity is higher the smaller and the more uniform the grain sizes are (Fig. 3 and Table 1). Sediments transported by wind tend to be well sorted, i.e., display a narrow range of grain sizes. Since the transport and deposition of sediments by water is controlled by characteristic relationships between grain size and flow velocity, one may also expect sediments deposited in river channels and floodplains to be well sorted. However, flow velocities in such environments may vary considerably in space and time. Across the river valley, the grain size distribution of such sediments therefore may exhibit significant variability. Sediments deposited from ice generally are expected to be poorly sorted and thus may display a wide range of grain sizes. The shape and packing of the grains are further factors affecting the porosity of unconsolidated sediments. Compaction by overlying rock and cementation by chemical precipitates transforms the unconsolidated sediments to consolidated sedimentary rock. Primary porosity is reduced by this process of lithification, which is why secondary porosity gains importance in this type of rock.

Secondary porosity generally denotes porosity developed after the original formation of the rock and comprises all types of discontinuities separating intact blocks of consolidated rocks. We distinguish fracture porosity, which includes discontinuities formed by a variety of processes, such as lithostatic or fluid pressures, tectonic forces, and thermal effects, from conduit porosity, which develops where the dissolution of rock widens fractures (Fig. 4). Consequently, conduit porosity is sometimes referred to as *tertiary porosity* (Ford and Williams, 2007). Rocks that are sufficiently soluble to enable the development of conduit porosity are termed karst rocks and, in particular, include carbonate rocks (e.g., limestone) and evaporite rocks (e.g., gypsum). It is important to note that several types of porosity can occur simultaneously. For example, sedimentary rocks such as sandstone can be fractured but still may have significant primary porosity. Likewise, dissolution may create conduits in carbonate rocks, while the majority of fractures may be little affected by dissolution and primary porosity may exist as well.

It is common to name aquifers after the geological material or the type of porosity primarily enabling groundwater flow. Hence, permeable unconsolidated sediments, such as sand and gravel, where groundwater is transmitted through primary porosity, are

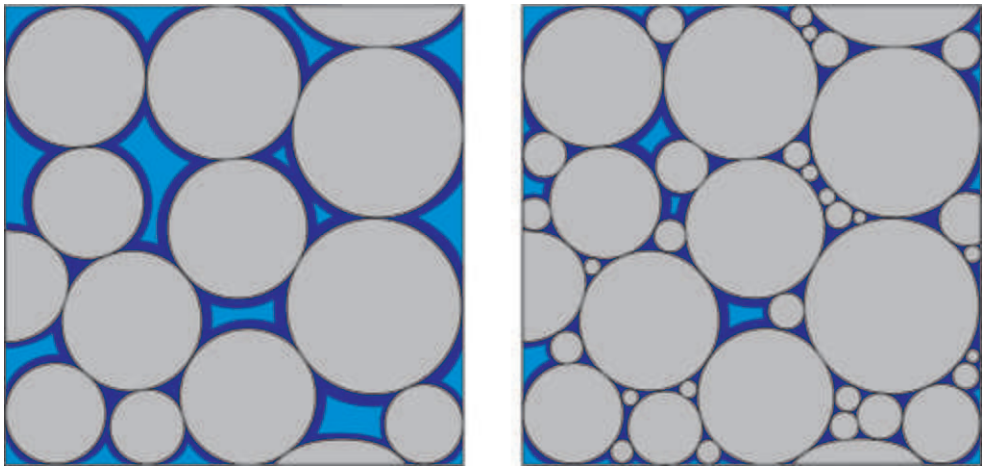

Fig. 3 Schematic sketch of the primary porosity (blue colors) of an unconsolidated sediment. The relatively coarse and well sorted sediment on the left has a higher total porosity than the poorly sorted sediment on the right, which contains fine grains filling spaces between the coarse grains. Dark blue color indicates immobile water surrounding the grains; only the light blue colored part of the pore space is available for groundwater flow (effective porosity).

Table 1 Approximate ranges of total porosity, effective porosity, and hydraulic conductivity for selected geological materials.

Geological material		*Total porosity*[a] *(%)*	*Effective porosity*[a] *(%)*	*Hydraulic conductivity*[b] *(m s^{-1})*
Unconsolidated rocks	Gravel	28–34	15–30	10^{-3}–1
	Sand	35–50	10–30	10^{-6}–10^{-2}
	Silty sand	33–40	8–12	10^{-7}–10^{-3}
	Silt	40–50	5–20	10^{-9}–10^{-5}
	Clay	40–60	1–5	10^{-13}–10^{-9}
Consolidated rocks	Karstified limestone	10–25	0.5–10	10^{-6}–10^{-2}
	Fractured basalt	5–30	2–10	10^{-7}–10^{-2}
	Sandstone	15–30	5–25	10^{-10}–10^{-6}
	Unfractured igneous or metamorphic rock	0–5	0–3	10^{-13}–10^{-10}

[a]From Singhal BBS and Gupta RP (2010) Applied Hydrogeology of Fractured Rocks (2nd edn.). Dordrecht: Springer; Hölting B and Coldewey WG (2019) *Hydrogeology*. Berlin: Springer for silty sand.
[b]From Freeze RA and Cherry JA (1979) *Groundwater*. Englewood Cliffs, NJ: Prentice-Hall.

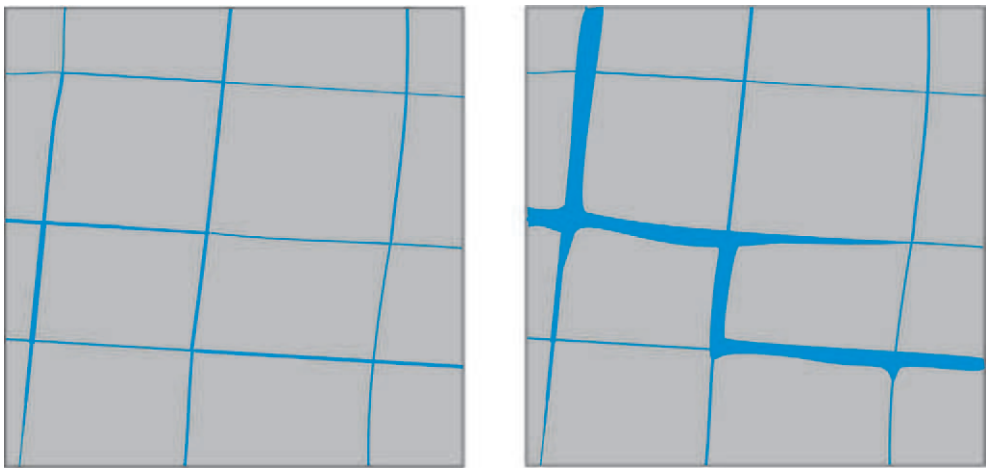

Fig. 4 Schematic sketch of fracture porosity resulting from discontinuities separating intact blocks of consolidated rocks (left). Conduit porosity develops where fractures are widened by dissolution of rock (right).

termed *unconsolidated aquifers* or *porous aquifers*. Correspondingly, the term *consolidated aquifer* refers to all types of permeable consolidated rocks. Commonly, these rocks are fractured and thus the aquifers are termed *fractured aquifers*. Some consolidated rocks, for example sandstone and basalt, the latter of which originates from volcanic lava flows, additionally may have primary porosity. Nevertheless, they usually will be classified as fractured aquifers, as flow typically occurs through open fractures rather than through the narrower pore spaces provided by the primary porosity. Similarly, solution conduits, which commonly have openings ranging from centimeters to meters, are expected to be more effective in conducting water than the pores or fractures of karst rocks. Aquifers where conduit porosity controls groundwater flow thus are termed *karst aquifers* or *karstified aquifers*.

The transmission of groundwater requires interconnected pore spaces of sufficient size to overcome adhesive forces attracting the water molecules to the mineral surfaces. The volume percentage of such pore spaces is termed *effective porosity*. The pore size in unconsolidated sediments tends to decrease with decreasing grain size. As a consequence, large parts of the pore space of fine-grained materials, such as clay or silt, is occupied with immobile water (Fig. 3). Hence, these materials have effective porosities considerably lower than their total porosity (Table 1). As a consequence, clay or silt are hardly capable of transmitting water and are classified as confining units rather than aquifers. Coarse materials such as sand and gravel, particularly if well sorted, tend to have high effective porosity that might come close to their total porosity (Table 1). Such materials represent aquifers, even though their total porosity generally is lower than that of fine-grained materials. The capability of rocks to transmit water thus appears to be related to their effective porosity rather than their total porosity. In this regard, the major difference between the two sediments sketched in Fig. 3 is not so much their different total porosity, but that the coarse and well sorted material has larger openings and thus higher effective porosity than the poorly sorted sediment. Yet, particularly some consolidated rocks may have low total porosity and consequently low effective porosity, but if few interconnected fractures or conduits have large openings these rocks are still able to transmit water. A more quantitative measure of aquifer permeability thus is needed and introduced below.

Flow properties

With some exceptions, such as flow through highly conductive conduits or flow in the vicinity of highly productive pumping wells, groundwater flow is very slow, in the order of meters per day or even well below that. Under such conditions, the *specific discharge q*, i.e., the volumetric rate of flow per unit area of flow cross section, is found to be proportional to the *hydraulic gradient i*, the slope of the water table (or piezometric surface). This is defined by Darcy's law (Darcy, 1856)

$$q = K\, i \tag{1}$$

where the proportionality constant K is termed *hydraulic conductivity*. Hydraulic conductivity estimates can be obtained by solving Darcy's law for K and inserting values of specific discharge and hydraulic gradient measured in lab or field experiments.

Hydrogeologist often treat hydraulic conductivity as if it were a property of the rock. Strictly, this is not correct, because K is also dependent on the density and viscosity of the fluid. Yet, in many groundwater systems the aforementioned fluid properties are spatially and temporally nearly constant, such that variations in K almost entirely result from differences in geological materials. Assuming constant fluid properties, values of K for different materials vary by many orders of magnitude (Table 1). Hydraulic conductivities of unconsolidated aquifers such as sand and gravel typically range from 10^{-5} to 10^{-2} m s^{-1}, though lower or higher values are possible. Values of confining units, e.g., composed of silty or clayey sediments, are orders of magnitude lower. Similarly, consolidated rocks exhibit a wide range of hydraulic conductivity depending on the characteristics of their fracture or conduit porosity.

Assessing the hydraulic conductivity of rocks is complicated by their *heterogeneity* and *anisotropy*. The grain size distribution of unconsolidated sediments and the frequency as well as the size of fractures or solution conduits of consolidated rocks commonly vary in space. This heterogeneity is displayed in the spatial distribution of hydraulic conductivity values. As a consequence, measurements of K at different locations may yield very different results even within the same geological setting. As a further consequence, hydraulic conductivities obtained by lab or field experiments depend on the scale of observation. This is most obvious for consolidated rocks with several types of porosity, such as sandstone or limestone. Lab measurements conducted at small samples of such rocks mainly provide information about the hydraulic conductivity associated with the primary porosity, whereas the effects of fracture or conduit porosity can only be observed at large spatial scales. In addition, sediment structures, fractures, and conduits may have preferential directions. This leads to a directional dependence, i.e., anisotropy, of hydraulic conductivity. As an example, the hydraulic conductivity of unconsolidated sediments composed of multiple layers generally is higher in the horizontal than in the vertical direction. Consolidated rocks tend to exhibit even higher anisotropy of hydraulic conductivity, because the mechanisms creating fractures and conduits often favor distinct directions.

Characterizing an aquifer's ability to transmit water is further complicated when groundwater flow is fast. Darcy's law holds only if inertial forces and turbulent friction can be neglected, which is not met if the flow velocity is too high. This is generally expected in karst aquifers, where velocities are often in the order of kilometers per day, and also occurs in other highly conductive aquifers close to productive pumping wells. The additional forces increase the flow resistance and cause deviation from the linear relationship between hydraulic gradient i and specific discharge q stated by Darcy's law. One approach to account for this effect is the non-linear flow equation proposed by Forchheimer (1901).

$$i = a\,q + b\,q^2 \tag{2}$$

where $a = 1/K$ is the reciprocal of hydraulic conductivity and the Forchheimer coefficient b an aquifer property controlling the non-linear deviation from Darcy's law. Estimates of b for various geological materials are provided by Zeng and Grigg (2006), Chin et al. (2009), and Sidiropoulou et al. (2009). Compared with hydraulic conductivity values of rocks, the non-linear flow properties of geological materials have been considerably less investigated though.

The ability of an aquifer to transmit water, characterized by its hydraulic conductivity K (and under the above specified conditions the Forchheimer coefficient b), is one important control on the interaction of groundwater systems with other components of the water cycle. A highly conductive aquifer is able to transmit the entire recharge under a hydraulic gradient much lower than the slope of the land surface (Fig. 5, left). In such recharge-controlled systems, the water table of the elevated areas is at great depth and thus disconnected from the hydrological processes at the land surface. In contrast, the transmission of groundwater through lowly conductive rocks involves steep hydraulic gradients such that the water tables of the elevated areas are shallow and thus interacting with the evapotranspiration and runoff processes at the land surface (Fig. 5, right). In such topographically-controlled systems, the potential recharge exceeds the rate at which groundwater can be laterally transmitted by the aquifer, i.e., recharge is rejected (Theis, 1940; Cuthbert et al., 2019).

Storage properties

In a hypothetical groundwater system where recharge and discharge are in balance, the stored water volume remains constant in time. However, natural or artificial fluctuations in recharge and discharge commonly cause temporal changes in the stored water volume. For example, consider the situation where pumping is started in an unconfined aquifer. As pumping starts, water is withdrawn from the wellbore, causing the water level in the pumping well to drop. Continued pumping then requires that groundwater flows from the aquifer towards the well. As a result, groundwater is drained from the aquifer storage and the water table in the vicinity of the pumping well starts to decline (Fig. 6, left). Hence, water withdrawal from the aquifer storage involves changes in water levels. To characterize this relationship quantitatively, we define the *storativity* (or storage coefficient) of an aquifer as the water volume released from storage per unit surface area per unit decline in water level.

In the above example of an unconfined aquifer, the water is released by gravity drainage from the aquifer storage. The water volume per rock volume released by gravity drainage is termed *specific yield*; it is equivalent to the storativity of the unconfined aquifer. Since some percentage of the water is retained as thin films surrounding grains or as capillary water in narrow pores, the specific yield is lower than the total porosity. The approximate ranges for effective porosity given in Table 1 also apply to specific yield (Singhal and Gupta, 2010). Thus, the specific yield of unconsolidated sand or gravel roughly ranges between 0.1 and 0.3, while values of fined-grained sediments are lower. Highly fractured, consolidated rocks may reach values similar to those of

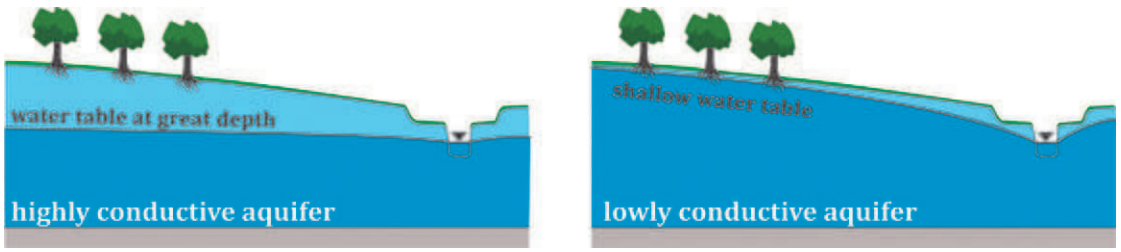

Fig. 5 The water table of a highly conductive aquifer (left) tends be at great depth below the land surface, whereas the transmission of groundwater through a lowly conductive rock requires a steep hydraulic gradient, thus leading to shallower water tables (right).

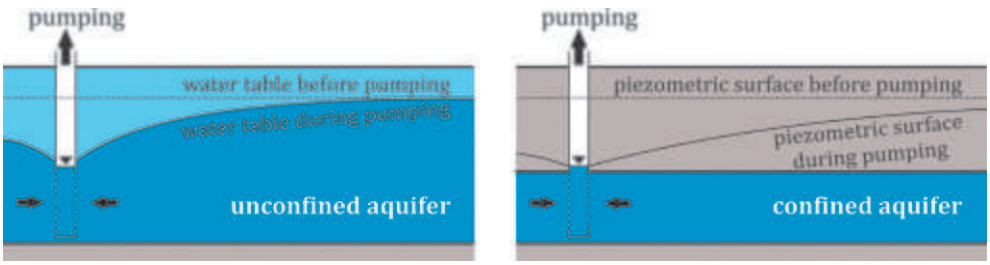

Fig. 6 Comparison of unconfined and confined aquifers when they are pumped. In the case of the unconfined aquifer (left) water is released by gravity drainage from the aquifer volume enclosed by the water tables before and during pumping. In contrast, the pore spaces of the confined aquifer (right) remain saturated during pumping; water is only released from the aquifer storage because the lowering of the piezometric surface corresponds to a reduction of pressure and thus leads to expansion of water and reduction of pore space.

coarse-grained unconsolidated rocks, but often the specific yield of consolidated aquifers is lower than that of unconsolidated aquifers.

Consider now a confined aquifer that is pumped (Fig. 6, right). As long as the aquifer is confined, the pore space remains saturated despite the lowering of the water level in the pumped well. Nevertheless, groundwater is released from the aquifer storage, because the decline of pressure, which corresponds to the lowering of the piezometric surface, results in an expansion of water and compression of the rock and thus the reduction of pore space due to the load of the overburden. The water volume that can be released by this mechanism and thus the storativity of confined aquifers can be estimated from the compressibilities of rock and water. The storativity of confined aquifers typically ranges in the order of 10^{-3} to 10^{-5}. This is much lower than typical values of specific yield and indicates that in unconfined aquifers the described effect of decompression generally is negligible compared with gravity drainage.

The greatly different values of storativity constitute an important difference between confined and unconfined aquifers. This can be understood by considering a pumping situation as described above (Fig. 6). Since the same decline in water level releases much less water per unit volume from a confined than from an unconfined aquifer, the confined aquifer requires a much larger aquifer volume to provide the same amount of water. As a consequence, after a given time the area affected by pumping will be larger for the confined than for the unconfined aquifer (assuming they have the same hydraulic conductivity). Similarly, disturbances by flood pulses or effects of droughts propagate faster (or over a greater distance in a given time) in a confined aquifer than in an unconfined aquifer of otherwise similar properties.

Chemical and thermal properties

Groundwater systems can also be characterized and classified based on their chemical and thermal properties. A comprehensive treatment of this topic is beyond the scope of this chapter. Yet, basic concepts and their interrelation with groundwater flow are briefly introduced below.

The water infiltrating into the soil after rainfall or snowmelt initially has a low solute concentration. As the water moves through the soil, it dissolves gases such as carbon dioxide and reacts with the soil organic matter and minerals. Thus, the water is already enriched in solutes when it reaches the water table. Depending on the geochemical conditions in the aquifer, the chemical composition of the groundwater further evolves through time.

The solute content of groundwaters reflects the processes involved in the hydrogeochemical evolution along the flow path. Thus, groundwaters can be classified into various types of hydrochemical facies based on the major ions they contain (Back, 1966). The cation facies can be characterized as calcium type, magnesium type, sodium and potassium type, or no dominant type; the anion facies can be classified as bicarbonate type, sulfate type, chloride type, or no dominant type (Fig. 7). The chemical composition of the geological material evidently is a major control on the hydrochemical facies. For example, limestone is composed of calcium carbonate and thus groundwater flowing through limestone that creates conduit porosity by dissolving the rock is expected to be of calcium-bicarbonate type. If water originating from limestone penetrates gypsum, which is composed of calcium sulfate, the increasing load of calcium leads to chemical precipitation of calcium carbonate and the hydrochemical facies changes towards calcium-sulfate type. Similar processes occur in other rocks such that the chemical composition evolves with increasing travel time and distance along the groundwater flow path. Generally, the content of dissolved solids increases with increasing distance and depth of the groundwater circulation, and the anionic facies is expected to change from bicarbonate to sulfate and chloride type, i.e., towards anions originating from highly soluble minerals (Tóth, 1999).

The chemical evolution of groundwaters is also influenced by thermal conditions within the aquifers, as changes in water temperature may disturb chemical equilibria and thus enable further dissolution or chemical precipitation of minerals. The surficial zone of the subsurface is influenced by seasonal temperature fluctuations, the amplitude of which decreases with depth (Anderson, 2005). At a depth of around 10–20 m below ground level, seasonal fluctuations are usually no longer observed (Todd and Mays, 2005), and thus the shallow groundwater exhibits temperatures close to the mean annual air temperature. In the geothermal zone that follows below, the temperature of the rock increases with depth according to the geothermal gradient (on average three Kelvin per 100 m). Since slowly circulating groundwater is in thermal equilibrium with the rock, the groundwater temperature increases with depth too. As a consequence, deep groundwater systems may exhibit high groundwater temperatures and thus constitute thermal water resources.

Changes in solution content and temperature involved in the deep circulation of groundwaters affect the density of the groundwater and thus potentially are able to induce density-driven flow processes. Moreover, the viscosity of water decreases with increasing temperature, which affects the hydraulic conductivity (see section "Flow properties"). Thus, potential changes in the density and viscosity of the water resulting from the chemical and thermal evolution along the flow path need to be considered in the assessment of deep groundwater systems. Similar effects can be found in coastal aquifers where freshwater and saltwater interact or in groundwater systems where thermal impacts resulting from human activities affect the density or viscosity of the water.

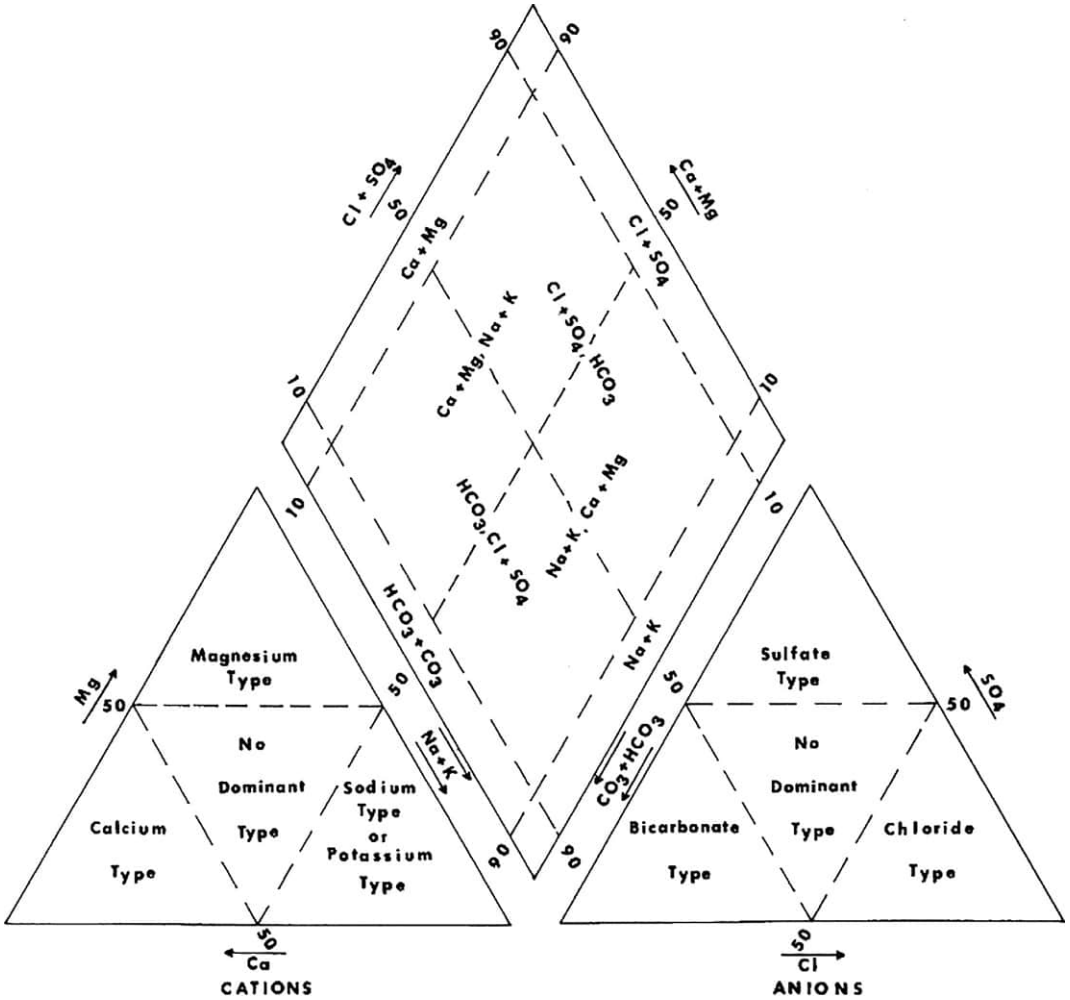

Fig. 7 Piper diagram showing hydrochemical facies. Numbers indicate percentages of major ion species based on ion concentrations in milliequivalents per liter (Ca = calcium, Mg = magnesium, Na = sodium, K = potassium, CO_3 + HCO_3 = bicarbonate, SO_4 = sulfate, Cl = chloride). From Back W (1966). *Hydrochemical Facies and Ground-Water Flow Patterns in Northern Part of Atlantic Coastal Plain. Geological Survey Professional Paper 498-A.* Courtesy the U.S. Geological Survey.

Conclusion

The hydrogeological typology of groundwater systems rests on two pillars, the distinction between unconfined and confined aquifers as well as the differentiation of porosity types. The first is defined by the position of the water table relative to the hydrogeological units; the second is determined by the characteristics of the geological material. The framework provided by this typology supports the understanding of aquifer properties governing flow and storage processes in groundwater systems. Groundwater systems can be further classified based on other aspects such as the chemical or thermal properties of the water. Possible interrelations between groundwater flow, chemistry and temperature need to be considered particularly in the hydrogeological assessment of deep groundwater systems, coastal aquifers, or settings affected by human impacts.

Knowledge gaps

- How to deal with scale effects resulting from the occurrence of several types of porosity in hydrogeological assessments of consolidated sedimentary rocks, for example, when measuring hydraulic conductivity values and when using these values in models predicting groundwater flow or the transport of heat or solutes.
- Properties of rocks controlling groundwater flow if inertial forces or turbulent friction cannot be neglected, particularly how properties of fracture or conduit porosity control groundwater flow dynamics and aquifer properties observed at large scale.
- Feedbacks between groundwater flow, chemical and thermal evolution of groundwater, and biological processes in different types of hydrogeological settings, including resulting changes in aquifer properties.

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Further reading

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Relevant websites

https://gw-project.org/—The Groundwater Project—Online Platform for Groundwater Knowledge.
https://www.un-igrac.org/what-groundwater—International Groundwater Resources Assessment Centre—Basics, Glossary, and Stories about groundwater.
https://www.usgs.gov/special-topic/water-science-school/science/groundwater—U.S. Geological Survey—Groundwater Science.
https://iah.org/education/—International Association of Hydrogeologists—Education Resources.

The Hydrology of Groundwater Systems - From Recharge to Discharge

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Introduction

Groundwater is the world's largest source of non-frozen fresh water (Gleeson et al., 2016) providing approximately half of the earth's population with drinking water (Velis et al., 2017). Groundwater systems are important parts of the hydrological cycle comprising the subsurface water itself, the geologic media containing the water, flow boundaries, groundwater recharge, point/areas of groundwater discharge or groundwater removal like springs or wells (Alley et al., 2002).

Quantitative understanding of groundwater systems' functioning is relevant for a wide range of research fields (Fig. 1). For instance, sustainable management of groundwater use is only possible if groundwater recharge, storage, discharge, and the impact of groundwater removal through pumping are well understood. Likewise, proper understanding of hydrological systems, especially during dry periods, can only be obtained when the interactions of surface water and groundwater are considered. Many ecosystems, e.g. wetlands, are dependent on groundwater. Hence, assessment of their present and future health require understanding of groundwater availability and quality. On the other hand, groundwater systems in agricultural and industrial regions are often exposed to pollutants that reach the phreatic zone posing a threat to drinking water supply and groundwater dependent ecosystems. Consequently, the characterization and simulation of transport of and storage of pollutants in groundwater systems has become a growing field of research. Similarly, accounting for the interaction of groundwater with subsurface constructions such as tunnels, building foundations, or mining has received increased attention in civil and structural engineering.

Fig. 1 Areas of research that require quantitative understanding of groundwater systems.

Definitions and structure of groundwater systems

In order to understand and quantify groundwater systems processes, some important technical terms need to be introduced. Groundwater storages are often referred to by the term aquifer. An aquifer is rock or sediment in a formation, a group of formations, or a part of a formation that is water saturated and sufficiently permeable to transmit economic quantities of water to wells or springs. Aquifers can be local (within the limits of a topographic catchment) or regional (crossing the boundaries of topographic catchments (Fig. 2, modified from Jones et al., 2019). An aquitard, or confining unit, is a low-permeability unit that can store

 https://doi.org/10.1016/B978-0-12-819166-8.00097-9

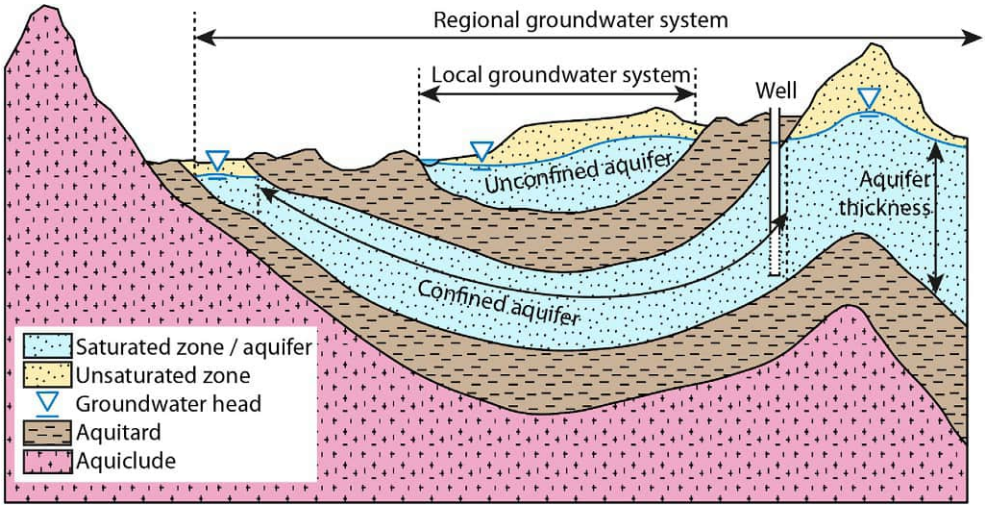

Fig. 2 Cross-section through a groundwater system. Modified from Jones MD, Abu-Jaber N, AlShdaifat A, Baird D, Cook BI, Cuthbert MO, Dean JR, Djamali M, Eastwood W, Fleitmann D, Haywood A, Kwiecien O, Larsen J, Maher LA, Metcalfe SE, Parker A, Petrie CA, Primmer N, Richter T, Roberts N, Roe J, Tindall JC, Ünal-İmer E, and Weeks L (2019) 20,000 years of societal vulnerability and adaptation to climate change in Southwest Asia. *Wiley Interdisciplinary Reviews Water* 6: e1330, doi:10.1002/wat2.1330.

groundwater and transmit it slowly from one aquifer to another. If completely impermeable, a geologic layer is called an aquiclude. The unsaturated zone, or vadose zone, is located between the land surface and the water table. Pores may contain some water but are not fully saturated. In the saturated zone, all pore space is filled with water at a pressure greater than the atmospheric. The water table of an aquifer is the level below which the material is saturated with water or, in other words, the boundary between fully-saturated and unsaturated pores. The vertical distance between the water table at the top and the aquitard or aquiclude at the bottom is often referred to by thickness of the aquifer. A well is defined as an excavation structure used to access groundwater stored in an aquifer. The water level measured in the well shows the hydraulic head of the groundwater (in the following referred to by "head" or "groundwater head") at this particular location.

Aquifers can be classified by their lithological setting. In a so-called unconfined aquifer when groundwater is in direct contact with the atmosphere through the pore spaces in the overlying rock or sediments. Its water table marks the upper surface of the groundwater. Within a confined aquifer, groundwater is overlain by an aquitard or aquiclude that limits upward movement of the groundwater. Its water table is at the same level as the lower boundary of the aquitard or aquiclude but its potentiometric surface, to which groundwater would rise in a pipe, is higher (Fig. 2). If groundwater would rise above the surface due to a confined aquifer setting, it would be referred to as "artesian." Locally limited aquicludes or aquitards within the unsaturated zone allow vertically percolating waters to also form perched aquifers that are at levels higher than the regional water table.

The water balance of an aquifer summarizes inflow, outflow and storage changes. It is defined by its inflows (groundwater recharge, lateral groundwater inflow), its outflows (groundwater discharge to springs or streams, pumping through wells, lateral groundwater outflows) and its change of storage. An aquifer is in a stationary state, when the inflow equals the outflow and the change of storage is zero. The components of the aquifer's water balance, from recharge to discharge and storage, will be described in the following sections.

Groundwater recharge

Groundwater recharge is defined in a general sense as the volume or process of downward flow of water reaching the water table, forming an addition to the groundwater reservoir (de Vries and Simmers, 2002). Water that contributes to groundwaters recharge originates from precipitation reaching the surface, rainfall or snow melt, that has infiltrated into the subsurface and that has percolated vertically through the unsaturated zone toward the water table. Three types of recharge can be distinguished (Fig. 3A): (1) Direct recharge that reaches the water table as a result of soil moisture excess and direct vertical percolation through the unsaturated zone, (2) indirect recharge that infiltrates and percolates through river beds or lakes, and (3) focused or localized recharge that results from local horizontal near(surface) concertation of infiltrating water, for instance through joints, depressions, sink holes or rivulets (not river beds or lakes). Global estimates of direct recharge range from very low annual volumes, e.g. in the deserts, to larger than 1000 mm per year in the tropics (Fig. 3A). In addition to direct recharge, focused or localized recharge have been shown to produce large volumes of groundwater recharge at very short time scales (Hartmann et al., 2015, 2017). For all three types of recharge, evapotranspiration will reduce the volumes that finally reach the groundwater. Evaporation and water uptake through roots substantially reduce the water volumes percolating downwards as direct recharge. Recharge can decrease even to zero

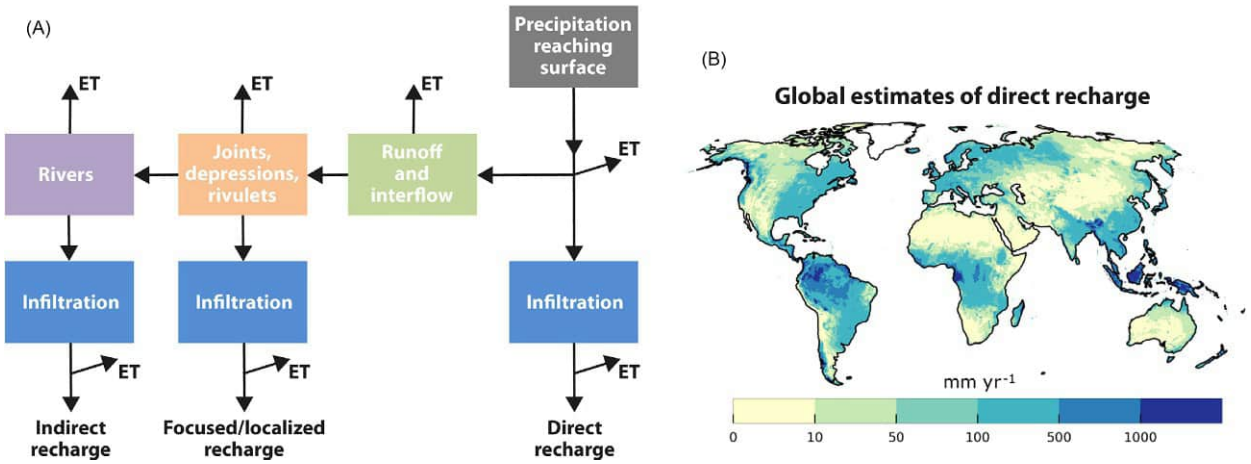

Fig. 3 (A) Mechanisms of groundwater recharge (Lerner, 1997; ET: evaportranspiration) and (B) global estimates of direct recharge under pre-industrial conditions (ensomble mean of eight global hydrological models Reinecke et al., 2021).

depending on the climate, season and vegetation (Jasechko, 2018). However, recharge can also make up >90% of infiltrating rainfall and snow at regions were soils are thin and temperatures are low, e.g. mountain areas (Chen et al., 2018).

Due to its occurrence in the subsurface, measurement of recharge is not straight forward. At well-defined catchments, where surface runoff and evapotranspiration can be estimated independently, long-term, average groundwater recharge can be obtained through the catchment's water balance. Water table observations at locations with negligible influence of lateral groundwater contributions, e.g. close to a groundwater divide, allow the assessment of groundwater recharge through water table fluctuations over time (Crosbie et al., 2005). Direct measurement of vertical percolation, as a proxy of groundwater recharge, is possible with so-called lysimeters that measure the water balance components of isolated and undisturbed soil monoliths. Baseflow analyses of discharge observations, modeling and, especially in arid regions, environmental tracer techniques also allow indirect assessment of groundwater recharge (Scanlon et al., 2002).

Groundwater storage

Groundwater is stored in the voids between the solid matrix of the subsurface. The space available for groundwater is described by the porosity of the aquifer material. It develops either when a rock or sediments are formed (primary porosity) or when fractures or weathering create additional voids after original formation of the rock or sediments (secondary porosity). Sometimes the term 'tertiary porosity' is used to describe voids formed by chemical weathering alone, e.g. karstification (Ford and Williams, 2007). Aquifers that store groundwater mostly in unconsolidated material are classified as unconsolidated aquifers; aquifers that mostly use their secondary porosity to store groundwater are classified as consolidated rock aquifers (sedimentary rock, metamorphic rock, or igneous rock, see Fig. 4, modified from Winter, 2001). Two metrics to quantify porosity exist, total porosity and effective porosity both of them quantifying the ratio of pore space against total volume of voids and solids. While the total porosity describes the entire pore space including voids that are sealed from their surroundings, the effective porosity describes only the part of the pore space that is penetrable by water. Consequently, the effective porosity is the more important measure when it comes to groundwater flow and storage. It ranges from values <1% (e.g., crystalline rock) up to 25% or larger (e.g., gravel).

However, when an unconfined aquifer is pumped, not all water that is stored in the effective pore space will be drained. Due to capillary forces and adhesion, part of it will be retained in the pore space. The other part, i.e. the volume of groundwater that can be drained by gravity, is called specific yield. Similar to the porosity, it is defined as the volume of drainable water per total volume of voids and solids. It ranges from 0% (clay) to >20% (gravel). When a confined aquifer is pumped, no drainage of pore space takes place but still water is released. This water is originating from decompression of the aquifer that results in expansion of the water itself and compaction of the effective pore space. How much water can be released per meter of aquifer thickness is quantified through the specific storage. It usually ranges from 0.1–1% m^{-1}. Both specific yield and specific storage (times the aquifer thickness) combine to the storativity of an aquifer but due to the huge differences in amount by orders of magnitude, the specific storage can be neglected when considering unconfined aquifers, while the specific yield of a confined aquifer is zero by definition.

Groundwater flow and discharge

Groundwater flow within an aquifer depends on the "slope of the aquifer", i.e. the difference of groundwater heads over a distance, the inverse of resistance to flow within the aquifer material, and the cross-sectional area (Fig. 5). The first who experimentally

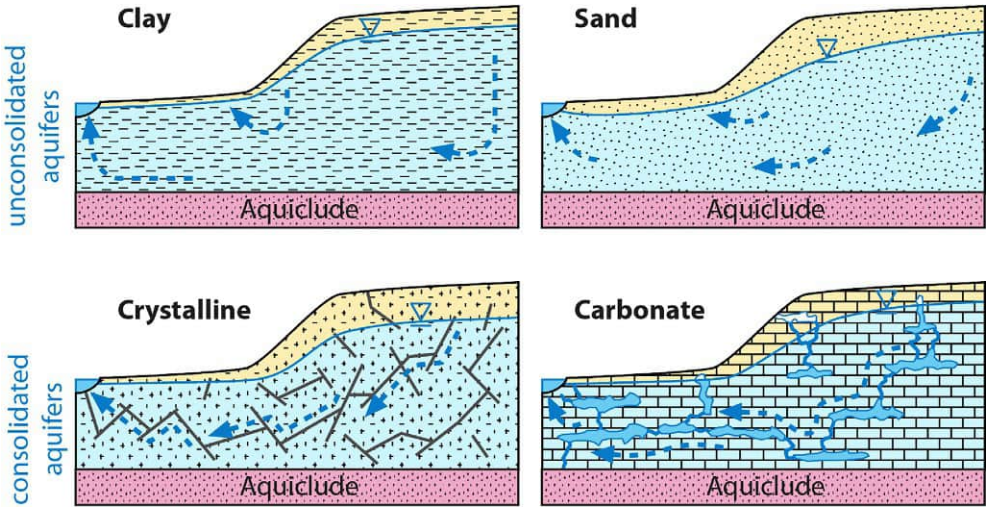

Fig. 4 Different rock types. Modified from Winter TC (2001) The concept of hydrologic landscapes. *Journal of the American Water Resources Association* 37: 335–349, doi:10.1111/j.1752-1688.2001.tb00973.x.

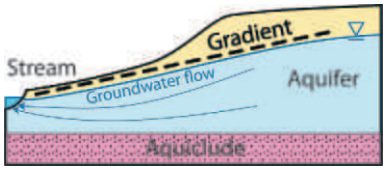

Fig. 5 Groundwater discharge to the stream following the gradient of the water table.

described the relationship between groundwater flow and the three variables mentioned was Henry Darcy in 1856. Using a saturated pipe filled with unconsolidated material, a pre-defined cross-sectional area, and by setting up a constant head difference between inlet and outlet of the pipe, he could show that groundwater flow is linearly correlated with the head difference, the cross-sectional area, the reciprocal of the flow distance and a linearity constant that was defined as the hydraulic conductivity. Darcy's equation is defined as

$$Q = A \cdot k_h \left(\frac{dh}{dx}\right) \tag{1}$$

$$q = k_h \left(\frac{dh}{dx}\right) \tag{2}$$

Where A [m^2] is the cross-sectional area, k_h [m/s] the hydraulic conductivity of the aquifer, and dh/dt [–] represents the change of groundwater head dh [m] over a distance dx [m]. Since this first experiment, Darcy's equation has been used to quantify volumetric groundwater flow or specific groundwater flow (normalized by the cross-sectional area) in a wide range of hydrogeological applications. But it was also shown that there are limits of its application for very low head gradients where electrostatic forces hold the water as well as with very high head gradients where groundwater flow becomes turbulent (e.g. in karstic caves or enlarged fractures).

Values of the hydraulic conductivity depend on the aquifer type (rock/unconsolidated), and span over more than 10 orders of magnitude, from 10^{-13} m/s for unfractured crystalline rock until 10^{-2} m/s for gravel or karst aquifers (Freeze and Cherry, 1979). The hydraulic conductivity results from the properties of the fluid, e.g. water, and the surrounding material, e.g. unconsolidated gravel. Cancelling out the properties of the fluid (specific weight and dynamic viscosity), the permeability of the aquifer material can be obtained (Hubbert, 1956), which can be combined with any other fluid that can move through the material (e.g. oil or contaminants in the fluid phase).

Despite the simplified example of a groundwater system in Fig. 2, real aquifer systems usually show a lot of heterogeneity at different scales. Due to the history of deposition, sand and gravel aquifers may expose strong changes of effective porosities and hydraulic conductivities within the scale of a few centimeters. At the range of some meters of depth, unconsolidated sediments may be followed by fractured crystalline rock or weathered carbonate rock (karst). If the saturated zone of an aquifer comprises such heterogeneities, it is necessary to weigh the hydraulic conductivities of the different layers by their thickness to obtain the effective hydraulic conductivity of the aquifer. If hydraulic conductivities differ for different directions, the aquifer is anisotropic; if they are the same, it is isotropic. For groundwater development by wells, the horizontal hydraulic conductivity and the aquifer thickness

(Fig. 2) are critical properties as they define how much water can be pumped without emptying the well. They are summarized in the transmissivity of the aquifer, which is defined by the effective hydraulic conductivity over all horizontal layers times the aquifer thickness.

The velocity of flow through an aquifer v [m/s] can be derived by dividing the specific groundwater flow (Eq. 1) by the effective porosity (therefore $v \geq q$). Because of wide ranges of v, hydraulic conductivities, and aquifer sizes (up to several Mio. km^2; Richts et al., 2011), groundwater travel times can range from several hours, e.g. in a karstic setting, to millennia or longer (Sprenger et al., 2019). As a consequence, changes of groundwater flow and discharge following changes of boundary conditions, e.g. reduced recharge volumes due to changing climate, may therefore occur with a substantial delay (Cuthbert et al., 2019).

Conceptual models of groundwater systems

A hydrogeological conceptual model synthesizes our understanding of a groundwater system. It includes information about geology and lithology, level and gradient of the potentiometric surface, the type of aquifer (e.g. confined or unconfined), groundwater recharge and discharge areas, and the direction(s) and scale of groundwater flow. It therefore summarizes all available information about the aquifer characteristics introduced in the preceding sections. Following Enemark et al. (2019), the components of a conceptual model consist of (a) a conceptual process structure, (b) a conceptual physical structure, and (c) a spatial variability structure (Fig. 6). The process structure defines the occurring groundwater recharge (Section "Groundwater recharge") and groundwater discharge processes (Section "Groundwater flow and discharge") and the locations where they are taking place. The conceptual physical structure defines the location and geometry of the aquifers, aquitards and aquicludes (Section "Definitions and structure of groundwater systems"), the aquifer types (Section "Groundwater recharge"), and the general boundaries of the groundwater system. The spatial variability structure defines how aquifer properties, such as hydraulic conductivities, specific storage, specific yield or effective porosity, vary in space and directions therefore describing the degree of heterogeneity and anisotropy of the aquifer system (Sections "Groundwater storage" and "Groundwater flow and discharge").

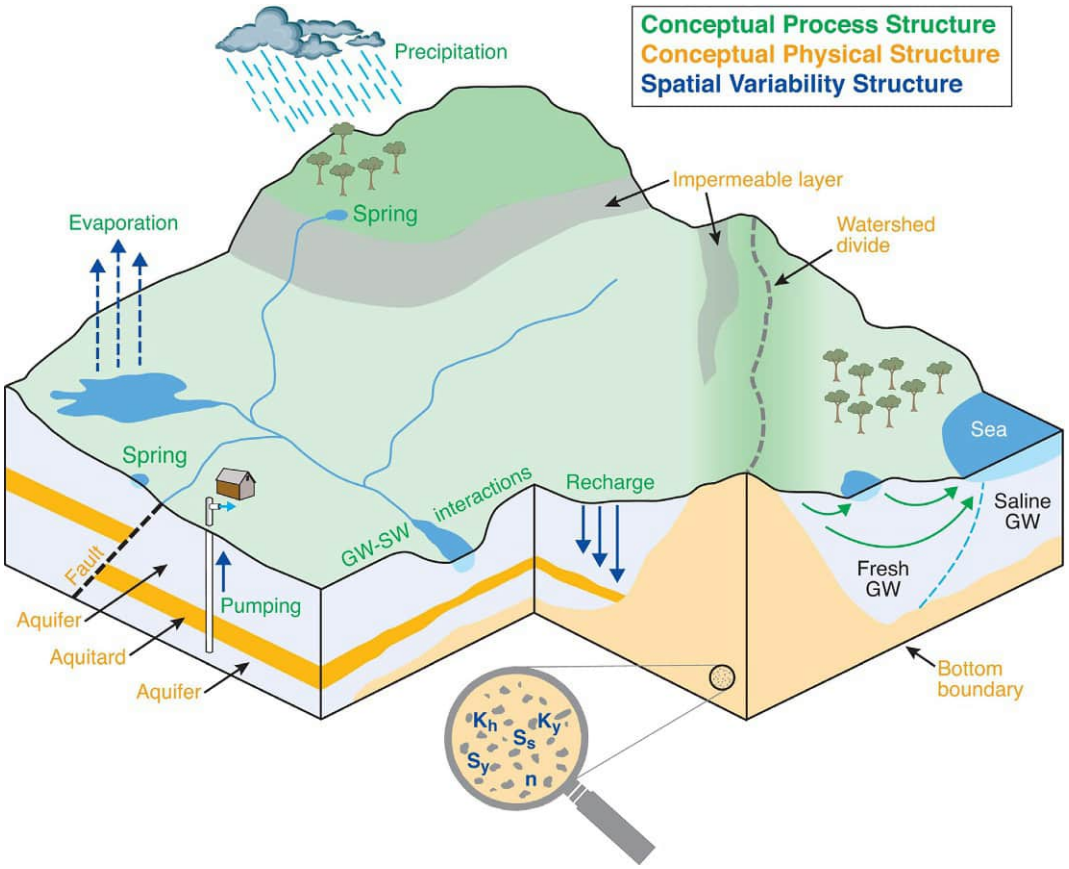

Fig. 6 Example sketch of a conceptual model considering separately the conceptual process structure, the conceptual physical structure, and the spatial variability structure of a groundwater system (Enemark et al., 2019; K_h/K_v: horizontal and vertical hydraulic conductivities, S_s: specific storage, S_y: specific yield, n: effective porosity). From Fig. 2 of Enemark T, Peeters LJM, Mallants D, Batelaan O (2019) Hydrogeological conceptual model building and testing: A review. *Journal of Hydrology* 569: 310–329, doi:10.1016/j.jhydrol.2018.12.007

The availability of data to develop a conceptual model of a chosen groundwater system is case dependent. Usually, existing data, reports or maps with information about topography and lithology exist at varying spatial resolutions to establish a priori knowledge about the conceptual physical structure. Maps and time series of hydrometeorological information, such as precipitation, evapotranspiration, streams and their discharge volumes, springs and their discharge volumes, etc., are often available to get a first understanding of the system. However, information about the spatial heterogeneity of a groundwater system is seldom available at the desired scale and may require additional field work and/or more sophisticated approaches for their definition (de Marsily et al., 2005). Bringing together all this information will allow establishing a visual sketch of the chosen groundwater system that can be regarded as an information-based hypothesis of the system functioning. It can be used for discussion with other hydrologists and be tested using additional observations or modeling (Enemark et al., 2020; Mudarra et al., 2019). With more and more global hydrogeological datasets available (see Table 1 in Gleeson et al., 2020), coarse conceptual models can also be established for regional groundwater systems or large-scale groundwater assessment. They will provide directions for a better representation of groundwater processes in large-scale modeling, e.g. the decrease of groundwater storages due to pumping and climate variability (Scanlon et al., 2018), the impact of focused groundwater recharge on recharge volumes and contamination risk (Hartmann et al., 2017, 2021), or inter-catchment groundwater flow (Fan, 2019; Liu et al., 2020).

Conclusion/synthesis

This chapter provides a brief overview of the hydrology of groundwater systems. The most relevant technical terms are defined and the most relevant processes, from groundwater recharge over groundwater storage to groundwater discharge, are explained. The use of conceptual hydrogeological models is introduced as a valuable tool to summarize and present available information in a combined way to prepare a chosen groundwater system for discussion among colleagues and for the application of groundwater models. The chapter focusses on natural groundwater systems. For an introduction into groundwater systems highly affected by pumping, please refer to Alley (2009) or Alley et al. (2002).

Knowledge gaps (among many others)

- Quantifying groundwater recharge
- Interactions of groundwater systems and surface catchments/rivers
- Behavior of complex pollutants like pharmaceuticals or pesticides in aquifers
- Measurement of spatial variability of hydraulic properties especially in heterogeneous settings like karst
- Understanding the long-term impacts of climate change and land use change on aquifers especially those with long transit times
- Regional or large-scale quantification of groundwater resources

Acknowledgments

A. H. was supported by the Emmy Noether-Programme of the German Research Foundation (DFG, Grant Nos. HA 8113/1-1). Thanks to Jürgen Strub at the University of Freiburg for designing some of the figures.

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Relevant websites

http://www.groundwater.org/—The Groundwater Foundation.

https://iah.org/—The International Association of Hydrogeologists (IAH) - the Worldwide Groundwater Organization.

https://karst.iah.org/—The IAH Commission on Karst Hydrogeology.

https://www.un-igrac.org/—The International Groundwater Resources Assessment Centre.

https://blogs.egu.eu/network/water-underground/ and https://blogs.agu.org/waterunderground/—Blog page run by global collective of hydrogeologists.

The Vadose Zone—A Semi-Aquatic Ecosystem

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Capillary fringe The zone of water above the groundwater table or phreatic zone where water is held by capillary forces and which is saturated, not aerated and under subatmospheric pressure.
Field capacity Soil water content that is supposed to remain in a soil 2 or 3 days after having been wetted with water and after free drainage is negligible.
Hydraulic conductivity The proportionality factor in Darcy's Law, as applied to viscous flow of water in soil, that represents the ability of soil to conduct water and is equivalent to the flux of water per unit gradient of hydraulic potential. Its value combines properties of the porous media and the fluid.
Matric potential Matric potential is attributed to intermolecular cohesive and adhesive forces acting within and between liquid, gaseous and solid phases. These forces lead to surface tensions at the interfaces of adjacent phases and fluid can be hold in the pores against gravity.
Porosity The volume of pores V_p in a known volume—soil sample or drill core sample in solid rock—divided by the bulk control volume V.
Preferential flow Free water and its constituents moving by preferred pathways through a porous medium.
Vadose zone The aerated region of soil or un-/weathered rock above the permanent water table.
Volumetric water content The volume of water V_w in a control volume related to the bulk control volume V.

Introduction, with aim of the chapter

Aim

The vadose zone is the variably saturated zone between the ground surface and the permanent water table of the groundwater. It is an important part of the water cycle and stores at least 8.5 times more water than is held by rivers (Oki and Kanae, 2006). Processes in the vadose zone contribute to food and water security by providing water to plants and contributing to recharge groundwater, which is the main source for drinking water worldwide. The aim of this chapter is to provide an overview of the vadose zone, its function as an ecosystem and how hydraulic properties influence flow processes. We give definitions about the vadose zone and explain the key soil hydraulic properties that influence how water flows through this part of the underground.

Definition of the vadose zone

The vadose zone is the aerated region of soil (SSSA, 2008) or un-/weathered rock above the permanent water table (Fig. 1). An almost synonymous term is the "unsaturated zone." The porous medium of this region is typically soil, but may also be sediments, porous rock, or any other material that occurs near the earth's surface (Nimmo, 2009). Soil might be defined as the

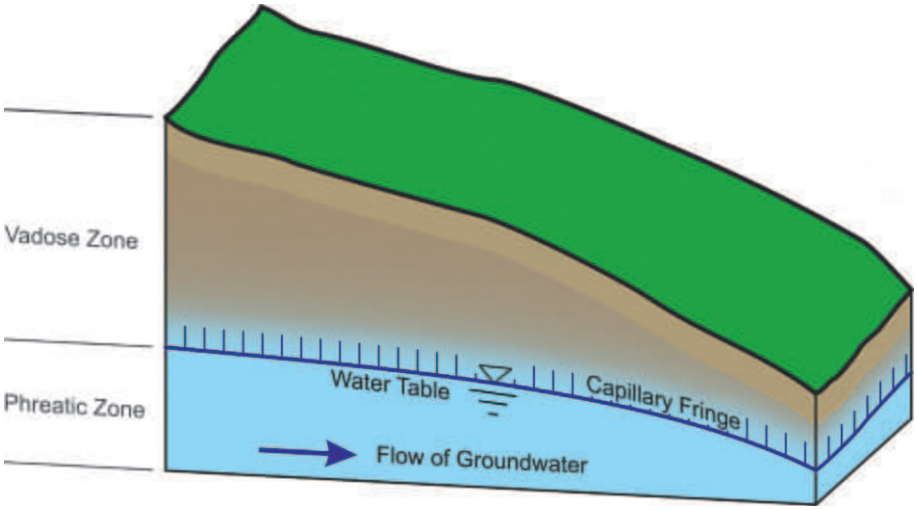

Fig. 1 Scheme of the vadose zone which is the aerated region of soil or un-/weathered rock above the permanent water table.

layer(s) of generally loose mineral and/or organic material that are affected by physical, chemical, and/or biological processes at or near the planetary surface, and usually hold liquids, gases (SSSA, 2008). The vadose zone may also include a capillary fringe which is the zone of water above the groundwater table or phreatic zone where water is held by capillary forces and which is saturated, not aerated and under subatmospheric pressure.

In contrast to surface waters and groundwater, flow and transport processes in the vadose zone are mainly vertical; lateral flow components become important in strongly layered systems with different hydraulic properties or in fractured systems according to the fracture orientation. Processes within the zone are percolation—a gravity driven, relatively fast downward movement—, capillary rise, root water uptake, and wetting and drying as increases and decreases in water storage within the profile of the vadose zone.

It is not only water and air that move through the pores in the vadose zone; the liquid phase may contain nutrients (e.g., carbon, nitrogen, phosphorus), contaminants (e.g., pesticides, fertilizer components, antibiotics), or any other substances dissolved in water or transported in colloidal or fine particulate form. The vadose zone is the living environment for plants and other soil biota comprising microorganisms (bacteria, fungi and archaea), viruses, as well as vertebrates and meso- and macroinvertebrates. Microbial biomass is generally highest in surface soils and declines with depth within the vadose zone (Holden and Fierer, 2005). The total biomass is still similar to groundwater whereas the interface of those two compartments is considered a hotspot for microbial activity (Griebler and Lueders, 2009; Holden and Fierer, 2005). More information about microbial processes in the vadose zone can be found in Holden and Fierer (2005).

Importance of the vadose zone in the hydrological cycle and its role as an ecosystem

The vadose zone is an important part of the water cycle. Generally, water enters the zone from above as infiltration from precipitation, snow and ice melt, as well as irrigation or any other water sources applied on the land surface. Depending on the soil hydraulic properties and topographic features, the soil surface regulates the infiltration process and its accumulation (i.e., ponding) on the surface that can contribute to overland flow. Water can enter the vadose zone also from the bottom due to capillary rise from the permanent water table or through infiltration from surface water bodies. Water leaves the system to the atmosphere as evaporation from bare soil and transpiration by plants. It can also leave at the bottom by recharging groundwater or discharges water to surface water bodies. Water may be held against gravity by capillary forces or flow upwards or downwards according to the hydraulic gradient.

The vadose zone provides several ecosystem services (Robinson et al., 2013). Those include climate regulation through buffering extremes of heat and cold, as well as contributing to greenhouse gas sinks and sources. Buffering floods and consequences of droughts and the storage of water are hydrological regulations. The vadose zone is often the foundation for buildings and infrastructure and a source of sediments and dust. The vadose zone is a habitat for biota and provides a gene pool impacting biodiversity. Geochemical cycling, mineralization of organic matter, natural attenuation processes and the ability to retard or eliminate contaminants define the quality of water which is important for both food and water security. The geochemical and biological processes are fundamental for the provision of clean groundwater as drinking water or the water use for industrial and agricultural purpose.

Porous media

The porous medium of the vadose zone has two components: the solid matrix and the pores in between (Fig. 2). The volume of the solid matrix V_s is composed of particles with distinct size, shape, density, and chemical composition. Inorganic matter e.g., quartz, clay minerals, or limestone dominates, but organic matter and in particular humus are also present. When the vadose zone is comprised of porous rock, the particles are strongly packed to monoliths; those in soils might be structured in aggregates of different types or in a singular granular form with only a few intergrain contacts. Particle size distribution is one of the most important physical properties of the solid phase. The international scale for particle size (in mm) ranges from clay ($\leq$0.002) to silt (0.002–0.063), sand (0.063–2.0), gravel (2.0–63), cobbles (63–200), boulder (200–630), and large boulder (>630). The United States Department of Agriculture classifies the finer soil particles with a diameter $d < 2$ mm into main mass fractions of clay ($\leq$0.002), silt (0.002–0.05), and sand (0.05–2.0). The percentages of these three fractions—independent of the reference scale used—partition soil texture into 12 classes. Soil texture characterizes the soil, and it is also the primary input parameter for pedotransfer functions, which are functions that estimate soil hydraulic properties based on easily measured soil or sediment properties, such as texture.

The pores in between the solid phase can be filled with air or water (Fig. 2), and the ratios of those filled with air or water are variable over time and space. The variation of air and water phases is the basis for the microbiological activity and most of other geochemical, flow and transport processes in the vadose zone. Earthworm holes, fissures, voids, gaps, cracks etc. are some of the many sources or origins of the pore spaces and their many different shapes and configurations. The pores are also the result of soil formation and rock weathering processes, such as shrinking, root growth, frostbites, soil cultivation, and biochemical transformation.

The size and number of pores, described by the pore size distribution, are key determinants of the physical behavior of water in the soil. The pore size distribution can only be indirectly determined with the help of the capillary law. The porosity n of a soil sample or drill core sample in solid rock is determined as volume of pores V_p in in the sample or core divided by its bulk volume V. The porosity of vadose zone matrices is typically larger than in groundwater bodies, ranging from a few percent in slightly weathered rocks to 40% in agricultural soils and up to 80% or more in peat and bog soils. For determining the porosity, the volume V of a sample needs to be analyzed, which is not straightforward in porous media. Either an undisturbed soil or rock sample has to be taken with a cylindrical stainless steel cup or the drill core with given dimensions or a displacement method for soil clods or not bearing material can be used. The pore volume ($V_p = V - V_s$) is calculated after removal of all liquids in the sample from the mass of the solid material m_s and the known particle density ρ_s ($\rho_s = m_s/V_s$).

Whereas porosity of a material is treated as a constant in most physical process descriptions (exceptions are e.g., shrinking and swelling effects or consolidation processes), the amount of water in the vadose zone is highly variable in space and time. An important parameter describing water quantity is the volumetric water content θ, which is the volume of water in a sample V_w related to the bulk volume of the sample V. The reference method for determination of V_w is evaporation of the water with the mass m_w in the sample after drying at 105 °C until constancy of mass. Some soils contain a certain amount of water even after long dry periods without fresh supply. This residual water content is a minimum value for θ, its maximum is approximately equal to the porosity. Another quantity for the amount of water in a soil is the degree of saturation S, defined by the ratio of water volume V_w and the total pore volume V_p; $S = 1$ refers to full saturation.

When the pore space is only partially saturated, the remaining space in the pores is filled with air with the volume V_a, giving a volumetric air content $n_a = V_a/V$. The volumetric portions of water, air and solid material constitute the phase concept in soil physics, together with the assumption that all phases exist in each infinitesimal point of a known volume despite their spatial separation in particles and pores filled with either water or air. Aside of the one gaseous phase in the soil and the aqueous phase liquid, in some cases other non-aqueous phase liquids, such as oils or other organic liquid substances, occur with a density greater or smaller than water.

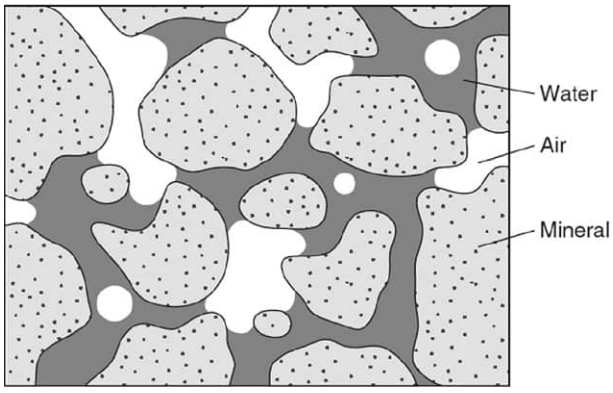

Fig. 2 Pore space of a hypothetical unsaturated medium, illustrating the arrangement of solid, liquid, and air phases. From Nimmo JR (2009) Vadose water. In: Likens GE (ed.) *Encyclopedia of Inland Waters*. Oxford: Elsevier.

Hydraulic properties and water flow

Water content and matric potential

The presence of water in the vadose zone does not necessarily mean that the roots of a plant are able to take it up or that water flows downwards. This illustrates the need for a further measure of quantity, the matric potential ψ_m, which describes how strongly water is bound in the porous medium and is part of the total energy level of soil or sediment water. ψ_m is always negative, as free water in contact with unsaturated soil or sediment will always flow into the soil or sediment, and not the opposite. ψ_m has a dimension of work but can be related either to the volume or the weight of the soil or sediment water and thus is given as a dimension of pressure or length (matric potential head), respectively. Matric potential is attributed to intermolecular cohesive and adhesive forces acting within and between liquid, gaseous and solid phases. These forces lead to surface tensions at the interfaces of adjacent phases and in particular at the liquid-air-interface, e.g., the meniscus in a thin pore. When a soil or sediment sample is submerged in a water bath and then its upper boundary is lifted to the level of the water table, the sample is completely saturated and its matric potential is zero. Reduction of the energy level leads then to a certain decrease in water content. This also means that when lifting the sample above the water level, the matric potential is only equal zero (=atmospheric pressure) at the bottom of the sample and negative above, resulting in water draining from the sample that cannot be held by the matric forces in the pores. This also illustrates that there is a strong relationship between matric potential and water content which is often called soil water characteristics $\theta(\psi_m)$ or soil water retention function.

A physical explanation of matric potential starts with splitting the forces into adsorptive and capillary forces. Capillary forces are responsible for the rise h_c of water in cylindrical tubes (capillaries) with a curved meniscus at the interface with the atmosphere. Under the assumption of full wetting (contact angle between meniscus and solid surface is zero), the pressure difference between the liquid and the gaseous phase or h_c are inversely proportional to the radius of the tube (Jurin's law for capillary rise). If only capillary forces were present and all pores were cylindrical tubes, the pore size distribution would be closely related to the integral of the soil water characteristics $\theta(\psi_m)$. However, soil and sediments also exhibit adsorption, which forms hydration envelopes over the particle surfaces. The presence of water in films is most important in clay which has a large surface area because of the small particle sizes, but relatively insignificant in sand where the capillary effect dominates (Tuller and Or, 2005). Further, real pores are not cylindrical but can have a variety of complex forms making it necessary to measure the soil water characteristics $\theta(\psi_m)$. Soil water characteristics can be determined by simultaneous measurement of matric potential and water content, either in the field or in laboratory experiments by e.g., conducting drainage experiments under known pressure conditions.

Numerous models exist for parametrization of the soil water characteristics $\theta(\psi_m)$; the most commonly used are the models introduced by Brooks and Corey (1966) and van Genuchten (1980). Fig. 3 below shows the water retention curves for a typical sand, clayey loam, and clay parametrized with the van Genuchten approach. There is a steep change in water content of sand at a matric potential head of -10^1 to -10^2 cm, which occurs because the majority of pores in a sand are relatively large and uniform. On the other hand, the pore sizes of a clay are more evenly distributed and mainly smaller, and thus the desaturation, i.e., the slope of the curve in the inflection point, is gentler. Simultaneous measurements of matric potential and water content over long periods often reveal a hysteretic behavior of $\theta(\psi_m)$ and thus the wetting and drying curves are different not having the same unique functional relationship.

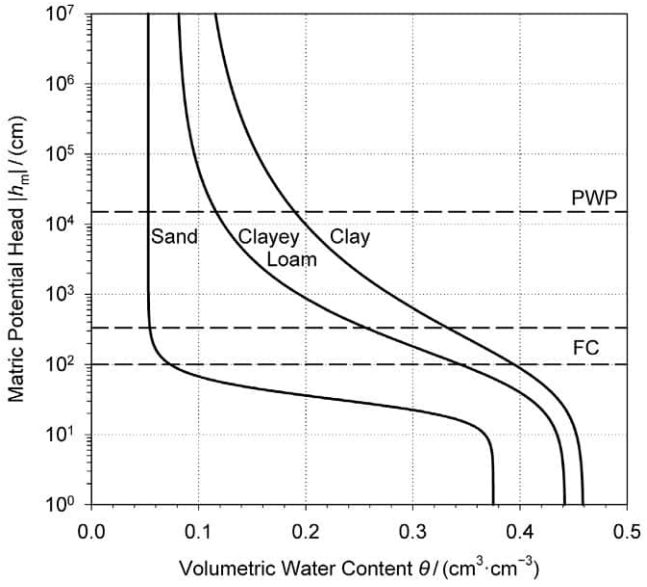

Fig. 3 Soil water characteristics for three typical soil types, modeled with van Genuchten function; PWP, permanent wilting point; FC, field capacity.

The soil water characteristic is not only required when describing flow (see next chapter), it also gives information about the soil water status and whether water is accessible by plants. To avoid the analytical complexities of determining the whole relationship $\theta(\psi_m)$, practitioners tend to focus on two specific measures of soil water. One is field capacity θ_{FC}, a moderately wet condition that gives the water that is expected to remain in the porous medium 2 or 3 days after having been wetted with water and after further drainage is negligible (SSSA, 2008). The other one, a relatively dry status is the permanent wilting point θ_{PWP}. This point represents the largest water content at which indicator plants, growing in that soil, wilt and fail to recover when placed in a humid chamber. Instead of conducting laborious standardized experiments, θ_{FC} and θ_{PWP} are taken from the soil water characteristic. Whereas θ at a matric potential head of -1.5×10^4 cm is considered a good estimation for θ_{PWP} in all soils, field capacity varies from -10^2 cm in sand soils to -3.3×10^2 cm in clays (Fig. 3). The respective pore radii according to the law for capillary rise delimit the range of medium-sized pores. The difference $\theta_{FC} - \theta_{PWP}$ reflects the plant-available water and is an important characteristic of the storage behavior of soils and sediments. The typical number of medium-sized pores is obviously similar in clayey loams and clays ($\theta_{FC} - \theta_{PWP} \approx 0.20$) and much smaller in sands (≈ 0.03). These values from Fig. 3 are consistent with long-term experience in agriculture: poor soils typically have 90 mm of plant available water per meter rooting depth, whereas favorable soils have 250 mm.

Uniform water flow

For describing water flow through porous media, we have to travel back in time to 1856, when Henry Darcy came up with his fundamental empirical relationship of quantifying water flow through a saturated porous filter system (Darcy, 1856) which is still the basis for describing water flow in porous media and was extended by Buckingham (1907) for unsaturated porous media. In an experimental setup (Fig. 4), Darcy calculated that the volumetric water flow Q through a porous filter column is directly proportional to the area A ($A = \pi r^2$; r, radius) of the column and the difference in hydraulic head ΔH and inversely proportional to the length of the column L; the hydraulic potential is the sum of gravitational head and pressure head. The proportionality factor is the hydraulic conductivity K. The water flux q can be calculated by referring the volumetric water flow to the area:

$$q = \frac{Q}{A} = v \cdot n = -K \cdot \frac{\Delta H}{L}$$

The water flux has the same dimension as velocity, but for calculating the average pore water flow velocity v, we must consider that water flow only takes place through the pore space and therefore, we have to additionally consider the porosity n. The hydraulic conductivity combines properties of the porous medium (e.g., pore sizes, pore connectivity) and the fluid (viscosity and density). For porous media with smaller pores, such as in clay, hydraulic conductivities are much smaller compared to media with larger pores, such as in sand.

For unsaturated media, Darcy's law has to be extended as the hydraulic head difference is not only dependent on the gravitational potential, but also on capillary forces and interactions of the liquid and solid phase, which are given by the matric potential. Therefore, the difference in hydraulic potential for unsaturated media equals the difference of the gravitational potential $d\psi_z$ plus the difference of the matric potential $d\psi_m$ over the flow length difference ds. Further, the hydraulic conductivity no longer is

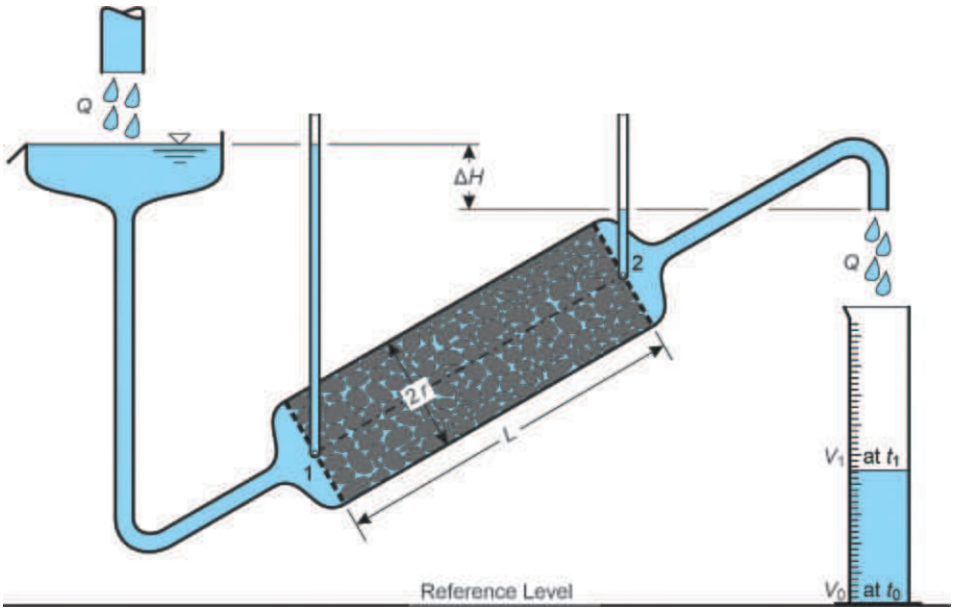

Fig. 4 Setup of a Darcy experiment to quantify water fluxes through porous media. From https://info.bmlrt.gv.at/dam/jcr:8d7b2b61-c5f1-4d54-903a-f02e37b81144/Sammelband_Wasser-im-Boden_BMLRT.pdf.

a constant value, but a function of the matric potential or volumetric water content θ. Both, the pore connectivity and radius of pores filled with water decreases with decreasing matric potential as the larger pores empty first. Thus, fewer and only smaller pores are filled with water being less conductive and increasing the flow paths through the system resulting in lower hydraulic conductivity. The vertical one-dimensional Darcy-Buckingham Law is

$$q = -K(\theta(\psi_m)) \cdot \frac{d(\psi_m + \psi_z)}{dz}$$

This law is all what is needed to describe average water fluxes under steady-state conditions. However, flow processes in the vadose zone are mainly transient and not steady-state. We have to consider that there is water stored and that water fluxes into the vadose zone are not equal to the water fluxes leaving it. Water fluxes—as well as state variables like θ and ψ_m—change over time t and space z ($dq/dz = d\theta/dt$), and therefore, the change in water volume in a specific control volume is no longer equal to zero. Combining this assumption of continuity (mass conservation) with Darcy's law gives the Richards equation (1931) describing transient water fluxes in variably saturated porous media, here given for vertical one-dimensional flow

$$\frac{\partial \theta(\psi_m)}{\partial t} = \frac{\partial}{\partial z} \cdot \left[K(\psi_m) \cdot \left(\frac{\partial \psi_m}{\partial z} + 1 \right) \right]$$

There are different forms of the Richards equation due to the interdependency of θ and ψ_m. For details, more information is available in text books on soil physics (see "Further reading"). The equation can be solved numerically, and in the present form describes uniform, vertical water flow in variably saturated, homogeneous porous media. It can be further expanded by a sink/source term considering plant-soil water interactions or any other sources and sinks of water. There are software programs available for simulating the movement of water (as well as heat and multiple solutes) in variably saturated media, such as HYDRUS-1D (Šimůnek et al., 2009).

Challenges of using the Richards equation have been discussed as numerical solutions are not always straightforward (Farthing and Ogden, 2017). Its applicability at larger scales is also computationally expensive and affects the accuracy of the modelling (Vogel and Ippisch, 2008), and it is complicated by nonlinearity and heterogeneity (Beven, 2001). Further, important processes like preferential flow are not considered in the form introduced above. Still, it is one of the main concepts for describing water flow in porous media, simulations with the Richards equation are consistent with measurements observed at the local scale, and it has also been extended to describe flow in heterogeneous porous media.

Non-uniform water flow

Preferential flow in the vadose zone is the rule rather than an exception. Preferential flow is defined as water and its constituents moving by preferred pathways through a porous medium. This preferential water flow is typically some orders of magnitude faster than flow through the remainder of the porous medium. Preferential flow can thus result in water and matter fluxes bypassing large parts of the vadose zone. Consequently, it influences the water cycle and can impact the quantity and quality of water in and leaving the vadose zone.

Preferential flow can be categorized into three types (i) macropore flow, (ii) funneled flow, and (iii) fingered flow. Macropores are pores that are larger in size, greatly continuous or have other properties enabling fast water flow velocities. Typical structures favoring macropore flow are fractures, root holes, or animal burrows. Funneled flow describes spatially variable water flow as a consequence of heterogeneities in hydraulic properties. It develops, for example, in layered medium or in the presence of differently textured lenses (e.g., clay lenses) compared to the surrounding. The contrasting hydraulic properties of those features cause a concentration of flow in the most conductive, wetter zones. Fingered flow is caused by heterogeneities resulting from different flux distributions or moisture states. A prominent example is the instability of infiltration fronts favoring flow into the wettest, most conductive pathways. Independent of the type of preferential flow, it still remains a challenge to measure, quantify and predict preferential flow due to its complexity, as outlined in detail in Nimmo (2021).

It also remains a challenge to measure other structural heterogeneities that cause non-uniform flow. Here, artificial or environmental tracers have been applied in field and laboratory studies to visualize or quantify flow processes (e.g., Flury and Wai, 2003; Stumpp and Maloszewski, 2010; Weiler and Flühler, 2004). Such use of tracers is limited to the upper part of the vadose zone that is accessible for doing those experiments or installing sensors for measuring volumetric water content or matric potential. For deeper parts of the vadose zone, measurements are even more challenging, and information about flow can be gained, for example, from drilling and water stable isotope analysis (Sprenger et al., 2016; Chesnaux and Stumpp, 2018) or installation of specific vadose zone monitoring systems (Dahan, 2020).

It remains difficult to quantify the importance of structural heterogeneities and their consequences for flow and transport at various scales. Factors such as texture (grain size distribution) and structure (aggregates) can vary vertically and laterally, and so do hydraulic properties. Determining those variable properties in the field is nearly impossible, and including spatial heterogeneity of hydraulic properties in three dimensional flow models based on the Richards equation is computationally only feasible at the plot scale. For simulation of water fluxes in the vadose zone at the catchment scale, homogeneity of hydraulic property often needs to be assumed, the impact of heterogeneities on larger scale remains unknown, and/or hydrological models with less complex flow assumptions for describing flow in the vadose zone are used.

Despite the challenges of quantifying non-uniform flow resulting from structural heterogeneities, there have been several approaches developed. These include the assumption of bimodal soil water and hydraulic conductivity characteristics (Durner, 1994; Priesack and Durner, 2006) and dual-porosity (Šimůnek and van Genuchten, 2008) or dual-permeability approaches (Gerke and van Genuchten, 1993). These approaches each divide the pore system into two or more components with different hydraulic properties. For quantification of macropore flow, kinematic wave approaches have been used (Germann and Beven, 1985) to simulate advective and gravity-driven transport processes.

Synthesis

Here, we provided an overview of the vadose zone, its function as an ecosystem and how hydraulic properties influence flow processes. We showed that hydrological processes are controlled by the ratios of solid, liquid and air phase and the size distribution of grains and pores. Due to adhesion and cohesion forces, water can be held in the porous medium against gravity. Both, gravitational and matric forces constitute the direction of water flow. Porous media have different soil water characteristics and hydraulic conductivities with a clear relationship to texture. Knowing those dependencies, uniform water flow can be quantified through a combined Darcy and mass conservation approach. Water flow in the vadose zone is, however, not always uniform; structural heterogeneities cause preferential or other non-uniform water flow. These processes are difficult to quantify or to even measure in the field. Particularly hydrological processes in the deeper parts of the vadose zone and the scaling of processes from the plot to the catchment scale and vice versa remain challenges in vadose zone research. We further showed that the flow processes in the vadose zone are highly variable and thus, they impact the amount and quality of water fluxes and are essential for food and water security.

Knowledge gaps

- Determination of spatial variabilities of hydraulic properties in the field and its consequences for water flow and transport
- quantification of non-uniform flow including preferential flow
- scaling of soil hydraulic properties and processes (plot vs. catchment scale)
- deep vadose zone processes and missing observations there
- interaction of physical, chemical and microbiological processes
- fate of contaminants in the vadose zone
- groundwater recharge quantification

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Relevant websites

https://open.oregonstate.education/soilhydrologyandbiophysics/—Online textbook on Soil Hydrology and Biophysics.

https://www.youtube.com/channel/UCoMb5YOZuaGtn8pZyQMSLuQ/playlists—Videopodcast of textbook on Soil Hydrology and Biophysics.

https://www.pc-progress.com/de/default.aspx—HYDRUS software for modelling processes in the vadose zone.

https://ddp.tereno.net/ddp/index.jsp—Terrestrial Environmental Observatories.

https://www.soils.org/—Soil Science Society of America.

https://www.cuahsi.org/education/resources-for-online-education/—Resources for online education in the field of hydrology offered by the Consortium of Universities for the Advancement of Hydrological Sciences, CUAHSI.

Groundwater Dependent Aquatic and Terrestrial Ecosystems

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Base-flow The sustained contribution of water from springs and seeps that maintains flow in streams and wetlands in the absence of inputs from rainfall and surface runoff.
GDE Groundwater dependent ecosystem.
Groundwater depth The distance from the surface to the groundwater table.
Groundwater flux The rate of groundwater flow.
Groundwater quality The physical and chemical properties of groundwater that determines its suitability for a specific purpose.
Groundwater pressure The force exerted by the groundwater as a consequence of its depth, the aquifer matrix and presence of over and underlying geological layers.
Groundwater regime A combination of groundwater conditions including pressure, flux, depth and quality of groundwater and the timing of its availability to meet the needs of an ecosystem.
Phreatophytic vegetation Deep-rooted plants that draw water from the saturated zone in the soil profile.
Stygofauna Aquatic subterranean fauna that are adapted to life in caves and aquifers.

Introduction

Groundwater dependent ecosystems (GDEs) are natural systems that require access to groundwater to maintain the diversity of plants and animals, ecological processes and ecosystem services provided by that ecosystem (Richardson et al., 2011). They need access to, and thus have a dependency on groundwater, which can be permanent or intermittent, and required by all or only a few species in the ecosystem, yet remains essential for the long-term persistence of the ecosystem in the landscape (Murray et al., 2003; Richardson et al., 2011).

Groundwater dependent ecosystems have played a critical, yet often unrecognized role in the development of ancient and modern civilizations and folklore. Groundwater springs and desert oases have been the nucleus for major cities that arose along ancient trade routes. For example, many cities along the silk road were established around springs and oases where the stable supply of water sustained populations, provided relief to parched travelers, and supported an ecosystem that provided food, resources for shelter, and enabled agriculture. Early hominids relied on the sustained flows in groundwater-fed wetlands of Tanzania (Ashley et al., 2009). Indigenous cultures of central Australia have had a close association with springs, soaks and groundwater fed swamps that were an integral part of their culture and beliefs (Moggridge, 2020). Today, major cities such as Las Vegas, USA have arisen around desert oases and others such as Bath, UK arose in c. 60 AD around thermal springs (springs chapter; Stevens, 2020). Indeed, more than half of the world's mega cities with >10 mill inhabitants are reliant on groundwater as their primary source of drinking water (Morris et al., 2003), and many major cities globally have significant groundwater issues (Foster, 2020).

Groundwater dependent ecosystems are found in a range of biomes and climate zones, and on all continents of the world, including Antarctica (e.g., Gooseff et al., 2013), and include terrestrial, freshwater and marine ecosystems. Despite their global distribution, they can be classified into three groups based on the ecosystem location (terrestrial/aquatic) and the water resource being used (above ground/below ground) (Box 1). This classification created by Eamus et al. (2006) encompasses all GDEs, including marine and subsurface systems, which are not always included in some regional classifications. In Australia, this

Box 1 Types of groundwater dependent ecosystems (from Eamus et al., 2006).

(I) Aquifer and cave ecosystems, also referred to as subterranean GDEs. Includes ecosystems occurring within karstic, fractured rock and alluvial aquifers (see Humphreys, 2006), as well as hyporheic zones of rivers (see Hancock et al., 2005), which often support a mixture of surface and groundwater organisms.

(II) All ecosystems dependent on the surface expression of groundwater. Also referred to as surface aquatic GDEs or groundwater associated aquatic (GWAA) ecosystems. This includes rivers, streams and wetlands that depend on groundwater for base-flow, springs, coastal lagoons and marine and estuarine areas receiving groundwater discharges.

(III) All ecosystems dependent on the subsurface presence of groundwater. Also referred to as surface terrestrial GDEs or groundwater dependent terrestrial (GWDT) ecosystems. This class includes terrestrial vegetation that accesses deep or shallow groundwater, in either the saturated or vadose zone. No surface expression of groundwater is required in this class of GDE.

classification system has been adopted as part of the National GDE atlas (BOM (Bureau of Meteorology), 2021). This classification is also consistent with the classification of GDEs established by the European Union, which recognizes Groundwater Associated Aquatic (GWAA) and Groundwater Dependent Terrestrial (GWDT) ecosystems (European Commission, 2012, 2015). The aim of this chapter is to provide an overview of the types of groundwater dependent ecosystems, their global extent, their biota, and the current threats to their integrity and existence.

Defining GDEs

In the context of GDEs, groundwater is water that is sourced from subsurface geological layers (aquifers). Groundwater can be utilized or accessed while still underground or used once it emerges at the surface. Groundwater dependent ecosystems rely on (are dependent on) the presence of groundwater to maintain the structure and composition of the ecosystem. Put another way, dependent ecosystems, or species there in would, over time, become locally extinct if the requirements for groundwater were not met. The dependence of an ecosystem on groundwater may vary with seasonal or climatic fluxes (e.g., drought), only requiring infrequent or occasional connectivity. As such, species may only require access to groundwater at specific life stages, or to supplement surface water supplies during drought. In addition, subsurface ecosystems depend entirely on consistent access to groundwater.

Each GDE, or species in it will, have its own set of groundwater "requirements" that must be met for that species or ecosystem to persist. Together, these requirements are referred to as the groundwater regime that is needed. Understanding the thresholds of these attributes for a GDE is critical for setting groundwater management targets and monitoring strategies.

In general, there are four key elements of a groundwater regime that are essential to GDEs (Eamus et al., 2016). These are:

1. Groundwater depth
2. Groundwater pressure
3. Groundwater flux
4. Groundwater quality

The importance of each of these attributes to each GDE type is outlined in Table 1 and is considered further in the following sections as each type of GDE is discussed.

Table 1 Importance of groundwater attributes to different types of GDEs.

GDE type	*Depth*	*Pressure*	*Flux*	*Quality*
Subterranean GDEs	• Provide habitat • Maintain groundwater stratification	• Fauna of deep aquifers may be pressure adapted	• Supply nutrients including organic matter and oxygen	• Maintain physico-chemical conditions to sustain biota and geochemical processes
Surface aquatic GDEs	• Provide open water or water-logged environment • Prevent activation of acid-sulphate soils • Maintain hydraulic gradient for groundwater discharge	• Sustain groundwater discharge to springs and surface waters	• Sustain above ground water levels including base flows • Prevent saltwater intrusion (estuarine/coastal environments) • Flow sufficient to modify conditions in surface environment	• Maintain suitable chemical composition of water for biota
Surface terrestrial GDEs	• Accessible water at root zones • Prevent water-logging		• Sustain water uptake rate (supplement transpiration losses)	• Maintain suitable chemical composition of water for biota

Adapted from Eamus D, Fu B, Springer AE, and Stevens LE (2016) Groundwater dependent ecosystems: Classification, identification techniques and threats. In: Jakeman AJ, Barreteau O, Hunt RJ, Rinaudo JD, and Ross A (eds.) *Integrated Groundwater Management*. Cham: Springer.

GDEs include a range of environments that support highly specialized species and ecosystems and possess unique biotic and abiotic characteristics that make them uniquely different from other ecosystems. GDEs all rely on groundwater for the maintenance of some or all, of their ecological functions (Murray et al., 2003). This dependence on groundwater can range from partial and infrequent dependence, such as seasonal or episodic groundwater use, to total continual access to groundwater and dependence. GDEs can range in area from small springs that may be less than 1 m^2 to forests that may cover hundreds of square kilometres.

Subsurface GDEs

Aquifers, and the groundwater within, account for over 95% of the available global freshwater reserves (Cantonati et al., 2020), making subsurface GDEs the world's largest freshwater biome. Subsurface aquatic GDEs are those that occur in saturated zones below the surface. These include water-filled voids in a variety of geological matrices such as karst (caves), fractured rock and alluvial ecosystems (Fig. 1A and B). They also include hyporheic ecosystems that occur in the sediments of surface waters and form an ecotone between surface and groundwater ecosystems. The hyporheic zones (Fig. 1C), their fauna and processes are discussed in detail in other chapters of this volume and are not discussed further here. Aquatic cave ecosystems (Fig. 1A) are also addressed in other chapters and will be mentioned only briefly below.

Subsurface GDEs may be further categorized based on the geology of the aquifer matrix. The geology strongly determines the size of the voids, which dictates the size of animals able to inhabit the aquifer, and the rate of flow of water. Caves and karst aquifers can have large voids able to support large invertebrates and even vertebrates and have high flows that can deliver large amounts of nutrients and oxygen from the surface. In contrast, aquifers comprised of gravels, sand and silt have smaller void spaces and because of that are constrained to supporting only small-bodied organisms (Dumnicka et al., 2020).

Groundwater environments are void of light, low in nutrients and oxygen, and habitat availability is limited by the size of the pores or fractures in the geological matrix. The groundwater environment is harsh, yet it supports an array of organisms including viruses, Archaea and Bacteria, Protozoa, Fungi and where habitat permits, invertebrates known collectively as "stygofauna" (Humphreys, 2006). It is estimated that 40% of prokaryote biomass on earth is located in the terrestrial subsurface, with microbial density estimates ranging from 10^2 to 10^6 cells per cm^3 in water and 10^4 to 10^8 cells per cm^3 in saturated cave and aquifer sediments (Griebler and Lueders, 2009). The majority of microbes within groundwater environments live in small colonies and biofilms attached to the sediment and rock matrix and provide a food source for larger organisms (stygofauna) to graze upon (Griebler et al., 2014).

Groundwater ecosystems are unique environments. With the lack of photosynthetic organisms in the dark subterranean environment, groundwater ecosystems heavily rely on external sources of carbon, filtering in from the surface. Heterotrophic bacteria, which rely on those allochthonous inputs of organic matter for energy, dominate microbial assemblages, but chemoautotrophic bacteria, which derive energy from inorganic sources, also occur (Gregory et al., 2014).

Stygofauna are essential in groundwater environments as they maintain effective porosity by burrowing, and grazing microbial biofilms and thus, control microbial communities (Griebler et al., 2019). Stygofauna are responsible for bioturbation within groundwater, assisting in biochemical circulation of essential nutrients, including carbon cycling, within aquifers and maintaining groundwater flow (Hose and Stumpp, 2019). Furthermore, stygofauna biodiversity has been linked to ecosystem functioning and services (Stein et al., 2010; Boulton et al., 2008).

Groundwater environments are influenced by a range of factors, all of which contribute to this unique environment. Geological factors including rock type, mineral composition and matrix porosity, combine with hydrological parameters such as hydraulic conductivity to create the physical and chemical habitat conditions that influence the irregular distribution of oxygen and nutrients throughout groundwater ecosystems (Schmidt et al., 2017). Together with the water chemistry (pH, dissolved oxygen concentration, nitrogen and salinity concentrations), these factors influence the distribution of organisms within groundwater (Johns et al., 2015; Korbel and Hose, 2015). However, water chemistry is also influenced by biogeochemical processes undertaken by the microbes living in groundwater (Chapelle, 2000).

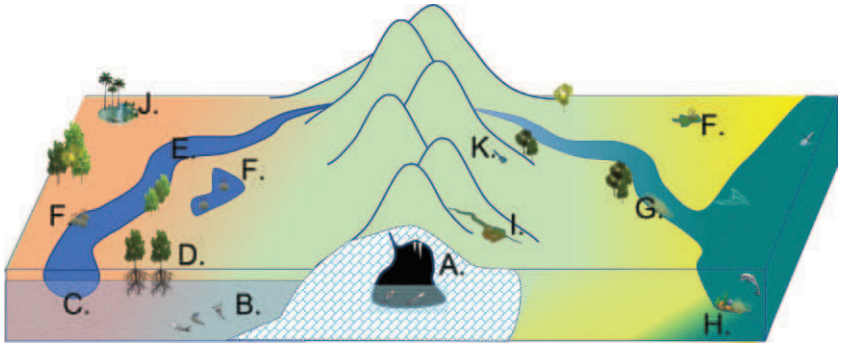

Fig. 1 Example types of groundwater dependent ecosystems in the landscape. A. cave and karst ecosystems, B. aquifer ecosystems, C. hyporheic ecosystems, D. phreatophytic vegetation, E. base flow of rivers and streams, F. wetlands, G. estuarine ecosystems, H. near-shore marine ecosystems, I. swamps and fens, J. springs and oases, K. hypotelminhoreic ecosystems.

Events linked to the hydrological cycle, such as precipitation and flooding, leading to recharge, are important parameters influencing biological assemblages in aquifers. Korbel and Hose (2015) show that the seasonality (during and after drought) accounted for a significant proportion of variation in microbial functional assemblage, while Reiss et al. (2019) showed major shifts in the composition and activity of bacteria, protists and invertebrates following an extreme flooding event. In both cases, aquifer recharge processes were strongly linked to changes in the aquifer ecosystem.

Terrestrial GDEs

For most plants, rainfall is the primary source of water but there are many plant species that routinely make use of groundwater to support their ecological functions and the ecosystem services they provide (Loheide and Booth, 2011; Kath et al., 2014). Vegetation will prioritize drawing water from areas of the soil profile where the least energy is required. This means that vegetation will use shallow soil water first before seeking deeper soil water or groundwater (Eamus and Froend, 2006). Plants will thus become increasingly dependent on groundwater as soil water becomes depleted (Howe et al., 2007).

In terms of water dependence, terrestrial plants span a continuum from vadophytes that rely solely on rainfall and do not access groundwater, to obligate phreatophytes that continually access groundwater and can cope with having some or all roots permanently inundated (Fig. 2). Facultative phreatophytes require groundwater at some stage of their life cycle, and although not requiring continuous access as do obligate phreatophytes, the availability of groundwater at those times may be critical for their survival. Phreatophytes often access groundwater via the capillary fringe or vadose zone (Eamus et al., 2006). Trees mostly take up groundwater from the capillary fringe because the direct uptake from below the water table is difficult due to the saturated and often low oxygen conditions (Eamus et al., 2006). Riparian and aquatic vegetation require continual access to water, which in many cases may be provided by groundwater base flows. Such plants typically have morphological and physiological adaptations to cope with having roots continuously in saturated soils and sediments.

In arid and semi-arid regions, groundwater is a critical resource for the local vegetation, as plants are often exposed to extensive dry periods where surface water is scarce, and transpiration exceeds precipitation (Eamus et al., 2006). Most groundwater-dependent vegetation relies on the availability of the groundwater being within the root zone just below the surface (Eamus et al., 2006). Large trees, for example, can persist for long periods of time without any rainfall, by sending tap roots down to the water table to access the groundwater below (Johansen et al., 2018, Fig. 1D). The *Banksia* woodlands of south-western Australia, and riparian forests of the San Pedro River Arizona, USA, are all examples of GDEs that require a supply of groundwater within rooting depth to maintain their structure and function (Zencich et al., 2002; Stromberg et al., 2006).

Methods for identifying vegetation using groundwater are outlined in O'Grady et al. (2006), Doody and Benyon (2011), Eamus et al. (2016), Doody et al. (2017), European Commission (2014) and others, and range from measurements of water use by individual trees, to remote sensing of canopy cover and "greenness" of large stands of vegetation over climatic cycles (Eamus et al., 2016; Doody et al., 2017; Dabovic et al., 2019). The identification of GDEs is often challenging because of the general limited availability of spatial information or even site-specific data on vegetation types, geology, soil properties and groundwater levels in many areas (Eamus et al., 2015). Information on groundwater levels, particularly in relation to the root depth of the vegetation, are critical for identifying groundwater-dependent vegetation, and this factor, as well as groundwater quality are the most critical attributes of the groundwater regime for this GDE type.

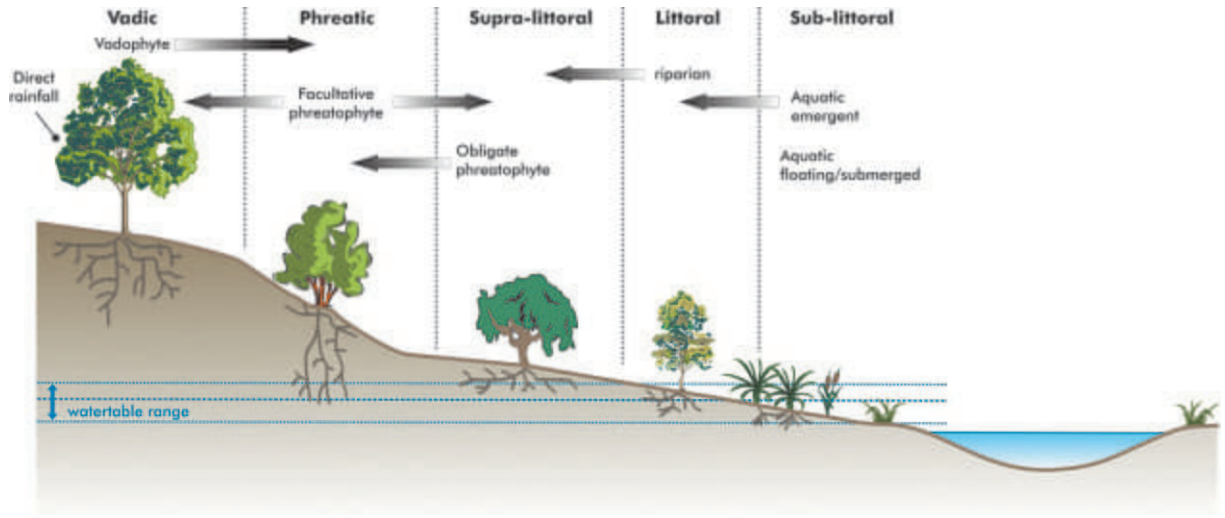

Fig. 2 Example types of groundwater dependent vegetation across a gradient of groundwater depth. From Pettit NE, Edwards T, Boyd TC, and Froend RH (2007) *Ecological Water Requirement (Interim) Framework Development: A Conceptual Framework for the Maintenance of Groundwater Dependent Ecosystems Using State and Transition Modelling.* A Report to the Department of Water. WA, Australia: Centre for Ecosystem Management, Edith Cowan University.

Aquatic GDEs

Aquatic GDEs include rivers and streams (Fig. 1E), wetlands (Fig. 1F), and marine and estuarine systems (Fig. 1G and H) that receive groundwater discharges. The discharge of groundwater to rivers and wetlands most commonly provides continuity of water supply, particularly in dry times when surface flows are limited, and groundwater discharge provides a base level flow. In many cases, the discharge of groundwater is essential for maintaining minimum levels of saturation or keeping river pools topped up so that they may provide a refuge habitat until surface flows return. The discharge of groundwater, often starting as a spring that seeps into surface waters to provide base-flows are critical to the survival of surface water ecosystems and their biota. This is particularly the case in arid and semi-arid environments where surface water flows are unpredictable.

In marine and estuarine environments, the discharge of groundwater often shapes the local physico-chemistry of water in the receiving environment and alters ambient conditions to suit a particular plant or animal species or processes. For example, the discharge of groundwater to nearshore marine systems can lower salinity and provide unique habitat (Leitão et al., 2015) and discharge of warm groundwater to rivers and streams provides habitat for spawning salmon (Saltveit and Brabrand, 2013).

The flow provided by groundwater discharges is essential to maintaining permanently wetted habitat in rivers and streams. Under increasing climate variability and changing rainfall patterns associated with global warming, groundwater discharges are increasingly important for maintaining constant flows in rivers and streams. Under hot and drought conditions, base flows are vital for maintaining refuge habitat. Even in temperate areas, base flows provide sufficient water depth and flow velocity over riffle habitat, and maintain permanent stream pools to support spawning and growth of stream biota (e.g., Hunter and Gillespie, 2011; Larsen and Woelfle-Erskine, 2018). In these cases, the ecosystem is likely dependent on a volume (or rate) of groundwater discharge, which is influenced by the groundwater depth (for unconfined aquifers) and pressure (for confined aquifers) and the flux, which defines the rate of groundwater moving through and out of the aquifer.

Wetlands are highly diverse and are generally characterized into five types (riverine wetlands, lacustrine wetlands, palustrine wetlands, estuarine wetlands and marine wetlands) (Cowardin et al., 1979), which each may be dependent on groundwater (Howe et al., 2007). Wetland vegetation across all wetland types is highly reliant on the degree of soil saturation and as such, wetland species are particularly vulnerable to hydrological changes (Le Maitre et al., 1999; Johansen et al., 2018). Currently the focus of research and management has been on understanding the environmental flow requirements of wetland communities and species (e.g., Powell et al., 2008; Roberts and Marston, 2011; Hernández-Guzmán et al., 2019), and the dependence of wetlands on groundwater is rarely quantified and not well understood (Howe et al., 2007; Johansen et al., 2018).

Some wetlands may be completely dependent on groundwater discharges to maintain water levels or soil saturation, whilst others may have limited dependence, such as at different times of year or stages in the plant life cycle (Thorburn et al., 1994a, b; Mudd, 2000). However, even small amounts of groundwater can be ecologically important, with small seepages supporting unique plant and animal communities, or trickling flows that maintain water levels in river pools. The physico-chemical properties of groundwater are critical to the biochemical processes of the wetland. For example, alkaline groundwater buffers wetland sediments and pore water, prevents acidification (Boomer and Bedford, 2008) and reduces the phosphorus bioavailability (Wassen et al., 2005). Waterlogging limits nutrient and oxygen availability (Almendinger and Leete, 1998) yet can promote high species diversity through the consequent lack of competition (Kotowski et al., 2010). The water table dynamics also influence oxidation-reduction (redox) conditions in the sediments which control the binding and release of carbon and phosphorus in sediments, and its availability to support plant and algal growth and other processes (Pant et al., 2003; Lucassen et al., 2005; Villa and Bernal, 2018; Were et al., 2019).

Included in this category are some peatlands (Fig. 1I) which, although often capturing and retaining rainfall, also require groundwater inputs. Peat swamps in the temperate highlands of eastern Australia (Cowley et al., 2019) maintain a saturated sediment profile with water derived predominantly from local groundwater, however the relative surface water and groundwater inputs to these systems varies across the landscape. For these systems also, the key variables of the groundwater regime are flux and quality. Groundwater depth is often not such a critical concern as it is derived from seeps and springs higher in the catchment (Cowley et al., 2019). However, in fens (peat swamps) in central Oregon, USA, groundwater depth is critical to maintaining plant diversity and peat formation (Aldous and Bach, 2014).

The dominance of shallow-rooted vegetation in wetlands (Fig. 2) means that wetland plants may be more susceptible to water table declines than deep-rooted phreatophytic vegetation (Dillon et al., 2009). A decline in water tables can result in the loss of water tolerant species, which will be gradually replaced by woody terrestrial species and those with broader ecohydrological ranges. In response to water table decline, many wetlands display a proportional response to drawdown, in which the magnitude and rate of water level change is critical in determining the magnitude of impacts (Froend et al., 2004; Dillon et al., 2009).

Along with wetlands, many flowing surface water ecosystems are dependent on groundwater to maintain flow during dry (low rainfall) periods when runoff is insufficient to maintain inundated habitat. In such systems, base flow is maintained by the surface discharge of groundwater. Base flow discharges are critical for maintaining habitat in rivers and streams (Beatty et al., 2010; Choi et al., 2018) and the degree of dependence strongly influences the structure and function of the fish, invertebrate, plant and microbial communities, and the connectivity among habitats within the landscape (Nevill et al., 2010).

Baseflow streams require groundwater depth, pressure and flux that enable sufficient surface discharge. For many streams that gain water from adjoining aquifers (termed “gaining streams”), the groundwater level must be similar to the river or stream water level. Groundwater flux must also be sufficient to maintain a gradient toward the river so that the stream continues to gain water from the aquifer and not lose water to it (termed “a losing stream”). The physico-chemical properties of the groundwater must be

suitable to support life in the stream. For example, the discharge of contaminated groundwater can be problematic to rivers, streams and coastal areas (e.g., Welch et al., 2019), or a change in groundwater temperature may affect the suitability of habitat for fish spawning (e.g., Ficke et al., 2007).

Springs (Fig. 1J), as surface discharge points for groundwater, are widespread globally (Olarinoye et al., 2020). They include desert oases, emergent cave streams and artesian mound springs, and globally are under multiple threats (Cantonati et al., 2020). The ecology of springs is described in detail in other chapters of this volume.

Small groundwater seeps can create permanent, but localized pockets of saturated soil that provide habitat for a unique fauna that often contains species characteristic of subterranean habitats. These small seeps are referred to as hypotelminorheic habitats (Fig. 1K, Culver et al., 2006). Environmental conditions in these systems are rather unique, with a mixture of groundwater and saturated, highly organic soils and leaf material (Culver et al., 2006). They support highly localized, short-range endemic species (occupying a range <5 km (Culver et al., 2006)) and have a species richness that rivals some cave systems. Hypotelminorheic habitats are suggested to be a key pathway for the colonization of subterranean ecosystems by surface fauna (Culver et al., 2006).

The discharge of groundwater to the near-shore marine and estuarine environments (Fig. 1 G.H) is critical to maintaining conditions in sea grass and other habitats that are essential for biota and ecological processes. Although beyond the scope of this chapter, near shore marine GDEs are discussed in more detail in Lecher and Mackey (2018) and Taniguchi et al. (2019).

Threats to GDEs

Groundwater dependent ecosystems are of considerable economic and ecosystem service value (Murray et al., 2006). They provide recreation and tourism opportunities, tangible goods in terms of water, timber and agricultural products, as well as providing valuable ecosystem functions such as maintaining groundwater geochemistry, carbon and nutrient sequestration, stabilizing soil, limiting erosion, maintaining land and water quality, capturing runoff, and preventing dryland salinity (Murray et al., 2006; Kløve et al., 2011; Griebler et al., 2019).

GDEs are under threat the world over because of the growing global demand for groundwater (Kløve et al., 2011). In addition, land clearing and the removal of riparian and terrestrial vegetation, as well as alterations to the hydrology of aquifers, wetland and rivers results in the destruction of GDEs (Kløve et al., 2011). Urbanization, particularly the replacement of natural surfaces with concrete and other impervious surfaces can reduce water infiltration, such that groundwater levels are not readily replenished, and have been linked to the degradation of GDEs (Fryirs et al., 2016; Bugnot et al., 2019).

In addition to habitat loss or change, land use change poses a significant threat to GDEs due to the risk of contamination and change in groundwater quality (Korbel et al., 2013). Groundwater quality is a critical element of the groundwater regime for all GDEs (Table 1, Hose et al., 2004). Heavy metals, pesticides, nutrients and organic chemicals derived from urban development, mining, agriculture and many other activities have the potential to alter subsurface ecosystems impacting their ability to provide necessary functions, such as water purification. There is an established body of ecotoxicological data that are applicable for protecting surface aquatic GDEs but data for terrestrial and subsurface GDEs (e.g., Castaño-Sánchez et al., 2020) remain limited (Hose et al., 2004).

The second threat is primarily associated with the extraction and pumping of groundwater for industrial purposes (Nevill et al., 2010) and occurs when groundwater is extracted at a faster rate than the water is replenished, resulting in a lowering of the water table and reduction of groundwater flow (Nevill et al., 2010). Deep-rooted plant species can become stressed when the water table drops below the rooting depth, which can have a flow on effect to the functioning of the surrounding ecosystem (Cramer et al., 1999).

Groundwater drawdown also has direct effects on subsurface GDEs. Lowering groundwater tables amounts to habitat loss for subsurface GDEs as previously saturated sediments become dry and uninhabitable for groundwater fauna (Stumpp and Hose, 2013). The effect of groundwater extraction can be to lower water tables (increase depth to groundwater), particularly for unconfined aquifers, and a reduction in pressure for confined aquifers. The reduction in aquifer pressure is manifest as decreased flow for example from artesian springs, and lesser volumes discharged to support surface aquatic GDEs (Hayashi and Rosenberry, 2002). Changes in groundwater flow and pressures due to pumping also changes interactions with surface water ecosystems (Sophocleous, 2002). Related impacts include the reduction of nutrients and oxygen inputs as connections with rivers and wetlands are lost, while in coastal areas, ingress of marine water impacts coastal groundwater quality, as reduced flow and pressure of fresh groundwater allows saltwater intrusion. The threat of groundwater abstraction is often unintended and the consequences for all GDE types are poorly understood (Eamus et al., 2016).

Knowledge gaps

1. The global distribution of different GDE types
2. Details and thresholds of change in groundwater attributes that affect GDEs
3. Degree of dependency of ecosystems on groundwater attributes
4. The impact of water quality changes on GDEs
5. Impacts of climate change on groundwater regimes and GDEs

Important case studies

Name of site	*Country*	*Coordinates*	*Main topic/concept*	*Key reference*
Fremont-Winema National Forest, Oregon, USA	USA	42.57°, –121.57°	Using hydro-ecological relationships to determine groundwater thresholds for swamps and fens	Aldous and Bach (2014)
Various sites a across five continents	Global		Analysis of coastal lagoon GDEs	Erostate et al. (2020)
Pilbara region	Australia	115–112°, 20–25°	Extensive survey of groundwater fauna	Halse et al. (2014)
Australia	Australia		Assessment of groundwater dependent ecosystems at continental scale	Doody et al. (2017)
Global review	EU, USA, South Africa, Australia		GDE policy	Rohde et al. (2017)
New South Wales	Australia		GDE prioritization	Dabovic et al. (2019)
California	USA	–124 to –116°, 42–32°	GDE mapping	Howard and Merrifield (2010)

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Groundwater and Surface Water Interaction☆

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This is an update of H.M. Valett, R.W. Sheibley, Ground Water and Surface Water Interaction, In Encyclopedia of Inland Waters, Edited by Gene E. Likens, Academic Press, 2009, https://doi.org/10.1016/B978-012370626-3.00019-3.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Amphibite Animals (typically invertebrates) with phases of their life cycle adapted to both groundwater and surface environments.
Baseflow Both a temporal distinction of channel flow describing flow that occurs without the influence of recent precipitation and a spatial orientation where groundwater flowpaths are generally perpendicular to the channel.
Damköhler numbers Numbers adopted from chemical engineering that relate alternative fates of solutes (transport or transformation) in a reactor; used to quantitatively describe reactive transport dynamics in environmental systems.
Groundwater Water present beneath the Earth's surface in rock and soil pore spaces and in the fractures of rock formations.
Hydrodynamic driver Relating to pressure gradients on the surface of the streambed primarily resulting from the momentum of channel water molecules interacting with geomorphic features that cause water to flow into the hyporheic zone; hydrodynamic forces strongly influence shallow hyporheic fluxes at fine to moderate spatial scales (e.g., bedforms, pool-riffle sequences).
Hydrostatic driver Relating to the pressure gradients on the streambed surface driven by the depth of the overlying water; hydrostatic forces influence hyporheic fluxes over coarse spatial scales (e.g., reaches or greater).
Hyporheic zone Subsurface volume beneath and lateral to a river or stream characterized by the bidirectional exchanges of water and resources with the stream channel.
Phenomenological models Models that quantify GW-SW exchange or related processes with mathematics that represent the influence of numerous physical drivers without simulating them explicitly.
Physically-based models Mechanistic models that quantify GW-SW exchange or related processes as a function of a suite of physical drivers.

☆*Change History*: November 2021. HM Valett prepared the update. Sections/figure/tables are updated within the article.

Stygobite Obligate groundwater animals (typically invertebrates) with evolutionary history shaped by subsurface environments.
Underflow Groundwater flow that is generally parallel to the longitudinal axis of the stream channel.

Introduction

The hydrologic processes of infiltration, recharge to groundwater, and discharge to channels illustrate the implicit connectivity between groundwater and surface water. Historically, the existence of streams has been argued to be a manifestation of groundwater-surface water (GW-SW) interaction because channel flow typically originates from groundwater discharge. Hence, it is not surprising that hydrologists and ecologists working on streams have led the way in pursuit of understanding GW-SW interactions.

In particular, research addressing GW-SW in streams has focused on the hyporheic zone (Orghidan, 1959), defined here as the subsurface zone beneath and laterally adjacent to a stream channel, characterized by the bidirectional exchange of water between the surface and subsurface (Boulton et al., 1992). Thus, exchange with the hyporheic zone is a type of 'hydrologic exchange flow' (Harvey and Gooseff, 2015), flow that includes lateral and vertical transport of water, materials, and energy between rivers and their surrounding marginal surface and subsurface waters.

This chapter addresses the ecological and hydrologic properties of hyporheic zones, and also reviews GW-SW influences on other inland waters. We first consider how GW-SW exchange has the potential to alter hydrologic, biogeochemical, and biological conditions associated with streams. It then covers flow systems, drivers of GW-SW interaction, and how such exchange flows are measured across scales of assessment. Sections on the modeling of hyporheic flow and reactive transport in the hyporheic zone address an active area of investigation, exploring both theoretical and applied research challenges. Finally, a short overview of GW-SW interactions in the floodplains of larger rivers and in lakes and wetlands is followed by an assessment of knowledge gaps and areas for future research in the context of environmental change.

Implications of hyporheic GW-SW interactions for aquatic ecosystems

Historically, the hyporheic zone has been studied as habitat for unique invertebrate fauna. Classification systems categorizing types of subsurface animals rely on the evolutionary history of the biota and the nature of their affiliation with groundwater habitats (Gibert et al., 1994). Macroinvertebrate assemblages in environments that receive water from and return water to the channel (i.e., hyporheos or stygophiles) are dominated by insects, often similar to benthic forms found on the stream bottom (Boulton and Stanley, 1995). In contrast, groundwater environments that are more isolated from hyporheic systems (i.e., phreatic water) support invertebrates with marine ancestry, predominantly crustaceans with obligate groundwater affinity (i.e., stygobites) frequently lacking eyes and pigment (Dole-Olivier et al., 1993). Other invertebrates that utilize both hyporheic groundwater and benthic environments (i.e., amphibites) share taxonomic affiliation with surface assemblages and emerge from streams as adults, but also display evident evolutionary adaptation to life underground (Stanford and Gaufin, 1974; Stanford and Ward, 1988). These kinds of affiliations underpin why the direction and magnitude of exchange can dictate the taxonomic composition and abundances of animals that live at the GW-SW interface.

Hyporheic exchange also influences habitat for surface biota. Purposefully borrowing terminology from oceanographers, areas of losing (i.e., influent) reaches are 'downwelling zones' and gaining (i.e., effluent) reaches are 'upwelling zones,' emphasizing the potential for nutrient delivery to alter benthic biological conditions (Valett et al., 1994). For instance, in nutrient-poor desert streams, upwelling nutrient-rich water promotes growth of algal forms that flourish among abundant nutrients (Fig. 1A) while downwelling portions of the reach are dominated by nitrogen-fixing cyanobacteria (Fig. 1B). Similarly, patterns of distribution and abundance of aquatic plants have been tied to the direction of exchange (Hendricks and White, 1988; Jones et al., 2008). The distribution of salmonid redds is also strongly related to distinct patterns of hyporheic exchange (Baxter and Hauer, 2000). The spatial configuration of discharge and recharge may organize responses by algae and aquatic plants, benthic macroinvertebrates, as well as fishes and water fowl that occupy surface environments in freshwater systems (Jones and Holmes, 1996).

Hyporheic zones themselves are well recognized as metabolically active systems that support mainly heterotrophic food webs linked to surface inputs of organic matter (Grimm and Fisher, 1984; Jones Jr. et al., 1995a; Fellows et al., 2001) Moreover, they are biogeochemically distinct environments. In many systems, downwelling of water that is rich in organic carbon supports metabolic activity in near-stream groundwater (Findlay et al., 1993) while mineralization of organic material in the subsurface can increase inorganic nutrient pools (Triska et al., 1994). The juxtaposition of electron donors and acceptors that occur at the GW-SW interface supports unique transformations (Dahm et al., 1998). Thus, the direction of exchange is a critical aspect of GW-SW interaction because surface and groundwater environments often differ markedly in their physicochemical composition (e.g., heat, redox potential, pollutants). For instance, surface water systems are generally characterized by turbulent flow and, thus, are typically oxic as compared to subsurface environments where dissolved oxygen content is reduced by chemical and biological demand. Accordingly, the hyporheic zone is often characterized by steep gradients in concentrations of oxidized and reduced compounds (Triska et al., 1989), rendering them biogeochemical hotspots (sensu McClain et al., 2003).

Hyporheic zones support diverse assemblages of microbes (Hendricks, 1993, 1996; Storey et al., 1999) that respond to and alter biogeochemical constituents introduced via GW-SW interaction (Feris et al., 2004, 2009). Because of the microbial and geochemical capacity for hyporheic zones to process a broad array of constituents, hyporheic zones have been referred to as the river's liver

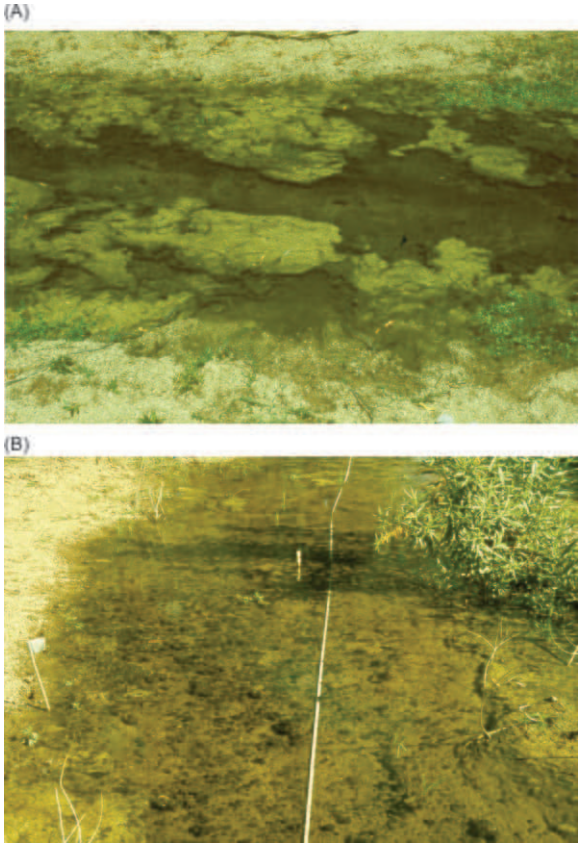

Fig. 1 Benthic algal responses to groundwater-surface water exchange in Sycamore Creek, Arizona, United States. (A) Groundwater discharge in upwelling zones supplies nitrogen from nutrient-rich interstitial environments and supports luxurious blooms of the green alga *Cladophora*. (B) Just 150 m downstream, in a downwelling zone, surface nitrogen concentrations are lower and the benthic flora is dominated by nitrogen-fixing blue green bacteria of the genus *Nostoc*. Photographs by H.M. Valett.

(Fischer et al., 2005). Hyporheic zones have been shown to be instrumental in terms of changing the form and abundance of nutrients that may potentially limit surface water productivity. For instance, studies have documented active hyporheic nitrification and denitrification (Triska et al., 1990; Jones Jr. et al., 1995b; Triska and Duff, 1996; Sheibley et al., 2003). Similarly, nutrient processing in the hyporheic zone of smaller streams (Mulholland et al., 1997; Lapworth et al., 2011) and larger rivers (Vervier et al., 2009) alters phosphorus abundance.

Hyporheic zones also have the capacity to provide critical ecosystem services. For instance, hyporheic zones attenuate transport of mining-derived pollutants (Gandy et al., 2007). Microbial and geochemical processes in the hyporheic zone of contaminated systems influence the concentrations, oxidation states, and mobility of metals, including manganese (Harvey and Fuller, 1998), arsenic (Nagorski and Moore, 1999), chromium (Yang et al., 2018), uranium (Fritz and Arntzen, 2007) and selenium (Arnold et al., 2016) among others. Many organic contaminants are also susceptible to hyporheic transformation and degradation (Lewandowski et al., 2011; Peter et al., 2019). The efficiency with which hyporheic zones process materials results from the catalytic role of microbiota and the balance between material reaction and transport.

The hydrology of hyporheic flow paths is thus a critical organizer of the magnitude and character of chemical loads and associated water residence times (i.e., amount of time spent in flows linking surface and subsurface environments). In this way, the nature of GW-SW exchange sets a physical potential for delivery of water and materials that is acted upon by biological and chemical processes. In combination, these drivers determine conditions experienced by biota that manifest as ecological structure and function within the hyporheic zone with implications for functioning at the whole-system scale (Fig. 2, Valett et al., 1996).

A number of studies have illustrated the potential influences for GW-SW exchange and biogeochemical processing within the hyporheic zone to influence the spiraling of nutrients at the whole-stream scale. Metabolic activity in the hyporheic zone has been tied to shorter spiraling lengths for phosphorous (Mulholland et al., 1997) while greater GW-SW interaction was associated with shorter uptake lengths (i.e., downstream distance required for removal from the water column) for nitrate-nitrogen across streams with different parent lithologies and propensity for hyporheic exchange (Valett et al., 1996). In tropical systems, Gücker and Boëchat (2004) found that stream geomorphology, including measures of hyporheic zone size, determined uptake of ammonium-nitrogen. In fact, Runkel (2007) championed a transport-based assessment of nutrient spiraling that directly linked GW-SW exchange to uptake dynamics, emphasizing the intimate links between them. Conversely, Sheibley et al. (2014) showed that hyporheic exchange is a poor predictor of spiraling in agricultural streams wherein rates of water and nutrient exchange between the surface and subsurface are typically low.

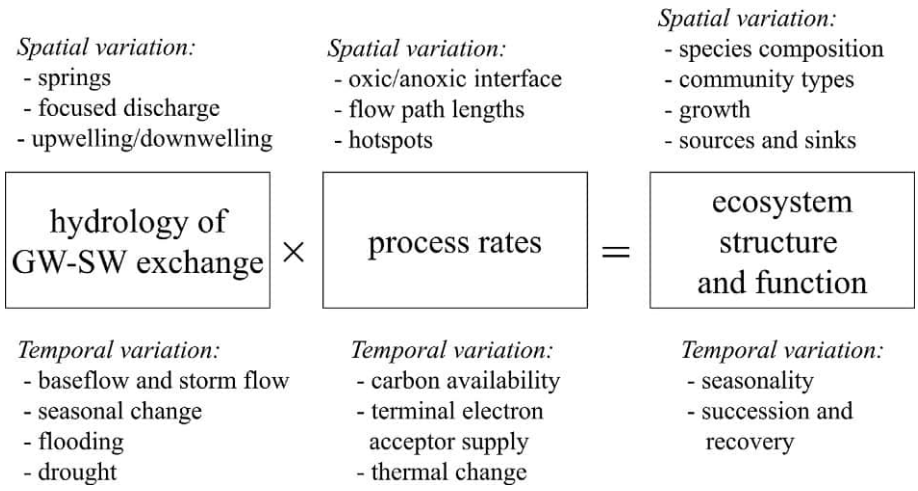

Fig. 2 A general schematic model relating how hydrologic and both geochemical and biological processes dictate the influence of groundwater-surface water exchange on various aspects of inland water environments. Determinants vary with space and time at multiple scales. Hydrologic influences include the magnitude, timing, and locations of interactions between groundwater and surface water. Moreover, hydrologic variance dictates water residence times with implications for how processes influence water availability and composition. Geochemical and biological processes alter water abundance and chemical quality and interact with hydrologic vectors to determine the net influence of exchange on physical, chemical, and biological aspects of inland aquatic ecosystems. Modified from Valett HM, Morrice JA, Dahm CN and Campana ME (1996) Parent lithology, surface-groundwater exchange, and nitrate retention in headwater streams. *Limnology and Oceanography* **41**: 333–345, with permission.

Flow systems, scales, and drivers of GW-SW characterization

Aquifers are linked to above-ground bodies of water at multiple spatial and temporal scales that constrain and characterize the hydrologic character of GW-SW interaction. Early work by Tóth (1963) recognized regional, intermediate, and local 'flow systems' and classified them by the temporal and spatial scales that link precipitation and recharge to groundwater discharge and channel runoff (Table 1). Our addition of a 'proximate' scale emphasizes flow paths of smaller extent that embrace much of the GW-SW interaction associated with hyporheic zones.

In running waters (i.e., lotic systems), water fluxes across the streambed are dictated by the gradient in hydraulic head (i.e., energy per unit weight). At smaller scales, the influences of flow velocity and the pressures created by water interacting with geomorphic features, such as bedforms or point bars, represent 'hydrodynamic' contributions to total head and dictate the magnitude and character of exchange. In contrast, the 'hydrostatic' component of the total head reflects the influences of elevation and the height (i.e., pressure) of overlying water. Water velocity does not contribute to hydrostatic pressure head. Hydrostatic forces are predominant drivers of exchange at larger spatial scales.

Hyporheic exchange flows have a wide range of water velocities and vary widely in terms of subsurface distances travelled. However, flow regimes emerge wherein GW-SW exchange is closely coupled to distinct elements of the stream channel because the mechanisms driving exchange differ in magnitude and etiology across spatial sales (Fig. 3). As emphasized by Boano et al. (2014), this coupling results in predictable patterns between hyporheic residence times and the length or depth of the geomorphic feature associated with the exchange, giving rise to 'characteristic residence times' and 'characteristic flowpath lengths', respectively. Fluid residence times and distances travelled shape how GW-SW exchange influences ecosystem structure and function (see Section "GW-SW interaction, reactive solutes, and the Damköhler number" below).

Table 1 Flow systems linking surface and groundwater at multiple scales.

Flow System	*Connection with Surface Recharge*	*Flow Rates ($m\ d^{-1}$)*	*Oxygen Status*	*Potential for transport form the surface*	*Example*
Regional	Virtually nonexistent	Almost stagnant	Anoxic/Anaerobic	Virtually nonexistent	Deep basin/petroleum reservoirs
Intermediate	Small	Slow	Generally Anoxic/ Anaerobic	Moderate	
Local	Extensive	0.0001–0.001		High	Confined aquifer
Proximate	Extensive	Fast	Often Oxic and Aerobic	Extremely High	Water table aquifer
		0.001–0.01	Fully Anoxic		Hyporheic zones, Seepage lakes
		Extremely Fast	Fully Oxic		
		1–1000	Mixed		

Adapted from Chapelle FH (1993) *Ground-Water Microbiology and Geochemistry*. New York: Wiley, with permission.

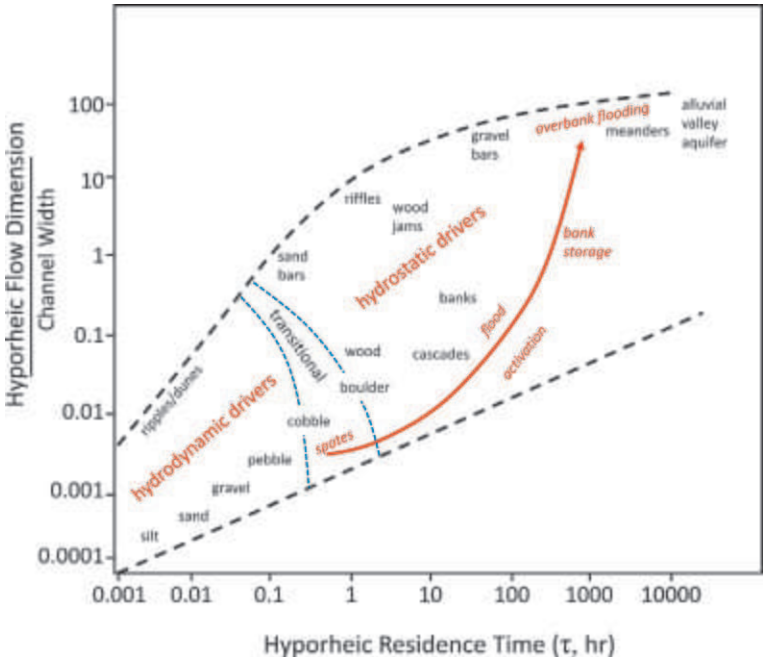

Fig. 3 Schematic representation of the scaling of hyporheic zone size (normalized to river channel width) vs. the time water spends involved in GW-SW exchange. Dashed black lines are boundaries on the spatial and temporal behavior of hyporheic flow. Features of lotic systems that influence exchange are listed within the described functional space at locations commensurate with their characteristic spatial and temporal behavior. Terms in red denote important regimes of hyporheic flow and the role of channel flow in activating them (red arrow). The dashed blue lines illustrate transitional conditions where exchange flows are influenced by both hydrodynamic forces (i.e., velocity and momentum) and hydrostatic drivers (depth, slope). Redrawn from Boano F, Harvey JW, Marion A, Packman AI, Revelli R, Ridolfi L and Wörman A (2014) Hyporheic flow and transport processes: Mechanisms, models, and biogeochemical implications. *Reviews of Geophysics* **52**: 603–679. doi: 10.1002/2012RG000417, Published with permission.

Hydrodynamic drivers are responsible for generating flow through shallow pathways shorter than the stream's depth and are closely associated with streambed substrates. They are highly influential in systems with bedforms composed of silt and sand, typically at the scale of centimeters to tens of centimeters in small streams. However, these types of exchange flows can also occur through mega-bedforms of several meters height and over hundreds of meters in rivers like the Mississippi, Amazon, and Parana (Boano et al., 2014). In contrast, hydrostatically driven exchange reflects changes in stream slope associated with transitions among riffles, runs, and pools, and with gravel bars and meanders. These flowpaths may extend far from the river, up to many hundreds of meters (Stanford and Ward, 1988) with residence times of many hundreds of days (Helton et al., 2014). While these exchange regimes are better described for streams and rivers, similar mechanisms apply to shallow areas of lakes, reservoirs, estuaries, and shoreline oceanic habitat, driven by currents and wave forces.

Biological processes and structures can also influence GW-SW exchange. For example, beaver dams (Lautz et al., 2010) and salmon redds (Gottesfeld et al., 2004) alter exchange as a result of changing instream features. Even small invertebrates such as crayfish (Johnson et al., 2011) and caddisflies (Tumolo and Albertson, 2020) can influence streambed hydraulics; additionally, the biological activity of a wide range of invertebrates can induce flow (i.e., bioirrigation) via activities that alter and organize sediment structure (bioturbation). Finally, aquatic plants and algae can alter stream bed roughness, influencing water residence times and streambed exchange (Hendricks and White, 1988).

Measuring GW-SW interaction: Methods and approaches

Measuring GW-SW exchange

Two general classes of methods for measuring GW-SW interaction can be recognized: physically-based and phenomenological methods. These distinctions apply to direct measures of GW-SW exchange, simulation modeling (see Section "GW-SW interaction, reactive solutes, and the Damköhler number"), or a combination of both. Physically-based methods rely on understanding the physics of the hydrological processes controlling exchange. Approaches in the second class are considered 'phenomenological'. These require observations collected from the system that are interpreted to assist in the quantitative characterization of GW-SW exchange. While data are required for either approach, phenomenological methods are so named because patterns in direct observations are represented with math based on empirical relationships or "phenomena", as opposed to representing mechanisms directly.

Flumes and laboratory studies

Use of flumes and laboratory studies to address GW-SW exchange provides opportunities to experimentally establish forms of roughness elements, to directly control flow, and to alter a single feature, and the physics associated with it, via experimentation. These approaches allow for the development and verification of physically-based simulation models (see Section "Modeling GW-SW exchange") and also facilitate direct measures of the forces and pressures responsible for exchange. Accordingly, they typically address hydrodynamic exchange associated with small-scale bedforms using chemical tracers (e.g., dye or salt).

Field assessment of GW-SW exchange

Measures of GW-SW exchange at field scales include indirect measures via stream flow gauging, hydrometric approaches, and tracer-based methods. The different techniques used involve tradeoffs between specificity and generality related to the spatial scale at which they are employed.

Mass-balance approaches

The magnitude of GW-SW exchange can be determined indirectly through mass-balance approaches that rely on measuring channel flow at designated locations, accounting for tributary inputs, and quantifying exchange by difference. The approach is challenging in complex channels that are shallow and wide, and in larger channels where flow is swift and often associated with unstable streambeds. A combination of dilution gauging (i.e., tracer dilution along a stream reach, see Section "Tracer-based methods" below) and use of acoustic velocimeters has increased the applicability and accuracy of this approach. The same mass-balance approaches apply to lakes and wetlands but require more accurate measures of loss from the water body to the atmosphere via evaporation and evapotranspiration.

Hydrometric approaches

Exchange fluxes can be estimated directly using hydrometric approaches that include measuring hydraulic head gradients vertically and horizontally in the stream bed (Fig. 4A), estimating streambed hydraulic conductivity (K; Chen, 2000), and calculating flux via Darcy's Law. Accurate measures of K are notoriously difficult to obtain, in part due to extensive spatial heterogeneity. Basic estimates

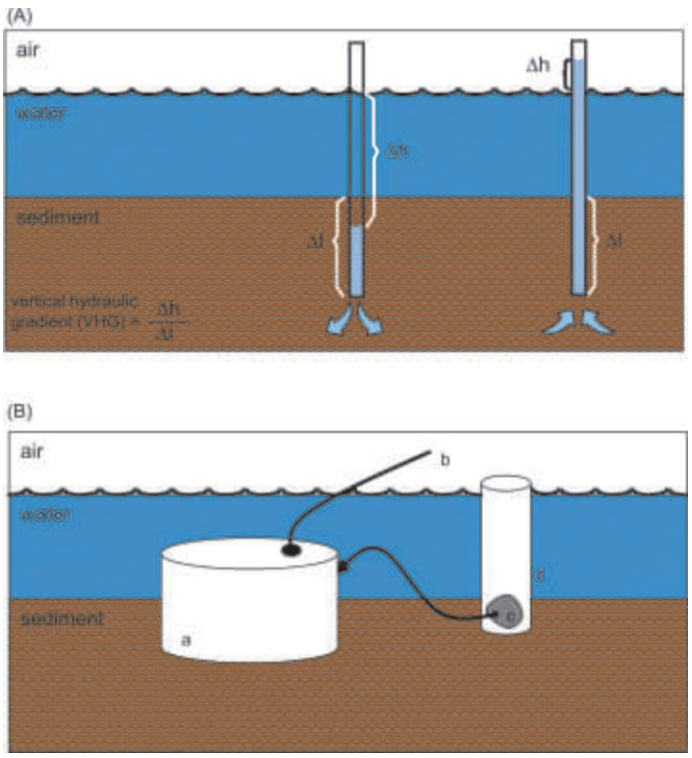

Fig. 4 Schematic representations of the use of (A) mini-piezometers to measure vertical hydraulic head gradients, and (B) seepage meters to quantify volumetric groundwater-surface water exchange in streams. Mini-piezometers allow for comparison of hydraulic heads at depth with surface water potentials. The vertical hydraulic gradient (VHG) is then calculated as the head difference divided by the depth of the piezometer, combined with measures of sediment hydraulic conductivity, and used in Darcy's Law to calculate exchange. Seepage meters measure volumetric flux directly and include an open cylinder (a) inserted into stream sediments and vented to the atmosphere (b). Groundwater discharge is collected in a plastic bladder (c) placed in a stilling well (d).

of K can be derived from laboratory analysis of grain sizes derived from sediment cores. Other methods of assessing K involve pump tests and monitoring wells that provide information on larger scales.

Direct measures of the volumetric flow of water across the surface-subsurface boundary can be provided by seepage meters (Fig. 4B). A seepage meter typically consists of a bottomless cylindrical chamber vented to a plastic bladder. Under conditions of groundwater discharge, flow from the substrate to the water column will collect in the bladder at a measurable rate. Infiltration from the surface to subsurface may be measured as a loss of water purposefully placed into the bladder at the time of chamber deployment. These types of seepage meters have been used extensively in lakes, estuaries, and reservoirs, and less frequently in streams.

Tracer-based methods

Whether direct or indirect, hydrometric methods are effective at relatively small scales ranging from gravel bars to features as large as relatively short (i.e., 10–100 m) reaches. Environmental tracers are often employed when investigators desire information on GW-SW interaction at larger scales. Often, traditional hydrometric approaches (e.g., use of wells and piezometers) are combined with the use of tracers to address spatially distributed measures at larger scales. Below, we provide a brief introduction to the use of tracers; for a recent detailed review of the use of environmental, biological, and anthropogenic tracers, see Abbott et al. (2016).

Environmental tracers are ambient natural or human-derived compounds found widely distributed in the Earth's shallow environments that may be used in hydrologic studies to discern sources, pathways, and timescales of interaction between surface and subsurface waters. To be useful, environmental tracers should naturally occur at different concentrations characteristic of potential sources (e.g., groundwater vs. channel water). The concentration in different water types allows calculation of mixing proportions among proposed sources. Examples of commonly used environmental tracers include specific electrical conductivity, chloride and other major ions, or stable isotopes of water (i.e., ^{18}O, ^{2}H). A range of radioisotopes have also been used to assess GW-SW exchange. More recently, human-derived compounds like caffeine or pharmaceuticals have been employed as environmental tracers with particular focus on materials derived from waste water treatment plants.

Heat in groundwater and surface water can also be used as a tracer to assess GW-SW exchange, an approach that has grown in popularity with the advent of inexpensive, easily-deployable temperature sensors. Most studies of this type employ vertical arrays of sensors to track GW-SW mixing across the streambeds, but also in wetlands and floodplain environments. Quantitative information is also being obtained by applying heat transport equations that account for both conductive and convective transport and heat balance. With this approach stream temperature is the function of groundwater discharge rate, differences in stream and groundwater temperature, stream flow, and heat exchange from the stream surface. Thus, net heat (and water) flux from groundwater is derived by difference.

Efficacy of studies utilizing tracers can be improved by introducing known tracers via solute releases (i.e., solute injections). Injections introduce conservative (i.e., unreactive) tracers—typically inorganic anions like Cl^- or Br^- or fluorescent dyes like rhodamine—that are tracked downstream both in surface and groundwater environments to address mixing between the channel and hyporheic zone. Sampling of the tracers over time generates breakthrough curves (Fig. 5) that can be analyzed to characterize GW-SW exchange. Breakthrough curves from channel water locations can also be used to determine stream flow via dilution gauging (Gordon et al., 1992) where integration of the concentration versus time curve yields flow magnitudes that can be used in mass-balance approaches. Breakthrough curves can also be used in modeling approaches assessing exchange (see Section "Modeling GW-SW exchange" below). Combining tracer methods with hydrometric measures of exchange includes measuring differences in tracer concentrations among wells and piezometers to derive spatial distributions of the extent and rates of exchange. Recently, investigators have combined geophysical imaging techniques that track electrical resistivity with release of electrically conductive salt tracers (e.g., Cl^-) to measure subsurface dynamics.

Modeling GW-SW exchange

Determination of GW-SW exchange and its influences on geochemical and biotic processes remains a major challenge due to variation in catchment lithologies, geomorphologies, land uses, biotic communities, and atmospheric inputs, along with the problems of integrating across scales of investigation (Harvey et al., 2019). Consequently, computer modeling approaches are useful as they allow researchers to isolate and manipulate components of streams systems in ways that are intractable or impossible in empirical studies.

Modeling studies assist researchers in explaining existing patterns through hypothesis generation, refinement, and testing of predictions addressing system behavior. As a method for assessing GW-SW interaction, modeling studies of stream systems also fall into the two broad categories described in Section "Measuring GW-SW exchange": physically-based and phenomenological (Boano et al., 2014). The current section provides a broad overview of these models and their value as tools for understanding GW-SW interaction.

Physically-based models

Physically-based models rely on quantifying key mechanisms driving GW-SW interactions by operationalizing the physical principles of mass and momentum balance as mathematical equations in code (Boano et al., 2014). Such models focus on the

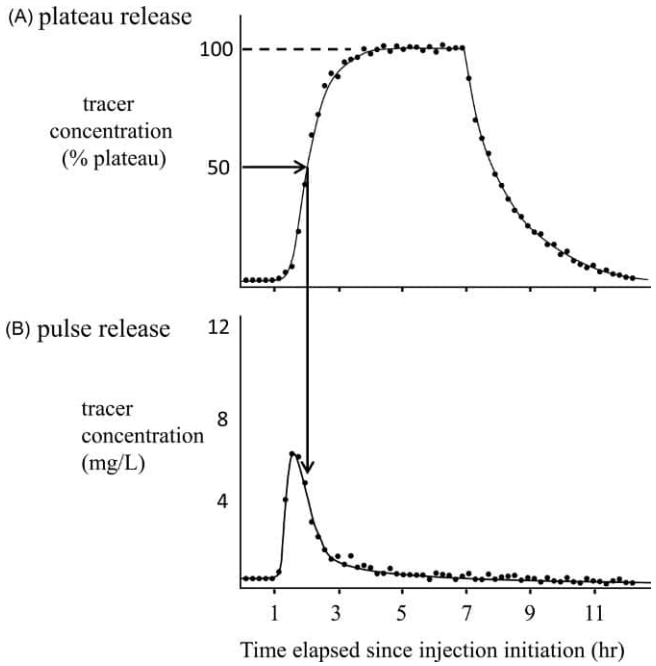

Fig. 5 Simulated tracer response (breakthrough) curves illustrating (A) plateau and (B) slug (or pulse) tracer profiles (black dots) generated by each release design. Plateau releases involve adding tracer upstream at a constant rate for a specified period of time. Once the tracer is well-mixed within the study reach, tracer concentration at the downstream monitoring site are at 'plateau' and will not change with continued tracer addition (panel A). Slug releases entail instantaneous addition of a given volume and mass of tracer that passes the downstream monitoring location and create a pulse profile downstream (panel B). Dashed line denotes plateau concentration. Arrows indicate time after initiation when tracer concentration is 50% of plateau (A) which is the same time at which 50% of tracer mass in a pulse release has arrived at the sampling transect (B). Solid lines are best-fit representations of continuously measured tracer response derived from numerical modeling (see Section "GW-SW interaction, reactive solutes, and the Damköhler number").

factors and forces that control water fluxes between the channel, banks, streambed, and subsurface. Advantages of physically-based models include that they have high mechanistic explanatory power, and help advance scientific understanding of how stream flow and morphology interact to govern GW-SW exchange. However, compared with phenomenological models (see Section "Tracer-based methods" below), physically-based models have a greater number of input parameters that must be determined from empirical study of the hydrosystem (i.e., morphology, sediments, and hydrodynamic drivers therein). Thus, the level of detail required to parameterize physically-based models has resulted in their being focused on spatial scales ranging from small bedforms (Elliott and Brooks, 1997a, 1997b) to sediment bars (Tonina and Buffington, 2007) to river bends (Boano et al., 2006). Physically-based models become more difficult to construct at coarser spatial scales because the number of physical mechanisms and their interactions increases with increasing spatial scale, leading to the widespread application of phenomenological models at the scales of stream reaches to whole catchments.

Phenomenological models

Phenomenological models differ from physical models in that they aim to capture and predict system behavior (i.e., GW-SW exchange) without directly modeling the mechanisms giving rise to them. Thus, phenomenological models do not include equations that physically represent and relate the individual hydrostatic and hydrodynamic forces influencing GW-SW exchange. Instead, they capture the influence of these forces in ways that are consistent with empirical observations and theory.

Phenomenological models rely on signals derived from physically-based models, tracer-release studies, or a combination of both to assist in accurately describing hydraulic behavior. Among the critical components addressed, the residence time distribution for water has received the most attention (Boano et al., 2014). The residence time distribution is among the most important components of many phenomenological GW-SW exchange models because it quantitatively describes the duration that parcels of water will spend in a given spatial domain (e.g., reach, channel, hyporheic zone). Characterization of the residence time distribution is imperative for most phenomenological models of contaminant transport, stream-solute sorption-adsorption dynamics, and coupled biogeochemical-hydrological processing.

Phenomenological modeling has a rich history and remains an active area of research. In a recent review, Boano et al. (2014) described several phenomenological models employed in GW-SW research: the advection dispersion equation (ADE); space and time fractional advection-dispersion equations (S-FADE, T-FADE, and ST-FADE), transient storage model (TSM), multirate mass

transport (MRMT); advective storage paths (ASP); decoupled continuous time random walk (CTRW); and solute transport in rivers (STIR). Details of these models is beyond the scope of this chapter, but we name them here to facilitate further investigation. Of these models, the TSM has been the most influential and widely adopted model of GW-SW exchange in stream ecology (Webster and Valett, 2007).

The TSM model (Bencala and Walters, 1983) predicts how solutes will move through a stream by considering their movement through two compartments: the advection-dominated stream channel and a connected zone which provides temporary (i.e., transient) storage for a volume of water and mass of solute. The TSM approach includes modified advective-dispersion equations that account for two-way hydrological exchange between these compartments. Thus, transient storage describes areas where the stream flow is slowed relative to the bulk advective velocity. Transient storage of stream flow may result from pools, backwaters, eddies, side channels and floodplains, as well as hyporheic exchange. Historically, transient storage was interpreted to represent hyporheic exchange, but surface features (e.g., eddies, pools) contribute to storage under appropriate conditions.

The popularity of the TSM relates to the elegance of the underlying conceptual model, the minimal number of model parameters it requires, and the availability of user-friendly software, which offers a finite difference approximation to the TSM (i.e., OTIS, Runkel, 1998). However, hydroecological modelers have been actively researching ways to overcome some of the simplifications of TSM (e.g., application of exponential residence time distributions and mathematics representing transient storage zones as well-mixed compartments). Many of the phenomenological modeling advances over the last 25 years (i.e., models listed above) have been made to address simulating GW-SW exchange in systems wherein the simplifications in the TSM cannot capture the key drivers and ecosystem patterns of interest, particularly over longer timescales than TSMs can simulate well.

GW-SW interaction, reactive solutes, and the Damköhler number

In a seminal paper, Gerhard Damköhler addressed the efficiency of chemical reactors (Damköhler, 1936) by considering how solutes were influenced by the alternative fates of reaction and transport. The elegance of Damköhler's conceptual approach and mathematical framework has resulted in it being broadly integrated into hydroecological research in a wide range of flow systems. Flow systems, like chemical reactors, have the capacity to transport and process solutes, prompting characterization of groundwater-surface water interactions through use of Damköhler numbers.

Different forms of Damköhler numbers exist (Oldham et al., 2013), but the version applicable to stream systems (Da_I) embraces advective flow and—to date—has employed 1st-order reaction-rate kinetics following Eq. (1):

$$Da_I = \frac{\tau_t}{\tau_r} = \frac{k \cdot l}{u} = k \cdot \tau_t \tag{1}$$

where τ_t is the characteristic transport time (T), τ_r is the characteristic reaction time (T), k is the reaction rate constant (T^{-1}), l is the length of the stream reach (L), and u is the mean water velocity (LT^{-1}). Conceptually, a larger Damköhler number ($Da_I >> 1$) indicates that a system is "reaction dominated" (transformation outpaces reactant delivery) whereas a smaller Damköhler number ($Da_I << 1$) indicates that a system is "transport dominated" (reactant transport through the system outpaces transformation).

Given the assumption of first-order kinetics, the characteristic reaction time (τ_r) occurs when e^{-1} (or 36.8%) of the original reactant remains. With knowledge of transport rates (solute delivery) and reaction rates (solute uptake or transformation), the Da_I quantitatively describes the efficiency of a flowpath, stream reach, or hyporheic zone. The Da_I can also be calculated as function of the initial (C_0) and remaining (C) reactant concentrations as follows:

$$Da_I = \log(C_0) - \log(C) \tag{2}$$

In GW-SW research, Da_I was first used to describe the behaviors of conservative tracers as a tool to improve the design of tracer release studies that quantified hyporheic exchange (Wagner and Harvey, 1997). In more recent studies, focus has shifted to addressing reactive tracers—i.e., nutrients and contaminants—and their behavior in stream systems. Studies describing reactive transport dynamics with Damköhler numbers have expanded greatly since their introduction and have influenced current hydroecological thinking. Quantitative integration of transport and reaction dynamics with Damköhler numbers has led to new ways of characterizing the significance of hyporheic-zone reactions for whole-stream and whole-network biogeochemical budgets. Through calculation of the Reaction Significance Factor (RSF) this approach addresses the tradeoffs between GW-SW fluxes, residence times, and reaction rates for a given exchange zone (Harvey and Fuller, 1998; Harvey et al., 2013). Use of the RSF, and Da_I more generally, has prompted an active and exciting area of research (Oldham et al., 2013; Abbott et al., 2016; Harvey et al., 2019) with implications for understanding controls over water quality.

Expanded use of the Damköhler number reflects the utility of the metric for capturing stream function and its broad applicability. Damköhler numbers are relevant across multiple spatial scales, solute types, and reaction mechanisms. Damköhler numbers have been used to describe the reactive transport dynamics at spatial scales ranging from pores (Briggs et al., 2015) to gravel bars (Zarnetske et al., 2012) and entire river networks (Schmadel et al., 2018; Harvey et al., 2019). Likewise, Damköhler approaches are suitable for characterizing reactive transport for a wide range of solutes and can be used to describe both biotic (e.g., biogeochemical) processing as well as geochemical (e.g., sorption-adsorption) dynamics (Abbott et al., 2016). For these reasons, many hydroecologists have converged on the utility of viewing hydrosystems as reactors whose efficiency can be described using Damköhler numbers.

GW-SW interaction across the inland hydrosphere

Rivers and floodplains

In rivers, the spatial and temporal scale of geomorphic features, flow paths, and fluid residence times associated with GW-SW exchange are increased compared to streams (Fig. 3) including important links to adjacent floodplains, geomorphic entities absent from streams. At the scale of the river basin, two fundamental types of flowpaths exist, (a) underflow, and (b) baseflow (Fig. 6). Underflow occurs when groundwater paths are parallel the river (Fig. 6A), more typical of steeper alluvial river valleys. Baseflow, a term often used to describe flow uninfluenced by recent precipitation, also reflects groundwater flow paths oriented perpendicular to the channel (Fig. 6B). When gradients are low and rivers are highly sinuous, baseflow promotes interaction with the channel through influent or effluent flowpaths. Mesic models of river systems emphasize groundwater inputs along river reaches while river flows in xeric environments typically also include losses to alluvial storage.

Baseflow and underflow can combine to create highly integrated river-aquifer-floodplain systems (Hauer et al., 2021). Complex flow paths generating GW-SW exchange result from changes in the direction of vertical hydraulic gradients responding both to channel constrictions (i.e., nick points) and to snowmelt recharge and baseflow discharge. Evidence for these complex flow paths

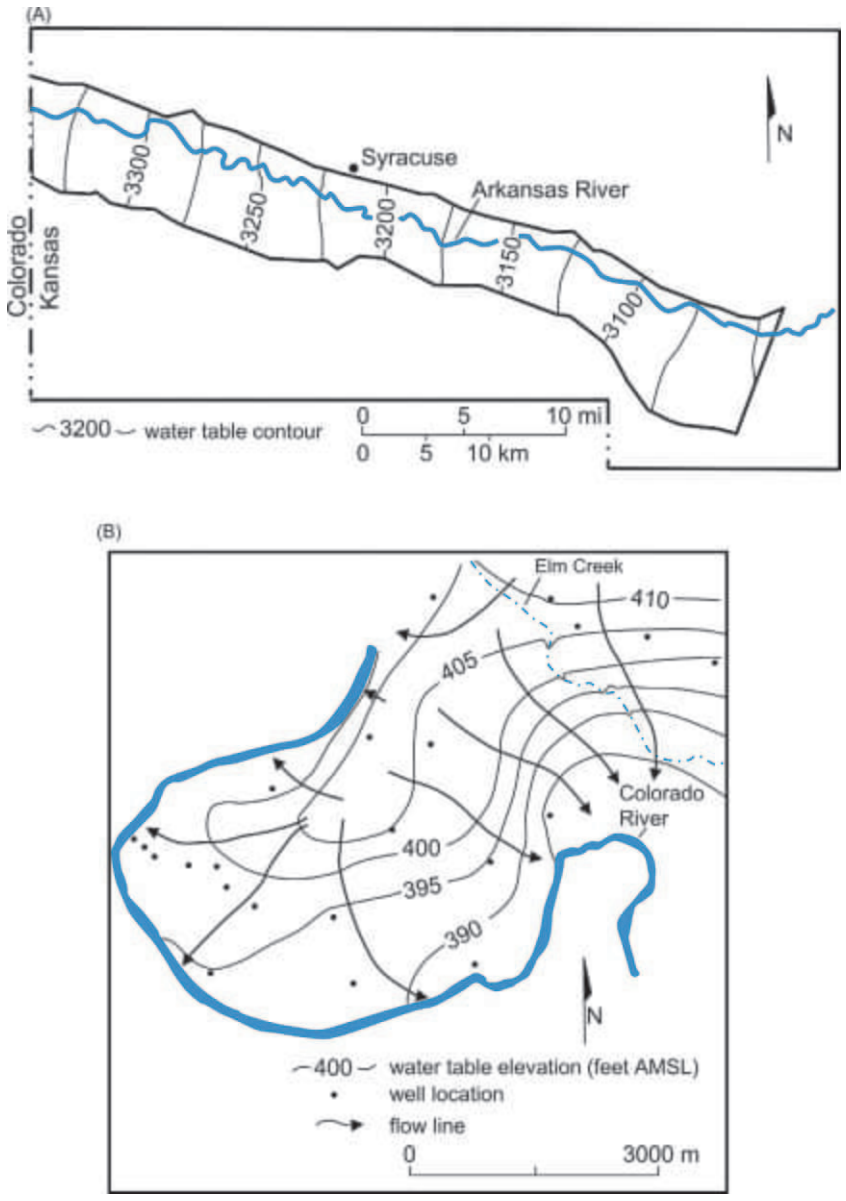

Fig. 6 (A) Groundwater flow parallel to the Arkansas River channel illustrates 'underflow' conditions characteristic of higher valley gradients. (B) Flows paths oriented perpendicular to the Colorado River, Texas generate 'baseflow' exchange between the alluvial aquifer and river channel. Adapted from Larkin RG and Sharp Jr RJM (1992) *Geological Society of America* **104**: 1608–1620.

includes changing groundwater chemistry, but is also apparent in subsurface biological communities. Researchers have documented the emergence of amphibiotic stoneflies from wells and septic fields up to 1 km from the waters of Flathead River, Montana, United States (Stanford and Ward, 1988). These same groundwater denizens have been found in other gravel bed rivers and along saturated beaches of montane lakes suggesting a long history of evolution and dispersal.

River flow can produce floodplain lakes and ponds by both overland flow and groundwater discharge as the water table rises above the land's surface in areas of low elevation. These hydrologic links with groundwater may seasonally connect lakes and ponds of the floodplain to main channel environments. Groundwater that emerges onto the surface of floodplains can also create highly productive 'springbrooks', reflecting groundwater inputs of nutrients and heat. At the same time, changing water table elevations alters metabolism and nutrient cycling in soils and subsurface sediments; inundation may accelerate or retard organic matter processing, and can influence productivity of riparian vegetation. For instance, research on cottonwood growth rates has shown that riparian trees in gaining reaches support larger and longer-lived trees (Harner and Stanford, 2003). Together, these hydrologic exchange flows contribute to the renowned diversity of floodplains worldwide.

Lakes and wetlands

Hydrologic exchange between lake water and groundwater occurs in three basic ways that can be used to categorize GW-SW interaction in lake systems. First, hydrologically mounded lakes receive virtually all of their water from precipitation and have seepage losses to groundwater throughout their beds. Second, terminal groundwater-discharge lakes receive water from adjacent aquifers throughout their beds. Third, pathways for water gain and loss in throughflow lakes is highly variable and dependent on geomorphic context. Because lakes exist in low points on the landscape, they may be influenced by flow systems ranging from local to regional with co-occurring proximate flow paths that influence their functioning as ecosystems.

In the process of GW-SW exchange, physical, chemical, and biological conditions are altered as water enters or leaves lakes. This phenomenon has been well documented for throughflow lakes in glacial and dune terrain where they are underlain by highly permeable deposits and are characterized by groundwater inflow along one shore and outflow along the opposite shore. Biological processes within lakes may provide critical protection from perturbations like acid rain by generating acid neutralizing capacity that is exported through seepage and provided to down-gradient water bodies. Concurrently, groundwater inflow can provide physical and chemical conditions that promote the growth of littoral algae and plants that influence the distribution of invertebrates and water fowl within and among lakes. Under these conditions, throughflow patterns may be relatively stable, but the boundaries of inflow and outflow along the lake bed change with time as the water table rises or lowers. Over varying time periods, precipitation and groundwater inflow may fail to match rates of evaporation, resulting in drastic declines in lake levels, increased concentration of dissolved solutes, and shifts in flow paths that alter GW-SW interaction. Accordingly, drought in the lake districts of Wisconsin and Minnesota, United States, resulted in very different loss of water from lakes that appear identical in most ways other than the character of GW-SW exchange (Webster et al., 1996).

Wetlands exist in climates and landscapes where groundwater discharge overwhelms rates of water loss via drainage or evapotranspiration. Their interaction with groundwater is similar to that of lakes since both wetlands and lakes may be heavily influenced by inflow, outflow, or some combination. However, unlike lakes, wetlands do not always occur at low spots on the landscape and their location influences how they are influenced by GW-SW exchange and how they act as aquatic ecosystems.

Typically, wetlands have been categorized by their hydroperiods (time of annual inundation and saturation). Wetlands such as fens may occur on slopes and act as groundwater donors to down-gradient systems. Bogs typically occur where groundwater flow systems converge or divide; some have no appreciable drainage or throughput (i.e., act as groundwater receivers). Many wetlands have both groundwater inflow and outflow and, thus, act to some degree as groundwater conveyors. Wetlands are highly diverse hydrologically and biologically, occur in both simple and complex flow fields, may be associated with slopes, perched in bottom lands, or integrated via river floodplains. Historic and recent emphasis on geographically isolated wetlands (GIWs, defined as those lacking surface inlets or outlets) has emphasized the importance of GW-SW interaction and the emergence of linkages at the landscape scale that suggest these types of wetlands are far from isolated.

Conclusion and synthesis

Ecological responses to GW-SW exchange are founded on the exchange flows that link water bodies in inherently complex ways. Among the most influential of all legislative accomplishments related to environmental protection, the Clean Water Act (CWA) of the United States regulates discharges of pollutants into the waters of the United States (WoTUS). Generally, WoTUS are defined as navigable waters and the tributaries that supply them. In decisions addressing whether links exist and establish a water body as WoTUS, GW-SW interaction has been identified as potentially representing a 'significant nexus', a condition identified as a legal precedent for inclusion. While much confusion exists around what is needed to establish a significant nexus, there is no doubt that GW-SW interaction influences the physical, chemical, and biological integrity of the waters involved and must be considered in the definition of WoTUS. Accordingly, the US Environmental Protection Agency has embraced issues of connectivity in addressing whether a water body is covered by the CWA. While receiving very different support from successive administrations, court rulings in summer of 2021 have supported expansion of the CWA protections. It is not, therefore, unreasonable to imagine that near-stream environments like hyporheic zones, groundwater flow paths that link lakes and wetlands to adjacent drainage systems, and,

potentially, riparian zones that border these aquatic systems may be regulated by the CWA in the foreseeable future. Beyond the scientific merit of understanding the integration of ecosystems across an array of landscapes, the study of GW-SW interaction plays a pivotal role in regulation, management, and stewardship of aquatic resources.

The realities of climate change, population growth, and energy demands combine to require the convergence of basic and applied research addressing GW-SW interaction across an array of challenging areas. Work remains to address how to build scaling relationships (i.e., mathematical relationships that predict behavior over scales that differ by orders of magnitude) that bridge hydrodynamic and hydrostatic realms of GW-SW exchange. There is an urgent need to understand the coupled spatial and temporal dynamics of GW-SW interaction as climate change alters the quantity, distribution, timing, and magnitude of precipitation. In addition, the propagation and retention of contaminant and wastewater influences in ground and surface waters further emphasize the need for better understanding of GW-SW exchange. Fortunately, the fundamental methods, approaches, and models reviewed here provide a broad and encouraging range of tools that can be applied to better understand GW-SW interaction in both theoretical and applied contexts in the face of rapid environmental change.

Knowledge gaps and environmental change

Human influences are evident at all scales in the natural environment and this is equally true for the processes and effects of GW-SW exchange (Hancock, 2002). Increasing documentation and appreciation of GW-SW exchange has drawn attention to the need to address how it will respond to environmental change, with particular focus on the potential influences of changing climate conditions. Here, we address some of the research needs associated with GW-SW exchange in the Anthropocene.

Water resource depletion and GW-SW linkages

Human activities rely on water availability and use, features that are at odds with one another in the face of climate change (Famiglietti, 2014). Decline in groundwater levels associated with pumping water creates gradients near surface water that may induce infiltration and lead to surface water losses, including streamflow depletion. Streams sourced primarily by shallow groundwater flowpaths are particularly susceptible (Hare et al., 2021). When groundwater depletion and induced recharge attenuates streamflow, water rights associated with groundwater become rights to divert stream waters, linking entities that are initially legally distinct in the United States. More work is needed to address how different approaches to water use and storage will influence key vectors of GW-SW exchange and their influences on water resource allocation.

Hydrosphere modifications

Hydroengineering, including construction of dams and impoundments, gravel extractions, channel straightening, and canalization have resulted in disconnection of rivers from their floodplains with implications for flow regimes and aquifer recharge (Tockner and Stanford, 2002; Nilsson et al., 2005). Changes in the distribution and timing of precipitation associated with climate change will interact with human modifications to the inland hydrosphere with unknown implications for GW-SW interaction and its influences. Increased efforts to address how climate change will interact with the development and operation of engineered water systems has been recognized by the US Army Corps of Engineers as part of their Climate Preparedness and Resilience Community of Practice. Understanding how these diverse drivers will collectively alter GW-SW interaction is a key component of proactive management approaches that will require research focusing on integrating these flows with water policy priorities.

Land use influences—Urbanization and agriculture

Urbanization can dramatically alter GW-SW exchange in streams through increases in impervious surface cover, reducing or eliminating infiltration, and promoting overland routing via flashy storms flows (Walsh et al., 2005). Reduced GW-SW exchange can increase erosion, cause bank failures, and cause urban streams to become dry during low flow periods. Furthermore, urban systems are often built along waterways and urbanization typically involves many of the engineered features described above. These features often eliminate GW-SW interaction, truncate network processes that reduce material transport, and enhance runoff as pulses of contaminants from sewage treatment plants, fluid storage tanks, landfills, industrial lagoons, and storm waters drain. Fundamental research on how urbanization alters GW-SW interaction should be integrated with urban water resource planning as the timing and distribution of water supply changes with climate in urban settings.

Agricultural conversion of land cover influences aquatic systems via erosion and sedimentation, irrigation, and application of agricultural chemicals (Hancock, 2002). These processes may change ecosystem function by altering hydrologic or biogeochemical aspects of GW-SW exchange (see Fig. 2). Erosion and sedimentation introduce fine-grained, often organic-rich, particles that may clog stream-sediment exchange, introduce sediment-bound contaminants, and alter biogeochemical function at the GW-SW interface. Irrigation often includes extensive canals and underground drains (i.e., tiles) that short-circuit flow paths linking surface water to groundwater. In some cases, irrigation returns increase recharge, elevate water tables, and enhance groundwater inputs to surface bodies. Agricultural chemicals, including pesticides and herbicides, may then enter groundwater via these modifications to the hydrologic system. Irrigation from groundwater sources, on the other hand, may result in groundwater decline, stream flow

depletion, and the drying of springs, marshes, and riparian areas, issues of particular concern in semi-arid lands. GW-SW interaction needs to be a central focus of research addressing how to better integrate agricultural practices with water quality and quantity needs, especially as extended drought becomes more challenging to food supplies in a world with changing climate.

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https://www.usgs.gov/mission-areas/water-resources/science/groundwatersurface-water-interaction?qt-science_center_objects=0#qt-science_center_objects—USGS Groundwater Information Pages.
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http://smig.usgs.gov/SMIG/reading_refs.html—Surface-water Quality and Flow Monitoring Interest Group.

Ecology of the Hyporheic and Parafluvial Zone

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Benthic zone The area at the bottom of a stream or river including the sediments.
Benthos The community of organisms living in the benthic zone.
Biocenosis An association of different organisms forming a closely integrated community.
Biofilm An assemblage of surface-associated microbial cells that is enclosed in an extra-cellular polymeric substance matrix.
Decomposition rate The rate at which dead organic substances are broken down into simple organic or inorganic compounds.
Ecotone A transitional habitat between two adjacent biological communities.
Hyporheos The community of organisms living in the hyporheic zone.
Macroinvertebrates Invertebrate fauna that can be captured on a 500 μm sieve.
Meiofauna Invertebrate fauna who pass through a 500 μm sieve but are captured on a 45 μm sieve.
Redox potential Tendency of a solution to gain or lose electrons when a new chemical species is introduced. It is used to characterize the oxidation-reduction status of an environment.
Riparian zone The interface between the land and a river or stream.
Stygobites Aquatic organisms that complete their whole life cycle, and are only found, in subterranean environments such as aquifers, springs and hyporheic zones.

Introduction

A significant milestone in freshwater research was the move away from a unidimensional perception of streams and rivers as pipes that move water from the source to the sea. It is now well established that complex multidimensional flow exchanges connect the river channel with the water table and the riparian zones through the bed sediments (Bencala, 1993). The volume of saturated sediments beneath the open channel through which these exchanges occur is known as the hyporheic zone (HZ; from the Greek *hypo* = under and *rheos* = flow or current) (Triska et al., 1989), which in turn is laterally linked to the terrestrial system through the parafluvial zone (the region of the river channel that is dry during low flows (Goldman et al., 2017, Fig. 1). The hyporheic-parafluvial zone (PHZ) is therefore a connected interface which receives aquatic, atmospheric and terrestrial inputs and in which biogeochemical processes occur (Goldman et al., 2017).

This sedimentary interface is an ecotone of enhanced energy and nutrient exchange, supporting diverse communities with taxa unique to the parafluvial and hyporheic zones as well as those from adjacent habitats (e.g., groundwater stygobionts, terrestrial colonizers). Important ecological processes take place within the PHZ, such as nutrient and water storage, cycling of nutrients and organic matter, contaminant detoxification, and fertilization of riparian zones (Boulton, 2007). In addition to their importance in biogeochemical cycling and as biodiversity reservoirs, PHZs are surprisingly large even though they might not be very visible compared to other parts of the riverine ecosystem. Battin et al. (2016) suggest that the bed sediments of streams and rivers have a surface area of between 100 and 1000 m^2 per cubic meter of sediment. Assuming a river bed depth of 1 m and approximating the global surface area of streams and rivers as 662,000 km^2 (from Downing et al., 2012), Battin et al. (2016) estimate a global surface area of beneath stream sediments of up to 662,041,000 km^2 (four times the area of the Pacific Ocean).

In recent years, PHZs have been a research focus for multiple disciplines (hydrology, zoology, microbiology, ecology, environmental engineering), resulting in significant advances in our understanding of their biodiversity, functioning and contribution to

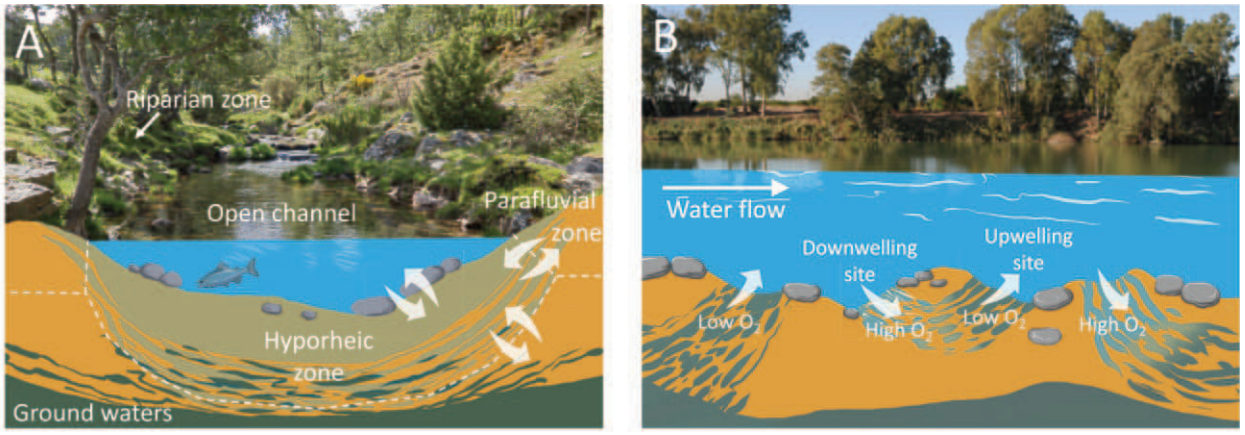

Fig. 1 Transversal (A) and longitudinal (B) representation of a river section. White arrows represent flow paths, which result in the hyporheic interchange.

ecosystem services. These achievements have been facilitated by the development of new analytical methods to capture subsurface hydrodynamics and biochemistry at very fine scales (e.g., Mechelke et al., 2019; Jaeger et al., 2019; Schaper et al., 2019; Martone et al., 2020; Coulson et al., 2021), and supra-disciplinary approaches that have led to the recognition of parafluvial-hyporheic habitats as active bioreactors with an impressive water-purifying capacity (Peralta-Maraver et al., 2018b, 2021).

However, together with their ecotonal nature, the existence of multiple field-specific definitions makes it difficult to delimit hyporheic and parafluvial zones from adjacent habitats, although this is central to quantification of their contribution to riverine ecosystem processes. Additionally, parafluvial habitats have received considerably less attention than hyporheic zones although this is beginning to change, for example a body of emerging research reports the important consequences of dry-rewetting cycles in parafluvial habitats for the biogeochemistry of soil and sediments in the whole river-floodplain landscape (Boye et al., 2017; Goldman et al., 2017; dos Santos Pinto et al., 2020). Furthermore, global knowledge of PHZ functioning is heavily skewed towards temperate zones at the expense of boreal and (sub) tropical regions (Peralta-Maraver et al., 2021). This is an important knowledge gap because temperature varies strongly across latitude and also determines community metabolism, and the ecosystem processes that communities sustain.

The overarching aim of this chapter is to provide a comprehensive framework for understanding the composition, complexity, diversity and functioning of the hyporheic and parafluvial habitats. We first describe how the abiotic habitat, the surface-groundwater hydrodynamics and flood pulses, redox gradient, and geomorphology of the sedimentary matrix define the hyporheic-parafluvial biotope. We then explain how the hyporheic-parafluvial biocenosis is organized through the habitat before moving to the ecological processes and services provided by PHZ. We pay particular attention to biologically driven decomposition processes, specifically organic carbon cycling and pollutants bioremediation. Finally, we propose important knowledge gaps, and suggest fruitful areas for future research.

Hydrodynamics within the sediments is the master variable controlling oxygen availability and parafluvial—Hyporheic zone functioning

Surface water penetrates into the PHZ and travels through the saturated sediments before returning to the open channel. During this journey surface water mixes with groundwater, changing its physicochemical properties due to microbial activity and sediment geology (Jones and Mulholland, 1999). The hyporheic compartment is the interface between oxidized surface waters and reduced groundwater, oxygen levels are typically at their highest in water entering the hyporheic zone from the surface stream and decrease thereafter. Groundwater, upwelling from underlying aquifers has lower levels of oxygen and, as it mixes with surface water entering the PHZ, a complex and spatially and temporally dynamic oxygen landscape comprising patches with differing oxygen concentrations is formed (Fig. 1). The full redox gradient is represented enabling biogeochemical processes such as nitrification and denitrification to occur. These processes are mediated by microbial consortia which in turn are influenced by other groups of the hyporheic zone food web (Krause et al., 2011). Thus the hyporheic zone attenuates nutrients and contaminants although the magnitude of this function varies with local conditions. Water temperature in the PHZ also varies depending on whether water is upwelling from groundwater (when temperature will be lower) or downwelling from the surface stream (when temperature will be higher). In any case temperature fluctuations in the PHZ are dampened compared to the surface stream (Lewandowski et al., 2019). The aquatic-terrestrial interface through the parafluvial compartment has been also recognized as a hot-spot of biochemical activity as a consequence of the drying-rewetting cycles and the resultant sequence of oxic and anoxic conditions. During wet episodes, oxygen is rapidly consumed within the pore space and anaerobic processes, such as denitrification and production of nitrous oxide, increase (Marcé et al., 2019; dos Santos Pinto et al., 2020). However, when desiccation occurs, aerobic pathways are favored again, reducing methane and nitrous oxide emissions, but promoting carbon dioxide emission (Gómez et al., 2012; Reverey et al., 2016).

The surface-groundwater exchange and the flood pulse are variable in space and time and drive the direction and magnitude of flow within the pore-spaces, and consequently, the expansion and compression of the size of the PHZ (Boano et al., 2014; Harvey and Gooseff, 2015). Sediment morphology (e.g., grain size), sediment migration rates, streambed topology (e.g., wavelength of sediment dunes), shape of the river channel, presence of obstacles, and flow regime result in heterogeneous hydrodynamic landscapes within the parafluvial-hyporheic sediments (Magliozzi et al., 2018) that determine the transport of solutes between riverine compartments (Ward et al., 2012) and the chemistry within the pore water (Triska et al., 1990; Bencala, 1993). Importantly, hydrodynamics also regulate the residence time or turnover capacity of pore-water within the PHZ. Short residence times are generally more common in the upper sediment layers, at the surface-hyporheic interface, creating hot spots and moments of enhanced biochemical activity (Briggs et al., 2014; Kaufman et al., 2017). In contrast, deeper sediment layers are generally characterized by longer residence times, low redox potential and slower biochemical reactions (Bardini et al., 2012). As a result, deep subsurface sediments tend to be a sink for recalcitrant compounds (Peralta-Maraver et al., 2019a). Parafluvial habitats and floodplains are also a trap for sediment, water and nutrients since they are exposed to drying-rewetting cycles due to inundation phenomena (Baigún et al., 2008; Walalite et al., 2016; dos Santos Pinto et al., 2020).

Pore-space hydrodynamics can therefore be viewed as the "master variable" of the PHZ functioning (e.g., Dole-Olivier, 2011; Peralta-Maraver et al., 2018b). Thus, quantifying the direction and magnitude of surface-subsurface water exchange, and consequently the size of the parafluvial-hyporheic zones, is of pivotal importance to further study of both the organization of biological diversity within the PHZ and also its role in biogeochemical cycling. A suite of techniques has been developed during the last decade for this purpose (e.g., Kalbus et al., 2006; Brunner et al., 2017). Initially, these approaches were almost exclusively employed in studies of hydrology and engineering (Boulton et al., 2010), but they are increasingly used in ecological sampling protocols (Peralta-Maraver et al., 2018b; Lewandowski et al., 2019).

Thermal sensors are often used to quantify vertical and longitudinal hydrodynamics within the PHZ (Lewandowski et al., 2019) because surface waters and groundwaters differ in temperature. The variation in the recorded temperature gradient is then transformed to vertical flux using well-established 1D heat diffusion-advection equations (Rau et al., 2010). This method is non-destructive, simple and low-cost, and can be easily combined with community and biochemical sampling methods (e.g., Peralta-Maraver et al., 2018b). However, vertical measurements of temperature variation ignore horizontal flow components (Lewandowski et al., 2011; Angermann et al., 2012) that demonstrate the hydrological connectivity with the parafluvial compartment. Recently, hydrologists and environmental engineers have developed active heat pulse sensors to quantify dynamic 3D flows within streambed sediments (Banks et al., 2018) allowing accurate characterization of connectivity and residence times of water across stream compartments. These tools are as yet virtually unused in ecological research on the PHZ.

Hydrological connectivity across PHZs and the natural shift between wet and dry states supports the establishment of diverse aquatic and terrestrial communities within these zones (Fig. 2). It also maintains several ecosystem services on which human well-being depends, such as contaminant attenuation, aquifer recharge and nutrient supply to the alluvial plain. However, traditional flood management techniques such as river clearance, channelization and cementing the river bed have encouraged rapid movement of water through rivers to the sea and global disruption of the vertical and lateral hydrological connectivity between rivers and their PHZs to the detriment of river functioning (Loheide and Gorelick, 2006; Boulton, 2007). Recent river rehabilitation approaches aim to restore connectivity between the surface stream and the PHZ encouraging increased hyporheic exchange flows and biogeochemical processing mediated by the hyporheos (Kasahara and Hill, 2006). Techniques are used that promote hydraulic gradients (e.g., wood debris, step-pools, dam removal) and geomorphological heterogeneity (i.e., bedforms, sediment sorting, meandering, realignment), while reducing sediment load and clogging (e.g., sediment traps) (reviewed in Magliozzi et al., 2019). However, implementation of such restoration strategies is still very recent (Boulton, 2007), and thus,

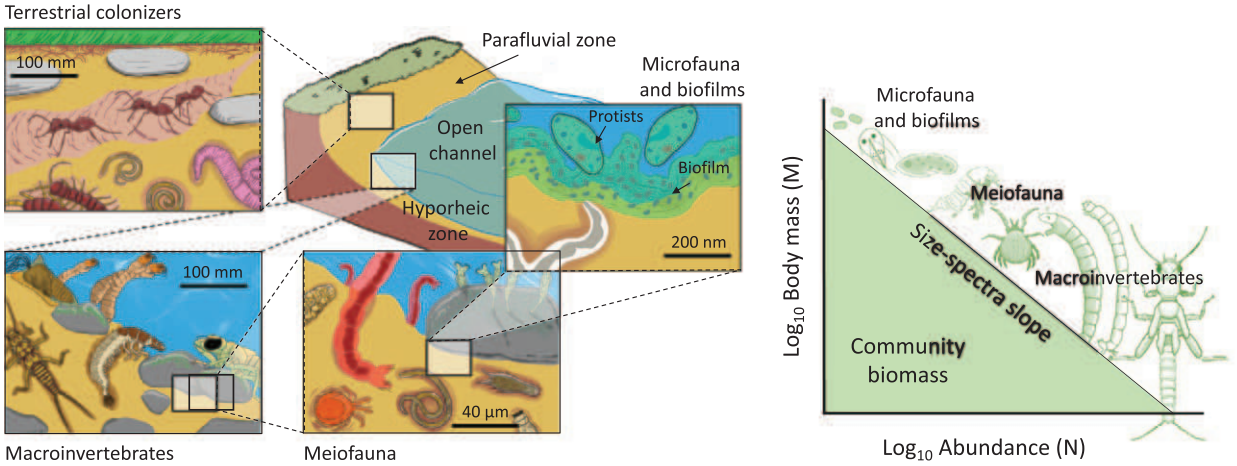

Fig. 2 Conceptual depiction of parafluvial-hyporheic biodiversity across body-size groups, and theoretical body mass (M)/abundance (N)-relationship of the community.

only a very few studies have examined the effect of these measures on the ecology and biochemistry of the PHZ. Robertson et al. (2021) examined the effects of removing an impoundment on the hyporheos and the benthos of an English chalk stream at multiple time points over a 5-year period. They found that both the hyporheic and the parafluvial compartments responded differently to restoration. Morley et al. (2021) found that the density and taxon richness of the hyporheos was significantly higher in reaches where the hyporheic zone had been restored compared to reaches with unrestored hyporheic zones. Given the importance of the hyporheic zone in the provision of ecosystem functions and services, it should undoubtedly be included in future monitoring protocols that aim to assess river restoration success.

An ecotonal interface full of life

The high surface area of the sedimentary matrix in the PHZ can create real hotspots of biodiversity. These habitats are multi-dimensional ecotones across surface-groundwaters and aquatic-terrestrial habitats (Sabater and Vila, 1991). They harbor complex and diverse consortiums that include organisms from across the tree of life (Fig. 2). Permanent inhabitants include biofilms composed of fungi, bacteria and archaea that grow attached to the sediment grains as a microbial skin within the pore space (Battin et al., 2016). Single cell eukaryotes (protists) and metazoa invertebrates also live permanently within these interstitial spaces, swimming in the pore-space or digging into the sediments. Invertebrates include many taxa of crustaceans, worms, rotifers, water mites and insects (reviewed in Rundle et al., 2002), and are characterized as meiofauna or macroinvertebrates. In addition to the permanent communities, surface and subterranean organisms temporarily colonize the parafluvial-hyporheic sediments (Robertson et al., 2000). Furthermore, the lateral transition between aquatic and terrestrial conditions results in cyclic succession of aquatic and terrestrial macroinvertebrates colonizing parafluvial habitats. For example, macroinvertebrates, such as Plecoptera, Trichoptera, isopods and amphipods are replaced by nematodes, annelids and arthropods (e.g., ants) during dry phases, supporting nutrient cycling in the whole river ecosystem (Prather et al., 2013) (Fig. 2).

From the surface, organisms enter the PHZ to find resources, or even refuge (Dole-Olivier, 2011; Stubbington, 2012). Vertical movements are well known in the case of invertebrates. The early larval instars of benthic insects such as stoneflies and mayflies use the small pore spaces of the PHZ as predation refuges (Williams and Hynes, 1974; Stubbington, 2012). Furthermore the HZ is critical in salmonid life histories; salmonids bury their eggs in the HZ of gravel bed streams, and the developing embryos remain there for several months before emerging as free-swimming fish (Malcolm et al., 2004). Vertical migration of multiple taxa from the surface into the PHZ also occurs during surface flow cessation, because the PHZ remains wetted for longer periods (Wood et al., 2010). When flow resumes, these groups rapidly recolonize the surface (Stubbington and Datry, 2013; Datry et al., 2014). Additionally, surface taxa can use the hyporheic zone as a thermal refuge as PHZ temperatures are typically lower than those of the surface sediments (Vander Vorste et al., 2017). Surface taxa may also use the PHZ as a refuge during high flow disturbance (see summary in Robertson and Wood, 2010). The PHZ will be most effective as a refuge from high flow disturbance when it is laterally and vertically extensive with large particle sizes because these provide greater living space. Interstitial architecture in turn influences dissolved oxygen concentrations, the degree of connectivity between the benthic and the hyporheic zone and the ease with which benthic organisms are able to penetrate into the hyporheic zone (Robertson and Wood, 2010). Furthermore, species will differ in their ability to utilize the PHZ depending on the biological traits they possess. Typically, taxa are small and so able to inhabit pore spaces within the PHZ, vermiform enabling movement through the sediments, highly mobile and with no attachment devices so that individuals can move into the HZ during disturbances, and a burrowing habit allowing penetration of the HZ. In fact many permanent residents of the PHZ (e.g., meiofauna such as Copepoda, Nematoda) possess these traits (Robertson and Wood, 2010). In addition to this "top-down" use of the PHZ as a refuge, stygobiotic taxa also colonize the PHZ during adverse conditions in the groundwater environment when extremes of anoxia or pH may occur (Marmonier et al., 2004; Wood et al., 2010). Interestingly, the use of the PHZ as a refuge is not exclusive to invertebrates. Biofilms also use the PHZ as a refuge from desiccation, although they are transported by hydrological pathways through the sediments rather than entering by active migration. During dry conditions at the surface, the PHZ supports prokaryotes associated with the infiltration of water and the maintenance of wet conditions within the sediment; when water exchange is restored during flood events, biofilms recolonize the surface habitats (Febria et al., 2012). Lastly, expansion and contraction of aquatic and terrestrial habitats also occur laterally through the parafluvial interface, even in perennial systems. Parafluvial habitats have different characteristics to those of adjacent riparian, terrestrial and fully aquatic habitats. Thus, PHZ can support unique communities, including inundation-tolerant terrestrial colonists (Tockner and Stanford, 2002; Steward et al., 2011) and desiccation-tolerant aquatic organisms (Stubbington and Datry, 2013; Datry et al., 2017).

Parafluvial–hyporheic communities include therefore a very heterogeneous set of organisms with diverse distribution patterns along the ecotone both in space and time. Dynamic environmental filters at a sediment-scale, driven ultimately by gradients of sediment size, changing hydrodynamics and depth within the streambed, constrain the ability of different taxa to colonize the PHZ (Williams et al., 2010; Robertson and Wood, 2010; Descloux et al., 2014). Consequently, distinguishing between parafluvial–hyporheic communities and those from adjacent habitats, such as benthic or riparian habitats, can be extraordinarily challenging. Traditional approaches define the habitat boundaries operationally, rather than based on the actual distribution of the organisms (e.g., Smock et al., 1992). However, accurately defining natural boundaries is a key aspect of designing ecological studies and for the interpretation of results, and is also central to defining ecosystems (Post et al., 2007). It is only recently that quantitative biocenosis analysis has shown unequivocally that PHZ communities are discrete communities with individual ecological integrity, and that vertical hydrodynamics influences their boundaries (Peralta-Maraver et al., 2018a).

As a rule of thumb, streambed sediments contain assemblages with relatively large invertebrates at the surface that are gradually replaced by a suite of numerous but small-bodied organisms with increasing depth (Schmid-Araya, 1994; Stead et al., 2004; Peralta-Maraver et al., 2018a,b). This is mainly because the reduction of oxygen and nutrients at greater depth and under upwelling conditions limits the colonization capacity of organisms with larger body size and high metabolic requirements (Strayer et al., 1997; Briggs et al., 2012; Descloux et al., 2014). As a result, communities inhabiting the streambed are strongly structured by body size (Schmid et al., 2000), which is inversely proportional to their abundances. When organisms are grouped into body-size classes, irrespective of taxonomic identity, the negative slope of the size-abundance relationship on a logarithmic scale (i.e., size-spectra; White et al., 2007) provides a measure of community size structure. The intercept reflects the carrying capacity, and the area under the slope and intercept gives a measure of total biomass (Fig. 2). Furthermore, the body size of different groups is a relatively good approximation of the trophic level they occupy within the parafluvial-hyporheic food webs (Kerr and Dickie, 2001), although there are some exceptions (e.g., parasites; Leaper and Huxham, 2002).

The size-abundance relationship is therefore an integrative metric of the community structure and the biomass depletion through food chains (White et al., 2007). Thus, size-abundance coefficients can be used to quantify the deviation of a natural community from a reference status due to natural constraints (e.g., oxygen limitation) or anthropic stressors such as organic pollution (Petchey et al., 2002). Size-abundance coefficients from parafluvial–hyporheic communities, including unicellular organisms, meiofauna and macroinvertebrates, are very sensitive to depth, hydrodynamics and anthropogenic stressors. In streambed sediments, the size-abundance intercepts are higher and the size-spectra slopes are flatter under downwelling conditions and in the upper sediment layers, while the opposite occurs under upwelling conditions and at deeper sediment layers (Peralta-Maraver et al., 2019a). Also, there seems to be a strong dependence of the size-abundance coefficients on the presence of emerging organic contaminants in streambeds, to the point of even shielding the effect of important environmental drivers such as temperature, pH, and productivity (Peralta-Maraver et al., 2019b). The size-spectrum coefficients scale with the efficiency of energy transfer across trophic levels (Brown and Gillooly, 2003), and curves typically become steeper as metabolic efficiency decreases. As we discuss in the following section, the variation in the size abundance relationship has therefore important implications for the functioning of the PHZ.

The parafluvial-hyporheic zone is an active interface with an impressive self-purifying capacity

The high surface area of the sedimentary matrix within the PHZ plays the functional role of a bioreactor with the capacity to decompose a wide range of allochthonous organic substrates, and it is sustained by the diverse and active communities that inhabit it (Peralta-Maraver et al., 2018b, 2021). The potential of the PHZ to process dissolved and particulate organic nutrients is well known in temperate streams and rivers (Lewandowski et al., 2011; Follstad Shah et al., 2017). For example, there is a body of literature on the decomposition of leaf litter within the PHZ (e.g., Burrows et al., 2017; Risse-Buhl et al., 2017). Additionally, the formidable bioreactor capacity of the PHZ enables it to decompose a wide range of emerging organic contaminants (EOCs). These include compounds of anthropogenic origin with trace concentrations in natural systems (up to several micrograms per liter), but disproportionately high biological activity (Stamm et al., 2016). Thousands of daily-use synthetic chemicals, such as antibiotics and other medications or pesticides, with hazardous effects on aquatic communities and human health occur among EOCs (Pal et al., 2010). Research in the temperate lowland river Erpe (Germany) provides strong evidence of the capacity of the PHZ to remove EOCs (Schaper et al., 2019; Rutere et al., 2020; Mueller et al., 2021). Unpublished analysis of surface water and pore-water chemistry at a sediment scale shows reductions of diverse EOCs through a depth gradient in the streambed of the River Erpe (Germany, Berlin). EOC concentrations declined strongly with increasing depth, while the artificial sweetener acesulfame increased (Fig. 3). Acesulfame is a good marker of EOC contamination in management and water regulation because it is very persistent and it is hydrophilic enough to penetrate into, and accumulate in, waterbodies (Peralta-Maraver et al., 2019c). Even though reduction of EOCs could be attributed to different processes than biodegradation, these results illustrate that the PHZ acts as a barrier against the contamination of near-surface groundwater aquifers, which are vital to the production of drinking water.

Decomposition of such a wide array of substrates is mainly explained by the fact that prokaryotes embedded in the streambed biofilms have a great enzymatic capacity and develop diverse metabolic pathways; they form consortia to maximize the range of nutrients and contaminants that can be processed and the rate at which their consumption occurs (e.g., Kolvenbach et al., 2014). Furthermore, water flow is strongly reduced within the pore space, resulting in long residence times, allowing time for microbial decomposers to perform these biochemical reactions. Lastly, while biofilms undertake most of the decomposition processes, protists and invertebrates also influence microbial decomposition rates. Life activities of protists and invertebrates inhabiting the PHZ could enhance the hydraulic properties of sediments through burrowing (bioturbation) and maintaining open pore spaces (Hose and Stumpp, 2019). Protozoa grazing on biofilms augment water mixing, increase biofilm surface, and ultimately, promote bacterial activity (Peralta-Maraver et al., 2018b). However, the contribution of protists and invertebrates to organic matter decomposition processes in the PHZ remains poorly characterized (Majdi et al., 2020).

A recent survey across 30 UK streams and rivers has shown that productive communities including flagellates, ciliates and invertebrates promote microbial decomposition within streambed sediments (Peralta-Maraver et al., 2019a). As body size and metabolic requirements constrain the distribution and biomass of organisms within the PHZ, it is reasonable to think that efficiency of the bioreactor will vary with these factors and also with environmental drivers such as depth and hydrodynamics. The size-spectra slope (derived from the size-abundance relationship described above) is a powerful linear predictor of the microbial decomposition

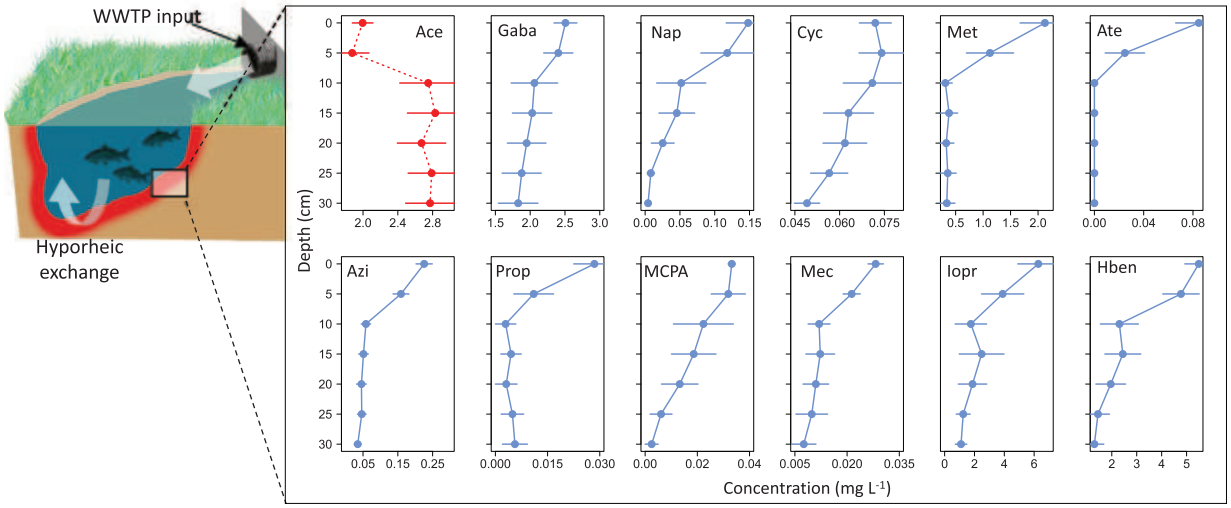

Fig. 3 Depth profiles of emerging organic contaminants (EOCs) measured in the surface and streambed sediments in six reaches of the River Erpe (Berlin, Germany). River Erpe is affected by the water release of a municipal wastewater treatment plant (WWTP). The sampling procedure is described in Peralta-Maraver et al. (2018a). Profiles show mean values and standard error of dissolved compounds measured in the pore-water of the PHZ. The marker acesulfame (*Ace*, in red) accumulates through depth while the other drugs show a strong reduction. Analyzed compounds include: Gabapentin (*Gaba*); naproxen (*Nap*); clofibric acid (*Cyc*); metformin (*Met*); acetaminophen (*Ate*); azithromycin (*Azi*); propanol (*Prop*); MCPA (herbicide); metoprolol (*Mec*); lopromide (*Iopr*); 1H-benzotriazole (*Hben*).

rate within streambed systems (Peralta-Maraver et al., 2021) and may be used to determine the limit of the PHZ bioreactor depurating capacity and the resilience of the system towards anthropic stressors. This metric can integrate information for the whole community, and also allow the effect of environmental factors to be incorporated within the analysis. The decomposition rate can be easily modeled as a response of the interaction between the size-spectra slope and the environmental variable under study (see Peralta-Maraver et al., 2021).

Functional diversity (the range of species' functional traits) is another tentative metric to further study decomposition processes at community level, as it underpins a key mechanistic link between species richness and ecosystem functioning. This approach can also be used to compare potential decomposition processes across biogeographic regions. Evidence from surface freshwaters, where it is well established, suggests that community functional diversity predicts ecosystem functioning better than species based indices (e.g., Gagic et al., 2015; Griffin et al., 2008). However, in the PHZ, the development of functional trait databases and the use of a functional trait approach is in its infancy (but see Robertson et al., 2021; Dunscombe et al., 2018; Claret et al., 1999; Robertson and Wood, 2010; Descloux et al., 2014; Bona et al., 2016; Mathers et al., 2017; Magliozzi et al., 2019). Developing the functional trait approach for the PHZ is a fruitful avenue for future research given the likely role of the hyporheic community in riverine ecosystem functioning. Currently, our knowledge of the capacity of the PHZ to process organic substrates is mostly limited to descriptive field surveys. The complexity of natural systems and the multiple variables interacting during microbial decomposition in these settings limits mechanistic knowledge of the functioning of the PHZ. For example, we do not yet know how protists or invertebrates grazing on biofilms promote microbial activity. This may result from the selective consumption of senescent bacteria, the control of biofilm overgrowth, or the increase of biofilm surface due to moderate grazing (Shapiro et al., 2010; Neury-Ormanni et al., 2016; Peralta-Maraver et al., 2018b). Nevertheless, these explanations remain largely hypothetical. Therefore, experimental approaches such as controlled microcosm experiments, as well as descriptive studies are required to assess the complex mechanisms behind the functioning of the PHZ.

Conclusions

Research on ecotones is challenging because they display aspects of the bordering habitats as well as their own emerging characteristics. A mix of research approaches and theories originally developed for the neighboring habitats is often required, making their study cumbersome; this is definitely the case for the PHZ. Humans prefer to work with clearly delineated systems, unfortunately (or maybe encouragingly), nature rarely works like this. Indeed, ecotonal areas are typically where we find new ecological processes or where those processes occur at a higher rate. The methodological difficulties encountered explain to a large extent why our understanding of PHZ functioning lags far behind those of other inland water habitats, with the notable exception of groundwaters. For the same reason, most of the historical research on the ecological processes driven by the PHZ, such as microbial decomposition, is limited to a local scale. Whilst this is certainly changing, and the latest research on PHZ functioning encompasses larger spatial and temporal scales, we are still unable to scale important processes up to global levels over longer periods of time. For example, benthic habitats in lentic inland waters (e.g., lakes, wetlands, reservoirs) are well established sources of greenhouse gasses

including CO_2, CH_4, and N_2O at a global scale (e.g., Tranvik et al., 2009; Bastviken et al., 2011; Soued et al., 2016). In contrast, the existing estimates of global greenhouse gas emissions from the PHZ are highly uncertain (Schelker et al., 2016; Boodoo et al., 2019), even though we know that the PHZ is a very active interface, because they are based on limited local observations that do not represent the variability that exists in PHZs globally. We began this chapter by stressing the advance in our understanding of riverine ecological processes gained by moving from a unidimensional to a multidimensional perception of rivers. We are convinced that the next great milestone will be to scale the ecological processes occurring within the PHZ in a macroecological context.

Knowledge gaps

- Communities inhabiting the PHZ are strongly influenced by the timing, frequency, duration and magnitude of hydrological connections with the surface and groundwaters. In addition, hydrological exchange conditions and flood pulse varies enormously at different time scales, from a short-term daily basis up to a climatic scale. However, the relative importance of circadian, seasonal and climatic scales on ecological processes of the PHZ have not been explored yet.
- Taxonomic knowledge on organisms inhabiting the PHZ lags far behind that of surface counterparts. These taxonomic impediments become especially severe among small size fractions such as protists and biofilms. The lack of a solid taxonomic knowledge critically limits advances in ecological research and monitoring of the PHZ. The recent surge in molecular-based identification methods is a promising approach to unravel the hidden diversity of PHZ communities in the future.
- Carefully designed microcosm experiments are needed to determine how the predator-prey interactions between biofilms and grazers affect the rate of microbial decomposition of nutrients and contaminants. Combined with knowledge from experimental trials this is a feasible strategy to unravel the inherent complexity of natural ecosystems.
- Parafluvial-hyporheic inhabitants and colonizers must be incorporated into our understanding of the energetic connectivity between terrestrial and aquatic ecosystems. This is especially relevant considering that climate change is expected to alter the frequency, intensity, spatial extent, duration and timing of extreme floods and droughts.
- Our understanding of the impact of novel pollutants such as emerging organic contaminants and microplastics on PHZ food webs and thus the functioning of the bioreactor is limited to non-existent. This knowledge gap should be addressed through field surveys and laboratory experimentation.
- Scientific interest in the production of CO_2, CH_4 or N_2O within PHZ is very recent, and research on this field is still limited to local-scale studies. Therefore, global estimates or even prediction of the role of the PHZ as sources or sinks of greenhouse gasses are largely unknown. This knowledge is however essential to anticipate the rate of global warming.

Important case studies

Site	*Country*	*Main topic*	*Key references*
River Erpe	Germany	This study reports how environmental filtering at a micro-scale determine diversity, productivity and composition of the whole streambed assemblage through depth and with the direction of vertical water exchange	Peralta-Maraver et al. (2018b)
River Erpe	Germany	Authors analyze changes in molecular composition of seven dissolved organic compounds, and the attenuation of 17 emerging organic contaminants within the hyporheic sediments of an urban stream receiving treated wastewater	Mueller et al. (2021)
8 streams from two regions located in humid subtropical east-ern Australia	Australia	Authors analyze particulate organic carbon decomposition, as well as rates of microbial respiration, to quantify rates of organic carbon processing in surface and parafluvial-hyporheic environments of intermittent and perennial streams	Burrows et al. (2017)
2 catchments in each of 3 geologies (chalk, limestone, sandstone). 4 sites per catchment	UK	Authors used a functional trait approach. They found that HZ community structure varied between streams draining different geologies. However, HZ community biomass and functional measures did not vary across geologies, suggesting that the HZ functions equally across geologies	Dunscombe et al. (2018)
Traisen River (Danube tributary)	Austria	Novel study assessing the effects of water fluctuation on the magnitude of greenhouse gasses emissions in the parafluvial zone of a restored river floodplain	dos Santos Pinto et al. (2020)

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Presence and Role of Prokaryotic Viruses in Groundwater Environments

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Glossary

Auxiliary metabolic genes (AMGs) Viral genes frequently encoding enzymatic functions which optimize the metabolism of the host for viral reproduction during infection.
Chronic infection Viral infection which leads to the stable integration of the phage genome (prophage) in the host cell (i.e. lysogeny). In contrast to lytic reproduction, viral progeny is released continuously without rupture of the host cell.
Kill-the-Winner model Describes the hypothetical trade-offs between defense and competition specialists among unicellular planktonic microorganisms. Predicts that more abundant and/or more active prokaryotes become preferentially targeted by lytic phages.
Lysogenic/temperate infection Viral infection which leads to the stable integration of the phage genome (prophage) in the host cell. Depending on the phage, a lysogenic infection may either turn out to be chronic or lead to a (delayed) lytic reproductive cycle.
Lytic infection Viral infection directly leading to the reproduction of viral progeny whose release results in the rupture (lysis) of the host cell.
Metabolic standby Metabolic state in which microorganisms are ready to perform translation (protein synthesis) but are otherwise metabolically inactive.
Phages Viruses infecting prokaryotes (i.e. bacteria and archaea). Often also limited to those infecting bacteria.
Prokaryotes Microorganisms without cell nucleus belonging to the domains bacteria and archaea.
Viral ecology Research field investigating the ecological role of viruses in the environment.
Viral shunt The lysis-mediated release of dissolved and particulate organic matter which can stimulate the activity of surrounding microorganisms.
Virus-like particles (VLPs) Particles with the morphological and/or biochemical characteristics of viruses.

Introduction

Microorganisms are ubiquitous and abundant with a distribution limited by only a few environmental factors, i.e. extreme temperature, extremely acidic or alkaline pH, and water availability (Hendry, 2006). Microbes are found around almost every corner on this planet, and occur even in environments like hot springs, glacier ice, the atmosphere and the terrestrial subsurface including groundwater ecosystems (Griebler and Lueders, 2009). What has been overlooked for a long time is that every microbe has its virus, or two or three. Along with their hosts, viruses have been found in rocks, soils, all kinds of aquatic ecosystems, inside of organisms including human beings, as well as in the atmosphere (Reche et al., 2018). Although viruses pathogenic to animals and humans make most of the news, the large majority of viruses in natural ecosystems infect single-celled microorganisms without a cell nucleus named prokaryotes (i.e. bacteria and archaea, Jacquet et al., 2010). This chapter will focus exclusively on viruses of

prokaryotes which are here referred to as phages. Nonetheless, since most methods do not discriminate between phages and other viruses, occasionally we will also use the more generic term 'virus.'

Based on an estimated 4×10^{30} virus-like particles (VLPs) in the ocean alone, phages are considered to be the most abundant biological entities in the biosphere (Suttle, 2005). In many freshwater habitats, like streams and rivers (Peduzzi, 2016), lakes and ponds (Hennes and Simon, 1995), and man-made impoundments (Peduzzi and Schiemer, 2004), phages occur in concentrations comparable to those found in the ocean. Nonetheless, overall estimates of the total abundance of viruses in freshwater are missing so far. Besides the immense diversity of freshwater habitats, this is due to the fact that very little is known about phages in the largest freshwater ecosystem on our planet, i.e. groundwater. As is explained in detail in other chapters of this section, groundwater ecosystems form the largest freshwater biome on earth. While only 2.5% of the world's water resources are fresh and about 69% thereof is solidified in ice and snow, almost all of the remaining 31% are contained within groundwater. Taken together, rivers, lakes and ponds contain less than 1%. In fact, nearly ~100 times more freshwater occurs in the terrestrial subsurface than in surface water bodies (Danielopol et al., 2003). Recent estimates also indicate that >80% of all prokaryotic biomass on earth, including many novel phyla, is located in the subsurface (e.g. terrestrial aquifers, vadose zones, and below the seafloor; Bar-On et al., 2018; Castelle and Banfield, 2018). However, covered by soils, sediments and rock, hidden below the surface and with no light as energy source groundwater ecosystems are typically poor in organic carbon and energy and thus exhibit a comparatively low productivity (Aiken, 2002; Regan et al., 2017; Hofmann et al., 2020). This results, to some degree, in a dependence on organic matter, nutrients and energetically favorable combinations of electron donors and acceptors coming from the surface along with groundwater recharge (Pabich et al., 2001; Goldscheider et al., 2006; Shen et al., 2015). In consequence, the concentration and activity of prokaryotes, the predominant hosts of viruses in groundwater, is much lower compared to surface waters (Kyle et al., 2008; Roudnew et al., 2012; Kieft and Phelps, 1997; Lopez-Fernandez et al., 2018). As a result, groundwater environments have long been perceived as microbiological deserts (Griebler and Lueders, 2009) and, with the exception of human pathogens, viruses, and in particular phages have been very rarely studied. To our knowledge, this is the first compilation of data on prokaryotic viruses in groundwater ecosystems.

Groundwater environments as a habitat for phages

The large majority of studies on viruses in groundwater focused on human pathogenic viruses like noro- and hepatitisviruses (e.g. Macler and Merkle, 2000; Borchardt et al., 2007; Krauss and Griebler, 2011). While in rare cases, pathogenic viruses in groundwater have been shown to be responsible for outbreaks of water-borne diseases, these viruses do not reproduce in groundwater and at standard conditions they occur in very low numbers and are only occasionally detectable. As such, they do not contribute to groundwater habitats in an ecological sense, i.e. in terms of organic carbon supply and microbial food web interactions. Therefore, viruses specific to humans and/or animals are not the subject of this chapter and interested readers are referred to respective reviews (e.g. Krauss and Griebler, 2011). The following paragraphs will focus on ecological aspects of viruses infecting prokaryotes and build on basic concepts in phage biology.

In surface waters, be it salty or fresh, phages have been shown to affect basically all prokaryotic-driven processes via (i) the short-circuiting of nutrients within the microbial food web (Wilhelm and Suttle, 1999), (ii) the alteration of host-metabolism (Puxty et al., 2016; Zimmerman et al., 2020; Kieft et al., 2021), and (iii) the control of microbial community composition (e.g. Bouvier and Del Giorgio, 2007). However, groundwater deviates from surface waters in several aspects. The water saturated subsurface is composed of a complex sediment and rock matrix providing an enormous surface for microbial colonization. In fact, most microbes in aquifers are epilithic, forming colonies or even biofilms attached to rocks and loose sediment grains. These microbes outnumber the pore water suspended microbial fraction by 10–100 fold (Griebler and Lueders, 2009), a fact that may also be true for phage particles (e.g. Mindl et al., 2015). Due to the severe carbon and energy limitation, microorganisms in groundwater typically display low productivity and occur in 10 to 1000-times lower concentrations than in surface waters (Griebler and Lueders, 2009; Fillinger et al., 2019a; Griebler et al., 2014). On the other hand, the dark and comparably 'cold' environments – groundwater temperatures are rather constant and resemble the annual mean temperature at the land surface shielding subterranean microorganisms from extreme hot or cold conditions – may also substantially slow down the decay of viruses (Krauss and Griebler, 2011).

Taken together, this is expected to have several important outcomes for virus-host relationships in groundwater: (i) Contact rates between phages and hosts in the water column (proportional to the concentrations of both partners) can be expected to be extremely low. (ii) Carbon and energy limitation likely result in a small fraction of prokaryotic cells with pronounced metabolic activity and/or short time periods in which the prokaryotic community is metabolically active and able to support the reproduction of phages. Combined with an assumed long-term persistence of phage particles in groundwater, this might lead to an uncoupling of prokaryotic and phage abundances. (iii) Due to the intimate interaction between pore water and the huge sediment and rock surface area with its biofilms, phage particles frequently collide with surfaces leading to adsorption and potentially inactivation of phages (Fig. 1). However, contrasting the expected low contact rates of prokaryotes and phages in pore water, at the same time, this might also increase the likelihood of encounters between dispersed phages and epilithic host cells.

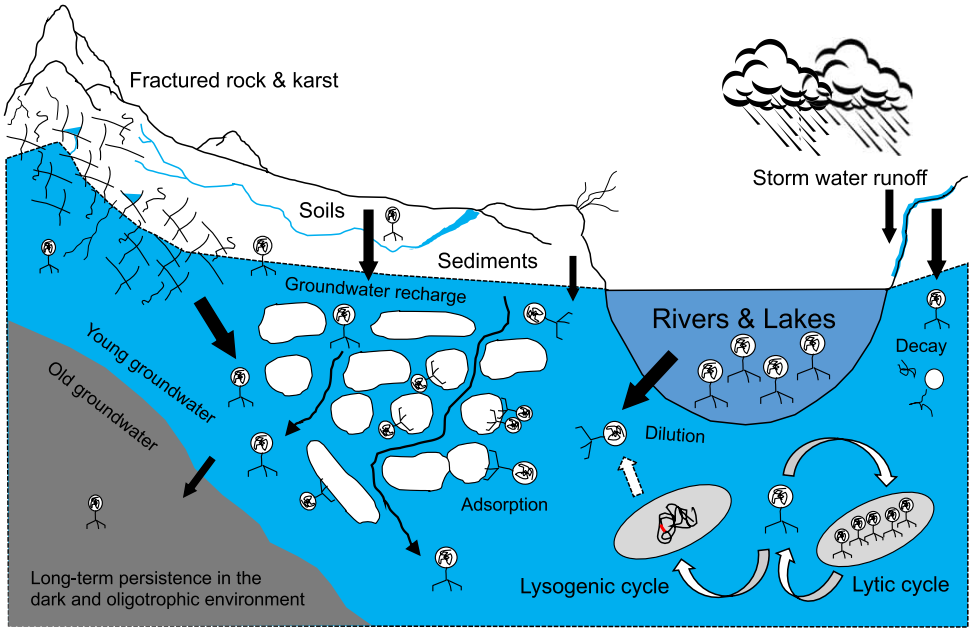

Fig. 1 Conceptual drawing of sources of viruses and processes that act at phages in groundwater ecosystems.

Virus abundance and the virus-to-prokaryote ratio (VPR) in groundwater

In groundwater ecosystems, phages and their potential ecological role have been ignored until the 2000s. Since then microbial ecologists have started to quantify phages in groundwater, repeatedly in the context of contaminated groundwater sites (e.g. Costeira et al., 2019; Holmes et al., 2015; Pan et al., 2017), but also in natural settings such as unconsolidated porous aquifers (Roudnew et al., 2014), karst systems and springs (Malki et al., 2020; Wilhartitz et al., 2013), as well as fissured aquifers like the Äspö Hard Rock Laboratory (HRL; e.g. Eydal et al., 2009; Kyle et al., 2008). Since viruses are extremely small and difficult to quantify, their abundances are often given as virus-like particles (VLPs), i.e. particles with the morphological and/or biochemical characteristics of viruses. The production of phage particles is based on prokaryotic cells and their metabolism. Therefore, prokaryotic and phage abundances are typically strongly correlated across ecosystems (e.g. $r = 0.86$, $P < 0.001$, $n = 524$ in Parikka et al., 2017). In an attempt to define a central parameter reflecting the relationships of phages and hosts in a given habitat, viral ecologists frequently determine virus-to-prokaryote ratios (VPRs) by measuring phage and prokaryote abundances in natural environments. However, the authors of the thus far most extensive meta-analysis of VPRs advise extreme caution with the interpretation of this ratio (Parikka et al., 2017). While VPR values of 10 have frequently been used as a rule-of-thumb, re-examinations of data on prokaryotic and viral abundances also suggest that VPRs are better described by a non-linear, power law function than linear relationships (Wigington et al., 2016). Parikka et al. (2017) found VPRs in groundwater averaging to 5.9 ($n = 11$), which is significantly lower than in marine waters (VPR of 26.5, $n = 233$). This could be explained by low nutrient concentrations and temperature in groundwater which, for other phage-host systems, have been found to lead to longer latent times and lower burst sizes and therefore lower viral production (Zimmerman et al., 2020). However, with only 11 samples, the data set for groundwater is ridiculously small and further studies are needed. For an overview of available data on viral abundances and reported VPRs in groundwater see Table 1.

Based on the estimated 4×10^{30} VLPs in the ocean (Suttle, 2005) at this point we may also attempt a quick estimation of total viral abundances in groundwater: Considering that (i) 2.5% of all water on earth is freshwater (= 2.56% of the amount of sea water), (ii) 30% of all freshwater is groundwater (Danielopol et al., 2003) of which 3% is less than 100 years old (termed young groundwater; Gleeson et al., 2016) and that (iii) young groundwater hosts prokaryotes and phages in concentrations comparable to those in the deep sea (below 200 m depth) which exceeds the volume of the sunlit ocean by 18-fold, we may estimate a minimum of about 10^{27} viruses (almost exclusively phages) suspended in young groundwater. Furthermore, assuming that $10\times$ more viruses are adsorbed to the sediment and rock matrix than are dispersed, this number rises to 10^{28} phage particles. This likely still underestimates actual abundances of phages in groundwater since in our simple calculation we have neglected 97% of the aquifers that are deep and contain old groundwater with so far unknown concentrations of phages. Reminiscent of the estimated prokaryotic biomass in the subsurface (Bar-On et al., 2018), it would not be a big surprise if subsurface phage biomass equals that of surface waters.

Table 1 Viral abundances and virus-to-prokaryote ratios (VPRs) in groundwater collected from monitoring wells, piezometers, and springs.

Viral abundance (VLPs L^{-1})	*Method*	*VPR*	*Habitat type*	*References*
10^8–10^{10}	EFM	1.1–18 (avg. 12)	Fissured granite aquifer	Kyle et al. (2008)
4.8×10^7–8.8×10^8	FCM	0.2–6	Unconfined and confined aquifer	Roudnew et al. (2012)
2.85×10^7–5.77×10^9	FCM	0.08–7.28	Unconsolidated porous aquifer	Roudnew et al. (2014)
4.6×10^{10}	EFM	NA	Alluvial sandy & gravel aquifer[a]	Pan et al. (2014)
1.4×10^7–2.1×10^8	SEM	5	Alluvial sandy & gravel aquifer	Mindl et al. (2015)
8×10^7–10^9	EFM	1.1–8.0 (avg. 3)	Uranium-contaminated alluvial sandy & gravel aquifer	Pan et al. (2017)
9.2×10^{10}–1.55×10^{11}	FCM	10–250	Tar oil-contaminated alluvial sandy aquifer	Zhou, Deng, Griebler unpupl. data
4.6×10^6–2.4×10^9	FCM	1.2–728 (avg. 94)	Alluvial sandy & gravel aquifers	Pleyer, Retter, Griebler unpubl. data
5.5×10^7–3.2×10^9 (avg. 9.4×10^8)	EFM	8–43 (avg. 20)	Limestone-spring	Wilhartitz et al. (2013)
1.1×10^7–3.8×10^8 (avg. 1.1×10^8)	EFM	3–12 (avg. 8)	Dolomite-spring	Wilhartitz et al. (2013)
9.6×10^6–1.1×10^8	EFM	2–10 (avg 5)	Springs	Malki et al. (2020)

EFM: Epifluorescence microscopy; FCM: Flow cytometry; SEM: Scanning electron microscopy; avg.: average.
[a]Sediment slurry with acetate and nitrite addition.

Controls of viral abundance in groundwater

Due to the limited amount of data on viruses in groundwater, general factors and principles governing viral abundance in aquifers have not been ruled out yet. For this reason, short summaries of individual case studies are presented in the following.

The first paper addressing the occurrence of phages in groundwater in an ecological context was published in the year 2008. Kyle et al. (2008) explored the occurrence of viruses in deep granitic groundwater in terms of quantity and morphology. Fluorescence microscopy counts of 10 groundwater samples originating from 69 to 450 m depth below land surface (b.l.s.) revealed 10^8–10^{10} VLP L^{-1} (VLP, virus-like particles) and 10^7–10^9 TCC L^{-1} (TCC, total prokaryotic cell counts). The authors reported a positive correlation of VLP with TCC ($r = 0.91$, $P = 0.0003$) and an average VPR of 12 (Kyle et al., 2008). Investigations of the vertical distribution of VLP in the water saturated terrestrial subsurface have been conducted by Roudnew et al. (2012) a few years later at the Ashbourne site in southern Australia. At this site, nested wells allowed sampling of groundwater from various depths between 15 m and 90 m below land surface. Ranging between 4.8×10^7 (90 m depth) and 8.8×10^8 VLP L^{-1} (60 m depth), VLP abundances varied significantly with depth ($p = 0.009$) but no general trend was observed. Also the VPR varied over the depth profile with values ranging from 0.2 to 6 (Roudnew et al., 2012). No relationship between either TCC or VLP abundance and inorganic nutrients was observed. The study revealed that, similar to their prokaryotic hosts, VLPs may experience small- and large-scale heterogeneity in groundwater systems, explained mainly by the geological setting and hydrological conditions, such as the groundwater recharge rate and the hydraulic conductivity of the system.

The first data on VLP abundance in karst waters was reported by Wilhartitz et al. (2013) who collected water from two hydro-geologically contrasting alpine springs, i.e. a limestone spring and a dolomite spring, for 3 years. Besides the long observation period, this study recorded for the first time the seasonal dynamics of naturally occurring microeukaryotes, prokaryotes and viruses in karst water. VLP abundance in the limestone spring and the dolomite spring averaged 9.4×10^8 and 1.1×10^8 VLP L^{-1}, respectively while TCC had mean values of 5.1×10^7 and 1.3×10^7 cells L^{-1}, respectively. The data revealed a strong dependence of the microbial communities on the prevailing hydrological situation. Unlike in the dolomite spring, the dynamic limestone spring revealed a clear difference between base flow and high discharge conditions. The VPRs in the dynamic limestone spring spanned a larger range of 8–43 (avg. 20) than the hydrologically less dynamic dolomite spring with VPRs of 3–12 (avg. 8). In general, the VPR at higher average water residence times was 2–3 fold lower (Wilhartitz et al., 2013).

Pan et al. (2014) performed laboratory experiments to investigate the production of phages and changes in microbial community structure within shallow alluvial aquifer sediment slurries amended with ^{13}C-labeled acetate and nitrate. This bio-stimulation resulted in phage production, concurrent with acetate oxidation, $^{13}CO_2$ production and nitrate reduction. Interestingly, the change in phage abundance was positively correlated to acetate consumption and CO_2 production whereas the change in prokaryotic cell abundance was not. Phage-mediated cell lysis had implications for microbial community composition. In the course of the incubation, representatives of the initially dominant Betaproteobacteria decreased in relative abundance while members of the Gammaproteobacteria increased. Interestingly, bio-stimulation also resulted in the production of filamentous phages from *Pseudomonas spp.*, which constituted >80% of the gammaproteobacterial community at late stages of the incubation. Although the experiment was conducted under quite artificial conditions, the authors concluded that phages are linked to carbon biogeochemistry and microbial community composition in terrestrial subsurface sediments (Pan et al., 2014).

Later the same authors assessed TCC and VLP abundances in groundwater from a uranium impacted alluvial aquifer adjoining the Colorado River near Rifle, CO (Pan et al., 2017). VLP abundance ranged from 8.0×10^7 to 1.0×10^9 L^1 and exceeded the number of prokaryotic cells in all samples analyzed (range 5.8×10^7 to 6.1×10^8 L^1). The VPR was between 1.1 and 8.1

(mean 3.0 ± 1.6 SD) with VLP abundance strongly correlated to prokaryote abundance (Spearman's $\rho = 0.73$, $p < 0.001$). Moreover, both VLP and prokaryotic cells were positively correlated to dissolved organic carbon (DOC). Groundwater uranium concentration was also strongly correlated with DOC content, VLP and TCC. Taken together the data indicates that local geochemical conditions likely control microbial host cell abundance which in turn controls phage abundance (Pan et al., 2017).

High-resolution depth-resolved quantification of prokaryotes and VLPs in a shallow tar oil polluted porous aquifer in north-west Germany, unveiled steep small-scale gradients in close relation to contaminant concentrations. A thin BTEX (mix of benzene, toluene, ethylbenzene, xylenes) plume with a vertical extension of only 50 cm exhibited a decline of contaminant concentrations by more than one order of magnitude within a few centimeters in the upper and lower fringe zone (Fig. 2, Zhou, Deng and Griebler, unpubl. data). High microbial activities and biomass, especially at the plume fringes and the slope of chemical gradients supported the concept that the latter are regulated by microbial processes and transverse dispersion, i.e. vertical mixing of electron donors and acceptors (Anneser et al., 2008, 2010). While prokaryote abundance was highest in sediment porewater collected at the plume fringes, the ratio of VLP to prokaryotic cells peaked at 250 m in the contaminant plume center (Fig. 2).

A lack of correlation between prokaryotic cell counts and virus-like particles in groundwater was found recently in a study in southern Austria (Fig. 3A). Following the River Mur valley in the federal provinces of Styria and Salzburg, 61 samples were collected from October to November 2020 during a five-week sampling campaign spanning a distance of around 300 km and an altitudinal gradient of around 1800 m. For a detailed description of the study area see Retter et al. (2020). Analysis of the whole data set, consisting of groundwater wells ($n = 46$), springs ($n = 2$), the Mur River ($n = 11$), and two tributaries ($n = 2$) revealed a reliable positive correlation between TCC and VLP for the river water samples alone (Fig. 3B). These river samples even force a correlation in the data set containing all water samples (Fig. 3C). However, the correlation disappears when groundwater samples are analyzed separately, without surface water samples (Fig. 3D). Also the VPR of river water and groundwater differed impressively. While the VPR was between 2.3 and 17.5 for the river samples (mean 7.6), it ranged between 1.2 and 728 (mean 94) within all groundwaters tested. This huge range indicates a pronounced heterogeneity within the groundwater sites sampled, revealing no detectable common relationship between prokaryotic abundance and viral production at the large scale. VLP and selected physico-chemical parameters showed only weak correlations, i.e. VLP were positively related to NO_2^- ($R^2 = 0.25$) and temperature ($R^2 = 0.20$) in groundwater, but negatively related to ammonium ($R^2 = 0.21$) and dissolved oxygen ($R^2 = 0.20$). However, as found for chloride ions by Kyle et al. (2008), groundwater electrical conductivity and VLP were significantly negatively correlated ($R^2 = 0.50$). Drawing from these findings as well as experimental results showing that virus particles may aggregate through changes in pH and salt concentration (Gerba and Betancourt, 2017), one might speculate that the quantification of VLP via direct counting may be significantly more sensitive to sample preparation than assumed previously. Moreover, the quantification of VLP from natural environments with pronounced heterogeneity in hydrochemistry and particularly with highly mineralized groundwater may be prone to underestimation.

Data on VLP in shallow groundwater has also been reported from an artificial groundwater recharge (AGWR) site. Here, Mindl et al. (2015) investigated the removal of bacteria and viruses during infiltration of surface water into the shallow aquifer through sandy and gravel sediments in infiltration ponds. The initial abundance of VLP in surface water was 5×10^{10} particles L^{-1}, which increased 3–4 fold to 1.5×10^{11} VLPs L^{-1} in interstitial water of the upper sediment layer of the infiltration basin before it decreased by a factor of 10–15 within the first meter of water saturated sediment. VLP attached to the sediment grains displayed only a minor decrease in abundance declining from about $3–30 \times 10^{11}$ VLP dm^{-3} down to 1×10^{11} VLP dm^{-3} with depth in the upper meter of sediment. It was shown that the number of viruses attached to the sediment matrix exceeded the number of free viruses by a factor of 2–20. VLPs were also quantified in the adjacent groundwater from up-gradient and down-gradient of the infiltration pond, accounting for 1.4×10^7–2.1×10^8 L^{-1}, respectively. The VPR in these latter groundwater samples was 5 (Mindl et al., 2015).

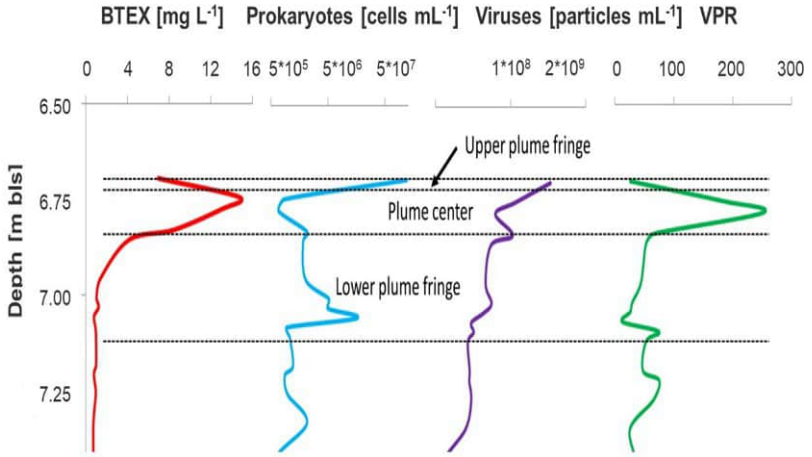

Fig. 2 Vertical profiles of organic contaminants (BTEX), prokaryotic cell numbers, the number of virus-like particles, and the virus particle to prokaryotic cell ratio (VPR) in a shallow tar-oil contaminated sandy aquifer.

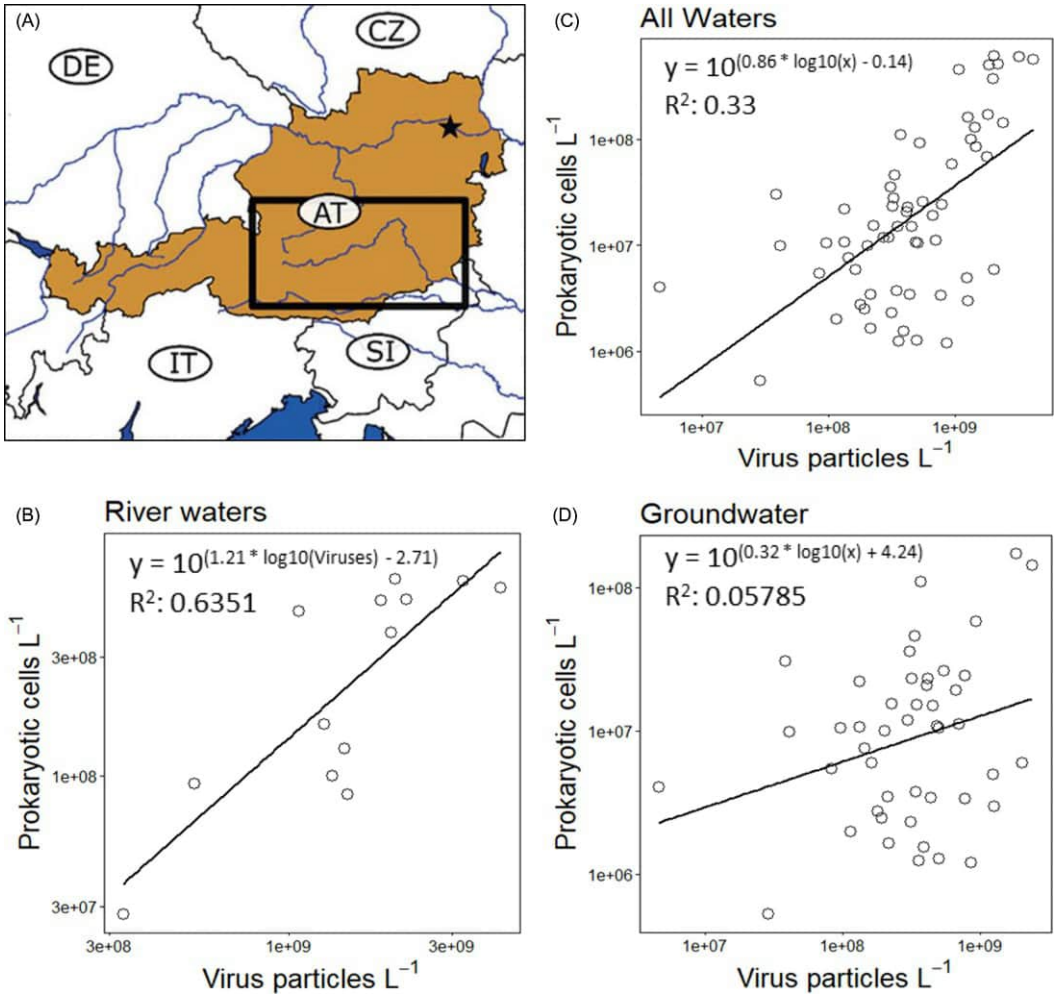

Fig. 3 The number of prokaryotic cells and virus-like particles in river water ($n = 13$) and shallow groundwater ($n = 45$) collected in the River Mur valley, Austria.

Viral diversity in groundwater: Phage morphologies, isolates and metaviromic data

In groundwater ecosystems, viral diversity is almost untapped, with culture-dependent and culture-independent studies being rare. To our knowledge, the only study characterizing the morphology of VLPs in groundwater was performed by Kyle et al. (2008). The authors observed VLPs down to a depth of 450 m in the Äspö HRL and found a diverse set of viral morphotypes resembling tailed phages (43% of observations, $n = 110$), polyhedral phages (31% of observations, $n = 78$), filamentous phages (8% of observations, $n = 21$) and fusiform archaeal phages (5% of observations, $n = 12$). Qualitatively, these results resemble viral morphotypes commonly found in surface waters (Brum et al., 2013) but more extensive datasets are needed to allow any further conclusion.

Eydal et al. (2009) isolated lytic *Podoviridae* with a very long latent period of ~70 h and a burst size of ~170 from five cultures of *Desulfovibrio aespoeensis* originating from the granitic aquifers in the Äspö HRL. This is in contrast to a recent report of a phage infecting *Pseudomonas* sp. isolated from groundwater which showed a short latent period of <2 h and a small burst size of ~20 (Hylling et al., 2020). In the same study, Hylling and coworkers isolated another phage infecting *Bacillus mycoides*. The genomes of both phages were sequenced and deposited under the genbank accession MK473373.1 and MG983742.1, respectively. It is important to note that the latent periods and burst sizes above were obtained under laboratory conditions and allow no inference of latent periods and burst sizes under in situ conditions in groundwater. Although virus particles resembling the morphology of archaeal phages have been observed in groundwater from granite aquifers (Kyle et al., 2008), no representatives have been isolated so far.

Since viruses lack a single conserved gene to be used for phylogenetic analysis and taxonomic classification, the only available method for investigating their genetic diversity in the environment is their metagenomic characterization. This process usually involves the separation of viruses and cellular organisms by filtration and the sequencing of the smaller virus fraction. However, science still has to deal with existing gaps and biases in sequencing databases which lead to a large proportion of unclassified reads (i.e. unexplored diversity) in metaviromes and an overrepresentation of well-studied phage groups such as the Caudovirales (Ackermann, 1998; Bruder et al., 2016). In addition, several studies have indicated that the morphological composition of viral communities in aquatic environments do not fully correspond to their metagenomic-based representation which results in prominent viral groups being overlooked (Kyle et al., 2009; Brum et al., 2013; Kauffman et al., 2018). In consequence, the large majority of metagenomes targeting viruses (metaviromes) in aquatic systems, including groundwater, show viral communities which are predominantly composed of double stranded (ds) DNA tailed phages or *Caudovirales* (Fig. 4; Costeira et al., 2019, Holmfeldt et al., 2021). As one of the first metagenomic, transcriptomic and proteomic studies targeting phages in groundwater, Holmes et al. (2015) circumvented these issues by only targeting phage-related sequences which the authors identified in five publicly available genomes of different *Geobacter* species. *Geobacter* sp. are important bacteria for the bioremediation of organic and metal contaminants in the subsurface. During a field experiment in which acetate was added to stimulate *Geobacter* activity in a contaminated aquifer, highly similar phage-sequences were detected in metagenomes suggesting that related phages were also present in situ. Further, concomitant with increased *Geobacter* activity, increased transcripts and peptide fragments relating to these phage-sequences could be detected which indicates also higher activity of the targeted *Geobacter* phages.

Another early metaviromic groundwater study by Smith et al. (2013) reported a high proportion of viral sequences in microbial and viral biomass collected on 0.2 μm filters, i.e. either very large viruses, viruses attached to cells or viruses within cells. A large proportion of these sequences were classified as ssDNA phages of the *Microviridae* family. Unfortunately, Smith et al. (2013) did not analyze the freely suspended fraction of viruses in their groundwater samples. Support for a high prevalence of ssDNA phages in groundwater also comes from a recent metagenomic study analyzing metaviromes of five springs fed by the Floridan aquifer (Malki et al., 2020). Furthermore, Roux et al. (2019) re-analyzed genomic and metagenomic datasets from various ecosystems which extended the 56 known members of the (ssDNA) *Inoviridae* family by >5000 putative *Inoviridae* genomes. While the newly identified sequences occurred in all major ecosystems they were especially prevalent in groundwater metagenomes.

Prokaryotic and viral activity in groundwater: Metatranscriptomic data

Recently Lopez-Fernandez et al. (2018) found metatranscriptomic evidence for the metabolic activity of all three domains of life (approximately 99% bacteria, 1% archaea and < 1% eukaryotes) in both 'young' (residence time of <20 years) and 'old' (thousands of years) groundwater. Many of the transcripts of the small ribosomal subunit (SSU) could not be mapped and included newly described candidate prokaryotic phyla (3%–31% of SSU-transcripts). Foremost, these findings indicate that microorganisms in groundwater ecosystems are active but still widely unexplored in terms of microbial diversity. In the young groundwater, microorganisms were inferred to carry out a diverse set of metabolic strategies, whereas microorganisms in the old groundwater were predominantly in 'metabolic standby' (i.e. ready to carry out translation but metabolically inactive). Notably, mapping of transcripts against Metagenome Assembled Genomes (MAGs) from the same sites yielded only a few hits for viruses. However, it

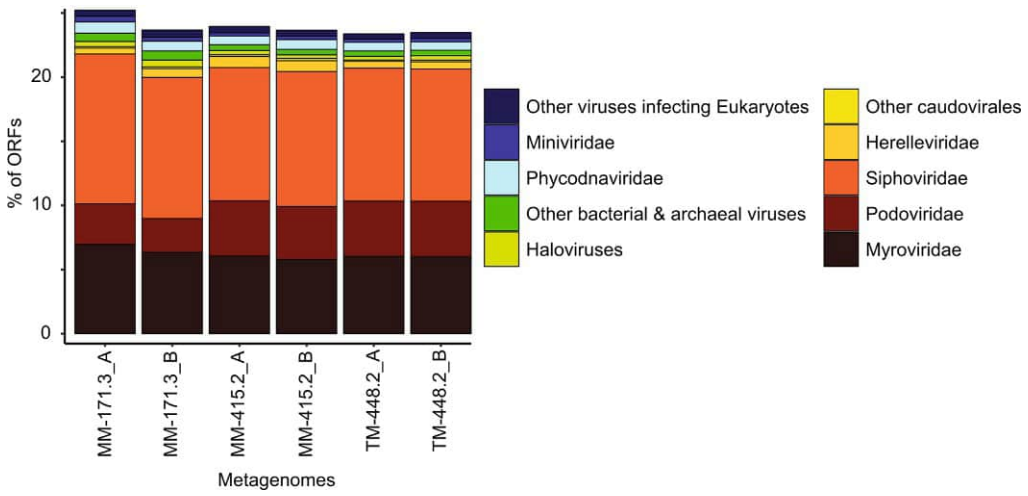

Fig. 4 Composition of the viral community in Aspö Hard Rock Laboratory based on gene homologies with known viral sequences. Three metaviromes at 171m (MM-171.3), 415m (MM-415.2) and 448m depth (TM-448.2) in two replicates (A and B). Myo-, Podo-, Sipho-, and Herelleviridae belong to the order Caudovirales. From Holmfeldt K et al. (2021) The Fennoscandian shield deep terrestrial virosphere suggests slow motion 'boom and burst' cycles. *Communications Biology* 4(1): 307.

should be mentioned that, especially in environments underexplored by metagenomic analysis, low fractions of identifiable viral reads are common (Bruder et al., 2016). In a more recent metagenomic and metatranscriptomic study with samples from the same sites, Holmfeldt et al. (2021) found that in the young groundwater up to 84% of identified viral genotypes showed transcriptomic activity. Paralleling the earlier findings for microorganisms, viruses in the old groundwater were mostly inactive or in 'metabolic standby' (0.1–3.8% active viral genotypes).

Phage lifestyles in groundwater

The relative importance of lytic and lysogenic phages in groundwater has not been addressed so far. Consequently, important variables like the frequency of visibly infected cells (FVIC), which have been seminal for initial estimates of the extent of phage mediated lysis in marine systems, are not available for groundwater (Fuhrman, 1999). From ultraoligotrophic arctic and Antarctic lakes extremely high FVIC (mean 26.1%) but low burst sizes and a large proportion of ssDNA phages have been reported (Säwström et al., 2007; De Cárcer et al., 2015). These findings indicate that highly oligotrophic environments do not necessarily prevent lytic dynamics but might keep them at an extremely slow rate or temporary halt their progression in a phenomenon called 'pseudolysogeny' until the environmental conditions change to their favor and allow the continuation of the infection cycle (Anesio and Bellas, 2011). While data on the frequency of lysogenic cells in groundwater is lacking, traditionally high frequencies of lysogenic cells have been reported from oligotrophic environments (Paul, 2008). Therefore, we might also expect a relatively high frequency of lysogenic cells in groundwater. The recent Piggyback-the-Winner model which postulates that temperate phages are more frequent under high microbial densities appears to be badly applicable to the diluted conditions in groundwater (Knowles et al., 2016). In addition, the validity of this model has been questioned based on contradicting experimental findings and theoretical considerations (Knowles et al., 2017; Weitz et al., 2017). Single stranded DNA phages of the *Microviridae* and *Inoviridae* families somewhat blur the dichotomous description of phage life strategies as either being lytic or lysogenic. While *Caudovirales* are known to encode complex machineries triggering the lysis of their host (Fernandes and São-José, 2018), *Microviridae* have significantly smaller genomes and employ much simpler mechanisms of cell lysis which are closely tied to their hosts growth (Székely and Breitbart, 2016). Both properties appear to be well suited for life in groundwater, where energy and nutrient limitations control viral production and drive organisms to a smaller genome size (Anderson et al., 2013; Tian et al., 2020). *Inoviridae* on the other hand cause chronic infections which lead to a continuous release of viral particles without lysing their host. Most of our knowledge about these phages stems from human pathogens like *Pseudomonas aeruginosa* and *Vibrio cholerae* where they have been found to impose only a low burden on their host (Hay and Lithgow, 2019). Despite their potential ecological roles only a handful filamentous phages have been isolated from aquatic environments (Wang et al., 2007). Their high frequency of occurrence in groundwater metagenomes and implication in biofilm formation raise the possibility that chronic infections by *Inoviridae* play a significant role in aquifers.

Potential ecological roles of phages in groundwater

Phages interact with their hosts but also with other phages and mobile genetic elements like plasmids. These interactions can either be antagonistic or synergistic (Díaz-Muñoz et al., 2017; Kothari et al., 2019). The interplay of phages and its consequences in aquatic ecosystems are therefore inherently complex and difficult to predict. For instance, in ocean waters a single prokaryotic strain can be targeted by more than 25 different phages at the same time (Deng et al., 2014). In groundwater, prokaryotic communities typically constitute hundreds to thousands of operational taxonomic units (OTUs or ASVs; e.g. Fillinger et al., 2019b). Due to the scarcity of studies investigating prokaryote-phage interactions in groundwater, this section on the potential ecological roles of phages in aquifers is speculative by nature. To further explore the potential role of viruses in groundwater ecosystems in the following, we address two related questions: (1) If the environmental conditions in groundwater impede viral production, why do we consistently find suspended phages in groundwater? (2) How could phage infection and reproduction be sustained under extreme carbon and energy limitations and in an environment where phages and hosts are extremely diluted? Possible answers include (i) insufficiently understood phage-host interactions between communities in pore water and those attached to sediment and rock surfaces (Hansen et al., 2019), (ii) 'boom and burst' cycles in slow motion (i.e. shifting regimes of metabolic activity and inactivity of prokaryotes and phages in groundwater, Lopez-Fernandez et al., 2018; Holmfeldt et al., 2021), (iii) frequently overlooked non-lytic viral life cycles (i.e. lysogenic and chronic infections) and (iv) groups of phages like *Microviridae* and *Inoviridae* which appear to be well adapted to carbon, nutrient and energy limitations but are hardly investigated in an ecological context (Székely and Breitbart, 2016; Roux et al., 2019).

Do phages sustain prokaryotic functional diversity in groundwater?

It is unknown how prokaryotic functional diversity can be sustained over extended periods of time when basic nutritional and energy requirements restrict essential cellular functions (especially in deep and old groundwater) such as the repair of damaged enzymes and DNA or the maintenance of the electrochemical potential (Jørgensen and D'Hondt, 2006). Phages might play an important role in this process by recycling nutrients from currently active members of the community to inactive members, e.g.

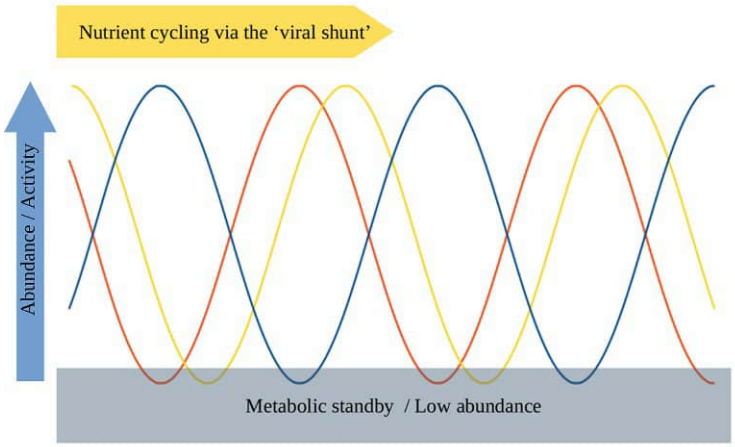

Fig. 5 Phages sustain prokaryotic functional diversity by oscillating between 'metabolic standby' and activity. Each line represents an idealized group of prokaryotes targeted by the same phages. These phages control the abundance of their hosts in a 'Kill-the-Winner' dynamic i.e. by preferentially targeting the most abundant and/or most active prokaryotes. Through host lysis metabolites are released which are recycled by other members of the prokaryotic community and thereby stimulate their activity and thereby ensure their persistence.

through 'boom and burst' cycles in slow motion (Danovaro et al., 2008; Heinrichs et al., 2020; Holmfeldt et al., 2021). In this concept, individual populations of prokaryotes oscillate between phases of metabolic activity and 'metabolic standby'. During an active phase, both prokaryotes and phages start to reproduce and phages impact the prokaryotic community following a 'Kill-the-Winner' (KtW) dynamic, i.e. the most abundant and most active prokaryotes would be preferentially targeted by lytic phages (Thingstad, 2000). As a consequence, phages would release nutrients through the lysis of their hosts via the 'viral shunt' (Wilhelm and Suttle, 1999) which could subsequently drive the activity of other members of the prokaryotic and phage community (Fig. 5). As proposed by the 'constant diversity' model, KtW is also expected to select against single prokaryotic genotypes which outcompete other, less competitive genotypes in terms of nutrient acquisition and energy usage. This allows other metabolic strategies to thrive as well and in consequence leads to a more efficient exploitation of resources by the prokaryotic community (Rodriguez-Valera et al., 2009). Both mechanisms could be essential for sustaining the functional diversity of prokaryotic communities in groundwater over long time scales. Lysogenic phages could play a key-role in the regulation of this process by either inhibiting its dynamic (e.g. by conferring resistance to other phages through 'superinfection exclusion,' van Houte et al., 2016) or promote it by switching from lysogeny to lytic reproduction. Oscillations between 'metabolic standby' and activity would also require stable intermediate stages for phages in times of 'metabolic standby' to counteract viral decay. A number of such intermediate stages like 'pseudolysogeny' (i.e. stalled stages of viral infections, Anesio and Bellas, 2011), lysogeny or chronic infections are known, which could play a key role in the persistence of phages in groundwater (Hobbs and Abedon, 2016).

Do phages alleviate metabolic bottlenecks?

Many phages contain auxiliary metabolic genes (AMGs) which during infection serve to optimize the host cell for viral reproduction by alleviating metabolic bottlenecks (Hatfull and Hendrix, 2011). Since the first description of AMGs (Mann et al., 2003), numerous examples have been identified in phages (e.g. Hurwitz et al., 2013; Kavagutti et al., 2019). Certain groups of AMGs are thought to have significant impact on the global carbon (Puxty et al., 2016) and sulfur cycle (Kieft et al., 2021). In groundwater, AMGs could keep the metabolism of an infected prokaryotic cell running even under conditions when it would normally enter starvation and halt metabolic functions. AMGs might therefore 'lubricate' the wheel of biogeochemical cycling in groundwater. How far AMGs are also involved in anabolic functions is currently unknown. As a recent example, Coutinho et al. (2020), identified AMGs in Lake Baikal which are presumably involved in dark carbon fixation and methylotrophy. These functionalities could also play a role during viral infections in groundwater.

Conclusion

Although our knowledge about the abundances and extent of metabolic and biogeochemical activities of subsurface prokaryotic and phage communities is still immature, a few conclusions can be drawn: (i) prokaryotes and phages are present in aquifers, (ii) some of these prokaryotes show metabolic activity which makes them potential hosts for phage reproduction, (iii) infective

phages are present and have been isolated from groundwater and (iv) viral RNA and viral peptides have been found to be expressed in recently recharged groundwater. Besides these facts, our knowledge about life strategies and the ecological role of phages in groundwater ecosystems is rather limited. While some studies underlined a statistical relationship between the number of prokaryotes and VLPs, other studies found no obvious connection. Moreover, no common key physical-chemical parameters have been identified governing phage abundance and production. A huge range in VPRs from less than one to >700 has been observed. Taking into account the substantially decreased contact probability of phages and their potential hosts in groundwater, in many aquifers prokaryotic and viral production (via the lytic cycle) seem to be decoupled. There is early evidence that also life strategies other than the lytic cycle, i.e. lysogeny, pseudolysogeny, and chronic infection, could play key roles in the persistence and reproduction of phages in groundwater.

Knowledge gaps

1. Which environmental factors drive viral abundances in groundwater?
2. Which environmental factors govern the activity of phages in groundwater?
3. Interactions of prokaryotes and phages in groundwater biofilms?
4. Frequency of visibly infected cells in groundwater?
5. Which lifestyles (lytic, (pseudo)lysogenic, chronic) do phages in groundwater preferentially adopt?

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The Groundwater Mycobiome: Fungal Diversity in Terrestrial Aquifers

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Anamorph Asexual, mold-like reproductive stage of members of Dikarya.
Barcode Conserved to highly variable gene segments, such as the ribosomal gene cluster, proteins, or enzymes, that are universal within the target group of organisms. They are, for instance, utilized in metabarcoding efforts for rapid species identification of environmental samples.
Convergent evolution Organisms not closely related that develop traits with similar form or function, also called homoplasies.
Cryptic Morphologically indistinguishable.
Dark matter fungi Fungal taxa that are uncultured and poorly known, mostly belonging to lineages diverging early in the fungal tree.
Diversity The number and relative abundance of taxa, which are often species or functional groups of organisms, as well as the genetic variation within a taxon.
Fungi Taxonomically, fungi constitute their own kingdom. They are eukaryotic, heterotrophic, mostly mesophilic organisms that produce spores for reproduction and dispersal and branching hyphae (that make up the so-called mycelium) for propagation, organic matter decomposition, and uptake.
Groundwater Water that is located beneath the earth's surface in pore spaces and cracks of the solid, rocky crust of the earth.
Next-generation sequencing (NGS) Inexpensive, routine, high throughput method for sequencing short genetic barcodes, often from environmental samples.
Oogamy Fertilization by the fusion of a small, usually motile male gamete and a large, much less motile female gamete.
Teleomorph Sexual lifecycle stage of members of Dikarya, often producing macroscopic fruiting bodies.

Introduction

Fungi are among the dominating lineages within the ecosphere, ubiquitously present in both terrestrial and aquatic habitats. Evidence from fossil records even suggests that fungi/fungal-like organisms may have existed in the deep biosphere as early as about 2.4 billion years ago (Bengtson et al., 2017; Loron et al., 2019). Owing to their diverse life strategies as decomposers, symbionts, parasites, and pathogens, fungi play vital ecological roles in the organization of different biological communities and contributed to shaping the world as we know it in its present form. Fungi can survive and thrive under a wide range of oxygen, pH, temperature, water potential, and nutrient level conditions (Schlosser, 2012). Thus, these fantastic creatures have managed to establish themselves in various types of ecological niches and habitats such as the snow and ice as found naturally in glaciers, the tropics, deserts, the oceans, and any kind of freshwater habitat—which simply means that fungi are everywhere. Along with this omnipresence, global fungal diversity has for some time been estimated to lie between 3.5 and 5.1 million species (Blackwell, 2011). In contrast, a more recent study showed that fungal diversity probably ranges between 2.2 and 3.8 million worldwide

(Hawksworth and Lücking, 2017). However, with only ~150,000 formally described species so far (Kirk, 2021), the fungal inventory is far from being fully explored.

Fungi are talented decomposers of dead organic matter (saprotrophs) and recyclers of inorganic materials (e.g., N and P), and their bioavailability constitutes a critical factor for fungal activity. In aquatic environments, fungi display various trophic modes, often occurring as parasites or pathogens, harming the host's cells, which can be animals, plants, or sometimes even other fungi. Apart from being saprobes or pathotrophs, fungi can form mutualistic associations (symbiotroph) with animals, plants, and various microorganisms that bring forth a multitude of phenotypically distinct lifestyles, some examples being mycorrhizae or lichens (Fig. 1).

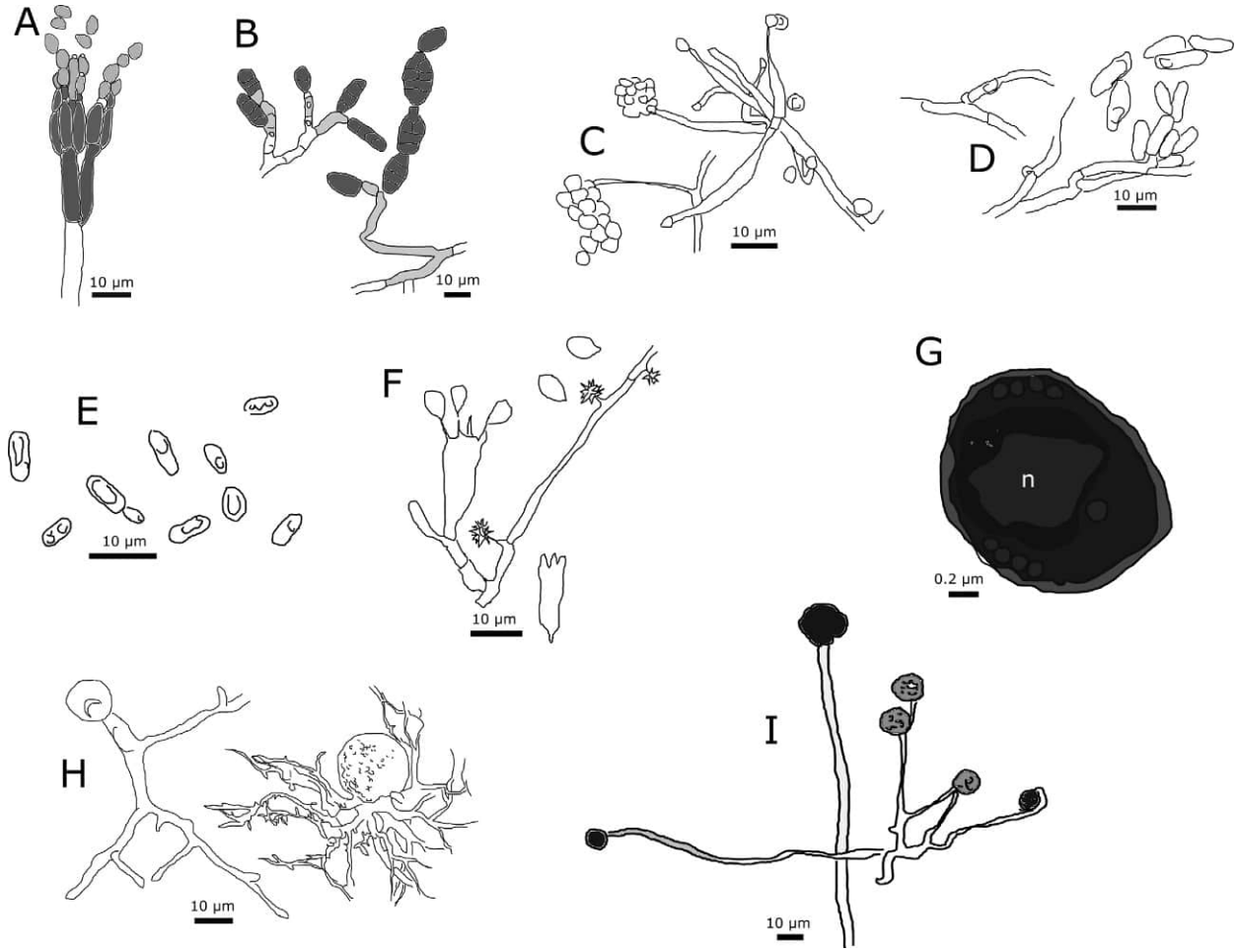

Fig. 1 Some examples of the variety of fungal lifestyles found within groundwater. (A) Ascomycetous saprotroph and plant pathogen/parasite (*Penicillium oxalicum*). (B) Ascomycetous plant- and animal pathogen, wood saprotroph (*Alternaria sp.*). (C) Animal pathogen (*Pochonia sp.*). (D) Saprotrophic, basidiomycetous yeast with filaments (*Dioszegia sp.*). (E) Low temperature tolerant, basidiomycetous budding yeast (*Vishniacozyma* sp.). (F) Saprotrophic basidiomycete (*Resinicium* sp.). (G) Microsporidian hyperparasite spore (n = nucleus). (H) Freshwater chytrid (Rhizophydiales). (I) Endophyte/saprotroph (*Mortierella* sp.).

About 90% of existing plants form such mycorrhizal associations, which, among other things, promote plant growth, increase plant resistance to biotic and abiotic stressors, and help plants acquire absorbed soil nutrients through fungal hyphae. Interestingly enough, some early diverging lineages of fungi, for instance, neocallimastigomycetes, even co-evolved within the digestive tracts of ruminant mammals, insects, and other invertebrates (Moore et al., 2011; Picard, 2017; Stefani et al., 2016). Consequently, fungi can take on a broad range of metabolic roles, naming just a few examples in Table 1. Fungi reproduce and disperse by means of spores,

Table 1 Metabolic roles of fungi.

Decomposing of OM (organic matter)
Organic and inorganic nutrient cycling (e.g., C, H, O, N, P, S, metals)
Translocation of water and nutrients
Change in local geochemistry (e.g., redox potential, pH, O_2)
Production of metabolites and exopolymers
Degradation of xenobiotics (e.g., pesticides, drugs, radionucleotides), complex compounds (polysaccharides, lipids, and proteins, and other complex structure polymers), and contaminants (e.g., fuel, oil, gas, explosives)
Mineral formation (e.g., carbonate, limestone) and dissolution (e.g., weathering and leaching)

Modified from: Watkinson SC, Boddy L and Money NP (2015) *The Fungi*, 3rd edn., pp. 189–190. Elsevier Ltd.

which are formed during meiotic- or mitotic reproduction. Different taxa can bring forth a great variety of spore types, all with an individual morphological and functional identity. Many aquatic fungal species, such as members of Chytridiomycota, and Blastocladiomycota can produce motile, flagellate spores (zoospores) (Fig. 2), or non-motile spores with a variety of unique shapes, optimal for dispersal in aquatic environments.

It is well established that fungi sometimes have complex and obscure life cycles that may involve stages of different growth forms (e.g., filamentous and/or unicellular, such as yeasts) (Fig. 1), hosts, and sexual states (e.g., anamorphs and teleomorphs in Dikarya) (Naranjo-Ortiz and Gabaldón, 2020). Fungi are largely cryptic, driven for instance, by convergent evolution, which is widespread throughout the fungal tree of life and can be caused by mechanisms such as interspecific hybridization (Shang et al., 2016; Steensels et al., 2021; Sun et al., 2019; Torruella et al., 2015). Traditional morphological taxonomic species identification is, in reality, often not possible, as stages of the life cycles in which fungi form characteristic fruiting bodies are unknown or not inducible during

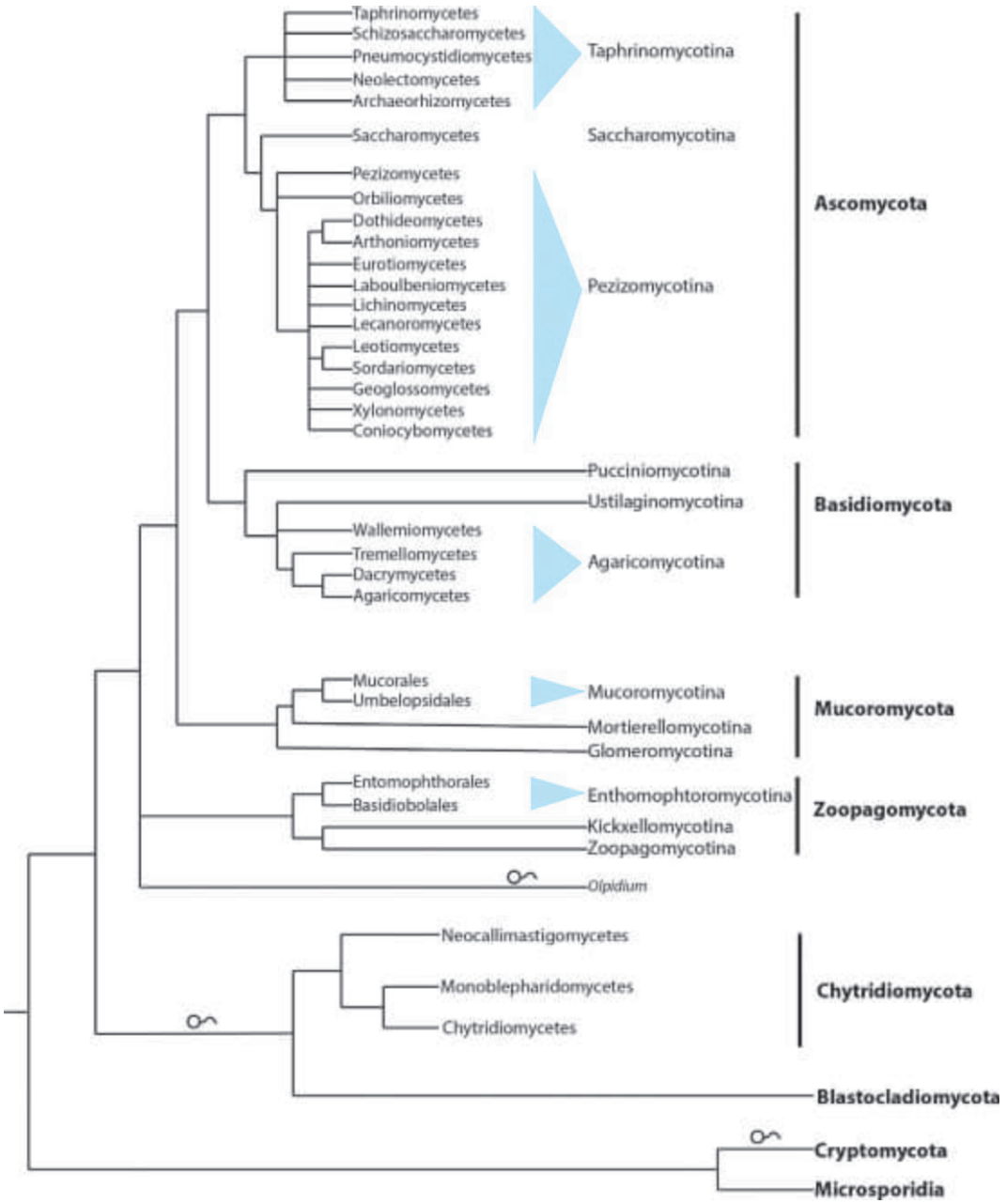

Fig. 2 Current understanding of the phylogenetic backbone of the fungal kingdom, compiled and negotiated from several phylogenetic studies (Gazis et al., 2012; Hibbett et al., 2007; James et al., 2006, 2013; Nguyen, 2015; Rosling et al., 2011; Schoch et al., 2009; Sekimoto et al., 2011; Spatafora et al., 2016; Tedersoo et al., 2018; Zhuang and Liu, 2012). Polytomies are representing yet unresolved relationships between lineages. Zoosporic fungi are indicated by a schematic drawing of a zoospore (James et al., 2006).

cultivation, and their somatic structures only show limited cell differentiation (Watkinson et al., 2015). Thus, purely phenotypic recognition of fungi is difficult, and it is no wonder that the taxonomic history of fungi resembles a roller coaster ride (Naranjo-Ortiz and Gabaldón, 2020).

The lack of knowledge about the sexual states of fungi and the fact that many species cannot be cultured in the laboratory consistently results in formal species descriptions being ambiguous or missing altogether. The large amount of molecular data derived from environmental sequencing creates an additional layer of complexity to this problem. Environmental sequencing, such as Next-generation sequencing (NGS) or Third-generation sequencing, is based on classifying a molecular barcode into a hypothetical species. These techniques enable rapid species identification in unprecedented numbers, utilizing subregions located in the nuclear ribosomal gene cluster, such as the formally accepted internal transcribed spacer (ITS) barcodes ITS1, or ITS2, or other, sometimes longer or more conserved parts of the rDNA (ribosomal DNA) (Heeger et al., 2018, 2019; Nilsson et al., 2019; Wurzbacher et al., 2019). The exactness of the classification depends a lot on the comprehensiveness and up-to-dateness of the various classification databases of choice. Additionally, these sequencing techniques are subject to several factors that may lead to biased species classifications, such as choice of primers, barcode, or sequencing technology (Tedersoo et al., 2015).

Unknown fungal richness in groundwater

Compared to the earth's terrestrial ecosystems, where many fungal global datasets are available, the aquatic environment has been historically understudied regarding its fungal diversity. It is important to mention that despite the huge estimates of ~2.2–3.8 million extant fungal species, currently, only a little over 4000 have been classified as aquatic (Jones et al., 2014) (Fig. 3). Such a small proportion of aquatic fungi within the global fungal diversity estimates may not hold when acknowledging that around 70% of the earth is covered with water and aquatic environments are potentially ideal habitats for many fungal species (Wurzbacher et al., 2011). This highlights the need to revise the extent of aquatic fungal diversity in the light of recent advances in molecular methods and their broader applications in biodiversity estimates of various ecosystems.

Similar to the deep oceans, the world's groundwater habitats are seriously underexplored for fungi (Grossart et al., 2019). Especially fungal members belonging to early diverging lineages (Fig. 2) are mostly underrepresented in fungal studies of aquatic systems (Picard, 2017; Retter et al., 2019). There are several reasons for such underrepresentation of aquatic fungi: first, many aquatic ecosystems/landscapes of the world are still not very well explored for their fungal inventory; second, reproduction life cycles in which fungi produce distinct fruiting bodies are often entirely missing (or yet undiscovered) for many fungal taxa; and third, due to molecular bias caused, for example, by choice of primers or the DNA barcode marker. The ITS—region, for instance, is not sufficient to target and resolve the taxonomy of fungi at a deeper level (Berbee et al., 2017; Grossart et al., 2019; Nilsson et al., 2019; Picard, 2017; Tedersoo et al., 2015).

Groundwater food sources and replenishment

The groundwater hydrosphere is generally regarded as an oligotrophic environment regarding the abundance and bioavailability of organic material. Due to the complete absence of light, an important energy source for primary production is missing. Even though chemoautotrophic organisms, for instance, as part of microbial biofilms, can sometimes contribute substantially to biomass production in groundwater, most of the energy is derived from the land surface (Herrmann et al., 2020). This includes organic material mainly in the form of allochthonous DOM (dissolved organic matter), which is supplied with seepage water. The availability and composition of DOM and essential nutrients are crucial for the survival and flourishing of the fungal communities

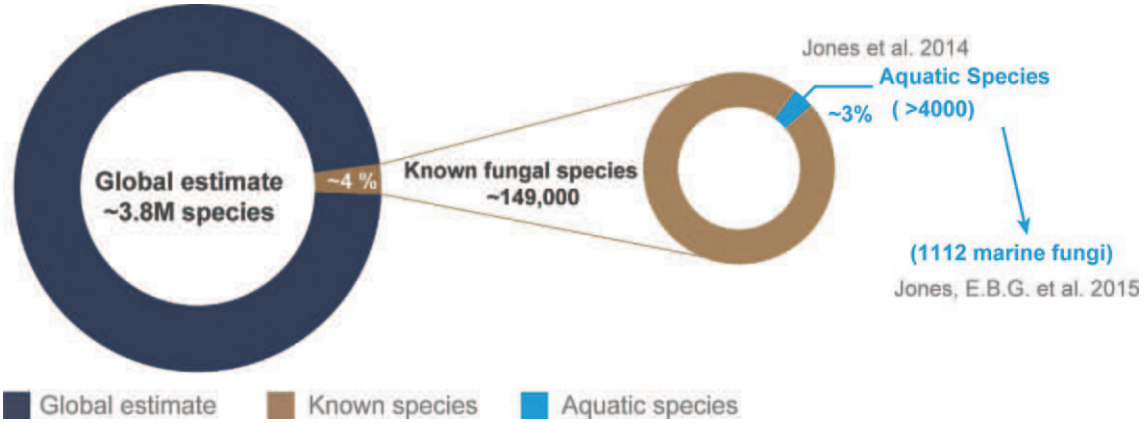

Fig. 3 The actual representation of known/described species of aquatic fungi (Jones et al., 2014, 2015) in the overall fungal diversity estimates.

in groundwater. In groundwater, the input of organic material will usually change dynamically during periods of precipitation and subsequent recharge or drought. Likewise, the quality and quantity of DOM that ultimately reaches the saturated zone is influenced by various biotic and abiotic factors, such as the surface land cover, surface water to catchment connectivity, the porosity, and the geology of the unsaturated zone, as well as the distance of the land cover to the aquifer (groundwater table depth). It is also dependent on the chemical and physical properties (e.g., polarity) of the dissolved organic compounds, if they have undergone photodegradation on the surface, and the degree of biodegradation by resident microbial communities in the soil layers through which the DOM passes (Shen et al., 2015). As a result, typical groundwater DOM is largely deprived of lignin-derived phenols, which are derivatives of secondary metabolites of vascular plants, and higher molecular weight (HMW) compounds (Shen et al., 2015). These fractions of DOM are highly reactive and have the ability to readily adsorb to the surface of solids (Rutlidge et al., 2021; Singh et al., 2016). Therefore, in terms of DOM composition, groundwater is similar to the deep ocean (Shen et al., 2015).

In contrast, in rivers, streams, and lakes, POM (particulate organic matter), e.g., animal and plant detritus, is an essential energy source. However, POM is not present in significant quantities in groundwater, as it is attenuated or degraded already within the pedosphere. From this point of view, groundwater represents a rather hostile environment for fungal organisms. On the other hand, some limiting factors such as UV-irradiation, competition for food or host species, or extreme temperature fluctuations do not exist or are less pronounced, which in turn may prove advantageous for the survival of various fungal species and their spores.

Not surprising, groundwater is different to surface water systems in several other aspects, such as high-water residence times (sometimes decades or millennia) and limited space, mainly in the form of (interconnected) pore cavities in unconsolidated sediments or fractures in the rock matrix. As a result, the groundwater hydrosphere may only serve to a limited extent as a vector for (long-distance) dispersal of fungal taxa and their spores. In summary, groundwater, represented by water in various types of aquifers, underground streams, and cave waters, forms a unique ecosystem with some potential limitations and advantages for its fungal and overall microbial life, on which the stability of this ecosystem is founded. Since groundwater is usually recharged by rain and snowmelt, as well as surface water passing through soil and sediment zones, this ecosystem provides a rare opportunity to study both transient and resident fungi in their natural settings.

The diverse ecological roles of fungi

Despite the challenging conditions prevailing in groundwater, there have been several studies conducted within the last decades that were able to detect both total and active proportions of fungal communities in various groundwater environments (Ekendahl et al., 2003; Jasrotia et al., 2014; Livermore and Mattes, 2013; Nawaz et al., 2018, 2019; Perkins et al., 2019; Schwab et al., 2017; Sohlberg et al., 2015; Wurzbacher et al., 2020). A study that has been published as early as 1989 already points at the highly diverse and distinct microbial communities, including fungi that could be recovered from a deep coastal plain aquifer (Fliermans, 1989), and fossilized fungi have also been reported from the subsurface (Reitner et al., 2006).

Concrete examples highlight the potentially important and yet unexplored roles that fungi play in the oligotrophic environment of the water-saturated subsurface. The first is that they can potentially restructure the groundwater matrix through their mineral weathering and mineralization properties, and thus also provide essential minerals for their (and other microorganisms) growth and metabolism (Ivarsson et al., 2018).

Second, they are excellent degraders of complex organic compounds, which they may mineralize to CO_2 and water in the presence of oxygen. Macropolymers often have a poor biological degradability, making them persist in the groundwater environment over a long period of time. Poorly biodegradable leftovers (refractory OM) of organic matter can be decomposed and transformed by fungi via particular enzymatic pathways, and they are also believed to have the capability to produce highly aromatic organic compounds themselves (Collado et al., 2018; Masigol et al., 2019). Some lignin-derived compounds, such as humic substances, make up a significant part of the refractory DOM available in groundwater (Hofmann and Griebler, 2018; Perkins et al., 2019). The effective degradation of such humic compounds by fungi seems to be dependent on, e.g., its concentration, oxygen availability, and temperature (Collado et al., 2018), possibly leading to slower degradation rates (i.e., supporting long-term growth) of complex organic substances by fungi in groundwater.

If pulses of DOM passing through the aquifer are long-lasting, at least bacterial communities were found to adapt and utilize the labile fraction of DOM. However, it appears that the more labile carbon there is available, the less it is converted into bacterial biomass for reasons that are still ambiguous (Hofmann et al., 2020). On the other hand, it seems that a more diverse composition of DOM promotes a higher bacterial diversity (Hofmann et al., 2020). Bacterial and fungal communities do not seem to be intimately connected, but as the structural setup of DOM is a primary driver for both, these scenarios could prove to be true for fungi as well (Fabian et al., 2017).

In other words, this could mean that if pulses of DOM are short, labile DOM is not converted into biomass to the same extent, as the microbial communities are highly adapted to the energy-poor conditions prevailing in groundwater. Thus, labile DOM may be retained in the gravel matrix or transported further down into the aquifer depending on hydrology and sorption capacities (Hofmann and Griebler, 2018). Fungi, especially saprotrophic taxa such as yeasts, are known to degrade substantial amounts of labile carbon (de Vries and Caruso, 2016), therefore potentially playing an important role in the degradation of this "unused" DOM fraction. Taking all of this into account, one can still only speculate about the dimension of the groundwater fungal biomass.

In situ sources of OM include microbial biofilms that form on the gravel matrix and rock surface of aquifers, byproducts of mineral-fluid interactions, chemolithoautotrophic primary production, production of secondary metabolites, fungal spores, as well

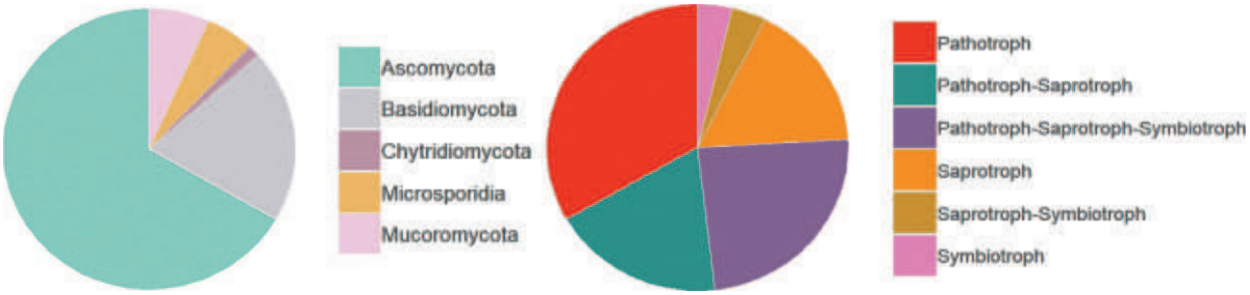

Fig. 4 Taxonomic affiliation on phylum level (left) and their trophic state (right) of 78 fungal taxa that represent the most commonly recovered fungi from groundwater habitats so far, summarized from several environmental sequencing studies (Bohu et al., 2016; Ekendahl et al., 2003; Euringer and Lueders, 2008; Fester, 2013; Grabner et al., 2020; Hoque and Fritscher, 2016; Jasrotia et al., 2014; Livermore and Mattes, 2013; Nawaz et al., 2018; Purkamo et al., 2018; Sohlberg et al., 2015; Wurzbacher et al., 2020). Trophic states of taxa were annotated, where possible, with FUNguild (Nguyen et al., 2016).

as dead groundwater biota (Drake and Ivarsson, 2018; Ivarsson et al., 2018; Kagami et al., 2014; Reitner et al., 2006). Although a certain percentage of groundwater fungal communities consist of saprotrophic species, Sohlberg et al. (2015) did not find a correlation between fungal diversity and activity and the input of dead organic material in their study of a deep groundwater mycobiome. This suggests that fungi potentially take on different ecological roles within the groundwater than those of pure decomposers, again emphasizing that fungi have complex life cycles and lifestyles within the groundwater habitat. This would be in line with the discovery that significant parts of fungi recovered from groundwater are parasites and pathogens (Fig. 4). For example, fungal members of Microsporidia have been found to parasitize groundwater amphipods - an ecological role that is still awaiting a more thorough exploration (Grabner et al., 2020). Other studies hint at the important role of fungi sustaining anoxic (deep) subsurface environments, for example, by recycling fossil DOM stocks (Perkins et al., 2019). Here they act as producers of substrates, such as small organic compounds or hydrogen gas that are readily available for autotrophic processes of other members of the microbial loop (Drake and Ivarsson, 2018; Pomeroy et al., 2007; Purkamo et al., 2018). Another study hints at the role fungi play in providing and transporting dissolved iron in anoxic to suboxic karstified groundwater environments (Schwab et al., 2017). These specific metabolic abilities indicate that fungi could play a role in sustaining bacterial communities locally, where bacteria are known to play an essential role in OM decomposition and biomass generation and effectively contributing to groundwater biomass themselves (Watkinson et al., 2015).

Where do groundwater fungi originate from?

The question of what the source of fungi recovered from groundwater forms is not so easy to answer. Nevertheless, aquatic fungi in general and groundwater fungi, in particular, can be divided into two broader groups. These are "resident fungi" and "transient fungi." Resident fungi are those specimens that can complete their life cycle in the aquatic realm and are not encountered in terrestrial habitats. In contrast, transient fungi are those that enter the aquatic environment from terrestrial sources and can adapt well to local conditions or remain inactive in the form of spores (Shearer et al., 2007). For instance, a robust adaptive capacity is exhibited by groundwater fungi found in karst aquifers, which make up the majority of the fungal OTUs found in these landscapes. These are presumably transported from the surface into the groundwater system, facilitated by fractures, underground drainage systems, as well as the large voids of karst during recharge events (Nawaz et al., 2016). The presence of terrestrial fungi in aquatic systems (transient fungi) raises a relevant question about the ability of different fungal taxa to adapt to the aquatic environment.

A recently published study on subterranean aquifers has shown the presence of various fungal OTUs of the terrestrial origin or known to be parasitic fungi of various crops in the active fraction of groundwater fungal communities recovered (Nawaz et al., 2018). This raises the question of whether and how the fungi have undergone specification in groundwater and whether obligate groundwater species exist at all. With the current state of information available on groundwater fungi, these questions are difficult to answer unless there are hypothesis-driven studies on these topics either in natural settings or in well-designated lab experiments.

Taxonomic composition and systematic overview of groundwater fungi

Fungal taxonomic and functional diversity in groundwater habitats is manifold, although there is currently no systematic overview of groundwater species. Keeping the fungal tree of life (Fig. 2) in mind, fungal taxa recovered from groundwater habitats so far are mostly affiliated with pathogenic and/or saprotrophic lineages, and a major part of them belong to Dikarya (Ascomycota + Basidiomycota) (Fig. 4). Wurzbacher et al. (2020) found that around 8% of the fungal diversity recovered from volcanic springs was made up of early diverging lineages of fungi, and a significant part belonged to yet unexplored yeast lineages. Yeasts, exclusively occurring within Dikarya, are especially remarkable, as they could be recovered from basically every habitat of the world (McLaughlin and Spatafora, 2015; Rojas-Jimenez et al., 2020).

Early diverging lineages

The following paragraphs attempt to address the ecology and systematics of the individual fungal phyla against the background of groundwater ecosystems. According to most recent phylogenetic studies, the branch diverging earliest in the fungal tree is the clade uniting members of Cryptomycota, and Microsporidia which are sister to the rest of the fungi. This clade is found to be almost as old as the entire fungal tree of life, and emerges mostly from environmental sequencing efforts, most often in marine ecosystems, but also from groundwater (Grabner et al., 2020; Letcher et al., 2018; Richards et al., 2012; Wurzbacher et al., 2020). Many cryptomycetes and microsporidians are endoparasites, for instance, of other fungi or fungal-like organisms (Gleason et al., 2012). Cryptomycetes have likely secondarily lost their chitin cell wall—a feature most members of the fungal kingdom share—in certain stages of their life cycle, such as during host infection (James et al., 2013; Jones et al., 2011; Richards et al., 2012). They also seem to have a degenerate mitochondrion, emphasizing the parasitic signature this group of early diverging fungi shares. Members of Microsporidia are also intracellular parasites that have evolved to infect a wide range of organisms, from insects to mammals, including aquatic species (McLaughlin and Spatafora, 2014). Microsporidians have to harvest their energy from a host as they have lost their mitochondria in the course of evolution, being left only with a reduced version called a mitosome (James et al., 2013).

Members of another ancient branch of fungi comprised of zoosporic chytrids and blastocladiomycetes have been found within groundwater ecosystems (Jasrotia et al., 2014; Nawaz et al., 2018; Sohlberg et al., 2015). The emergence of zoospores within this aquatic sister group to the "terrestrial fungi" once again underlines their adaptation to the aquatic realm. They are ubiquitous in various habitats, the majority of them being found in water. They have also been recovered from highly challenging environments, such as hydrothermal vents in the deep ocean (Le Calvez et al., 2009). Nawaz et al. (2018) discovered that the chytrid fraction made up the third-largest phylum detected in their groundwater study site. In the groundwater, chytrids are mainly parasites of other fungi or invertebrates. In surface water ecosystems, they also infect amphibians, and plants, including algae and phytoplankton. Some orders within Chytridiomycotina are also known to saprotrophically feed on various structural polymers (e.g., keratin and chitin). Monoblepharidomycetes, on the other hand, are exclusively saprotrophic and form a distinct clade, which is attributable to their oogamous sexual reproduction (McLaughlin and Spatafora, 2014). Neocallimastigomycetes are obligate anaerobic species, which can be found in terrestrial and aquatic anaerobic environments but are best known for their occurrence in the guts of ruminant herbivores. In the course of evolution, they came forth with a degenerate version of a mitochondrion that allows them to break down complex compounds, such as cellulose, by fermentation. Thus, together with facultative anaerobic fungal species, which include some members of Blastocladiomycota, they have the potential to sustain oxygen-deprived groundwater environments (Moore et al., 2011; Risse-Buhl et al., 2013).

Fungi belonging to the Zoopagomycota and Mucoromycota are thought to only occur sparsely within aquatic habitats. On the other hand, these claims are potentially obsolete as it is now well established that this group of fungi is underrepresented in environmental sequencing efforts, primarily due to molecular biases. They are non-flagellate fungi and known to comprise the earliest terrestrial lineages that are important to understand the transition of fungi from water to land (Heitman et al., 2017). Members of Zoopagomycota are mostly predators (for instance, of nematodes and their eggs, or amoebae), parasites (e.g., of other fungi), but also obligate symbionts, for instance, in the gut of arthropods (Heitman et al., 2017; Spatafora et al., 2017). Mucoromycetes are predominantly characterized by their associations with plants, for example saprotrophic, or mycorrhizal, and their most recent ancestors probably gave rise to the modern fungus-plant relationships. Evidence in favor of the theory of a molecular bias towards these lineages of fungi is given by Grossart et al. (2019), who name this phylum as one of the dominant lineages recovered from groundwater aquifers.

Dikarya

Most sequences recovered from groundwater metabarcoding efforts are affiliated with Dikarya, many of them yeast or yeast-like taxa (Fig. 4). In other words, they are probably dominating the subsurface hydrosphere from what we know so far. The largest fungal phyla are Ascomycota, containing around 65,000 described species, and Basidiomycota, which encompasses approximately 31,000 described species. All known yeast species are placed within Dikarya but do not form a monophyletic group. Yeasts consist of those taxa that are known to grow vegetatively by budding or fission, and they are usually single-celled, although there exist exceptions that can produce hyphae. They can be free-living, attached to the substratum, or living within a host. Besides that, the majority of members of Dikarya grow in filaments on all kinds of organic substrates, such as carbohydrates, some being able to function well even under oxygen-deprived conditions (facultative anaerobes). Many members cannot be unambiguously placed within existing phylogenetic clades (Jones et al., 2014), and a significant number of described species within this group have their binomial name only linked to their asexual state, and the description of sexual morphs is often missing.

Moving from unknowns to knowns of aquatic fungal diversity

As in the previous sections, we have established that aquatic fungi are highly diverse in their taxonomic composition and functional abilities. Unlike the conventional microbiology tools such as microscopic or direct observations of different fungal spores, the molecular-based environmental surveys employing metabarcoding techniques (e.g., NGS) helped to explore unusual aquatic fungal

niches, for instance, deep-sea sediments, subseafloor, hydrothermal vents, and terrestrial groundwater. However, apart from the environmental sequences that could be taxonomically assigned, a significant proportion of the sequences remained unclassified, a common observation in most aquatic fungal surveys. Likewise, from DNA and RNA-based analysis of groundwater samples from terrestrial aquifers, Nawaz and colleagues reported that a significant proportion of fungal sequences remained unclassified (Nawaz et al., 2018, 2019). Such high proportions of unclassified fungi detected in the sequence-based datasets from the aquatic habitats are primarily due to the lack of their representation in the reference databases (Grossart et al. 2019, Heeger et al. 2019; Hibbett et al., 2011) and Grossart et al. (2016) has termed these unknown/unclassified aquatic fungi as "fungal dark matter—FDM"—the composition and ecology of which is largely unknown.

At present, the fungal databases are dominated by sequences from two major lineages, namely Ascomycota, and Basidiomycota with little representation of early diverging lineages, such as Cryptomycota, Chytridiomycota, and Zoopagomycota. This explains the possible reason for a considerable proportion of unclassified aquatic fungal query sequences against the available databases. One way forward to resolve the problems associated with fungal dark matter is the unambiguous communication of such unclassifiable fungal species (Kõljalg et al., 2020), or the application of single-cell omics, which involves the lysis and subsequent single-cell whole-genome sequencing of uncultured fungi. In 2018, a team of scientists from the Joint Genome Institute (JGI) and the University of Michigan has successfully amplified the whole genomes of a group of uncultivated fungi (Ahrendt et al., 2018). Application of such methods in aquatic fungal diversity studies will help to expand the current scope of information of aquatic fungi from mere pieces of barcoding regions of fungal DNA to whole genomes of the representatives of different fungal lineages, which consequently not only help to catalog the early diverging fungal species but also to understand their evolution and unique metabolic potentials.

Outlook on fungal groundwater diversity and their protection

In aquatic ecosystems, both organic and inorganic matter sources are altered by influences such as human activities, changed groundwater characteristics, or extreme meteoro-hydrological events (climate change) (Retter et al., 2020), which ultimately affects the resident fungal communities. These events can also potentially influence important drivers for fungal diversity, such as pH (e.g., leading to possible heavy metal leaching), temperature, or salinity. A change in local salt concentration could have very specific consequences, as it is relatively more difficult for land and freshwater species to conquer marine habitats, and salinity, therefore, plays a fundamental role in shaping fungal diversity (Jones and Pang, 2012). To better protect fungal communities in groundwater and the aquatic realm, there is an urgent need to improve the understanding of their diversity, as well as functions they provide, to protect their habitats, to act against climate change, to reduce anthropogenic influences on water bodies, such as the unrestricted use of fertilizers and fungicides in agriculture, and to accelerate the description and accurate classification of yet undescribed fungal species.

Conclusion

In this article, we underlined the diversity and capabilities of groundwater fungi as well the bottlenecks and way-outs in studying groundwater fungi using next-generation molecular platforms. There is a general agreement that fungi in terrestrial habitats are well studied and researched compared to aquatic ecosystems and that terrestrial fungi can be described as both richer and more diverse. However, the advent and application of new molecular biological tools in the field of mycology has revolutionized the approach and understanding of mycologists towards aquatic fungi. Despite this technological progress, groundwater mycologists are still faced with fragmented, or distorted information and literature on certain fungal groups and taxa, while research on others is entirely lacking.

It is worth noting that although groundwater represents only a small fraction of the water available on the planet, nearly 1.6 billion people worldwide depend on this underground reservoir for domestic, agricultural, and industrial purposes. From this context emerges a lack of consensus on the occurrence of diverse fungal taxa in groundwater, as the focus lies mostly on disease-causing taxa or few others that provide potentially interesting functions for biotechnology. All of this gives rise to an incomplete puzzle of groundwater mycology.

Conversely, it can be concluded from the available information on groundwater fungi that, in terms of species diversity and occurrences, we are currently only scratching the tip of the iceberg. A coherent message from recently published literature on groundwater fungi using the most-recent molecular methods (based on sequencing) is that largely, fractions of unknown fungi represent the mycobiome of groundwater. This indicates a significant knowledge gap regarding the contribution of groundwater fungi to the sustainability of such a unique ecosystem, along with their evolution, ecology, metabolic properties, and interaction potential with other organisms in the aquatic groundwater food web.

Knowledge gaps

- Accounting for the proportion of fungal respiration in groundwater.
- Estimating the proportion of fungal biomass in comparison to other microorganisms, such as bacteria.

- Exploring ecological roles that fungi cover within groundwater and defining their contributions to the groundwater food web, carbon, and nutrient cycling dynamics, as well as quantifying their turnover rates.
- Determining fungal diversity and formally describing novel fungal species living in groundwaters to reduce the number of "dark taxa" and accurately assess the full taxonomic and functional potential of fungi in groundwater.
- Investigating the fungal spore hydrodynamics and their dispersal in groundwater.
- Determining the number of obligate and facultative groundwater species.

Important case studies

Name of site	*Country*	*Coordinates*	*Main topic/concept covered*	*Key references*
Marching spring	Germany	48.820217, 11.715458	Biodiversity survey; mercury-removal function analyzes	Hoque and Fritscher (2016)
Former gasworks site	Germany	51.222720, 6.817301	Biodiversity survey; microeukaryote-targeted PCR/T-RFLP fingerprinting	Euringer and Lueders (2008)
Former uranium mining district	Germany	50.854577, 12.147187	Mn(II)-oxidizing microbial communities structures	Bohu et al. (2016)
Äspö Hard Rock Laboratory	Sweden	57.433191, 16.660323	Cultivation, phenotypic, and phylogenetic analysis of yeasts	Ekendahl et al. (2003)
Constructed wetland	Germany	51.325078, 12.027310	Arbuscular mycorrhizal bioremediation; phylogenetic analysis	Fester (2013)
	Germany, Belgium, Luxembourg, France, Poland, Great Britain, Ireland, The Netherlands, Czech Republic		Microsporidian diversity survey; barcoding	Grabner et al. (2020)
OakRidge Integrated Field Research Challenge	USA	35.979929, –84.290411	Biodiversity survey; ITS sequencing	Jasrotia et al. (2014)
Deep Archaean bedrock fracture aquifer	Finland	64.218147, 29.944645	Biodiversity survey; metabolic functionality	Purkamo et al. (2018)
Collaborative Research Centre AquaDiva	Germany	51.112186, 10.436933	rDNA, rRNA ITS sequencing	Nawaz et al. (2018)
Deep saline groundwater	Finland	61.236213, 21.478502	rDNA, rRNA ITS sequencing	Sohlberg et al. (2015)
Groundwater springs along volcanic zone	Iceland		biodiversity survey; ITS sequencing	Wurzbacher et al. (2020)

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Relevant websites

https://unite.ut.ee/—The Unite database.
https://mycocosm.jgi.doe.gov/mycocosm/home—Mycocosm—A fungal genomics resource.
http://www.funguild.org/—The FUNguild database.
https://www.gbif.org/—Global Biodiversity Information Facility.
http://www.speciesfungorum.org/—The fungal database of the Species 2000 project.
https://fungidb.org/fungidb/—FungiDB—An integrated Bioinformatic Resource for Fungi and Oomycetes.
https://www.fungaltaxonomy.org/—The International Commission on the Taxonomy of Fungi.

Microbial Biodiversity in Groundwater Ecosystems

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Glossary

Abundance The total number of individuals of a taxon or taxa in an area, population, or community.
Aquifer An underground geological formation of sand, soil, gravel and rock able to store and yield water.
Dormancy Not active or growing but has the ability to be active at a later time.
Ecosystem services Benefits people obtain from ecosystems. (1) Provisioning services such as food and water; (2) Regulating services such as regulation of floods, drought, land degradation, and disease; (3) Supporting services such as soil formation, nutrient cycling and habitat provision; and (4) cultural services such as recreational, spiritual, religious and other non-material benefits.
Eveness The uniformity of abundance between species in a community.
Functional group Groups of organisms that respond to the environment or affect ecosystem processes in a similar way.
Genetic diversity A measure of the amount of distinct genetic characteristics within and among individuals of a population, a species, an assemblage, or a community.
Metabarcoding High throughput DNA-based identification of multiple species from environmental DNA.
Metagenome Complete DNA sequences recovered from an environmental sample, containing information on community structure and genetically encoded functions.
Natural habitat Areas composed of viable assemblages of species of largely native origin and/or where human activity had not essentially modified an area's primary ecological functions and species composition.
Phylogeny The evolutionary relationships among organisms; the patterns of lineage branching produced by the true evolutionary history of the organisms being considered.
Population A group of individuals of the same species, occupying a defined area, and usually isolated to some degree from other similar groups.
Species richness The number of species within a given sample, community, or area.
Syntrophy Interaction of different species of microorganisms that are mutually dependent on each other for growth and existence.
Taxonomy A system of nested categories (taxa) reflecting evolutionary relationships or morphological similarity.

Introduction

The term biodiversity (or biological diversity) describes the variability of life. It covers multiple scales spanning from the genetic to the ecosystem level. In general, the differences between the entities apply to the taxonomic, phylogenetic and the functional diversity (Escalas et al., 2019; Horner-Devine et al., 2004; Prosser et al., 2007). Looking into the microbial diversity, early microbiologist Lourens Baas-Becking (Baas-Becking, 1934; Wit and Bouvier, 2006) famously wrote "*Everything is everywhere*, but *the environment selects*." His statement acknowledges the ubiquity of microorganisms, and assumes virtually no dispersal limitations but a dominant structuring role of the environment. Almost 100 years later, this tenet of microbiology has been proven inaccurate as ecologists start to unravel the underlying mechanisms for the spatial and temporal distribution patterns of microbial communities. In this chapter we will discuss the available tools to measure and estimate microbial diversity in groundwater ecosystems, we will examine the drivers of diversity and the relevance of biodiversity for ecological processes.

Microbes, including all living single-cell organisms such as *Bacteria*, *Archaea*, protozoa, and some fungi, are ubiquitous in aquifers. Their diversity and versatility makes them the most important drivers of biogeochemical processes in the subsurface. A clear distinction to terrestrial and aquatic surface microbial communities is the absence of light and thus phototrophic life but also the limited supply of easily available organic carbon. The groundwater habitat (the terms groundwater, aquifer, and subsurface ecosystem are used synonymously) comprises a vast, mostly nutrient-limited and often heterogeneous environment. The different challenges for its inhabitants have been described for metazoans (Fišer et al., 2014) and microbes (Goldscheider et al., 2006; Griebler and Lueders, 2009) in aquifers alike.

Historically, microbiologists have focused on Eubacteria as the dominant group of microorganisms in most groundwater ecosystems, but recent analysis draw a more complete picture including all domains of life. Due to the enormous extent of the water-saturated subsurface, it forms the largest inland aquatic habitat for microbes and an immense pool of carbon on earth.

Groundwater ecosystems present not only vast but complex habitats for diverse microbial biocoenosis. Sequences of different geological layers and large vertical gradients for nutrients, substrates, temperature, pressure and redox conditions are characteristic for the subsurface. Especially, the mixing zones of groundwater and surface ecosystems are active spots of biogeochemical processes and high microbial biodiversity (Küsel et al., 2016).

Shallow groundwater systems are also highly impacted by the input of organic matter and nutrients from surface environments (Hofmann et al., 2020; Stegen et al., 2016). In terrestrial habitats land-use and meteorologic events, such as heavy rain, affect the shallow subsurface. Nonetheless, groundwater is most often characterized as a nutrient-deprived environment. Microbes deprived of carbon, nutrient and energy sources display several adaptions such as a reduced metabolism, dwarfism or even dormancy. In caves and aquifers, where organic input from upper layers is restricted, chemolithoautotrophic microorganisms may shape the ecosystem processes (Chen et al., 2009; Hutchins et al., 2016). Chemolithoautotrophs capture energy from oxidizing inorganic compounds and provide the base for foodwebs, which establish pathways of energy flow that give the system its character (Levin, 1998).

The microbial communities that drive the processes in the subsurface differ in their composition and structure from surface environments (Taubert et al., 2019). Despite the typically nutrient-poor conditions in the subsurface, microbial communities in groundwater can display high diversity. However, measuring microbial diversity in any environment is not a trivial task. The current estimates for the global microbial species richness ranges from several millions up to 10^{11} taxa (Locey and Lennon, 2016; Schloss et al., 2016). The great variability of estimates is related to technical and methodological shortfalls (Amann and Rosselló-Móra, 2016). Still, being aware of the different methods and concepts to describe biodiversity (e.g. depict the number of species, their relative abundance and distribution) allows us to draw informed conclusions.

A short history of groundwater microbiology

The first microscopic investigations of groundwater bacteria date back to van Leewenhoeck (1677) who observed, what he called "animalcules" in little droplets of well water. In the mid-19th and early 20th century several observations of microbes (e.g. methane-, iron-, and manganese-oxidizing bacteria) in diverse subsurface habitats (e.g. raw water from water works, salt mines, deep subsurface, oil-field water and reservoirs) were reported (Cohn, 1853; Ginsburg-Karagitscheva, 1933; Hassall, 1850; Namyslowski, 1913). It took until the 1980s that modern, aseptic sampling techniques allowed a more comprehensive analysis of inherent microorganisms within aquifers (Kölbel-Boelke et al., 1988; Ventullo and Larson, 1985; Webster et al., 1985). At that time, groundwater contamination and its effect on microbial communities were already in the scientific spotlight (Harvey et al., 1984; Tangley, 1984; West and McKinley, 1983) and would act as the main topic for the years to come. The vast amount of contaminated sites (e.g. gasworks, landfills, industrial waste) fostered a hands-on approach that led to new discoveries on bioremediation, corrosion and degradation processes. Following this hike in applied groundwater microbiology, more fundamental research started and ecological questions and patterns were studied. Groundwater microbiology is nowadays a multidisciplinary research field including geomicrobiology, hydrogeology, and biogeochemistry. Recurring questions in microbial ecology regard the distribution, structure and function of the communities often stated as "Who eats what, where and when" (Neufeld et al., 2007; Xu et al., 2014).

Methodological approaches

> As is the case with other statistics, such as the mean, the median, the mode, and the standard deviation, evenness (diversity) values are merely numbers: their relevance to an ecological problem must be judged by the ecologist on the basis of observed correlations with ecological or environmental variables of his or her interest.
>
> Molinari (1989)

Richness is the number of species present in a community, without considering their abundances, while diversity indices like Shannon or Simpson also take into account species abundances. Evenness is a measure of how evenly abundances are distributed among species in a community. Therefore, estimating diversity requires the observation and quantification of community members (i.e. individuals) and their classification into discrete units [i.e. species, operational taxonomic units (OTUs), amplicon sequence variants (ASVs), genes, functional traits] in a defined area or volume.

In addition to characterizing different features of community diversity (i.e. alpha diversity), geographic or temporal variation across communities can be quantified (i.e. beta diversity), and the total observed richness of all samples (i.e. gamma diversity) can draw a picture of biodiversity across scales (Hill, 1973; Jost, 2006; Walters and Martiny, 2020).

For the observation of microorganisms, the advances and availability of molecular tools since the 1990s have shifted the analysis from laborious, and bias-prone culture-dependent methods to gene-based community profiling [e.g. denaturing gradient gel electrophoresis (DGGE), automated ribosomal intergenic spacer analysis (ARISA), terminal restriction fragment length polymorphism (T-RFLP)] in the past decade and more recently to metabarcoding and high through-put sequencing methods.

The amplification and identification of the ribosomal 16S SSU rRNA (small subunit ribosomal ribonucleic acid) and functional genes has become a standard practice in microbiology (e.g. Earth Microbiome Project). The approaches have dramatically increased the resolution with which microbial community diversity and composition can be analyzed over previous gene fingerprinting techniques. However, although these approaches are now widely used and standardized, they present new challenges as they are also prone to bias the results by the choice of methods (e.g. DNA extraction, primers, polymerase chain reaction, etc.). Furthermore, the taxonomic classification of microorganisms is not always unambiguous as different, partially conflicting classification systems exist and reaching a consensus currently still is an active and evolving field (Parks et al., 2018; Waite et al., 2020).

DNA fingerprinting methods rely on the separation of amplicons (i.e. the product of an amplification reaction), based on different sequence composition (e.g. GC content, size). Each band or fragment represents and is counted as a distinct taxonomic unit. These techniques allow only a qualitative or at best a semi-quantitative measure for the abundance of OTUs.

With next generation sequencing (NGS) the sequence of nucleotides for each amplicon can be recorded. Bioinformatic tools (e.g. OTU clustering, or inference of ASVs) group similar amplicon sequences into distinct units, and abundances are computed based on the number of sequence reads for each of these units. The taxonomic classification can be inferred from alignments of the obtained sequences in relation to sequences of known taxa in a database. The acquired nucleic acid sequence information may be used to infer species similarity, which can be approximated using phylogenetic diversity indices (Faith, 1992; Leinster and Cobbold, 2012; Lozupone and Knight, 2008). In brief, microbial communities of low phylogenetic diversity consist of populations that are genetically more similar and are thus more likely to share a common ancestor and functional traits and *vice versa*.

The analysis of functional marker genes has been widely used to screen environmental samples. Typically, conserved genes encoding the key enzymes of catabolic pathways or dissimilatory electron transfer reactions are targeted. Functional groups that are regularly encountered in groundwater environments are methanotrophs and ammonia oxidizers, lithoautotrophs, sulfate-reducing microorganisms, denitrifiers and methanogens. With the advent of non-targeted sequencing methods such as high-throughput sequencing and metagenomic analysis, complete or nearly complete microbial genomes can be analyzed (Anantharaman et al., 2016; Lau et al., 2014) and led to the discovery of novel clades and metabolic pathways.

A metagenome analysis utilizes the entire genetic composition of microbial communities. After the extraction of nucleic acids from an environmental sample, direct sequencing yields a collection of genetic fragments (i.e. reads) that can be assembled using bioinformatic algorithms (Teeling and Glöckner, 2012). Consequently, metagenome sequences allows high resolution genomic analysis of phylogenetic and functional features.

Metagenomic analysis tackles two important questions: "Who is there?" and "What are they potentially capable of doing?" These investigations have provided unprecedented insights into the microbial life within aquifers and subsurface ecosystems. Recent studies have revealed a great micro-diversity within single taxonomic groups that can be described in terms of a pan-genome (i.e. all the genes present in a given species, across all isolates). This analysis allows to differentiate between core genes (common to all isolates) and accessory gene content, which would indicate the preference to a specific environmental setting (Brockhurst et al., 2019). The advances in sequencing technology allow high resolution analysis of microbes. Still, all the methodological approaches require a trade-off between comparability (e.g. same processing) and suitability (e.g. highest efficiency). In groundwater, the most common restrictions to community analysis are: low cell densities and activities, presence of PCR inhibitors (e.g. iron, humic acids) and underrepresentation of sequences from subsurface ecosystems in reference databases (Smith et al., 2018). It is absolutely necessary that the efforts in sequencing and bioinformatic data analysis are matched with a thorough investigation of the environmental conditions. In a pointedly critique, Prosser and Martiny (2020) warn of purely descriptive look-and-see studies which often mistake correlation and causality. The theoretical frameworks to study microbial diversity are available and should be used.

Microbial biodiversity in groundwater ecosystems

Ecological and evolutionary dynamics

Ecological and evolutionary processes (i.e. selection, drift, mutation, gene flow) determine the assembly of microbial communities. Abiotic factors (e.g. pH, temperature, nutrient concentrations and composition) affect the fitness and metabolism (i.e. biochemical reactions) of each individual microbe. The metabolic rate constrains the ability to grow, to be active and to reproduce (Brown et al., 2004) and thus influences population dynamics. The availability of nutrients and energy governs the microbial growth and activity in natural groundwater (Hofmann et al., 2020; Hutchins et al., 2016). The interaction rates (i.e. trophic dynamics: consumption, predation, parasitism) and population growth are determined by rates of individual metabolism. In natural aquifers large areas are populated by low numbers of microbes, phages and eukaryotic predators, which will narrow the chances for encounters and interactions. These mechanisms will be more important when microbial activity is increased. There is a direct link between the rates of ecological interactions and species diversity. This further illustrates that comprehensive analysis of the microbial biodiversity cannot be achieved isolated from the environment and the conditions in which the taxa live and processes are taking place.

In an aquifer, the most important abiotic factors are often described by the physico-chemical properties of groundwater such as the pH, electrolytic conductivity, temperature and oxygen concentration. In addition, major ions, dissolved gases and nutrient availability are factors that define the niches in groundwater. Furthermore, the hydrogeology (i.e. sediment structure and mineral composition as well as hydrodynamics) shape the environmental conditions in the subsurface (Humphreys, 2009). As a consequence, species lacking the relevant traits to thrive under those conditions will fail to colonize this groundwater environment, which is referred to as environmental (or abiotic) filtering (Kraft et al., 2015).

In addition, species interactions (e.g. competition, predation, mutualism and commensalism) will determine the community assembly (Little et al., 2008). Even though, little is known about the ecological role of heterotrophic protozoa (mainly flagellates) and phages (i.e. viruses) in the subsurface, they are considered to be important predators of microorganisms (Kyle et al., 2008; Novarino et al., 1997; Weinbauer et al., 2007). In addition, phages have been shown to be important drivers of microbial diversity by targeting the dominant species, but also acting as agents of gene transfer (Edwards and Rohwer, 2005). Besides predation, syntrophic and mutualisitc interactions between prokaryotic partners appear to be wide-spread in the subsurface. Especially in nutrient deprived groundwater, ultramicrobacteria (Anantharaman et al., 2016; Luef et al., 2015) with particularly small genomes and cell sizes (<0.1 μm) that may even lack essential biosynthetic pathways, are common. For these organisms syntrophy (i.e. species living off the metabolic products of another species) and interconnected populations are required for growth and survival.

The assembly of microbial communities is defined by the establishment and maintenance of local communities through the colonization and immigration of individuals from a regional species pool (Fukami, 2015; Leibold et al., 2004). Perturbations and disturbances create new chances for new populations to establish. In groundwater such perturbations and stressors can be related to water level fluctuations, temperature changes, nutrient inputs or pollution with xenobiotics (Cho et al., 2000; Griebler et al., 2016; Hemme et al., 2010; Herzyk et al., 2017; Pilloni et al., 2019).

Biodiversity and its impact on groundwater ecosystems

Why do we care about the microbial diversity in groundwater? Despite the high microbial diversity present in the environment, most biochemical reactions are driven by a limited set of metabolic pathways. Describing communities as functional entities (i.e. ecological guilds or clades) which encode enzymes for the same energy-yielding metabolic reactions reveals patterns of community structure (Louca et al., 2018). The functional diversity can be quite different from the taxonomic diversity which has major implications for the ecosystem functioning (i.e. the capacity of natural processes and structures to provide goods and services). Phylogenetically different microbes belonging to the same functional group contribute to the ecosystem functioning under varying environmental conditions. This functional redundancy will ensure that biochemical processes are carried out by substituting one species in case of disturbance by a functionally equivalent species.

In Cardinale et al. (2012) formulated consensus statements based on meta-analyses that describe the impact of biodiversity on ecosystem functioning. For marine environments, it has been shown that microbial functional diversity increases with taxonomic diversity (Galand et al., 2018). The following should also be considered for microbial communities in groundwater ecosystems:

- Diversity increases the efficiency, as differences in functional traits increase the total resource capture by which ecological communities capture biological resources, produce biomass, decompose or recycle nutrients.
- Biodiversity increases the stability of ecosystem functions over time through functional redundancy.
- The correlation between biodiversity and ecosystem processes is nonlinear.
- Diversity across trophic levels influences ecosystem functions more strongly than diversity within trophic levels.
- Functional traits of organisms have a large impact on ecosystem functions which may change after extinction of the organism.

Does scale matter? Species distribution across spatial and temporal scales

The number of observed individuals varies in relation to the spatial and temporal scale under investigation. Aquifers have long been considered as large uniform and unproductive environments, and are still underrepresented in global biodiversity studies. Even though the subsurface is immensely large, it is far from a homogenous and inactive biome. The comparatively low cell densities

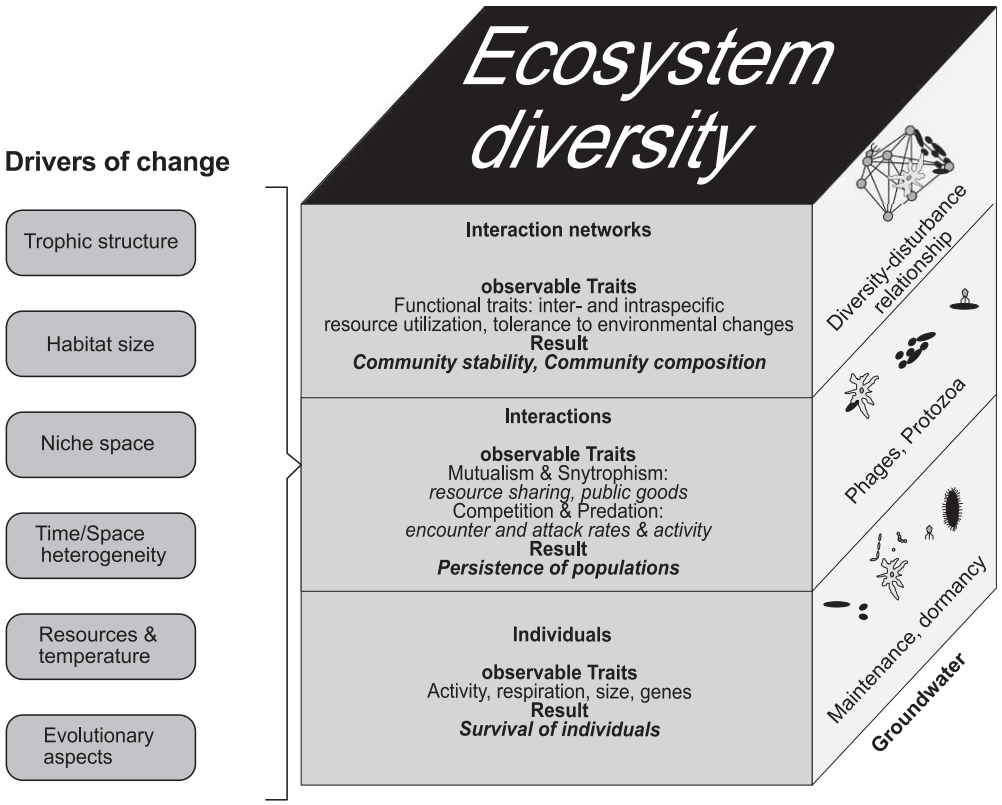

Fig. 1 From genes to ecosystems. The hierarchical structure of microbial biodiversity is driven by eco-evolutionary dynamics connecting one level to another. Trophic interactions dominate the energy flow through the ecosystem and thus shape diversity patterns. Examples relevant for the groundwater environment and measurable traits are given.

commonly found in those environments is compensated by the sheer volume and surface area the microbes colonize. These niches are shaped by abiotic (reduction-oxidation) and biotic (species interactions) gradients (Fig. 1). While the interaction range of microorganisms is in the range of a few μm to cm, fluctuations of the groundwater table can span several meters, and aquifers may extend over hundreds of kilometers. But even then, hydrological dynamics as well as small scale substrate heterogeneities are important when considering the microbial biodiversity. More than 90% of the microbial biomass in aquatic ecosystems are attached or bound to the sediment matrix (Griebler and Lueders, 2009). Hence, the free floating cells that are sampled by pumping groundwater represent only a limited fraction of the total microbiome. High resolution monitoring has revealed different populations within the range of a few millimeters to centimeters (Anneser et al., 2010; Meckenstock et al., 2015; Pilloni et al., 2019) where physical-chemical gradients occur. On the smallest scales (micro- to centimeter scale) species interactions and mass effects are important, but the importance decreases as spatial scales become larger where community composition becomes more affected by environmental selection, dispersal, and drift (Langenheder and Lindström, 2019). The small-scale variation and the restricted accessibility to groundwater has so far limited the success of identifying clear biogeographical patterns.

However, colonization of pristine sediments seems to follow the same mechanisms (i.e. succession) that are found in non-subsurface environments (Fillinger et al., 2019b). The subsurface seems to be also strongly influenced by the local terrain structure, which can be more relevant to landscape-scale ecosystem patterns (Fan, 2015).

Although recent meta-analyses of aquatic ecosystems suggest that biogeographic patterns exist across microbial taxa, they are weaker than for macro-organisms (Barberan et al., 2012; Hillebrand, 2004; Philippot et al., 2010; Stein et al., 2012). Moreover, with microbes a decoupling of taxonomic and functional community composition has been observed, which can be due to lateral gene transfer or functional redundancy (Boucher et al., 2003; Louca et al., 2018). In contrast to macroorganisms, many microbial functions are not continuously expressed and directly dependent on the environmental conditions (e.g. activity, community interactions) (Kundu et al., 2020). Several studies show that microbial populations contribute disproportionally more to the active community functions than their abundance may suggest (Jewell et al., 2016; Wegner et al., 2019). Hence, a conflict between the measured diversity of genotypes (conserved gene regions (i.e. 16S rRNA)) and the realized functional diversity (i.e. inferred from databases) arises. In microbial ecology, a trait-based approach which focuses on the ecological strategies and functions of a microbe is pursued (Escalas et al., 2019; Krause et al., 2014; Martiny et al., 2013).

In the subsurface the large range of spatial scales is match by the temporal variability of processes. Climatic change and seasonal patterns are typically dampened and time-delayed with the depth gradient. Most studies have investigated short-term effects of biodiversity on ecosystem functioning, but often relevant changes (i.e. climate) appear on much larger time scales. Investigating the temporal scale of groundwater biodiversity is limited by the few longterm monitoring sites (e.g. Hainich in Germany, Rifle in CO, USA or Äspö in Sweden). Shallow aquifers with a high hydraulic conductivity can exhibit seasonal fluctuations affecting biodiversity (Ben Maamar et al., 2015; Lohmann et al., 2020; Zhou et al., 2012). Seasonal effects such as the influx of allochthonous (i.e. originating from elsewhere) microorganisms (i.e. dispersal) and substrates can influence community composition but are mitigated compared to surface ecosystems.

Global groundwater models estimate highly variable groundwater turnover times ranging from decades in shallow aquifers to several thousands of years in less accessible and deep strata. This illustrates the different environmental conditions and process dynamics that groundwater microorganisms are facing. While some subsurface microorganisms are directly affected by adjacent ecosystems (e.g. losing streams, water table within plant root depth) others are more or less isolated from surface environment (Fig. 2).

In this respect, also the role of dormant and non-active microbes needs to be considered. Apparently a large proportion of microorganisms in the subsurface exhibit low activity or metabolically resting due to unfavorable conditions (e.g. starvation). Nonetheless, these microbes contribute to the potential microbial diversity (i.e. seed bank, (Lennon and Jones, 2011)) and are thus part of the metacommunity. Resuscitation of dormant cells is mostly coupled to changing environmental conditions. Considering the bias of blending active and dormant cells or even extracellular DNA when analyzing sequence data is especially important in groundwater systems where starvation is likely to be the rule, rather than the exception (Kundu et al., 2020).

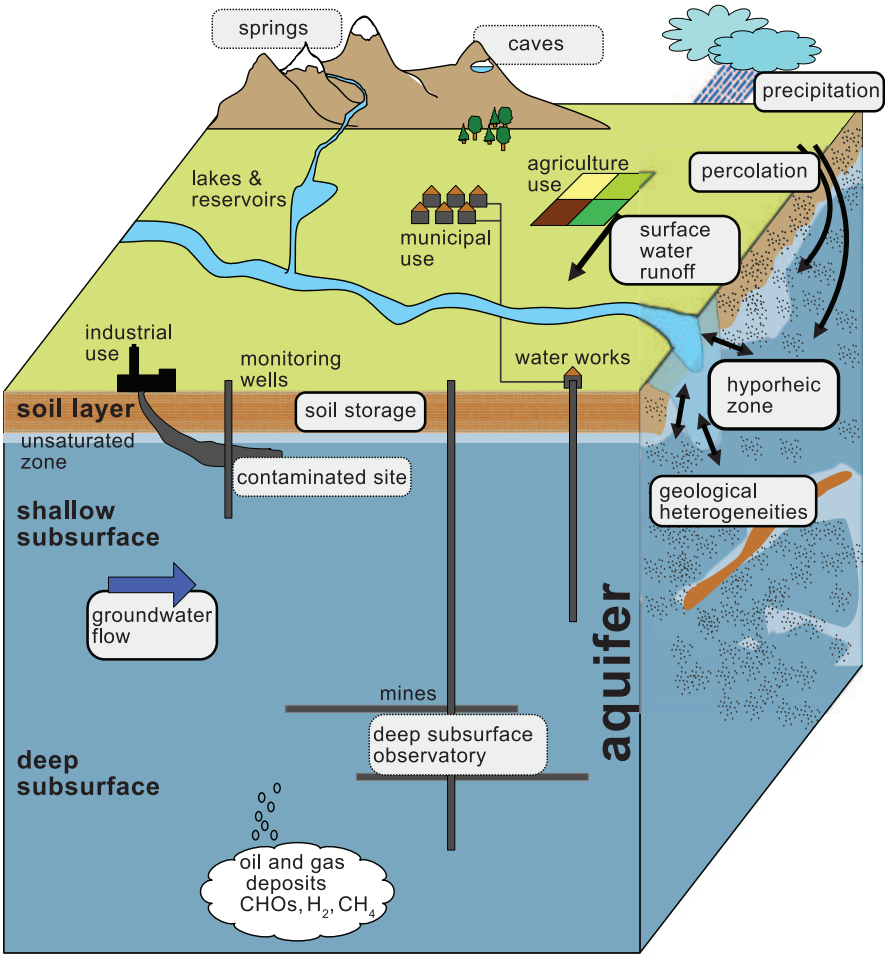

Fig. 2 A schematic overview of the subsurface and adjacent habitats. The groundwater environment links terrestrial and aquatic ecosystems. The intact water cycle provides humans with invaluable ecosystem services.

The characterization of microbial groundwater communities

Despite the great variability of subsurface ecosystems several parameters have been used to characterize the indigenous microbial biocoenoses. The total cell counts (i.e. abundance of prokaryotes) range from 10^2 to 10^6 cells suspended in one mL groundwater and a hundredfold more (10^4 and 10^8 cells per cm^3) can be found attached to the sediment matrix (Griebler et al., 2002). In all aquatic environments, microbes will attach to sediment particles, rock surfaces, larger organisms, and organic detritus. The physical aggregation of organic material at the water-solid interface makes the attached mode of life especially advantageous in carbon- and nutrient-poor environments. Furthermore, it has been shown that the phylogenetic, metabolic and functional diversity of planktonic and attached cells differs substantially (Alfreider et al., 1997; Smith et al., 2018; Stoodley et al., 2002).

Abiotic factors (e.g. pH, temperature) affect the microbial activity (i.e. biochemical reactions) of each individual cell. The metabolic rate constrains the ability to grow, to be active and to reproduce (Brown et al., 2004) and thus influences population dynamics (Fig. 1). The rates of individual metabolism (e.g. transformation and uptake kinetics, foraging) determines the interaction between cells (i.e. trophic dynamics: consumption, predation, parasitism) and population growth. Several methods have been developed mainly based on the incorporation of labeled substrate to estimate in situ microbial activities. Bacterial carbon assimilation rates based on uptake of radiolabeled substrate, revealed bacterial doubling times between a few days and thousands of days for groundwater sediments (Phelps et al., 1994).

The readily measured ATP (i.e. Adenosine triphosphate) concentration in groundwater gives a fairly good indication of the active microbial biomass. In pristine natural aquifers the ATP concentrations will be as low as a few picomol per litre (1 pM = 10^{-12} mol) and even lower in deep subsurface strata.

Where to look? Case studies of biodiversity in groundwater habitats

Today we know that the entire earth's underground (within the strict limits of life) is colonized by microbes. That microbial communities in the subsurface consist mainly of Bacteria and Archaea, but also of Protozoa and Fungi occur, and that these microbial communities are relevant for biogeochemical processes. The species richness in groundwater is highly variable ranging from highly specialized communities in extreme environments (e.g. deep hot subsurface, acid mine drainage) dominated by a few species to highly diverse microbiomes.

Microbial communities in groundwater can be very diverse and, depending on the depth and the hydraulic conductivity, they are more or less influenced from above (soil) layers or intrusion of surface water. Even though naming a complete list of microbial lineages in groundwater is elusive, several taxa are recurring and are likely to be found in aquifers (Griebler and Lueders, 2009).

The large and diverse bacterial phyla of Proteobacteria is also the most common in groundwater. The composition of the major subgroups alpha-, beta-, and gammaproteobacteria may indicate ecological gradients (Philippot et al., 2010). For example, Betaproteobacteria are abundant in freshwater, while they are less common in saline waters. Other phyla comprise: nitrite-oxidizing Nitrospirae (Gülay et al., 2019); Firmicutes, often as indicators of recent groundwater (Flynn et al., 2013); Bacteroidetes, associated with the breakdown of polysaccharides (Wegner et al., 2019); and Acidobacteria, which share a close ecological connection to the Proteobacteria (Kielak et al., 2016) The recent discovery of nanobacteria (Luef et al., 2015) and episymbiotic bacteria belonging to the Candidate Phyla Radiation (CPR, or Patescibacteria) demonstrate the potential for new discoveries (Anantharaman et al., 2016).

Archaea may be less abundant in shallow aquifers and often associated with extreme environments. However, they take a central part in mediating biogeochemical processes throughout the subsurface (He et al., 2021; Probst et al., 2014; Purkamo et al., 2018). Especially striking is the high efficiency of their chemolithoautotrophic pathways. *Nitrosopumilus*, a member of the phylum Thaumarchaeota is involved in nitrification and is capable of CO_2 fixation for the utilization of inorganic electron donors. Although evolutionary distinct, it shares this trade with several other lineages affiliated to the phylum of Crenarchaeota and Bathyarchaeota (Lazar et al., 2017). These phyla appear to be common, but are not abundant in groundwater.

The tight interconnection of Archaea and Bacteria is best illustrated by the methane metabolism. Archaea, are so far the only known microorganisms that conserve energy for ATP synthesis by producing methane gas (CH_4) called methanogensis. In the absence of oxygen, methanogens produce considerable amounts of methane from the decay of carbon (Kotelnikova, 2002) in the subsurface. Closely related to this process, is the anaerobic methane oxidation, which is hypothesized to be a reverse methanogensis (Hallam et al., 2004). A syntrophic consortium of archaea, termed (ANME), and a bacterial partner link the oxidation of methane to a wide range of electron acceptors (i.e. sulfate, nitrite, nitrate and metals). Specifically, in contaminated aquifers these processes might be dominant and structure community composition.

Fungi have long been neglected in microbial community analyses of groundwater ecosystems. The eukaryotic microbes are known saprophytes and parasites, mostly thriving from the decomposition of organic and inorganic materials. Thus, they are considered for monitoring groundwater quality (Lategan et al., 2012), and anthropogenic impacts (Nawaz et al., 2018). Consequently, the presence of fungi in the absence of organic deposits has been linked to a parasitic lifestyle and the fungal degradation of bacterially produced polysaccharides (Cunningham et al., 1995; Drake and Ivarsson, 2018). Recently, the discovery of deep diverging fungal lineages in aquatic systems (Grossart et al., 2016) has spurred the interest of microbiologists to expand the picture of the microbial biodiversity in the subsurface.

In the following, we provide some examples of groundwater habitats (Fig. 3) that resembles the breadth of investigations.

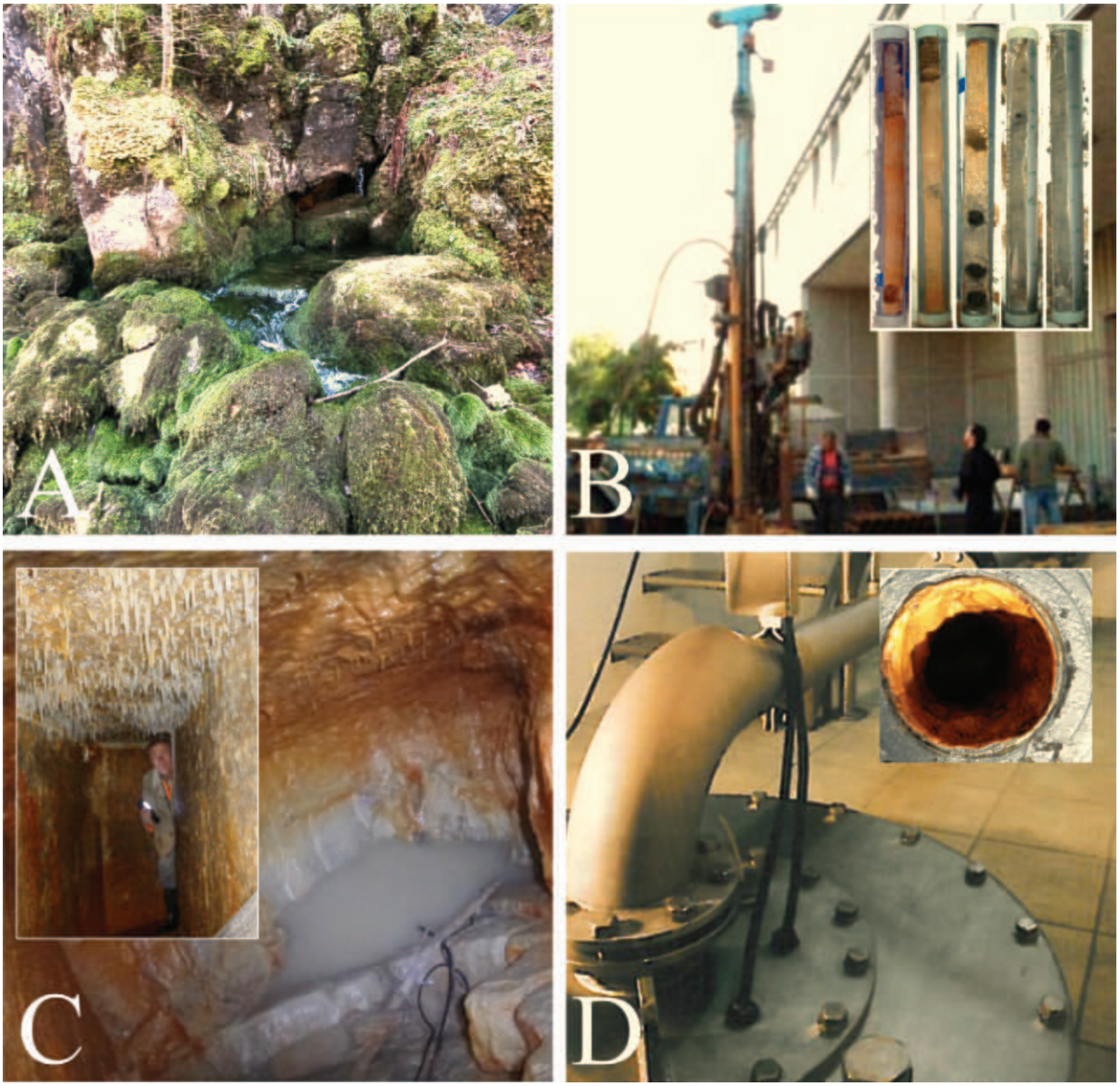

Fig. 3 (A) Groundwater emerges at the surface at a natural alpine spring. (B) Drilling monitoring wells and recovering borehole sediments from a contaminated aquifer to assess bioremediation processes. (C) Caves can host massive microbial biofilms, which often thrive on chemolithoautotrophic resources. (D) Drinking water distribution systems host a distinct microbiome.

Shallow groundwater ecosystems

Large metagenomic and proteomic studies have revealed novel bacterial and archaeal phyla in shallow aquifers. At the Rifle Integrated Field Research Challenge site close to the Colorado river (USA), biogeochemical processes in the subsurface have been studied in great detail (Campbell et al., 2012; Jewell et al., 2016). Sediment cores and groundwater were sampled from the shallow aquifer. The high levels of microbial biodiversity resulted in several thousand near-complete metagenome-assembled genomes. In addition to the well known bacterial phyla (e.g. Proteobacteria, Bacteroidetes, Actinobacteria) they found 47 newly discovered phylum-level lineages were found (Anantharaman et al., 2016).

Most often, not a single population will comprise more than 1% of the microbial community, indicating a very high species evenness. The relevance of this high biodiversity was shown by the metabolic analysis. Only few organisms within the community can handle multiple sequential redox transformations. Hence, metabolic byproducts need to be passed on to adjacent microorganisms that carry out specific steps in redox pathways (Hug and Co, 2018). The so-called metabolic handoffs highlights the importance of syntrophic interactions in subsurface environments.

A collaborative research project at the long-term monitoring site Hainich (Germany) investigates the soil-groundwater interface (termed the critical zone) of aquifers (Akob and Küsel, 2011; Küsel et al., 2016). There, a recent study (Yan et al., 2020) found fundamental differences in the microbial communities and biogeochemistry of multi-storey aquifer complexes. The availability of inorganic energy sources governs the microbial community, resulting in hot spots for chemolithoautotrophic processes (e.g. nitrification and anaerobic ammonia oxidation) (Wegner et al., 2019). In addition, differences were correlated to the distinct land uses in the respective recharge areas and the effects of precipitation events and groundwater recharge dynamics (Küsel et al., 2016) (Fig. 2). The interdisciplinary approach, combining molecular, geological and hydrological data which ultimately feed into conceptual models promotes the qualitative and quantitative characterization of subsurface processes.

Caves and karst pools

The accessibility of caves facilitates the observation and sampling of groundwater biota. However, there are some characteristics of caves that make them special in comparison to other groundwater environments. The different types of caves that form from hydrological and biogeochemical processes reflect the connection between the surface and subsurface. Most caves are structured into an entrance and twilight zone, where photosynthesis is still feasible and animals and debris may enter from the surface. In contrast, the deep cave zone is considered to be a low-energy environment, that resembles a "true" subsurface ecosystem.

The biodiversity differs within and between caves, because of the rock type, hydrological conditions, and biological properties such as larger animals inhabiting the cave. The habitat conditions are resembled in the active microbial metabolism, which connects to the overall biogeochemistry of the system (Shabarova and Pernthaler, 2010). Some groundwater filled caves have been studied in detail describing these metabolic and biological diverse ecosystems. The Movile Cave in Romania (Sarbu, 2000), the Frasassi Caves in Italy (Desai et al., 2013; Jones et al., 2012) and the Nullarbor Caves in Australia (Holmes et al., 2001) are only a few fascinating examples of habitats for chemolithoautotrophic microbes that form massive biofilms (Fig. 3C). Sulfidic caves, where supplies of reduced sulfur, hydrogen or methane support rich chemolithoautotrophic activity, feature microbial mats and pendulous biofilms (also known as Snottites). Multispecies aggregates of acidophilic, sulfur-oxidzing *Thiotrichaceae*, hydrogen-oxidizing "Knallgas" bacteria (e.g. *Aquificaceae*) and methylotrophic microbes dominate and actively form (i.e. biogenic speleothems) the cave habitats through mineral dissolution and breakdown products (i.e. moonmilk) (Boston et al., 2009; Engel et al., 2004). Another example of massive biofilm growth but fueled by methylotrophic production was described at the Sulzbrunn cave in Germany (Karwautz et al., 2017). Geogenic methane from deeper layers enters the shallow cave where a diverse microbial community resembles a clear zonation along the cave walls resulting in different rates of methane oxidation.

In contrast, the energy dynamics of carbonate and volcanic caves are less well-defined. The bacterial communities from these oligotrophic environments often display low phylogenetic diversity, but with a remarkable diversity of CO_2 fixation pathways (Barton et al., 2004; Ortiz et al., 2014; Tebo et al., 2015).

The deep subsurface

Deep drilling and ore-mining allows examining the microbial communities that thrive several thousand meters below the surface. Microorganisms at these depths are often classified as extremophiles. This refers to the extreme environmental conditions such as high temperature, high pressure, acidity, alkalinity or elevated concentrations of halides. In deep groundwater anaerobic microorganisms take over as the primary degraders of organic matter, as oxygen has been used up in the shallow subsurface. Hydrothermal fluids and reduced gases (e.g. methane, hydrogen) support the metabolic processes (Hallbeck and Pedersen, 2008; Newman and Banfield, 2002). Subsurface microbial communities are involved in hydrogen oxidation which is associated with autotrophic methanogenesis and contributes to the biogenic methane production. Therefore, it is necessary to take into account the activity of methane-producing Archaea and methane-oxidizing bacteria in groundwater when estimating the impact of subsurface environments to global warming (Kotelnikova, 2002).

Microorganisms might even contribute to ore deposition over geological time frames as they precipitate metals from solution. In contrast, microbes are also involved in the dissolution of minerals and metals [e.g. pyrite (FeS_2), spalerite (ZnS)]. Low-diversity communities of autotrophic and heterotrophic archaea and bacteria which catalyze iron and oxidize sulfur have also been found in acid mine drainage and deep subsurface environments (Baker and Banfield, 2003; Hallbeck and Pedersen, 2008; Tyson et al., 2004).

Notably, it was shown that metabolic active fungi in deep groundwater are present and that the fungal communities react to changes in the concentration of organic carbon sources in their environment (Sohlberg et al., 2015). They form synergistic consortia with sulfate reducing bacteria in deep granitic subsurface, where the role of the fungi is to provide H_2 for sulfate reducers (Drake et al., 2017). It is very likely that the fungi consume carbohydrates for their own heterotrophic metabolism by degrading microbial biofilms (Drake and Ivarsson, 2018). In turn the fungi release small carbon compounds that can function as electron donors and carbon source for bacteria and archaea.

Drinking water

Groundwater is the major source of drinking water in many regions of the world. The legal frameworks to safeguards high drinking water quality (e.g. Directorate-General for Environment, 2009; EC Council Directive, 1998) sets limits to the concentrations of microbial pathogens (e.g. Legionella) and fecal indicators (e.g. Enterococci). The microbial biocenoses of drinking water treatment

plants and distribution system (Fig. 3) has been the objective of numerous studies (Berry et al., 2006; Pinto et al., 2014). Drinking water production systems are an engineered environment providing different conditions to the microorganisms when compared to aquifers (Fig. 3D). While the milieu in aquifers seems to be mainly governed by sediment heterogeneity and microbe-mineral interactions as wells as nutrient availability, drinking water distribution systems are mainly governed by extreme hydrodynamics and pipe material characteristics (Yu et al., 2010). Even though cell densities and metabolic activity in drinking water are typically low (Hammes et al., 2008) the distribution system is colonized by diverse microbial communities (Fig. 3), typically dominated by Proteobacteria. Temporal variations of the microbial communities could also be of interest to drinking water providers that aim at proliferating water of continuous high quality (Pinto et al., 2014). In a rare study about fungi in drinking Göttlich et al. (2002) reported a significantly lower fungal diversity in the distribution network than in raw water and house installations, indicating a low durability under these conditions.

Contaminated aquifers

The anthropogenic impact has hit all earth ecosystems. Even the somewhat hidden and isolated aquifers are threatened by contamination and over-exploitation (Mammola et al., 2019). Especially, contamination with aromatic hydrocarbons and halogenated organic compounds poses a long-lasting hazard. The various pollutants (i.e. heavy metals, pesticides, pharmaceuticals, radionuclides) display differences in the way of entry (e.g. point and diffusive sources), concentrations, degradability and transport dynamics. The detrimental impact of contamination on human and environmental health has initiated immense efforts in understanding microbial communities in contaminated aquifers. In most cases, organic pollutants will increase the local microbial diversity and shift the community towards dominating degrader populations (Pilloni et al., 2019; Röling et al., 2001. In some cases, this increase in diversity is related to the dispersal of microbes introduced with the contaminant, such as manure (Cho et al., 2000). However, contamination of an aquifer will most often cause considerable stress to the autochthonous microbial communities and leads to biodiversity loss and long-lasting, potentially irreversible changes in microbial community composition and functioning (Herzyk et al., 2017; Ma et al., 2015).

In case of organic pollution, microbes will rapidly consume the available oxygen in groundwater to oxidize the contaminants (Fig. 3B). Therefore anaerobic degradation pathways are prevalent in organically contaminated aquifers. Consequently, microbes will reduce different electron acceptors such as nitrate, iron (III), manganese (IV) and sulfate, which will then determine the respiratory processes (Meckenstock et al., 2015). Pilloni et al. (2019) provided a good example that the composition of the degrading communities are far from being stable so that key degraders within the bacteria are replaced by functionally redundant counterparts under changing environmental conditions. Key degraders and microbial communities in contaminated aquifers can grow, mineralize or co-metabolize toxic substances. Nonetheless, this process known as bioremediation is severely limited by abiotic and biotic factors (Table 1).

Table 1 Important case studies dealing with microbial diversity and the role of microorganisms in biogeochemical processes in various groundwater environments.

Research focus	*Study site*	*Reference*
The microbial groundwater communities of shallow aquifers	Europe	(Wegner et al., 2019)
	• Hainich	(He et al., 2021)
	North America	(Lategan et al., 2012)
	• Rifle	
	Australia	
	• New South Wales	
The microbial groundwater communities of deep aquifers and fracture fluids	Europe:	(Hallbeck and Pedersen, 2008)
	• Äspö	(Gihring et al., 2006)
	Africa:	
	• Kalahari	
Caves	Europe:	(Macalady et al., 2006)
	• Frassasi	(Chen et al., 2009)
	• Movile	(Holmes et al., 2001)
	Australia	(Cunningham et al., 1995)
	• Nullabor	(Lennon et al., 2017)
	North America:	
	• Lechuguilla	
	Asia	
	• Vietnam	
Contaminated aquifers and biodegradation	• Petroleum hydrocarbons	(Meckenstock et al., 2015; Watanabe et al., 2000)
	• Chlorinated organic compounds	(Bælum et al., 2013, Jugder et al., 2016)
	• Toxic metals and metalloids	(Feris et al., 2004)
	• Pesticides and micropollutants	(Fenner et al., 2013)
Ecological processes determining community diversity and composition	Environmental selection	(Fillinger et al., 2019a; Yan et al., 2020)
	Dispersal	(Graham et al., 2017; Stegen et al., 2016)
	Species interactions	(Hug and Co, 2018)

Knowledge gaps

The challenges in groundwater microbial ecology remain very much the same as they were ten years ago (Larned, 2012). Many ecological questions that have been explored in surface-water systems remain unexplored in subsurface habitats. The wealth of observational studies based on pattern-detection and description needs to be matched by hypothesis-testing and mechanistic explanations (Prosser and Martiny, 2020).

Access to groundwater ecosystems is generally limited by the availability of monitoring wells and the logistical efforts (i.e. costs, regulations, flow of information) to create new study sites. Furthermore, groundwater sampling (i.e. pumping) provides only an overview of relatively narrow zones around wells and differences between attached and planktonic microbes are often neglected.

Attached microorganisms can be assessed by sampling borehole sediments (Anantharaman et al., 2016), introducing sediment cages into monitoring wells (Fillinger et al., 2019a, b; Griebler et al., 2002) or establishing groundwater mesocosm systems (i.e. columns, indoor aquifers) (Griebler et al., 2016; Herzyk et al., 2017).

Another challenge is the limited information about ecosystem boundaries and spatial heterogeneity, a lack of detailed habitat templates (Larned, 2012; Stein et al., 2012). Sampling design guided by hydrogeological methods can increase the spatial resolution by optimizing well positioning and interpolation between them.

In aquifers, the geology and distribution of sediments creates structural and hydraulic heterogeneity, which establish the spatial variation of nutrients and organic matter and thus biogeochemical processes. Groundwater flow models can characterize these heterogeneities of a study area and may help to identify ecologically relevant hydrological variables (e.g. preferential flowpaths, recharge zones, and aquifer boundaries).

Even with the wealth of molecular data, many groundwater microbes remain undescribed and uncultured. A greater effort to cultivate groundwater microorganisms will be needed to characterize their physiology, ecology and evolutionary processes (Imachi et al., 2019; Thrash, 2019).

Conclusion and outlook

The subsurface is one of the earth's largest yet for the most part untapped reservoir of microbial diversity. Multiple environmental gradients foster an immense biodiversity displayed in the genomic and functional versatility of groundwater ecosystems. Ecosystem functioning and services are a direct consequence of this biodiversity.

A large part of the scientific literature focuses on the characterization and remediation of contaminated groundwater sites. Nonetheless, even in low energy, pristine and natural systems microbes can display a great taxonomic and functional diversity which reflects their adaptability.

Factors that control microbial diversity in aquifers include physicochemical conditions, spatial heterogeneity, temporal variability and disturbances such as pollution with chemical anthropogenic contaminants. First insights into the importance of individual biogeochemical processes have been obtained from surveys of microbial diversity within functional groups and direct links to groundwater ecosystem functioning have been established for selected research sites (CRC AquaDiva, IFRC). Such long-term monitoring programs are essential to the understanding of microbial diversity and biogeochemical processes.

The rapid advances in microbiology have reshaped the scientific scope of biodiversity research in groundwater ecosystems. Metagenomic data and bioinformatic tools allow elucidating unprecedented details of the diversity and metabolic potential of microorganisms. Including all life forms (Bacteria, Archaea, Fungi, protozoa, metazoa, and viruses) in biodiversity analysis, and deciphering their interactions as well as how these interactions link to biogeochemical processes, is the next big step in the census of subsurface ecosystem research.

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Biogeochemical Cycling of Carbon and Nitrogen in Groundwater—Key Processes and Microbial Drivers☆

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

☆*Change History*: October 2021. M Herrmann and M Taubert introduced a new section "Lysis of microbial cells", added new text to some of the sections, added two new points to section "Knowledge gaps", added new references to section "References", and made minor changes throughout the manuscript to address the comments and suggestions of two reviewers.

Glossary

Anammox Anaerobic oxidation of ammonium with nitrite to form N_2 as end product.
Chemolithoautotrophy Lifestyle that employs CO_2 as carbon source and obtains energy from the oxidation of inorganic compounds.
Denitrification Reduction of nitrate to gaseous nitrogen compounds (NO, N_2O, N_2).
DNRA Dissimilatory nitrate reduction to ammonium.
Fluid flow Movement of water driven by physical influences like gravity or capillary action.
Heterotrophy Lifestyle that employs organic carbon compounds as carbon source.
Metagenomics/Metatranscriptomics/Metaproteomics Study of the entirety of DNA/RNA/proteins present in a selected habitat at a selected point of time.
Microbiome Entirety of the microorganisms living in a specific habitat.
Mixotrophs Microorganisms able to use CO_2 and organic carbon as carbon source, concomitantly and/or consecutively.
Necromass Remains of dead microorganisms, including cell debris, biopolymers and dissolved molecules.
Nitrification Oxidation of ammonia to nitrate via nitrite.
Symbiosis Close and long-term biological interaction between two species. Can provide benefit and/or harm to the involved organisms.

Introduction

Role of microorganisms in biogeochemical cycles in aquifers

Microbially mediated biogeochemical processes in aquifers are central to the chemical composition of groundwater and its suitability as drinking water resource. Groundwater chemistry and the sources and sinks of key chemical compounds, including potentially hazardous chemicals, have been well studied for decades. Our understanding of microbial activities in these environments, microbial key players and the factors driving their community composition, distribution and activity, however, is still in its infancy. Heterogeneity of biogeochemical processes in aquifers is often directly linked to hydrogeological heterogeneity and the dynamics of groundwater flow (Utom et al., 2020), emphasizing the need for interdisciplinary research combining microbiology, biogeochemistry, and hydrogeology to improve our understanding of microbially driven transformation processes in these environments (Küsel et al., 2016).

Generally low microbial cell numbers and biomass in groundwater environments may substantially limit process rates compared to surface freshwater environments, marine environments, or engineered systems. However, as residence times in aquifers may range from several years to centuries, even processes that occur at very low rates may significantly contribute to shaping groundwater chemistry. In this chapter, we want to focus on nitrogen cycling and carbon cycling as two major biogeochemical cycles in aquifers that are tightly interconnected and that are also strongly linked to other element cycles like the sulfur or iron cycle. We introduce key processes and key microbial players, and explore how the role of these microbes in biogeochemical cycling is linked to their life styles and strategies to survive in oligotrophic groundwater.

Sources of carbon and nitrogen compounds in groundwater

Pristine groundwater is characterized by low concentrations of organic carbon and other nutrients. Traditionally, the shallow subsurface is believed to be driven by surface inputs, supporting a low biomass of heterotrophic microorganisms. Besides these surface inputs, heterotrophic life in the subsurface can also be fueled by the release of organic compounds from sedimentary rocks and the lysis of cells in the groundwater itself (Fig. 1) (Benk et al., 2019; Schwab et al., 2019). Increasing evidence of the relevance of chemolithoautotrophic CO_2 fixation by microorganisms for subsurface carbon cycling, however, has challenged this view of a predominance of heterotrophy (Akob and Küsel, 2011). Autotrophic microorganisms rely on fixation of inorganic carbon to produce all of their biomolecules, and are thus independent of external organic carbon. The availability of inorganic carbon strongly depends on the local geology but is also influenced by microbial activity and transport processes.

Similarly, nitrogen compounds in groundwater largely originate from surface sources but can also be derived from degradation of organic matter, cell lysis, and nitrogen fixation in the aquifer itself (Fig. 1). Due to its higher mobility in soils and subsurface, nitrate is usually the major surface-derived inorganic nitrogen compound. Nitrate is also one of the central chemical compounds in groundwater strongly affected by human activities. Increased nitrate levels resulting from excess fertilizer applications are a serious threat to the suitability of groundwater for drinking water production and may cause eutrophication of groundwater-fed water bodies (Vitousek et al., 1997; Stark and Richards, 2008). This has led to increasing interest in naturally occurring processes that enable or control nitrate attenuation in aquifers (Rivett et al., 2008). In contrast, subsurface transport of ammonium is largely controlled by sorption as a result of cation exchange processes occurring at negatively charged mineral surfaces such as clay minerals, and, quantitatively less important, by biological attenuation via incorporation into microbial biomass (Buss et al., 2004).

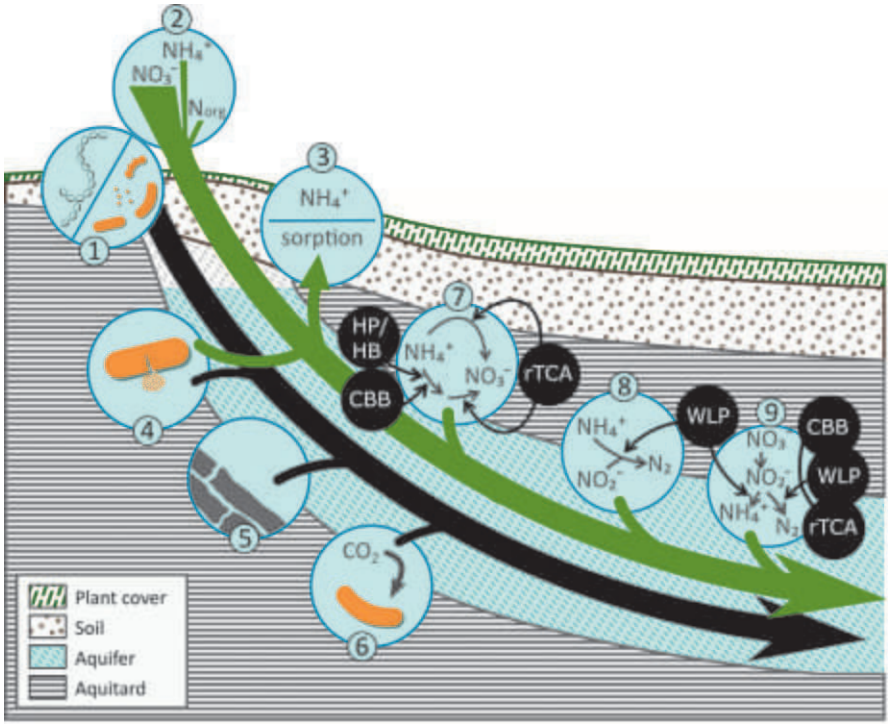

Fig. 1 Conceptional model of the surface input, flow and transformation reactions of carbon and nitrogen compounds in groundwater. Individual nitrogen transformation processes are linked to CO_2-fixation pathways utilized by the respective microbial groups (black circles). 1: surface input of organic carbon and microbial cells; 2: surface input of nitrogen compounds; 3: attenuation of ammonium by sorption processes; 4: cell lysis; 5: rock-derived organic carbon; 6: CO_2-fixation; 7: nitrification; 8: anammox; 9: denitrification and DNRA. CBB = Calvin-Benson-Bassham cycle; rTCA: reductive tricarboxylic acid cycle; WLP: Wood-Ljungdahl-pathway; HP/HB: 3-hydroxy-propionate/4-hydroxy-butyrate pathway.

As consequence, ammonium derived from microbial processes such as organic matter degradation or dissimilatory nitrate reduction to ammonium (DNRA) is likely the major source for ammonium-dependent transformation processes such as nitrification or anammox in the subsurface (Böhlke et al., 2006; Jahangir et al., 2017).

Effect of geologic setting on biogeochemical cycles in groundwater

Geologic setting shapes microbially driven biogeochemical cycles via two major factors: (i) its effect on groundwater chemistry, in particular pH and availability of suitable electron donors or electron acceptors for microbial metabolisms, and (ii) its effect on porosity and the structure of the aquifer bedrock material, affecting fluid flow, surface connectivity, water travel times or residence times, and linked to that, oxygen supply, and the structural heterogeneity of microbial habitats (West and Chilton, 1997).

Porous aquifers with low flow conditions versus fractured aquifers with rapid flow conditions may differ substantially regarding the prevalence of anoxic conditions or the extent of fluctuations in redox conditions. Fractured or karstic aquifers with locally or episodically rapid water flow can provide close connections between surface and subsurface, supporting oxic conditions even in deeper groundwater. In turn, systems with long water residence times are more likely to undergo oxygen depletion, resulting in a prevalence of anoxic conditions. While high surface connectivity in fractured or karstic systems may also enable more frequent and intense supply of fresh surface-derived organic carbon, low surface connectivity and long water residence times may favor the growth of slow-growing autotrophic bacteria (Taylor et al., 2013).

Effect of oxygen availability

Oxic conditions

Oxygen availability is one key driver of groundwater biogeochemical cycles. Oxic conditions in groundwater require an input from the surface (Lovley and Chapelle, 1995), which can occur via fluid flow, or via fluctuations of the groundwater table that rapidly suck air from the surface into the subsurface (Lehmann and Totsche, 2020). Along the groundwater flow path, oxygen is consumed by a variety of microbial processes. The higher the concentrations of reduced organic and inorganic compounds, the faster oxygen is depleted by the microbial activity, leading to anoxic conditions.

Anoxic conditions

Upon depletion of oxygen, the use of alternative electron acceptors such as nitrate becomes energetically more favorable, and a large range of facultative anaerobic microorganisms are capable of switching from aerobic respiration to nitrate reduction. Once nitrate is depleted, other terminal electron acceptors may become relevant, such as manganese, iron (III), sulfate, and finally hydrogen and CO_2 resulting in the formation of methane. These alternative electron acceptors can be derived from surface inputs, or from minerals of the aquifer rocks, such as sulfates and oxidized metal species (Fe^{3+}, Mn^{4+}, As^{5+} etc.) (Schippers et al., 1996; Oremland and Stolz, 2005; Kohlhepp et al., 2017). Furthermore, organic carbon can act as electron acceptor for regeneration of nicotinamide adenine dinucleotide (NADH) during fermentation, or during acetoclastic methanogenesis, where acetate acts both as electron donor and acceptor, leading to the release of CO_2 and methane (Demirel and Scherer, 2008).

Nitrogen cycling in groundwater

Microbially mediated nitrogen transformation processes

Nitrogen compounds leached from surface environments are subject to further transformation by complex dynamics and interlinkages of different biogeochemical processes in the groundwater, including mineralization of organic matter, nitrification, denitrification, DNRA, anaerobic ammonium oxidation (anammox), and sorption processes (Fig. 1). These processes can occur simultaneously in spatially structured heterogeneous environments, and linkages between aerobic and anaerobic nitrogen transformation processes may be especially intense under micro-oxic conditions or along transition zones from aerobic to anaerobic conditions. Altogether, they result in changes in the initial concentrations of the nitrogen compounds and may lead to their conversion into new nitrogen species (Burgin and Hamilton, 2007). While denitrification and anammox lead to nitrogen loss as dinitrogen gas, DNRA results in the conservation of inorganic nitrogen as ammonium.

Traditionally, heterotrophic denitrification coupled to the oxidation of organic electron donors was believed to be the most important pathway for nitrate removal from groundwater. However, recent findings suggest that chemolithoautotrophic denitrification linked to the oxidation of inorganic electron donors, anammox, and DNRA play a more important role than previously thought. Potential factors that determine which process prevails include electron donor availability and identity, and electron donor/nitrate ratios (Tiedje et al., 1982; Burgin and Hamilton, 2007; Strohm et al., 2007; Rütting et al., 2011).

Nitrification

The nitrification process

Nitrification is a key process of the nitrogen cycle, transforming ammonium to nitrate in a two-step process, ammonia oxidation (1) as the first and rate-limiting step, and nitrite oxidation (2).

$$2NH_4^+ + 3O_2 \rightarrow 2NO_2^- + 4H^+ + 2\,H_2O \quad (1)$$

$$2NO_2^- + O_2 \rightarrow 2NO_3^- \quad (2)$$

As such, in addition to surface-derived inputs, nitrate can be formed in situ in the groundwater, and reported nitrification activities range from 0.012 μmol NO_x per L per day in oligotrophic, pristine groundwater to 6.72 μmol NO_x per L per day in groundwater contaminated with ammonium (Smith et al., 2006; Opitz et al., 2014). The process is primarily controlled by the availability of ammonium and oxygen, pH, and the presence of substances which might act as inhibitors of nitrification, such as heavy metals or organic contaminants (Buss et al., 2004). Nitrification can proceed at high rates even if apparent concentrations of ammonium are low, since ammonium is usually continuously replenished from the degradation of organic matter. Recently, Utom et al. (2020) also reported nitrite oxidation coupled to manganese reduction in an anoxic alluvial aquifer.

Microbial key players involved in groundwater nitrification

Although some of the microorganisms involved in nitrification have been isolated as early as 1890 (*Nitrosomonas europaea, Nitrobacter winogradsky*) (Winogradsky, 1890), the nitrification process has provided many surprises for researchers until today. These include the discovery of ammonia-oxidizing archaea (AOA) in Könneke et al. (2005), extending the metabolic capacity of ammonia oxidation beyond two distinct phylogenetic groups within the Proteobacteria, and the discovery of complete ammonia oxidizers (comammox bacteria of the genus *Nitrospira*) in Daims et al. (2015) and van Kessel et al. (2015). Until then, division of labor in nitrification had been an unchallenged concept, i.e., the strict separation of nitrification into a two-step process carried out by different guilds of organisms, the ammonia-oxidizing bacteria (AOB) or archaea, and nitrite-oxidizing bacteria (NOB).

Despite the high relevance of in situ nitrate formation for groundwater quality, studies addressing nitrifying microbial populations in groundwater are still scarce. Both AOA and AOB were reported from aquifers (Reed et al., 2010; Opitz et al., 2014) (Table 1). Interestingly, comammox bacteria are present or even especially abundant in engineered systems related to groundwater such as groundwater-fed biofilters (Fowler et al., 2018; Gülay et al., 2019) or drinking water systems (Pinto et al., 2016), suggesting that they might also play an important role in groundwater nitrification. In fact, the genus *Nitrospira*, including nitrite oxidizers as well as comammox bacteria, accounted for about 11% of the bacterial community in oligotrophic groundwater (Herrmann et al., 2020; Yan et al., 2020) (Table 1).

Table 1 Prominent examples of microbial taxa involved in nitrogen transformations, carbon cycling, or other biogeochemical processes, which have been reported from groundwater environments.

Process	*Respective microbial taxa in groundwater*	*References reporting these organisms in groundwater*
Nitrogen transformations		
Nitrification (ammonia oxidation)	*Nitrosomonas*, *Nitrosospira*, *Nitrosoarchaeum*, *Nitrososphaera*	Opitz et al. (2014), Herrmann et al. (2015), Starke et al. (2017), Herrmann et al. (2019), Lavy et al. (2019), Wegner et al. (2019) and Fillinger et al. (2021)
Nitrification (nitrite oxidation)	*Nitrospira*	Converse et al. (2015), Herrmann et al. (2015) and Yan et al. (2020)
Nitrification (comammox)	*Nitrospira*	Yan et al. (2020) and Herrmann et al. (2020)
N_2-fixation	*Geobactera*, *Sulfurimonas*, *Brocadiales*	Wrighton et al. (2014), Starke et al. (2017) and Probst et al. (2018)
Denitrification	*Azoarcus, Hydrogenophaga, Sulfurimonas, Sulfuricella, Sulfuritalea, Thauera, Gallionellaceae*	Hubalek et al. (2016), Jewell et al. (2016), Probst et al. (2017), Herrmann et al. (2017), Lueders (2017) and Kumar et al. (2018)
Anammox	*Cand.* Brocadia, *Cand.* Jettenia, *Cand.* Kuenenia	Jewell et al. (2016), Kumar et al. (2017), Starke et al. (2017) and Wegner et al. (2019)
DNRA	*Burkholderiales*, Ca. Omnitrophica, Nitrospirae	Anantharaman et al. (2016)
Carbon cycling		
Organic carbon degradation		
Plant polymers	Bacteroidetes, DPANN Archaea, Firmicutes, Chloroflexi, *Cand.* Parcubacteria, saprotrophic fungi	Wrighton et al. (2014), Nawaz et al. (2016), Danczak et al. (2017), Castelle et al. (2018) and Taubert et al. (2019)
Aromatics and aliphatics	*Azoarcus*, *Thauera*, *Aromatoleum*, *Geobacter*, *Peptococcaceae*, *Microbacteriacaea*	Kuntze et al. (2011), Kleinsteuber et al. (2012), Taubert et al. (2012), Taubert et al. (2018) and Lueders (2017)
C1 compounds	*Methylobacterium*, *Methylobacter*, *Methylocystis*, *Methylophilaceae*, *Rhodobacteraceae*, *Hyphomicrobiaceae*	Lindner et al. (2007), Taubert et al. (2018), Lazar et al. (2019) and Kuloyo et al. (2020)
CO_2 fixation pathways		
Calvin-Benson-Bassham cycle	*Thiobacillus*, *Thiomicrospira*, *Nitrosomonas*, *Nitrosospira*, *Hydrogenophaga*, *Gallionellaceae*	Alfreider et al. (2009), Herrmann et al. (2015), Emerson et al. (2016) and Probst et al. (2017)
Reductive tricarboxylic acid cycle	*Nitrospira*, *Sulfurimonas*, *Sulfuricurvum*, *Helicobacteraceae*	Handley et al. (2013), Handley et al. (2014), Ortiz et al. (2013), Herrmann et al. (2015), Probst et al. (2017), Probst et al. (2018) and Wegner et al. (2019)
Wood-Ljungdahl pathway	*Brocadiales*, *Cand.* Altiarchaeum, *Desulfobacteraceae*, *Syntrophobacterales*	Jewell et al. (2016), Probst et al. (2017), Starke et al. (2017), Probst et al. (2018), Herrmann et al. (2019) and Wegner et al. (2019)
3-hydroxypropionate/4-hydroxybutyrate cycle and dicarboxylate/4-hydroxybutyrate cycle	Thaumarchaeota	Opitz et al. (2014), Herrmann et al. (2015) and Wegner et al. (2019)
Other biogeochemical processes		
Iron reduction	*Geobacter*, *Dechloromonas*, *Desulfotalea*, *Desulfitobacterium*, *Ferribacterium*	Wrighton et al. (2014), O'Mullan et al. (2015), Schwab et al. (2017) and Lueders (2017)
Iron oxidation	*Gallionellaceae*, *Acidithiobacillus*, *Sideroxydans*	Converse et al. (2015), Herrmann et al. (2015), O'Mullan et al. (2015), Jewell et al. (2016), Herrmann et al. (2017) and Probst et al. (2018)
Sulfate reduction	*Desulfobacca*, *Desulfosporosinus*, *Desulfotomaculum*, *Desulfovibrio*	O'Mullan et al. (2015), Hubalek et al. (2016), Lavy et al. (2019), Wegner et al. (2019) and Lueders (2017)
Oxidation of reduced sulfur compounds	*Thiobacillus*, *Thiomicrospira*, *Sulfurimonas*, *Sulfurifustis*, *Sulfuricella*, *Sulfuritalea*, *Acidithiobacillus*	Herrmann et al. (2015), O'Mullan et al. (2015), Emerson et al. (2016), Probst et al. (2017), Probst et al. (2018) and Herrmann et al. (2019)
Hydrogen formation	*Bacteroidales*, *Cand.* Omnitrophica, Melainabacteria, Chloroflexi	Wrighton et al. (2014) and Probst et al. (2017)
Hydrogen oxidation	*Hydrogenophaga*, *Geobacter*, *Sulfuritalea*, *Syntrophobacterales*	Wrighton et al. (2014), Converse et al. (2015), Probst et al. (2017), Herrmann et al. (2017) and Herrmann et al. (2019)

Under ammonium-limited conditions, utilization of alternative nitrogen sources that yield ammonia, such as urea or amino acids, has been described for all three groups of ammonia oxidizers (Koch et al., 2019) and could also be an important mechanism in groundwater nitrogen cycling (Reed et al., 2010). Nitrification is also tightly coupled to groundwater carbon cycling, as most nitrifiers are chemolithoautotrophs and employ different CO_2-fixation pathways such as the Calvin-Benson-Bassham cycle (AOB), the reductive tricarboxylic acid cycle (*Nitrospira*), and the 3-hydroxypropioniate/4-hydroxy-butyrate pathway (AOA) (Fig. 1; see also section "Pathways and key players").

Denitrification

The denitrification process

Denitrification is the stepwise reduction of nitrate to dinitrogen gas, including the following steps and intermediates (3) (Zumft, 1997):

$$2NO_3^- \rightarrow 2NO_2^- \rightarrow 2NO \rightarrow N_2O \rightarrow N_2 \quad (3)$$

Reported in situ denitrification activities in aquifers range from <0.001 to 0.986 μmol N L^{-1} d^{-1} under pristine or nitrate contaminated conditions, respectively (Kumar et al., 2017; Smith et al., 2004, 2015). The denitrification capacity of groundwater is mainly determined by the availability of reduced compounds acting as suitable electron donors. Lack of organic carbon as electron donor has been considered as the most significant factor limiting denitrification rates in groundwater and may further be influenced by the nature of DOC with low-molecular weight compounds such as acetate or organic acids being more biologically reactive than high-molecular weight compounds (Starr and Gillham, 1993; Baker and Vervier, 2004). Many denitrifiers can also reduce nitrate chemolithoautotrophically, with sulfide, thiosulfate, ferrous iron, and hydrogen as common electron donors. Availability of these alternative electron donors will strongly depend on the geological setting, e.g., availability of pyrite (see section "Electron donors"). Denitrification does not require completely anoxic conditions but takes places at oxygen levels below 2 mg L^{-1} (Rivett et al., 2008).

Denitrifying microorganisms

The ability to perform denitrification is a wide-spread feature across multiple bacterial and archaeal phyla. Consequently, denitrifier communities in groundwater are usually diverse but may be dominated by a few key players depending on the prevalent electron donor (Table 1). Kumar et al. (2018) found a large fraction of organisms affiliated with the genera *Sulfurifustis*, *Sulfuricella*, and *Sulfuritalea* in a karstic aquifer, pointing to a high relevance of sulfur compounds as electron donors. Most denitrifiers are facultative anaerobes that perform oxidative respiration as the most energy efficient process as long as oxygen is available and switch to nitrate reduction once oxygen is depleted. Many of the denitrifying microorganisms are also capable of switching between heterotrophic and chemolithoautotrophic denitrification depending on the availability of electron donors. Moreover, while some microorganisms are capable of doing the complete denitrification pathway, others can only perform selected steps out of the whole cascade, resulting in complete denitrification by exchange of intermediates within microbial consortia.

Anaerobic ammonia oxidation (anammox)

The anammox process

Anaerobic ammonia oxidation (anammox) is the oxidation of ammonia with nitrite under anoxic conditions to form dinitrogen gas (4) (Strous et al., 1999).

$$NH_4^+ + NO_2^- \rightarrow N_2 + 2H_2O \quad (4)$$

Aquifers often provide suitable conditions for the anammox process to occur—presence of ammonium, nitrite and nitrate simultaneously, absence of oxygen, and slow movement of water. However, while the huge relevance of the anammox process for the nitrogen cycle in marine systems has been recognized for two decades now, the role of anammox for nitrogen loss in aquifers has to date only been addressed by a few studies. Recent findings by Wang et al. (2020) suggest that anammox is a major nitrogen sink in aquifer soils of a few meters down to 28 m depth on a global scale. In situ ammonium concentrations appear to affect anammox activities in groundwater with higher rates at contaminated sites (72–432 nmol L^{-1} d^{-1}) compared to pristine sites (<10 nmol L^{-1} d^{-1}), while the contribution of anammox to overall nitrogen loss, ranging from 18% to 90% across studies, was not linked to the contamination level (Moore et al., 2011; Smith et al., 2015; Kumar et al., 2017; Wang et al., 2017).

Anammox bacteria

The ability to carry out anaerobic ammonia oxidation is confined to a very distinct phylogenetic group within the Planctomycetes, the *Brocadiales*. Anammox bacteria are characterized by rather slow growth rates with doubling times of up to 2 weeks. As a consequence, they are thought to be only competitive in environments with minor water exchange rates, which might apply to a broad range of groundwater environments. In fact, a recent survey studying the distribution of anammox bacteria across different habitats even suggested that groundwater might be the preferred habitat for anammox bacteria (Wang et al., 2019).

Anammox bacteria are mostly known as obligate autotrophs using the Wood-Ljungdahl pathway for CO_2-fixation (see section "The Wood-Ljungdahl pathway") (Fig. 1). Molecular surveys revealed that the fraction of anammox bacteria in the total groundwater bacterial population can be as high as 10% under both low and high levels of nitrate or ammonium contamination. All five known genera of anammox bacteria—*Cand*. Brocadia, Jettenia, Kuenenia, Anammoxoglobus, and Scalindua—have been reported from groundwater environments but the genus *Brocadia* seems to be the most widely distributed in groundwater, represented by the species *Cand*. Brocadia anammoxidans and *Cand*. Brocadia fulgida (Kumar et al., 2017; Wang et al., 2017, 2020) (Table 1).

Dissimilatory nitrate reduction to ammonium (DNRA)

The DNRA process

DNRA is a two-step process that shares the first step of nitrate reduction to nitrite with denitrification but then performs direct reduction of nitrite to ammonium in a second step (5).

$$NO_3^- \rightarrow NO_2^- \rightarrow NH_4^+ \quad (5)$$

DNRA can be coupled to the oxidation of organic carbon compounds as well as to the oxidation of inorganic electron donors such as sulfide or hydrogen (Brunet and Garcia-Gil, 1996; Simon, 2002). Evidently, the potential relevance of DNRA for nitrogen cycling and its contribution to nitrate reduction had been by far overlooked and underestimated in many different environments such as soils (Rütting et al., 2011) or sediments (Bernard et al., 2015). In groundwater environments, DNRA has been considered insignificant for nitrate attenuation (Buss et al., 2005). However, this view was challenged by the observation that DNRA contributed 40–63% to total nitrate reduction in shallow groundwater beneath a constructed wetland system (Jahangir et al., 2017). Occurrence of DNRA was recently linked to low groundwater recharge conditions in an anoxic alluvial aquifer (Perovic et al., 2020).

Microorganisms performing DNRA

Similar to denitrification, the capacity to perform DNRA is widespread across the bacterial and archaeal domains. Many known denitrifiers also possess the genetic machinery for DNRA and may switch between the two different nitrate reduction pathways depending on environmental conditions. To date, our knowledge of the taxonomic affiliation of DNRA-performing microorganisms in groundwater primarily originates from metagenomic approaches. Those revealed that members of the Proteobacteria but also less well studied groups such as Nitrospirae or *Cand.* Omnitrophica harbor the genetic capacity to perform DNRA in groundwater (Anantharaman et al., 2016) (Table 1), suggesting that this metabolic feature is even more wide spread than previously recognized.

Carbon cycling in groundwater

Heterotrophy

Sources of organic carbon

Surface input

At the Earth's surface, the overwhelming majority of organic carbon is formed by photosynthetic primary production. Almost all heterotrophic organisms depend on this organic carbon produced. In terrestrial environments, mostly higher plants are responsible for the primary production. Structural polymers make up the largest part of plant biomass (Lynd et al., 2002). Consequently, the majority of plant-derived organic carbon is present as polymers of carbohydrates (e.g., starch, cellulose, hemicellulose) and polymers of phenolic compounds (e.g., lignin). This organic carbon is transported into the subsurface by fluid flow of infiltrating rain water (Baker et al., 2000; Griebler and Lueders, 2009; Küsel et al., 2016; Perrette et al., 2015). During transport, it undergoes major transformations (Kalbitz et al., 2000; Kaiser and Kalbitz, 2012). Already in soils, plant-derived polymers are broken down and assimilated by microorganisms. Microbial cells are lysed, and the resulting necromass is recycled again and again. The plant-derived organic matter is transformed into microbial-derived carbon (Roth et al., 2019). Within days to decades, depending on the conditioning of the groundwater microbial community (Einsiedl et al., 2007; Hofmann et al., 2020), only a minor part of the carbon transported into the subsurface still consists of remaining, more recalcitrant plant-derived organic matter.

Lysis of microbial cells

Together with dissolved and particulate organic carbon, also microbial cells are transported downwards (Herrmann et al., 2019; Pronk et al., 2009; Shabarova et al., 2013). When transitioning from the soil to the rock parent material, these cells experience drastic changes in environmental conditions. The pH, for example, can change from acidic conditions of pH 3–5 in soils by up to five orders of magnitude to slightly basic conditions of pH 7–8 when reaching carbonate rock (Yun et al., 2016). Such changes can lead to the excessive lysis of cells, increasing the input of microbial-derived biomass into the groundwater. Likewise, viral lysis leads to the release of bacterial necromass. Although there are about 10 times as many viral particles as prokaryotic cells in groundwater, we are still in the early stages of understanding the impact of viruses in the groundwater microbiome (Kyle et al., 2008; Smith et al., 2013). The top of the food web is formed by eukaryotes such as protozoans and metazoans that feed on prokaryotes or on other protozoans (Schmidt et al., 2017). This grazing may also contribute to the release of dissolved organic material originating from sloppy feeding (Møller, 2004, 2007) as described for marine environments.

Rock carbon

An alternative source of organic carbon in the groundwater are the rocks making up the aquifers (Nowak et al., 2017; Schwab et al., 2019). During the formation of sedimentary rocks, hundreds of millions of years ago, organic matter and microorganisms were trapped between the mineral particles. During diagenesis and aging, the organic carbon introduced underwent structural changes.

Exposure to high pressure and temperature resulted in a decrease in heteroatoms and an increase in the number of unsaturated bonds, leading to a higher fraction of aromatic and aliphatic compounds (Benk et al., 2019).

Microbial activity in the groundwater leads to the dissolution of rock material (Sánchez-Cañete et al., 2018). For example, microbial respiration releasing CO_2 as carbonic acid locally decreases the pH of the groundwater, which is compensated by the dissolution of carbonate minerals. Through the progress of dissolution, the aged organic carbon is released and becomes available for microbial degradation. Due to the high age and the chemical composition of these carbon compounds, they closely resemble organic material present in marine sediments (Benk et al., 2019).

In situ primary production

The primary production by autotrophic organisms (see section "Autotrophy") provides another source of organic carbon in the groundwater (Griebler and Lueders, 2009; Akob and Küsel, 2011). Compounds produced by this process can be released when autotrophic cells are lysed. The resulting microbial necromass is then available for heterotrophic growth. Furthermore, autotrophs might be involved in symbiotic interactions with heterotrophic organisms, supplying specific carbon compounds directly.

Other processes typically not considered "primary production" per se closely resemble the mode of carbon distribution through the microbial food web from CO_2 fixation. The assimilation of methane by methanotrophs is one example of such a process. Methane, a C_1 compounds like CO_2, is only available to a small number of organisms, which use it as carbon and energy source (Smith et al., 2010). Similar to chemolithoautotrophs, methanotrophs are frequently observed to supply more easily available carbon compounds to a heterotrophic microbial community, forming the basis of a microbial food web (Ruff et al., 2015; Yu and Chistoserdova, 2017; Taubert et al., 2019).

Compounds and key degraders

Plant polymers

Structural plant polymers, including carbohydrates and lignin, are typically too large for a direct uptake into bacterial cells. Extracellular enzymes, attached to the cell wall or outer membrane, or released into the environment, are used for the extracellular breakdown (Warren, 1996; Schellenberger et al., 2010). Carbohydrates are degraded by glycoside hydrolases, which hydrolyze glycosidic bonds and release oligo- and monomers. Glycoside hydrolase genes can be found in a variety of groundwater microorganisms (Danczak et al., 2017; Castelle et al., 2018) (see Table 1), and the expression patterns of these genes show independence of groundwater hydrochemistry (Wegner et al., 2019). Lignin is degraded by radical-producing peroxidases and laccases, yielding low molecular weight phenolic compounds. Fungi are mayor key players in this process in the groundwater (Nawaz et al., 2016, 2019), but also certain bacteria are involved (see Table 1).

Necromass

The composition of bacterial necromass resembles to large extents that of living bacterial cells. Proteins and nucleic acids are the main components of the bacterial cell, making up 50% and 20% of cell carbon, respectively. These polymers are broken down via proteases and nucleases. The resulting amino acids and nucleotides can be directly used for biosynthesis (Orsi et al., 2018; Starr et al., 2018; Hanajima et al., 2019). To make use of this easily available carbon source, groundwater microorganisms employ a range of transporters for amino acid and nucleotide uptake (Wrighton et al., 2012; Castelle et al., 2018) (see Table 1). Despite a widespread genetic potential for its degradation, assessing the importance of necromass to the microbial community is difficult due to its chemically diverse nature and rapid turnover.

Aromatics and alkanes

Aromatic and aliphatic compounds originate as ancient carbon from rocks (Benk et al., 2019; Schwab et al., 2019), from lignin degradation or as minor components of microbial necromass. These energy-rich but very stable compounds are degraded using mono- and dioxygenases under oxic conditions. Under anaerobic conditions, peculiar biochemical reactions are required for degradation, such as fumarate addition, O_2-independent hydroxylation and reductive dearomatization (Fuchs et al., 2011). Organisms able to perform such reactions are often found in pristine groundwater (see Table 1). In contaminated groundwater, these organisms become central key players and make up the majority of the microbial community.

C_1 compounds

C_1 compounds, containing no carbon-carbon bonds, can be assimilated by methanotrophic and methylotrophic microorganisms. In the groundwater, these compounds are derived from different sources: Methane can originate from volcanic activity, or from methanogenic microorganisms (Mills et al., 2010; McCollom and Seewald, 2013). Methanol is a byproduct of the degradation of plant material, and methylated amines are breakdown products of nitrogen-containing biomass (Neff et al., 2002; Gray et al., 2010). The corresponding assimilation pathways are highly modular (Chistoserdova, 2011), allowing methanotrophs and methylotrophs to use multiple C_1 compounds. Such pathways are primarily present in various *Proteobacteria*, but also *Bacilli* and *Verrucomicrobia* are C_1 utilizers occurring in groundwater (see Table 1).

Autotrophy

Requirements

Electron donors

As in groundwater no photosynthesis is possible, primary production has to rely on chemolithoautotrophic processes utilizing inorganic electron donors such as reduced nitrogen and sulfur compounds. The latter as well as metal ions like ferrous iron can be available from minerals in the aquifer rock, such as pyrite (Schippers et al., 1996; McCollom and Seewald, 2013; Kohlhepp et al., 2017). Various microorganisms able to oxidize reduced sulfur compounds were observed in groundwater (see Table 1). As ferrous iron is rapidly oxidized abiotically under oxic conditions, biological iron oxidation is primarily occurring in microoxic or anoxic groundwater. While arsenic is a common problem for drinking water production from groundwater due to its toxicity, arsenic-oxidizing autotrophic bacteria use it for autotrophic growth under oxic as well as anoxic conditions (Garcia-Dominguez et al., 2008).

Apart from inorganic compounds, also organic compounds can be oxidized to provide energy for CO_2 fixation via autotrophic pathways. Oxidizing organic carbon to CO_2 and then fixing CO_2 to produce biomass seems energetically expensive at first. Certain organisms, however, are employing such a 'chemoorganoautotrophic' strategy (Kang et al., 2011; Winkel, 2013; Taubert et al., 2017, 2018), which might provide an advantage when diverse organic carbon sources difficult to be channeled into the central metabolism are used.

Inorganic carbon

In aquifers made of carbonate rock, ample dissolved inorganic carbon for chemolithoautotrophic growth is available, as the groundwater is saturated with carbonate due to dissolution processes (Kohlhepp et al., 2017). However, the presence of cations forming carbonates with low solubility might restrict the availability of inorganic carbon. In contrast, in aquifers made of siliciclastic rock, the supply of inorganic carbon from carbonates is highly limited (Kunkel et al., 2018). In these environments, the input of inorganic carbon from the surface and the oxidation of organic carbon to CO_2 might be the only sources for inorganic carbon. Chemolithoautotrophs hence are restricted to re-fixing the carbon released by heterotrophic organisms.

Pathways and key players

The Calvin-Benson-Bassham cycle

The Calvin-Benson-Bassham (CBB) cycle is the dominant pathway for CO_2 fixation at the surface, due to its tolerance to oxygen (Berg, 2011). Despite being the energetically most expensive CO_2 fixation pathway, it is also widely distributed in subsurface habitats (Alfreider et al., 2009; Herrmann et al., 2015; Probst et al., 2017) (see Table 1). Transcripts of the key enzyme, Ribulose bisphosphate carboxylase/oxygenase, can represent up to 4% of all metatranscriptomic reads obtained from groundwater samples (Jewell et al., 2016; Wegner et al., 2019).

The reductive tricarboxylic acid cycle

The reductive tricarboxylic acid (rTCA) cycle is present in microaerobic and anaerobic bacteria of the phyla *Chlorobi*, *Proteobacteria*, *Aquificae* and *Nitrospirae* (Berg, 2011). In groundwater, it is employed by nitrite-oxidizing *Nitrospiraceae* (Herrmann et al., 2015; Wegner et al., 2019) (see Table 1). Despite the sensitivity of some involved enzymes to oxygen, the rTCA cycle is also found in oxic groundwater. The mechanisms behind this oxygen tolerance are yet not fully understood.

The Wood-Ljungdahl pathway

The Wood-Ljungdahl pathway represents a highly versatile metabolic module: It can be used for autotrophic growth by converting CO_2 to acetyl-CoA, but it can also run in reverse to oxidize acetate, or be used for the assimilation of C_1 compounds (Berg, 2011; Lemaire et al., 2020). Its presence thus is not strictly linked to autotrophy. In groundwater, it is used for autotrophic growth of anammox-performing *Planctomycetes* (Jewell et al., 2016; Wegner et al., 2019). Methanogens and acetogens also use it for autotrophic growth. The latter, however, also employ it during heterotrophic growth (Lemaire et al., 2020). It is also present in sulfate-reducing *Deltaproteobacteria* that can grow heterotrophically or autotrophically (Probst et al., 2017, 2018). This versatility makes it difficult to assign the Wood-Ljungdahl pathway to a clear lifestyle.

Other autotrophic CO_2 fixation pathways

Three other metabolic pathways for CO_2 fixation in autotrophs are known: The 3-hydroxypropionate cycle used by members of the *Chloroflexi*, and the 3-hydroxypropionate/4-hydroxybutyrate (HP/HB) cycle and dicarboxylate/4-hydroxybutyrate (DC/HB) cycle present in members of the *Crenarchaeota*. These organisms are present only in low abundance in groundwater habitats. The expression of genes of the HP/HB cycle by ammonia oxidizing *Archaea* has been reported (Ortiz et al., 2013; Wegner et al., 2019). As these pathways lack specific marker genes, it is difficult to determine whether they are used for CO_2 fixation by particular organisms, and activity-based measurements are required for support.

CO_2 uptake by heterotrophs

In addition to autotrophs, heterotrophs fix CO_2 during anaplerotic reactions (Alonso-Sáez et al., 2010; Erb, 2011). The carbon assimilated in this way can contribute 1–8% to total cell carbon (Braun et al., 2021). Certain carbon assimilation pathways lead to a

much higher contribution of CO_2. Type II methylotrophs obtain up to 50% of carbon from CO_2 via the serine cycle (Chistoserdova, 2011; Braun et al., 2021). Likewise, organisms assimilating acetate while lacking the glyoxylate cycle typically require the fixation of one or two molecules of CO_2 per acetate, resulting in 33–50% CO_2-derived carbon (Taubert et al., 2012). Hence, also in heterotrophs, a substantial amount of carbon can be derived from CO_2.

Methods

Sampling

Difficulties/challenges with accessibility

The special conditions encountered in the subsurface pose a number of challenges when investigating the groundwater microbiome. Methods to sample groundwater microbial communities available to date are limited in their ability to resolve spatial and temporal heterogeneity on the micro scale level, which is the relevant scale for growth and activity of microorganisms (Schmidt et al., 2017). Due to micro scale heterogeneity, not all microorganisms at a given location, e.g., defined by the volume of the sampled groundwater, are exposed to the same environmental conditions in situ (Thullner and Regnier, 2019). However, to obtain suitable amounts of biomass for analysis, high volume filtration of thousands of liters of groundwater might be necessary. This results in the mixing of water from different (micro scale) sources and in the integration of effects of several micro-environments with their distinct microbial communities. Moreover, the ultra-small cell sizes below 0.2 μm reported for various groundwater microbes are best captured using a sequential filtration approach (Castelle et al., 2015; Herrmann et al., 2019).

Similar to the observations on spatial scales, understanding temporal microbial community dynamics is generally limited by the temporal scales at which sampling can be conducted. To understand the assembly of groundwater microbial communities, the biogeochemical parameters influencing them and the role of surface input, a complex infrastructure as well as data acquisition in time series are advantageous (Küsel et al., 2016).

Methods of molecular biology

16S rRNA gene amplicon sequencing

Due to their low requirements for biomass and the high information on taxonomy and functional potential, primarily DNA-based methods were used to acquire first insights into the groundwater microbiome. 16S rRNA gene-based profiling has revealed a highly distinct makeup of communities encountered in the subsurface and allowed insight into parameters driving the assembly of groundwater microbial communities (Stegen et al., 2013, 2016; Hubalek et al., 2016; Yan et al., 2020; Fillinger et al., 2021).

Metagenomics, metatranscriptomics and metaproteomics

Advances in metagenomics have opened a window into the functional potential of groundwater microorganisms by providing thousands of metagenome-assembled genomes (MAGs) (Anantharaman et al., 2016; Parks et al., 2017). Genomic investigation of many groundwater bacteria has shown a high metabolic diversity, a widespread potential for chemolithoautotrophic growth and key roles in nitrogen and sulfur cycling (Anantharaman et al., 2016, 2018; Emerson et al., 2016; Probst et al., 2018; Wegner et al., 2019). These functional predictions have allowed researchers to develop hypotheses about microbial lifestyles in the groundwater, such as the frequent occurrence of metabolic handoffs between microbes (Wrighton et al., 2014; Anantharaman et al., 2016). Such hypotheses now warrant verification by using methods other than metagenomics that can illuminate microbial activities.

Activity measurements

Determination of bulk metabolic rates

A first step to unravel microbial activities in the groundwater is the determination of bulk rates on whole community level. Methods relying on the detection of heavy isotopes, both radioactive and stable, in substrates and products of microbial conversion reactions are ideal tools for this purpose, as they allow a distinction against environmental concentrations of the analytes and offer a supreme sensitivity. Analysis of natural ^{15}N isotope abundances in nitrate, nitrite, and ammonium, combined with the assessment of ^{18}O values in nitrate and nitrite, can provide first insights into potential sources and sinks of these compounds and which nitrogen transformation processes are likely to co-occur (Wells et al., 2016; Minet et al., 2017; Nikolenko et al., 2018). Short-term incubations following the transformation of ^{15}N-labeled ammonium, nitrate, or nitrite into oxidized or reduced nitrogen species allow the quantification of process rates of nitrification, denitrification, anammox, and DNRA, and of potential linkages between these processes (Berg et al., 2015; Roland et al., 2018).

The essential question regarding the contribution of in situ CO_2 fixation to the microbial carbon can currently be addressed by ^{13}C and ^{14}C-based methods to quantify the incorporation of CO_2 derived carbon in total microbial biomass (Nowak et al., 2015; Beulig et al., 2016; Akinyede et al., 2020; Overholt et al., 2021). For both nitrogen and carbon cycling, estimations of turnover rates for the whole aquifer system need to take into account that in many aquifers, the greatest proportion of subsurface process activity probably occurs in association with biomass present on mineral surfaces (Fredrickson and Fletcher, 2001).

Towards a generalized understanding of the subsurface

To understand the contribution of microbial taxa to ecosystem functions, their adaptation and strategies for survival in the groundwater, approaches connecting taxonomy, function and activity are required. Metabolic labeling techniques such as stable isotope probing (SIP) allow the identification of active microbial key players. Provided with heavy isotope labeled substrates, active microbes will incorporate isotopes like ^{13}C, D or ^{15}N into their biomolecules. This heavy isotope incorporation can be determined on the community level using omics techniques targeting different classes of biomolecules (Neufeld et al., 2007; Taubert et al., 2012). Furthermore, using Raman microspectroscopy or nanoSIMS, the isotope incorporation can also be detected on the level of individual cells (Musat et al., 2008; Berry et al., 2015; Taubert et al., 2018). Novel developments in the SIP methods are currently moving beyond the identification of key players, towards a quantitative assessment of carbon and nitrogen fluxes (Koch et al., 2018; Taubert et al., 2019, 2021).

However, these approaches typically rely on laboratory experiments conducted under conditions that aim to mimic but also strongly simplify the aquifer environment. Natural porous media are complex and often heterogenous structures, which imposes severe challenges in determining the exact physical, chemical and ecological conditions the microbial community is exposed to in situ (Thullner and Regnier, 2019). Future challenges lie in a better approximation of the micro scale heterogeneity of these conditions, and of the respective micro scale distribution patterns of microbial communities and processes.

A final challenge that scientists are facing is linking microbially driven processes on the micro scale level to landscape level observations. Refined modelling approaches that integrate micro scale heterogeneity are key to understanding individual systems on the catchment level as well as developing a generalized understanding of microbially mediated biogeochemical transformations in the subsurface (Fig. 2).

Synthesis: Strategies of the groundwater microorganisms combining lifestyles

Autotrophy and heterotrophy

One of the most interesting questions about microbial life in groundwater concerns the relative importance of CO_2 versus organic carbon as carbon source. Approaches targeting genetic potential for autotrophic or heterotrophic growth typically result in a clear bisection of the microbiome (Herrmann et al., 2015; Jewell et al., 2016; Long et al., 2016). However, here, we would like to address this aspect from the perspective of the groundwater microorganisms: aiming for survival. How can microorganisms utilize their genomic potential to thrive under the conditions present in the groundwater? What strategies have they evolved to be successful? Which energy-providing reactions are linked to these lifestyles, and how do they connect to biogeochemical cycles?

The "all-rounder"

In the sections above, multiple examples of organisms using both CO_2 and organic carbon were outlined. In oligotrophic groundwater, mixotrophy is a successful strategy allowing microbes to expand the range of accessible resources. Groundwater

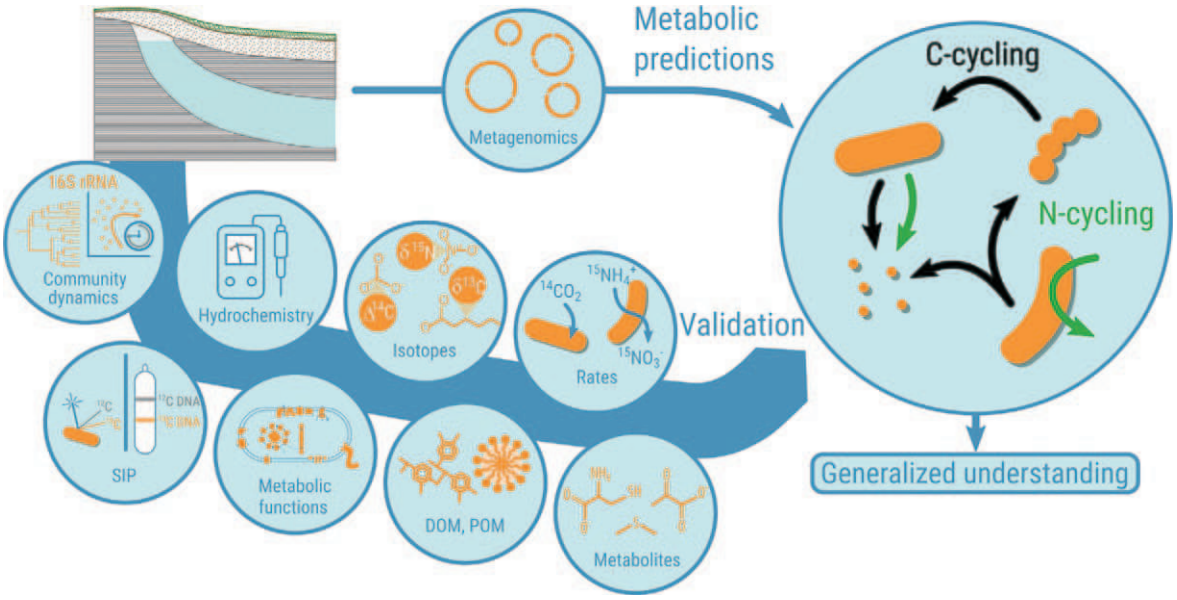

Fig. 2 Overview of methods employed in a comprehensive approach to understand microbially driven biogeochemical cycling in groundwater, interaction and metabolic handoffs between the key players, and key environmental controls on microbial consortia.

microbes with the potential to fix CO_2 thus often also exhibit uptake and assimilation mechanisms for various organic carbon compounds (Emerson et al., 2016; Probst et al., 2017) (see Table 1). To further enhance their metabolic capabilities, such organisms employing an "all-rounder" strategy can be able to utilize inorganic energy sources, such as reduced nitrogen and sulfur compounds, and multiple electron acceptors, such as oxygen and nitrate (Jewell et al., 2016; Wegner et al., 2019; Taubert et al., 2021). Similarly, many facultative anaerobic microorganisms are able to switch from oxygen respiration to nitrate reduction and thus adjust to fluctuating redox conditions. Using nitrate as electron acceptor, some microbial taxa found in groundwater can perform both denitrification and DNRA and can choose the nitrate reduction pathway that will be energetically more favorable under the given conditions.

The "minimalist"

A large amount of microbes found in groundwater feature ultra-small cell sizes below 0.2 μm (Castelle et al., 2015; Luef et al., 2015; Herrmann et al., 2019). These organisms are characterized by a minimalistic strategy, featuring reduced genomes that lead to restricted metabolic capabilities. The members of the Candidate Phyla Radiation (CPR), which are often present in high abundance in groundwater habitats, are prime examples of this strategy (Rinke et al., 2013). The CPR possess various glycoside hydrolases for the breakdown of carbohydrates and a high range of transporters to satisfy their minimal nutritional requirements: amino acids, nucleotides, and sugars for fermentation (Castelle et al., 2015, 2018; Danczak et al., 2017). Lacking pathways for synthesis of essential amino acids and nucleotides, these organisms likely exhibit a symbiotic lifestyle (Nelson and Stegen, 2015). Successful examples of co-cultivation of CPR with putative hosts have confirmed this assumption (Gong et al., 2014; Bor et al., 2020).

Individual strategies and links to biogeochemical cycles

Like autotrophic and heterotrophic lifestyles, the all-rounder and minimalist strategies should be seen as extremes on a wide gradient. Even minimalists like the CPR are proposed to contribute individual metabolic steps in the nitrogen or sulfur cycle to complement the capabilities of other organisms (Hug et al., 2016; Danczak et al., 2017; Castelle et al., 2018). Metabolic hand-offs can occur, where each of the involved organisms carries out some steps of a metabolic pathway (Anantharaman et al., 2016; Hug and Co, 2018). Mixotrophic all-rounders were found to rely less on CO_2 fixation the more organic carbon compounds they were able to utilize, and vice versa (Taubert et al., 2021).

To date, a huge body of literature exists where research either focused on biogeochemical processes in groundwater, or diversity and functional potential of groundwater microbial communities based on molecular surveys. New concepts and perspectives, along with a rapidly expanding toolbox of novel methodological approaches to link microbial identity, activity, and element flow within microbial consortia, will allow us to eventually achieve a mechanistic understanding of the groundwater microbiome. Starting from there, we will be ready to face the next challenge: To link microscale studies and concepts of microbial metabolism and interactions to aquifer-level observations of microbially-driven biogeochemical processes.

Knowledge gaps

- What is the contribution of planktonic versus attached microbial populations to nitrogen transformation processes in aquifers?
- How can we adequately account for large-scale and microscale heterogeneity in biogeochemical processes and microbial distribution patterns in our groundwater sampling designs?
- Which factors determine the major nitrate reduction pathway—denitrification, DNRA, or anammox—in groundwater, and what is the impact of geologic setting and land use?
- To what extent can we predict the groundwater's capacity for a given biogeochemical process based on abundances of the corresponding key microbial players?
- What is the fate of microbial-derived carbon in groundwater?
- What is the relative importance of heterotrophy and autotrophy in the groundwater, and which factors influence it?
- How does the genomic potential of groundwater organisms translate into phenotypes and metabolic strategies?
- How does interaction with symbiotic organisms like CPR affect groundwater microbial community composition and activity, and what is the role of CPR in biogeochemical processes?
- What is the role of viral lysis and protist grazing for the provision of labile organic carbon in groundwater?

Important case studies

See Table 2

Table 2 Collection of important case studies dealing with groundwater microbial diversity, functional potential, and the role of microorganisms in biogeochemical processes in aquifers.

Research focus	*Study site*	*References*
Genome-resolved study at the community level, allowing insight into interconnected biogeochemical processes	Aquifer adjacent to Colorado river (Rifle, CO, United States)	Anantharaman et al. (2016)
Effect of availability of energy and nutrient sources, determined by surface connectivity or deep geological processes, on subsurface microbial communities	Äspö HRL tunnel sites (Sweden)	Hubalek et al. (2016)
Interdisciplinary approach to study links between the surface and subsurface biogeosphere	Hainich CZE (Germany)	Küsel et al. (2016)
First comprehensive metagenomic study of ultra-small bacteria affiliated with the candidate phyla radiation in groundwater	Aquifer adjacent to Colorado river (Rifle, CO, United States)	Luef et al. (2015)
Statistical framework to quantify mechanisms of community assembly of groundwater microorganisms	Hanford site (Washington State, United States)	Stegen et al. (2013)
Environmental drivers of microbial diversity in groundwater	Hainich CZE (Germany)	Yan et al. (2020)

Acknowledgment

M.T. gratefully acknowledges funding by the DFG under Germany's Excellence Strategy—EXC 2051—Project-ID 390713860.

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The Ecology of Microbial Contaminant Degradation in Groundwater

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Aquifer A geological formation in which subsurface water is transported and stored.
BTEX Complex contaminations of petroleum hydrocarbons including benzene, toluene, ethylbenzene and xylenes.
Co-metabolism Degradation of contaminants, often at low concentrations, by the fortuitous activity of enzymes expressed to degrade substrates other than the actual micropollutant.
Functional marker gene Catabolic or respiratory gene conserved within a functional group of microorganism, the targeting of which allows to detect and quantify respective process potentials in the field.
Microbiome A characteristic microbial community found in a defined habitat, including their specific metabolic activities and ecological interactions.
Micropollutants Pollutants typically found at low concentrations (ng–μg L^{-1} range) in the water cycle, often of emerging concern due to their bioactivity and toxicity at trace amounts.
Organohalides Halogenated hydrocarbons, aliphatic or aromatic.
Priority pollutants A list of the most widespread and concerning groundwater pollutants compiled by regulatory authorities.
Stable isotope probing Detection and identification of process-relevant populations within complex environmental microbiomes based on labeling with stable isotopes.

Introduction

Aquatic microbiomes are of crucial importance for the quality of inland waters. They regulate the turnover of carbon and nitrogen inputs, they degrade pollutants, and are crucial for hygienic water quality. While surface waters such as rivers and lakes are often more prominent in public awareness, the quantitatively most significant component of the terrestrial water cycle is groundwater (Shiklomanov, 1993). The use of groundwater is especially important for drinking water supply. A lack of access to hygienically safe drinking water is estimated to result in up to half a million of human mortalities p.a., mostly in less developed countries (World Health Organization, 2019). However, also chemical groundwater pollution is of increasing global concern. Rising environmental pollution, changes in land use, population growth and climate change are just a few of the most relevant factors leading to changes in the amounts of solutes entering our groundwater.

Chemical water contaminants can generally be defined as elements or compounds foreign to a water body, or with concentrations significantly raised compared to natural background concentrations, that are toxic, persistent and liable to bioaccumulate (Tornero and Ribera d'Alcalà, 2014). The canonical lists of ground- and drinking water "priority pollutants," routinely compiled by regulatory authorities (European Commission, 2008; US EPA, 2015), include many organohalide solvents, aromatic hydrocarbons and other petrochemicals, metals and other inorganics, but also certain biocides (Table 1). Many of these are considered as so-called "legacy contaminants," which have been released to and accumulating in the environment due to anthropogenic activities over many decades. Concentrations of such legacy contaminants in polluted groundwater can be quite high, typically in the mg L^{-1} range or even higher. In contrast, a further group of compounds summarized as "emerging contaminants" or "micropollutants" is typically found in the ng–μg L^{-1} range. Despite these low concentrations, they are of increasing stakeholder concern

 https://doi.org/10.1016/B978-0-12-819166-8.00180-8

Table 1 Examples of frequent ground- and drinking water pollutants, including priority pollutants.

Pollutant class	*Example compounds*	*Source*
Petroleum hydrocarbons	Alkanes, BTEX (benzene, toluene, ethylbenzene, xylenes), phenols	Petroleum industry
Polyaromatic hydrocarbons	Napthalene, anthracene, phenantrene, benzo(a)pyrene, fluoranthenes	Chemical industry, asphalt, combustion products
Halogenated hydrocarbons	Chloromethanes, chloroethanes, polychlorinated biphenyls (PCBs), pentachlorophenol (PCP), dioxins, polybrominated diphenylethers	Chemical industry, dry cleaning, degreasing, lubricants, flame retardants
Pesticides, other biocides	Atrazine, DDT, diuran, endosulfanes, isoproturon, triclosan	Agriculture, food industry, disinfection
Pharmaceuticals	Ethinyl estradiol, diclophenac, ibuprofen, metformin, carbamazepine	Hospitals, households
Additives	Methyl-*t*-butylether (MTBE), phthalates, bisphenol A, nonylphenols	Chemical industry, plastic production
(Heavy) metals, metalloids	Lead, cadmium, chromium, copper, mercury, nickel, arsenic, antimony, uranium and their compounds	Geogenic, mining industry
Other inorganics	Nitrate, ammonia, sulfuric acid, sulfide	Fertilizers, animal husbandry, mining

Curtailed from European Commission (2008), US EPA (2015) and based on the pollutants discussed in this chapter.

(Schwarzenbach et al., 2010). Micropollutants include many bioactive compounds such as pesticides, pharmaceuticals, hormones and antibiotics, but also chemical detergents, personal-care products, flame retardants or disinfection by-products (Table 1). In contrast to our understanding of the degradation of many legacy contaminants (a.k.a. "macropollutants"), research on the microbiology and biochemistry of micropollutant degradation remains a major analytical challenge today (Fenner et al., 2021).

Microbial contaminant degradation via redox processes

Microbes and especially bacteria, typically more abundant in aquifers than archaea or microeukaryotes, actively control groundwater quality with their biogeochemical activities. To understand the principles of microbial contaminant degradation, it is relevant to first classify the different pollutants into fundamental redox schemes (Fig. 1). I.e., petroleum hydrocarbons and other reduced organic pollutants like pesticides or pharmaceuticals will typically be utilized as electron donors and thus are subject to oxidative biodegradation. At the same time, the general redox setting of the water body and the availability of electron acceptors like oxygen, nitrate, ferric iron or sulfate will determine, whether oxidative degradation is driven by either aerobic or anaerobic degraders (Lueders, 2017). In contrast, some of the most widespread organohalide pollutants are higher-chlorinated ethylenes (perchloroethylene, PCE, and trichloroethylene, TCE), which are highly oxidized compounds, making them unattractive as electron donors or even inaccessible for oxidative biodegradation (Mattes et al., 2010). Here, biodegradation essentially relies on reductive processes and actually the use of the pollutant as electron acceptor by anaerobic degraders (Fig. 1). The redox setting of the aquifer will thus not only determine the mode of biodegradation, but control whether a pollutant can be degraded at all. The same also applies to another very prominent, but inorganic groundwater pollutant: Nitrate can typically also be eliminated from groundwater via reductive processes alone, canonical denitrification being the responsible respiratory process and dependent on the absence of oxygen, as well as the availability of suitable electron donors to fuel denitrifying microbial populations. Finally, reduced inorganics

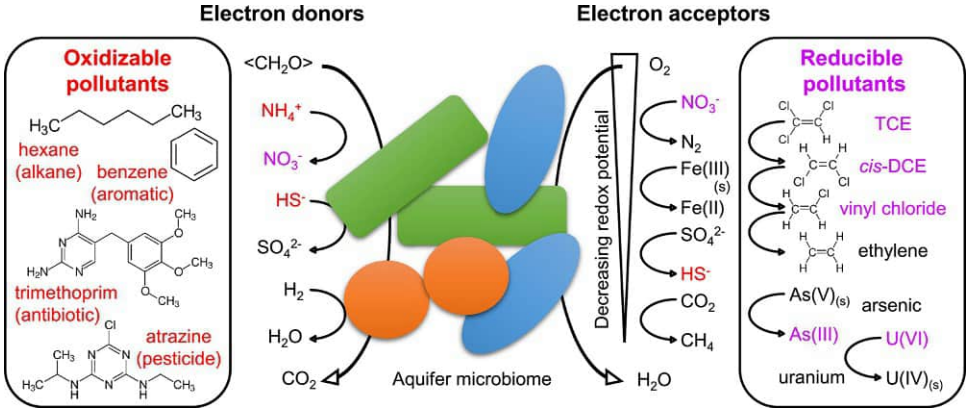

Fig. 1 Scheme of the coupling of electron donors and electron acceptors in redox processes mediating the degradation of pollutants by aquifer microbes. Oxidizable organic and inorganic pollutants are given in red, reducible water pollutants in purple. Modified from Meckenstock RU, Elsner M, Griebler C, Lueders T, Stumpp C, Aamand J, Agathos SN, Albrechtsen H-J, Bastiaens L, Bjerg PL, Boon N, Dejonghe W, Huang WE, Schmidt SI, Smolders E, Sørensen SR, Springael D, and van Breukelen BM (2015) Biodegradation: Updating the concepts of control for microbial cleanup in contaminated aquifers. *Environmental Science & Technology* 49: 7073–7081. doi:10.1021/acs.est.5b00715.

like ammonium or sulfide can also contaminate groundwater as a result of anthropogenic inputs. Their removal again depends on oxidative processes and their use as electron donors, mostly by aerobic chemolithoautotrophs incl. nitrifiers and sulfide oxidizers.

Thus in summary, the nature and ecophysiology of the microbes involved in the degradation of macropollutants in groundwater will primarily be dictated by the redox state of the pollutant itself (i.e., is the pollutant an attractive electron donor or acceptor?), and by the availability of appropriate partner reactants needed to drive the respective redox processes. In contrast, micropollutant degradation is taken to mostly rely on co-metabolic (or fortuitous) degradation mechanisms (Fenner et al., 2021; Schwarzenbach et al., 2010). These will be discussed in more detail further down.

Oxidative catabolism of groundwater pollutants

The most common way of contaminant biodegradation is oxidative catabolism, in which the organic contaminant serves as electron donor and carbon source for degraders. It may be surprising, but many of the above mentioned xenobiotic compounds are easily accessible substrates for a wide diversity of microbes. Since petroleum hydrocarbons (e.g., aliphatic alkanes and aromatic hydrocarbons) are amongst the most frequent groundwater pollutants, we have a deep knowledge on the oxidative microbial degradation of these compounds today. Especially monoaromatic hydrocarbons, such as benzene, toluene, ethylbenzene and isomers of xylene (the so-called BTEX compounds) pose the highest environmental hazard. Thus, their biodegradation pathways are well-characterized (Fig. 2). Under aerobic conditions, the initial step of degradation is always the activation of the aromatic ring in peripheral or upper pathways of degradation, catalyzed by a wide variety of mono- and dioxygenase enzymes. The largest group of enzymes that can activate the aromatic ring are the Rieske non-heme iron-dependent oxygenases. These enzymes play an important role in the degradation of benzene, toluene, phthalates, naphthalene and biphenyls (Gibson and Parales, 2000). They are multi-component enzyme complexes consisting of a terminal oxygenase component and various electron transport proteins. During the reaction catalyzed, two oxygen atoms are incorporated into the aromatic ring, eventually forming an aromatic *cis*-dihydrodiol. Followed by a dehydrogenation step, depending on the substrate, this results in a substituted or non-substituted catechol molecule. In the case of toluene, the product is 3-methylcatechol. Another important group of aromatic ring activating enzymes is the soluble di-iron monooxygenases, some of which are capable of monooxygenating benzene or toluene and thereby converting them to phenol or methylphenol, respectively. Subsequently, these are also further transformed to catechols. Their best-known representatives are toluene monooxygenases, which are able to hydroxylate toluene in all three possible positions (Parales et al., 2008). In the following step, the phenol or methyl-phenol will be transformed to a catechol or methyl-catechol. Eventually, all peripheral or upper pathways result in a catecholic molecule, which is the central intermediate of this aerobic degradation. These catecholic molecules will be further transformed by enzymes of the central or lower pathways of aromatic hydrocarbon degradation, in which the key step is the cleavage of the aromatic ring. Only two types of dioxygenases catalyze this ring cleavage: intra- or extradiol dioxygenases. Intradiol dioxygenases (ortho-cleavage dioxygenases) selectively cleave the aromatic ring between the hydroxyl groups of the catecholic substrate, while extradiol dioxygenases (meta-cleavage dioxygenases) cleave the C–C bond outside the two hydroxyl groups of catechols. Also methyl substituted aromatic compounds (toluene, xylenes) are metabolized via meta-ring cleavage. A well-characterized group of extradiol dioxygenases is adapted to limited oxygen availability (Kukor and Olsen, 1996), a favorable property in contaminated subsurface environments. Microbes harboring this type of ring-cleavage enzyme can play prominent role in the degradation of monoaromatic hydrocarbons in hypoxic aquifers (Táncsics et al., 2018).

Given the fact that the availability of oxygen is often limited in contaminated aquifers, microbes capable of degrading petroleum hydrocarbons under anaerobic conditions play a pivotal role in the clean-up of the contaminated subsurface environments. The most common mechanism for the anaerobic activation of aromatic compounds is fumarate-addition (Fig. 2). In this process, a glycyl radical enzyme decreases the stability of the aromatic ring by the addition of a fumarate molecule to the aromatic compound (i.e., to the methyl group of toluene). This process of benzylsuccinate formation, first described for the nitrate-reducing *Thauera aromatica*, is now widely recognized as a conserved key mechanism for the anaerobic activation of methylated aromatics and even alkanes (von Netzer et al., 2016). Such benzyl- and alkylsuccinate-synthases are highly conserved, and can be found not just in nitrate-reducing, but also in sulfate- and iron-reducing bacteria that degrade petroleum hydrocarbons. In analogy to the catechols in aerobic aromatics degradation, benzoyl-CoA is formed as the central intermediate then entering downstream catabolic routes. For alkanes, the alkysuccinates go through a carbon chain rearrangement, followed by a decarboxylation, resulting in a branched chain fatty acid, which can then enter central metabolic pathways and canonical β-oxidation. Overall, prokaryotic microorganisms have evolved many efficient oxidative pathways for the degradation of organic molecules, even for those having complex aromatic structures, or showing minimal solubility in water.

Reductive elimination of groundwater pollutants

Subsurface environments are typically oxygen-limited, thus providing a niche for bacteria which use electron acceptors other than oxygen for their respiration (Fig. 1). These alternative electron acceptors include both inorganic (sulfate, nitrate, ferric iron) and organic compounds (e.g., trimethylamine N-oxide). The fact that some organic contaminants can serve as electron acceptors is relevant in the bioremediation of groundwater ecosystems contaminated with chlorinated aliphatic (tri- and perchloroethylene—TCE/PCE) or aromatic compounds (e.g., chlorobenzenes, polychlorinated biphenyls, dioxins). Specific obligate anaerobic microorganisms, members of the class *Dehalococcoidea* in the phylum *Chloroflexi* (Löffler et al., 2013), can perform this organohalide respiration, resulting in the reductive dechlorination of the above mentioned compounds. This mechanism, which is catalyzed by

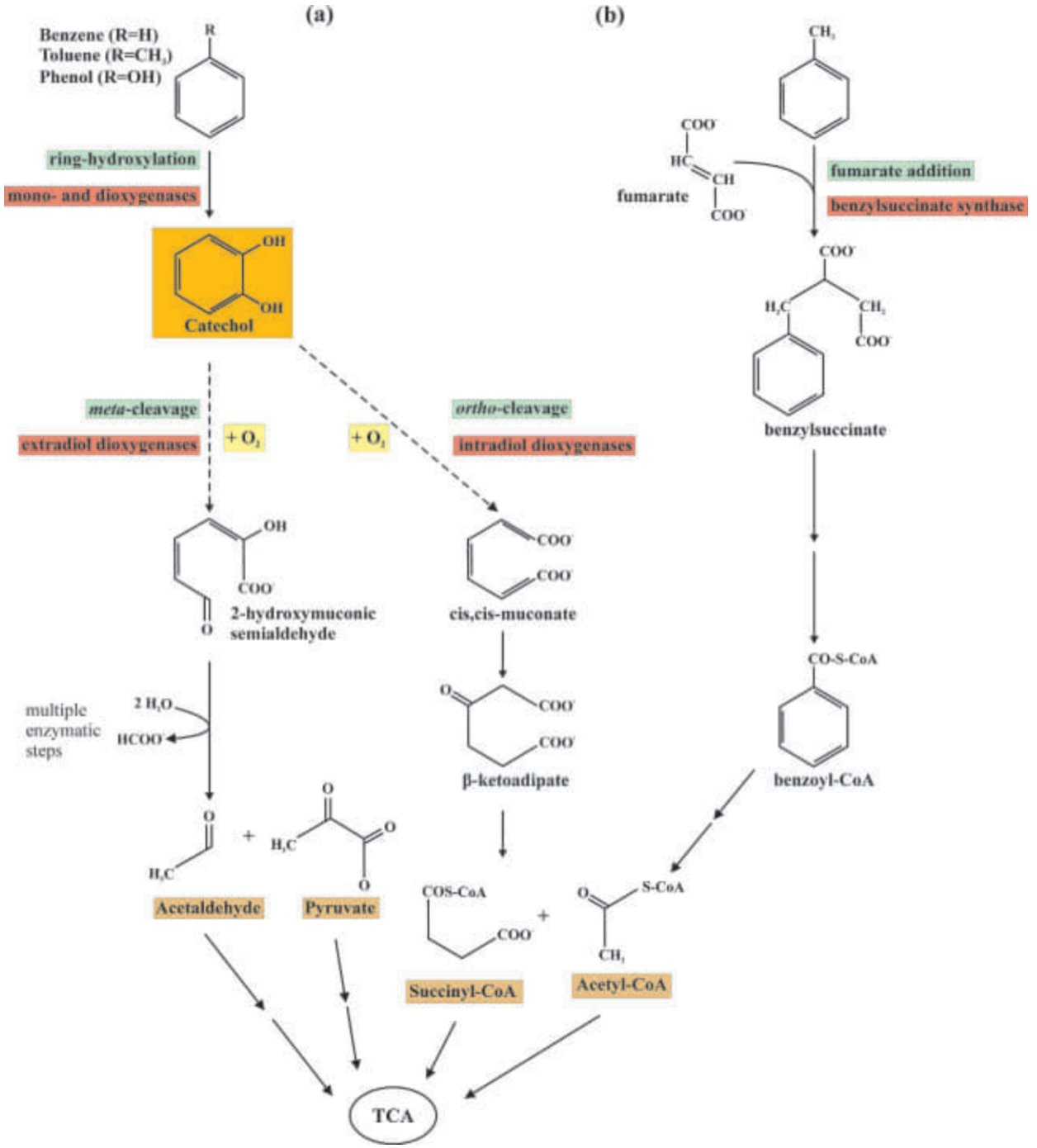

Fig. 2 Schematic representation of conserved (A) aerobic and (B) anaerobic degradation pathways of monoaromatic hydrocarbons. During aerobic degradation, enzymes of the upper or peripheral pathway are responsible for the activation of the aromatic ring, resulting in a catecholic central intermediate. Thereafter, enzymes of the lower pathway are responsible for the ring-cleavage of the chatecholic molecule. During anaerobic degradation, fumarate-adding enzymes play a key role in the initial activation of the aromatic ring. Ultimately, both aerobic and anaerobic degradation end-products can enter the TCA-cycle.

reductive dehalogenase (RDase) enzymes, involves the removal of the chlorine substituents as halogen ions and their replacement by hydrogen. The RDase homologous (*rdh*) genes are often used as molecular markers to reveal the diversity and activity of organohalide-respiring bacterial communities. One of the RDases, called vinyl chloride reductase (*vcrA*), plays a crucial role in the complete reduction of PCE and TCE into the harmless ethylene by catalyzing the reduction of vinyl chloride. This enzyme is mostly harbored by members of the genus *Dehalococcoides*, often obligate organohalide-respiring bacteria. Therefore, the bottleneck of the complete bioremediation of TCE/PCE-contaminated subsurface ecosystems is the presence of *vcrA*-harboring *Dehalococcoides* populations. The absence of such bacteria can lead to the accumulation of vinyl chloride, which is more harmful than the parent compounds.

A common inorganic electron acceptor in anoxic groundwaters, nitrate, is one of the most widespread and important groundwater contaminants if present in higher concentrations (typically above 50 mg L^{-1}). Its appearance in groundwater is mainly due to human activities, especially animal husbandry and the release of manure, fertilization, the desiccation and field application of sewage sludge, or irrigation with domestic wastewater. Given the fact that nitrate is a rather mobile anion, it is readily leached into groundwater when applied to surface soils. Nitrate, and nitrite as its initial reduction product, have serious health effects. It may form carcinogenic n-nitroso compounds in the intestinal tracts, and can cause methaemoglobinaemia in infants, thus prohibiting the use of nitrate-burdened groundwater for human consumption. Bioremediation of nitrate-contaminated aquifers is mostly based on the activity of heterotrophic denitrifying bacteria. However, denitrification will only be efficient in groundwater, when oxygen is absent and adequate electron donors are present. Aquifers are usually oligotrophic environments, thus the metabolic activity of denitrifiers can be stimulated by providing them with easily available carbon- and energy sources, such as methanol, ethanol, acetate or molasses. In canonical denitrification, nitrate will ultimately be transformed into nitrogen gas, thus eliminating the pollutant from the system. However, also inorganic electron donors like reduced sulfur species and hydrogen gas have been reported to drive autotrophic denitrification within aquifer microbes (Kumar et al., 2018).

Besides nitrate, also the reduction of other oxidized inorganics is of relevance for pollutant fluxes in groundwater (Fig. 1). Specifically, the microbial reduction of water-insoluble arsenate (As(V)) to soluble arsenite (As(III)) is a major mechanism for the mobilization of this known carcinogen in regions where aquifer sediments are naturally rich in arsenic, but human impact has caused oxygen depletion in previously oxic groundwaters (Hug et al., 2020). In contrast, the reductive immobilization of dissolved U(VI) to insoluble U(IV) by metal respiring aquifer microbes is an important and actually applied strategy for the containment of radioactive pollution at sites with respective subsurface contamination, e.g. at sites of former nuclear weapon testing (Williams et al., 2011). In summary, not only the catabolic but also the respiratory activities of aquifer microbes are involved in many ways in the degradation and attenuation of groundwater pollutants.

Co-metabolic degradation of micropollutants

In addition to the microbial elimination of notorious legacy pollutants, the widespread emergence and accumulation of a considerable range of micropollutants in the water cycle, complex mixtures of anthropogenic chemicals not only present, but also of concern in low concentrations, is receiving increasing attention (Schwarzenbach et al., 2010). As mentioned above, many of these compounds are biocides, detergents, pharmaceuticals and other bioactive chemicals (Table 1), entering the water cycle mainly via outflows of urban wastewater treatment, agriculture or industry. In contrast to the catabolism of macropollutants by degraders specialized to capitalize on the resulting carbon and energy fluxes, the degradation of micropollutants mostly depends on co-metabolic processes. The low concentration of micropollutants is recognized as the major limitation to potential degraders, effective availability mostly being below thresholds to trigger the induction of catabolic pathways. Co-metabolic degradation involves the fortuitous activity of enzymes expressed to degrade substrates other than the actual micropollutant, but capable to transform the latter due to structural or mechanistic promiscuity. While it is far from clear today, whether lower thresholds for catabolic degradation can be predicted by compound- or strain-specific parameters, there is an increasing understanding of the primary metabolic activities in aquatic microbiomes that can result in an increased co-metabolism of micropollutants. Intriguingly, next to "expected" metabolic activities by unspecific oxidative enzymes of heterotrophs such as laccases (Margot et al., 2013), there is increasing evidence for a role of autotrophic co-metabolism in wastewater systems. Hence, the monooxygenase enzymes of lithotrophs such as ammonia oxidizers and methanotrophs are also capable to oxidize certain micropollutants. For example, the elimination of a range of micropollutants typically subject to oxygenation reactions was significantly correlated to the abundance of ammonia-oxidizing Archaea in activated sludge (Helbling et al., 2012). Future research will have to show whether it is possible to more specifically stimulate and harness such co-metabolic activities, to counter micropollutant accumulation in the terrestrial water cycle. For this however, major challenges still remain to be met, both from a microbiological and an analytical perspective.

The ecology of contaminant degrading microbes in groundwater

Research on the microbial biodegradation of environmental contaminants such as alkanes dates back more than 100 years. A Dutch microbiologist, N. L. Söhngen, was the first to report on the microbial biodegradation of oil slicks floating on water and to describe that these hydrocarbons can serve as a source of carbon and energy for microorganisms (Söhngen, 1913). In the following decades of the era of classical microbiology, enrichment and isolation approaches have increased our knowledge on the diversity of xenobiotic degrading bacteria. Today, it is known that the ability of xenobiotic degradation is widespread among members of the bacterial domain, even some members of the Archaea have this ability. Until now, more than 320 genera of Bacteria and 12 genera of Archaea have been reported to include hydrocarbon-degrading species (Prince et al., 2018). As compiled in the first section of this chapter, the physiology and biochemistry of many microbial pollutant degraders with relevance in groundwater are now fairly well understood. That is, given that these microbes have been isolated and can be cultivated in the laboratory, and that biodegradation in laboratory culture is relevant to pollutant concentrations typically found *in situ*. Over the last 1–2 decades, considerable research efforts have addressed the retransfer of this understanding back to the field, to identify important degrader populations and the controls of their biogeochemical activities directly in contaminated subsurface ecosystems (Lueders, 2017; Meckenstock et al., 2015). This motivation has advanced the canonical field of biodegradation research toward a more ecological and microbiome-based perspective.

One primary approach facilitating this perspective involves the detection of degraders *in situ* by the use of so-called functional marker genes. On the oxidative side, this is relatively straightforward and firstly involves the development of PCR assays for catabolic genes conserved and ideally distinctive for a certain biodegradation pathway. Typically, this will be genes of initial activating enzymes of pollutants, or of the turnover of central metabolites. For aromatic hydrocarbons, this can be illustrated e.g. by work done on substrate-activating mono- and dioxygenases and on ring-opening dioxygenases for aerobic degraders (Junca and Pieper, 2009; Táncsics et al., 2010), or on fumarate-adding and dearomatizing enzymes of anaerobic degraders (von Netzer et al., 2016). The development of primer pairs with required specificity but still optimal coverage of diverse degrader lineages is often a major challenge. Still, the application of such functional marker gene assays to nucleic acids extracted from contaminated aquifer samples offers a number of important advantages over classical laboratory-based enrichment-and-isolation of degraders, and over pure biogeochemical assessment of biodegradation *in situ*. First, functional marker gene sequencing allows to trace degrader populations truly established at a given site, to affiliate them either to known degraders available in laboratory culture, or to provide evidence for as-yet unidentified degraders to be of relevance. Second, when applied in a quantitative manner (in qPCR), spatial distribution patterns or temporal dynamics of degrader populations at sites can be assessed. All insights generated via such marker gene approaches are utile to unravel important drivers and limitations of biodegradation processes at a given site, and to inform population-based monitoring and biostimulation measures in bioremediation.

Also on the reductive side of pollutant transformation, a host of utile functional marker genes is at hand. This especially concerns enzymes involved in the reductive dehalogenation of chlorinated ethylenes, where the terminal vinyl chloride reductase, detoxifying the highly toxic penultimate sequential reduction product of PCE, can be correlated to effective pollution levels and biodegradation potentials (van der Zaan et al., 2010). For other pollutant-reducing reductases, e.g. genes involved in canonical denitrification, a functional interpretation of field monitoring data can be less informative. In example, since many denitrifiers are not obligate but facultative anaerobes, the presence or local abundance of respective functional marker genes (e.g., the dissimilatory nitrite reductase (Yan et al., 2003)) may not be directly correlated to potential or actually ongoing denitrification in groundwater. In a general notion, the more strictly a certain gene product is associated with a specific pollutant-attenuating function, the more utile the respective functional marker gene is in bioremediation research. Beyond direct marker gene sequencing and qPCR of field samples, respective catabolic and respiratory gene patterns can also be targeted in metagenome mining, or genome bins assembled therefrom. This can produce evidence for a potential involvement of yet unidentified or uncultivated microbial lineages in pollutant degradation in the field.

A second, not gene-targeted strategy to detect specific pollutant degraders in contaminated aquifer samples relies on the use of labeled substrate queries. In what is called "stable isotope probing" (SIP), typically ^{13}C-labeled pollutants are exposed to complex degrader microbiomes, mostly in laboratory microcosms, with the idea of an assimilatory labeling of the microbes most actively involved in pollutant catabolism. A density- or mass-dependent resolution of biomarkers such as DNA, RNA or proteins of active degraders from unlabeled backgrounds then allows to unambiguously identify microbial lineages involved in a given biodegradation process, even if previously unknown or uncultivated, and even if no à-priori knowledge on catabolic routes involved is available. The SIP approach has been widely applied to unravel hydrocarbon-degrading microbial key-players in groundwater (Lueders, 2017; Vogt et al., 2016). That said, the approach also comes with its weaknesses, requires laboratory incubations or elaborate labeling microcosms deployed in the field, and a comparably high concentration of pollutants for efficient assimilatory labeling. This clearly limits its applicability to reductive pollutant degradation processes, or to the degradation of micropollutants degraded in a co-metabolic manner (Fenner et al., 2021). Still, no matter which experimental or analytical strategy is chosen, a successful detection and identification of the microbes involved in biodegradation at a contaminated site is always a prerequisite for the further delineation of their ecophysiology and ecology *in situ*.

Bottlenecks of pollutant degradation

One of the most paramount objectives of understanding degrader ecology in the field is the unraveling of the limitations of biodegradation processes *in situ* (Fig. 3). Aquifers contaminated with pollutants subject to oxidative biodegradation are often heavily overloaded with these electron donors, in a habitat, which would otherwise be mostly oligotrophic (Griebler and Lueders, 2009). This reductant overload typically exceeds local electron acceptor availability, making the replenishment of suitable electron acceptors for microbial pollutant oxidation one of the primary limitations of catabolic biodegradation in groundwater (Lueders, 2017; Meckenstock et al., 2015). Within contaminated aquifers, this typically results in highly reduced plumes of organic pollutants transported from the source area by groundwater flow, surrounded by zones of elevated biodegradation activities and degrader abundance at the plume fringes (Meckenstock et al., 2015). These are a result of the absence of efficient turbulent mixing in groundwater, and the very limited mixing by transversal dispersion and diffusion being the only mechanisms of sustainably replenishing both dissolved electron donors (from inside the plume) and acceptors (from outside) to degrader populations established in these "hot zones" (hot spots would not be correct in a 3D conception). Stakeholder measures aimed at enhancing natural attenuation at a given site should optimally capitalize on an understanding of both, the physicochemistry and the microbiology of the contaminated system. E.g., the injection of electron acceptors such as nitrate or oxygen into a plume of petrochemicals may be of limited use, if the dominant degraders established at the site belong to iron-reducing lineages.

Vice versa, electron donor supply is often a primary limiting factor for the reductive elimination of oxidized pollutants such as chlorinated solvents. Most organohalides-respiring bacteria rely on electron donors such as molecular hydrogen and other fermentation products, resulting in the introduction of cheap and fermentable organics such as molasses, or reactive barriers with

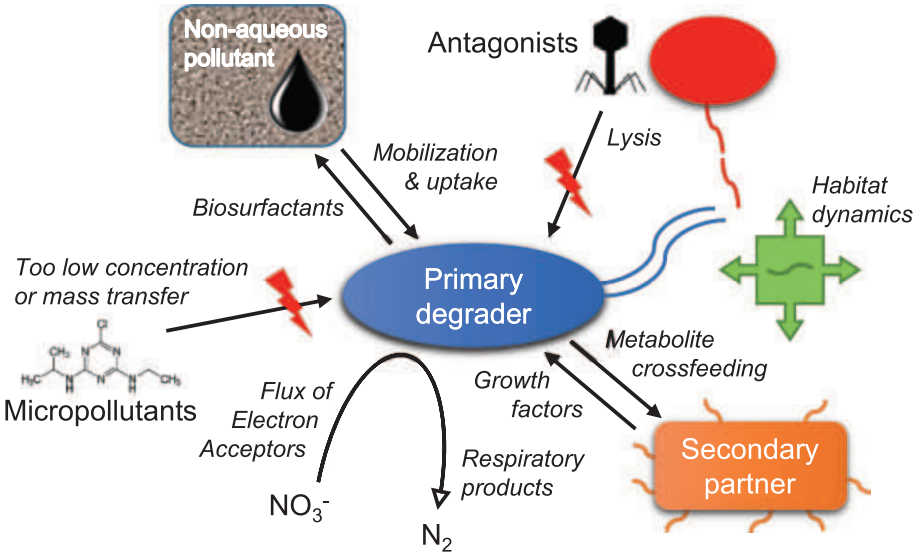

Fig. 3 Summary of key ecological factors that can positively or negatively influence biodegradation activities of organic pollutants by aquifer microbes.

hydrogen-releasing zero-valent iron into contaminated aquifers to stimulate degraders (Kocur et al., 2016). However, since hydrogen and other fermentation products are also attractive to many other anaerobic microbes in aquifers, reductive dehalogenation will typically only be efficient at comparably low redox potentials (<−250 mV), when other electron acceptors are mostly depleted.

Next to the supply of redox partners for pollutant turnover, access to and bioavailability of the pollutant itself can also represent a major limiting factor for biodegradation. This becomes especially apparent where (a) pollutants are present at high mass loads, but hardly water soluble, or (b) when pollutants are present at very low concentrations (in the ng–μg L^{-1} range), as discussed above. In the first case, as known also from natural oil reservoirs (Head et al., 2006), many hydrocarbon oxidizers can release biosurfactants to mobilize and internalize small micelles of non-aqueous phase liquids such as mineral oil. However, this strategy will be viable for degraders mostly in diffusion- and transport-limited microenvironments, such as within biofilms or the micropores of aquifer sediments. Vice versa, at low pollutant concentrations, the limitations of efficient mass transfer into the cell and cellular maintenance energy demands have been shown to cease the biodegradation of atrazine by *Arthrobacter aurescens* TC1, a well-known aerobic pesticide degrader, at the limits of ∼10 μg L^{-1} and below (Kundu et al., 2019). The further exploration of the adaptive strategies of degraders in the degradation of anthropogenic pollutants at limitingly low concentrations represents another prime challenge of environmental microbiology today.

Ecological adaptations and interactions within degrader microbiomes

While many of the factors influencing degrader ecology discussed above relate to habitat characteristics and reactant fluxes, there is also important ecological, population- or community-level adaptations that influence biodegradation outcomes (Fig. 2). Wherever a natural ecosystem is first exposed to a new incoming pollutant of anthropogenic origin, extant microbiomes will react by selecting for microbes capable of capitalizing on the new substrate, either as electron donor or acceptor, and under prevailing habitat conditions. Thus an enrichment of pollutant degraders within total microbiomes will become apparent especially in habitats with complex or highly concentrated contamination scenarios. The time scales for such adaptations to occur, however, will depend on the selective pressure and the natural background of microbes with a respective catabolic or respiratory capacity in the system before contamination, or on the influx of such organisms by organismic dispersal. In line with the postulate of Baas Becking, "Everything is everywhere, but the environment selects" (de Wit and Bouvier, 2006), it can be assumed that for all anthropogenic pollutants, there are natural sources or at least natural substrate analogs, which have resulted in the evolution of respective biodegradation pathways long before man-made pollution. Still, evolutionary processes within contaminant-degrading microbiomes have been reported and can result in the emergence of degradative enzymes with altered functionality, or which are newly acquired and integrated into its metabolism by a given strain. Many of these adaptations have been associated with the mobilization and redistribution of auxiliary functions within complex communities under contaminant exposure, resulting in novel recombinations of previously evolved catabolic functions and pathways in newly emerging degraders (van der Meer, 2006). Only rarely, such mechanisms may result in the emergence of completely novel catabolic functions with relevance to ground- and drinking water quality. One recent example may be the emergence of catabolic capacities for the degradation of acesulfame in wastewater treatment, a widely used artificial sweetener which had long been considered to be persistent in the water cycle (Kleinsteuber et al., 2019).

But even if the oxidative or reductive routes for the elimination of a given pollutant are known for specific microorganisms, these are present within a pollutant-exposed aquifer microbiome same as the needed reactants, this does still not imply that

biodegradation is always efficient. Adaptations and interactions within degrader microbiomes can also involve community-level responses to abiotic habitat dynamics. In example, a transient cease of contaminant degrading activities and a subsequent switching between dominant populations of sulfate-reducing toluene degraders has been reported upon hydrological fluctuations of the groundwater table and connected rearrangements of the redox zonation of a comprehensively characterized BTEX plume (Pilloni et al., 2019). Furthermore, in anoxic groundwater, pollutant degradation is often a community effort, involving essential metabolic interactions between different members of a degradative consortium, such as the mutual provisioning of metabolites and enzymatic cofactors for biodegradation (Fig. 2). In example, such aspects have been elaborately demonstrated for microbial interactions between primary pollutant degraders, secondary metabolite consumers, and even bacterial necromass scavengers in a benzene-degrading, sulfate-reducing enrichment culture from groundwater (Taubert et al., 2012). Similar interactions between primary hydrocarbon-oxidizing fermenters and methanogens as their syntrophic partners have long been established for methanogenic hydrocarbon degradation. Moreover, the activity of organohalide-respiring bacteria can essentially dependent on appropriate corrinoid cofactors of reductive dehalogenases to be provided by associated microbes within dechlorinating consortia (Yan et al., 2016). These examples illustrate that within contaminated aquifers, microbial pollutant degradation is often more a community effort than the activity of a single microbial population.

Beyond such mutualistic microbial interactions in pollutant degradation, antagonistic biological interactions can also shape contaminant degrading bacterial communities. As an example, members of the still enigmatic candidate phylum *Saccharibacteria* are widely distributed and have also been detected in contaminant degrading microbial communities (Figueroa-Gonzalez et al., 2020). These only 200–300 nm ultra-small bacteria have an extremely reduced genome (~1 MB) lacking the capacity of de novo biosynthesis of several important building blocks of the bacterial cell. They seem to be obligate host-parasitic epibionts, thriving on the surface of microbial cells and disrupting their hosts to consume released cellular compounds. The impact of such antagonistic microbial interactions on pollutant-degrading populations in contaminated aquifers is not at all understood, but subject to ongoing scientific investigation. Taken together, the relevance of such ecological controls of and interactions within groundwater pollutant degraders may still be vastly underestimated.

Conclusions

In summary, the extraordinary importance of understanding groundwater microbiomes for the protection and sustainable use of our ground- and drinking water resources is clearly apparent. For many present and future problems in drinking water supply, such as increasing pollution with nitrate and the spread of micropollutants, solutions may be offered via the modulation and harnessing of groundwater microbiomes, possibly upstream of drinking water wells. Also for currently still uncertain and unregulated hazards in our water cycle, such as microplastic pollution, a microbial perspective may contribute to solutions. Even at sites highly contaminated with legacy contaminants, groundwater microbiology has provided sometimes surprising new insights into the control of degradation processes and the degraders involved. A more precise understanding of these degrader populations and their activities and ecology *in situ* will be key to advance current measures and future options for protecting our groundwater resources.

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Epikarst: An Important Aquatic and Terrestrial Habitat

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Aquifer A groundwater reservoir, usually a rock of high permeability capable of delivering water to wells or springs.
Chao estimates Estimates of total species richness based on the abundance or incidence of species occurring in one and two samples.
Hypotelminorheic A persistent wet spot, a kind of perched aquifer; fed by subsurface water in a slight depression in an area of low to moderate slope; rich in organic matter; underlain by a clay layer typically 5–50 cm beneath the surface; with a drainage area typically of less than 10,000 m^2; and with a characteristic dark color derived from decaying leaves which are usually not skeletonized.
Karst A terrane, generally underlain by limestone or dolomite, in which the topography is chiefly formed by the dissolving of rock, and which may be characterized by sinkholes, sinking streams, closed depressions, subterranean drainage, and caves.
Milieu souterrain superficiel (MSS) Interconnected cracks and crevices in the superficial layer of rocks, in scree slopes and similar habitats, usually covered with soil or vegetation.
Percolation water Autochthonous karst water which permeates directly through karst limestone without using a surface watercourse.
Recharge The process of addition of water to the saturated zone.
Secondary porosity Porosity created after rock formation due to fracturing, dissolution, etc.
Stygobiont Obligate, permanent resident of aquatic subterranean habitats.
Stygophile A species that completes its entire life cycle in subterranean waters but can also complete its entire life cycle in surface waters.
Vadose zone The zone above the water table in which water moves by gravity and capillarity. Water does not fill all the openings and does not build up pressures greater than atmospheric.

Introduction

Since its identification as a distinct feature of the karst landscape nearly 50 years ago, epikarst has drawn increasing attention from both hydrogeologists and biologists. It is an important component of most if not all karst regions, and is the source of significant

fraction of the subterranean biodiversity of many regions. We first briefly summarize the physical and hydrological aspects of epikarst, and then turn to epikarst communities.

Hydrogeological perspective

Epikarst as a perched aquifer

Epikarst was first described, studied and named by Mangin (1973), Bakalowicz et al. (1974), and Williams (1983) as the uppermost zone of karst that served as a perched aquifer, and among other things, providing an explanation of the persistence of cave streams during periods of drought. While perched above the major aquifer, it can have a large impact on water recharge and quality (Trček, 2007). Many hand dug wells, now primarily of historical interest, tapped into epikarst. In many road cuts and quarries, it forms an obvious top to the rock layer (Fig. 1), but perhaps not surprisingly, epikarst is difficult to precisely define. Participants in a workshop sponsored by the Karst Waters Institute on epikarst (Jones et al., 2004) decided on the following definition, which also illustrates some of the complexities of epikarst:

> Epikarst is located within the vadose zone and is defined as the heterogeneous interface between unconsolidated material, including soil, regolith, sediment, and vegetative debris, and solutionally altered carbonate rock that is partially saturated with water and capable of delaying or storing and locally rerouting vertical infiltration to the deeper regional, phreatic zone of the underlying karst aquifer.

The standard terminology is that water moving vertically out of the epikarst is percolating water, and the entire zone above the water table is the vadose zone. In a study of three German caves, using tritium as a dating method, water was retained in epikarst for one to 3 years (Kluge et al., 2010). While residence times certainly vary more widely than this, it shows the important feature of epikarst—it retards the downward movement of water.

Berthelin and Hartmann (2020) emphasize the diffuse nature of epikarst recharge, and explicitly do not include recharge through sinkholes and stream losses (swallets), although the Karst Waters Institute definition does not seem to exclude this direct recharge. A sketch of the epikarst is shown in Fig. 2.

The epikarst zone is also a very active zone of carbonate dissolution (Berthelin and Hartmann, 2020). The transformation of organic matter into CO_2 in the soil is the source of acidification and hence dissolution. The structure and thickness of epikarst is greatly influenced by soil conditions.

Another way to conceptualize epikarst is as a series of very small drainage basins. Kogovšek (2010) showed that the area drained in some epikarst drips in Postojna Planina Cave System in Slovenia was between 0.1 and 245 m^2, depending on both the year of measurement and the particular drip. The areas are not necessarily contiguous but it is useful as a way of scaling the system. Another small scale perched aquifer, the hypotelminorheic, which occurs at very shallow depths and underlain by clay, is a non-karst equivalent of epikarst, and a habitat that also harbors species specialized for subterranean life in small basins (less than 1 ha in size in Rock Creek Park in Washington, D.C., Keany et al., 2018). Basins are better defined but shallower in the hypotelminorheic than in the epikarst.

Fig. 1 Photo of an Acme Quarry in Greenbrier County, West Virginia. Epikarst here is between 4 and 10 m thick, generally becoming thicker to the right. Photo by William K. Jones, used with permission.

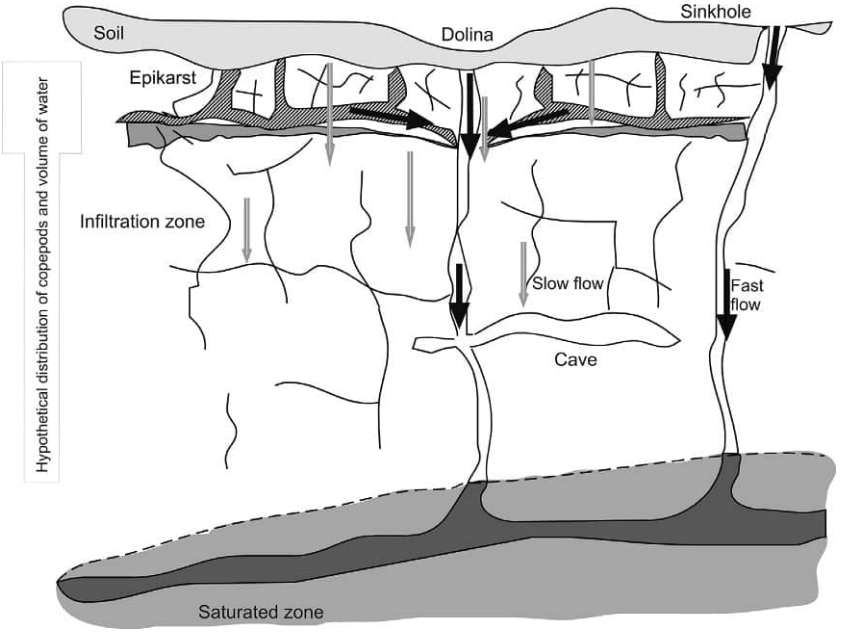

Fig. 2 Conceptual model of epikarst. Gray arrows indicate the direction of diffuse water flow and black arrows are faster flow. Some authors do not include the faster flow as part of epikarst. From Pipan T (2005). *Epikarst—A Promising Habitat*. Ljubljana, Slovenia: Založba ZRC, used with permission.

Physical structure of epikarst

Secondary porosity, as a result of carbonate dissolution is high, perhaps as high as 30% according to Williams (2008) or 10% according to Klimchouk (2004). The epikarst is rarely open enough to be enterable by humans, but some authors include upper level vadose cave passages only a few meters from the surface (Bichuette and Trajano, 2004; Fong, 2004). There are some cases where the epikarst layer becomes more open and uncovered, such as the stone forests of China (Williams, 2008). The depth of epikarst varies with soil and rock conditions, but Klimchouk (2004) states that it can be up to 15 m deep. According to the models of Gabrovšek (2004), it is nearly universal in its occurrence. The boundary between epikarst and the percolation zone can be gentle or abrupt (see Fig. 1).

Biological perspective

Epikarst as habitat

Although the term epikarst was first used in 1973, earlier biological studies included the epikarst fauna. Racovitza (1907) pointed out the cave-adapted organisms commonly occur in cracks and crevices, and that cracks and crevices may be the primary habitat of many species. Not all cracks and crevices are part of the epikarst, because they occur in the vadose and phreatic zones as well, but at least some of Racovitzan cracks and crevices belonged to the epikarst. It was the pioneer of ecosystem studies in karst areas, Raymond Rouch (1986), who demonstrated that zones containing spots of permanent water-saturation (what we now call the epikarst) occur above caves in the Baget basin in France, and harbor an abundant and diverse fauna. Other French biologists have studied the epikarst as well, but in general it was part of a more general study of the fauna of small interstitial habitats, including the vadose zone and the hyporheic zone (e.g. Delay, 1968; Gibert, 1986). Although little known, Petkovski (1959), working in the Dinaric karst, was an early pioneer who observed stygobiotic copepods in caves with no water aside from percolating water accumulating in drip pools. He called the small water filled depressions in cave walls the "realm of Parastenocarida." Brancelj's (2002, 2015) discovery of a rich copepod fauna in drip pools in the shallow Slovenian cave Velika Pasica, which has no other water, but with relatively few reproducing individuals, led him to conclude that reproduction was occurring in small cracks around the cave.

Sampling the epikarst fauna

Generally, it is impossible to sample directly in the epikarst itself because the solution holes and crevices are not large enough to enter. However, there are circumstances where caves are so shallow that they are either directly in or directly below the epikarst zone, depending on one's definition of epikarst. For example, Knapp and Fong (1999) used drip pools that drained the epikarst in a very shallow section of Organ Cave, West Virginia, to do a mark-recapture study of an epikarst dwelling amphipod, *Stygobromus emarginatus*.

Until the development of a device for sampling dripping water (Pipan, 2005, see below), the aquatic fauna was known exclusively from drip pools. After individuals fall from epikarst into drip pools, they may reproduce and establish populations. Copepods and other microcrustacean routinely fall out of epikarst because they are dislodged from the substrate in a manner analogous to particle mobilization in the water column (Hjulstrom curves). This process probably differentially dislodges smaller organisms (see Pipan and Culver, 2007 for details).

Brancelj and Pipan (Pipan and Brancelj, 2001; Brancelj, 2004; Pipan, 2005) developed a technique, while not sampling the epikarst directly, did sample dripping water continuously with the potential for measuring water volume as well. In their sampling device, water from a ceiling drip is directed via a funnel into a 500 ml rectangular filtering bottle fitted on two sides with plankton netting of 60 μm mesh size, and the filtering bottle is placed within a sampling container (Fig. 3). Each sampling container has a drain 3 cm from its base such that collected animals and a small amount of water remain in the filtering bottle while most of the water passes through the filtration unit. Samples, which typically have a volume of about 50 mL, are preserved in either formalin or alcohol, formalin having the advantage of requiring less volume of liquid. Samples are then sorted and identified in the laboratory. Pipan and Culver (2007) provide guidelines for how many such filters need to be used and for how long in order to sample completely the epikarst fauna.

Aquatic fauna

The epikarst fauna of a hotspot cave in Spain

Ojo Guareña is a large (>110 km) cave in Spain and also one of the most biodiverse caves in the world with 187 aquatic species, 49 of which are stygobionts (Camacho and Puch, 2021). The epikarst fauna, known only from the repeated sampling of 10 drip pools in the cave is likewise biodiverse (Camacho et al., 2006). The drip pool fauna, derived from the epikarst, contained a total of 53 species, 15 of which were stygobionts (Table 1), approximately 30% of the entire stygofauna of the cave. The data for pools is almost certainly an underestimate of the total epikarst fauna, based on Pipan et al.'s (2010) analysis of Slovenian cave data which showed that drips contained on average two more stygobiotic copepod species than the associated pools. In any case, the fauna is rich and highly endemic. No figures on the percentage of single cave endemics are present in the entire stygofauna, but it is 67% for epikarst pool stygobionts based on the Slovenian cave data. Camacho et al. (2006) found that pools with carbonate oversaturation, low pCO_2, and overall stability had the most stygobionts. Crustaceans, especially copepods had the most stygobionts, and copepods have been more intensively studied than other components of the epikarst fauna.

The copepod fauna – Patterns of biodiversity

Epikarst copepods are the most diverse and best studied group, although the best studied cases have been limited to Italy, Romania, Spain, Slovenia, and the United States (Table 2). While the numbers may seem low to the non-specialist, these species numbers often rival or even exceed the number of aquatic species specialized for other cave habitats. Especially impressive in this regard is Županova jama (Table 2; Blatnik et al., 2020) with 13 copepod species. A total of 10 copepod species were found in a single drip in

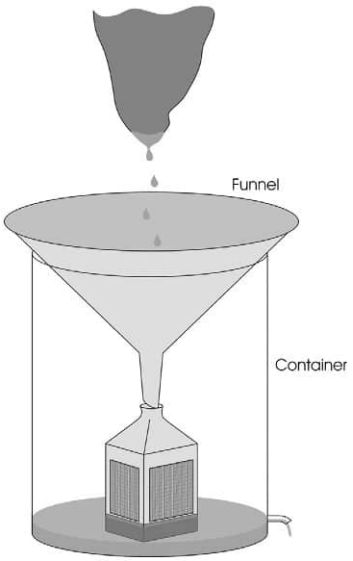

Fig. 3 Diagram of filtering device to continuously collect invertebrates from drips. From Pipan T (2005). *Epikarst—A Promising Habitat.* Ljubljana, Slovenia: Založba ZRC, with permission.

Table 1 Species list from Ojo Guareña and pools in Ojo Guareña.

	Ojo Guareña			*Ojo Guareña pools*			
	Total	*Stygobionts*	*Stygophiles*	*Total*	*Stygobionts*	*Stygophiles*	*Endemics*
Rotifera	1	0	1	0	0	0	0
Cnidaria	1	1	0	1	1?	0	0
Nematoda	1	?	?	0	0	0	0
Turbellaria	5	1	0	2	1	0	0
Hirudinea	3	1	0	0	0	0	0
Tardigrada	13	0	0	4	0	0	0
Oligochaeta	49	5	8	15	2	2	1
Mollusca-Gastropoda	11	2	1	1	0	0	0
Mollusca-Bivalvia	5	0	0	2	0	0	0
Crustacea-Cladocera	1	0	0	0	0	0	0
Crustacea-Ostracoda	22	8	9	7	2	0	2
Crustacea-Copepoda	37	9	12	16	5	0	3
Crustacea-Amphipoda	8	4	0	0	0	0	0
Crustacea-Isopoda	3	2	1	2	2	0	2
Crustacea-Bathynellacea	7	7	0	2	2	0	2
Acari-Limnohalacarida	1	1	0	1	1	0	0
Acari-Hydrachnidia	19	8	1	0	0	0	0
Total	187	49	33	53	15	2	10

Data summarized from Camacho et al., 2006 and Camacho and Puch, 2021.

Table 2 Number of obligate subterranean dwelling copepod species found in epikarst drips or pools.

Country	*Cave*	*Number of epikarst stygobiotic copepod species*
Italy	Grotta A del Ponte di Veja	4
	Covolo della Croce	3
	Grotta di Roverè Mille	2
Romania	Peştera Ciur Izbuc	4
	Peştera Ungurului	3
	Peştera Vadu Crişului	2
	Peştera cu Apă din Valea Leşului	2
	Peştera Doboş	2
Slovenia	Županova jama	13
	Škocjanske jame	8
	Pivka jama	8
	Dimnice	8
	Črna jama	8
	Velika pasica	7
	Zguba jama	6
	Postojnska jama	4
	Jama pod Babjim zobom	3
	Pološka jama	3
	Zadlaška jama	2
	Snežna jama	2
	Huda luknja	2
Spain	Ojo Guareña	5
United States	Organ Cave	7

Modified from Blatnik M, Culver DC, Gabrovšek F, Knez M, Kogovšek B, Kogovšek J, Liu H, Mayaud C, Mihevc A, Mulec J, Năpăruş-Aljančič M, Otoničar B, Petrič M, Pipan T, Prelovšek M, Ravbar N, Shaw T, Šebela S, and Zupan Hanja N (2020) Changing perspectives on subterranean habitats, In Knez M, Otoničar B, Petrič M, and Pipan T. *Karstology in the Classical Karst*. pp. 183–205. Gland, Switzerland: Springer Verlag.

this cave (Pipan, 2005; Pipan et al., 2018). Overall, the median number of copepod species for the data in Table 2 is 4, and most of the species rich caves are in Slovenia and Spain, and most of the species poor caves are in Italy and Romania.

Although the discovery and description of the epikarst fauna are in the very beginning stages in most regions, recent taxonomic work (Table 3) suggests a rich, largely undescribed fauna, and that this fauna is global in its distribution. Of the 21 species of epikarst copepods described since 2000, 10 are from Thailand (and one from Vietnam), suggesting that tropical epikarst may also

Table 3 List of copepod species from epikarst water taxonomically described in the last 20 years.

Species	*Cave/country*	*Year of description*
Morariopsis dumonti Brancelj	Mala pasjica, Slovenia	2000
Parastenocaris andreji Brancelj	well bore, Slovenia	2000
Paramorariopsis irenae Brancelj	Letuška jama, Slovenia	2006
Elaphoidella tarmani Brancelj	Velika pasjica, Slovenia	2009
Elaphoidella millennii Brancelj	Velika pasjica, Slovenia	2009
Elaphoidella namnaoensis Brancelj, Watiroyram & Sanoamuang	Tham Yai Nam Nao Cave, Thailand	2010
Bryocamptus (*Rheocamptus*) *stillae* Cottarelli & Bruno	Grotta Conza, Italy	2012
Parastenocaris diversitatis Cottarelli & Bruno	Grotta Conza, Italy	2012
Bryocyclops maewaensis Watiroyram, Brancelj & Sanoamuang	Tham Nam Phar Ngam Cave, Thailand	2012
Bryocyclops maholarnensis Watiroyram, Brancelj & Sanoamuang	Wat Tham Maholarn, Thailand	2015
Elaphoidella thailandensis Watiroyram, Brancelj & Sanoamuang	Tham Khun Cave, Thailand	2015
Elaphoidella jaesornensis Watiroyram, Brancelj & Sanoamuang	Tham Phar Ngam Cave, Thailand	2015
Elaphoidella sanoamuangae Watiroyram & Brancelj	Payanakarst Cave, Thailand	2016
Stammericaris destillans Bruno & Cottarelli	Molara Cave, Italy	2017
Elaphoidella paraaffinis Watiroyram, Sanoamuang & Brancelj	Phra Kayang Cave, Thailand	2017
Elaphoidella ligorae Watiroyram, Sanoamuang & Brancelj	Khao Plu Cave, Thailand	2017
Siamcyclops cavernicolus Boonyanusith, Sanoamuang & Brancelj	Chom Phon Cave, Thailand	2018
Metacyclops thailandicus Boonyanusith, Sanoamuang & Brancelj	Khao Bin Cave, Thailand	2018
Pseudograeteriella longiaesthetascus Sanoamuang, Boonyanusith & Brancelj	Thien Duong, Vietnam	2019
Cottarellicaris sanctiangeli Bruno & Cottarelli	Grotta Superiore di Sant'Angelo, Italy	2020
Stammericaris vincentimariae Bruno & Cottarelli	Grotta dello Scoglio, Italy	2020
Proserpinicaris specincola Bruno & Cottarelli	Grave Grubbo, Italy	2020

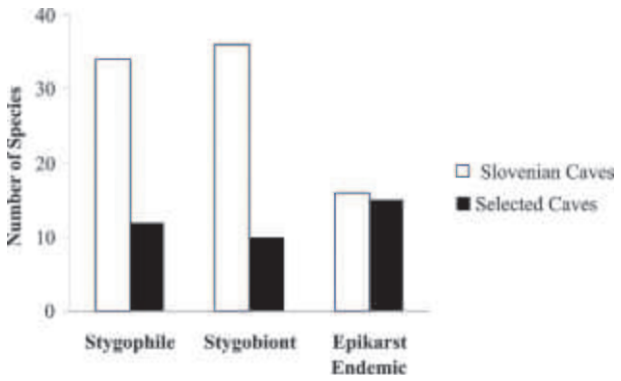

Fig. 4 Relative contribution of within drip (α-diversity), among drip, among cave, and among region (all β-diversity) to the overall diversity of 30 Slovenian epikarst copepod species, relative to random expectation. From Pipan T, Culver DC, Papi F, and Kozel P (2018) Partitioning diversity in subterranean invertebrates: The epikarst fauna of Slovenia. *PLoS One* 13: e0185991.

have a rich fauna (Table 3). Even in the case of relatively well studied Slovenia and Italy, 11 new species have been described from these two countries since 2000.

At the regional scale within Slovenia, the Dinaric karst had the richest epikarst fauna, with 25 copepod species, compared to 5 for the Alpine karst, and 3 for the Isolated karst (Pipan et al., 2018). A similar pattern is present with the aquatic and terrestrial cave fauna, but it must be noted that the Dinaric karst is much more thoroughly sampled for all the subterranean fauna. Overall, the epikarst copepod diversity is largely variable between sites, with regional differences (β-diversity) accounting for 60.9% of total richness, richness between caves in a region accounted for 19.7%, richness between drips in a cave 9.4%, and within drip richness (α-diversity) only 9.9% (Pipan et al., 2018, Fig. 4). The between-site diversity was largely due to replacement of species geographically (not surprising given the small ranges of many epikarst species) but nestedness (the occurrence of hotspots) was important as well (as evidenced by the hyper-diverse drip in Županova jama).

Even at the level of different drips within a cave, distances that range from 1 to 100 m reveal very high levels of heterogeneity. Hotspot caves like Županova jama are hotspots because of only a handful of drips (Table 4), and this heterogeneity has proven difficult to explain, or at least to draw general patterns. A number of authors have sought explanations, typically through Canonical Correspondence Analysis (CCA). A striking example is the negative correlation of the presence of most epikarst copepods with

Table 4 Distribution of number of epikarst copepod species per drip in 13 Slovenian caves.

	Number of species in individual drip											
	0	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*Cave total*
Črna jama			2	1		1	1					8
Dimnice		2	1			1		1				8
Huda luknja	9	2	1									2
Jama pod Babjim zobom	1	2		2								3
Pivka jama			1		3		1					8
Pološka jama		2	2	1								3
Postojnska jama	6	3	1									4
Snežna jama	2		3									2
Škocjanske jame		1		3		1						8
Velika pasica					2		2					7
Zadlaška jama	2	2	1									2
Zguba jama	5	1	1	1	2							6
Županova jama		1			1	2					1	13
Total	25	16	13	8	8	5	4	1			1	30

From Pipan T, Culver DC, Papi F, and Kozel P (2018) Partitioning diversity in subterranean invertebrates: The epikarst fauna of Slovenia. *PLoS One* 13: e0185991.

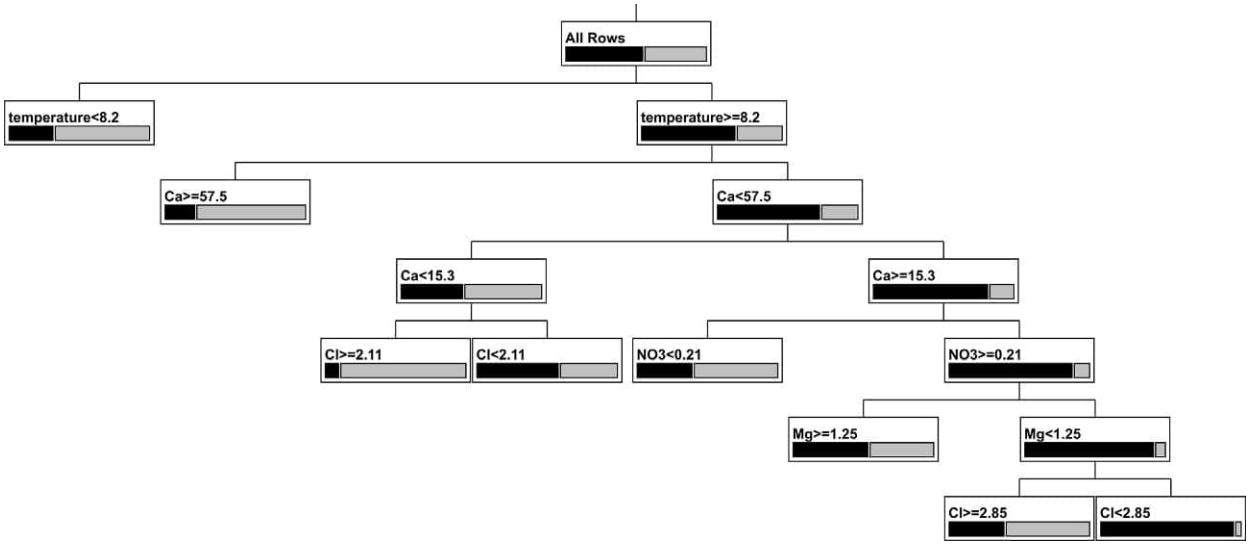

Fig. 5 Classification tree for presence or absence of epikarst copepods in Slovenian caves. The size of the black rectangle is the relative number of empty samples and the size of the gray rectangle is the relative number of samples with copepods. From Pipan T, Christman MC, and Culver DC (2020) Abiotic community constraints in extreme environments: Epikarst copepods as a model system. *Diversity* 12: 269, with permission.

ceiling thickness found by Pipan in her study of six Slovenian caves (Pipan et al., 2006) and the reverse in Zguba jama by Kozel and Pipan (2020). And when there does seem to be some generality emerging, such as the influence of NO_3^- (Pipan et al., 2006; Liu et al., 2017), it is difficult to explain. There are a number of possible reasons for this difficulty (see Moldovan et al., 2018), but one of them may be that there are too many variables that are correlated among themselves. Pipan et al. (2020) used the technique of recursive partitioning and random forests (Strobl et al., 2009) to create a decision tree for the presence/absence of epikarst copepods from drips in the six Slovenian caves originally studied by Pipan (2005). They found temperature, Ca^{2+}, and NO_3^- to be influential (Fig. 5).

The non-copepod aquatic fauna

There is a variety of non-copepod species found in dripping water, that are little studied, but likely are specialized for subterranean life in general or epikarst life in particular. Camacho and Puch (2021) reported that Cnidaria, Rotifera, Turbellaria, Tardigrada, Nematoda, Hirudinea, Acari, Diptera, Gastropoda, Oligochaeta, Ostracoda, Syncarida, Amphipoda, and Isopoda were present in

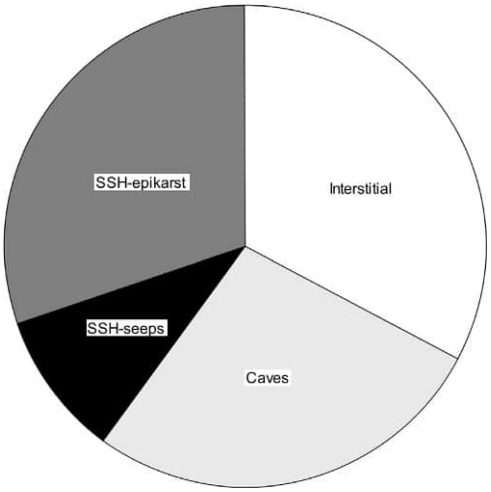

Fig. 6 Subterranean habitats of 125 species of the exclusively subterranean amphipod genus *Stygobromus* from eastern and central North America. From Culver DC and Pipan T (2014) *Shallow Subterranean Habitats. Ecology, Evolution, and Conservation.* Oxford, UK: Oxford University Press, based on data from J. Holsinger.

epikarst pools in Ojo Guareña, Spain (Table 1). In Pipan's (2005) study of Slovenian caves several of these groups were much more common in pools, including Ostracoda, Gastropoda, Oligochaeta. It is not surprising that some of these groups are rare in dripping water, even if they are common in the epikarst, because of their ability to cling to the substrate, such as Gastropoda. Among the non-crustaceans, nematodes and oligochaetes were the most common inhabitants in Ojo Guareña.

In eastern and central North America, one of the most common inhabitants of drip pools are amphipods of the genus *Stygobromus* (Culver and Pipan, 2014). Of 125 species, all are subterranean, but only 34 are known from caves. More are known from drip pools and presumably epikarst, i.e. 38 (Fig. 6). No phylogenetic analysis of the genus is available so far, but many of the epikarst species were previously placed in the genus *Apocrangonyx* (Holsinger, 1969).

Morphological adaptations of crustaceans and amphipods to epikarst

Habitat size is an important constraint and selective force in subterranean environments, and there is an overall correlation between body size and habitat size of subterranean habitats (Pipan and Culver, 2017). Slovenian copepods that are epikarst specialists tend to be smaller than non-specialists, both ones limited to subterranean habitat and ones found in surface habitats (Culver et al., 2009). North American *Stygobromus* amphipods that are epikarst specialists are smaller than cave stream species as well as species from other subterranean habitats with larger habitat size such as phreatic lakes (Fig. 7; Culver et al., 2010).

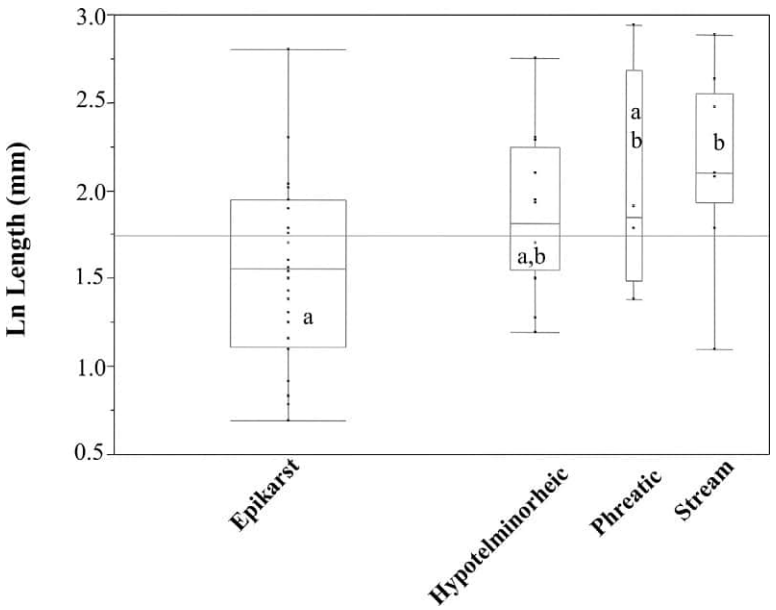

Fig. 7 Box and whiskers plots of ln female body length of species of the amphipod genus *Stygobromus* for epikarst, hypotelminorheic, cave streams, and phreatic habitats in North America. Overall mean represented by the line across the entire. Boxes: 50% of the data, line across each box: group median; whiskers: minimum and maximum values. The widths of the rectangles are proportional to sample size. Dots are individual data points. Plots with the same letter (a or b) do not differ according to the Tukey-Cramer HSD test. From Culver DC, Holsinger JR, Christman MC, and Pipan T (2010) Morphological differences among eyeless amphipods in the genus Stygobromus dwelling in different subterranean habitats. *Journal of Crustacean Biology* 30: 68–74.

Brancelj (2006, 2009) provided a number of intriguing suggestions about uniquely convergent features of epikarst copepods. Working with the genera *Morariopsis* and *Paramorariopsis*, he pointed out that animals living in the epikarst must have some morphological adaptations to prevent or minimize their transport downward. Combined with what he considers a low supply of organic carbon, he proposes that the following convergent features are present in specialized epikarst copepods to avoid being displaced by water flow:

- Reduction in endopodal segmentation to two or one;
- Reduction in number of spines and setae on the terminal segments of both endopods and exopods;
- Reduction in spines and setae on the caudal rami to one terminal seta;
- Tips of the terminal setae of the caudal rami are far apart;
- Short and robust setae on the endopodal lobe of fifth leg (P5) as well as very strong spinules at the base of the caudal rami.

Brancelj (2009) demonstrated that the genus *Elaphoidella* shows similar convergent features, especially the last two features listed above. He also proposed that there is convergent reduction on length of the antennules and that robust setae are probably an adaptation for moving through small spaces in fractured rock as well as a protection against washout.

Terrestrial fauna of epikarst

The terrestrial habitat

Epikarst is primarily considered an aquatic habitat because it was first described as a perched aquifer. However, it is not a permanent aquifer, or at least it is not always water-saturated. Drip samples almost always have some terrestrial species. While a few species may have gotten into the samples from the cave (flying or hopping), most are resident in the epikarst. Huda luknja in Slovenia is the most extreme example of the terrestrial nature of some epikarst. It had more terrestrial individuals than aquatic individuals (Pipan et al., 2008).

Epikarst also has a close connection with the MSS (milieu souterrain superficiel). The MSS has been defined variously since its discovery by Juberthie and his students in the 1970s, generally to become more inclusive of shallow subterranean terrestrial habitats. Mammola et al. (2016) define the MSS as "the underground network of air-filled voids and cracks developing within multiple layers of rock fragments usually covered by soil." The MSS is a very active research area, and Mammola et al. (2016) reported 235 papers on the MSS. While typically considered a non-karst habitat, the MSS, or its equivalent depending on definition, does occur on karst and grades into the epikarst. For example, Pipan et al. (2011) reported on closely adjoining terrestrial epikarst and MSS sites in a deep doline in Slovenia, the bottom of which is the entrance to the cave. The epikarst site, accessible from the surface, was directly connected to the cave while the MSS site was about 25 m distant. The primary difference between the two habitats was that the limestone at the MSS site was no longer solid, but consists of separated rock and boulders (the multiple layers of Mammola et al.'s, 2016 definition). Ortuño et al. (2013) suggested that a major MSS type is alluvial MSS, which is along streams and periodically floods. Environmental conditions in the alluvial MSS are likely very similar to terrestrial epikarst.

Inhabitants of terrestrial epikarst

The most extensive sample of terrestrial epikarst inhabitants comes from Huda luknja in Slovenia (Pipan et al., 2008), where terrestrial species and individuals outnumber their aquatic counterparts (Table 5). A wide variety of groups were found and it seems likely that many of these were soil inhabitants, given the close proximity of soil and epikarst. The aquatic fauna is depauperate, with only two copepod species reported, both species are rare. Either the relative isolation of the cave or the quality of the epikarst in terms of water retention may explain the low species numbers. While unusual with respect to the high numbers of terrestrial species, the near universal presence of terrestrial species suggests they are part of the overall community and worthy of further study.

Critiques of the epikarst concept from the biosciences

While the term epikarst is widely used in the speleological sciences, Sket et al. (2004) argued there is no distinct epikarst fauna. Part of this disagreement echoes back to Šušteršič's (1999) claim that epikarst is just a consequence of the karst erosional cycle, hence unimportant. But part of this disagreement stems from our inability to sample epikarst directly. To summarize the physical setting of epikarst, it rests at the top of the vadose zone, and is the site of primary water storage above the phreatic zone. Water in the epikarst moves laterally within the epikarst, analogous to small drainage basins (see Kogovšek, 2010), and it moves vertically as percolation water. The sampling of drips is the sampling of percolation water that originated from epikarst. There is likely few if any reproducing populations in vertically moving percolation water per se, but there are likely to be small water bodies in the vadose zone below the epikarst that do harbor epikarst populations. Sampling percolating water then samples both epikarst water and any other vadose water. An example of such a non-epikarst habitat are the "*Parastenocaris*" pools described by Petkovski (1959). Because most of the water (i.e., habitat) is in the epikarst, it is likely the most important habitat for animals trapped by percolating waters. It is a major habitat of the vadose zone. There are perhaps no species that never occur outside the epikarst zone, but the majority of populations

Table 5 List of taxa found in 12 epikarst drips during a 1 year sampling in Huda luknja in northeast Slovenia.

Higher Group	*Class*	*Order*	*Genus and/or Species*	*Terrestrial **T** or Aquatic **A***
Acari		Rhabditida	Unidentified	**A**
Annelida	Clitellata	Oligochaeta	Unidentified Enchytraeidae	**A**
			Unidentified Lumbricidae	**T**
Arthropoda	Arachnida	Palpigrada	*Eukoenenia* cf. *austriaca*	**T**
		Araneae	*Troglohyphantes diabolicus*	**T**
		Mesostigmata	Unidentified	**T**
		Oribatida	Unidentified	**T**
	Crustacea	Amphipoda	*Niphargus scopicauda*	**A**
		Ostracoda	Unidentified	**A**
		Copepoda	*Parastenocaris nolli alpina*	**A**
			Bryocamptus balcanicus	**A**
	Chilopoda		Unidentified	**T**
	Diplopoda	Acherosomatida	Unidentified	**T**
			Polyphematia moniliformis	**T**
	Insecta	Collembola	Unidentified Poduridae	**T**
			Unidentified Sminthuridae	**T**
			Unidentified Entomobryidae	**T**
		Diplura	*Plusiocampa* sp.	**T**
		Coleoptera	cf. *Atheta* sp.	**T**
			Laemostenus schreibersi	**T**
			Otiorhynchus anophthalmus	**T**
		Diptera	Unidentified Sciaridae	**T**
			Unidentified Trichoceridae	**T**
			Unidentified larva	**T**

From Pipan T, Navodnik V, Janžekovič F, and Novak T (2008) First studies on the fauna of percolation water of Huda luknja, a cave in the isolated karst of Northeast Slovenia. *Acta Carsologica* 37: 141–151.

are almost certainly in the epikarst. Perhaps a more accurate term for the habitat is vadose macropore, to borrow a term from soil science. However, in our view, adding this term does little except add terminology to a discipline already suffering from an excess of jargon (see Martínez and Mammola, 2021).

Conservation

The protection of epikarst communities poses special challenges (Culver and Pipan, 2014). The main sites of collection for many species are drip pools, although drip pools are often not the primary habitat. The area immediately above known sites (drip pools and drips) is of the utmost importance in any protection scheme. Given the small drainage area of each drip, the population structure of epikarst species is likely to be that of a metapopulation, with subpopulations "blinking" on (colonization) and off (local extinction) (Moldovan et al., 2012). Adequate protection requires protection of the entire landscape of the metapopulation, regardless of whether a particular site currently harbors a population.

Each site, and its protection, has its own idiosyncrasies. Županova jama in Slovenia, the cave with the most diverse epikarst fauna known, is a show cave, with four main galleries with a total length of 682 m. The drips are in the midst of the highly decorated sections of the cave, but not near adjoining tourist trails. It has been a show cave since its discovery in 1926. The land above the cave is forested. In Slovenia, caves cannot be privately owned, but show caves are typically managed by local caving clubs, and this is the case for Županova jama. The land above the cave is privately owned, and the likelihood of logging above the cave is uncertain but logging in this area is typically selective and sustainable, with only a few trees taken at any one time. The cave itself is well protected since all Slovenian caves are protected by Slovenian national legislation, including the 2004 decree on the protection of wild animal species, including species living in caves and subterranean waters, and a 2004 act on cave protection, including restrictions on number of visitors and on amount of collecting.

Another kind of protection is that for Piddling Pit in West Virginia, USA. It has three species of amphipods in drip pools less than 200 m inside the cave—*Stygobromus emarginatus* (Hubricht), *S. nanus* (Holsinger), and *S. parvus* (Holsinger). This is a remarkable assemblage of epikarst amphipods, and no other epikarst site in the state has so many species of *Stygobromus* amphipods. Because of its unique biological characteristics, The Nature Conservancy, a non-governmental conservation organization, purchased the cave entrance in 1993, and fortunately purchased the land above the cave as well. Access to both the largely forested land and the cave are highly restricted.

Conclusion

Epikarst, the fractured and solutionally modified uppermost layer of karst, harbors an often rich aquatic fauna, with many species specialized for existence of this highly heterogeneous, variable habitat. Epikarst copepods may be a significant part of the aquatic fauna, as is the case in Ojo Guareña cave in Spain. Species show a number of morphological modifications, including small body size. Because of difficulties in sampling, the epikarst fauna has only been thoroughly sampled in a few European countries, especially Slovenia, Romania, and Spain. There appears to be terrestrial fauna, likely derived from the soil fauna, but it has been little studied. Because of its proximity to the surface, epikarst and epikarst fauna are highly vulnerable to environmental changes.

Knowledge gaps

- Many more caves will need to be studied before any continental or global pattern emerges.
- A careful study of the taxonomy of terrestrial epikarst species is needed to determine if it is distinct from the deep soil fauna.
- Long term studies of the epikarst fauna from a handful of caves, such as has been done by Pipan (2005) and Brancelj (2015), are likely to yield important insights in the temporal dynamics of epikarst populations.
- Studies of convergent morphology, beyond body size, are needed.

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Relevant websites

General information about karst and karst research.
https://izrk.zrc-sazu.si/en/predstavitev#v—Karst Research Institute ZRC SAZU.
https://karstwaters.org—Karst Waters Institute.
https://speleogenesis.info—SPELEOGENESIS Scientific Network.

The Ecology of Aquatic Cave Environments

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Allopatric speciation (also vicariant speciation, or geographic speciation) A mode of speciation occurring when the ancestors of two or more closely related species became geographically separated in the past, preventing (or drastically reducing) gene flow among them.
Aquifer An underground water body in porous rock, rock fractures/voids/caves or unconsolidated alluvial deposits.
Biospeleology A branch of biology dedicated to the study of organisms that live in caves.
Capillarity A physical phenomenon where water, due to surface tension, rises in small voids/tubes ($<$ 1 mm dimensions).
Chemoautotrophic bacteria Bacteria getting their energy from oxidizing inorganic compounds, like iron, manganese, nitrogen, or sulfur compounds.
Doline Usually, rounded depression on a karst landscape, several tenth of meters in diameter and several meters/tenth of meters in depth; a result of chemical or mechanical dissolution/destruction of limestone; bottom with a layer of soil ("terra rossa"); an entrance into a vertical pit, or sometimes as temporary pool after heavy precipitation.
Drift Animals or organic particles (from plants or animals) transported by water flow, along with inorganic sediment.
Perched aquifer An aquifer which is situated between the main aquifer and the infiltration zone; it is disconnected from the main aquifer below the infiltration zone.
Scrapers Animals, collecting their food from substrate with specialized appendages (mouth parts or swimming legs) in a form of small particles rich in bacteria or mold.
Sinkhole A spot where surface water enters subterranean environment either temporarily (through local depressions after heavy rain) or continuously (permanent streams, rivers).
Source/sink habitats Source habitats support viable populations of stygobionts for long (geological) periods. Sink habitats are places where stygobionts are regularly/accidentally transported from source habitats; cannot reproduce or establish persistent populations and die within a generation.
Stygobionts Obligate dwellers in aquatic subterranean environment; when accidently conveyed to surface environment, they die soon due to light, temperature or predation.
Water flux A volume of water flows per area per unit of time; expressed as liters per square meter per hour ($L\ m^{-2}\ h^{-1}$).

Introduction

For a long time, cave habitats, both terrestrial and aquatic, were considered unfavorable environments (dark, cold, and monotonous), largely devoid of fauna and hosting only few, highly specialized species that have taken refuge there and became prisoners of their habitat (Danielopol, 1992). This view of cave ecology was based on the very first taxonomic descriptions of cave-dwelling

species, such as the olm (*Proteus anguinus* Laurenti, 1768) in the Dinaric Karst (south-eastern Europe) (Aljančič, 2019). This now-famous cave animal was discovered in a Slovenian karstic spring by Johann Weikhard von Valvasor, believing it to be a young dragon. Later, it was scientifically described by Laurenti (1768), who did not recognize it as a cave animal. During the century of research that followed, sampling sites were frequently designated as only "cave" or "spring," alongside with little geographical information (i.e., country, region). It was Emil Racoviță's essay (Racovitza, 1907) that turned the studying of cave biology became a real scientific discipline. The Romanian scientist is considered the founder of biospeleology, and one of the fundamental impediments of modern ecology is named in his honor (the "Racovitzan impediment": Ficetola et al., 2019). The Racovitzan impediment simply states that one cannot describe, map, analyze, and conserve the biodiversity of the environments that are unexplored and unmapped. Caves belong to the least explored environments on Earth. Sampling caves and their spring outlets requires intense fieldwork on small spatio-temporal scale, with hard-to-reach habitats, and often requires advanced caving techniques that further complicate overcoming the Racovitzan impediment (Pipan et al., 2020). Research in the past was mainly devoted to describing or studying the morphological or physiological adaptations of organisms that live in these dark environments, especially loss of eyes and pigments (troglomorphy *sensu* Christiansen, 1962). Nowadays, it is well known, that groundwater-dwelling fauna in caves is rich and the cave-spring continuum has been recognized (Botosaneanu, 1986). In a later paper, Botosaneanu (1998) called springs the "gates of Styx" and from this ancient myth, obligate groundwater-dwelling organisms are named stygobionts.

Caves are widely spread across the Earth's subsurface (Klimchouk et al., 2017). Most of them are formed in sedimentary carbonate rocks (limestone and/or dolomite, i.e., the true karstic environment) although some cave-like formations are common in other geological context too, like lava tubes, sandstones, gypsum formations as well as large crevices in metamorphic or igneous rocks (Gunn, 2004). All limestone/dolomite depositions started in ancient oceans and were later, due to tectonic activity, uplifted to present-day mountain ridges or plateaus, sometimes more than 2000 m above sea level. In this chapter we mainly focus on the true karstic environment, i.e., caves which developed in carbonate rocks. From an anthropogenic point of view, caves are defined as vertical or horizontal channels (pits and galleries) accessible by humans, i.e., spaces large enough to be practicable by human beings. This is a limited, partial vision of the subterranean karstic environment, which comprises two interconnected (eco)systems: terrestrial and aquatic. They consist mainly of very tiny fractures, cracks, and crevices, while caves – accessible to humans – are only a small part of the karstic environment. Undiscovered galleries, as well as galleries filled with sediments from older geological periods, complete the picture of the karstic environment. Present-day caves and karstic springs are only "windows" that open an immense subterranean karstic environment (Culver and Pipan, 2019).

Karstic zones as vertically connected functional systems

Over the last four decades, studies divided the karstic ecosystem into four distinct zones, from the surface to deeper aquifers: (I) epikarstic zone, (II) vadose zone, (III) epiphreatic (= flooded, amphibian) zone and (IV) phreatic zone (Fig. 1; Table 1) (Brancelj and Culver, 2005; Culver and Pipan, 2019). Each of the zones is connected with the surface environment through water

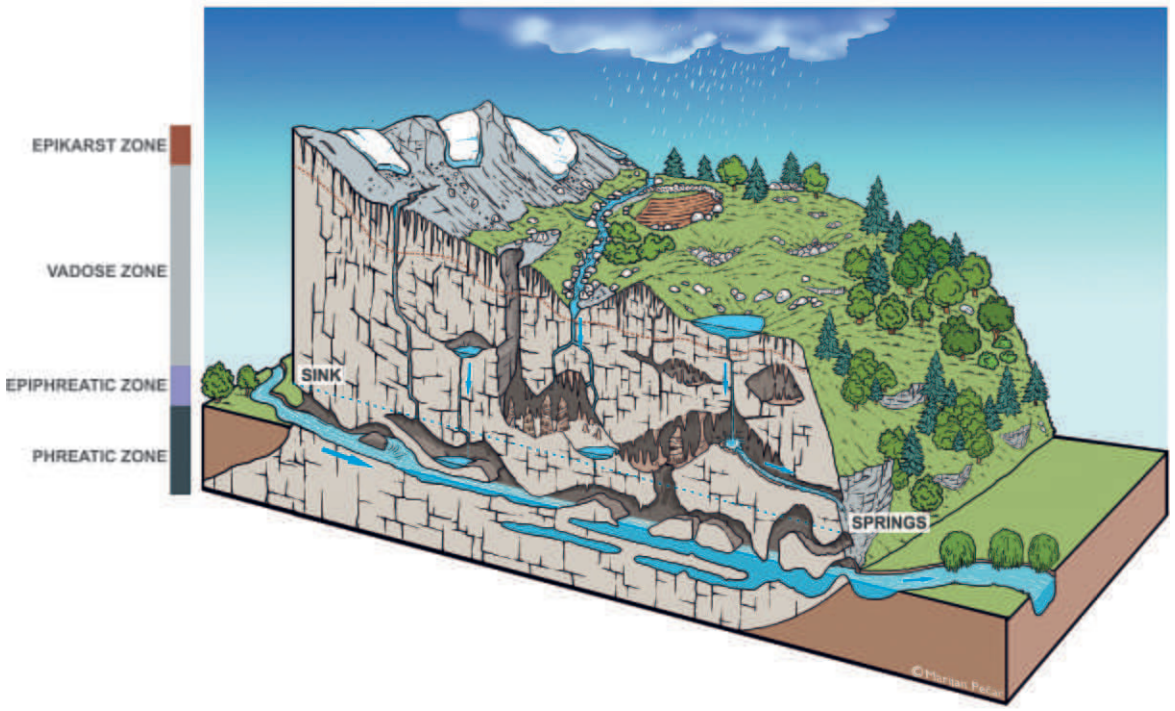

Fig. 1 Cross section through a karst massif with hydrological connections. Author: M. Pečar.

Table 1 Some characteristics of physical environment of the four main vertical zones (= habitats) in the karstic caves, including springs as horizontal connection with surface.

	*Epikarst zone**	*Vadose zone*	*Epiphreatic zone**	*Phreatic zone*	*Springs*#
main source of water	infiltrating precipitation (as rain or snowmelt)	epikarst zone and temporary sinking streams	epikarst and vadose zones, combined with sinking rivers and phreatic zone	epikarst, vadose and epiphreatic zones, combined with sinking rivers and/or sea	depends on their position along the vertical profile of a karst massif; includes also submarine springs
intensity of water flow	depends on weather conditions; single drops or low flow during droughts, intensive or very intensive soon after precipitations (within hours)	depends on weather conditions; low or high flow with some time delay after precipitations (usually hours/ days)	depends on weather conditions; heavily affected by discharge of sinking rivers (in a range of days) and less with infiltrating precipitation	depends on hydrological and hydrostatic conditions in an epiphreatic zone	depends on hydrological conditions in a catchment area and cave hydrological system
water flow direction	prevails vertical direction with some localized oblique and horizontal orientation	vertical in drips; oblique in torrents and streams; combination of riffles and pools	horizontal, with riffles, pools and lakelets; zone of floods	horizontal, as the galleries are completely filled with water	usually oblique or horizontal, with riffles or pools at a mouth; sometimes as a siphon from phreatic zone
water temperature oscillations	correlates with intensity of precipitation and soil temperature; normally in a range of few degrees (°C) around local average of annual air temperature	usually in a range of 1–2 °C around local average annual air temperature	depends on seasonal water discharge from surface rivers and distance from entrance/sink points; can vary by several degrees °C; higher at sink point and lowest near springs	low oscillations; usually in a range of 0.1–1 °C around local average annual air temperature	dependent on discharge and distance from sinking points
space size (maximal diameter)	usually < mm to cm	m or tenth of meters	m or tenth of meters	m or tenth of meters	depends on their position along the vertical profile of the karst massif (mm to meters)
food source for metazoan fauna (other than prey)	POM, bacteria+	POM, bacteria+, guano, dead animals"	POM, bacteria+, guano, dead animals", leaves, twigs	POM, bacteria+	POM, bacteria+

* – ecotone; # – discharge of water from four zones either temporary or permanent; POM – particulate organic matter:" – animals from surface or troglophiles/troglobionts;
+ – includes heterotrophic and chemoautotrophic bacteria.

inlets (sinkholes, crevices) and outlets (temporary or permanent springs), which reflect the hydrological and ecological "fingerprint" of their catchment area. Zones (= habitats) are determined by hydrological, energetic (= food), and biological parameters, including organisms' size and diversity. In the vertical direction, these zones are functionally interconnected through voids and channels of varying dimensions, which determine the physical, chemical, and biological parameters of flowing waters, driven by infiltration rate, volume, and speed of water flow. While cracks and fissures reduce speed and water flux and mainly retain groundwater (capacitive zones), pits, sinkholes, and galleries increase it (conductive zones) (Di Lorenzo et al., 2018).

The epikarst (Bakalowicz, 2019)

It is a thin zone just below the karst surface, extending from several dozens of centimeters to a few meters in depth. It is typically intensively fractured, enhancing the porosity and permeability of the carbonate rock. It is very heterogeneous and usually supports a perched aquifer, where vertical water flow prevails, even when some restricted lateral flow is also present. Flow is fed exclusively by precipitation and thus is very dynamic over hourly, daily, and seasonal scales (Kogovšek, 2010). Precipitation (rain or snowmelt) is collected from a relatively small surface area and directed to a specific drip-point within a cave. The area above each drip-point effectively represents an "island" from an ecological point of view (Brancelj and Culver, 2005; Pipan and Culver, 2013). Water from drip-points is discharged either into galleries, where it accumulates in small pools (from milliliters to tens of liters in volume), or into voids connected to the vadose zone. The living space in the epikarst is small, as crevices and voids are normally in the millimeter scale. This represents the primary, or exclusive, habitat for very specialized aquatic fauna, dominated by Copepoda (Cyclopoida, Harpacticoida), followed by other crustacean orders (Ostracoda, Syncarida), Oligochaeta, and free-living Nematoda, which may drift downwards to the vadose zone (Rouch, 1968; Brancelj, 2002).

The vadose zone (Hopmans and van Genuchten, 2005)

It is located just below the epikarst. Here, water flows through voids and channels with a more stable discharge, even though some trickles may dry-out during periods of no precipitation. This results in pools of drip water, with a volume up to several hundreds of liters, or permanent subterranean streams with riffles and pools, usually associated with compact speleothems such as stalactites and stalagmites. The living space for groundwater animals ranges from millimeters to several meters in size. This zone is controlled by daily precipitation, but with some time delay and a dampening of extreme values. In principle, the vadose zone represents the old and inactive part of a cave, which could be, over long time periods, filled with sediments from soil and deposition processes in sinking rivers or by formation of speleothems as a result of dissolution and deposition within the karstic massifs. This is also the zone usually visited by tourists in the show-caves.

The epiphreatic zone (Audra and Palmer, 2011)

It is also called the amphibious zone or flood zone. From a biological aspect, it is the most intensively studied, because many parts of the galleries are relatively easy to access for the cavers during low water level. An important source of water for this zone is from sinking streams and rivers, which flow through permeable and impermeable slopes entering caves. This zone can oscillate in its vertical extent over several tens of meters (Mihevc, 2004) as a result of differences in the infiltration rate from the surface and in the discharge rate of siphons and offers a virtually unlimited living space for stygobionts. It is characterized by fine sediment deposition (silt and clay mud), sometimes decorated with speleothems. This zone is characterized by seasonal inputs of allochthonous organic material during floods when connectivity with sinking rivers is high. During low water levels, stygobionts from the phreatic zone are trapped in pools, siphons and dead arms of subterranean rivers. When water levels rise, the epiphreatic zone becomes an ecotone between the unsaturated (vadose) and saturated (phreatic) zones.

The phreatic zone (Audra and Palmer, 2011)

It is more difficult to access, usually through natural or artificial wells and boreholes, or by speleodivers and remote-control vehicles. Alternatively, phreatic waters are sometimes accessed through deep-feeding springs. Water quality and discharge as well as the composition of fauna and biodiversity are relatively stable over long time periods, and the living space for stygobionts is unlimited as channels can be up to several meters in diameter and several kilometers in length. Food resources are quite limited but rather constant, except in cases where local surface eutrophication is present, or in phreatic habitats that are connected to sinking river channels (Di Lorenzo et al., 2019; Strona et al., 2019), or sulfidic water layers (Brad et al., 2021). Some phreatic aquifers in karstic caves close to the sea are a mixture of fresh and sea water, forming the so-called anchialine caves. Here voids or channels connect inland aquifers to sea water, and usually a density gradient is established (chemocline), with dense sea water underneath freshwater. The example of this type of habitat are the cenotes in the Yucatan peninsula, Mexico (Beddows, 2004), but similar examples can be found in all continents.

Springs

They are ecotones between subterranean and surface water habitats where surface and groundwater species co-exist. They often appear as tiny seepage-like springs (heleocrene) fed by the unsaturated karstic zone on the slopes of hills, as running springs (rheocrene) or in the valleys as lake-like springs (limnocrene). Like caves, springs can be present in other, non-karstic terrains, too, but with ecological parameters quite different from those on limestone/dolomite rocks (Stoch et al., 2011). Water coming from the karstic massifs is discharged through well-defined springs (usually called resurgences) when limestone rocks encounter alluvial sediments or less permeable terrains (Gibert et al., 2009; Brancelj et al., 2020). Spring ecology is quite specific and intensively studied. In this context, it is noteworthy to mention that they host both surface species, usually dominated by snails, crustaceans, insect larvae, and subsurface stygobiotic species, dominated by snails and crustaceans, rising to the surface from deeper aquifers (Stoch et al., 2016). The hydrology of karstic springs depends on the hydrological dynamics within the karstic massifs, and the dynamics of the discharge of subterranean fauna have been recently studied (Di Lorenzo et al., 2018). During high discharge periods, springs may convey a high number of stygobionts to the surface, from invertebrates to amphibians and fish. Figuratively, loss of groundwater animals was called the "hemorrhage" of karstic aquifer fauna (Rouch, 1970).

Springs connected to the phreatic zone are of different types. Estavelles (or inversacs), depending on weather conditions and seasonality, alternate between serving as sinkholes or true springs. Large karstic lakes and fields (named polje) are frequently fed by this type of springs. Another important category is represented by the Vauclusian springs (named after the famous Fontaine de Vaucluse in France) that originate from deep karstic system. Springs are not limited to continental areas. Several examples of submarine karstic springs (vruljas in the Mediterranean area) are peculiar habitats worth studying. As stygobionts are related to the groundwater that feed karstic springs, their use as hydrological biotracers to identify different aquifers that mix at a spring outlet has been advocated (Mori et al., 2015; Stoch et al., 2016; Brancelj et al., 2020).

Functional structure of the aquatic karstic environment

Structure of karstic habitats

The karstic ecosystem is a very complex three-dimensional system of locally interconnected small voids and fissures on a scale of fractions of millimeters to centimeters in size, as well as larger galleries, accessible by human. The Veryovkina Cave in Abkhazia, Georgia, is the deepest cave in the world (2212 m), followed by the Krubera-Voronja Cave (both located in West Caucasus), that ends in a siphon of phreatic water. The latter has been studied in detail and revealed an interesting subterranean community that lives over 2000 m below the surface, including several groundwater crustaceans described later as new to Science (Sendra and Reboleira, 2012). However, the community there includes both stygobionts and surface species that were transported 2140 m below the surface as drift. As with most caves, even the Krubera ecosystem depends on allochthonous sources of organic carbon originated from the surface. Nevertheless, there are few caves, which are energetically based on chemolithoautotrophic processes and microbial biomass; the most well-known examples are sulfidic caves (Palmer and Hill, 2019; Brad et al., 2021).

Limestone sediments, deposited in marine environments hundreds of millions of years ago, were uplifted to the surface as a result of tectonic activity and orogenesis. In addition, parts were exposed to the terrestrial environment because of the sea-level drop that occurred during the ice-age period. After the retreat of Quaternary glaciers, the sea level rose up to 130 m and lower parts of the caves near the shoreline were re-submerged in sea water, as was the case in several cenotes in the Yucatan, the Blue Hole complex in Florida, or the vruljas along the Mediterranean coasts (Stevanović, 2015). Formation of karstic caves is a result of water activity, including dissolution of carbonate rocks, corrosion, and erosion, i.e., increase of the channel diameter due to sediment transport (sand, stones, and gravel) by water flow. Very deep and long caves are frequently formed as a network of parallel and branched horizontal galleries, sometimes formed in two or three levels on an area of several tens of square kilometers. The galleries accessible for human there could be several tens or even hundreds of kilometers long (i.e., Mammoth cave system, Kentucky) (Buckner, 2019). Each level within these caves reflects different geological periods with different climate and hydrological cycles (Dumitru et al., 2021). Together with these type of caves (called epigenic caves), hypogenic caves were formed by rising, often solutionally aggressive, groundwater (Sendra et al., 2014; Klimchouk et al., 2017) with the most famous examples being sulfidic caves (Sarbu et al., 2018).

Pits and larger crevices act as entry points for relatively large particulate organic matter (POM) and surface organisms into the caves. Small crevices and fissures allow the transport of mainly dissolved organic matter (DOM) and occasionally fine POM, including drift from the epikarst (Pipan and Culver, 2013). Another common and important sources of surface water and organic material into the subterranean environment are sinking streams and rivers connected to the galleries, located at the level of the epiphreatic zone or sometimes directly feeding the phreatic zone. Water discharge varies from a few L sec^{-1} to hundreds of L sec^{-1} depending on rain and snowmelt, and has significant impact due to the considerable transport of POM and DOM.

It is evident that the living space, i.e., the size of fractures/voids/galleries in the subterranean environment, determines the size of animals living in these habitats as well as community structure (Dumnicka et al., 2020). Some of the worm-like organisms (free-living nematodes, flatworms, oligochaetes, and some tiny harpacticoid copepod crustaceans as well) can move easily between narrow spaces in micro-crevice habitats, together with rotifers and protozoans. The same is true for different developmental stages, like eggs or juveniles that can be passively carried through narrow passages by water flow, in contrast to adults, especially those with a rigid exoskeleton. For that reason, large-body representatives of crustaceans (like larger Amphipoda, Isopoda, and Decapoda), cave fish and amphibians can be found only in caves, i.e., in galleries or large springs.

Physical and chemical characteristics of karstic subterranean waters

Karstic subterranean waters are fed by precipitation and sinkholes (Fig. 1). A typical example of a catchment area with subterranean rivers is the network of the Ljubljanica river (Slovenia, Europe), which includes the well-studied Postojna-Planina Cave system (Zagmajster et al., 2021). It is a network of two branches of sinking rivers which enter caves several times (actually 11 times), before finally re-appearing as the Ljubljanica river in a series of springs south of Ljubljana that is part of the Danube river catchment.

Following the paths through the karstic system, water experiences changes in physical and chemical properties. Changes are determined by the distance from the surface as well as by seasonality and endogenous processes. Near the entrance points, water characteristics are defined by epigean parameters but get more uniform in the most remote parts of the karstic ecosystem, i.e., next to the springs. During intensive weather events, "fingerprints" of surface parameters last longer in time but are usually limited to few hours or occasionally days. In distance, they can extend several kilometers from the sink point, but this depends on flux and speed of water flow. During these events, discharge from storms or intensive snowmelt may substantially increase for a short period of time (i.e., hours) by factors of up to 10^1–10^2 in sinking rivers or even up to 10^3 in the epikarst/vadose zone (Kogovšek, 2010; Brancelj, 2015) (Fig. 2).

Carbonate geology defines the water pH in the karstic massif as neutral or slightly alkaline (i.e., pH 7.0–8.5), although there are some oscillations and the presence of aggressive waters (like in sulfidic caves) can turn the pH to acidic, either permanently or only in some seasons. Precipitation may also influence chemical and physical water properties for a short time (i.e., hours), including temperature, electrical conductivity, or the concentration of major ions (Ca^{2+}/HCO_3^-, Mg^{2+}, NO_3^-, SO_4^{2-}, . . .). This happens over a short distance of a few meters in the vertical direction in the epikarst zone (Kogovšek, 2010; Brancelj, 2015). Changes during intensive rain/snowmelt events are a result of the "piston effect", as incoming water from the surface push out resident water rich in

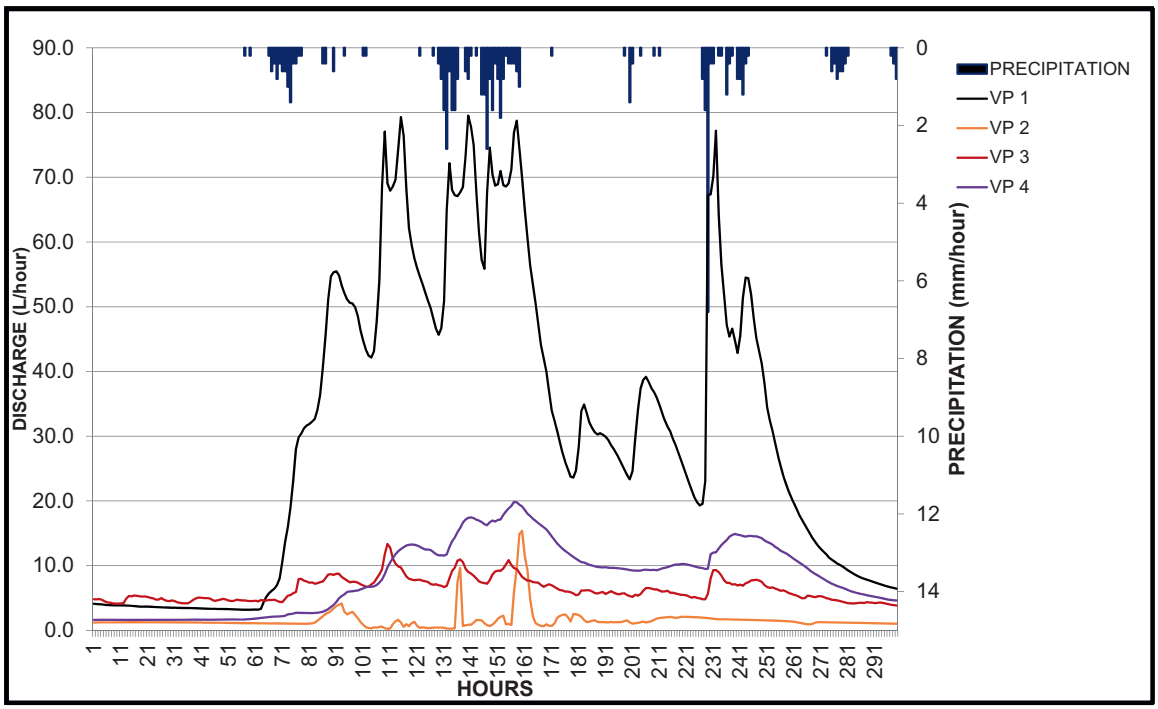

Fig. 2 Discharge of four drip points (VP1–VP4) from the epikarst zone of the Velika Pasica cave (Slovenia) related to precipitation. Distance from surface to a specific drip-point is between 5 and 8 m. Author: A. Brancelj.

ions from crevices. Later, the concentration of ions drops because of dilution with incoming water. Water temperatures at entry points (i.e., in the epikarst, as diffuse sources), or at sinkholes (as point sources), reflect surface weather conditions. Along their route in the subsurface, water temperature approaches the mean annual local air temperature, albeit controlled by discharge.

Food sources and feeding habits

For a long time, the karstic environment was considered a "truncated ecosystem" (Gibert and Deharveng, 2002) due to the absence of primary producers represented by photoautotrophs (green plants). This statement was based on the fact that most karstic ecosystems (except small parts of sinkholes and springs, measured at a meter scale) are in permanent darkness – as one of the most recognized and distinctive characteristics of the subterranean environment (Romero, 2009). The only source of organic material in caves were for a long time considered leaves, twigs, guano, and carcasses of epigean animals that actively entered, drifted by water flow, or accidentally fell into the caves, most of them through man-accessible openings (like pits, horizontal galleries, or sinkholes). More recent research indicates that important sources of food also include other organic material, either DOM or small fragments of POM as a substrate for decomposing bacteria (Kevin, 2019), which can subsequently be consumed by some cave-dwelling organisms, i.e., scrapers. An additional, and important source of food and energy in caves are chemoautotrophic bacteria using inorganic compounds (mostly reduced iron, manganese or sulfur species) in combination with oxygen for gaining energy used for proliferation and biomass production, which forms the food base of surface-independent chains/webs. These bacteria are in majority attached to mineral particles or rock walls and can sometimes form extensive mats, which are consumed by scrapers. Examples are the sulfidic caves such as the Movile cave in Romania (Sarbu et al., 2018; Palmer and Hill, 2019; Brad et al., 2021).

To date, there are about 3500 species worldwide that are recognized as stygobionts, both from unconsolidated (i.e., interstitial) or fractured (i.e., rocky) aquifers. There is not yet a clear separation between both systems possible based on smaller organisms (like Turbellaria, Oligochaeta, Ostracoda, Copepoda), although there are obvious differences in ecological parameters between the systems, like living space, food, hydrological conditions. At the same time, both systems share some common characteristics, like absence of light, scarcity of food, relatively stable physical and chemical parameters.

The most common invertebrate representatives in the karstic habitats are Mollusca (especially Gastropoda – several hundred species), Annelida (mainly Oligochaeta – several dozen species), Crustacea (among others, Ostracoda, Copepoda, Amphipoda, Isopoda, Syncarida, Decapoda – each group with several hundred species) and Coleoptera (especially the rich families Dytiscidae and Elmidae – several tens of species each). Most of the other aquatic invertebrate taxa have at least one or few representatives in the karst environment. For example, among Vertebrata, there are over 200 described species of obligate cave fish, most of them found in tropical or subtropical areas, albeit one stygobitic population of the genus *Barbatula* was recently discovered in caves of Germany

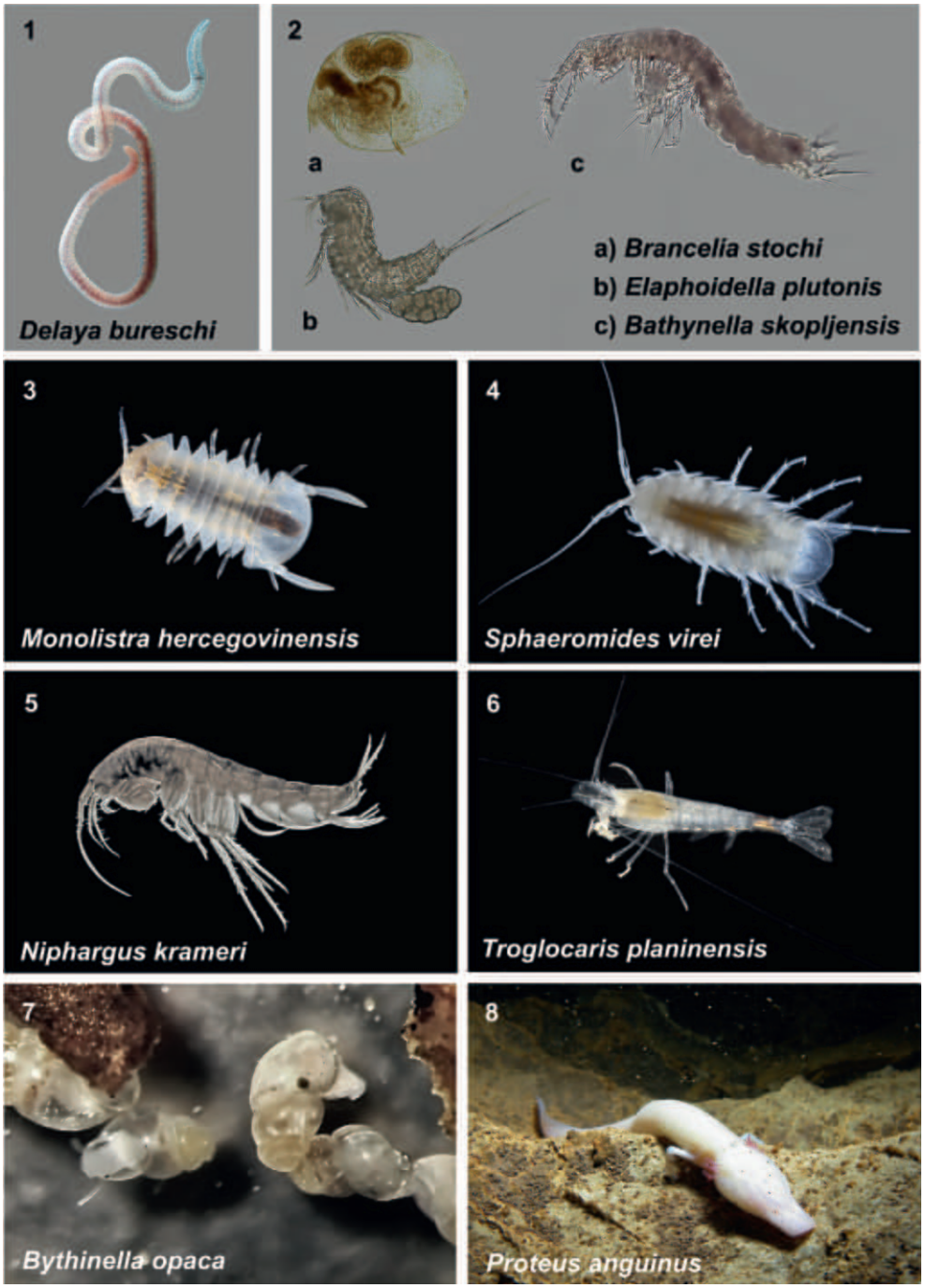

Fig. 3 Some stygobionts inhabiting aquatic cave environments. Photos by G. Balázs (8), A. Brancelj (2a), T. Delić (1, 3, 4, 6), F. Stoch (2b, 2c, 5, 7).

(Behrmann-Godel et al., 2017). Finally, Amphibia are represented in Europe by the famous olm (*Proteus anguinus*), while other species of aquatic cave salamanders are present in the U.S.A. Some representatives of karstic groundwater-dwelling species in Europe are presented in Fig. 3. Stygobionts share some common characteristics, like loss of pigments, eye reduction, elongation of body appendages, increased number of chemoreceptors and mechanoreceptors and lower metabolic rates (Christiansen, 1962).

Stygobionts practice several modes of food gathering, because distribution and amount of food do vary in time and space. For that reason, they can ingest fine sediment particles or scrape on surfaces of mineral or organic material, both covered with bacterial biofilms. This is practiced by most small-bodied animals, including Planaria, Gastropoda, Annelida, some families of water beetles (Coleoptera), and some microcrustaceans (Cladocera, Ostracoda, some Copepoda). Different groups of arthropods, especially representatives of crustaceans (some Copepoda, Isopoda, Amphipoda, Mysidacea, Decapoda) combine a detritivorous diet with predation – in principle they are omnivores, including the largest cave-dwelling species, *Proteus anguinus* (Bizjak-Mali and Bulog, 2004). Predators are represented by copepods, isopods, crayfish, crabs, dytiscid beetles, and several blind fish. Only a few

stygobionts are specialists, like some sessile filter-feeders, usually inhabiting caves near sinkholes (sponges – *Eunapius subterraneaus* Sket & Velikonja, 1984; mussels – *Congeria kusceri* Bole, 1962; polychaetes – *Marifugia cavatica* Absolon & Hrabe, 1930). These organisms are frequently associated with certain surface-dwelling relatives, that can survive for some time in such environments and were in the past often considered (erroneously) as representatives of cave-dwelling fauna, too. Planktonic filter-feeders are very rare in karstic environments and are represented worldwide by only about 10 species of Calanoida (Copepoda) (Brancelj and Dumont, 2007). They are not able to resist water current; thus they can only establish viable populations in environments with low water flow or standing water bodies.

Sampling methods for cave-dwelling aquatic fauna

Sampling methods for cave-dwelling aquatic fauna include most well-known and standardized techniques applied also for epigean aquatic environments (Downing and Rigler, 1984) alongside more specific devices.

(I) Pick-up sampling of larger individuals by hands, small hand nets, tweezers, and cups.
(II) Different types of traps usually left on site for one or exceptionally few days, with baits (usually rotten meat/liver) to sample fish or crayfish. For smaller mobile organisms, traps can be adequately modified; they are made from plastic bottles and equipped with fine mesh along the sides (Beladjal et al., 1992).
(III) Kick-up sampling for sediment-associated fauna with hand nets in the knee-deep sections of rivers/streams and pools.
(IV) Plankton nets for larger standing water bodies within caves used either from boat (vertical tow-samples) or from the shore.
(V) Plankton nets positioned horizontally in the spring-mouth to collect drift.
(VI) Specially designed filtering bottles connected to plastic sheets or funnels for sampling drips and trickles from the epikarst to collect specimens for several days/weeks (Fig. 4) (Brancelj, 2015).
(VII) Small pools (like rimstone pools) of one or tens of milliliters of water are sampled using plastic pipettes or sucking pumps (Fig. 5).
(VIII) Piezometers or man-made wells are usually sampled with small-size plankton nets or Cvetkov's nets (Cvetkov, 1968).
(IX) Samples can be collected by rotating pumps from piezometers and wells, but only small motile organisms can be collected undamaged (Copepoda, Ostracoda, Syncarida), and larger organisms (Amphipoda, Isopoda) are likely damaged by the pump's rotor, although some specific body fragments may be sufficient to identify animals to species/genus level (Brancelj et al., 2016).
(X) Environmental DNA (eDNA) techniques to detect whole communities (eDNA metabarcoding) or species within karstic systems collected in water samples, were applied for example to *Proteus anguinus* (Gorički et al., 2017; Vörös et al., 2017) or the North American amphipod *Stygobromus* (Niemiller et al., 2018).

Fig. 4 Sampling device used to collect physical data (water temperature and discharge) and specimens of groundwater fauna (by a filtering bottle) at a drip point from the epikarst. Location: the Velika Pasica cave, Slovenia. Photo: A. Brancelj.

Fig. 5 Sampling devices for rimstone pools (upper image) and the community living there (lower image, with representatives of Oligochaeta, Ostracoda and Copepoda Harpacticoida). Location: the Cave Pocala, Italy. Photo: F. Stoch.

Groundwater pollution

Historically, caves were used as shelters, sacred sites for graves of respected members of their community or were used for certain religious rituals/offerings. In more recent decades they become "dump sites," i.e., places heavily affected by factories, agriculture, and local communities as sites for waste deposition (Foster, 1987).

Karstic aquifers are very vulnerable to anthropogenic impacts from the surface, as galleries can act as corridors (channels) for fast and long-distance distribution of pollution. Assessing the vulnerability of karstic aquifers to pollution and other threats is essential for their conservation (Machiwal et al., 2018). Under the term "pollution," we may consider two main processes. One of them is eutrophication (as discharge of un-treated wastewater from households, farms as well as part of urban waters) leading to an increased productivity and the second one is a discharge of harmful or poisonous chemicals (from industry, traffic, agriculture) leading to a decreased productivity. Sources of both types could be point-sources and/or diffused in a karstic massif.

Eutrophication is caused by an increase of organic matter and nutrients triggering an elevated production in surface sections of sinking rivers or direct discharge into groundwater from septic tanks of households or farms. Organic material, either as POM or DOM, transported into the subterranean environment has a two-fold effect. During decomposition, it can induce (locally and/or temporally) anoxic conditions and exterminate local cave fauna. At the same time, increased energy sources (i.e., food) can support the presence of epigean species, even alien species, which can out-compete, and consequently trigger extinction of cave-dwelling organisms (Mazza et al., 2014).

Persistent and toxic chemicals may reflect actual surface activities (leaks/discharge from local factories, oil spills from traffic accidents, road maintenance during de-icing or weed removal) or past waste dumping of industrial or urban deposits. This kind of pollution can last in the karstic environment for decades and their effects depend on the quality and quantity of deposits. Heavy water extraction represents yet another pressure and karstic aquifers close to the coast are already subject to salt-water intrusion (Kresic, 2012).

Conclusion

Caves have been important for humans for almost 50,000 years, as shelters against harsh environmental conditions. People left striking signs of their presence in the caves in form of fireplaces, leftovers of food consumption (bones, seeds), artifacts or ritual places, including impressive mural paintings and burial places.

Nowadays scientists focus their attention to the evolution of karst formation from geological, geographical as well as biological aspects. From an ecological point of view, the karstic groundwater environment is still hardly explored. Many new species are discovered every year, especially since the development of modern molecular techniques, and/or in poorly sampled areas, particularly in sub-tropical and tropical regions in Asia, Australia, South America. Phylogenetic and genomic research revealed a very dynamic and highly diverse situation in this rather "conservative" environment. The karstic environment is much more diverse as was considered in the past. Its fauna is rich, specialized for peculiar environmental conditions (i.e. absence of light, constant temperature, low food levels), and with plenty of endemics mainly due to allopatric speciation in isolated karstic areas. More than one century after Racovitza's (1907) essay, overcoming the Racovitzan impediment in karst environments is still one of the major challenges for aquatic ecology.

Future research

- holistic approach to research of karstic habitats/ecosystems, i.e., combining physical, chemical, hydrological and biological parameters in the same studies
- study of karstic habitats/ecosystems in different geographical/climate zones
- biodiversity and phylogeny of stygobionts
- reactions of groundwater fauna to pollution, eutrophication and climate changes

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Karst Groundwater Dependent Ecosystems—Typology, Vulnerability and Protection

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Calcrete Carbonate deposits that form in the vicinity of the water table as a result of the evaporation of groundwater.
Convergence The independent evolution of similar traits in distinct evolutionary lineages, often as a result of similar selective pressures.
Divergence The independent evolution of different traits in distinct evolutionary lineages, often as a result of different selective pressures.
Ecological specialist Species that generally occupies a very restricted range or even a single habitat and feeds on a small range or even a single food source. In the case of subterranean habitats, animals are absolutely dependent on and they complete their life cycle in subterranean habitats.
Hyporheic Interstitial spaces with the sediments of a streambed; a transition zone between surface water and groundwater.
Karst Landscape in soluble rock where solution rather than erosion is the primary geomorphic agent, typically with caves, sinkholes and springs (see Fig. 2).
Phreatic zone The lower, saturated part of the aquifer where flow through the (sub)horizontal network of conduits predominates.
Stygobiont Obligate, permanent resident of aquatic subterranean habitats. Troglobiont is an analogy with terrestrial species.
Troglomorphy The occurrence of convergence, especially in morphology, due to natural selection acting upon subterranean populations or species.
Vadose zone The upper, unsaturated part of the aquifer, where the fast drainage through a vertical network of fissures and voids interacts with the slow percolation through low permeable volumes.

Introduction

Karst covers about 15% of the global land surface and more than a fifth in Europe alone (Chen et al., 2017). Among a variety of karst environmental assets, groundwater resources are certainly the most important (Bakalowicz, 2005). Karst aquifers meet around a quarter of the world's drinking water needs (Ford and Williams, 2007; Hartmann et al., 2014). They are important for agriculture, industry and hydropower, and their significance is gradually increasing.

At the same time, karst areas are also important due to the presence of unique ecosystems. Many of these ecosystems reside within or are reliant to karst groundwater and, like other groundwater dependent ecosystems, form complex communities of organisms in which groundwater is a key element for their existence (Merz et al., 2001). Karst groundwater dependent ecosystems (KGDEs) represent an essential interface between the biosphere and the karst hydrological systems. They often harbor a high regional biodiversity, especially at springs, and communities with a high portion of endemic species. KGDEs provide various ecosystem services, including water purification, ecological productivity, photosynthesis above ground and carbon sequestration (Goldscheider, 2019). Some are recognized as recreational areas, others are of religious, spiritual and cultural significance. KGDEs make an important contribution to water and food supply, improve water and air quality, and are of particular importance for flood mitigation (especially wetlands).

Although groundwater dependent ecosystems, and among them KGDEs in particular, are increasingly recognized for their ecological and socio-economic values, they have not yet been adequately documented and investigated (Bonacci et al., 2009; Cantonati et al., 2020). Studies in which groundwater ecohydrology has been discussed so far are few in number, at least as far as karst groundwater ecosystems are concerned, and focus mainly on surface water bodies. Only a few studies have been published where karst groundwater habitats and complex processes within them were closely investigated. Such integrated approaches are rare, mainly because underground biotic communities are hardly accessible and because conducting experiments and monitoring underground may require logistical, financial and physical efforts. As a result, KGDEs are poorly investigated and known and face major knowledge gaps in karst science (Culver and Pipan, 2014; Goldscheider et al., 2006; Kløve et al., 2011a).

To fill this gap, the present contribution provides an overview of karst groundwater and associated ecosystems, with a special focus on foremost ecohydrological processes and environmental conditions, as well as on the interactions between animate and inanimate nature.

Although groundwater is generally defined *sensu stricto* as subsurface water occupying the phreatic zone up to the water table (Fryar and Mukherjee, 2021), some authors allow the definition *sensu lato* referring to all water underneath land surface (Kresic, 2010). In karst, this is reasonable because the water table is not always continuous and hydrological systems can be quite anisotropic and heterogeneous. A special part of the vadose karst zone is its upper layer, called epikarst, which can form perched aquifers and is an important contributor to other parts of the aquifer, especially during baseflow conditions. It also represents a special karst habitat and is therefore considered here as part of the KGDEs. In order to better assess the vulnerability of KGDEs and to achieve proper adaptation strategies for their management, the most representative KGDEs types are presented together with indicator communities.

Ecohydrogeological processes and environmental conditions in karst

Karst is formed by the dissolution of host rock along discontinuities. Therefore, its internal structure is characterized by a unique triple porosity (Fig. 1). The primary porosity is related to the intergranular permeability of the rock matrix as well as small voids and microfissures. The secondary porosity consists of discontinuity planes, including joints, faults and bedding planes. The presence of well-developed solution channel pathways, which form the tertiary porosity, is a major difference with other types of aquifers (Atkinson, 1977; Jeannin and Grasso, 1997; White and White, 2005). A hierarchically organized network of hydraulically connected voids, the size of which varies from slightly enlarged cracks to conduits many meters in diameter and many kilometers long, enables flow over long distances (Gabrovšek and Dreybrodt, 2001; Worthington and Ford, 2009).

A large part of groundwater recharge takes place through openings either as rapid diffuse or concentrated infiltration, while the other part moves slowly through the matrix. In the subsurface, the flow through conduits and channels, where water storage is limited, is often fast and turbulent (Bakalowicz, 2005; Aquilina et al., 2006). The flow velocities can even reach several hundred m/h, in contrast to velocities in intergranular aquifers, where the maximum velocities are in the order of a few tens of m/day. The flow through micropores in the carbonate bedrock, where considerable storage occurs, is much slower, diffuse and often laminar (Ford and Williams, 2007; Fig. 1).

Due to the predominant channel flow, another specificity of karst hydrology is the fast and strong variability in response to meteorological conditions. This results in changes from open-channel to pressurized flow and changes from laminar to turbulent flow (Worthington, 1991; White, 2003; Williams, 2008). Water table fluctuations can reach several dozen meters within a short time and flow velocities can vary by several orders of magnitude. As a result, water overflows onto the surface and extensive surface-groundwater interactions may occur, such as the activation of temporarily active springs, swallow holes, intermittent lakes, etc. (Naughton et al., 2012; Mayaud et al., 2019). The hydrological status of estavelles also changes. Variations in flow directions and thus in contribution of different parts of the aquifer to a particular spring are also frequent (Ravbar et al., 2011).

In contrast to other (subterranean) ecosystems, where the hydrological conditions are much more stable (Boulton and Brock, 1999), the described flow characteristics have a significant influence on the buoyancy, structure and functioning of KGDEs. Baseflow periods are characterized by stable environmental conditions and generally higher water quality. Since the chemical composition of groundwater in carbonate aquifers is represented by the predominant dissolution products of carbonate minerals, groundwater carries continuous flux, rich in calcium-bicarbonate and low turbidity (Jeannin and Grasso, 1997; Bakalowicz, 2005).

Recharge events induce spatial and temporal variability of the flow, which has many implications for groundwater distribution, its physical and chemical properties. Water flow velocities, temperature and turbidity, transport of nutrients and concentrations of other substances can be subject to considerable variability (Ford and Williams, 2007; Bonacci et al., 2009). The temperature variance occurs because the water adapted to the surface temperature cannot fully adapt to the subsurface temperature on its way due to the rapid transfer of infiltrated water toward the spring (Petrič and Kogovšek, 2010). Water quality may deteriorate due to rinsing of soluble contaminants from an adjacent aquifer or other parts of the aquifer. Similarly, nutrients and particles of different shapes and sizes (dissolved and particulate organic matter, sediments along with small organisms and seeds) entering the system by various pathways can spread rapidly over long distances. Various types of pollutants may be attached to the transported particles (Pronk et al., 2006).

In the underground, very special environmental conditions prevail and animals have adapted in a very special and unique way (Table 1; Christiansen, 2012; Fišer, 2019). Darkness is the most defining factor that has the greatest influence on the organisms and is manifested by the reduced energy flux through food webs. In nearly all ecosystems, light-driven photosynthetic production by

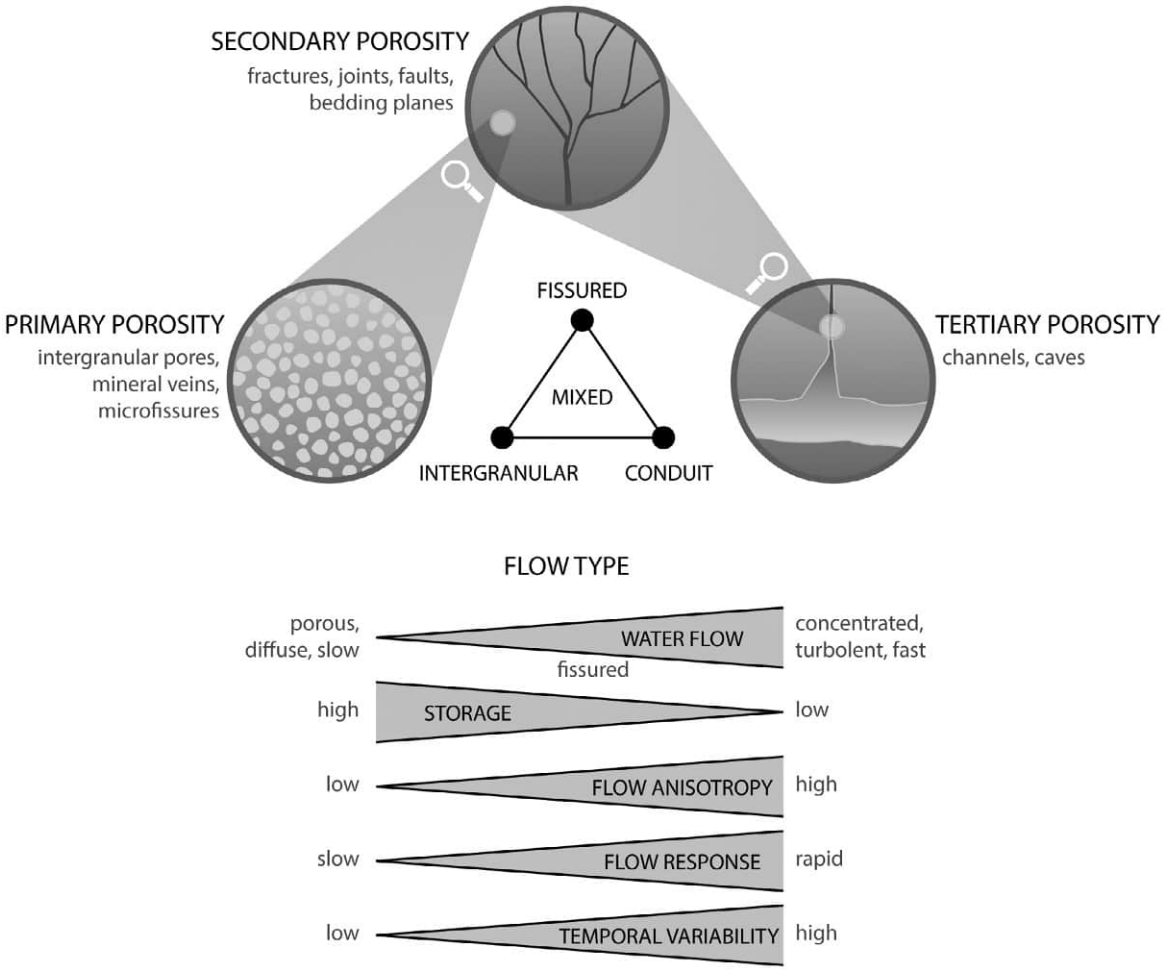

Fig. 1 Schematic description of the porosity types and the associated flow properties in karst. Modified from Atkinson TC (1977) Diffuse flow and conduit flow in limestone terrain in the Mendip Hills, Somerset (Great Britain). *Journal of Hydrology* 35: 93–110; Ford D and Williams P (2007) *Karst Hydrogeology and Geomorphology*. John Wiley and Sons; Gillieson D (1996) *Caves: Processes, Development and Management*. John Wiley & Sons.

Table 1 Morphological, ecological, physiological, and behavioral adaptations of aquatic and riparian fauna to subterranean life.

Morphological	*Ecological and physiological*	*Behavioral*
Reduced eyes, pigments and brain parts connected with processing sensory information	Reduced metabolism	Reduced aggregation
Specialization of extra-optic sensory organs	Resistance to starvation	Reduced response to alarm cues
Cuticular thinning	Reduction of circadian rhythm	Increased sensitivity to vibrations
Modification of feeding structures	Reduced egg number; increased egg volume	Reduced intraspecific aggressive behavior
Reduction of scales and swim bladder (fish)	Increased life span	
Elongation of appendages		

microbes and plants is the key source of energy for heterotrophs, but in the absence of light primary production can only be based on chemical sources to produce microbial biomass. This chemical-driven microbial production, chemoautotrophy, can support food webs in caves and other subterranean habitats (Brad et al., 2021). The other source is dead organic matter from plants, detritus, dead animals, feces, or other material which is imported from the surface (Simon, 2019).

Compared with related surface-dwelling species, subterranean animals are characterized by the absence or reduction of a series of features, particularly eyes and pigments. Subterranean animals are also characterized by an elaboration of extraoptic sensory

structures as well as other morphological, ecological, physiological, and behavioral adaptations (Table 1). This represents a remarkable convergence among subterranean animals, the morphological aspects of which are called troglomorphy (Christiansen, 1962). But not all features are convergent. For example, interstitial and epikarst species tend to be smaller than surface-dwelling sister taxa while cave species tend to be larger (Fišer et al., 2012).

KGDE types and their representative subterranean communities

A prerequisite for better understanding of interactions between environmental elements and complex feedback mechanisms of KGDEs, of their vulnerability to specific environmental pressures and adequate protection is their classification (Fig. 2, Table 2). Addressing changes in ecosystem structure and functions requires an integrated approach from the (sub)surface to the vegetation and atmosphere, across scales and ecosystems, and it entails combining observation, ecosystem theories and modeling. Challenge of framing the KGDEs as a whole system approach, combining human-environment interactions, and cross-scale interactions with feed-back loops, is triggered by the theoretical basis and practical implementation. To identify the most representative ecosystem types, the position within the hydrological system, the morphology of the environment, the main hydrogeological processes (i.e., extent, duration and frequency of groundwater inflow), main biota and factors limiting the evolution of the species (e.g., darkness) are considered and briefly described.

The most spatially distributed habitat in karst and a major ecotone between surface and cave water is the soil–rock interface known as the epikarst (Bakalowicz, 2004). From a hydrogeological perspective, it represents an upper layer of the vadose zone, which can be from a few meters to several tens or even hundreds of meters thick. Due to its origin by weathering and corrosion processes, it is structurally different and much more karstified than the lower part of the unsaturated zone. As the degree of fracturing and the hydraulic conductivity decreases with depth, the concentration of infiltrated water is promoted. Consequently, perched aquifers are formed enhancing temporal storage of the water and its lateral flow before it is diverted to the main flow paths in the deeper parts of the system (Mangin, 1975; Williams, 2008; Berthelin and Hartmann, 2020). This is particularly important for the gradual recharge of the phreatic zone and springs during baseflow conditions (Perrin et al., 2003; Trček, 2003).

The epikarst layer also acts as a natural filter for pollutants and other substances contained in the seepage water. Due to its morpho-hydrological conditions, it hosts a variety of different microhabitats of rich and diverse aquatic fauna, e.g., in pores, voids, fissures, cavities and conduits that are permanently or temporarily flooded, as well as in drips, riffles, pools and ponds (Culver and Pipan, 2013). Direct sampling of epikarst habitats is not possible and epikarst communities are best sampled by collection and filtration of drip water over extended periods of time. Animals in dripping water are the ones that have been swept out of their primary habitat above the cave passage. Drips exhibited considerable environmental and biodiversity heterogeneity, represented mainly by copepod species (Pipan, 2005a).

At regional scale, however, the water enters the underground karst system via ponors and swallow holes and, together with the water percolating through the vadose zone finally reaches a cave stream (Fig. 3A–C), which in turn exits at a spring and flows into a surface river (White and White, 2005). The part that is located in the area of water level fluctuations is called the epiphreatic zone

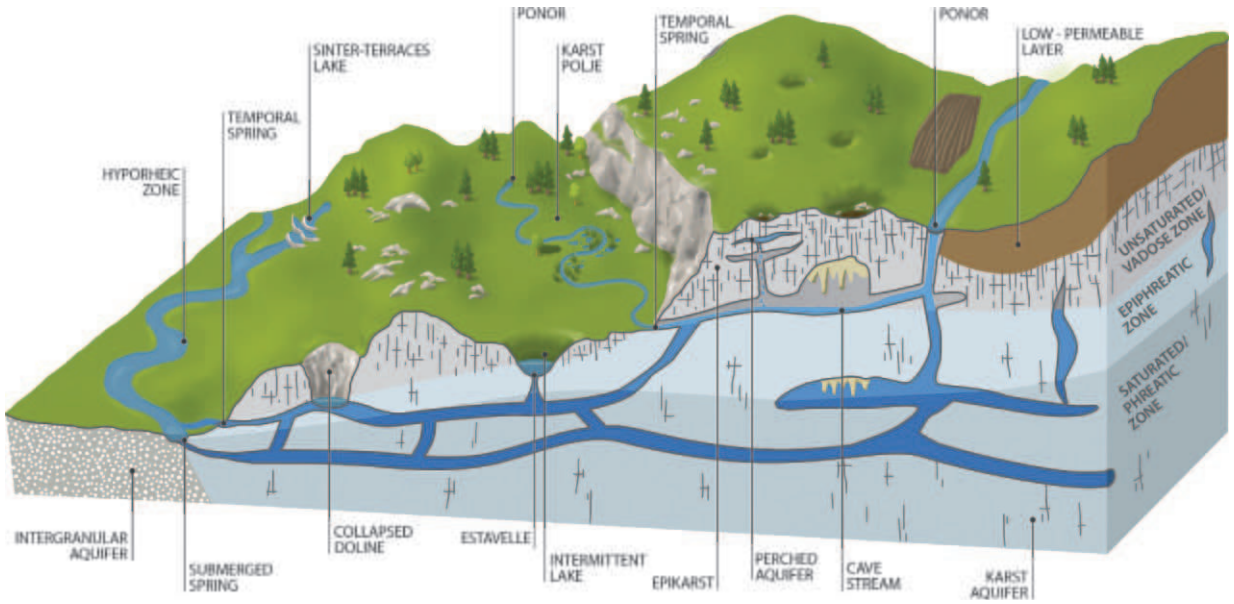

Fig. 2 Schematic presentation of the most representative KGDE types. The figure is not in scale. Modified from Ravbar N and Šebela S (2015) The effectiveness of protection policies and legislative framework with special regard to karst landscapes: Insights from Slovenia. *Environmental Science and Policy* 51: 106–116.

Table 2 An overview of KGDE types, foremost ecohydrological processes and environmental conditions, with the main representative groundwater taxa.

Ecosystem type	*Position within the hydrological system*	*Main ecohydrogeological processes*	*Type of habitats*	*Representative groundwater taxa*[a]
Epikarst	Subterranean	Storage, filter, transport, lateral flow	Pores, voids, fissures, cavities, conduits drips, riffles, pools and ponds	Microcrustacea, Oligochaeta
Cave stream in epiphreatic and phreatic zones		Transport, high temporal variability of flow	Conduit network, sediments	Microcrustacea, Decapoda, Gastropoda, cave salamander, cave fish
Cave in phreatic zone		Slow flow		Microcrustacea, Decapoda, Coleoptera, cave salamander; cave fish
Cenote	Surface-groundwater interaction zone	Slow flow	Water cave	Microcrustacea, Copepoda, Decapoda, cave fish
Ponor		Transport, high temporal variability of flow	Opening in the ground	N/A
Spring			Pores, voids, fissures, cavities, conduits, sediment	Microcrustacea, Gastropoda
Karst polje, Intermittent lakes	Surface	Temporal variability of flow	Sediment, groundwater	Microcrustacea
Sinter-terraces lakes			Sediment, pools	Isopoda, Gastropoda
Calcrete aquifers	Subterranean	Slow flow	Sediment, water column	Coleoptera, Microcrustacea
Hyporheic	Groundwater		Sediment	Microcrustacea, Oligocheata, Insecta

N/A, not applicable.

[a]By representative groundwater taxa are meant the most diverse and best-studied subterranean groups known in the literature.

and is temporarily saturated, while the phreatic zone is permanently saturated. The habitats in these zones consist of networks of conduits of different sizes, from a few millimeters to dozens of meters in diameter. Usually during flood pulses they serve as transmitters of water, nutrients, mass and energy, which are of vital importance for cave biota (Gillieson, 1996). Transport in cave streams formed largely from percolating epikarst water tends to be more stable over time, while transport in cave streams formed largely from sinking surface streams shows greater temporal variability. The flow rates of cave streams range from a few mL/min to dozens of m^3/s.

The sinking rivers are usually inhabited by a rich assortment of stygophiles and accidental surface species, stygobionts are rare. Sinking rivers recharge aquifer in a concentrated manner and often have a direct link with the phreatic zone. Sometimes they develop a larger ponor-spring cave system, such as is the example of the Postojna-Planina Cave System (Slovenia; Fig. 3C). This cave system has a long history of biological research, dating back to the early 19th century and is considered as the cradle of biospeleology with at least 48 stygobiotic species known today. Representative communities in the cave river comprise European cave salamander *Proteus anguinus anguinus* (Fig. 4A), different species of snails and crustaceans, among which endemism is high, as well as hydrozoan *Velkovrhia enigmatica* and the cirolanid isopod *Monolistra racovitzae racovitzae*, both with a marine origin. Endemic cave salamanders are also known from caves of the south-eastern United States (i.e., *Eurycea spelaea, E. latitans, E. wallacei, E. tridentifera, E. rathbuni*, etc.). In terms of cavefish species diversity is richest in South China Karst, the Brazilian and Mexican karst regions with endemic species.

Aquifers are emptied through springs which usually feed streams or lakes (Fig. 3D). There are different types of springs in terms of geological, tectonic and morphological aspects and they can be permanently or temporarily active (Kresic, 2010; Kløve et al., 2011a; Culver and Pipan, 2013, 2014, 2019; Stevens et al., 2020). Springs are fed by a conduit network that contains abundant water and has highly variable flow rates of up to several dozen m^3/s (Bakalowicz, 2005), which are associated with recharge events. Accordingly, flow velocities, particulate and solute matter concentrations and temperature may strongly fluctuate. A particular hydrological form of the karst is the estavelle, through which the karst aquifer is fed or emptied and can therefore act as a spring when the water level rises or as a ponor when the water level falls. Where the aquifer empties in the riverbed or the seabed,

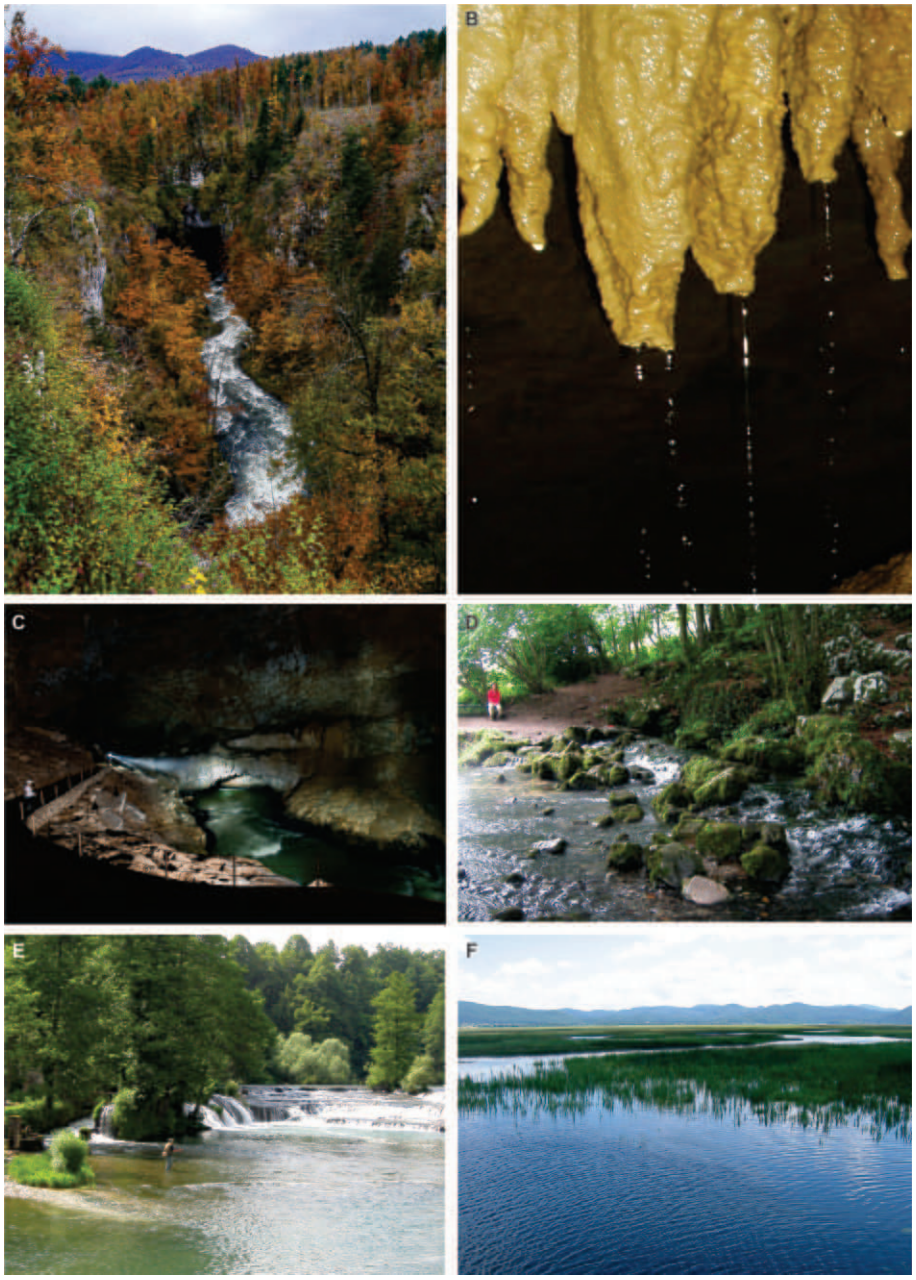

Fig. 3 Photographs of the most representative KGDE types: (A) ponor, (B) cave drip, (C) cave stream, (D) spring, (E) sinter-terraces, (F) intermittent lake. Photos: (A) M. Blatnik; (B) H. Hobbs; (C) B. Kogovšek, all with permission; (D, E, F) N. Ravbar.

subaquatic or submarine springs appear. In the later strong saline-freshwater interactions occur affecting both marine and KGDEs (Surić et al., 2015; Morrissey et al., 2020). Springs are ecotones between aquatic, riparian, or terrestrial habitats and are likely to affect habitat conditions, colonization, wildlife and human uses, as well as other ecosystem characteristics. Important microhabitats include springs' orifice, pools and streams, hyporheic zones, wet meadows, riparian habitats, waterfall spray zones, and barren rock habitats near springs. Springs are considered biodiversity hotspots, including calcifying mosses, cyanoprokariotes and diatoms, among macroscopic invertebrates, snail and crustacean fauna is rich (Cantonati et al., 2020; Culver and Pipan, 2013).

At some springs or in stream channels sinter- (tufa- or travertine-) terraces form (e.g., in Krka River and Plitvice Lakes in Croatia, Pamukkale in Turkey, Huanglong valley in Sichuan, China). Often a staircase of pools is created by CO_2 degassing from water in areas of strong aeration and under favorable temperature conditions (Fig. 3E). Predominantly chemical deposition of calcite arises through the intervention of biological activity (Wang et al., 2010). A range of cyanobacteria, algae, mosses and higher plants contribute to the retention and accumulation of tufa and in this way gradually form tufa barriers. When tufa is deposited, it covers the bottoms and sides of streams and even fossilizes other sediments and organic remains, such as fallen trees and leaves.

Fig. 4 Photograph of typical (A) *Proteus anguinus anguinus* and the pigmented, eyed subspecies (B) *Proteus anguinus parkelj*. Photo: G. Aljančič, with permission.

This chemically-precipitated porous limestone habitat is an ecotone between surface, mostly current water, and a vadose or occasionally shallow phreatic environment (Pentecost, 2005). It harbors also troglomorphic taxa, like isopod crustacean *Caecidotea stygia* in North America and snail species of *Iglica* and *Paladilhiopsis* in Slovenia (T. Novak, per. comm.).

Karst poljes are larger closed depressions in karst landscapes with flat bottoms. They are typical of the Dinaric karst, but can be found in most karst regions of the world (Ravbar et al., 2021). Common characteristics of the poljes are very complex hydrological and hydrogeological features of sinking water with outlets on the one side and swallow holes on the other, with cycles of extensive flooding (Fig. 4), followed by receding water levels and the formation of wetlands (Gams, 1978; Ford and Williams, 2007). Sometimes karst poljes follow one another in a row downgradient, so that the same water sinks and reappears several times (Bonacci, 2013).

Strong and direct interaction between the circulation and storage of ground- and surface water also occurs in areas of shallow karst, where bottoms of karst depressions reach the epiphreatic zone. The so-called intermittent lakes (in Ireland similar formations are termed turloughs) and other karst wetlands appear of widely varying sizes with different periodicities and have a role as reservoirs of biodiversity (Pipan et al., in press). In the case of Pivka intermittent lakes in Slovenia, for example, water flows underground most of the year, but after periods of intensive or long-lasting precipitation, the water table rises and emerges to the surface (Petrič and Kogovšek, 2005). Some of the intermittent lakes appear annually and last for up to 6 months, but some other lakes appear rarely, and only fill up in times of extreme hydrological events. Some of the smaller lakes recharge and discharge mainly through the alluvial sediments which cover their bottoms.

Extensive surface-groundwater interactions and flooding in these areas promote the exchange of nutrients and organisms between habitats. Human societies have developed grazing patterns for their domestic livestock and established cropland and agricultural methods that make optimal use of the fertilized land released after the floods. When the water is present, area is often used for agriculture and recreation. The transition from wet to dry (and vice versa) can be rapid, and thus karst poljes and areas of intermittent lakes create diverse habitats for specifically adapted communities. The crustacean fauna of the Pivka intermittent lakes includes two species of fairy shrimp (*Branchypus schafferi* and *Chirocephalus croaticus*; Fig. 5), three Cladocera species, nine Copepoda species, two Ostracoda species, one Amphipoda, and one Isopoda. While the species list is very incomplete and non-existent for insects, it includes stygobionts, generalist species, and species adapted to temporary waters (Pipan, 2005b; Pipan and Culver, 2019).

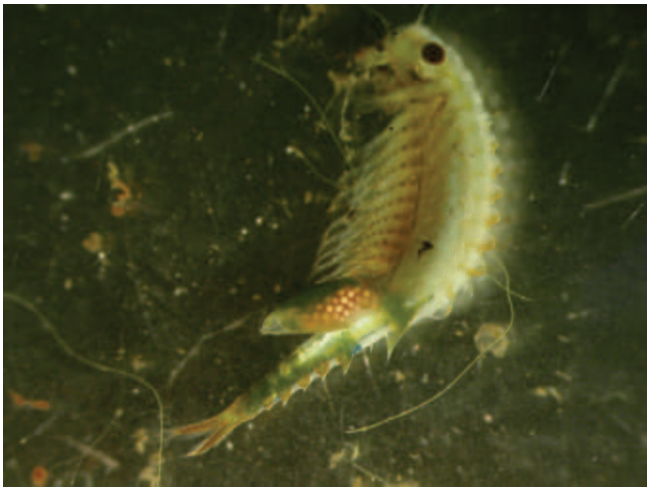

Fig. 5 *Chirocephalus croaticus*, a rare species of fairy shrimp limited to intermittent karst waters. From Pipan T (2005) Fauna of the Pivka intermittent lakes. *Acta Carsologica* 34: 650–659.

Typical of temporary wetlands, fairy shrimp have thick-shelled winter eggs that are resistant to desiccation. They also have a very high reproductive rate and in the case of *C. croaticus*, can complete their life cycle in 2 weeks, an obvious advantage in temporarily present waters. In general, open meadow-like flooded areas and dry meadows at the margin of the intermittent lakes are important habitats also for vegetation. In the areas that are flooded for longer periods, purple willow (*Salix purpurea*) overgrows meadows and pastures in the absence of cultivation or grazing. Due to zonation in the lake basin, related to flood duration, there are many endangered and rare species and plant communities still poorly examined (Pipan et al., in press), like mouse garlic *Allium angulosum*, Siberian iris *Iris sibirica*, wild gladiolus *Gladiolus illyricus*, and solitary clematis *Clematis integrifolia* (Mulec et al., 2005). Rare plant communities include the wild gladiolus—purple moor grass (Gladiolo-Molinietum), and tufted hairgrass—tall plantain (*Deschampsio-Plantaginetum altissimae*) communities.

Among the best known karst poljes is the Cerkniško Polje (Slovenia). Aquatic plant communities are very restricted, but adapted to hydrophilic conditions due to the intermittent nature of the lake that occurs in the polje (Fig. 3F). Most species die back during the dry phase. Among such species are *Charetea fragilis* and several species of *Potametum*. With regular draining and filling, the lake's reed beds provide shelter, food, and nesting sites for a variety of water and other birds. Amphibious species are ones where the species occur in both wet and dry phases and where the duration of the aquatic phase is at least 3–4 months. There are typical wetland species and species living on the edge of the inundation zone. Many of these wetland species are rare or endangered in Slovenia (Pipan and Culver, 2019). The Crustacea reported from Cerkniško Polje include a fairy shrimp, *Chirocephalus croaticus*, a rare species limited to intermittent karst waters. A total of 21 cladoceran species and 15 copepod species have been recorded from the lake, some species are obligate subterranean dwellers (stygobionts). The lake is also a hotspot for both Odonata and Trichoptera, with several species rare and endangered in Slovenia. The cave salamander *Proteus anguinus anguinus* has been reported from Cerkniško Polje and the Pivka intermittent lakes, where it washes in from subterranean channels as the lake fills (Pipan and Culver, 2019). During the dry season, these areas are an important terrestrial habitat for mammals, butterflies and beetles.

Other important aquatic habitats in karst landscapes include collapsed dolines when their bottoms reach the (epi)phreatic zone and form lakes (e.g., Red and Blue Lakes near Imotski, Croatia). This type of collapsed doline is also called cenote, which is characteristic of the low karst of the Yucatan in Mexico, where the term originated. Cases of collapsed dolines with a river flowing along the bottom are also common.

A specialized aquatic karst habitat has been found in extensive areas of western Australia. These are thin carbonate deposits in isolated, desert, though sometimes extensive pockets formed by evaporation of near surface waters in very arid climates (Humphreys, 2001). Shallow, up to 10 m thick calcrete aquifers are a feature of arid karst areas, that are colonized by a diverse fauna of stygobionts, including diving beetles (Dytiscidae), amphipods (Crangonyctoidea and Melitoidea), and isopods (Phreatocoidea; Halse, 2018). Because of their long geological history, some of the fauna is very ancient. The source of organic matter and nutrients is rain water percolating into the calcrete aquifers, and tree roots that penetrate the calcrete (Saccò et al., 2021). It is speculated that chemoautotrophy also occurs. Overall, regional diversity is high, but overlap among related species is low, and different isolated calcretes have different, but related species.

Vulnerability and protection

Karst groundwater dependant ecosystems and organisms living there are mainly threatened by human influence and pollution that changes the chemical or microbiological composition of the water. The use of fertilizers and pesticides in agriculture is the most

common contamination impact worldwide (Coxon, 2011). Due to the repeated, large-scale recharge of these pollutants, this activity is particularly problematic. Another important group of pollutants are hormonal disruptors that affect the reproduction of organisms. Other persistent contaminants and compounds of emerging concern (CEC), are used every day to promote human health and well-being (i.e., microplastic). Specific threats include spills from traffic accidents, illegal dumping in dolines and sinkholes. Epikarst is considered as one of the most vulnerable KGDEs as it acts both as a collector of toxic waste, because of its storage capacity and a dispersal path, and because of its vertical and horizontal connections (Loop and White, 2001).

Particularly threatening is the construction of various hydrotechnical structures that cause changes in water levels, e.g., hydraulic drainage of surface waters/flood reservoirs (Milanović, 2004; Zupan Hajna et al., 2010), and artificial aquifer recharge management (Daher et al., 2011). Such interventions destroy habitats, prevent the free passage of organisms and sediments and contacts between populations. The water regime and temperature may change and cause the oxygen content and water quality to decrease. Extensive water use is increasing worldwide due to growing water demand, leading to a decline in groundwater levels (Joodaki et al., 2014; OECD, 2015). Similar impacts are expected from changes in land use and vegetation cover (e.g., abandonment of traditional land use and natural vegetation encroachment; Kovačič et al., 2020).

Additional threats are associated with the introduction of invasive species, which often lack natural predators and thus proliferate rapidly. Invasive species may also be able to exploit a resource that native species cannot use, allowing them to establish themselves in the new environment. As a result, invasive species can rapidly decimate natural biota and cause widespread habitat loss (Mollot et al., 2017). An example of the spread of an invasive species is the release of a perch in an intermittent lake of Cerkniško Polje in the 1990s. Since then, its numbers have multiplied dramatically. The perch is a distinct carnivore that attacks and destroys natural populations in the lake and was recently tried to be removed.

In addition, poaching of rare and endemic species, which has recently become a very widespread activity, can also cause their extinction. Hundreds of illegal pitfall traps have been found in caves in Slovenia, Croatia, Bosnia and Herzegovina and Montenegro and organisms, especially beetles, would be sold on the black market (Simičević, 2017).

Proteus anguinus anguinus is the only European cave vertebrate, and by far the largest cave animal in the world, that lives in the subterranean waters of Dinaric karst. Around 300 localities (partly interconnected caves or cave springs) of proteus have been recorded, of which 200 are in Slovenia. In some localities proteus has become extinct due to negative anthropogenic influences from intensive agriculture, energy production (karst water damming), and unregulated urbanization (groundwater pumping and sewage disposal; Aljančič and Prelovšek, 2010). The morphologically most distinct of all proteus populations, discovered in 1986, is *Proteus anguinus parkelj* (the black proteus; Fig. 4B), limited to a single cave system in Bela Krajina (South East Slovenia, on less than 30 km^2) and thus extremely endangered. Even a single local pollution incident could have a devastating impact on the entire population.

Climate change can have a variety of serious negative impacts on ecosystems. Warming and precipitation changes already pose the greatest threat to World Heritage sites, which are protected at the highest level and a third of which are severely affected (Osipova et al., 2020). Little is known about the vulnerability of KGDEs to the direct effects of various environmental changes, and studies are urgently needed. However, observed records and climate simulations are consistent in projecting globally changing patterns of precipitation and temperature and in projecting impacts on the water cycle (IPCC, 2007).

Changes in the quantity, intensity and variability of precipitation could have implications on water quantity and quality in many karst areas. These may cause altered water level fluctuations and changes in seasonality of surface-groundwater interactions (Hartmann et al., 2014). As a result, smaller water bodies may be filled up or drained. Coastal areas can be severely affected by sea-level rise and saltwater intrusion. Consequently, the spatial extent or even ecosystem status of KGDEs may be changed.

In addition, changed abiotic conditions, intermittent exchange of oxic and anoxic conditions in sediments, conditions that accelerate the degradation of organic matter, and an imbalance of nutrients are to be expected (Urbanc-Berčič and Gaberščik, 2001). An increase in precipitation could cause acidification or accelerate pesticide leaching (Bertrand et al., 2012; Kløve et al., 2014). More frequent and more intense flood events could increase bacteria transport. On the other hand, a decrease in recharge may lead to decreased dilution, which is particularly important for the transport of pollutants concentration.

The temperature increase could pose a problem especially in smaller surface water bodies, such as intermittent lakes. It may have an impact on temperature dependant reaction rates and oxidation reactions, which further influence many biogeochemical processes (e.g., nitrogen and carbon cycle, fate and transport of pollutants; Kløve et al., 2014; Retter et al., 2020).

The species and habitats of KDGEs are regularly exposed to environmental stress and are therefore better adapted to natural fluctuations (water level, nutrients, temperature). However, changes triggered in fundamental ecological processes as a consequence of altered recharge and temperature regimes are difficult to predict and will most probably be regionally dependant. The composition and distribution of species will most likely depend on the intensity of environmental changes. It is likely that larger systems will be more resilient to environmental change. Nevertheless, the loss of specialist species can be expected.

The need to tackle the deterioration of aquatic ecosystems has been recognized by policy-makers and legislation has been adopted to halt further deterioration (Kløve et al., 2011b; Gunn, 2021). Some international treaties, such as the UN Convention on Biological Diversity, the Bern and Ramsar Convention on Wetlands, Natura 2000, IUCN Red List of Threatened Species and others, directly require preservation of biodiversity, water quantity and quality. Examples of legislation with similar aims on a regional level are e.g., European Water Framework Directive, Groundwater Directive and Habitats Directive, which form the basis for national legislation. In Switzerland, the Regulation for Water Pollution Control and in the USA the US Clean Water Act regulate water quality standards. On the other hand, the Slovenian Cave Protection Act represents a unique approach to the conservation of caves and the

monitoring of interventions, including their restoration (Ravbar and Šebela, 2015) but many sites still do not have any monitoring scheme or conservation action plan.

At least in the developed countries, many protection mechanisms have been evolved, but their provisions are rather general. They restrict selected human activities and determine, e.g., which species are protected to what extent, etc. However, not only selected species *per se* should be protected, but the entire ecosystem. Therefore, more precisely defined measures are necessary, but first a better understanding of the processes that determine groundwater dependant ecosystems, their biological function and their vulnerability needs to be assessed.

Conclusion

Karst groundwater dependant ecosystems are highly underexplored and lack information especially about the underground ecosystems and related ecohydrological processes. Although speleological research allows direct observation of water flow in aquifers, water caves are not always accessible and only form a part of the entire water network. Other access points to karst subterranean habitats, such as wells, provide easier access, but are also rare. Although surface KGDEs are more intensively studied, little is still known, how different environmental changes and pressures influence environmental conditions of individual KGDEs.

As KGDEs host a large number of endemic species, they are *a priori* threatened with extinction for this reason alone. Only a slight environmental change can cause the extinction of the most vulnerable species and possibly trigger complex feedback mechanisms that would lead to degradation of habitats. Since KGDEs (in particularly the subterranean ones) are unconnected habitats and not subject to majority of exogenous processes, repopulation is almost impossible. Once damaged, KGDEs may take a long time to recover, and the rehabilitation process is a difficult task. For these reasons, KGDEs must be holistically managed in an appropriate and careful manner. Because population worldwide rely on the same groundwater bodies that support KGDEs species for their freshwater needs, protecting groundwater quality and quantity benefits both wildlife and humans.

Appropriate protection requires a thorough understanding of the hydrogeology of karst aquifers and the specific processes of their groundwater dependant ecosystems. A step toward is the presented KGDEs classification that considers the special characteristics of karst environments and driving processes, and the interactions between different elements of the environment. By protecting these ecosystems, we also contribute to the benefit of mankind.

Knowledge gaps

- KGDEs are underexplored, therefore processes, vulnerability and impacts are poorly understood.
- More in-depth research and monitoring is needed, taking advantage of karst specific research methods and approaches (e.g., natural and artificial tracers monitoring, GIS and remote sensing, modeling).
- Due to the high regional biodiversity of the KGDEs with a high degree of endemism, regional studies are necessary.
- There are also gaps in knowledge about the impact of living organisms on the karst geomorphology.
- For proper protection of KGDEs, the recognition of indicator organisms, habitat specialists and the intensification of species variability and distribution monitoring is necessary.
- A more complete protection of KGDEs requires a shift of emphasis from protection of isolated groundwater ecosystem to protection of wider surface karst area. KGDEs are mainly ecotone habitats, below the surface or in the surface and land-use changes can pose a threat to populations.
- A fundamental understanding of KGDEs should lead to improved prediction of how KGDEs and their services will evolve and adapt under global challenges, with climate, land use and societal changes as the key drivers.

Important case study—Slovenian karst

Its location in the area of very high geodiversity and between different climate types place Slovenia among hot spots of biodiversity on a global scale (Culver et al., 2021). Slovenia is a small country within the EU, where half of the country is underlain by carbonate rocks. Due to long tradition of karst science development and an area of pioneering speleo(bio)logical research, it is considered the cradle of karstology (Gams, 2004; Shaw and Čuk, 2015).

The interaction between the orographic, climatic, hydrological and edaphic conditions, as well as the fact that the area served as a hub for various species and as a refuge during the glaciation periods determines the very high biodiversity of the country's karst areas. Due to deforestation in prehistoric times, man has even contributed to the diversification of the flora by creating space for the occurrence or expansion of habitats that are now considered natural (e.g., dry meadows; Kaligarič et al., 2006). An important factor for the preservation of a particularly rich diversity of karst flora and fauna is also the low level of human impact and the very well preserved landscape in its natural state.

A selection of the most important KGDEs in Slovenia is presented in Fig. 6 and Table 3.

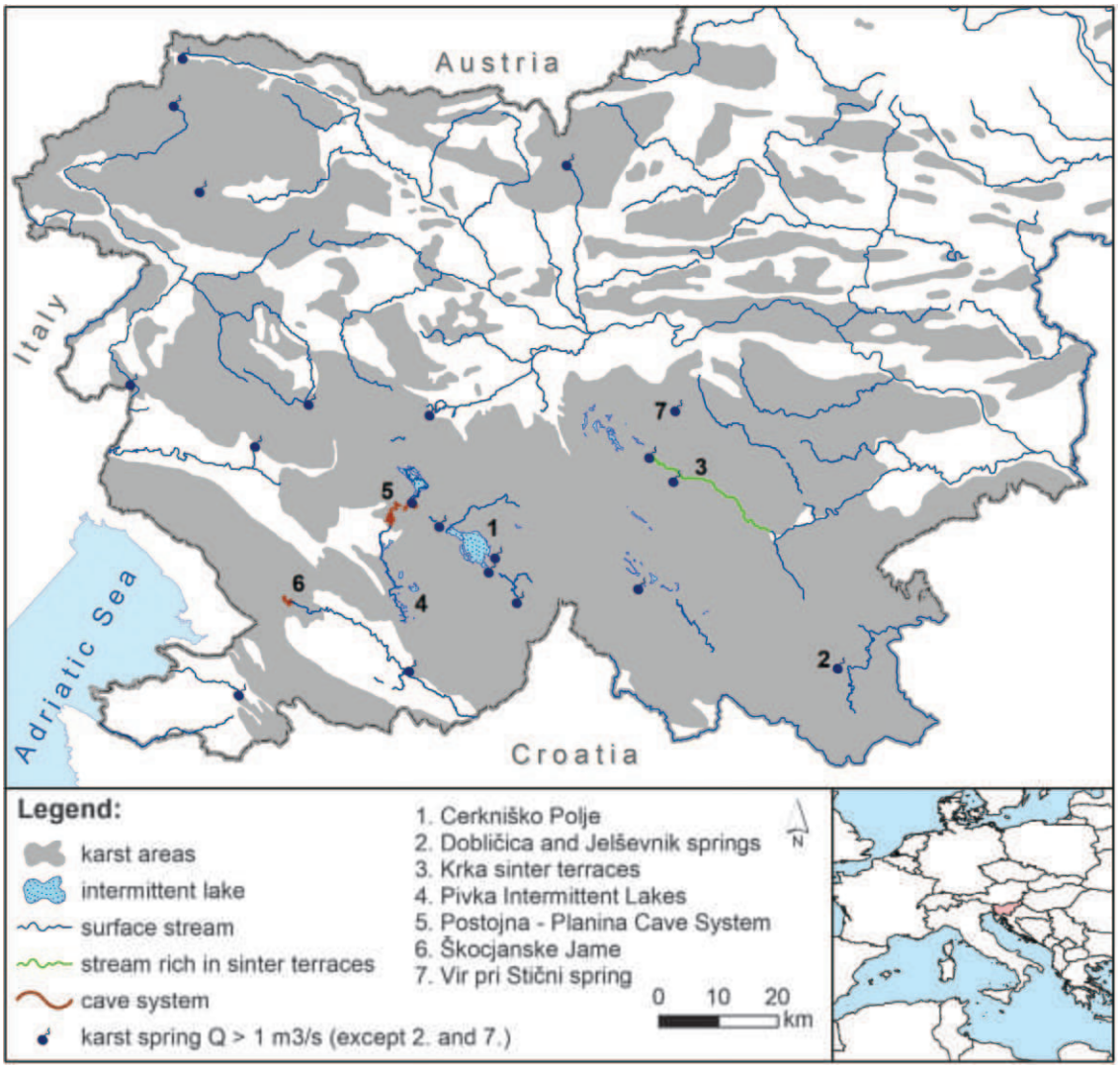

Fig. 6 Map of Slovenia showing karst areas and locations of selected KGDE sites. For more information about the selected sites see Table 3.

Table 3 A list of the main KGDE sites in Slovenia indicating type of ecosystem and charismatic groundwater species, compiled from the literature.

Name of location (in alphabetical order)	*Ecosystem type*	*Rare, endemic and/or iconic groundwater species*	*Selected reference*
Cerkniško Polje (Fig. 3F)	Karst polje	*Chirocephalus croaticus*	Brancelj (2003)
Dobličica, Jelševnik	Karst spring	*Proteus anguinus parkelj*	Sket and Arntzen (1994)
Krka sinter terraces (Fig. 3E)	Sinter terraces	*Kerkia kusceri, Paladilhiopsis kostanjevicae*	Bole et al. (1993)
Pivka Intermittent Lakes	Karst wetlands	*Chirocephalus croaticus*	Pipan (2005b)
Postojna-Planina Cave System (Fig. 3C)	Cave system, water cave	*Proteus anguinus anguinus*, *Velkovrhia enigmatica, Monolistra racovitzae racovitzae*	Culver and Pipan (2013)
Škocjanske Jame	Ponor cave	*Proteus anguinus anguinus*, *Zospeum spelaeum spelaeum, Marifugia cavatica, Dendrocoelum spelaeum, Elaphoidella karstica*	Prelovšek et al. (2021)
Vir pri Stični	Karst spring	*Proteus anguinus anguinus*	Sket and Velkovrh (1978)

For location of the sites see Fig. 6.

Acknowledgments

The contribution was prepared within the context of the projects Ecohydrological study of spatio-temporal dynamics in karst critical zones under different climate conditions, No. NK-0002, and Infiltration processes in forested karst aquifers under changing environment, No. J2-1743, and the programme Karst Research, No. P6-0119, all financially supported by the Slovenian Research Agency. Several EU projects are also acknowledged: eLTER Preparatory Phase Project (eLTER PPP), eLTER Advanced Community Project (eLTER PLUS) and "Development of research infrastructure for the international competitiveness of the Slovenian RRI space—RI-SI-LifeWatch."

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Groundwater Metazoans

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Biodeposition Deposition in the environment of biogenic material in the forms of feces and pseudofeces (expelled material unsuitable for food that has not passed in the digestive tract).
Bioturbation Reworking of sediments by animals by burrowing, ingestion, and defecation of sediment particles.
Chemolithoautotrophic bacteria Bacteria that acquire energy via the oxidation of inorganic compounds, including sulfide, methane, ammonium, iron, and manganese, which is then used to fix organic carbon for growth.
Ecosystem processes Ecological processes that control the fluxes of energy, nutrients and organic matter through the ecosystem. These include primary production, decomposition of dead organic matter and nutrient recycling.
Groundwater ecology The study of the interactions between groundwater organisms and their external environment, be it the immediate aquifer or a connected terrestrial system (*in* Hancock et al., 2005).
Groundwater habitats The subterranean open spaces within the rock and sediments that are partially or entirely filled with water. Habitats vary in terms of void space available to metazoans, interconnectedness of the voids and hydrological linkages to surface ecosystems.
Heterotrophic bacteria Bacteria that obtain their energy from the oxidation of organic compounds or fermentation. In groundwater, heterotrophic bacteria at the base of the food chain rely on inputs of dissolved and particulate organic matter from the surface environment.
Intrinsic vulnerability of aquifer The vulnerability of groundwater to human perturbations: it depends on the geological, hydrological, and hydrogeological characteristics of the aquifer but is independent of the nature of perturbations.
Molecular delimitation of species A diverse array of DNA-based methods to determine species boundaries.
Specialist groundwater species Species showing strict dependence on groundwater either because they complete their entire life cycle exclusively in groundwater or because they necessarily complete a part of their life cycle there. The term obligate groundwater species is also in use.
Species accumulation curve A plot of the cumulative number of species collected in a particular area as a function of the cumulative effort spent searching for them.
Troglomorphic syndrome A hypothesis predicting that specialist groundwater metazoans show convergent traits because of a convergent selective environment.

 https://doi.org/10.1016/B978-0-12-819166-8.00176-6

Introduction

Groundwater metazoans belong to the invisible component of biodiversity on Earth. Even groundwater scientists and managers outside the field of biological sciences have little awareness. For the public and media, life in groundwater is associated to the existence of a few hyper-specialized creatures that would naturally find their place in a cabinet of curiosities. As often, reality is very different from collective imagination: groundwater metazoans are many, show varying degrees of specialization and are likely to be found wherever there are open spaces within the water-filled subterranean rock and sediment matrix. Since shallow fresh groundwater represents by far the largest reservoir of liquid freshwater on Earth (Ferguson et al., 2021), and groundwater biologists have only explored a minor fraction of it, groundwater metazoans are likely to represent an important, yet largely underestimated, proportion of Earth's freshwater biodiversity (Culver and Holsinger, 1992; Sket, 1999).

The history of research on groundwater metazoans is marked by a series of influential events that explain the current state of our knowledge on their diversity, biological traits and roles in the ecosystem. The first mention of a blind and depigmented groundwater metazoan probably dates back to report of the Chinese hyaline fish *Sinocyclocheilus hyalinus* from the Alu Limestone caves, Yunnan, China by Jie in 1541 (Romero, 2001). Chen and Yang formally described that species in 1993. In Europe, J.W. von Valvasor commented in 1689 on the European cave salamander, *Proteus anguinus*, which was described 80 years later by J.N. Laurenti (Aljancic, 1993). However, the systematic inventory and sampling of groundwater metazoans only began at the beginning of the 20th century, notably with launching of the "Biospeologica" international research program (Racovitza, 1907). Biological exploration of groundwater was mostly restricted to caves until the sixties (Ferreira et al., 2007). Subsequently, it was extended to groundwater in all types of consolidated rocks and unconsolidated sediments thanks to the development of different sampling methods (Camacho, 1992a). Early attempts to explain geographic patterns of biodiversity focused on the importance of groundwater colonization from surface ancestors, leading to the formulation of different hypothetical scenarios of transition from surface to subterranean life (Howarth, 1987; Coineau and Boutin, 1992). This approach prevailed until the nineties when it was replaced by macroecological analyses that disentangled the relative influence of broad factors including spatial heterogeneity, climate and history on regional species richness and the size of species ranges (Culver et al., 2006; Eme et al., 2015).

Perhaps more than in any other habitat, evolutionary research is a hallmark of studies on life in groundwater (Juan et al., 2010; Kowalko et al., 2020). Since the sixties, the often-remarkable morphology of cave animals has stimulated on-going evolutionary research on the causes of reduced features, i.e. the lack of eyes and pigments, and the importance of convergent selective forces in shaping similar elaborated features—for example, the occurrence of elongated appendages—among distantly-related species (Christiansen, 1961, 1962). The search for convergent traits among specialist groundwater metazoans—a hypothesis often referred to as the troglomorphic syndrome—was extended to life history, behavioral and physiological traits in several taxon-specific studies (Ginet, 1960; Poulson, 1963; Hervant and Renault, 2002). Recent works have questioned the troglomorphic syndrome and emphasized divergent selective pressures that resulted in a diversity of phenotypes among groundwater metazoans (Culver and Pipan, 2015).

Until the seventies, caves were the basic physical unit in ecological studies. The concept of groundwater ecosystems, particularly the physical boundaries of groundwater ecosystems, were elaborated in the seventies thanks to Raymond Rouch's research at the Baget karst basin, France (Rouch, 1986). Rouch showed that the physical boundaries of the karst environment in which organisms interacted with each other extended well beyond the cave walls to include all the aquifer and its surface drainage basin. The concept of groundwater ecosystem was extended to groundwater in unconsolidated sediments (Marmonier et al., 2000; Danielopol and Griebler, 2008), and served as a basis for the study of the flow of energy and material in groundwater ecosystems (Simon, 2019). Groundwater ecology gained international recognition with the publication of the first textbook dedicated to that discipline in 1994 (Gibert et al., 1994a). The nineties brought new knowledge of the importance of interactions between surface water and groundwater in regulating fluxes of carbon, nutrients and organisms between the two ecosystems. A special emphasis was on the parafluvial—hyporheic zone, the interface between streams, groundwater and the riparian zone (Peralta-Maraver and Robertson, in press). Research led to the publication of the first book dedicated to the structure and function of surface water—groundwater ecotones (Gibert et al., 1997), a special issue on the hyporheic zone (Valett et al., 1993) and the first textbook on the interactions between streams and groundwater (Jones and Mulholland, 2000). Since the 2000s, functional ecology has become a prominent aspect of groundwater ecology. Major research developed along three directions: the structure and function of groundwater food webs (Venarsky and Huntsman, 2018), the role of metazoans on ecosystem processes (Marmonier et al., 2012), and the importance of metazoans in regulating important ecosystem services delivered by groundwater ecosystems to humans (Boulton et al., 2008; Griebler and Avramov, 2015).

Modern research on groundwater metazoans embraces concepts and tools from multiple disciplines to address questions on the evolution, distribution and functional role of biodiversity (Griebler et al., 2014). Studies are increasingly integrative to address intertwined questions such as (i) How many groundwater species are there? (ii) Where do they live and how are they distributed over space? (iii) How do they evolve? (iv) What are their roles in groundwater ecosystems? Here, we describe groundwater habitats, the composition of groundwater metazoan assemblages, and the characteristic features of specialist groundwater organisms. Then, we emphasize the role of metazoans in groundwater ecosystems and discuss how scientific knowledge on their diversity is reflected in current groundwater policies that frame the management of groundwater resources.

Groundwater habitats

It is difficult for most people to comprehend the notion of groundwater habitats because most are invisible to human eyes. For many people, their notion is limited to the subterranean areas they can access, the rivers and lakes in caves. For scientists and managers, it can be difficult finding a balance between using too specialized scientific terminology of habitat types and too broad and imprecise descriptions. The tendency among scientists to name each of the subterranean habitats that they discovered has led to a profusion of specialized terms that are impenetrable to most readers (Camacho, 1992b). Conversely, the typology of freshwater habitats used in the European red list of habitats includes 25 items devoted to surface water but all groundwater habitats are grouped into a single item "Underground standing and running waterbody" (Jansen et al., 2016). It is important, yet often difficult to avoid classifying groundwater habitats based on the organisms they contain. Here, we provide a physical characterization of groundwater habitats, emphasizing abiotic characteristic features that are likely to account for differences in the composition of metazoan assemblages among different groundwater habitat types.

A simple way to comprehend habitats is to view groundwater as a sponge-like matrix in which water circulates through an interconnected network of voids. Voids are open spaces within the rock and the sediments, which provide the habitats for groundwater metazoans. The voids can be partially or entirely filled with water, a characteristic that is used by hydrogeologists to distinguish between the unsaturated (or vadose) and saturated zones of aquifers. Three characteristics of the voids can be used to classify habitats: void size, their degree of connectedness and their degree of connection with the surface environment.

Void size influences the diversity of organisms by setting an upper limit on the maximal body size (Pipan and Culver, 2017). Void or pore size is different from porosity, which defines the entire volume of the void space in the aquifer. Hence, clay has a higher porosity than sand but pore size is too small (1–10 μm) for harboring metazoans other than burrowers. The pore space available between sand particles allows for the occurrence of meiofaunal organisms (body size: 63–1000 μm), whereas macroinvertebrates (body size >1 mm) can be found in gravel aquifers. Pore space is no longer a physical constraint in carbonate rocks where the size of fissures is considerably enlarged by weathering of the parent rock. Cave water bodies may thus harbor large groundwater organisms including amphibians and fish (Proudlove, 2006).

In groundwater, water flows from high to low energy-head locations but the ability of the aquifer to transmit water depends on having connected pores. This ability is referred to as permeability. Permeability is another important feature to classify groundwater habitats because it influences the fluxes of nutrients, dissolved oxygen (DO) and organic carbon that supports life. Interconnectedness of the voids may also influence the movement of animals, hence their foraging capacity, although no experiments have yet tested this hypothesis. Cornu et al. (2013) used information on groundwater flow type, void size and permeability contained in the international hygrogeological map of Europe to provide the first groundwater habitat map for Europe (Fig. 1). The map portrays the

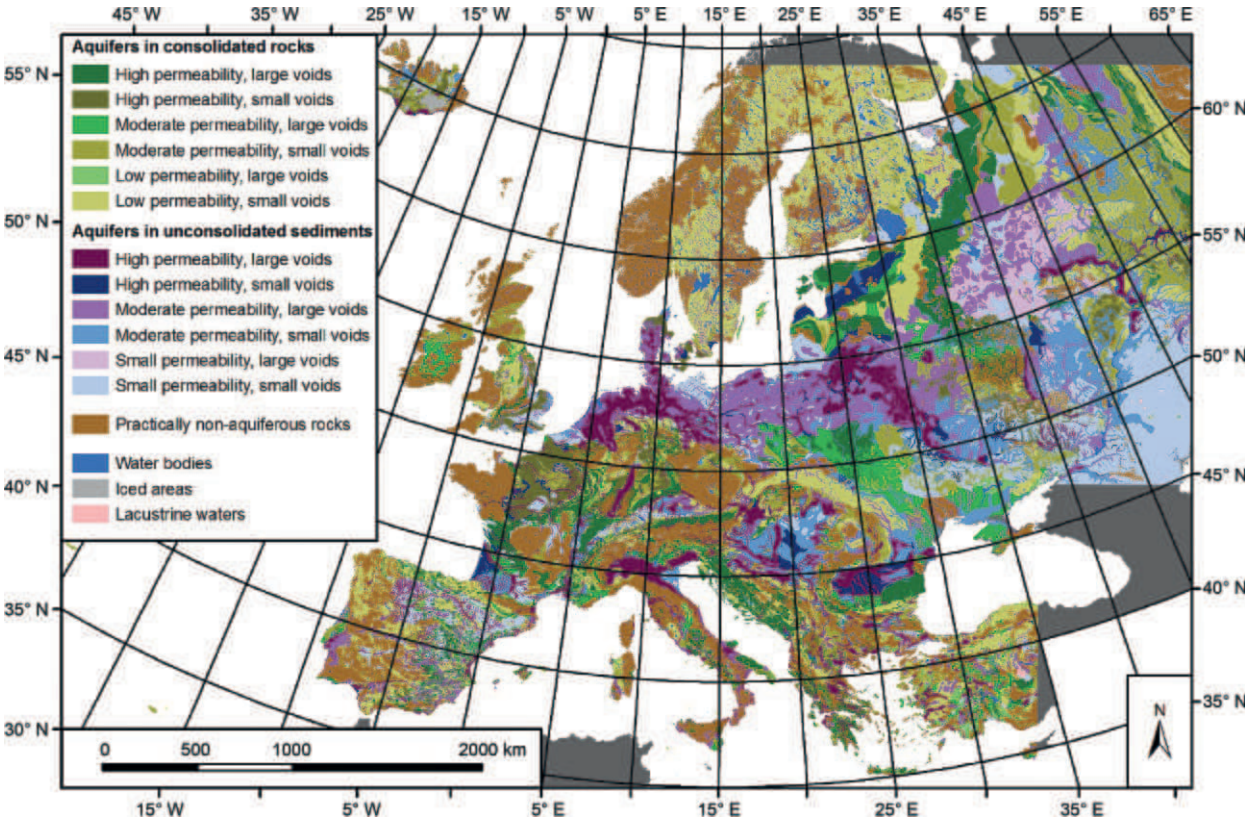

Fig. 1 The groundwater habitat map of Europe (Lambert azimuthal equal-area projection). From Cornu JF, Eme D, and Malard F (2013) The distribution of groundwater habitats in Europe. *Hydrogeology Journal* 21: 949–960.

areal distribution of 13 habitats types and it has provided a useful resource for testing the role of groundwater habitat area and heterogeneity on geographic patterns of species richness in Europe (Eme et al., 2015; Bregović and Zagmajster, 2016).

Another key feature for ecologically classifying groundwater habitats is their degree of connection to the surface environment, which strongly influences their temporal variability and the amount of organic resources they receive from surface terrestrial and aquatic ecosystems (Hahn, 2009). This feature was not integrated into the groundwater habitat map of Europe (Fig. 1). It is difficult to assess at the landscape scale but several hydrogeological surrogates are becoming available. One potential surrogate is depth to the groundwater table. The annual thermal amplitude of groundwater temperature decreases with increasing depth below the soil surface, until it becomes constant throughout the year at a depth of about 10–15 m. There is an inverse relationship between the concentration of dissolved organic carbon (DOC) in groundwater and vadose zone thickness, indicating stronger DOC retention with increasing water residence time in the vadose zone (Pabich et al., 2001). However, depth to the groundwater table may be a poor surrogate of hydrological connection to the surface in karst aquifers where conduit flow in pipe-like channels can result in short travel time of water despite considerable distances from the soil surface. Another surrogate is intrinsic vulnerability of the aquifer, a hydrogeological feature that is becoming easier to characterize and map due to the development of geographical information system-based methods (Machiwal et al., 2018).

Pore size, permeability and hydrological connectivity to the surface are hydrogeological features that have gained a large consensus among groundwater ecologists for characterizing groundwater habitats (Hahn, 2009; Cornu et al., 2013; Weitowitz et al., 2017). Hydrogeological criteria accounted for the largest proportion of variance in groundwater metazoan composition among sites in a number of studies (Dole-Olivier et al., 2009a; Hahn and Fuchs, 2009; Johns et al., 2015; Korbel and Hose, 2015). However, features such as permeability and pore size are often qualitatively assessed using geologic types of aquifers as surrogates rather than quantitatively measured in the field. However, most aquifers are intrinsically heterogeneous and exhibit changes in hydraulic conductivity and pore size over short distances, which may affect the distribution of metazoans. In addition, hydrogeological criteria do not account for regional variation in the composition of groundwater metazoans that may result from historical events such as the longstanding effect of Quaternary glaciers (Foulquier et al., 2008).

Composition and diversity of groundwater metazoan assemblages

Generalist and specialist species

Groundwater metazoan assemblages are often a mix of species that show different degrees of dependence on the groundwater environment. That extent of dependence has been widely used to classify groundwater species into different ecological categories. The categories shown in Fig. 2 were published by Gibert et al. (1994b) in the first edition of the Groundwater Ecology textbook. They apply specifically to aquatic species and groundwater in unconsolidated sediments, including the hyporheic zone. Yet, they are similar to earlier categories proposed by Schiner (1854) and Racovitza (1907) for the subterranean environment in general. Gibert et al. (1994b) recognized three top categories, two of them are further subdivided into subcategories. Stygoxenes have no affinities with groundwater: they occur accidentally in groundwater. For example, black fly insect Larvae (Simulidae) can be passively transported into caves. Stygophiles comprise three subcategories of species that all have higher affinities for the groundwater environment than do stygoxenes. The occasional hyporheos are essentially insects whose early instar larvae can reside in the hyporheic zone, whereas later life stages occur in the surface stream. Amphibite species have a life cycle that necessitates both a groundwater and surface water stage. The stonefly *Isocapnia* spends all its larval stage in deep layers of the hyporheic zone before dispersing to surface stream and emerging as mating adults (Stanford and Gaufin, 1974). The permanent hyporheos comprises species with no aerial stage, including nematodes, oligochaete worms, crustaceans and tardigrades that can complete their entire life cycle either in surface water or in groundwater. The last category, the stygobites (or stygobionts) are obligate groundwater species that complete their life cycle exclusively in groundwater. Gibert et al. (1994b) further distinguished between phreatobite (phreatobiont) species that are restricted to the deep strata of alluvial aquifers and ubiquitous stygobiont species that occur in a large variety of groundwater habitats.

In an article to be published in the second edition of the Groundwater Ecology textbook, Culver et al. (in press) argumentatively questioned the need and justification for such an elaborated classification and terminology of groundwater metazoans. Their argument is twofold. First, the terminology is meaningless to most non-subterranean biologists, whereas many terms have equivalence in the general ecological literature. Instead, they propose to use the more general terms of specialist and generalist species. Specialist groundwater species have a strict dependence on groundwater because they complete their entire life cycle exclusively in groundwater (stygobites) or because they necessarily complete a part of their life cycle there (amphibites). Generalist species exploit a wide range of resources that they can draw from both groundwater and surface water (occasional and permanent hyporheos), and trogloxenes can be referred to as surface water specialist species. Second, the terminology derives from the idea that the composition of groundwater communities shows a distinct zonation with predictable changes in the relative proportion of the different categories of species with distance to the surface environment. Yet, studies conducted in different surface water—groundwater transition zones (ecotones), including springs (Plenet et al., 1992), sinking karst rivers (Vervier, 1990) and the hyporheic zone (Peralta-Maraver et al., 2018) showed that zonation of groundwater communities, when it exists at all, are temporary and strongly influenced by the intensity and direction of water fluxes between surface and groundwater environments. Hence, groundwater specialists may occur in the upper sediment layers of the streambed in areas of groundwater upwelling, whereas generalists may occur at greater depths into the streambed in areas of strong surface water downwelling. Compositional shifts in

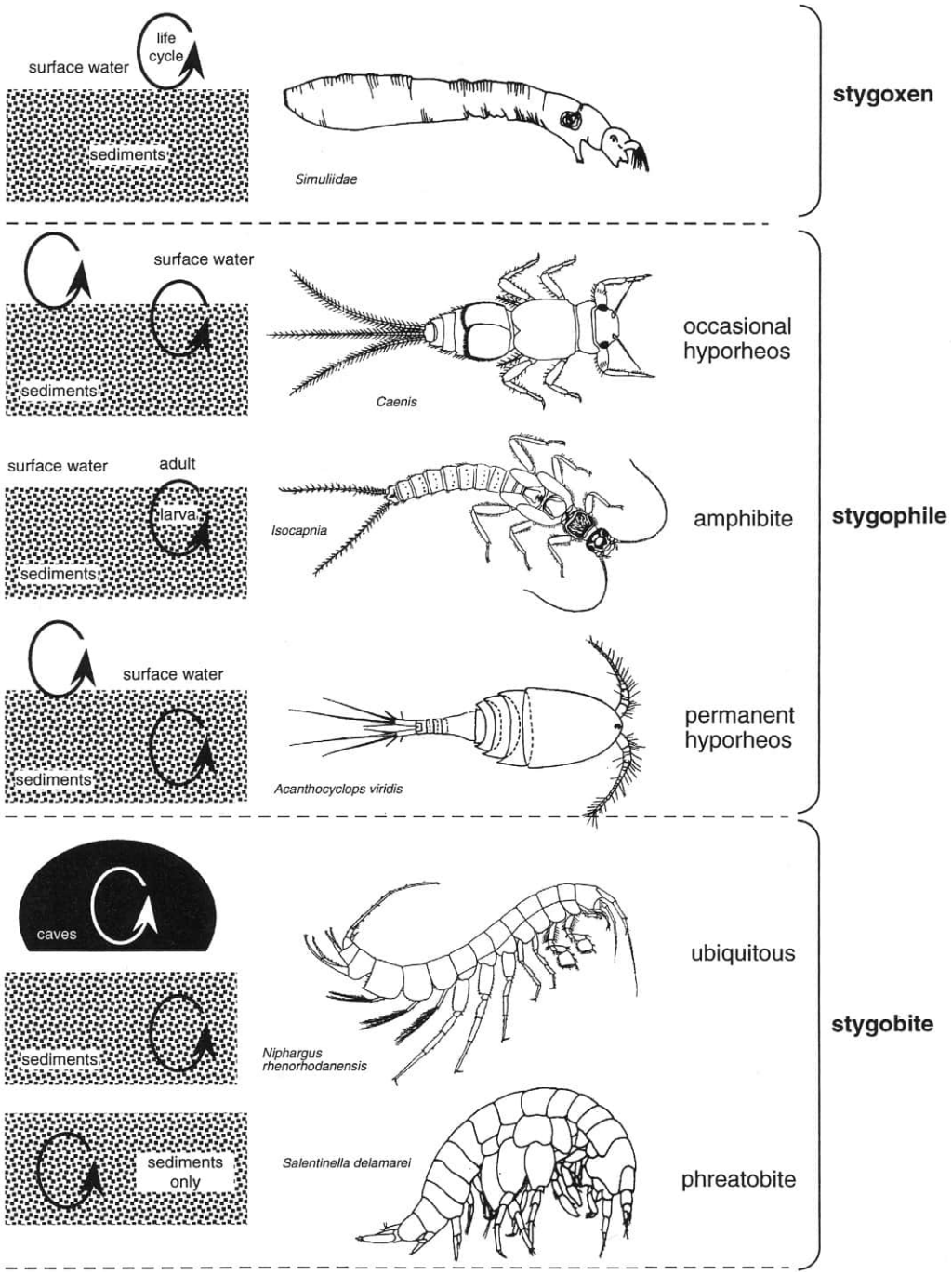

Fig. 2 A classification of metazoans based on their extent of dependence on groundwater. From Gibert J, Stanford JA, Dole-Olivier M-J, and Ward JV (1994) Basic attributes of groundwater ecosystems and prospects for research. In: Gibert J, Danielopol DL, and Stanford JA (eds.) *Groundwater Ecology*, pp. 7–40. San Diego, USA: Academic Press.

groundwater communities are also influenced by biotic factors. In their clinal model of interstitial communities, Brunke and Gonser (1999) proposed that the colonization of deep groundwater by generalist taxa was limited by the availability of organic matter, whereas the colonization of shallow groundwater by obligate groundwater species was restricted by interference competition with generalists. There may also be substantial variation in the habitats occupied by different populations within the same species. Eme et al. (2014) found that populations of the eyeless and depigmented isopod *Proasellus valdensis* were restricted to subterranean habitats of low elevation, whereas they formed dense populations in surface aquatic bryophytes extending several meters downstream of high-elevation Alpine springs.

How many species are there?

Estimates of the number of specialist groundwater metazoan species at global to continental scales are scarce. The faunistic, distributional and ecological synthesis of the World fauna inhabiting subterranean waters published by Botosaneanu (1986) contained more than 5500 species of metazoans. From the synthesis of the European PASCALIS research project, Deharveng et al. (2009) enumerated 1047 specialist groundwater metazoan species in western-central Europe (Belgium, France, Italy, Portugal, Slovenia and Spain). A total of 1570 obligate groundwater crustacean species are known from Europe (Zagmajster et al., 2014). Groundwater metazoans are dominated by crustaceans (Fig. 3; Dole-Olivier et al., 2015): they represent more than 70% of species known in western-central Europe, followed by mollusks (16%) and oligochaete worms (6.1%) (Deharveng et al., 2009). Stoch and Galassi (2010) showed that the number of obligate groundwater crustaceans in Europe exceeded the number of surface-dwelling crustacean species, even though their description lagged behind that of surface species (Fig. 4). Many groundwater crustacean taxa are either phylogenetic relicts (i.e., they have no close living relatives) or distributional relicts (i.e., relatives are in disjunct geographical areas) (Humphreys, 2000).

Species numbers provided above are underestimations of the true number of species for three reasons. First, a small fraction of the Earth's groundwater has been sampled. Second, even in highly sampled regions, species accumulation curves never reach saturation because of the high proportion of species with extremely narrow ranges (Dole-Olivier et al., 2009b). Third, molecular delimitation of species indicates many species are overlooked by traditional morphological taxonomy. In a Europe-wide study of groundwater niphargid amphipods and asellid isopods, Eme et al. (2018) found that molecular delimitation provided putatively 2.5 times more species than morphological delimitation. Breakthroughs in molecular methods can considerably speed up the inventory of groundwater species. Species molecular inventory has simultaneously shifted from the sampling of specimens to that of environmental DNA (eDNA) and to the identification of a single organism (barcoding) to the simultaneous identification of a whole community (metabarcoding) (Niemiller et al., 2018; West et al., 2020).

Explaining the richness of groundwater species within clades

Here, we briefly draw the reader's attention to the inherent difficulty of disentangling the relative influence of processes that influence the number of extant obligate groundwater species within a clade. That number directly depends on the addition of species through speciation and their subtraction through extinction over time (Scholl and Wiens, 2016). Extinction of groundwater

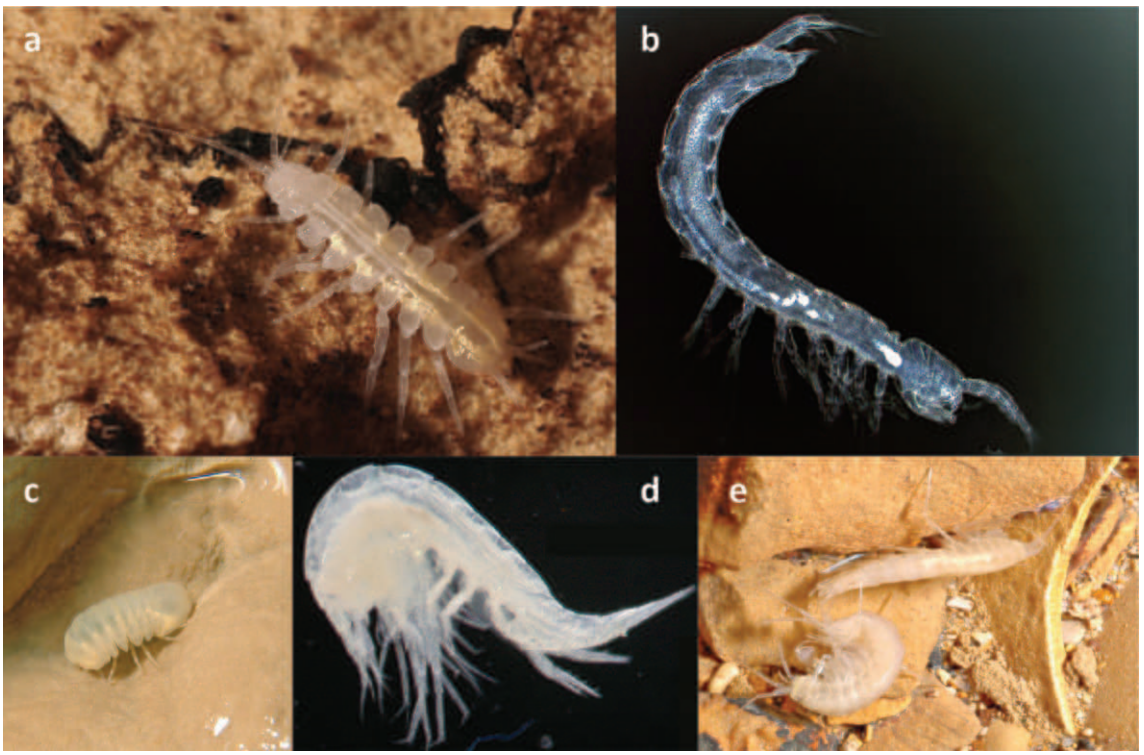

Fig. 3 Photos of obligate groundwater species. (A) *Proasellus valdensis* (Isopoda, Asellidae, body length (BL): 8 mm); (B) *Parabathynella* sp. (Bathynellacea, Parabathynellidae, BL: 1.5 mm); (C) *Caecosphaeroma virei* (Isopoda, Sphaeromatidae, BL: 10 mm); (D) *Salentinella* sp. (Amphipoda, Salentinellidae, BL: 2 mm); (E) *Niphargus rhenorhodanensis* (Amphipoda, Niphargidae, BL: 15 mm). (A), (C), (E) Courtesy of Robert Lepennec. (B) From Dole-Olivier M-J, Galassi DMP, Fiers F, Malard F, Martin P, Martin D, and Marmonier P (2015) Biodiversity in mountain groundwater: The Mercantour National Park (France) as a European hotspot. In: Daugeron C, Deharveng L, Isaia M, Villemant C, and Judson M (eds.) Mercantour/Alpi Marittime All Taxa Biodiversity Inventory. *Zoosystema* 37(4): 529–550.

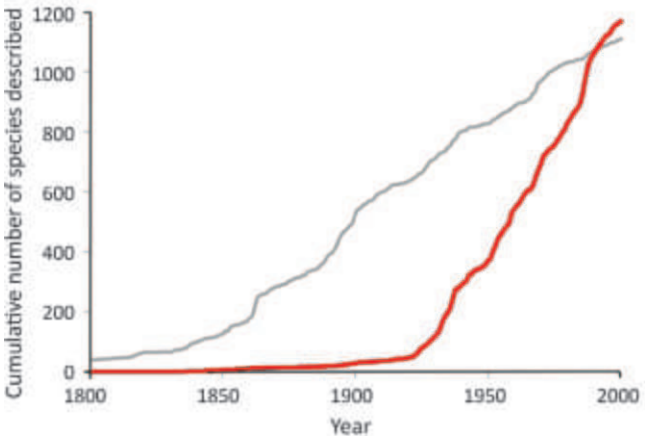

Fig. 4 Cumulative number of European crustacean species described against year for surface water (gray line) and groundwater (red line). Modified from Stoch F and Galassi DMP (2010) Stygobiotic crustacean species richness: A question of numbers, a matter of scale. *Hydrobiologia* 653: 217–234.

species is difficult to quantify in the absence of fossil records. It may be high because of the narrow ranges of many species (Hugueny et al., 2011) or low because of the environmental stability of deep groundwater layers (Mammola et al., 2018) and it is expected to vary strongly across regions (Zagmajster et al., 2014). Speciation events that can contribute to the addition of species are of two types. The first is that of a speciation occurring during the transition of a surface ancestor to groundwater. The second is that of a speciation caused by the divergence of populations of an obligate groundwater species. Ecological and/or non-ecological processes may drive both types of speciation (Van Bocxlaer, 2017). The difficulty is that the two types of speciation cannot be distinguished by phylogeny alone (Trontelj, 2019), unless molecular markers can be used to pinpoint when transitions from surface water to groundwater occurred along branches of a phylogeny (see e.g., Lefébure et al., 2017). Until these markers or any other alternative approaches are available and robust, the relative contribution of transition from surface to groundwater life and groundwater speciation events to groundwater species diversification cannot be quantified.

Geographic distribution patterns and their explanations

Species richness

Attempts to document global patterns of species richness of obligate groundwater metazoans are few. Culver and Pipan (2013) mapped the worldwide distribution of biodiversity hotspots, defined as sites containing more than 25 obligate groundwater species (see also Pipan et al., 2020). Zagmajster et al. (2018) mapped the number of obligate groundwater crustacean species per country (corrected for country area). Both studies indicated species richness was highest in temperate regions, not in the tropics. The reasons for this unusual pattern are unclear: the tropics are undersampled or some factors limit biodiversity at upper bounds of productivity.

Continental patterns of groundwater crustacean species richness are well documented for Europe (Deharveng et al., 2009; Eme et al., 2015). When mapped using 10,000 km^2 grid cells, species richness of crustaceans peaks at mid latitudes ranging from ca 42° to 46°N. At these latitudes, the combined beneficial effects of a high surface productivity and high groundwater habitat heterogeneity on groundwater species richness are not counteracted by cold (northern Europe) or arid (southern Europe) historical events (Eme et al., 2015). Mapping of biodiversity hotspots of groundwater harpacticoid crustaceans in Europe using a multi-metric approach also revealed the important roles of historical factors and habitat heterogeneity (Iannella et al., 2020).

Range size

Groundwater obligate species often exhibit a small range size, some being restricted to a single aquifer. Yet, range sizes show large geographic variation. In Europe, Zagmajster et al. (2014) showed that the median range size of groundwater crustacean assemblages increased markedly with latitude above a latitudinal threshold of 43°N (Fig. 5). They demonstrated that this pattern was best accounted for by the effect of temperature anomaly—the difference in mean annual temperature between the present and the last glacial maximum—which was used as a surrogate for long-term climatic variability. Three non-mutually exclusive explanations were proposed to explain why species showed larger ranges in northern regions of high historic climate variability. These are a disproportionate extinction of small-range taxa, a stronger selection for generalism and vagility, and colonization of vacant habitats by species showing high dispersal ability following cold periods (Zagmajster et al., 2014).

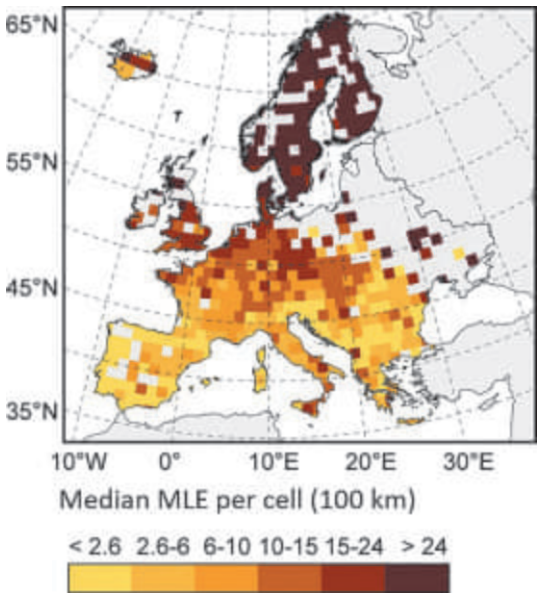

Fig. 5 Geographic distribution of median range size of obligate groundwater crustacean species in Europe. The maximum linear extent (MLE) is the straight-line distance between the two most distant known localities of a species. Grid cell area is 10,000 km^2. From Zagmajster M, Eme D, Fišer C, Galassi D, Marmonier P, Stoch F, Cornu JF, and Malard F (2014) Geographic variation in range size and beta diversity of groundwater crustaceans: Insights from habitats with low thermal seasonality. *Global Ecology and Biogeography* 23: 1135–1145.

Community composition

A striking feature of groundwater metazoan communities is their high spatial turnover. Species composition differs markedly among aquifers within a region as well as among regions within a continent. In Europe, Malard et al. (2009) showed that dissimilarity in species composition between karst aquifers and unconsolidated sediment aquifers of six European regions increased with increasing regional species richness. Dissimilarity among karst aquifers increased with regional species richness but there was no significant relationship for unconsolidated porous aquifers. Zagmajster et al. (2014) found that spatial turnover in species composition among regions increased with decreasing latitude. A number of explanations were put forward to explain these patterns. First, high species turnover in species-rich regions that have experienced a long historically stable environment reflects the addition of species over time and short dispersal from their place of origin. Second, competition among species may promote habitat specialization and reduction in species range. Third, lower hydrological connectivity among karst aquifers than among unconsolidated porous aquifers reduces dispersal.

Species traits

Describing and explaining the phenotypes of groundwater species, including morphological, behavioral, life history and physiological traits, would warrant a full chapter. Here, information is restricted to the description of two contrasted, yet non-mutually exclusive, views of trait variation among groundwater species. An organism's lifetime reproductive output depends on a number of components including fecundity, mating success and survival (Pincheira-Donoso and Hunt, 2017). Environmental selective pressures induce changes in phenotypic traits that influence each of these components of fitness. Of course, interactions do occur among these components, known as trade-offs (Stearns, 1992): a large body size female can produce more or larger eggs (fecundity increases), but the probability that it is caught by predator may increase (survival rate decreases).

An historical view of groundwater species traits is that of convergence by which distantly related species show similar phenotypes because of a convergent selective environment that includes no light, reduced food availability and low environmental variability (Culver and Pipan, 2015). This hypothesis referred to as the troglomorphic syndrome (Christiansen, 1962, 2012) was originally formulated for morphological traits but it was then extended to physiological and life history traits. Reduced eyes, loss of pigment and development of non-visual sensory systems occur in almost all groundwater obligate metazoans. Loss-of-function mutations under conditions of relaxed selection for pigmentation and light detection caused loss of pigment and visual photoreceptors in species as different as groundwater diving beetles (Leys et al., 2005), cave fish (Protas et al., 2006; Niemiller et al., 2013), cave planthoppers (Bilandzija et al., 2012) and asellid crustaceans (Lefébure et al., 2017). In the Mexican cave fish *Astyanax mexicanus*, the same pleiotropic genes control the reduction of eyes and development of non-visual sensory receptors such as the number of taste

buds (Yamamoto et al., 2009) and the number of superficial neuromasts within the cavefish eye orbit (Yoshizawa et al., 2012). A physiological trait that is supposedly common among specialist groundwater metazoans is their capacity to withstand starvation and hypoxia (Hervant and Malard, 2019). That capacity results from a combination of traits including a high-energy reserve (mainly lipid stores), low energetic requirements, and a depressed locomotory and metabolic activity during stress (Hervant and Renault, 2002). The troglomorphic syndrome hypothesis also predicts that specialist groundwater metazoans show *k*-selected life history strategies, which include maturity at older ages, slower growth rate, longer life span, fewer but larger eggs per reproductive event, and a higher or more irregular number of reproductive events per lifetime than their surface relatives (Fišer, 2019). However, data on physiological and life history traits of groundwater metazoans are few, concern a limited number of model taxa, and are from inter-specific comparative studies of groundwater and surface water species that do not account for phylogenetic relationships among taxa (Fišer, 2019).

Another more recent and potentially more realistic view emphasizes the non-uniform and hence divergent evolution of species traits among specialist groundwater metazoans (Culver and Pipan, 2015). Konec et al. (2015) examined morphological changes in two surface-subterranean population pairs of the isopod *Asellus aquaticus* and found that only 18 traits of 63 evolved convergently. There are at least two reasons why divergence may be common. First, the only selective pressure that acts repeatedly across all subterranean habitats is the absence of light. This important pressure may have cascading effects: prey may develop characteristic morphologies to escape predators, which rely on non-visual receptors for foraging. However, many other selective pressures including the size of voids, water current, temperature seasonality, and the availability of food and DO can vary markedly among groundwater habitats. Accordingly, a number of traits including body size and appendage length (Trontelj et al., 2012; Delić et al., 2016; Pipan and Culver, 2017), thermal tolerance (Mermillod-Blondin et al., 2013), resistance to starvation (Salin et al., 2010), and metabolic rate (Simčič and Sket, 2019) vary markedly among groundwater metazoans. However, identifying the combination of environmental pressures responsible for these variations has remained a difficult task. Second, a particular selective pressure may imply different responses in terms of trait evolution. The loss of eyes may be compensated by an increase in the size of sensory organs (e.g., antennae), the number of sensory units or a change in locomotory behavior leading to an improved food finding ability.

Functional roles of metazoans

Indirect and direct effects of metazoans

The potentially important role of organisms in maintaining hydraulic attributes of sediments and ecosystem processes in the hyporheic zone and shallow alluvial groundwater have been the subject of several reviews (Boulton, 2000; Boulton et al., 2008; Marmonier et al., 2012). Metazoans act as ecosystem engineers: they modify the habitats of microorganisms through their bioturbation and biodeposition activities. By building and irrigating biogenic structures such as tubes and burrows, they modify the movement of water (Hose and Stumpp, 2019), and they increase the fluxes of nutrients and DO available to microorganisms (Navel et al., 2012). Metazoans also expel fecal pellets and pseudofeces that inoculate the sediment with bacteria and serve as organic-matter rich substrates for microbial colonization and exploitation. Grazing of biofilm by metazoans promotes the turnover of microbial communities, thereby potentially stimulating their productivity and respiration activity (Boulton et al., 2008). Mermillod-Blondin (2011) proposed that the influence of metazoans on ecosystems processes in sediment was controlled by the interaction between functional species traits and interstitial flow rate (Fig. 6). They emphasized five species traits of importance for determining the significance of bioturbation and biodeposition: sediment mixing rate, burrowing depth, the type of biogenic structures (tubes and burrows), bioirrigation rate and biodeposition rate. They further proposed that the effects of bioturbators and biodepositors on sediment metabolism would be high in sedimentary habitats with low interstitial water flow rates (diffusion-dominated habitats in Fig. 6), but considerably reduced in habitats with high flow rates (advection-dominated habitats in Fig. 6). Thus, U-shaped tube burrowers and gallery-diffusor invertebrates increase microbial respiration in diffusion-dominated sediments by up to 250%, but only by up to 50% in advection-dominated sediments (Mermillod-Blondin, 2011). Although the proposal in Fig. 6 is essentially for water-sediment interfaces and it has been validated with aquatic surface metazoans such as tubificid worms, chironomid larvae and asellid isopods, it provides a solid conceptual framework for assessing the functional role of specialist groundwater metazoans.

Despite growing recognition of the potentially important role of metazoans in groundwater ecosystems, quantitative studies are still rare, essentially because of the difficulties to breed and manipulate obligate groundwater metazoans in the laboratory. Studies provided equivocal results, potentially reflecting large differences in the role of species and strong density effects. Foulquier et al. (2010) showed that the bioturbation/feeding activity of the amphipod *Niphargus rhenorhodanensis* significantly increased DO removal in the uppermost layers of flow through sediment columns, but it did not affect the number and biomass of bacteria. Microbial production and activity were essentially influenced by fluxes of DOC (bottom-up control) and the feeding rate of *N. rhenorhodanensis* was too low to regulate bacterial biomass (top-down effect). In contrast, the cave isopod *Caecidotea tridentata* was shown to stimulate the abundance and activity of attached bacteria (Edler and Dodds, 1996), and the cave amphipod *Gammarus minus* to reduce the bacterial production on rocks (Cooney and Simon, 2009). Weitowitz et al. (2019) demonstrated that the amphipod *N. fontanus* and isopod *P. cavaticus* increased protozoan abundance in biofilm attached to stone tiles, but they did not affect bacterial abundance. The number of protozoans also increased over time in the presence of the amphipod *N. kochianus* and the effect was more pronounced with high density of amphipods. Hose and Stumpp (2019) showed that even in low numbers,

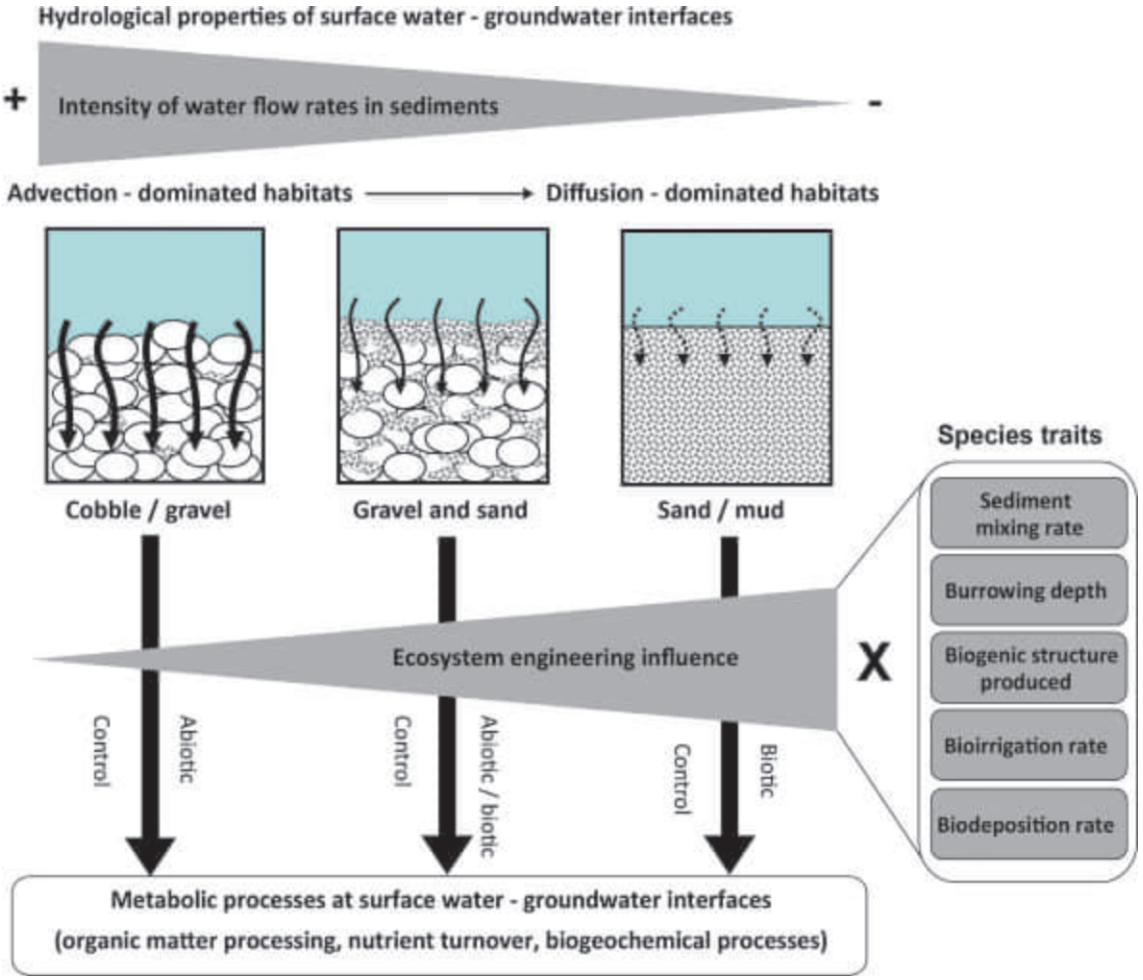

Fig. 6 The intensity of water flow rate in sediments and functional species traits interact to determine the influence of metazoans on metabolic processes. Modified from Mermillod-Blondin F (2011) The functional significance of bioturbation and biodeposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems *Journal of the North American Benthological Society* 30(3): 770–778.

the amphipod *N. inopinatus* maintained the amount of pore space that actively contributed to water flow in sediment columns. Although microcosm experiments provide growing evidence that metazoans influence hydraulic properties of sediment and ecosystem processes that sustain important ecosystem services such as groundwater provision and purification, research is needed to upscale these microcosm observations at the aquifer scale (but see Boulton et al., 2008).

Food webs

Metazoans directly contribute to energy flow through groundwater ecosystems via trophic linkages. Until the 2000s, groundwater food webs were predicted to be relatively simple, having no autotrophs and strict predators, and containing up to two trophic levels predominantly occupied by generalist consumers and omnivores (Gibert and Deharveng, 2002). However, the quantitative investigation of trophic linkages using stable isotope analysis, compound specific isotope analysis on amino acids and DNA metabarcoding of bacteria in the gut of metazoans is offering a new perspective of groundwater food webs (Saccò et al., 2019, 2021). First, groundwater food webs are primarily fueled by microbial biomass but the importance of biomass produced by chemolithoautotrophic bacteria relative to that of heterotrophic bacteria might have been under-estimated (Hutchins et al., 2016; Venarsky et al., 2018). The study by Herrmann et al. (2020) suggested that biomass produced by chemolithoautotrophy represented a rather stable resource that supported complex food webs with several trophic levels in oligotrophic groundwater. Second, François et al. (2016) recently challenged the assumption of generalist feeding by demonstrating that some cave isopod species showed a strong trophic specialization on sedimentary biofilm, a resource that is both abundant and stable in caves. Third, feeding sources appear to vary both among and within species with the abundance of resources in the environment. Francois et al. (2020) showed that asellid isopods, among which there are a number of obligate groundwater species, fed more selectively when the availability of

resources in the environment was high. Saccò et al. (2021) showed that high rainfall periods triggered a trophic cascade effect: increased input of organic matter led to proliferation of microbial biofilm that was grazed by primary and secondary consumers (copepods and amphipods), which constituted the prey of top predators (larvae and adults of beetles). Fourth, groundwater food chains are longer than previously thought because they contain four or even five trophic levels and include strict predators in the most species-rich aquifers (Hutchins et al., 2016; Premate et al., 2021).

Conclusion/outlook

Groundwaters contain diverse assemblages of metazoans that represent an important yet underestimated component of the Earth's freshwater biodiversity (Deharveng et al., 2009). The characteristic traits of obligate groundwater metazoans are sources of unexpected scientific discoveries that have wide theoretical and applied implications (Griebler et al., 2014; Mammola et al., 2020). Metazoans play a potentially important, albeit insufficiently documented role, in maintaining goods and services delivered by groundwater ecosystems to humankind (Boulton et al., 2008; Griebler and Avramov, 2015). Yet, they are neither recognized as conservation priorities, nor integrated into management policies of groundwater resources (Mammola et al., 2019). In Europe, the assessment of groundwater resources is still exclusively based upon criteria of water quality and aquifer productivity, whereas that of surface water bodies is largely based upon the concept of ecological status. This discrepancy has persisted since the 2006 iteration of the European groundwater directive, even though methods have been developed for assessing the health of groundwater ecosystems (Korbel and Hose, 2017), estimating the risk that groundwater alterations may pose to metazoans (Strona et al., 2019) and defining conservation priorities for groundwater metazoan communities (Michel et al., 2009; Asmyhr et al., 2014). Methods relying on metazoans are diverse, using either the composition of local metazoan communities (Korbel and Hose, 2017), exposure of sentinel organisms (Marmonier et al., 2018), or toxicity tests (Di Lorenzo et al., 2019; Castaño-Sánchez et al., 2021). Given the high diversity, important role and bioindicator value of groundwater metazoans, there would be substantial benefits in fully integrating them into conservation planning, monitoring practices, and assessment schemes for groundwater in the future.

Knowledge gaps

- The groundwater metazoan fauna is yet to be surveyed in many regions of the World: molecular methods for sampling, identifying and delimiting species can significantly contribute to fill knowledge gaps on the diversity and geographic distribution of groundwater metazoans.
- Comparative studies of surface and groundwater metazoans are key for understanding eco-evolutionary shifts during transition to novel habitats. This understanding has long been from comparisons of cave and surface dwelling populations. Phylogenetic comparative analyses of clades containing multiple surface and groundwater species are needed to consider evolutionary processes taking place over time periods longer than the lifespan of natural populations.
- Studies of species traits, including morphological, behavioral, physiological, and life-history traits, are crucial to understand how variation in selection pressures within groundwater shape the diversity of phenotypes. A next important step is linking phenotypes to the role of organisms in ecosystem processes.
- In functional ecology, a significant research effort is urgently needed to understand the links between the diversity of metazoans, their role in groundwater ecosystems, and the services these ecosystems deliver to humans.
- We lack knowledge about the tolerance of groundwater species to abiotic conditions, including temperature and toxicants. Acquiring such knowledge is important to forecast biodiversity change in response to global warming and developing environmental risk assessment of pollutants in groundwater.
- Scientific knowledge on the diversity and function of groundwater metazoans does not yet translate into policies that frame the characterization, management and assessment of groundwater. Solutions should be found for implementing the knowledge of groundwater biodiversity into management strategies for assessing the health of groundwater ecosystems and their capacity to deliver important ecosystem services.

See Also: Structures and functions of Inland Waters - Groundwater: Ecology of the Hyporheic and Parafluvial Zone

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Springs—Groundwater-Borne Ecotones—A Typology, with an Overview on the Diversity of Photoautotrophs in Springs

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Aquifer hydrostructure System of relationships between three-dimensional hydrogeological complexes, homogeneous within them, identified by the ways in which water circulation happens, and by the limits that separate them from adjacent complexes.
Crenobiont or Spring-dependent species Species well adapted, and confined, to springs.
Crenophile Species that live in springs, but not exclusively.
Cyanotoxin Secondary metabolite produced by cyanobacteria, of varied chemical nature and toxic effects.
Diazotrophic Diazotrophs are bacteria, cyanobacteria, and archaea that fix atmospheric nitrogen gas into a more usable form such as ammonia.
Euaerial Taxa colonizing habitats that receive moisture solely from the atmosphere.
Gushet Spring type, refers to a waterfall pouring out of a cliff.
Heterocyte A specialized nitrogen-fixing cell formed by some filamentous cyanobacteria.
Hydroperiod Length of time and portion of the year a waterbody holds water.
Hypocrene Spring type: groundwater doesn't reach the surface and is only recognizable by vegetation.
Invertebrates Animals without backbones.
Karst spring or Karstic spring Spring that is part of a karst hydrological system.
Karst Landform produced by the dissolution of soluble rocks such as limestone, dolomite, and gypsum. It typically has underground drainage systems with sinkholes and caves.
Phanerogams Seed plants.
Piston flow In hydrogeology, conditions under which any given water front would advance uniformly downwards to the aquifer, with the same velocity and negligible dispersion and mixing.
Pseudaerial Taxa thriving on rocks or other substrata moistened by a steady source of water, such as springs and waterfall spray.
Refugium An area in which a population of organisms can survive through a period of unfavorable conditions.
Rheophilic Organism preferring or living in flowing water.
Spring Concentrated point of outflow of groundwater.

Springs as habitats, ecosystems, multiple ecotones

By definition, a spring is a discrete site where groundwater emerges to the Earth's surface (e.g., Scarsbrook et al., 2007; Glazier, 2009), with its characteristics (e.g., hydroperiod) determined by the hydrogeological features of the parent aquifer (Van der Kamp, 1995).

Springs are widely recognized as important **habitats** (Cantonati et al., 2012a, 2015), and biodiversity hotspots (e.g., Taxböck et al., 2017; Cartwright et al., 2020; Pascual et al., 2020). More precisely, individual sites can be species rich or species poor (α-diversity) while diversity at the landscape level (γ-diversity, regional pool of diversity) is typically high (Cantonati et al., 2020a). When examined at the regional scale, springs harbor a very high total number of taxa, including several new species, and many Red-List taxa (Cantonati et al., 2012a, 2021). This pattern indicates that there is a high species turnover among springs, as well as

high distinctness of individual spring systems. This high regional species richness is generally linked to the variety of geological conditions (geodiversity, namely lithotypes and aquifer hydrostructure), which lead to wide variation in the hydrochemistry, especially in conductivity and pH. In addition, chemical conditions can be altered by agricultural and industrial activities, especially in the lowlands, resulting in nutrient enrichment and other forms of pollution. High geological diversity translates into high spring ecomorphological and hydrochemical diversity, which in turn, is reflected in high γ-biodiversity (Cantonati et al., 2020a). An applied consequence of the highly individualistic nature of springs, is that it is imperative to protect entire regional groups of springs, including representatives of the different ecomorphological spring types, lithologies, and degrees of human influence (Cantonati et al., 2020a). Springs also host many sensitive, rare, threatened, Red List relict, and exclusive species. Some springs, particularly desert springs, frequently support a rich collection of endemic flora and fauna (Rossini et al., 2018; Fahey et al., 2019). Spring snails are the poster child of endangered, highly stenotopic, spring endemic species, e.g.: 11 species of *Floridobia* silt snails in Florida, as well as hundreds of highly endemic truncatelloidean springsnails globally (Hershler et al., 2014; Cantonati et al., 2020b). Aquatic ecologists recognized springs as distinct habitats with unique biotas deserving their own discipline ("crenobiology") almost 60 years ago (Illies and Botosaneanu, 1963). The habitats of springs are heterogeneous both within, the mosaic of microhabitats recognized already by Illies and Botosaneanu (1963), and among sites. Stevens et al. (2020a) pointed out that large springs can include up to a dozen of different microhabitats, each with its own array of species and more or less interacting, but in any case strongly contributing to the way in which diversity builds up in springs. Taxböck et al. (2020), working on the diatom communities of Swiss springs, could show that diatom species richness increases with microhabitat complexity within springs and elevation. Some springs are extremely isolated (a typical example are artesian springs generating desert oases) and individualistic freshwater habitats, whereas many others (e.g., permanent flowing springs with medium to high discharge) are well connected to a surface system of running waters. Acknowledging this isolated nature, springs in general have been considered island-like, "azonal" habitats (e.g., Cantonati et al., 2012a). However, there are also many examples of well-connected springs. Cantonati et al. (2010), for instance, discovered a new species of diatoms in the Brenta Dolomites in the south-eastern Alps, and its ecological characterization showed that it is typical of the uppermost part of the headwaters (eucrenal) of streams on carbonate substrata (limestones, dolomite, etc.) while it is replaced by other species downstream. Stevens et al. (2021) underline that connectivity is generally not a positive feature for springs since it favors colonization by non-native invasive species. Many springs contain relict species (including glacial and Tertiary relicts), and provide hospitable refugia for many other taxa (e.g., Taxböck et al., 2017). In highly impacted geographic areas with dense human populations, species sensitive to disturbance (Least-Impaired Habitat Relicts: LIHRe) may be found only in springs, because the quality of other freshwater habitats is no longer sufficient to meet their needs (Cantonati et al., 2012a). In arid landscapes some springs may provide stable hydrologic refugia in drying climates (Cartwright et al., 2020).

Spring environments are very diverse and often extreme with respect to specific ecological factors (e.g., pH, electrolyte content, temperature, etc.). Spring organisms representing many kinds of taxa have thus evolved diverse biochemical, physiological, morphological, behavioral and life-history adaptations (e.g., Cantonati et al., 2015). Some organisms (crenobionts, or springs-dependent taxa according to Stevens et al., 2020b) only live in spring habitats. Gerecke et al. (2017) pointed out that no other group of invertebrates includes a share of species with a particular relationship to spring habitats as high as water mites (Hydrachnidia): in their revision of the European fauna, they found that about one fifth of the species has a preference for spring habitats, and 14% can be reliably classified as crenobiontic. However, the causes of "crenobiosis" are not yet completely understood. Several environmental factors might be important for a better understanding including a constant low temperature (e.g., Glazier, 2012), the existence of a permanently non-frozen area of wet soil around seepage springs (Fischer, 1996), lower levels of competition due to shorter trophic food chains and the sparsity of top predators. Crenophilous species, on the other hand, do not have their distributional center in springs but can reproduce in them. They can be of various origins (e.g., Martin et al., 2015), and, in addition to springs, prefer standing water (lentic crenophiles), streams (rhitrobiontic crenophiles), groundwater (stygobiontic crenophiles), or colonize aquifers and the hyporheic interstitial (stygo- and hyporheobiontic crenophiles). Finally, crenoxenic species have no relation to sources, but appear here as "random guests." However, they can play a dominant role in degraded springs (Gerecke and Di Sabatino, 1996).

Despite their usually small size springs have a high ecological value (e.g., Odum, 1971). They can also be viewed as **ecosystems** (see the conceptual model presented by Stevens et al., 2020a). The term "crenoecology" has been used sporadically in the literature over the last two decades (e.g., Cantonati et al., 2012a). In spite of springs having been the cradle of ecosystem ecology (Odum, 1957), only four large springs have been in-depth investigated from an ecosystem perspective: Silver Springs (e.g., Odum, 1957), Montezuma well (e.g., Blinn, 2008), springs in Yellowstone National Park (e.g., Payne et al., 2019), and Cuatro Ciénegas (e.g., Hendrickson et al., 2008). Permanent springs with stable discharge are excellent sites for long-term ecological research (Gerecke et al., 2011). Springs are unique systems, and their productivity levels may be among the highest worldwide (Odum, 1957; Perla and Stevens, 2008). Many springs are "keystone ecosystems" because they supply an important habitat together with other ecological resources and services for many kinds of organisms that live in them and neighboring terrestrial and downstream ecosystems (Perla and Stevens, 2008; Cartwright et al., 2020). Glazier (2012) pointed out negative nonlinear relationships between food-chain length and temperature as well as between macroinvertebrate species richness and temperature. Both deviated from predictions based upon metabolic theory, and the negative effect of temperature on species richness contrasted with positive relationships observed at larger regional scales. Thermal tolerance limits are likely to play a major role in causing these relationships. Fluxes of resources (water, nutrients, and food sources), i.e., complex multi-directional subsidy exchanges, between groundwater, springs and neighboring habitats are still poorly understood but essential for supporting life and basic ecological functions in these highly connected ecotonal "springscapes" (Reiss and Chifflard, 2017). Barzaghi et al. (2017) showed biomass subsidies (exchanges) between two aquatic ecosystems (cave and spring pools) driven by a biphasic predator, the fire salamander (*Salamandra salamandra*).

Environmental conditions (e.g., water temperature, chemistry and flow rates, resource availability, and substrate type and diversity) strongly influence the productivity, trophic complexity, species composition and diversity of springs, but much work still has to be done to improve our understanding of the ecological structure and functions of springs.

Geothermal springs are model ecosystems to investigate microbial biogeography as they represent discrete, relatively homogenous habitats, which are distributed across multiple geographical scales, encompass broad geochemical gradients, and have limited metazoan interactions (Power et al., 2018). Li and Ma (2019) analysed the microbiome of 165 hot spring samples at the global scale covering wide ranges of temperatures (7.5–99 °C) and pH (3.3–9), and assessed population- and community-level spatial heterogeneities using the quantitative models of Taylor's power law and its extensions. They found that hot-spring microbiomes located in different regions, in spite of different environmental conditions, shared a fundamental heterogeneity scaling parameter, which may vary slightly depending on altitude and latitude but is invariant overall.

A small number of springs, but including several of those best-studied from the functional (ecosystemic) standpoint, are very large, actually resembling lakes, and can themselves be considered ecosystems, with local energy and matter cycles, whereas the large majority of springs are small, and therefore maybe easier to conceptualize as transitional environments (ecotones). However, most of these smaller springs feed groundwater dependent ecosystems (GDE) such as spring-fed headwater streams, lakes, etc. More precisely, when viewed as ecotones, springs should be considered **multiple** (3-way) **ecotones** linking ground- and surface-water, aquatic and terrestrial environments, and the spring-source with the spring-fed stream (spring-brook) (Fig. 1). In some spring types (e.g., seepages) the aquatic-terrestrial ecotone is very developed, and these are thus excellent sites to study the transition from submerged to subaerial.

Springs are mostly small but numerous: according to Glazier (2014), who provides a well-grounded estimate, there are worldwide on land (not counting Antarctica) > 3 springs/10 km^2, which means a global total of >43 Mio springs on Earth (and >7 thermal springs/10,000 km^2, leading to a global total of >100, 000).

Springs also have an enormous societal, cultural, and economic relevance (e.g., Glazier, 2009, 2014; Knight, 2015).

The main aim of this chapter is to review the characteristics and reasons for the uniqueness of springs and how they have been and are classified against a background of the biodiversity of the photoautotrophs, mainly algae, that inhabit them. The effects of increasing anthropogenic stresses, and the current efforts for spring ecology, conservation, and restoration are discussed.

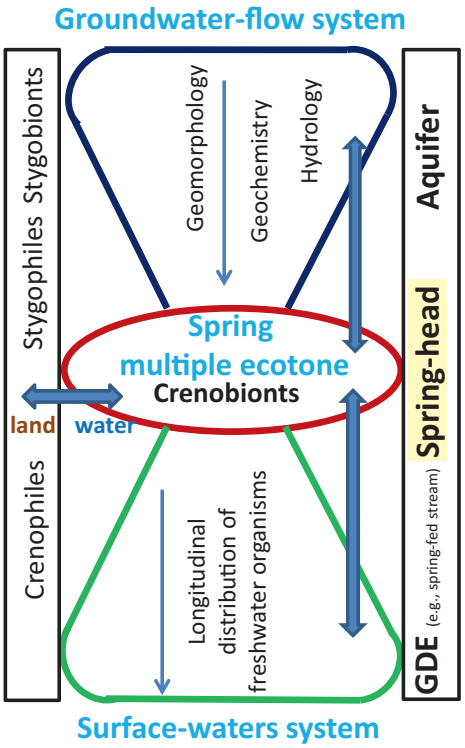

Fig. 1 Hourglass model pointing at the spring environment as a multiple—three ways—ecotone *(double arrows)*. Modified after Cantonati M, Stevens LE, Segadelli S, Springer AE, Goldscheider N, Celico F, Filippini M, Ogata K, Gargini A (2020b) Ecohydrogeology: The interdisciplinary convergence needed to improve the study and stewardship of springs and other groundwater-dependent habitats, biota, and ecosystems. *Ecological Indicators* 110. DOI: 10.1016/j.ecolind.2019.105803.

Springs as the iconic environments of ecohydrogeology

The disciplines of hydrogeology and ecology converge at spring sources, with emphasis on hydrogeology retreating in the post-emergence environment, while emphasis on ecosystem ecology generally increases from the point of emergence into ecotones in the surface environment (Cantonati et al., 2020b). Thus, for hydrogeologists the source is the final point of their targeted interest in the aquifer, while for freshwater ecologists the source is the initial point of interest, from which originating surface water generates a surface groundwater-dependent ecosystem seepage or a flowing channel, associated fens or mires, lakes, as well as lacustrine, palustrine, or fluvial riparian zones (Fig. 2).

Recently, an integration between the interdisciplinary approaches of the Earth's Critical Zone and hydropedology has bridged multiple spatial scales from the individual substratum type to the catchment and landscape (springscapes, Reiss and Chifflard, 2017). Springs represent a water-dominated critical zone at the interface between lithosphere, hydrosphere, and biosphere, but none of these fields of science by itself can fully embrace the phenomenology of physical, biological, and cultural interactions over time that constitute a spring ecosystem. On the geological side of spring research, hydrogeology is multidisciplinary among earth sciences and hydrological sciences, whereas ecosystem ecology is also multidisciplinary but emphasizes a strongly differing lexicon, suite of concepts, variables, and study approaches (Cantonati et al., 2020b).

Spring-ecosystem ecohydrogeology has been insufficiently studied by the scientific, and insufficiently recognized as worth of protection by the public and the management/governance communities.

"*Tales sunt aquae quales terrae per quas fluunt*" Pliny the Elder, *Naturalis historia*, 74 D.C. This statement ("Waters take on the properties of the rocks through which they pass"), which now constitutes the First law of Hydrogeochemistry, dates back almost 2100 years and yet is fully modern and topical. The physical and chemical characteristics of the water are indeed determined by the geological settings and regional climate features in pristine environments, and are modified by the indirect and direct impacts of human activity elsewhere (compare with Fig. 1 where the environmental influences and impacts on the aquifer-spring-surface-water system were not explicitly shown for the sake of clarity and simplicity). These interactions directly influence algal, macrophyte, invertebrate, and vertebrate spring biodiversity and assemblage structure.

The water demands of approximately one quarter of global human population are met using groundwater obtained from karst aquifers (Ford and Williams, 2007). The huge practical relevance of karst aquifers fostered, among other initiatives, the World Karst Aquifer Mapping (WOKAM) project (Chen et al., 2017). WOKAM succeeded in generating a world map and data-base of karst aquifers, also including selected karst springs and caves, acknowledging that karst springs are the "entrance" to karst conduits and

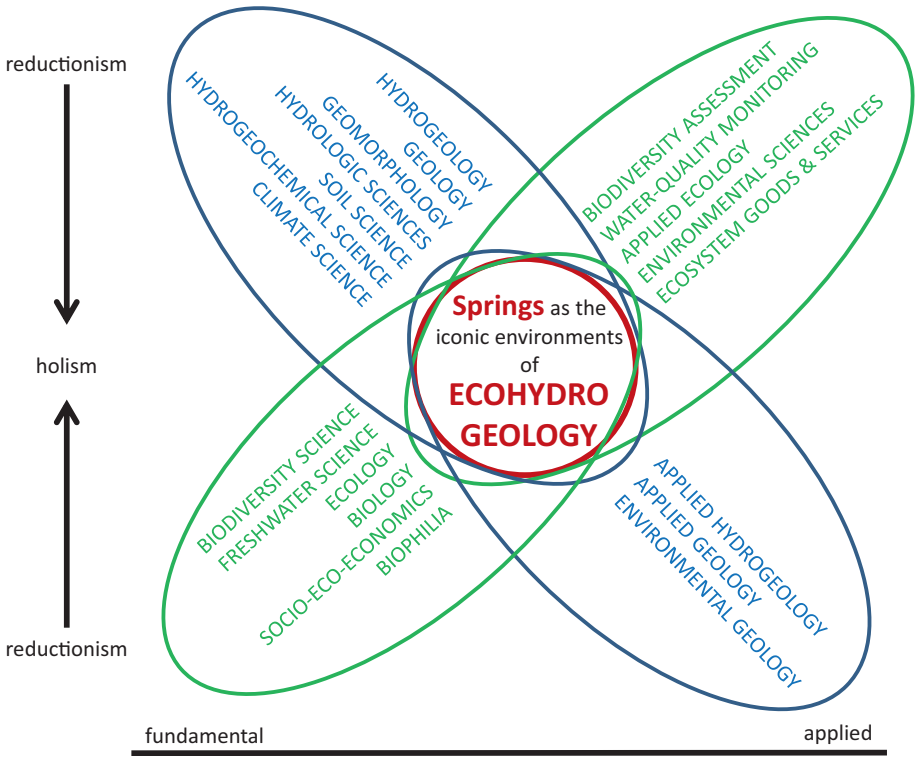

Fig. 2 The scientific domain of the unifying, integrative, multi-disciplinary field of ecohydrogeology. Modified after Cantonati M, Stevens LE, Segadelli S, Springer AE, Goldscheider N, Celico F, Filippini M, Ogata K, Gargini A (2020b) Ecohydrogeology: The interdisciplinary convergence needed to improve the study and stewardship of springs and other groundwater-dependent habitats, biota, and ecosystems. *Ecological Indicators* 110. DOI: 10.1016/j.ecolind.2019.105803.

caves. Cantonati et al. (2020b) used this as an example of the importance of interdisciplinary collaboration to improve understanding and management of karst ecohydrogeology.

Our knowledge on how the geological history of an environment shapes its physical and chemical properties and how these, in turn, influence community assembly is still limited. However, Payne et al. (2019), in a study of a moderately acidic hot spring (pH 5.6, 77.4 °C) in Yellowstone National Park, showed that geologic legacy (seismic activity) influences community assembly of archaeal-dominated and anaerobic microbial assemblages.

Sugiyama et al. (2018) determined signatures of direct impacts of rainfall on groundwater, using microbial, stable isotopic $\delta^{18}O$, and chemical analyses (silica concentration) to clarify the route of groundwater in systems at Mt. Fuji, Japan. Their findings indicated a rapid flow of rain through the shallow part of the aquifer, which appeared within a few weeks of torrential rain extracting abundant microbes from soil. Archaea were considered to be embedded in the geologic layer and to have been extracted to the examined groundwater by means of enforced piston flow caused by heavy rain.

On a similar note, Cantonati et al. (2020b) report the compelling correspondence between main precipitation peaks, flow-rate increases, and occurrences of depigmented, stygobiontic niphargid amphipods in basal springs. They hypothesized that the direct link between increased stygobiontic niphargid amphipods occurrences and electric conductivity values is due to enhanced spring flow rates, mainly caused by the arrival in the feeding aquifer of newly infiltrated waters with the consequent sudden increase in the hydraulic load. This abrupt increment and the subsequent pressure wave likely favor the mobilization of large volumes of deeper and more mineralized waters, along with the displacement of the hypogean organisms that live in the immediate vicinity of the spring.

Springs classification

The focus of this chapter is on land-surface springs but there are also springs emerging underwater in rivers, lakes (e.g., Ólafsdóttir et al., 2019), and oceans (Post et al., 2013).

The broad array of proposed classifications is generally related to "natural conditions," not to springs that have been diverted for human use or created by anthropogenic activities. However, the majority of springs in many landscapes have been dominated by human activities for millennia (e.g., Haynes, 2008 in North America; Cuthbert and Ashley, 2014 in the Old World), and are today partially or fully diverted, ecologically impaired, or obliterated (e.g., Stevens et al., 2021). Also, all spring types can be created or altered by human actions (e.g., Stevens et al., 2020a), with wells and fountains being the "artificial" counterparts of the springs found in nature.

Springs are usually regarded as very stable environments, but this applies only to some spring types, whereas in others (e.g., many karst springs), fluctuation of environmental factors/disturbance can be very high (e.g., Cantonati et al., 2012a).

Besides present-day, extant springs, paleosprings might be recognized as springs of the distant past but that no longer flow, and are identified from geologic or paleontological evidence (e.g., paleo deposits of spring-associated limestones). Paleosprings may contain important paleoclimate and archeological archives (Stevens et al., 2020a).

The existence of different spring types (from both the hydrologic and chemical points of view) is due to the interaction between different factors, such as (i) aquifer geology and geomorphology, (ii) vegetation and topsoil features, (iii) hydraulic properties of rocks and heterogeneity, (iv) groundwater pathways and residence time, (v) thermal gradients, (vi) weather conditions and precipitation regime, etc.

Many classification systems in several disciplines have been developed to define and identify spring types (Fig. 3), and one of the main features is the extreme diversity/heterogeneity of environments included in the definition of springs. Springs can be characterized by different regimes (variation of discharge over time) and cover an extremely wide range of water chemistry, temperature, and environmental settings. Spring types have been classified on the basis of diverse indicators (Alfaro and Wallace, 1994; Kresic, 2010): hydrology (discharge rate, e.g., Meinzer, 1923; recession coefficient, e.g., Gargini et al., 2008), hydrogeology (e.g., Civita, 1973), geology and morphology (e.g., Springer and Stevens, 2009), physical and chemical characteristics (e.g., electrical conductivity, Total Dissolved Solids, e.g., Clarke, 1924), temperature (cool, ambient, i.e., MAAT Mean Annual Air Temperature-, thermal, hot; e.g., Glazier, 2009), flow conditions at the spring head (Thienemann, 1924), and biological characteristics, in particular vegetation (bryophytes + vascular plants; e.g., Ellenberg, 2009) and invertebrate communities (e.g., Gerecke and Di Sabatino, 1996; Schröder et al., 2006; Martin and Brunke, 2012). Furthermore, biota-based spring types can be recognized by using benthic algae forming colorings and/or structures identifiable with the naked eye (Cantonati et al., 2012c), or their diatom microflora (Cantonati et al., 2012b). A comprehensive multi-taxon classification by "Procrustes" analysis showed that each group of organisms provides useful specific spring characters that however are related to other groups only at the level of broad ecological categories (e.g., photoautotrophs, meiofauna, etc.; Spitale et al., 2012). In the United States, 12 spring types were distinguished by geomorphology and recurring species (Springer and Stevens, 2009).

Springs are complex composite hydrogeological and ecological ecosystems and deserve a dedicated classification in order to provide a systematic framework necessary to study them. A variety of classifications have been presented in the literature from the hydrogeological stand-point, as well as from the ecological, crenobiological, and ecosystem services perspectives. These two groups of classifications are very useful and are utilized in an intra-disciplinary fashion by hydrogeologists or ecologists (Cantonati et al., 2020b).

From the hydrogeological standpoint, basic classifications rely simply upon: parent rock geology (lithology, stratigraphy) and structural geology of the groundwater basin; driving force mechanisms (gravity, pressure or density/temperature dominated discharge), groundwater quality including water temperature and/or geochemistry; discharge quantity (magnitude, variability,

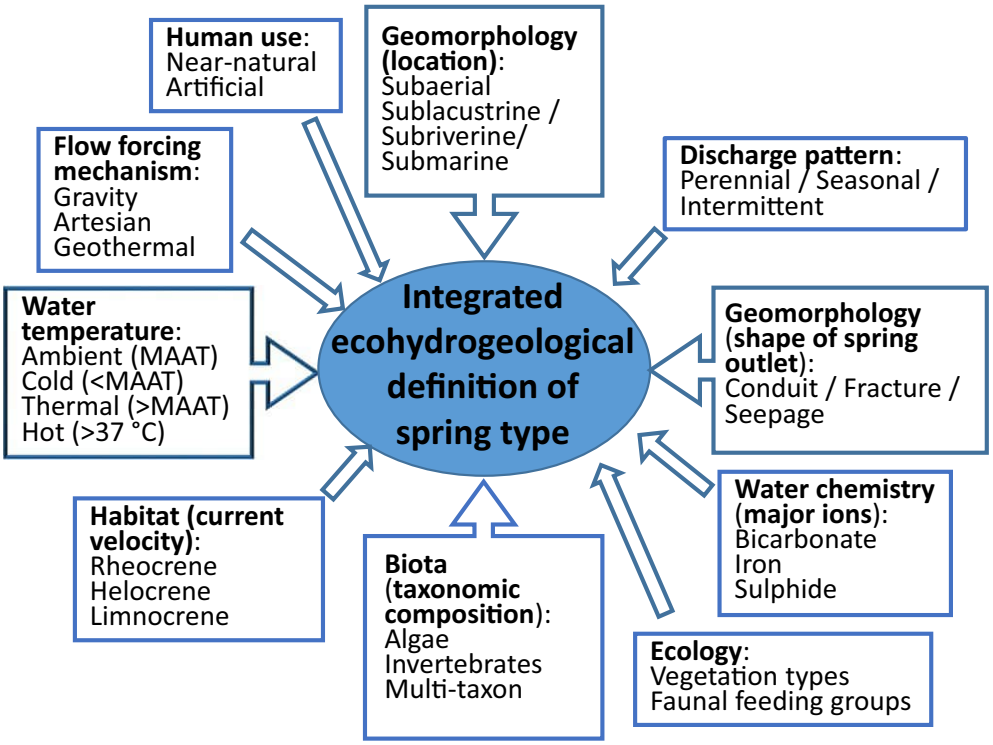

Fig. 3 Schematic diagram synthesizing spring classification approaches.

and recession); or the geomorphology of the discharge point of the spring (the "sphere of discharge" as landform pattern at the springs source; Meinzer, 1923).

From an ecological and anthropogenic uses perspective, the focus of the classification can be physical and/or biological, depending on taxonomic composition, and structural or functional parameters of the associated biota and assemblages. Early attempts to identify features determining spring characteristics particularly relevant for the colonizing biota are attributable to Van der Kamp (1995), who demonstrated that the hydrological stability of many springs and springs-associated biota is determined by the hydrogeological features of the parent aquifer.

Meinzer (1923), Alfaro and Wallace (1994), Springer et al. (2008), and Glazier (2009, 2014) review the many springs classification approaches that have been proposed (Springer and Stevens, 2009). There is a growing body of literature revealing a suite of species not only dependent on springs but selective of different spheres of discharge of springs (e.g., Sinclair, 2018).

Glazier (2009, 2014) provided an exemplary recapitulation of classification attempts, with detailed tables with cross-citation of references. Cantonati et al. (2020b) offer a synthetic review of the main classification approaches that have been proposed with a summarizing table, along with examples of references, some of which are collectors of other references. Stevens et al. (2020a) emphasize that of the proposed classification factors, only geomorphology clearly and unambiguously distinguishes spring types, and consequently propose a practical, geomorphology-based classification with a dichotomous key for 13 spring types. Their spring types are based on those identified by Springer and Stevens (2009) but also include paleosprings, differentiate between floodplain and upland subtypes of helocrenic and hillslope springs, and distinguish three subtypes of mound-forming springs. Besides common types discussed in this and the following section, they also deal with more peculiar ones, such as hypocrenes and gushets.

Kinds of springs

A limnological spring type is grounded only on the hydromorphological shape of the source (i.e., the discharge type). This becomes a spring typology when it is accompanied by information on the characteristic colonizing organisms (Martin et al., 2015). Based on preliminary work by Steinmann (1908) and Bornhauser (1913), Steinmann (1915) provided the first detailed definition of the three "classic" spring types according to hydromorphological criteria, the distinction of which is still valid today (they are shown in Fig. 4 using artwork by a German painter):

- **Flowing springs** or **rheocrenes** (German: *Sturzquellen* or *Rheokrenen*) are "characterized by a waterfall-like discharge." "The substratum is coarse, sandy or stony, mostly also poor in plants."

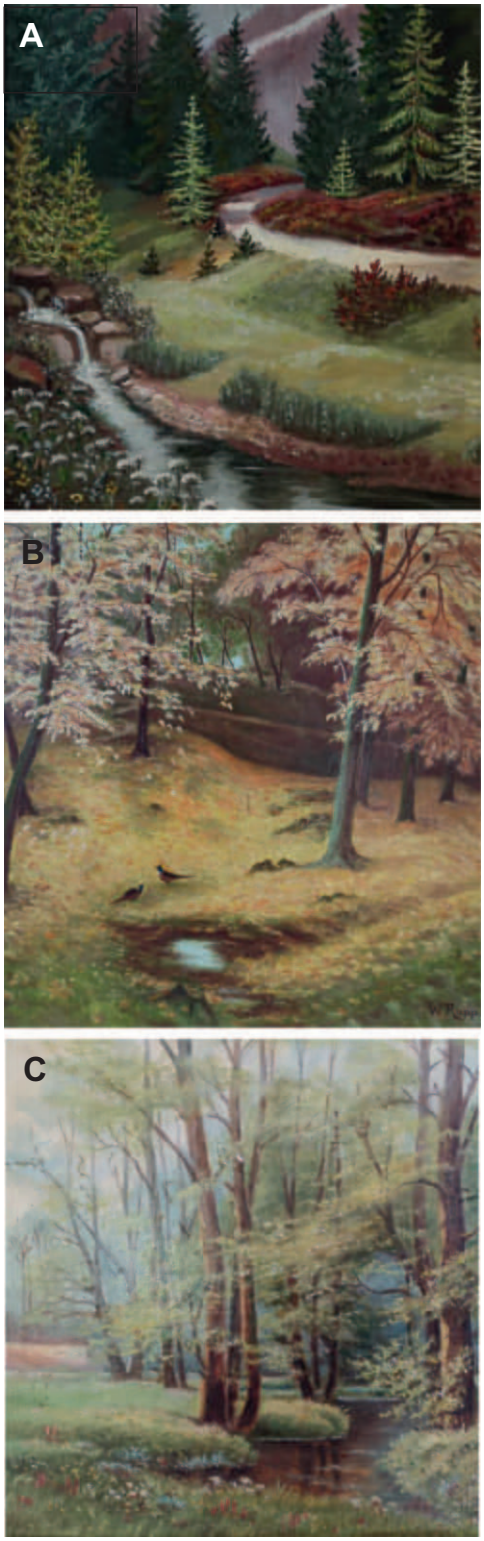

Fig. 4 An artwork representation of the three classic Naumann-Thienemann spring types A. flowing spring/B. seepage/C. pool spring using paintings by Wilhelm Rupp (Leipzig, 1899–1994).

- **Pool springs** or **limnocrenes** (German: *Tümpelquellen* or *Limnokrenen*) are "basin-like springs that are filled with water from below. The spring brook forms by overflow. The limnocrenes usually have a muddy or sandy substratum and sometimes abundant vegetation."
- **Seepages** or **helocrenes** (German: *Sickerquellen* or *Rinnquellen*, known as *Helokrenen* since Thienemann, 1922) are seen by Steinmann (1915) as a transition type between rheo- and limnocrenes, and he notes that these "show pronounced relationships with semi-terrestrial habitats."

Since Thienemann (1924) this division into three types of springs can be found in most textbooks, and has often been used uncritically for spring classification (Martin et al., 2015). More differentiated systems have only recently been developed for regional use (e.g., Howein and Schröder, 2006; Martin and Brunke, 2012). It often turned out to be useful to combine the classic terms for transitional situations (e.g., rheohelocrenes, limnorheocrenes, etc.).

The "linear spring" (German: *Wanderquelle*, Zollhöfer, 1997) represents a special type of spring, the springhead of which is not stable at one point but "migrates" up and down in the spring-brook channel, depending on the groundwater level. Hydromorphologically, these are mostly rheohelocrenes.

Relationships between spring types and settling organisms, i.e., spring typologies, have only recently been developed on the basis of thorough geomorphological descriptions (e.g., Zollhöfer et al., 2000; Howein and Schröder, 2006; Martin and Brunke, 2012), whereby the composition the inorganic substrata and the type of runoff proved to be the most important determinants of the invertebrate communities. Together with the geogenic variables (e.g., conductivity), shading, nutrients (especially nitrates), and elevation were the factors most important for the algae-based characterization of spring types in the Alps (Cantonati et al., 2012b, 2012c). A statistical comparison between the spring types obtained using different groups of organisms (diatoms, bryophytes, vascular plants, nematodes, molluscs, oligochetes, water mites, copepods, ostracods, chironomids, mayflies, stoneflies, and caddisflies) showed that the groupings obtained with the mentioned groups of organisms were different, and that the results obtained with one group of organisms, in particular for nature conservation concerns, cannot be transferred directly to other groups. However, of course there were affinities: the subdivisions of the photoautotrophs, of the meiobenthos groups, and of the EPT (mayflies, stoneflies, and caddisflies) groups were most similar to each other (Spitale et al., 2012). Broad-based, comprehensive biodiversity studies are therefore indispensable for thoroughly scientifically-informed nature conservation at springs.

In order to define targets for restoration measures, the representation of reference springs is of particular importance (Martin et al., 2015). The detailed knowledge required for this purpose of all spring types in a geographic area and their potential natural status is difficult to obtain in the many regions in which most springs have been anthropogenically impaired (Zollhöfer et al., 2000; Martin and Brunke, 2012). Spitale (2007) names as the most important typological parameters: (a) georeferencing, gradient situation and external appearance, (b) shape and area, (c) substrata, (d) discharge, (e) light conditions, (f) buffer zones and disturbances.

Hydrogeologically oriented classification systems (e.g., Schönborn, 2003) differ very much from the limnological typology in that they pay special attention to the characteristics of the groundwater (i.e., flow of the water underground before it reaches the spring-source). Some of the criteria investigated used there are unlikely to deeply influence the biological colonization of the spring. In principle, however, one should keep a close eye on the conditions in the aquifer when developing an ecological/biological regional spring typology, if possible in cooperation with hydrogeologists (Martin et al., 2015). Questions about the length of the time the water has stayed underground (flow path), the fracturing characteristics of the conductive rocks and their geological composition can be very important for understanding spring-dwelling communities (e.g., Van der Kamp, 1995).

Karst springs represent a special type of springs in this respect (Martin et al., 2015), in which water emerges from crevices and large underground cavities in karst areas (e.g., Schönborn, 2003). Since they only discharge as long as the groundwater level is higher than the lower edge of the runoff gap, their discharge is intermittent and difficult to predict, influenced by storms, snowmelt, and seasonal fluctuations in the amount of precipitation. Karstic springs are not only found in limestone mountains (very typical, e.g., in the Swiss-South German Jura) but occasionally (and surprisingly) also in landscapes in which limestone influences aquifers without being visible on the surface. The comparatively rapid groundwater passage, with little exchange with the conductive rock, determines the atypical characteristics of karstic springs (discharge fluctuations, turbidity after rainfall, oxygen content, often anthropogenic pollution), all phenomena that are related to a particular susceptibility to external influences. This also explains the peculiarities of the flora and fauna, which are often characterized by the occurrence of eurythermic running-water species, and occasionally by indicators of increased saprobicity (compare, e.g., Martin and Zaenker, 2007). Some karst springs have achieved real fame due to their exceptionally-high discharge, e.g., Vrelo Bune (Bosnia Herzegovina; with an average discharge of 43 m^3/s, is considered the spring with the largest discharge in Europe; Fig. 5A) (Martin et al., 2015).

The main characteristics of the different kinds of springs will succinctly be recalled in the following using seven "macro-types" (examples shown in Fig. 5):

- **Flowing springs** (**rheocrenes**): Springs are most common in mountainous areas, and rheocrenes are by far the most frequent kind of springs on mountains. Flowing springs can be characterized by swift current already in the spring-head area that degrades in the following spring-fed stream with few immediately-perceptible changes. In these last cases, morphological (e.g., changes in slope), physical and chemical (e.g., longitudinal temperature changes), or biological (e.g., overall bryophyte cover and presence of spring-dwelling invertebrates, such as water mites) criteria must be used to try to delimit the eucrenal (Cantonati et al., 2006, 2007).
- **Hygropetric springs** or **rock-face seepages** (Fig. 5B) are more common on carbonate substratum. Cantonati et al. (2012c) identified the cyanoprokaryotes *Rivularia* spp., *Plectonema tomasinianum*, *Ammatoidea normannii*, *Chamaesiphon minutus* (mainly as an epiphyte of other cyanobacteria), and *Calothrix parietina* as indicator taxa of this spring type. Gesierich and Kofler (2010) noted a large proportion of pseudaerial taxa (e.g., from the genus *Gloeocapsa*) in a carbonate rock-face seepage. Cantonati et al. (1996) found the highest number of cyanobacterial taxa in this spring type, and attributed this finding to the fact that hygropetric springs include transition microhabitats to other biotopes (dripping and wet rock walls).

Fig. 5 Examples of the seven spring macrotypes presented more in detail in this chapter: (A) large flowing spring (Vrelo Bune, karstic spring in Bosnia Herzegovina, photo credit: wikimedia); (B) small flowing spring in the Northern Apennines forming a rock-face seepage (p.c.: Dr. Stefano Segadelli); (C) seepage (helocrene in the south-eastern Alps; p.c.: Dr. Daniel Spitale); (D) large pool spring (Silver Springs, Florida; photo credit: Brad Stith and John Moran); (E) hot spring (Yellowstone; photo credit: David Mark from Pixabay); (F) iron spring in the south-eastern Alps (p.c.: MUSE—Museo delle Scienze); (G) limestone-precipitating spring in the south-eastern Alps (p.c.: Dr. Daniel Spitale); (H) Crescent spring in the Gobi Desert (photo credit: whitewaltz from Pixabay).

- **Seepages (helocrenes**; Fig. 5C): Helocrenic springs are those where groundwater emergence is diffuse and generates wetlands. Dystrophic habitats (seepages, mire pools) were pointed out to be of special importance, not only for the diatom assemblages (e.g., Cantonati et al., 2009a; Cantonati and Lange-Bertalot, 2011) but also for the meiofauna (e.g., Gerecke et al., 2011). Helocrenes are the most species rich habitats both for invertebrates and for diatoms (Gerecke et al., 2011). Spring-fed desert

wetlands, or *ciénegas*, spanning the borders of Arizona (United States) and Sonora in México are regions of high biodiversity in the American deserts. These environments contain an estimated 19% of endangered, threatened and candidate species (Minckley et al., 2013).

- **Pool springs (limnocrenes)**: Limnocrenes have played a very special role in springs science: Silver Springs (Fig. 5D) was the place where ecosystem ecology originated, and Montezuma Well is considered the site with the highest concentration of unique species of any point in North America (Schenk et al., 2018). Springs with a distinct pool at the springhead and an outflowing streamlet are classified as limno-rheocrenes. They are frequent only in specific geographic areas (e.g., Finland; Lehosmaa et al., 2017), and in many cases this special morphology has been accentuated by human alterations such as digging of the pool and/or damming of the outlet.
- **Thermal springs** (Fig. 5E): Recent, continuous progress in technologies (metagenomics, culturomics, high-throughput culturing, comparative genomics, 16S amplicon sequencing, etc.) have opened unprecedented possibilities to the study of spring (and groundwater) microbial communities (e.g., Pedron et al., 2019). This resulted in the overall spring-habitat literature of at least the last decade being dominated by microbiological studies of thermal springs (Cantonati et al. unpublished). Power et al. (2018) measured bacterial and archaeal community composition, 46 physical and chemical variables from 925 New Zealand thermal springs to identify factors that determine biogeographical patterns. They determined that diversity is primarily influenced by pH at temperatures $<70\,^{\circ}C$, with temperature having a significant effect only for values $>70\,^{\circ}C$. Further, community dissimilarity increased with geographic distance, with niche selection driving assembly at a localized scale, with two dominating genera (*Venenivibrio* and *Acidithiobacillus*). Decades of research into geothermal-spring Bacteria and Archaea have generated great insight into the diversity and adaptations to extreme environmental conditions while microbial eukaryotes (protists), which are also ubiquitous in most thermal springs, surprisingly remained understudied. Oliverio et al. (2018) used high-throughput sequencing to study the diversity and structure of microbial eukaryotic communities found in 160 New Zealand geothermal springs. Protistan communities were moderately predictable in composition and varied most strongly across the wide gradients in pH and temperature, and this variation mirrored patterns observed for bacterial and archaeal communities. While extreme pH values were associated with dropping protist diversity, high temperature springs still allowed for substantial amounts of protist diversity.
- **Mineral springs**: Springs that have waters that were enriched in dissolved substances during their underground flow path. They thus possess hard water, that can contain dissolved minerals, salts, sulfur compounds, and gases. Iron springs (Fig. 5F) are characterized by the regular occurrence of iron-oxidizing Proteobacteria (Dyer, 2003) whereas they are frequently very poor in macroscopically visible benthic algae (Cantonati, 2008). Aguilera et al. (2019) described a new fish species of the genus *Jenynsia* (Anablepidae) from a sulphide spring in Northwestern Argentina. Sulphide springs have extreme environmental (toxic and hypoxic) conditions that only few vertebrate species can tolerate. Cantonati et al. (2019) described a new diatom species in the genus *Halamphora* from a large, fast flowing, inland-saline (Triassic gypsum), mineral (chloride, sulphate, sodium, calcium) spring in the Northern Apennines, characterized by very high electric conductivity and slightly alkaline pH. Stepanek and Kociolek (2019) suggest that inland-saline habitats like this are of particular interest because diatom groups, such as *Amphora* and *Halamphora*, that have representatives colonizing smaller inland waters with high conductivity, might have used these waterbodies as potential intermediate habitats from which the colonization of surrounding freshwaters could have taken place. The diversity of mineral springs is amazing and includes for instance:
  - Chocolate Pots hot springs, which are present-day systems that support active Fe redox cycling, and can provide insight into how life could have functioned in such environments; iron redox-based metabolisms likely supported life on early Earth and may support life on other Fe-rich rocky planets such as Mars (Fortney et al., 2018).
  - Polyextreme springs, such as the unique Dallol hot springs (Northern Afar, Ethiopia), which are highly acidic (pH ca. 0) and saline (saturation) with maximum temperatures ranging between 90 °C and 109 °C, and from which Gómez et al. (2019) reported for the first time evidence of life existing within these hot springs using a combination of morphological and molecular analyses: ultra-small structures, identified as members of the order Nanohaloarchaea, were shown to be embedded within mineral deposits.
  - A nuclear geyser system, identified by Maruyama et al. (2019) as the most likely site for origin of life on Earth on the basis of the nine essential requirements for the first emergence of life on our planet.
- **Limestone-Precipitating Springs (LPS)** (Fig. 5G): LPS are ambient-temperature (non-geothermal) freshwater springs that achieve sufficient oversaturation for $CaCO_3$ by physical CO_2 degassing and activity of photoautotrophs to deposit limestone, locally resulting in scenic carbonate structures. The most characteristic organisms in these springs are those that contribute to carbonate precipitation, e.g.: the bryophytes *Palustriella* and *Eucladium*, the crenophilous desmid (green algae) *Oocardium stratum* (Rott et al., 2012; Linhart and Schagerl, 2015; Tran et al., 2019), and cyanobacteria (e.g., *Rivularia*). These organisms appear to be sensitive to phosphorus pollution. To verify if *Oocardium stratum* is often overlooked because it develops in a habitat type rarely visited by phycologists, Trobej et al. (2017) studied algal communities only in springs with associated SAL (Spring-Associated Limestones) deposits. They found the species in 50% of the sites studied, and concluded that this species is more common than often believed, but that it occurs exclusively in habitats with very specific hydrogeological characteristics, as described above for LPS (Cantonati et al., 2020b). Invertebrate diversity is modest, and highest in pools with an aquatic-terrestrial interface. Animal species able to persist in the petrified channels are mostly mountain-stream generalists which migrate from their preferred habitat into spring brooks. An exception is the case-less larva of the caddisfly *Rhyacophila pubescens*, which can be considered an outstanding element of LPS in Europe. Analysis showed a rather high genetic isolation of local populations, probably due to a

fragmentation of areas with suitable habitats, combined with a low dispersal rate of the adults (Engelhardt et al., 2011). LPS is the only widespread spring type included in the EU Habitat Directive, mainly because of landscape esthetics. Pre-requisites for the occurrence of LPS are: an aquifer lithology that enables build-up of high bicarbonate and Ca^{2+} to sustain $CaCO_3$ oversaturation after spring emergence, combined with intense groundwater percolation especially along structural discontinuities (e.g., fault zones, joints, schistosity), and a proper hydrogeological structure of the discharging area. The main threats to LPS are water diversion, nutrient enrichment, and lack of awareness by non-specialized persons and administrators (Cantonati et al., 2016a).

- **Desert springs** (Fig. 5H): Desert springs form oases in otherwise inhospitable landscapes and occur across the globe. They frequently support a rich collection of endemic flora and fauna (Fahey et al., 2019). Rossini et al. (2018) studied endemic biodiversity and its conservation value in Australia's artesian desert springs, and found 96 species and subspecies of fishes, molluscs, crustaceans, and plants endemic to these arid-climate freshwater springs. The majority of these endemic species are invertebrates with a limited geographical distribution pattern. Cantonati et al. (2015) highlighted that the ambient springs in warm climate settings, including the freshwater arid ecosystems, host rich, interesting, and diverse cyanobacterial communities, that, however, are typically poorly-known so far. Also, the diverse cyanobacterial and algal adaptations to the arid-climate freshwater spring habitats are understudied. However, Garcia-Pichel et al. (2002) studied a thermal spring in the Cuatro Ciénegas karstic region of the Mexican Chihuahuan Desert, and found unusual centimeter-sized water-warts built by an *Aphanothece*-like unicellular cyanobacterium: these were suspended within a central, conically-shaped, 6-m deep well by upwelling waters, and supported a community of other epiphytic filamentous cyanobacteria and diatoms. This unique structure of jet-suspended, calcite-ballasted, colonial cyanobacterial community shows relevant adaptations to this desert-spring habitat. The morphotaxonomic surveying by Shaaban et al. (2015) of the freshwater ambient-to-slightly hot springs (*ains*) and drilled wells (*birs*) in the El-Farafra Oasis in the Western Desert of Egypt highlighted that these important habitats are affected by direct human and cattle impacts (organic pollution). This was confirmed by the main cyanoprokaryote taxa found that were typical bioindicators of eutrophicated thermal freshwater habitats. The over-use of the Nubian aquifer system (NAS), the world's largest non-renewable (fossil) water resource, has already resulted in the abandonment of oasis settlements (Powell and Fensham, 2016). A clear relationship between the ever increasing number of wells and the dramatic decrease of active flowing springs has been observed (e.g., in oases of the Western Desert of Egypt) and is predicted to exacerbate due to the lack/non-compliancy with sustainable exploitation plans (Voss and Soliman, 2014). In most of the springs (and even wells) in oases of the Western Desert of Egypt, ecological integrity, as shown, e.g., by benthic algae, is low because of human impact due to the use of the water for drinking, cattle watering, irrigation, recreation, etc. Near-natural springs, likely to host unique biota, exist in protected areas and in remote, difficult-to-access sites. Fahey et al. (2019) described a new grass (Poaceae) species, *Chloris circumfontinalis* Fahey et Fensham, from arid-environment artesian springs of inland Australia. The new species occurs only in the saline scalds that form around the springs, and population surveys indicated a threat status of "Endangered" under the IUCN Red List criteria.

The main environmental determinants of photoautotrophs in springs

To complement a chapter in the present Encyclopedia by Williams (2022) on springs' biodiversity, which focuses on the fauna (namely invertebrates), an overview of the photoautotrophs ("flora") that can be found in springs is provided here.

According to Cantonati et al. (2007) "**phytobenthos**" in the broader sense includes not only benthic algae but also aquatic lichens, bryophytes, and vascular plants, i.e., all photoautotrophic organisms that live in close proximity to the water-influenced substrata (Figs. 6 and 7). The term "benthic algae" is also used there for a large number of lower plants that do not develop any real tissue, flowers or fruits. These groups differ from one another not only evolutionarily (both eu- and prokaryotes) but also in their biochemistry, physiology and metabolism. The phytobenthos of mountain springs (especially that of the rheocrenes) shows striking similarities to that of mountain streams. However, there are also a number of characteristic features, which are described below for the most important groups. In addition to cyanobacteria and diatoms, chlorophytes (green algae), rhodophytes (red algae), chrysophytes (golden-brown algae), and xanthophytes (yellow-green algae) also play an important role in springs (see Cantonati et al., 2007). A discussion of the relationship of the individual groups with springs, as well as with other habitats, is hardly possible without considering the following key environmental variables:

- **Lithology**: The relevance of lithology is expressed, for instance, in the fact that vicarious species of the same genus replace each other on siliceous vs carbonate rocks (e.g., the cyanoprokaryotes *Chamaesiphon fuscus*/*C. geitleri*—Fig. 6A–B, the diatoms *Meridion constrictum*/*M. circulare*). The importance of lithology-related abiotic parameters (conductivity, pH) has been confirmed many times (e.g., Cantonati et al., 2012b, 2020a). Werum and Lange-Bertalot (2004) showed that spring diatom communities in a lithologically heterogeneous region can be assigned to different geological formations on a statistically significant basis.
- **Current velocity**: Flow velocity is an important influencing factor, especially in rheocrenes (e.g., in large karst springs, gushets, or mountain springs emerging on steep slopes). Species that occur in rivers and springs with heavy pouring can also be found in small rheocrenes if there are microhabitats with particularly strong currents, e.g., the rheophilic golden-brown alga *Hydrurus foetidus* (Cantonati, 2008; Cantonati et al., 2009b) or the diatoms *Achnanthidium pyrenaicum*, *Hannaea arcus*, and *Cocconeis placentula* (Cantonati and Spitale, 2009). In contrast, other algae have developed adaptations to extremely reduced flow or even to dehydration, e.g., the cyanobacterium *Chamaesiphon polonicus*, and the diatoms *Humidophila perpusilla*, *H. contenta*, and

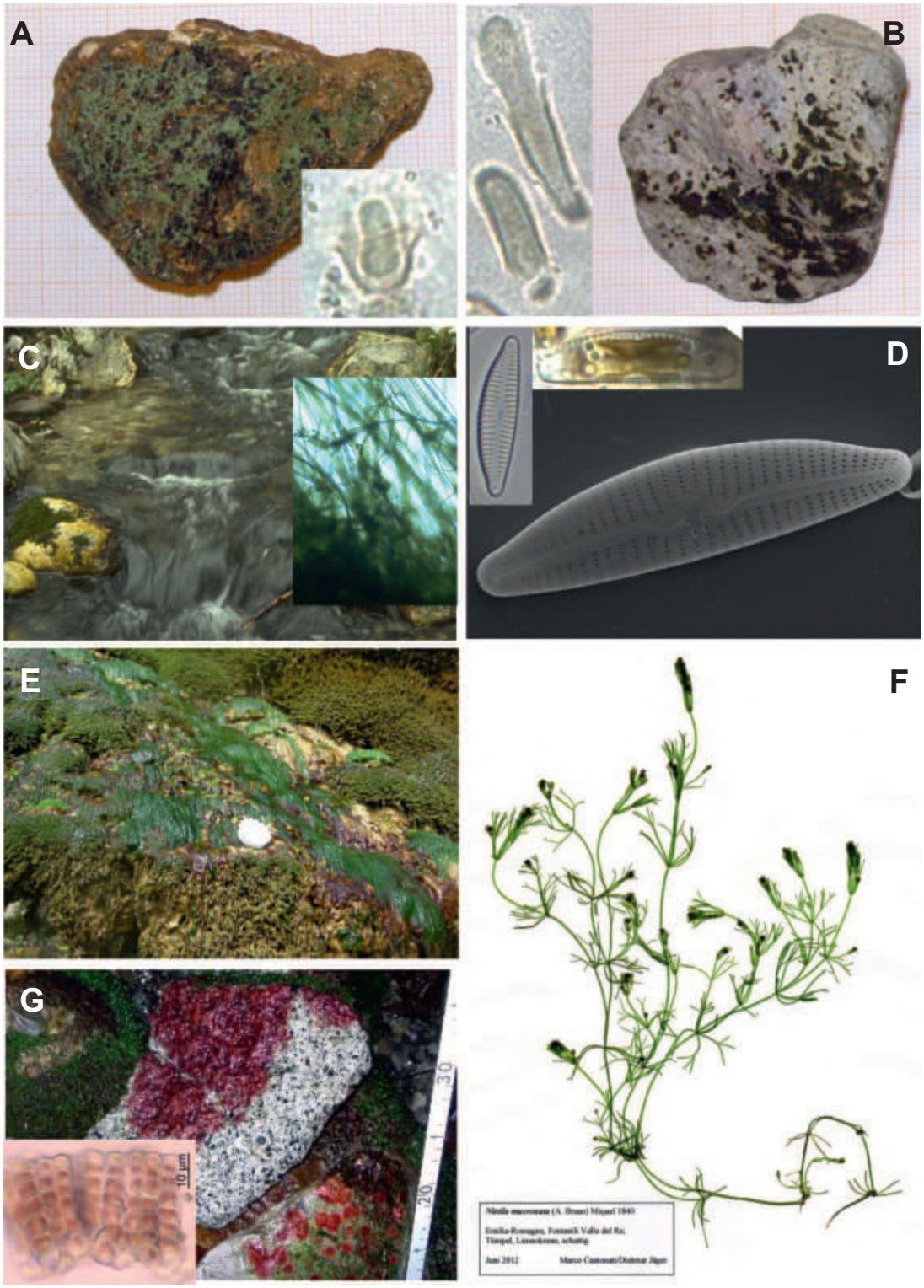

Fig. 6 Examples of spring (Northern Italy) benthic algae and cyanobacteria presented more in detail in this chapter: (A–B): macroscopic aspect of colonies of two vicariant species of cyanoprokaryotes: siliceous vs carbonate rocks, *Chamaesiphon fuscus* (A)/*C. geitleri* (B) (the inserted images show the microscopic aspect); (C) macroscopic aspect of a benthic bloom of the diatoms *Odontidium mesodon* + *O. hyemale* (the inserted image shows the microscopic aspect); (D) the diatom *Cymbella tridentina* seen at the scanning electron microscope (the inserted images show the aspect of this species under the light microscope: *left*: prepared material, *right*: living cell with plastid); (E) Macroscopic aspect of the filamentous red alga *Bangia atropurpurea*: red patches intermingled with the green patches of the green alga *Cladophora glomerata* (splash zone of a waterfall formed by a large limestone-precipitating spring in the Northern Apennines); (F) the stonewort *Nitella mucronata* (herbarium sheet) sampled from a shaded pool spring in the Po plain in Northern Italy (p.c.: Dietmar Jäger); (G) crusts of the red alga *Hildenbrandia rivularis* in a small shaded flowing spring in the south-eastern Alps.

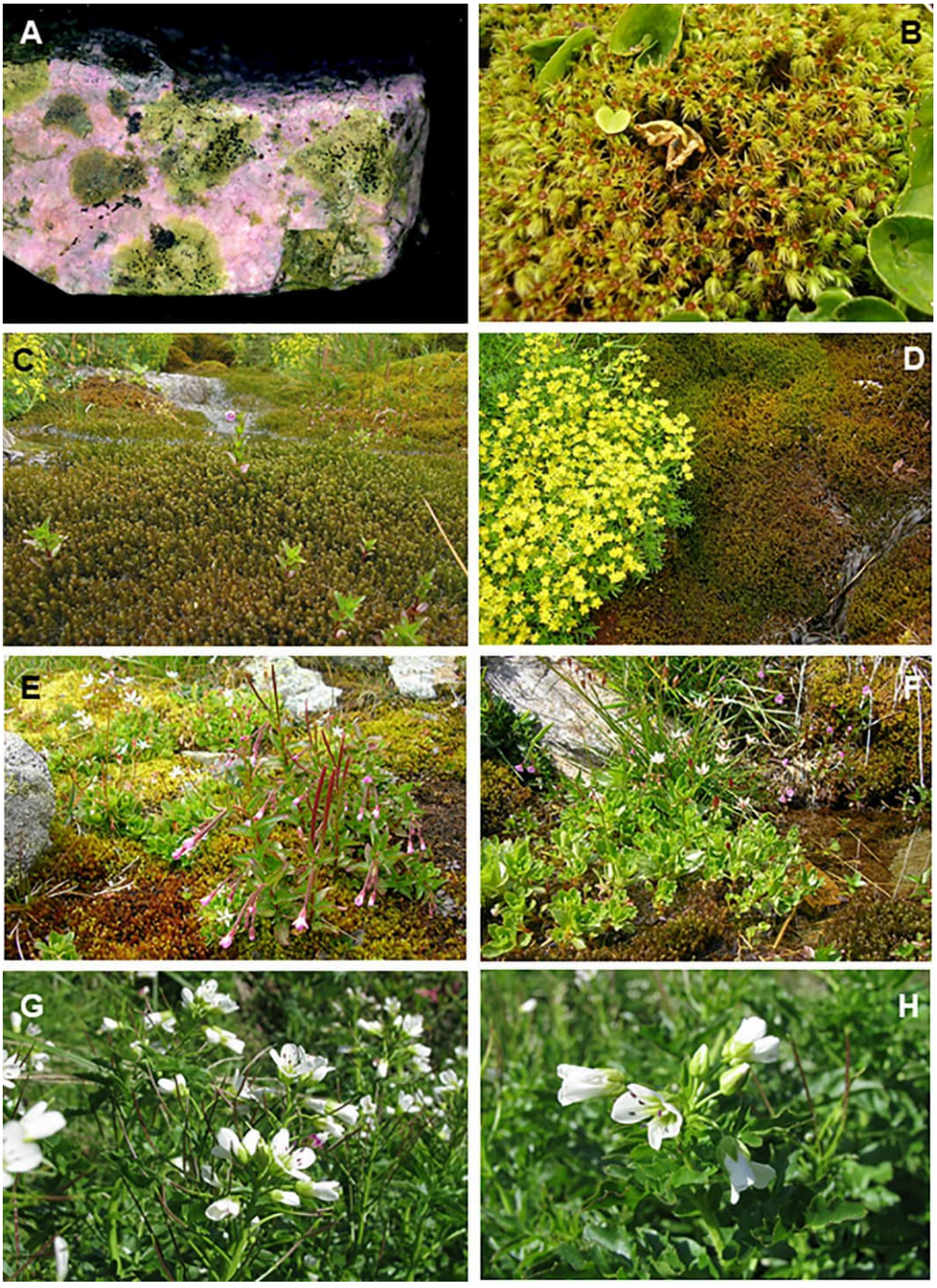

Fig. 7 Examples of common lichens, bryophytes, and vascular plants in springs of the Alps: (A) the epilithic aquatic lichen *Verrucaria funckii*; (B) the moss *Philonotis fontana*; (C) *Epilobium alsinifolium* (chickweed willowherb, Onagraceae) "immersed" in the moss *Palustriella falcata*; (D) *Saxifraga aizoides* (yellow mountain saxifrage, Saxifragaceae) and the mosses *Palustriella commutata* and *P. falcata*; (E) *Epilobium alsinifolium* and *Saxifraga aizoides*; (F) *Saxifraga stellaris* (starry saxifrage, Saxifragaceae); (G–H) *Cardamine amara* (large bitter-cress, Brassicaceae). (B–H): photo credit: Dr. Daniel Spitale.

Orthoseira roeseana (Cantonati et al., 2006, 2007; Cantonati and Spitale, 2009). Hofmann et al. (2018), in their diatom Red List, designate a number of species as (eu- and pseudo-)aerial. In a similar way, van Dam et al. (1994) designate species living at the periphery or mainly outside waterbodies with the numbers 4 and 5 in a moisture (M) scale of 1–5. Cantonati et al. (2012c) identified different spring types in the south-eastern Alps, which differ in environmental parameters and species communities of benthic algae (without diatoms). Their most common spring type was, for example, carbonate rheocrenes located at middle and higher elevations with medium conductivities, mainly characterized by shade-tolerant (Chroococcales) or rheophilic (*Tapinothrix varians*) cyanobacteria.

- **Light**: Another important determining factor are the light conditions. Benthic freshwater diatoms, like many cyanobacteria and red algae, can tolerate shading or are even specially adapted to it (e.g., Poulíčková et al., 2004). In contrast, at high elevations or periodically exposed sites that are affected by high levels of radiation, cyanobacteria can protect themselves against UV stress by producing the photoprotective pigment scytonemin, which is stored in the sheaths where it causes a yellow-brown color (e.g., *Ammatoidea normanni* and *Tolypothrix* spp.; Cantonati et al., 2007). Another strategy is the production of UV-absorbing mycosporine-like amino acids (MAAs), small, colorless and water-soluble molecules that effectively absorb wavelengths in the range between 309 and 360 nm. Presumably, such components generally play an important role above the tree line; Sommaruga and Garcia-Pichel (1999) found them in both planktonic and benthic taxa in high mountain lakes.
- **Nutrients**: Since nutrient levels in springs are generally low under natural conditions, nutrient availability is of fundamental importance in the ecology of spring algae. Nutrient enrichment can be direct (e.g., through grazing cattle or game) or indirectly (e.g., deposition of airborne nitrogen compounds). Even small amounts of nitrate obviously favor non-heterocytic cyanobacteria and certain diatoms (e.g., *Cocconeis placentula*, *Planothidium lanceolatum*; Cantonati et al., 2006). In springs exposed to organic pollution, diatom species indicating eutrophication are typically found (e.g., *Gomphonema parvulum*, *Navicula tripunctata*, *Nitzschia palea*; Cantonati and Spitale, 2009). Cantonati and Lange-Bertalot (2010) found the lowest number of species and the lowest Shannon-Wiener diversity values in springs with the highest nitrate concentrations in the north-eastern Alps, with an important occurrence of the eutraphentic diatom species *Planothidium lanceolatum* (56%) and *Gomphonema micropus* (7%). Anthropogenic disturbances and higher nutrient concentrations are obviously the main explanatory factors for differences in species composition between springs in more or less densely populated areas (e.g., Aboal et al., 1998; Angeli et al., 2010).

The main groups of photoautotrophs in springs

The following is a summary of photoautotrophs known to inhabit springs. In average ("normal") conditions, the bottom of a spring is not barren but sparkles with shades of color ranging from dark-brown or black, to reddish, to all nuances of green and blue-green. Springs owe their bright colors to algae, aquatic lichens, and bryophytes (whereby German scholars use the term *Vegetationsfärbungen* = colors due to aquatic vegetation) (Figs. 6 and 7). Also the land-water ecotone, unless artificially altered with concrete or otherwise, is never bare but richly covered with aquatic plants, bushes (and sometimes trees) which need increasingly less water and become more and more intolerant of submersion with distance from the spring. While aquatic and hygrophilous bryophytes are frequent in shaded springs while higher aquatic plants prefer the muddy bottoms of wetland springs, rheocrenic springs with fast moving waters are well colonized by benthic algae and aquatic lichens.

- **Cyanoprokaryotes** or cyanobacteria (Fig. 6A–B), the former blue-green algae, are one of the dominant groups in oligotrophic waters and thus also in springs. Their prokaryotic nature is meanwhile known since many decades but they are traditionally treated as algae due to their similar growth form but also because they carry out an oxygenic photosynthesis comparable to other photoautotrophs and thus play a comparable functional role in ecosystems. The term cyanoprokaryotes is a compromise trying to acknowledge both these aspects. Due to both under-appreciation of spring studies, and increasingly complex approaches required for the characterization of cyanobacteria assemblages in near-natural habitats, the literature on cyanoprokaryotes in ambient springs is very limited (Cantonati et al., 2015). However, some generalizations are possible. The marked heterogeneity of the spring habitat requires a diverse set of adaptations. Different ambient springs are thus colonized by rheophilic, UV and radiation resistant, shade-tolerant, non-diazotrophic, P-specialist cyanoprokaryotes. Cyanobacteria can successfully be used to statistically characterize the diverse types of ambient springs (Cantonati et al., 2012c). Some morphotypes, e.g., *Phormidium retzii* in large karstic springs at low elevation, and *Homeothrix juliana* in ambient springs in arid regions, are regularly reported from these habitats even from distant geographic locations. Coccoid types appear to dominate in ambient springs in temperate climate while filamentous types appear to prevail in ambient springs in warm and arid climates (Cantonati et al., 2015). The in-depth characterization of ambient-spring cyanoprokaryote assemblages is important because, if adequately known, spring cyanoprokaryotes might provide a valid contribution to the assessment of the ecological integrity, quality, and value for nature protection of spring habitats (Cantonati et al., 2015). In the last decades it has become apparent that cyanobacterial toxin production extends to many more freshwater habitats than previously believed. Aboal et al. (2005) demonstrated that also occurs in high-ecological-integrity calcareous Mediterranean streams, and Cirés et al. (2017) brought to the forefront the presence of cyanotoxins in extreme environments, including hot springs. The exact adaptive meaning of cyanotoxin production in these environments still has to be elucidated. One of the most plausible interpretations is that cyanoprokaryotes may use these toxins for successful competition for space and nutrients with other primary producers, in particular other algae, and as an anti-grazing defense.
- **Diatoms** (Fig. 6C–D): Diatoms, unicellular microalgae characterized by an amorphous silica frustule formed by two valves with a complex ultrastructure, are the most species-rich group of algae (Mann, 1999). The global diversity of diatoms may be one or more orders of magnitude higher than the current number of species described (Vanormelingen et al., 2008), with as many as ca. 100,000 but at least 30,000 extant diatom species (Mann and Vanormelingen, 2013). They contribute to global primary production with a proportion as large as 20%, possessing global significance in the carbon and silicon cycles (Mann, 1999). Diatoms can be found everywhere where there is a little bit of moisture, and in all aquatic habitats. Most of them have very precise preferences for ecological conditions of pivotal relevance in environmental quality assessments, such as pH, mineral

content, nutrients, etc. A combination of mechanisms (active urea cycle, probably used to improve nitrogen storage; fatty acids oxidation in mitochondria; chemical information exchange among cells; "melting pot genome" of ca. 10,000 genes with many diatom specific genes but also extensive documented gene transfer from bacteria to diatoms) may underlie the rapid diversification rates, and may explain why diatoms have come to dominate several contemporary systems in a relatively short period of time (Bowler et al., 2008). A large multi-disciplinary project (CRENODAT) allowed to study 110 ambient springs in the south-eastern Alps, considering a wide range of elevations, lithologies, types, mineral content, and pH. Diatoms in the different kinds of springs were found to be as follows. Iron springs typically harbored species-poor assemblages with low numbers of individuals. Helo- and rheohelocrenes and some very-low alkalinity rheocrenes had *Eunotia* as the most species-rich genus, and were characterized by the mire-species *Frustulia crassinervia*, the acidophilous *Tabellaria flocculosa*, the very low-alkalinity indicator *Psammothidium acidoclinatum*, and several *Eunotia* species (*E. borealpina*, *E. exigua*, *E. tenella*). Well-buffered rheocrenes on siliceous substrata had *Odontidium* as the most species-rich genus, and the following common species: *Odontidium mesodon*, *O. hyemale* (Fig. 6C), *Eunotia minor*, *Encyonema minutum*, *Navicula exilis*, *Planothidium lanceolatum*. Carbonate flowing springs with lower conductivities and/or affected by seasonal desiccation had *Humidophila* as flagship genus: *H. perpusilla*, *H. contenta*, *Planothidium frequentissimum*, *Meridion circulare*, *Achnanthidium dolomiticum*. Rheocrenes on carbonate substrata with different situations of current flow had *Achnanthidium* as characteristic genus: *A. pyrenaicum*, *A. lineare*, *Rossithidium pfisteri*, *Gomphonema elegantissimum*, *Nitzschia fonticola*. This group can be subdivided into sub-assemblages defined by decreasing *A. lineare* and increasing *A. pyrenaicum* with increasing current velocity. Carbonate rheocrenes affected by moderate nitrate enrichment and/or shading had *Cocconeis* as outstanding genus: *C. euglypta*, *C. lineata*, *C. pseudolineata*, *Amphora pediculus*, *A. micra*, *A. inariensis*, *Caloneis fontinalis*, *Reimeria* spp., *Eunotia arcubus*. Hygropetric rheocrenes and some LPS springs had *Encyonopsis* as most characteristic genus: *E. microcephala*, *E. cesatii*, *Delicatophycus delicatulus*, *D. minutus*, *Gomphonema lateripunctatum*, *Denticula tenuis*, *Cymbopleura austriaca*. Many diatom species showed a significant substratum preference for stones or bryophytes. Bryophyte-dwelling assemblages were found to have higher taxa numbers and species diversity but average diversity did not differ among the most frequent bryophyte species (Cantonati et al., 2012b). Our knowledge of diatoms in springs comes mainly from alpine regions and low mountain ranges. Żelazna-Wieczorek (2011) showed that they also abundantly occur in lowland springs with species-rich populations. Even if there is hardly any crenobiontic species there, diatoms allow well-founded nature conservation statements about springs. In addition to the ecological informative value of the species communities described above, it is possible to identify rare species according to the Red List of Diatoms in central Europe (Hofmann et al., 2018; Cantonati et al., 2021) gaining further scientific grounds to campaign for the protection of their habitats.

- **Green algae** (Fig. 6E–F): Among the chlorophytes (green algae) in the broadest sense, filamentous and unicellular algae of the orders Zygnematales and Desmidiales are abundant, especially in slightly acidic helocrenes (Cantonati et al., 2012c). The species *Klebsormidium rivulare* often grows on bryophytes or large stones, mostly in only partially water-covered areas. Species of the genus *Cladophora* (Fig. 6E) can be found in nutrient-richer springs of various types, and charophytes (stoneworts, Fig. 6F) typically occur in limnocrenes, including desert springs (e.g., Saber et al., 2021). *Rhizoclonium*, though reported from a variety of habitats, also seems to be more common in limnocrenic springs, for example in the lowland pool springs in alluvial deposits of the Italian Po plain, locally called *fontanili* (Saber et al., 2017).
- **Red algae** (Fig. 6E and G): Among the rhodophytes (red algae), tufts of species of the genus *Audouinella* are most common in mountain springs, epilithic crusts of *Hildenbrandia rivularis* (Fig. 6G) occur in heavily shaded sources, especially in low to medium-elevation locations (Cantonati et al., 2016b) while the long, branched, threadlike filaments of *Batrachospermum* species are most likely to be found at lower elevations, where they colonize rheocrenic springs as well as streams. In springs with large discharge where splash-zone, spray-zone microhabitats can develop the filamentous red alga *Bangia atropurpurea* (Fig. 6E red patches intermingled to the green patches of *Cladophora glomerata*) can sometimes be found (MC unpublished observation). The unicellular and colonial red alga *Chroothece* sp. was found in an inland-saline spring by Cantonati et al. (2019).
- **Yellow-green algae**: Xanthophytes (yellow-green algae) are particularly represented in springs of the Alps by species of the genus *Vaucheria* (e.g., Cantonati et al., 2012c), whose rough, cushion-like thalli on carbonate substrates can cover extensive areas. Filamentous representatives (*Tribonema*) of the yellow-green algae often appear in different source types including helocrenes.
- **Golden-brown algae**: The golden alga *Hydrurus foetidus* (chrysophytes) is widespread in the mountains in streams and rheocrenes. This species is rheophilic and does not tolerate water temperatures above 15 °C. Therefore, it occurs in streams only during a defined time window (late winter-spring) (Rott et al., 2006) but can be observed in springs all year round (Cantonati et al., 2016b).
- **Lichens** (Fig. 7A): Originating from a symbiosis between a "photobiont," an alga or a cyanobacterium, and a fungus, lichens are found with a restricted number of species in freshwater habitats. They are quite common in springs of the Alps, but so far they have received relatively little attention (e.g., Cantonati et al., 2007). One of the determining environmental factors for the distribution of freshwater lichens is light (Thüs, 2002). In addition to species that are adapted to very little light (e.g., *Verrucaria hydrela*, *Porina chlorotica*), others prefer higher light intensities. Most lichens are quite insensitive to dehydration, but some spring-dwelling species (e.g., *V. funckii*) cannot even tolerate short-term exposure outside the water (Cantonati et al., 2007). Dependent on stable lithic substrata, they are missing, for example, in wetland springs where fine detritus dominates among substrates. The different demands on light or moisture result in a characteristic vertical zoning in relation to the lowest or highest water level, which is typically visible on larger boulders at the margins of the spring (Cantonati et al., 2007). Other important environmental factors are the lithology (different species communities in silicate and carbonate springs) and the pH (acidification is hardly tolerated) (Thüs, 2002). In spring streams, especially on silicate substrates, Mühlenhoff (1994) was able to

identify typical associations of lichens and bryophytes, which are probably also suitable to provide information on the overall quality and integrity of rheocrenic spring habitats. Nascimbene et al. (2011) tried to apply to springs the bioindication potential of lichens widely applied in terrestrial habitats, and identified *Verrucaria elaeomelaena* on carbonate rocks and *V. funckii* (Fig. 7A) on silicate substrata as typical spring species.

- **Bryophytes** (Fig. 7B–D): Bryophytes (mosses and liverworts), treated together with the phanerogams in many spring studies and contrasted with the algae and fungi, with which they could be summarized as "cryptogams" (Martin et al., 2015), are often very narrowly restricted to the source area (eucrenal) in the longitudinal zonation (compare, e.g., Petraglia, 2007, Tomaselli et al., 2011), abundantly colonize the substrata available there (Ortler, 1997), and accommodate a characteristic microflora (see above) and fauna (e.g., Hajkova et al., 2011). Bryophytes proved to be more suitable than the higher plants for a classification of springs of the south-eastern Alps on siliceous and carbonate substrata, as they were more strictly bound to springs (Ortler, 1997). Out of 58 bryophyte taxa found by Ortler (1997), 12 had their ecological optimum in the springs (crenophiles: *Cratoneuron* spp., *Dicranella palustris*, *Brachythecium rivulare*, *Bryum pseudotriquetrum*, *Philonotis* spp. (Fig. 7B), and *Scapania undulata*), and another three were key species of bryophyte communities (*Fontinalis antipyretica*, *Chiloscyphus polyanthos*, and *Hygrohypnum dilatatum*). As regards carbonate springs, phytosociological characterization revealed three, mainly *Cratoneuron*-dominated, associations along an elevation gradient. With increasing altitude, the montane *Cratoneuretum commutati* is replaced by the subalpine *Cratoneuron decipiens*-association, and then, in the alpine zone, by the *Cratoneuretum falcati*. In springs on siliceous substratum, associations were more variable and bryophytes were altogether more frequent, especially springs with large discharge. In addition to lithology, the most important environmental variables turned out to be substrate-particle size, discharge, soil moisture, elevation, and contact-vegetation composition while light conditions were apparently only of secondary importance (Ortler, 1997). In boreal springs, in which bryophytes are as well the dominant group of plants, Heino et al. (2005) observed drastic shifts in the species spectrum between 1986 and 2000. Some species became noticeably rarer and were regarded as acutely endangered (e.g., *Philonotis fontana*, Fig. 7B), while *Sphagnum* species (e.g., *S. warnstorfii*) occurred more frequently. Depending on specific conditions in different areas, either water chemistry (in turn dependent on the lithology, the elevation, and on possible acidification; Beierkuhnlein, 1999, Beierkuhnlein and Schmidt, 1999) or light conditions (Peintinger and Beierkuhnlein, 1999) proved to be the main determinants of the spring-vegetation composition. Species occurring in forest seepages obviously differed both in their life cycle and in terms of their ability to adapt to different light and temperature conditions (Beierkuhnlein and Gräsle, 1998). Submerse mosses generally have great potential as bioindicators. The occurrence of the *Cratoneuron* association is one of the characteristics used to describe the EU Habitat Directive FFH priority habitat "Petrifying springs" (Natura 2000 code 7220; EU-HD, 1992). *Chiloscyphus polyanthos*, a characteristic species for non-acidic spring-brooks with stable discharge, is sensitive, for example, to pollution and fine-sand deposits, which may cover the vegetation after floods (Himmler and Tremp, 1992). *Fontinalis antipyretica* is typically found in cold, but rather nutrient-rich springs, is absent from acidic springs, and is a good indicator in spring waters with different pH values and different contaminant levels. Trace elements, such as Cd, Pb, Cr, Cu, and Hg, are strongly accumulated, and saturation is reached already after a few days to weeks but the release is slow and occurs over some months (Cenci, 2000). *Scapania undulata* lives in springs on siliceous substratum, submerged in acid water, both submerged and on exposed substrates in the spray zone at approximately neutral pH, but exclusively above the mean water-level line at pH values greater than 7 (Frahm, 1992). In forest seepages the species can thus be used as acidification indicator. In a study by Audorff and Beierkuhnlein (1999), calcium and magnesium could only be determined at neutral pH or when the springs were exposed only to rare acidification events; the concentrations of these elements in *S. undulata* were correlated with their concentrations in the water and the pH value.
- **Vascular plants** (Fig. 7D–H): In terms of degree of cover, bryophytes dominate in most spring habitats over higher plants (vascular plants or phanerogams) (Martin et al., 2015), which are also more likely to be found at the spring margins rather than inside the spring-head (Zechmeister and Mucina, 1994). Thus, in a spring study in the south-eastern Alps, out of 344 recorded species of higher plants, only 67 occurred exclusively in places directly influenced by the springs, and only seven could be described as character species of the spring vegetation in the phytosociological sense, namely *Arabis soyeri*, *Epilobium alsinifolium* (Fig. 7E), *Cardamine amara* (Fig. 7G–H), *Pinguicola alpina*, *Saxifraga stellaris* (Fig. 7F), *Silene pusilla*, and *Stellaria alsine* (Ortler, 1997). In the lowlands and in medium-altitude mountains *Chrysosplenium oppositifolium* is an important indicator of spring sites, occurring at and, in part, also in springs (compare Hinterlang, 1996). Higher plants appear generally unsuitable for a spring classification, although they can dominate the spring flora at lower elevations, where mosses are less competitive (Petraglia, 2007). Due to the special conditions in springs, rather unusual plant species grow here, which, for example, have to be adapted to the stenothermal conditions (Zechmeister and Mucina, 1994). The environmental determinants are similar to those for other groups of photoautotrophs, i.e.: water temperature, flow velocity, pH as well as nutrient availability and concentrations (Warncke, 1980; Audorff et al., 2011). Anthropogenic nutrient enrichments are quickly reflected in changes in the phanerogamic communities (see Tomaselli, 2007, also for an overview of the typical spring flora of the Alps). Plant communities at spring locations can serve as an indicator for the degree of naturalness, and their analysis can provide valuable information for nature conservation and biotope improvement measures (Hinterlang, 1993). Sources on siliceous substrata are particularly suitable as monitoring sites for acidification processes. When the pH value falls, the *Chrysosplenietum oppositifolii* association is replaced by the *Caricetum fuscae polytrichetosum communis* association, and this happens already at a stage in which the forest vegetation is not yet responding to acidification (Beierkuhnlein, 1996).

Conservation concerns and restoration efforts at springs

Stevens et al. (2021) conducted a preliminary global analysis on the ecological integrity of springs, reviewing information on an estimated 250,000 spring ecosystems from 78 countries. Literature on springs ecological integrity is sparse, widely scattered, and spatially erratic, with major gaps in knowledge. There are large differences in the quality and extent of information among countries and continents, with only moderate data availability even among developed countries, and limited information across most of the developing world. Where data are available, ecological impairment of springs is rampant everywhere, sometimes exceeding 90% in developed regions (Stevens et al., 2021).

Cantonati et al. (2020c) report that humans and their livestock impact springs in manifold direct and indirect ways. Many springs have been dewatered through aquifer overdraft. A striking example is that approximately 33% of the 259,000 km^2 Floridan Aquifer has been appropriated for human uses, and existing permitted withdrawals equal about 50% of the aquifer's recharge, which historically fed more than thousand artesian springs (Knight, 2015). Further impacts, directly or indirectly related to climate change and land-use alteration, include reduced precipitation and aquifer recharge, excessive nutrient enrichment (e.g., nitrogen from agricultural and urban development), non-native species introduction, physical disturbance, and geomorphic alteration, livestock watering and trampling, flow diversion, water-bottling operations, and recreation impacts (Cantonati et al., 2020c).

The Habitat Directive of the European Union (EU) recognizes only one major spring habitat type, namely Limestone Precipitating Springs (LPS; Annex I: "Petrifying springs with tufa formation—*Cratoneurion*" EU-Code 7220, Cantonati et al., 2016a). Australian artesian springs in the Great Artesian Basin are protected under Federal Australian Law by the Environment Protection and Biodiversity Conservation Act. However, few other nations have similar legislation, an exception being Finland, which protects its springs through the Water Act and the Forest Act. In the United States, groundwater and springs are scarcely considered in federal legislation, with jurisdiction over those waters largely deferred to individual states (Florida, New Mexico, Wisconsin, and a few other states recognize the importance of protecting their springs). Comprehensive local, national, and international legislation for conservation of springs is urgently required (Cantonati et al., 2020c).

According to Cantonati et al. (2020c), reducing the global loss of spring ecosystems requires reinvigorated scientific effort, education and outreach, and improved policy (Glazier, 2014). All spring types and their recharging groundwater basins should be included in relevant conservation and assessment legislation worldwide. On the scientific side, improved mapping, broad agreement on a consistent lexicon, and adoption of standardized inventory and assessment protocols are needed. Basic information about the location of springs is lacking for most areas of the world (compare Stevens et al., 2021).

According to Cantonati et al. (2020c) and Stevens et al. (2021), the global silent crisis of the demise of springs can be slowed or reversed by using sound scientific data and through informed debate among stakeholders. Global conservation efforts require the collective recognition of the importance of springs for humans and nature. Given their significance as biodiversity havens for many rare and endemic species, as well as their cultural and socio-economic values, improving stewardship of springs and their supporting aquifers will yield major environmental advantages and societal benefits.

Restoration efforts at springs (e.g., Martin et al., 2015) have so far only rarely been scientifically documented. Documentation of the pre-restoration state would have to be undertaken before the intervention, followed by a multi-year success-control study (e.g., Wächter and Rüther, 1994). In a flowing spring in pastureland, Zollhöfer (1997) observed a gradual increase in spring-dependent species after fencing of the spring-source area. A definitely important factor for a recolonization is certainly an existing potential for species re-establishment from the surrounding area. Unfortunately, technology and experience from case studies about using flow-splitters to allow for a residual ecological flow after spring capturing to feed purposely-designed secondary spring biotopes are still in a very early phase (Cantonati et al., 2009b). Barquín and Scarsbrook (2008) pointed out that unsustainable exploitation of springs also impairs their capability to provide ecosystems goods and services. Eller and Katz (2017) proposed the Nitrogen Source Inventory and Loading Tool, developed as an ArcGIS and spreadsheet-based approach that provides spatial estimates of current nitrogen inputs to the land surface and loads to groundwater from nonpoint and point sources within the groundwater contributing area, as an integrated approach toward restoration of water-quality impaired karst springs. One of the few countries in which spring-habitat restoration is a serious concern both politically and scientifically is Finland. Lehosmaa et al. (2017) evaluated the effectiveness of spring restoration using data from near-natural, restored, and human-impacted springs, the major impact being degradation of spring hydrology by forest drainage. They used both taxonomic (bryophytes, macroinvertebrates, and leaf-decomposing fungi) and functional (leaf breakdown) measures of restoration success. The contribution of surface water was greatly reduced, and thus restored springs were thermally more stable than impacted springs. Bryophytes and macroinvertebrate did not differ among restored and natural springs. Bryophytes were more abundant in restored than in impacted springs, and invertebrates differed between restored and impacted springs. Species diversity and functional attributes showed weaker responses to restoration. Due consideration of the responses of springs to climate change will foster the long-term effectiveness of their conservation and restoration (Cartwright et al., 2020).

Knowledge gaps

- Improve the theoretical framework of springs as ecosystems
- Springs, studied in an ecohydrological perspective, as ideal systems in which to further investigate and understand geo-biodiversity relationships

- Further develop efforts to raise societal and political awareness of springs as unique systems and effective protocols for springs conservation and restoration
- Build and strengthen a global network for spring ecology and conservation (compare Spring Stewardships Institute at MNA)
- Further expand knowledge on the theoretical foundations of spring-habitat restoration, and develop restoration technologies

Acknowledgments

I thank Colleagues who share my passion for springs and with whom I have repeatedly discussed, over the years, the topics of spring-aquifer relationships and spring typology, most notably: Larry Stevens, Rod Fensham, Doug Glazier, Reinhard Gerecke, Stefano Segadelli, Nico Goldscheider, Alessandro Gargini.
I am grateful to Christian Griebler, Managing Editor of the section on "Groundwater habitats" of the *Encyclopedia of Inland Waters*, and Paula Davies, Elsevier Ltd. Content Project Manager, for their assistance while I was preparing the chapter and their patience with delays.

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Relevant internet resources

https://springstewardshipinstitute.org/.

www.kalktuffquellen.de—Conservation and restoration of limestone-precipitating springs in Germany.

https://www.alpenquellen.com/.

Biodiversity of Invertebrates in Springs

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Introduction

From a simplistic hydrological viewpoint, a spring represents a concentrated point of natural discharge of groundwater that is sufficiently high to maintain flow on the land surface (Van Everdingen, 1991). The flow of water from a spring often comprises a mixture of water that has infiltrated the subsurface at different times and places. The rate of this recharge varies according to the balance between precipitation, infiltration, runoff and evapotranspiration, and as the contributions from different recharge points change, so too will the output of the spring vary. Van der Kamp (1995) illustrated such variation in hydrogeology with examples of two spring types: (1) a spring fed by slow seepage through small pore spaces (e.g., sand and rock with fine fractures, typically $<$0.1 mm wide) with strong filtration which produces stable flow and water devoid of any large particulate matter; (2) a spring fed through cavernous carbonate rock – such 'karst' springs typically have strong, but variable, flow and higher particulate loads. In some instances, a spring may be fed by a very shallow or small aquifer resulting in intermittent surface flow. Such contrasting discharge patterns can be predicted to radically affect the nature of the community capable of living in these respective springs. From an ecological perspective, springs have been traditionally subdivided into three broad types (Fig. 1): *rheocrenes* – in which the source emerges into a rapidly flowing stream; *limnocrenes* – in which the source first enters a basin with slow flow; and *helocrenes* – in which emerging water percolates into a marshy holding area, frequently rich in mosses (Bornhauser, 1913). There are, of course, some springs that do not fit neatly into these definitions, for example, where a limnocrene has sufficient discharge such that the water spills out of the basin forming a fast-flowing stream, which might be termed a 'rheolimnocrene.'

If we examine a simple water budget for springs, it is clear that groundwater is their primary source. Precipitation directly on the relatively small surface areas of, for example most rheocrenes, is likely to be low, although that on limnocrenes may be higher. Of the main water losses (outputs), evapotranspiration is likely to be low – but again related to spring surface area, together with the characteristics of local vegetation. Water lost to floodplains may be retained in wetlands or flow down-gradient in springbrook channels. In the case of helocrenes, water may diffuse away as overland flow into surrounding depressions, soil and vegetation. Depending on local topography and soil infiltration capacity, some spring waters may re-enter shallow downstream aquifers, perhaps to re-emerge at down-slope springs. Emergence of groundwater, as described above, occurs globally, making springs commonplace in all but the most arid or cold regions – although even the latter have their own characteristic upwellings (e.g., those found in the Chihuahuan Desert in Texas, Wallace et al., 2005; and on Axel Heiberg Island in the High Arctic, Lay et al., 2013).

The main aim of this chapter is to review the properties of springs and how they have been classified against a background of the biodiversity of the animals, chiefly invertebrates, that inhabit them.[1] Emphasis is placed on our past and current understanding of the structural and functional links between these organisms and their environment. The effects of increasing anthropogenic stresses are discussed.

Alternative typologies of springs

There is an over-abundance of imprecise terms to describe springs (e.g., spring source, spring-fed stream, springbrook, headwater spring, spring run, seep, spring seep). Some definitions are based on the immediate physical and chemical environment, while others focus on the communities of organisms living there. These differences stem, largely, from the disparate backgrounds of the

[1]Larger, permanent springs may sometimes support small fishes, such as bullheads, especially where underground, cave-dwelling populations come to the surface. However, such occurrences are rare.

 https://doi.org/10.1016/B978-0-12-819166-8.00072-4

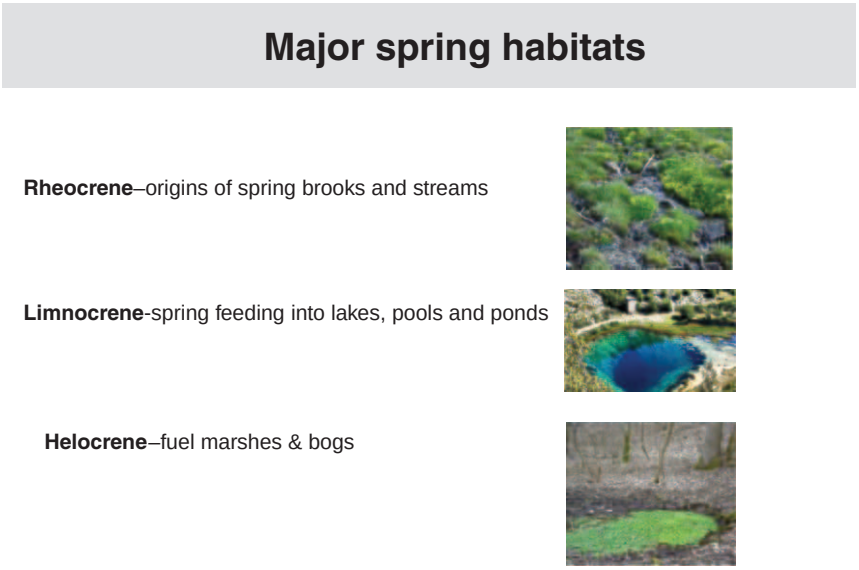

Fig. 1 The three broad types of spring: rheocrene (top), limnocrene (middle), helocrene (bottom).

scientists who study them. For example, geologists tend to define thermal springs with respect to temperatures more than 5 °C above the local mean-annual air temperature (Van Everdingen, 1991) – which reflects geothermal warming. Biologists customarily define thermal springs in reference to temperatures above the local annual mean (warm), as well as above the annual mean maximum (relatively hot), and above 40 °C (absolutely hot) (Tuxen, 1944). Biologists also sometimes categorize habitat temperatures in a manner that best coincides with the distribution of a given taxon. For example, Smith (1991) defined a 'hot' spring as one above 30 °C as none of the Canadian water mites he studied occurred in waters that hot. However, some insects and other invertebrates can be found in springs exceeding 40 °C, requiring a different cut-off level for 'hot' (for further discussion, see Pritchard, 1991).

In any given spring, all or some of these factors come together to characterize the size, rate and pattern of flow, temperature regime, and chemical composition of the habitat. The community of invertebrates that subsequently develops reflects tolerance of and/or adaptation to these factors, together with colonization abilities from neighboring or distant sources. The latter is particularly important in regions where new habitat has been created, such as by shifts in regional geology, affecting the level of the groundwater table, or by the retreat of glaciers during the Pleistocene (Williams and Williams, 1999). The role of these factors will be re-visited later in the chapter.

As noted, strictly speaking, a spring can be defined only in its proper geological setting, taking into account numerous variables that characterize its nature and potential as a habitat. These variables include some that are easily measured, such as pH, temperature, current speed, and dissolved oxygen, but others that are much more difficult to quantify, such as size of underlying aquifer and nature and length of groundwater flow paths (both of which may influence habitat stability). Given limitations in acquiring measurements of some of these variables, and in preference to a rigid classification of springs, for which there will always be exceptions, Danks and Williams (1991) proposed using a minimum of five key descriptors to characterize each habitat sampled for biological data (Table 1). These descriptors are seen as providing sufficient characterization of fundamental elements of springs as habitats, and comprise: source geometry; rate of water supply; temperature; chemistry; and persistence. Thus, for example, the following minimum description provides a useful and comparable characterization: 'low volume, warm, freshwater, annual, temporary rheocrene.' Where logistically possible, such a basic description should always be supplemented by additional information, measurements and photographs.

A few words about seeps

In addition to springs, *senso stricto*, most of the world's major biomes support another form of habitat fed by groundwater, namely 'seeps.' Unfortunately, the latter have been far less studied. While both these habitats are fed by groundwater and may have stable temperature and chemical properties, they can differ markedly in their physical characteristics. For example, springs are likely to have a more defined footprint at their point of issue, deeper water and greater discharge, whereas seeps are shallow (often just a film of water over rock surfaces), and typically discharge more diffusely – the water typically infiltrating into surrounding soil and/or vegetation, such as mosses. Their rate of flow is generally insufficient to form an outflow stream. The limited data available (Williams, 2016) show an apparent global absence of a few major taxa in seeps (e.g., bivalves, isopods, mayflies), and, at the genus level, approximately 41% of the diversity seen in springs. The two habitat types share 100 genera, which include many freshwater

Table 1 Recommended minimal key descriptors of springs for biological data.

Key descriptors	*Status observed*		
	Low	*Intermediate*	*High*
Nature of source	Helocrene (discharge or seep into marshy/mossy substrate)	Limnocrene (discharge into basin)	Rheocrene (rapid flow into defined channel on discharge)
Discharge at source	Low volume (<0.01 m^3 s^{-1})	Medium volume (0.01–0.5 m^3 s^{-1})	High volume (>0.5 m^3 s^{-1})
Water temperature	Cold (<10°C)	Warm (10–40 °C)	Hot (>40 °C)
Chemistry: as total dissolved solids	Fresh water (<1000 ppm)	Mineral (1000–35,000 ppm)	Saline ($>35{,}000$ ppm)
Persistence[a] (as approx. interval between major disturbances)	Intermittent (typically annual, but up to 5 years)	Apparently permanent (>5 years i.e., some signs of inconsistency)	Permanent (>50 years; no disturbance)

[a]Unless historical records are available (e.g., from paleoecological evidence - see Williams and Williams, 1996), interpretation here is likely to be largely subjective, based on observations of physical and biological conditions made at the site.

From Danks HV and Williams DD (1991) Arthropods of springs, with particular reference to Canada: Synthesis and needs for research. *Memoirs of the Entomological Society of Canada* 155:203–217.

generalists (e.g., *Ischnura*, *Hydroporus*, *Chironomus*, and *Hydroptila*), but there are 55 genera found only in seeps, which include some seep specialists (e.g., *Stolonicyclops*, *Trichothyas*, *Viehoperla*, *Oconoperla*, *Ochterus*, *Antillocladius*, *Orethalia*, *Chilostigma*, and *Clostoeca*). These records suggest that the invertebrate faunas of seeps contain a component that is a sub-set of the fauna found in springs, but also a second component that is comprised of seep specialists. Further studies are required to test these hypotheses.

General habitat conditions in springs

For aquatic invertebrates, it is important to remember that environment and community are intimately linked and that springs represent a range of habitats from the 'classical' highly stable (especially in terms of temperature and discharge) type to those with a more seasonably variable hydroperiod, such as those associated with wetlands (Danks and Rosenberg, 1987). Many factors influence habitat conditions in springs, including those associated with the terrain (e.g., local geology, topography, and groundwater reserves) and geographical position (e.g., latitudes and glacial history), alongside smaller-scale influences such as vegetation (submerged, emergent, and riparian, especially if it shades the water) (Danks and Williams, 1991).

Terrain features dictated by geology and topography determine the supply of water and how it varies, together with the level and variability of its temperature and chemical composition. Thus, large groundwater reservoirs buffer the habitats from erratic drying and other major changes, they tend to enhance the rate of flow but reduce its variation, and they stabilize temperatures. Longer groundwater residence in softer rocks increases mineralization, but depending on the composition of the rocks may either increase or decrease pH (Van Everdingen, 1991). Permanent springs are fed by groundwater with at least a 1-year residency underground, but the water of many springs is fossil water that emerges from the ground long after it entered, often 10,000 years later (Downing et al., 1977).

Conditions above the ground surface are modified on a broad geographical scale by local climate and other regional elements - such as photoperiod, known to promote the seasonal succession of invertebrate species and algae that occurs in springs despite oftentimes very constant temperature (Teal, 1957) - and on a yet smaller scale by the size of the spring, its vegetation, and habitat diversity. These influences especially affect temperature, primary productivity, allochthonous food (such as dead leaves) supply, and other ecological factors. Thus while a spring may have very uniform abiotic conditions, there may be considerable annual variation in its biotic conditions (Varza and Covich, 1995). High mineral content creates mineral springs, including salt springs (Ring, 1991); high temperature groundwater creates thermal springs (Pritchard, 1991); and erratic or surficial discharges produce intermittent springs. Discharge has an important effect on spring-bed substrates, which have a major influence on the invertebrate community. For example, constant or intermittent high flow rates remove fine particles thus increasing the mean particle size on the bed and reducing the amount of detrital food materials. In contrast, where the water wells up into a basin, fine particles accumulate. Highly mineralized springs may precipitate flocculent substrates.

Broad characteristics of the fauna

Within the last couple of decades, there have been several attempts to bring together the collective knowledge of spring faunas with the aim of galvanizing further study, synthesis, and conservation (Williams and Danks, 1991; Ferrington, 1995; Hinterlang and Lischewki, 1996; Botosaneanu, 1998; Glazier, 2014). However, while the spring faunas of some regions (e.g., Europe and North America) and some taxa (e.g., Trichoptera, Diptera, and Acari) are becoming better known, the information base for spring communities in most geographic regions of the world is very sparse (Yule, 2004).

In lotic systems, the diversity of invertebrates generally increases downstream. Typically, therefore, the section of channel immediately below the outlet (springbrook) will have a lower diversity than the stream, whereas the spring itself will have the least (Ward and Dufford, 1979). However, this is not always the case (Resh, 1983), and certain taxa may be particularly species rich at the source. For example, Gathmann and Williams (2006) recorded 38 species of Limoniidae (Diptera) from 30 coldwater springs in southern Ontario, Canada. Interestingly, of the total of 86 insect species found, 55% were found at three or fewer sites, and only for very few of these rare species were more than 10 individuals m^{-2} collected. Inter-annual differences were also apparent, with emergence records from a single year, on average, containing around 50% of the total number of species found in the entire study. Temperature and discharge correlated most strongly with insect community similarity among springs.

Invertebrates collected in or near springs range from permanent residents to those that are just visiting - to avail themselves of food or use these habitats as 'stepping-stones' in an attempt to reach other waterbodies. Many of these non-residents do not breed in springs yet they may dominate the fauna. For example, of the 33 species of aquatic beetle found in a spring in North Dakota, 64% were non-resident (Roughley and Larson, 1991). Resident species are derived from several different sources (Fig. 2). At the core, are species (termed 'crenobionts') that are confined to springs and/or seeps and which exhibit suitable adaptations to cold water and constant abiotic conditions (Danks and Williams, 1991). Another important component comprises the phreatic species of turbellarians, micro-crustaceans, mites, plecopterans, and other taxa that live in suitable, oxygenated groundwaters and enter the springs that emanate from them. Generalist species from downstream coldwater brooks also enter where there is sufficient flow (rheocrenes). Limnocrenes and helocrenes may contain some lentic species, although not those that cannot tolerate very cold water (e.g., pond species). Some species are associated with spring margins, especially where there is abundant moss or organic materials, or a distinct splash zone, for example, mites, collembolans, and various semi-aquatic dipterans. Other species may be derived from the wet soil at a spring's edge (e.g., rotifers, mites, nematodes, snails). Such species living in springs, but not exclusively so, are often termed 'crenophiles.' Hot springs and saline springs are populated by a low diversity of extremely tolerant species, typically, in the case of insects, belonging to the Diptera, Coleoptera, and Hemiptera (Ring, 1991) - additionally, Odonata may occur in hot springs (Pritchard, 1991).

Specifics of the fauna

The following is a summary of invertebrates known to inhabit springs. These records, wherever possible to the level of genus, are taken from a global synthesis (Williams, 2016) which should be consulted for greater details. The data-set is by no means complete, but hopefully will serve as a useful first step toward creating a global framework to which new occurrences of species in springs can

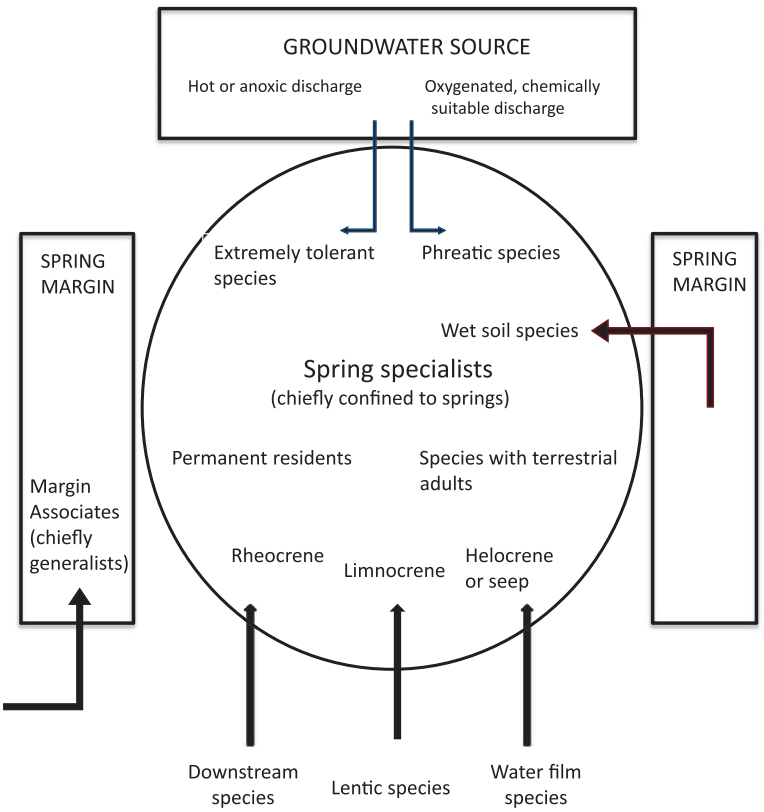

Fig. 2 Components of the faunas of springs and seeps. Modified after Danks HV and Williams DD (1991) Arthropods of springs, with particular reference to Canada: Synthesis and needs for research. *Memoirs of the Entomological Society of Canada* 155:203–217.

be added. Taxa range from the more sessile forms, such as sponges and hydrozoans, through small motile forms, such as gastrotrichs, rotifers and nematodes, to micro-crustaceans, mites and many insect orders. Groups that have freshwater representatives but appear to be absent from springs include bryozoans (more restricted to warmer lentic and lotic waters; Wood, 2010), branchiopods (more characteristic of lentic waters that have a drying phase; Williams, 2006), and aquatic orthopterans, lepidopterans, and hymenopterans. The data-set comprises 379 genera, across all taxa. See also photographs of some of these taxa in Fig. 3 (Tricladida, Gastropoda, Tardigrada, Ostracoda, Isopoda, Acari, Collembola, Coleoptera, Diptera - Chironomidae, Trichoptera).

- *Porifera* - freshwater sponges in the genus *Spongilla* are widespread in cold fresh waters, but also occur in thermal springs (Hooper and Van Soest, 2002).
- *Hydrozoa* - the widespread genus *Hydra* has been found in springs. *Velkvrhia enigmatica* (Family Bougainvilliidae), has been found in springs in Slovenia (Zagmajster et al., 2011).

Tricladida - over 100 species of freshwater planarian are associated with cold waters, with genera such as *Crenobia*, *Polycelis* and *Phagocata* occurring commonly in springs (Reynoldson, 1967). Habitats of the, largely unidentified, Microturbellaria include springs (Kolasa and Tyler, 2010).

Gastrotricha - freshwater gastrotrichs (Family Chaetonotidae) have been recorded from springs (Balsamo et al., 2008; Nesteruk, 2008).

Rotifera: rotifer species in the genera *Dipleuchlanis*, *Ptygura* and *Wierzejskiella* have been collected from spring/seep complexes (Segers, 2004), and species within the genus *Lindia* are known from hot springs (Wallace et al., 2005).

Nematoda: species within the orders Monhysterida and Plectida (Subclass Chromadoria) are among the most widely reported nematodes from fresh waters, likely including springs (Abebe et al., 2008). At least eight families of nematode contain species capable of living in hot springs (Poinar, 2004, 2010).

Oligochaeta: around 100 species of aquatic oligochaete are found exclusively in groundwater environments, some of which are deemed important centers of endemism (Martens et al., 2008). A number of tubificid genera (e.g. *Ilyodrilus*, *Limnodrilus* and *Varichaetadrilus*) are associated with karst systems (Webb et al., 1996). Several genera within the subfamily Naidinae have been recorded from springs and/or seeps (e.g. *Allonais*, *Dero*, *Pristina*, *Stylaria*).

Gastropoda: springs and springbrooks support snail taxa not typically found in larger running waters, although individual sites tend to have low species richness (1–6 species, but at very high densities). Regionally these habitats support highly diverse assemblages of snails – especially of hydrobiids (Strong et al., 2008). Other families known to live in springs include: Melanopsidae, Assimineidae, Pomatiopsidae (saline springs), Planorbiidae, and Physidae. The high level of endemism in gastropods occurring in spring and related groundwater systems is associated with the extinction of many freshwater snail species as these habitats become degraded or destroyed by human activities, such as water abstraction, trampling of outflows when used for watering livestock, and irrigation or mining (Williams et al., 1990; Keleher and Sada, 2012).

Bivalvia: while clams are important members of the benthic communities of rivers and lakes, their occurrence in springs appears to be much rarer. Indeed, the only records are of the sphaeriid genus *Pisidium*, which has a cosmopolitan distribution (Cummings and Graf, 2010) and is capable of living in a very wide range of waterbodies.

Tardigrada: most waterbears are 'limnoterrestrial,' living in the thin films of water on the surfaces of moss, lichens, algae and leaf litter. Some live in wet soils or in aquatic sediments, and others are associated with water margins (Garey et al., 2008). Five, widely distributed genera, from three families, live in springs or at their margins (*Bertolanius*, *Eohypsibius*, *Isohypsibius*, *Microhypsibius*, *Murrayon*).

Crustacea – Ostracoda: ostracods are common inhabitants of springs, where their ecology appears to be a complex product of many environmental variables, including water chemistry, thermal regime, and hydrogeology (Forester, 1991). Spring-dwelling ostracod are well represented by genera belonging to the Cyprididae and Candonidae. A number of genera are known from thermal springs, for example: *Chlamydotheca*, *Cypris*, *Potamocypris*, and *Thermopsis*.

Diplostraca: several of the more common genera (*Alona*, *Daphnia*, *Diaphonosoma*) contain species that are associated with springs, others live in wet *Sphagnum* moss.

Copepoda: a number of highly vagil and cosmopolitan species live in a range of subterranean waters, including springs (e.g., *Acanthocyclops*, *Diacyclops*, *Eucyclops*, *Attheyella*, *Bryocamptus*).

Peracarida - Isopoda: species within the genera *Asellus*, *Caecidotea* and *Lirceus* are found commonly in cool springs, and *Thermosphaeroma thermophilum* lives in hot springs (Wilson, 2008).

Amphipoda: amphipod diversity is highest in subterranean environments (45% of species), and especially so in the karst regions of Central and Southern Europe (Niphargidae), North America (Crangonyctidae), and Australia (Paramelitidae) (Vainola et al., 2008). Some genera are widespread, including in springs (e.g., *Gammarus*).

Decapoda: there appear to be relatively few decapods that inhabit springs per se (e.g., *Palaemonetes*), but there are burrowing crayfishes (e.g., *Fallicambarus*) that inhabit seepage areas where they excavate shafts down to the water table (Williams, 2006).

Acari: the super-order Acariformes contains a wide variety of aquatic mites, those belonging to: the Hydrachnidia (true water mites); the Halacaridae (a primarily marine family); and the Oribatida (a primarily terrestrial order).

Smith (1991) produced a detailed synthesis of the Hydrachnidia from springs in Canada and recorded, at that time, over 115 species in 57 genera and 25 families collected from springs across the country. He divided the water mite fauna into three ecological groups related to the mites' preferences for helocrene, rheocrene or limnocrene habitats. Families with genera very commonly found in springs include the Hydryphantidae, Lebertiidae, Pionidae, and Arturidae. The genus *Thermacarus* lives in hot springs.

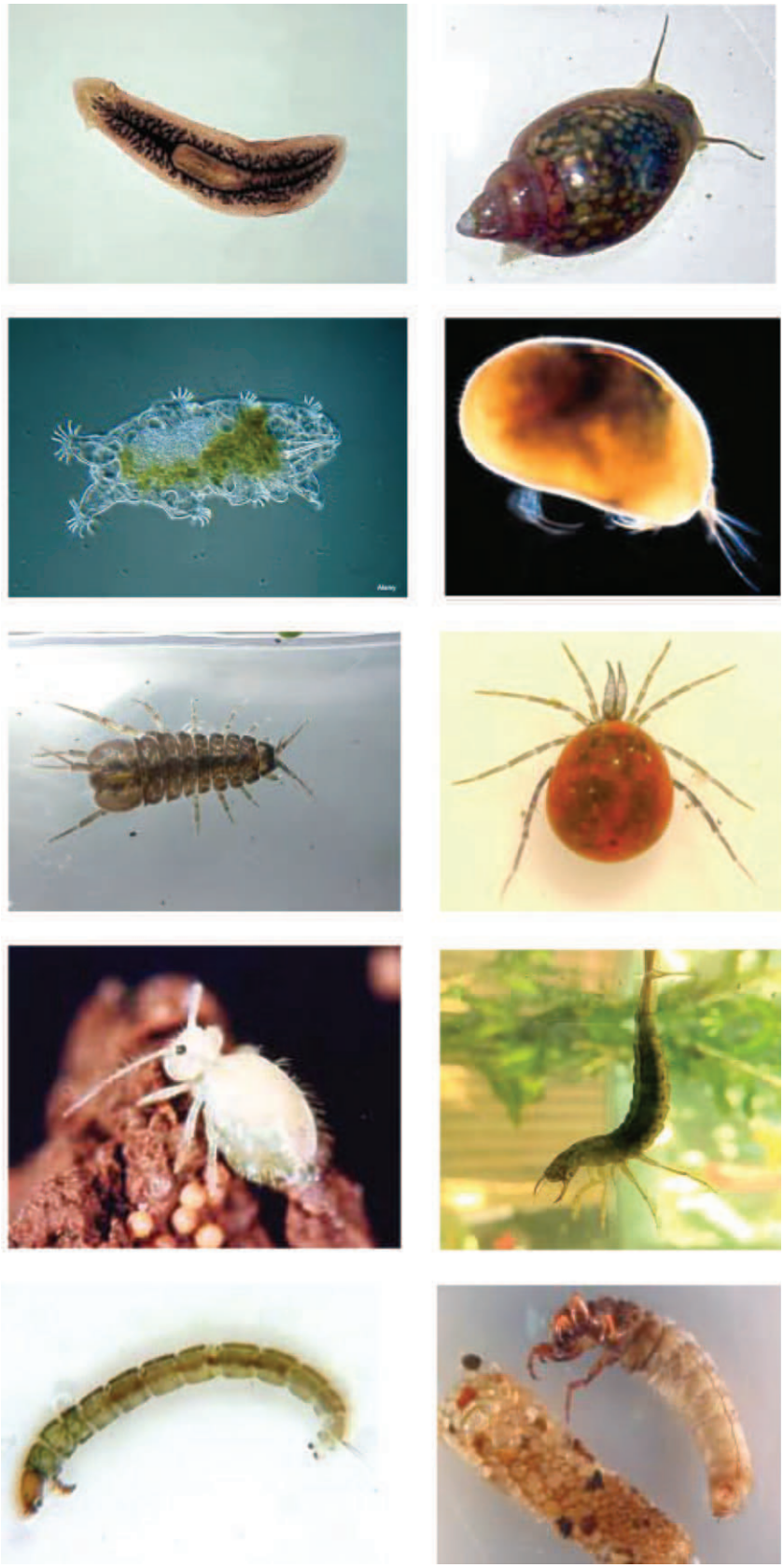

Fig. 3 Photos of representative invertebrate taxa found in coldwater springs.

Of the more than 1000 species of Halacaridae, only around 56 are known to occur in fresh water. These occur in both surface and subterranean waters, and have been recorded from springs. Genera collected from springs in Europe include *Copidognathus* and *Halacarellus* (Benfatti et al., 1989). Halacarids have a very low dispersal ability yet many genera and even some species are widespread (Bartsch, 2008).

Oribatid mites are largely associated with soil, forest litter, mosses and lichens, and only about 90 species, from 10 genera, can be considered truly aquatic. Habitat preferences in many are quite specific, and include springs (Schatz and Behan-Pelletier, 2008). Despite low diversity, aquatic oribatids can occur at very high densities. Some spring-dwelling species are very ancient, for example *Mucronothrus nasalis* is thought to pre-date the breakup of Pangea, about 200 million years ago. The distribution of this species is global, but discontinuous, and seems to be limited by temperature to cold, spring-fed water and cold bogs (Norton et al., 1988).

Collembola: springtails are particularly abundant in wetlands. In springs, they are most often encountered on the surfaces of helocrenes and limnocrenes, around the water margins, on saturated soil or on low vegetation (especially mosses) close to the water (Deharveng et al., 2008). Cosmopolitan genera commonly found in spring pools include *Isotomurus*, *Podurus*, and *Sminthurus*.

Ephemeroptera: despite being most often found in running waters, mayflies are neither abundant nor diverse in springs. Their life cycles are known to be tied closely to changes in water temperature, with small increases, for example, resulting in a different number of nymphal molts and early adult emergence. Perhaps the more constant temperature regimes of many springs lack cues essential to the timing of important mayfly life cycles events. Genera occasionally collected in springs\headwaters include: *Baetis*, *Serratella*, *Ecdyonurus*, *Epeorus*, *Rhithrogena*, and *Stenonema*.

Odonata: a number of dragonfly and damselfly genera, representing at least 10 families (Cordulegastridae, Petaluridae, Gomphidae, Libellulidae, Corduliidae, Hemicorduliidae, Calopterygidae, Coenagrionidae, Lestidae, and Megapodagrionidae), are associated with coldwater springs. Moreover, and perhaps reflecting their evolution in tropical regions, several genera support species that live in thermal springs, for example: *Cordulegaster*, *Ophiogomphus*, *Erythemis*, *Libellula*, *Orthemis*, *Pantala*, *Haeterina*, *Amphiagrion*, *Argia*, *Ischnura*, and *Lestes*.

Plecoptera: stonefly nymphs live, typically, in cold, clean running waters but are not particularly common in springs. A number of species (e.g., belonging to the Leuctridae, Nemouridae, Peltoperlidae, and Perlodidae) inhabit seeps and splash zones (Stewart and Stark, 1993).

Hemiptera: heteropterans can be found in a range of spring types. For example, corixids, notonectids and belostomatids occur in weedy limnocrenes and helocrenes, ochterids in shallow seeps with exposed rock surfaces, species of *Saldula*, *Micronecta*, *Anisops*, *Ambysus*, and *Limnocoris* in thermal springs, and species of *Diplonychus* in peat-mound springs.

Neuroptera: the megalopteran families Corydalidae and Sialidae have fully aquatic larvae that live in a wide variety of lotic and lentic waters (Cover and Resh, 2008). These include springs, with species of *Sialis* having been found in slow-flowing limnocrenes in several regions, and the corydalid genus *Neohermes* recorded from seeps in North America (Merritt et al., 2008).

Coleoptera: in Canada, up to 1991, the distribution of the 663 known aquatic beetle species among its major freshwater habitats was: lentic 61%, lotic 23%, springs 8%, other <1%, unknown 8%. The 63 spring-dwelling species belonged to: Dytiscidae (38 species), Hydrophilidae (9), Hydraenidae (8), Chrysomelidae (subfamily Donaciinae 6), Haliplidae (1), and Dryopidae (1)- (Roughley and Larson, 1991). Relatively diverse families deemed absent from the Canadian survey were: Gyrinidae, Scirtidae, Curculionidae, Amphizoidae, Elmidae, and Psephenidae. The occurrence or absence of these families broadly agrees with more global findings (Williams, 2016). Notable exceptions are the occurrence of Hydroscaphidae in seepages and thermal springs; the Scirtidae in seepages adjacent to lotic margins; the elmid genera *Heterelmis* and *Stenelmis* in springs (the latter also in warm springs); *Hydrochus* (Hydrochidae) in mound-springs and limnocrenes; and *Lutrochus* (Lutrochidae) in mineral springs.

Diptera: of the 150 families of Diptera, 27 can be considered to be 'marginally' to 'exclusively' aquatic. Nineteen of these have representatives that inhabit springs and seeps, many of them occurring on a global scale. Among the Nematocera, the following genera contain species that are especially notable for being spring/seep specialists: the tipulids *Brachypremna*, *Dactylolabis*, *Pedicia*, *Thaumastoptera*, and *Tipula* - further, many members of the subfamily Limoniinae are increasingly being captured in springs (see Gathmann and Williams, 2006). Among other nematocerans, the chironomids are well represented in springs: Podonominae – *Boreochlus*, *Paraboreochlus*, *Parochlus*; Tanypodinae – *Krenopelopia*, *Macropelopia*, *Pentaneurella*, *Zavrelimyia*; Diamesinae – *Diamesa*, *Pseudokiefferiella*, *Syndiamesa*; Orthocladiinae – *Antillocladius*, *Doithrix*, *Heleniella*, *Krenosmittia*, *Lymnophyes*, *Parachaetocladius*, *Parametriocnemus*, *Psilometriocnemus*, *Stilocladius*; Chironominae – *Krenopsectra*, *Neozavrelia*, *Stempellinella*. Many of the above genera specialize in specific temperature ranges. Alongside these stenotherms are generalist chironomid genera that frequently form part of the spring community: *Ablabesmyia*, *Procladius*, *Corynoneura*, *Cricotopus*, *Eukiefferiella*, *Heterotrissocladius*, *Orthocladius*, *Psectrocladius*, *Thienemanniella*, *Chironomus*, *Polypedilum*, *Micropsectra*, *Paratanytarsus*, *Stempellina*, and *Tanytarsus*. Ferrington (1998) estimated that at least 111 genera of chironomid, comprising at least 185 species, occur in North American springs, representing 19% of the total described species. For cold springs in Europe, the comparable statistics are 85 genera and over 200 species, representing 20% of the described fauna (Lindegaard, 1995). In springs in the Central High Plains of North America, Blackwood et al. (1995) found that the Orthocladiinae were more prevalent in rheocrenes, while the Chironominae were more abundant in limnocrenes.

Among the Brachycera, the following families contain species associated with springs and/or seeps: Stratiomyidae (*Beris*, spring margins); Empididae (*Hemerodromia*, *Oreothalia*); Dolichopodidae (raised peat-mound springs); Syrphidae (raised peat-mound springs); Sciomyzidae (snail-predators in seeps); Ephydridae (*Ephydra*, *Ephydrella*, *Paracoenia*, and *Scatella* in thermal springs).

Trichoptera: currently, 616 genera and 49 families of caddisfly are known (Trichoptera World Checklist, 2015). Of these, at least 21 families, comprising at least 59 genera, have larvae that live in springs and/or seeps, including both cased and net-spinning forms. Some genera show distinct microhabitat preferences (e.g., *Homoplectra* – rockface springs and seeps in montane areas,

Moselyana – subalpine forest seeps, *Chilostigma* – seeps in wet meadows, *Pseudostenophylax* – cool spring runs and small intermittent streams), whereas others encompass a wider range of habitats that include springs (e.g., *Cheumatopsyche*, *Polycentropus*, *Lepidostoma*, *Anabolia*, *Hesperophylax*, *Limnephilus*, *Platycentropus*, *Helicopsyche*, and *Oecetis*). An analysis of the caddisfly larvae living in springs across Canada showed some general trends together with some regional and habitat-related differences (Williams, 1991a, b). Notably, the number of species present in the springs increased with habitat diversity, and around 35% of the species recorded were from the Limnephilidae. Limnocrenes and rheocrenes with a weak current and small substrate particles supported few species, but often large populations. Grazers, shredders and predators were common, but filter-feeders were rare – an exception being the hydropsychid genus *Parapsyche*. Ordination of the data confirmed an east/west difference in caddisfly communities with influential variables including elevation, extent of groundwater source, and summer temperature. Factors strongly influencing the composition of the spring communities in both the west and east included riparian vegetation, substrate particle size, current, and pH. Springs in which caddisfly larvae were strongly involved in the processing of detritus were dominated by *Homophylax* in the west, but by *Frenesia* and *Lepidostoma* in the east. Predators and scrapers were abundant only in springs having relatively high microhabitat diversity, current speed, and pH.

Ecological controls

Comparisons among springs - Most permanent freshwater springs are stable environments, with many of their physical and chemical properties fluctuating less than in streams, rivers, and lentic waterbodies. In some springs, however, chemical composition, suspended solids, and even discharge and temperature, show both seasonal and sudden variation. This is especially evident in seasonal springs discharging from aquifers of limited storage capacity and in temporary springs discharging from shallow systems. However, it also occurs in some perennial springs (Van Everdingen, 1991). Springs characterized by such variation have not been studied extensively, but are known to be common in alpine headwaters (Maiolini et al., 2011). Most of the following discussion is aimed at 'classical,' coldwater springs, those with low environmental variability.

Although one of the first studies done on springs incorporated standing crop and energy flow models (Silver Springs, Florida; Odum, 1957), most of our knowledge on these habitats has come from a taxonomic rather than a quantitative ecological approach. Hence, there persists a weak understanding of the community dynamics of springs, and especially seeps, particularly in terms of how their communities develop, are organized and function. There is also much that is not known of the life histories and physiological properties of spring-dwelling species – adaptations that enable these organisms to live and persist in these habitats.

It is clear that springs support faunas that, collectively, include most of the major taxa of invertebrates capable of living in fresh waters. From sponges, hydras, gastrotrichs, rotifers, nematodes, and oligochaetes, to mollusks, mites, and a wide variety of insects, all have representatives that have adapted to the oftentimes constant physical and chemical environments that springs present. Further, their faunal composition has similarities across much of the world, even to the family and genera level. However, in some regions global processes have impinged on these patterns. For example, within the last 15,000 years coldwater springs in some temperate regions have been destroyed by Pleistocene glaciation. Springs re-formed since ice retreat often have had insufficient time to repopulate fully such that, in Southern Ontario, Canada, for example, faunas are dominated by the more vagil insects – typically, nemourid stoneflies, chironomids, and caddisflies (Williams and Williams, 1998). Unlike in non-glaciated parts of North America, mollusks and triclads are not well represented.

At the local regional level, studies show differences in species from spring to spring, and also in their abundance and time of adult emergence (e.g., in Plecoptera, Trichoptera, and Diptera; Erman, 1998; Gathmann and Williams, 2006). From a study of the insects living in 75 springs in the south-eastern Alps, Maiolini et al. (2011) concluded that springs have an island-like property, with each spring having its own specific history and abiotic characteristics which select for unique faunal patterns. In a separate study in the same vicinity, Stoch et al. (2011) concluded that, for the meiofauna (oligochaetes, mites, and crustaceans) spatial patterns of assemblages at the regional scale were best explained by altitude, water chemistry (related to geology), and water-flow regime – as was earlier found for macroinvertebrate assemblages by Barquin and Death (2006), Ilmonen et al. (2009), and Glazier (1991). To these controlling influences, Myers and Resh (2002) added spring permanence, lack of disturbance, and coldwater temperatures as factors responsible for explaining higher species richness of Trichoptera. Ferrington (1998) further added within-spring habitat heterogeneity, operating on a local scale, as a determinant of the taxonomic composition of individual springs. Mattson et al. (1995) provided evidence for spring-bed substrates being among such determinants in that woody substrates in karst-fed springs in Florida were dominated by chironomids, mayflies and caddisflies (with snails and amphipods occasionally abundant), but sandy substrates were populated with other chironomids, snails, bivalves, and oligochaetes. In Stoch et al.'s (2011) study, such microhabitat features, together with human disturbance, were less influential, but these authors conceded that where anthropogenic pressure is high (see Sarkka et al., 1997), it can become the foremost influence on spring faunal assemblage structure and distribution. For example, Ferrington (1998) showed that the chironomid genera of two North American springs that had become contaminated by cattle dung came to resemble those found in similarly enriched lower-order streams – the important spring specialists having been lost.

Specialists versus *generalists* - Another issue to address is what adaptations define spring and seep generalists and specialists. In an analysis of life history traits, Williams (1991a,b) concluded that, in terms of life history theory, the limited information available for spring species showed most support for a deterministic view, based on the predictions of r-, K- and A-selection (Greenslade, 1983). Permanent, coldwater springs are habitats characterized by low disturbance and low adversity – assuming that

low water temperature is not an adversity for lotic organisms, many of which have their ancestry in cold, headwater streams. According to the predictions, most of the fauna should be K-selected in that: (1) the community should show intermediate to high diversity (see Lindegaard, 1995; Ferrington, 1998), and consist primarily of sessile grazers/gatherers (see Anderson and Anderson, 1995) and filter-feeders with narrow, specialized niches due to heavy competition; (2) productivity and individual growth rate should be high (see Williams and Hogg, 1988), although growth may be low in non-cold-adapted species (Iversen, 1976); (3) survival rate may be low, and length of life, time to maturity, and fecundity intermediate (see Tilly, 1968); (4) population densities should be near carrying capacity; (5) incidence of dormancy should be low, as should that of parthenogenesis (but see Norton et al., 1988); (6) predators should be rare; and (7) vagility should be low to intermediate.

Community assembly - Permanent coldwater springs, perhaps more so than seeps, present highly persistent habitats for invertebrates and may contain a disproportionately high number of unusual species for their relatively small size (Erman and Erman, 1995). Species presence may be the result of several different entry pathways into the faunal assemblages of individual springs. These pathways result in various species statuses that include (with trichopteran species examples): (1) *habitat specialists* – (e.g., *Crunoecia irrorata*, *Anagapetus debilis*) which are largely crenobiontic species arriving from similar habitats that may be adjacent or at some distance, depending on migration abilities; (2) *habitat generalists* – (e.g., *Ptilostomis ocellifera*, *Hesperophylax designatus*) including crenophilic species that may arrive similarly, but also by range extension from downstream springbrooks; (3) *relict species* – (e.g., *Apatania muliebris*, *Rakiura vernale*) previously abundant species that have undergone range contraction (often through climate change, but increasingly through human activity) and now occur in only one or a few adjacent springs; and (4) *endemic species* – (e.g., *Agarodes ziczac*, *Lepidostoma ojanum*) species which originated in a single, stable and persistent spring locality that is ecologically isolated and to which they are now highly adapted. Given these different components to spring faunas, it is important to consider whether spring faunas are stochastic aggregates of habitat- (temperature)-limited species or true, coevolved communities. A relevant observation in this regard was made by Myers and Resh (2002), who found that among the caddisfly assemblages from 28 springs in the Great Basin, USA, although several springs had very similar physicochemical characteristics, none was identical, indeed the assemblage totals ranged from four to 18 per spring. Lack of assemblage repeatability suggests a more stochastic colonization process. Further, given the somewhat eclectic nature of the faunal source-pathways, it seems unlikely that such a resulting mix of species would be able to function as a true, cohesive and fully interactive community. Clearly, we need many more studies on the development of spring communities in order to resolve these issues. Toward this goal, the main environmental factors thought to shape the composition of these invertebrate assemblages/communities are outlined in Fig. 4.

As noted earlier, knowledge of spring invertebrates has arisen from two, largely uncoordinated, approaches: the first based on the taxonomy of particular invertebrate groups whose range of habitats includes springs (e.g., Feldman, 1974); the second comprising a relatively small, unconnected series of population or community studies from single springs (e.g., Teal, 1957; Tilly, 1968; Winterbourn, 1973). Specific, regional surveys of spring faunas have been rare in the past (e.g., Tuxen, 1944; Botosaneanu and Negrea, 1961), but are now becoming more common and informative. For example, from a study of the mayflies, stoneflies and

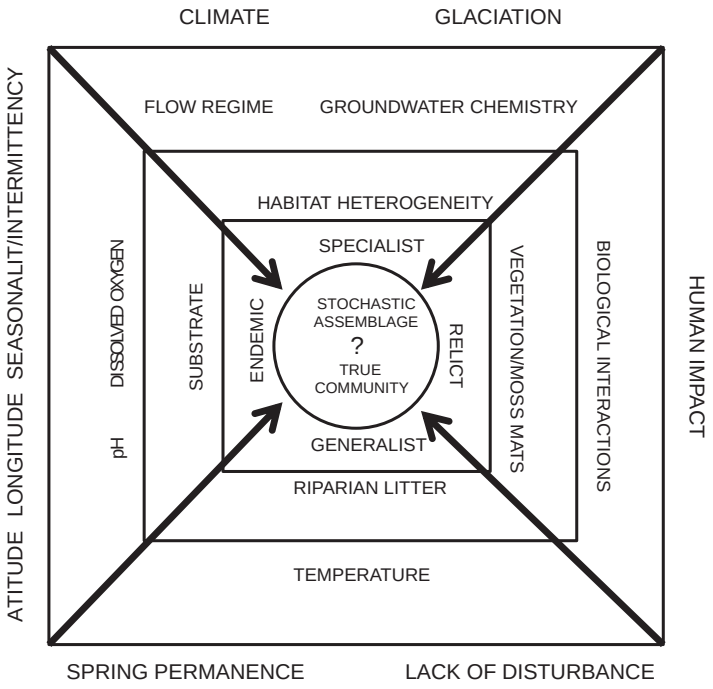

Fig. 4 Summary of the main environmental factors thought to shape the composition of invertebrate assemblages/communities in freshwater springs (the arrows indicate the general direction of flow of the factor influences).

caddisflies found in springs of the Trentino Region of Italy, Maiolini et al. (2011) were able to propose three important functions of coldwater springs in alpine landscapes: (1) in such harsh environments, the mild and stable environmental conditions of springs contribute to maintaining and enhancing the regional biodiversity; (2) springs act as refugia for stream biota, providing more benign conditions during spates and drought – common features in alpine headwaters; and (3) springs provide specialized habitats for strictly crenobiontic species.

Community and population ecology - Perhaps the greatest ecological utility that springs and seeps represent is their potential to contribute to our understanding of community ecology and ecosystem function. Indeed, Odum (1971) proposed that springs are natural, constant-temperature laboratories, and pointed out that their study had pioneered development of the trophic dynamics approach to ecosystem studies in general. In 1998, Williams and Williams identified the following features of springs that had the potential to advance community ecology: (1) their communities are naturally less complex than those occurring in most other aquatic habitats yet, as far as is known, they possess the structural (e.g., a wide range of species representing many major taxa) and functional (e.g., producers, various levels of consumers, and decomposers) elements seen in other communities; (2) the natural variation in community structure, and presumably in function, seen among natural springs represents an ideal testing ground for questions of community trophic efficiency, predator-prey dynamics, and competition – particularly in the more extreme spring types (thermal and saline) which have very simple community structures (see Collins et al., 1976). A number of population-level research avenues also could be explored using springs, for example: (1) given the high degree of specificity of many spring-dwelling species to this habitat type, alongside the oftentimes isolated nature of individual springs, they could provide ideal habitat island models for the experimental analysis of Metapopulation Dynamics Theory (Gathmann and Williams, 1998); (2) they could be used to compare the population traits of coexisting species that differ widely in their status (e.g., specialists versus generalists), as shown by spring species with very narrow habitat requirements (e.g., the endemic caddisfly *Lepidostoma ermanae*) and the widespread caddisflies *Chyranda centralis*, *Wormaldia occidea*, and *Rhyacophila grandis* (Erman and Erman, 1995); and (3) using thermal springs to tease apart the influences of important abiotic habitat variables, such as water temperature and chemistry, on populations – effective, natural elimination of thermal differences among adjacent sections of spring or seep complexes (and thus removal of a strong environmental variable) has been proposed as an ideal test condition for the study of the influence of habitat heterogeneity on species richness (Ferrington et al., 1995; see further examples in Williams and Williams, 1998).

Conservation concerns

Knowledge of spring faunas has the potential both to address zoogeographical issues and to monitor environmental change. An example of the former is the proposal that for mites, in Canada, springs have played important roles as both refugia and routes for migration. As in Europe, not only have present-day, temperate lowland springs allowed the survival of cold-adapted species after ice retreat, but they also may have allowed the survival of such species in marginal refugia during glacial maxima (through maintenance of interstitial spring habitats in glacial deposits near the southern limits of ice sheets). Refugial survivors then were able to repopulate newly created habitats upon subsequent glacial retreat. It is possible that such 'leading-edge' colonization at glacial margins may subsequently have produced a spatial assortment of genomes, perhaps promoting divergence and speciation (Hewitt, 1996).

Monitoring environmental change involves the very close relationship, as part of the hydrological cycle, between groundwater and the atmosphere, where changes to the latter (such as a rise in global air temperature) are likely to affect the former. Such a change is likely to have serious consequences for spring discharge, in that permanent springs may become intermittent, and also for the typically stenothermic communities of organisms that live in springs. A study of a spring in which the water temperature was artificially raised by 2 °C to 3.5 °C to simulate global warming, resulted in a suite of changes to the fauna including: a decrease in total invertebrate numbers; earlier onset of adult insect emergence; increased growth rates and precocial breeding in amphipods; smaller size at maturity in stoneflies; and altered sex ratios in caddisflies (Hogg and Williams, 1996). Such responses to environmental change make spring faunas very useful in detecting changes in water quality of their source aquifers and hence the potability of these important reservoirs (70% of freshwater is bound in ice and snow. 30% is freely available, in liquid form, of which 99.6% is groundwater). Williams et al. (1997) showed that, in a series of springs in Southern Ontario, Canada, there was a strong relationship between the fauna and chloride – a major contaminant of the groundwater in the study area and believed to be derived from the application of road de-icing salt. Several taxa were closely associated with high chloride levels (e.g., the dipteran families Tipulidae and Ceratopogonidae), whereas others occurred only in springs with low chloride (e.g., Turbellaria and *Gammarus pseudolimnaeus*). Not only can spring faunas be used as indicators of contemporary spring health, where sufficient sediment depth occurs coring can yield chitinous remains that may allow reconstruction of the past history of source aquifers and their catchments, especially during the Anthropocene. For example, a core taken from the bed of a Canadian spring showed evidence of changes in land use over a 200-year period. Fossil sclerites of, predominantly, caddisfly and chironomid larvae indicated a shift from pre-European settlement forest, through a land clearing/agricultural phase, to a present-day increase in urban development (Williams and Williams, 1996).

Spring faunas provide unique information on endemism and also on post-glacial colonization patterns. Springs are habitats where relict species of these former times have endured, protected from large oscillations in climate. Springs hold a position of importance as study areas that is far out of proportion to their size and number. However, the same cannot be said about their global knowledge base. Some collections of specific taxa from springs exist in the general holdings of national or regional museums,

but these collections seldom have sufficient accompanying habitat description or quantification to make them useful except in an introductory capacity. This dearth is occurring at a time when they and their source aquifers have come under extreme pressure from human activities. Springs themselves are being destroyed by, for example, use as stock watering holes, water-bottling sites, spas, and as a consequence of logging and transportation routes (Brune, 1981) - whereas their water sources are being rendered unfit for use by both invertebrates and humans (Liu and Liptak, 1999). Some causes of contamination are localized, while others, such as acid rain, may be widespread. However, contaminants may migrate along subsurface paths, many of which emerge at the surface as springs before flowing into streams, lakes and wetlands. This form of contamination is increasing primarily because the diversity of chemicals used in industry and agriculture is high and many of them persist in the groundwater zone (Bowler, 2014). Detection involves costly and repetitive sampling at depth. Biomonitoring of spring faunas has been proposed as a viable alternative, as these organisms are continually subjected to the emerging water and integrate the effects of geology, vegetation and climate over time (as many have at least a one-year life cycle) (Biological Survey of Canada, 1990). Where palaeoecological information is available, it is possible to build up an accurate index of groundwater quality and the history of individual aquifers.

Williams and Danks (1991) drew up a series of recommendations for the protection of springs that comprised: (1) preparing inventories of spring types and their distributions, at both regional and continental levels; (2) surveying their floras and faunas so as to enable the detailed study of representative spring types and regions; (3) making, alongside the biota, detailed descriptions of local geology, hydrology and climate, together with comprehensive analyses of water chemistry; and (4) preserving rare and regionally characteristic spring types and their biotas – the latter to be accomplished through: restricting the capping of springs for commercial use; establishing and enforcing protective areas (e.g., woodlands) around springs, including fencing to prevent trampling by livestock; raising public awareness of the importance of springs; and establishing appropriate protective legislation, perhaps most effectively focused on maintaining high quality groundwater. Groups identified as needing to take responsibility for the implementation of these recommendations include federal and local governments, natural history and other societies, individuals, and landowners. Such action is to be strongly encouraged.

Knowledge gaps

- expand the taxonomic base of spring faunas to cover poorly known groups, such as the porifera, hydrozoa, rotifers and nematodes.
- encourage autecological studies of individual, particularly keystone species, but also of species that may be widely distributed yet occur at very low densities in individual springs.
- undertake more quantitative analyses of spring communities, paying particular attention to food/energy pathways and to the link between species and their microhabitats.
- how are food resources shared given the high number of species feeding on the same materials (e.g., fine particular organic material and epilithon, via similarly-structured mouthparts, e.g., chironomid larvae and limoniid larvae) - are all of the food niches filled?
- determine the role of metapopulations, especially in the survival of regionally rare species.
- explore the utility of using spring communities as biological indicators of the health of source aquifers.
- examine the potential of springs to be used as natural, constant-temperature field laboratories in which ecosystem-level hypotheses on physiological and ecological properties can be tested - e.g., on cold stenothermy and climate change.
- seek answers to questions on endemism and zoogeography.
- further develop effective conservation protocols for springs subject to single or multiple human use - e.g., water abstraction or livestock grazing.

Acknowledgments

I thank colleagues past and present who have shared my interest in springs and their invertebrate faunas, but most notably the late Dr. Lazare Botosaneanu, Dr. Hugh Danks, Dr. Oliver Gathmann, Dr. Dirk Hinterlang, Dr. Ian Hogg, the late Prof. Noel Hynes, Dr. Nancy Logan, Dr. Ian Smith, and Dr. Catherine Yule.

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Importance of the Micro-scale for the Macro-scale—What Can We Learn From Groundwater Ecosystems?

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Aquifer Groundwater-bearing subsurface material; may be unconsolidated with sedimentary grains (boulders, gravel, sand, silt, clay) or consolidated rock. In the latter case, the groundwater flows through uncemented porosity or secondary porosity in the form of fractures and/or karst features (resulting from rock dissolution).
Contamination Input of unwanted or even poisonous substances. May be organic or inorganic, anthropogenic, or from a natural disturbance.
Eukaryotes Unicellular or multicellular organisms where cells have a nucleus.
Fauna Generic notion, usually meaning multicellular eukaryotes of the animal kingdom.
Groundwater Subsurface water that saturates all pores and voids and only moves by gravitational force; the limit to surface-characterized interstitial zone is imprecise.
Individual-based models (IbM) A type of agent-based model (ABM) where individuals or agents receive properties per cell or agent, not just average properties, and where they are equipped with behavioral rules and their stochastic likelihood. These stochastic parameters are set to be different in each run. Running this model many times though produces a range of results for the desired outcomes, which can be interpreted as emerging properties.
Metazoa "Higher" animals, i.e. eukaryotic, multicellular organisms.
Micro-scale In the strictest sense, the scale between the nanometer and millimeter scale; for the purpose of this chapter, in the wider sense, the scale of the water-saturated pore, or network of pores in sediments.
Microbes Summary notion for eukaryote and prokaryote microorganisms, i.e. unicellular organisms.
Natural attenuation Self-cleaning by abiotic and biotic processes.
Pore A void space in an aquifer material such as the space between the sedimentary particles or the fractures within rock.
Prokaryotes Unicellular organisms without a nucleus.
Protozoa Unicellular "animal-like" organisms; generic, non-taxonomical notion encompassing unicellular eukaryotes, i.e. flagellates, ciliates, amoebae.

Introduction, with aim of the chapter

The ecological patterns of groundwater systems are usually overlooked because they are out of sight, and thus, out of mind. However, groundwater ecosystems are as fascinating as the deep sea, harboring phylogenetically ancient organisms which have adapted to their environment, among which many are endemics (species that occur only within a geographically narrow area; Wilkens et al., 2000). Prokaryote functions unknown, or untypical, from other environments are found in deep groundwater

(Chivian et al., 2008). Groundwater organisms in karstic, porous and fissured aquifers generally consist of eubacteria and archaea, fungi, protozoa, and often also small metazoa such as worms (nematodes, oligochaetes, polychaetes), tardigrades, mites, and crustaceans (mostly amphipods, copepods, isopods, ostracods). More important than their diversity, their biogeographical distribution, and their ability to survive in a scarce environment, is the fact that groundwater organisms contribute to the self-cleaning of aquifers: groundwater microorganisms provide important ecosystem services (Griebler and Avramov, 2015) such as degrading organic carbon, be it natural or contamination ("natural attenuation"; Rivett et al., 2008), with fauna sometimes further increasing degradation rates by rejuvenating microbial growth, and keeping the pore spaces open (bioturbation; Schmidt et al., 2017). Increased pore space variability leads to increased flow variability. This in turn results in higher oxygenation of the subsurface water in some parts (Schmidt et al., 2017). Due to these—anthropocentrically speaking—ecosystem services, groundwater is—depending on the region—a major source for drinking water (Quevauviller, 2007). Worldwide, drinking water production relies on groundwater to almost 50% (The United Nations—World Water Development, 2009).

Natural attenuation, i.e. the natural self-cleaning of the groundwater, including contaminant degradation, is an ecosystem service which is threatened by climate change (Retter et al., 2020) and increasing contamination of all types. In addition, an increase in groundwater temperature accelerates changes in the groundwater food web diversity and composition (Brielmann et al., 2009), and fauna's behavior (Avramov et al., 2013) and consequently their ecosystem functions. Some of the groundwater fauna representatives are larger than 1 mm and thus, strictly speaking, use space beyond the micro-scale. But even on the centimeter or decimeter scale, observations in-situ in the aquifer are hardly possible, and laboratory observations are still rare. We will focus here on porous aquifers because that is where most of the studies are performed. Most studies were motivated by the need for removing contaminants, and thus, disproportionally many results from contaminated aquifers and laboratory set-ups are available. The aim of the chapter is to conceptually describe in which ways the micro-scale variability influences the larger scales in the aquifer, and then to show with three (complexes of) case studies what researchers have found. The case studies originate from laboratory experiments and computational exercises and thus lack a geographic reference. Field-investigation on the micro-scale, if micro is taken literally, as smaller-than-millimeter, and/or pore scale, are virtually non-existent.

Main topics/concepts

Concepts

We argue that micro-scale processes are the basis for the groundwater food web. The relevant transactions contributing to attenuation and degradation are shaped not only by macro- and meso-scale conditions such as net recharge, net carbon import, climate, hydrogeochemical background from rock weathering, but also by micro-scale processes which form e.g. through temporally and spatially small-scale redox reactions resulting in the overall biogeochemical transformations. Fig. 1 shows this conceptually—a

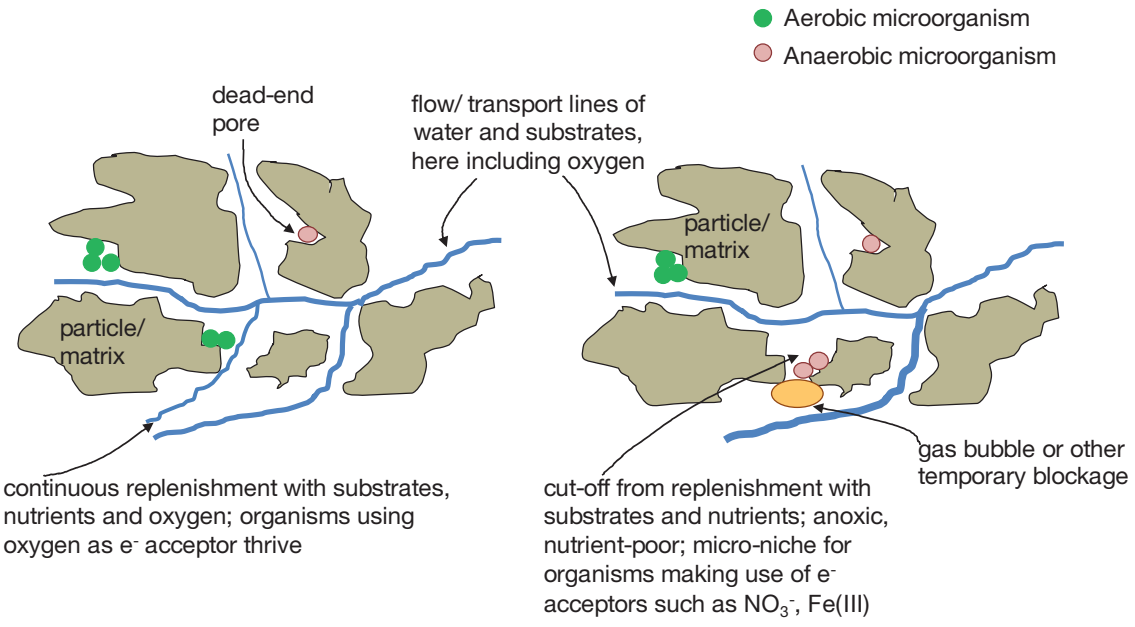

Fig. 1 Conceptual sketch of the micro-scale variability in pores and their hydraulic situation. Modified from Fig. 1 in Schmidt SI, Cuthbert MO, and Schwientek M (2017) Towards an integrated understanding of how micro scale processes shape groundwater ecosystem functions. *Science of the Total Environment* 592: 215–227, with permission from Elsevier B.V.

temporary blockage by gas bubbles or microbial growth creates zones that stop being replenished by flow-through (Thullner et al., 2002b). Gas bubbles have, depending on circumstances, however also the potential to reorganize sediments and thus increase flow diversity further (Liu et al., 2018).

Variabilities on the micro-scale interact with the meso- to macro-scale trends. The biogeochemical properties of groundwater are the result of the interplay of rock weathering and recharge from the surface—both replenish the aquifer with ions, nutrients, organic carbon, and electron acceptors. Inorganic carbon and ions enter the aqueous phase by dissolution and erosion, i.e. weathering, from the inorganic particles and the rock matrix. These processes depend on the physical and chemical properties of the rock matrix on the micro-scale properties, e.g. inclusions in the rocks. A considerable fraction of the weathering is mediated by microorganisms (Bennett et al., 2000). Microorganisms are known to occur patchily in aquifers, in micro colonies of up to 100 cells (Harvey et al., 1984; Fig. 2A). Such microcolonies have been confirmed in those laboratory settings, where resources were set to be limiting (Iltis et al., 2011; Fig. 2B).

Concurrently, the organisms act, use resources, and produce extracellular polymeric substances (EPS) and metabolites, in micro patches. However, they act not only by dissolving the mineral matrix and/or by shuttling electrons, they e.g. degrade organic material. Aerobic degradation reactions usually offer the highest energy gain for the organisms. Thus, such reactions will be performed preferably and fastest. This might lead on the micro-scale of the dead-end pore or colony to the complete depletion of oxygen, so that only compounds and ions such as nitrate, Fe(III), Mn(IV), sulfate, or CO_2 may act as electron acceptors. The energy that can be gained from such reactions is less than that gained from aerobic respiration. Since the products of these processes may be very different from those resulting from aerobic degradation reactions, the chemical conditions of the aquifer become a mixture of substances resulting from reactions at different redox states. The degradation of the substrate is limited by the transport of suitable reaction partners to the degradable compound and the microorganisms (Thullner et al., 2002b; Chu et al., 2005; the degradable compound may also be a contaminant: Anneser et al., 2008). In those cases, degradation was found to be most intense in the fringes where resources and favorable environmental conditions are in the optimum relationship to each other (van Breukelen and Griffioen, 2004). This fringe zone is often only a few millimeter wide (Bauer et al., 2008), but its effects are also measurable on the meso-scale in the field (Anneser et al., 2008). Natural attenuation and contaminant remediation thus rely on degradation in such fringe zones which themselves depend on the micro-scale environment (Meckenstock et al., 2015). Note that mass transfer limitations to the cells occur also when concentrations of contaminants decrease below a cell-relevant limit, independently of the amount and distribution of biomass (regime (ii) in Sun et al., 2021). However, if and where biomass has adapted after a contaminant was in abundance, degradation takes place even though the contaminant has decreased to a limiting level (regime (iii) in Sun et al., 2021). Such adaptation and the mass transfer limitation through the cell wall are usually not taken into account in models so far.

In Schmidt et al. (2017) we have conceptualized what difference the micro-scale might make for the degradation of organic matter and contaminants through the whole food web. In Fig. 3 the ways in which the micro-scale features may influence larger scales, and vice versa, are shown. The temporal dimension is given on the *x* axis in Fig. 3 and the spatial dimension on the *y* axis. The exchange with the surface is one dominant driver, in that it delivers overall organics, oxygen, but also e.g. contaminants. Despite the overall conditions, Fig. 3 shows how situations which are very different in their physical, chemical, and hydraulic properties, may exist in close vicinity both spatially and temporally within the same macro scale framework. They provide the environments for differing biological communities and ecosystem functions. These ecosystem functions vice versa shape their physical and chemical

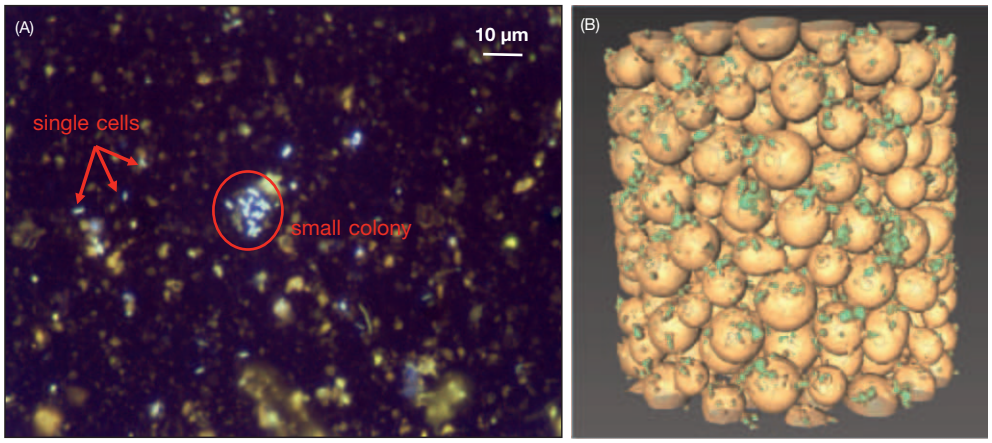

Fig. 2 (A) DAPI stained attached bacteria in a subsurface sediment sample. Reproduced with permission from C. Griebler, University of Vienna (pers. comm.). (B) Result of the three-dimensional X-ray computed microtomography (CMT) biofilm imaging. Biofilm (green) was grown in a glass bead pack of neutrally buoyant, silver-coated hollow glass microspheres (10 µm diameter; gold). The interpretation is that the silver particles have attached to the biomass that had grown within the bead pack and that the silver particles thus reflect the spatial arrangement of biomass. Reproduced from Iltis GC, Armstrong RT, Jansik DP, Wood BD, and Wildenschild D (2011) Imaging biofilm architecture within porous media using synchrotron-based X-ray computed microtomography. *Water Resources Research* 47: 1–5, with permission from the American Geophysical Union.

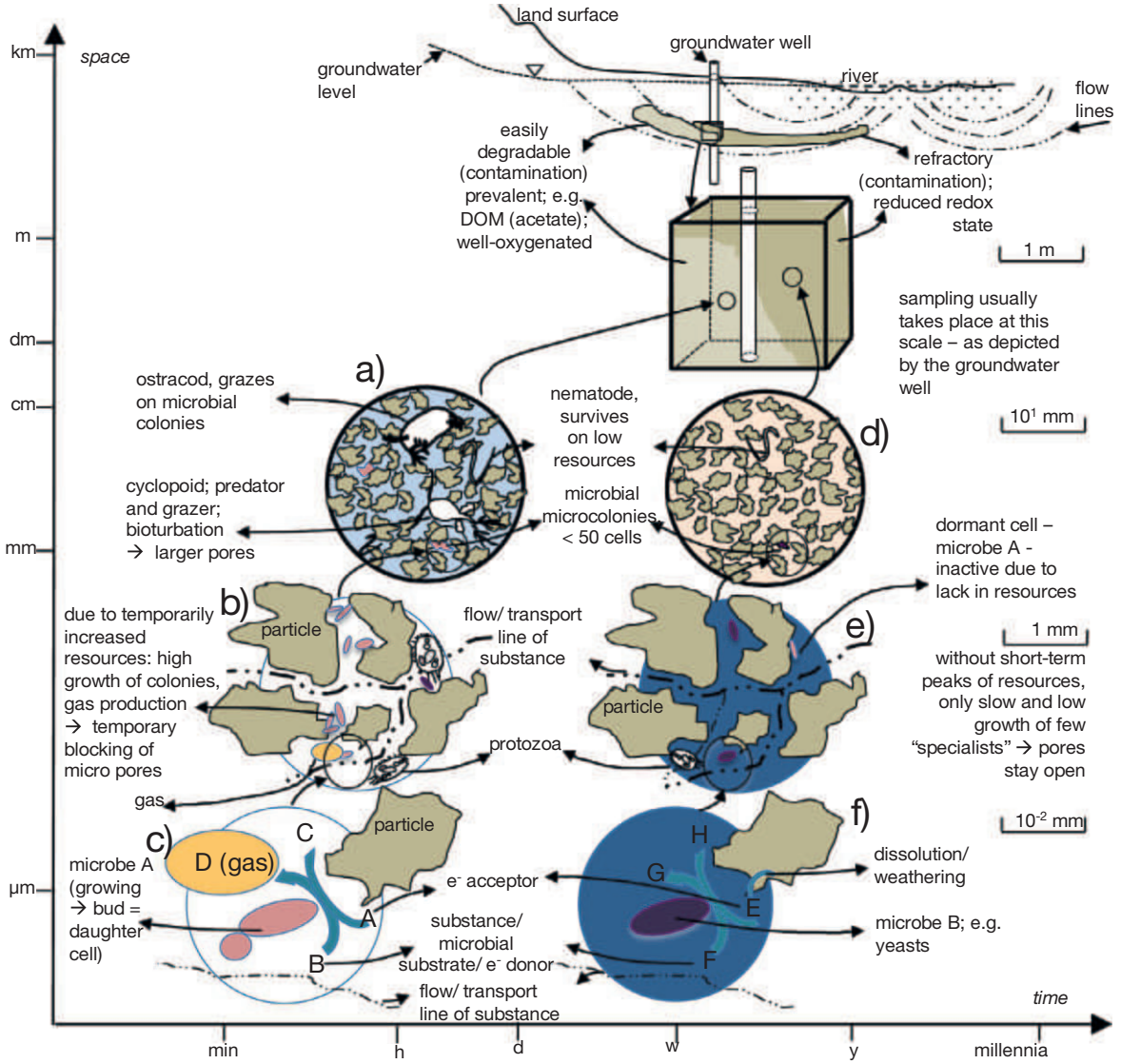

Fig. 3 Micro-scale conditions and their relation to patterns on larger scales. This is illustrated on two examples of zones that might be temporally or spatially apart. They might be different stages of an ongoing contamination degradation, which leads to different background with carbon compounds of varying complexity. The temporal scale is depicted on the *x* axis; and the spatial scale on the *y* axis. The axes give, however, only the general direction, but are not to scale. Further explanation in the text. Reproduced from Schmidt SI, Cuthbert MO, and Schwientek M (2017) Towards an integrated understanding of how micro scale processes shape groundwater ecosystem functions. *Science of the Total Environment* 592: 215–227, with permission from Elsevier B.V.

environment. While the macro scale sets the scene for organism growth, on the micro-scale, the actual food web depends on the prevalent pore environment, but also the consequently patchy microbial growth and how the micro environments then develop, and on the way in which the organisms react to them. Fig. 3A–C represents a well-replenished aquifer situation, with fast processes, while Fig. 3D–F depicts an impoverished situation, with fewer organisms, slower processes, and less transformations.

The situation in Fig. 3C builds the basis for the fast-growing food web on the left side, with Fig. 3B and A representing higher levels in the food web. The biochemical transformations yield energy for microbial growth. This microbial growth is grazed upon on the *meso* level by protozoa (Fig. 3B), and by small metazoa such as rotatoria. Further up the food web, larger metazoa such as crustacea feed on the small metazoa and protozoa (Fig. 3A). Since the degradation of the available substrates in a situation depicted in Fig. 3C, with higher concentrations of more easily degradable substrates than in Fig. 3F, yields more energy than in (F), more organisms find enough resources to thrive in (B) and (A), than in (E) and (D). Growth is faster in (C) than in (F), and microbial colonies may grow to larger sizes and maybe even higher diversity in (C) than in (F). E.g. resource-poor environments in deep mines, one extreme case of Fig. 3F, harbored microbial communities of less than 10 OTUs (operational taxonomic units; Chivian et al., 2008), while groundwater environments with regular input from the surface, represented in Fig. 3C, typically harbor several thousands of OTUs, or ASVs (amplicon sequence variant; Griebler et al., 2010). The reactions at the basis of the food web (Fig. 3C) might e.g. be the degradation of the molecule acetate (substrate B in Fig. 3C) under the reduction of nitrate (substrate A in Fig. 3C).

This denitrification yields among other products N_2O or N_2 (substrate D in Fig. 3C; Strohm et al., 2007) which might form gas bubbles (Bauer et al., 2008; Fig. 9). Such bubbles are (temporary) flow hindrances, even on the mm scale (Figs. 1 and 3B; Cuthbert et al., 2010).

In the right half (Fig. 3D–F), in contrast, less and more-difficult-to-break-down substrates, or less favorable conditions (high or low pH, etc.) prevail, and/or substrates such as the easily degradable acetate have been used up. Growth takes longer and is more resource-demanding: more activation energy is required, and consequently less biomass and products are the result. One example is the anoxic feldspar dissolution (feldspar represented by substrate E in Fig. 3F) which was shown to occur only where feldspar contains phosphorus which is limiting in many groundwater ecosystems (Bennett et al., 2000). The dissolution is enabled either by the local excess production of CO_2 forming an equilibrium with carbonic acid, or by organic acids produced from degradation of (contaminating) aromatic compounds, e.g. benzoic acid (Bennett et al., 2000)—these acids are represented by the letter F in Fig. 3F). The products are dissolved carbonate ions (letter H in Fig. 3F) and benzoate (letter G in Fig. 3F). Since this reaction is energetically not as yielding as denitrification coupled to the oxidation of acetate, the growth of individual microbial cells, and consequently, growth of colonies, is slower and sparser (right hand side of the μm scale in Fig. 3F) than that for acetate-grown cells (Fig. 3C). This low productivity only supports low numbers of protozoa and metazoa (e.g., nematodes; Fig. 3D and E).

In direct comparison with the situation where a less degradable substrate prevails, the situation of the easily degradable substrate (Fig. 3A–C), at the respective scales, shows that there are faster reactions on the cell level (around 0.001 mm), higher numbers of more active microorganisms (bacteria, archaea, fungi, protozoa) on the scale of 0.01–0.1 mm, as well as higher numbers of grazing metazoa on the millimeter to centimeter scale. Such increased growth leads to more and faster bioturbation (i.e., reworking of sediments by organisms, see also section "Additional remark on small scale food web—Fauna grazes on microbes and engineers the environment"), than with a refractory substrate. These two situations depicted may occur in close vicinity both spatially and temporally. The major reason for the right-hand side situations to occur are zones where hydraulic conductivity is lower (e.g., due to fine sand or clay) than in the left-hand side situation, or micro-scale spots that are clogged by fine materials and bioclogging. This clogging may, however, be unstable over time and thus, a left-hand situation may develop into a right-hand situation and vice versa. Conventional sampling which usually means pumping large volumes (liters), will mix this micro-scale variability. The spatial scale on which these two (or more) situations occur may be as small as from one pore to the next. Also, on the temporal scale, the two situations may occur at the same spot, but in succession.

Measuring on the micro-scale

Measuring on the micro-scale is challenging—the environment, the processes, and the biota in the system have to be measured simultaneously and over time, since all these features are in fact interconnected—hydrological and hydrogeological patterns shape chemical reactions, which provide the resources for organisms. Vice versa, organism by their actions change the chemical and physical environment and may change hydrogeological patterns such as flow paths. The results obtained on the micro-scale depend highly on specific circumstances. When doing experiments and ascertaining developments, particularly where microbial growth is involved, imaging may be one of the first aims. Depending on the imaging method, the resulting pictures emphasize certain properties and may ignore other properties. E.g. the colonies in Fig. 2B seem to be clearly delineated, while in reality, extrapolymeric substances (EPS) produced by the cells might not be as compact as the picture suggests but might be organized in thin threads of biomass, e.g. Flemming and Wuertz (2019), which are captured better with other methods, such as epifluorescence light microscopy (Nadell et al., 2017 and compare Fig. 4).

The results gathered from micro-scale investigations, be they observational, experimental (laboratory and field), or computational, depend thus highly on the methods. However, all observational and experimental methods applied so far to pore-scale biomass growth unequivocally demonstrate the patchy, heterogeneous growth where resources become limiting (e.g., Bauer et al., 2009; Davis et al., 2010; Iltis et al., 2011; Neu et al., 2004; Wagner et al., 2009; Fig. 3). Micro-scale growth patterns were found to be influenced by flow velocity (Coyte et al., 2017), Reynolds number (which is the ratio of inertial to viscous forces in a moving fluid; Wagner et al., 2010), permeate flux (Valladares Linares et al., 2016), Péclet and Damköhler numbers (the ratio of velocity to pore diameter, and the ratio of the rate constant to the velocity, respectively, Jung and Meile, 2019), and by pore throat size (Jaiswal et al., 2014). In turn, microbial growth and thus, the increase of biomass, influenced physical properties such as porosity (Thullner, 2010), conductivities (Peszynska et al., 2016), the ability of compressional waves to pass through a sediment core (Davis et al., 2010), the wettability of polar substances within water (Armstrong and Wildenschild, 2012; Khajepour et al., 2014), flow velocity and T2 magnetic relaxation which can be used to image flow (Seymour et al., 2004), and the arrangement of aggregates and thus the distribution of pores in soil (Bucka et al., 2019). Microbial biomass may block pores (Thullner et al., 2002a; Thullner and Baveye, 2008) and thus, prevent some cells from receiving nutrients. Most of these studies did not, however, focus on groundwater ecosystems explicitly, and almost none used groundwater ecosystem-specific conditions, neither in experiments nor in modeling.

Many studies with a clear connection to groundwater have been performed in the context of oil recovery or CO_2 storage—in both applications, knowledge on the pore structures and behavior is undeniably paramount (Steefel et al., 2013). However, such studies mostly ignore microorganisms and always ignore food webs. Here, we give three groundwater-specific case studies. With the first case study we briefly show experimental work related to biofilm response to pH changes which may be one side effect of CO_2 storage. The second "case study complex" collates work form one group using a microfluidic cell which has proven adequate for a high range of questions, including mineral precipitation which is one feature complicating CO_2 storage (Singh et al., 2015). The third case study demonstrates, in a proof-of-principle approach, the effect of colony size and colony location on degradation

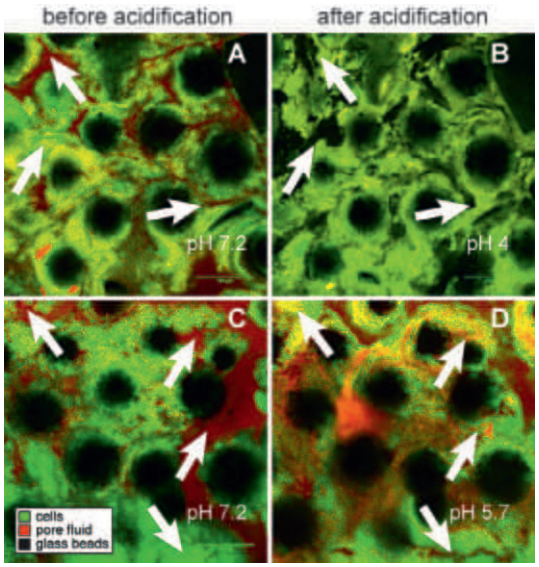

Fig. 4 Microbial biomass in porous media, visualized by confocal microscopy, before and after acidification to pH 4 (images A and B) and to pH 5.7 (images C and D). The legend specifies the material represented by each color in the images. Flow was from left to right through the porous media in the images. Arrows indicate spots where biomass shifted from one picture to the next. The contrast of the image (B) was adjusted to highlight the biomass in the image and therefore, the pore fluid in image (B) lacks red color. Reproduced from Kirk MF, Santillan EFU, McGrath LK, and Altman SJ (2012) Variation in hydraulic conductivity with decreasing pH in a biologically-clogged porous medium. *International Journal of Greenhouse Gas Control* 11: 133–140, with permission from Elsevier Ltd.

within an idealized single pore. Such set-ups allow to study competition among functional organism types and to study how food webs develop in detail in a controlled situation. Some studies have combined laboratory experiments with modeling (e.g., case study complex 2). This might result in bespoke models that may not be easily transferrable, neither in terms of the boundary conditions and implementation, nor in terms of the results. However, combining experiment and model is important for verifying modeling approaches and outcome. All three case studies so far cannot be generalized, and in all cases, upscaling to the meso-scale and further to the global scale is fundamental to the applicability of the results for field scale evaluations. The second and third case studies have tackled upscaling—a growing field, not discussed here.

Case study 1: Clogging of aquifer sediments due to pH changes—Experimental study

Kirk et al. (2012) devised micro columns (1 mm^2 cross-sectional area), filled with 105–150 μm diameter glass beads, which they studied under the confocal microscope, to clarify whether the microbial biomass involved in clogging of pores would survive a sudden pulse of low pH. This is important knowledge in developing strategies for carbon dioxide storage in geological structures. Sustainable storage relies on reservoirs that can be sealed against the surface so that the carbon dioxide remains trapped in the underground. Stimulating growth of microorganisms which clogs pores, could be one way to ensure that potential leakage pathways remain blocked, but the question arose whether the microbial biomass would stay intact, even if the microorganisms did not survive a pulse of super critical carbon dioxide which might result in a sharp decrease of pH. In the initial phase of the experiment, before acidification, microorganisms grew into colonies which clogged individual pores and reduced hydraulic conductivity (Fig. 4A and C). This was partly due to the formation of EPS. In the ensuing acidification phase, many cells died (Fig. 4B and D), and hydraulic conductivity increased measurably. However, much of the dead biomass remained in place, and continued to clog the pores considerably which would result in the cap on the carbon dioxide storage reservoir remaining in place. In this study, the medium and macro scale properties of the aquifer, i.e. hydraulic conductivity, were one of the response variables, but the low changes in hydraulic conductivity despite a pH detrimental to living cells, could only be understood by observing the distribution of live and dead biomass on the micro-scale.

Case study 2: Biomineralization alters porosity and flow patterns—Experimental and modeling studies

Microbial growth may develop in situations where electron donors and acceptors meet and occur in the optimal relations. This may happen e.g. during in situ bioremediation along the fringes of a point-scale input (e.g., contaminant plume) where oxygen from the ambient groundwater mixes with a dissolved organic pollutant from the plume. This mixing results in a narrow "reaction zone" which is habitat for organisms along the plume fringe. It was described for the centimeter and millimeter scale by Bauer et al. (2008). That such plume fringe effect scales up to the decimeter scale, was shown by Anneser et al. (2008). Werth and co-workers

(e.g., Nambi et al., 2003) have used 2-D micro fluidic pore networks to investigate such transverse reaction processes experimentally on the micro-scale. With a depth of 15 μm, a close-packed array of 300 μm diameter silicon posts separate 35 μm pore throats (Nambi et al., 2003). The flow chamber accepts two inlets, so that an electron donor can be fed into one inlet, and an electron acceptor into the other inlet. With the flow through the system, the two substrates meet around the central mixing zone. With this system, Werth and colleagues studied how biomineralization induced by urea hydrolysis and denitrification processes (Singh et al., 2015) altered porosity and flow patterns significantly, both in observations and accompanying models. In parallel to the laboratory-scale experiments, pore-scale numerical models were developed, capable of handling complex dynamic solid–liquid boundaries, in order to couple flow, solute transport, and biofilm growth at the pore scale (Fig. 5).

While the focus of this first set of studies was on the effects of microbial biomass on flow and mixing patterns, in another set of investigations the group concentrated on the effects of microbial degradation on distribution of chemical compounds in groundwater. They used the same experimental setup for this, but also a set up where the columns and thus the pore sizes varied—these had aggregates of small pore sizes, interrupted by larger pore sizes, thus introducing further flow heterogeneity (Zhang et al., 2010). Tang et al. (2013) injected as electron donor (*R*)-2-(2,4-dichlorophenoxy)propionate (*R*-2,4-DP) into one inlet. Dissolved O_2 served as electron acceptor and was fed through a separate inlet. The researchers inoculated the microcosm with the bacterial strain *Delftia acidovorans* MC1 and studied e.g. degradation rates. Both in the flow cell (Fig. 6E and F) and in the model (Fig. 6A–D) they showed how the biomass growth led to different flow and concentration fields. The interplay between biomass and substrate availability resulted in heterogeneity in the biomass, forming bridges between columns, and thus closing pores for flow (Fig. 6). The effects of bioclogging on hydraulic conductivity and flow were in agreement with comparable studies by e.g. Thullner et al. (2004), Bauer et al. (2008), and Sun et al. (2021).

For simulating the effect of the transverse mixing, Tang et al. (2013) used a Lattice Boltzmann code to model the 2-D pore-scale flow field and the advection–diffusion–reaction equations (with dual Monod kinetics), and coupled a Cellular Automaton model for biofilm spreading. Fig. 6 shows the good agreement between the growth pattern in the model (Fig. 6A–D) and the micromodel experiment (Fig. 6E and F). In the model, most of the biofilm developed on the downstream side of the cylindrical posts, and then extended out into the pore body.

Case study 3: Microbial colony growth patterns influence biodegradation of acetate—Modeling study

There is no "plug and play," "out of the box" model applicable straight away to any given problem in groundwater ecology, neither on the macro-scale nor on the micro-scale. It very much depends on the question, the framework, boundary conditions, the scales, the complexity, which method could be most useful to address the question. With the study presented in this third case, care was taken to represent groundwater conditions not only in terms of physical properties (temperature, and the temperature-dependent physical constants set accordingly), in terms of chemicals (hydrochemical concentrations representative for groundwater), but also in terms of the microbial kinetics (kinetical parameters adjusted from laboratory temperatures to groundwater temperature;

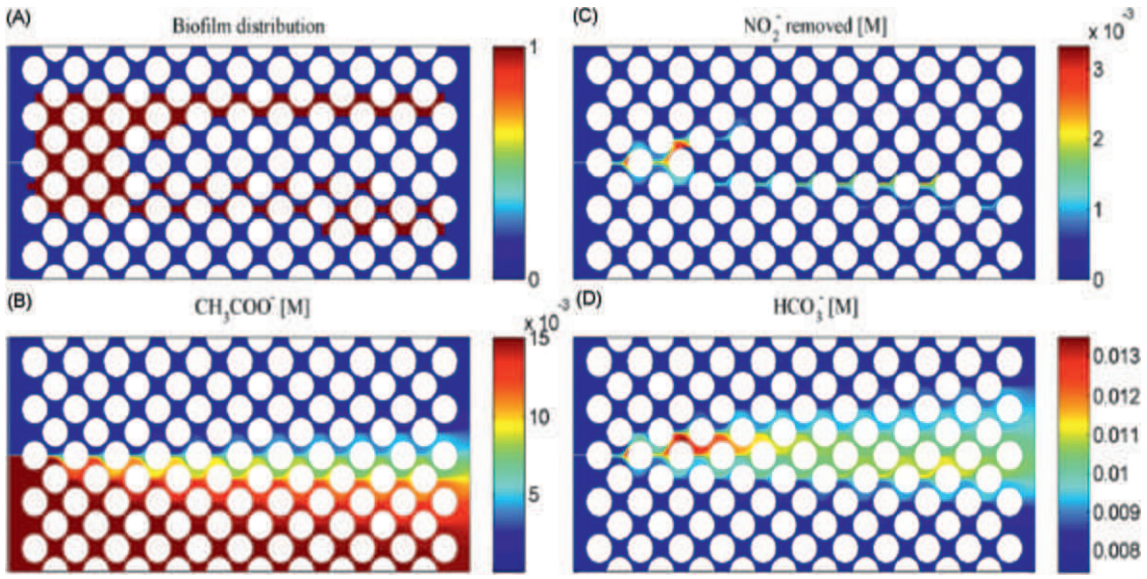

Fig. 5 Modeling biomineralization induced by urea hydrolysis and denitrification processes. Aqueous solution flow from left to right. (A) Spatial distribution of biofilm as observed in microfluidic cell experiments and implemented in the model. The following substrates and their spatial distribution were simulated: (B) CH_3COO^-, (C) removal of NO_2^-, (D) formation of HCO_3^-. All concentrations are in mol L^{-1}. Modified from Singh R, Yoon H, Sanford RA, Katz L, Fouke BW, and Werth CJ (2015) Metabolism-induced $CaCO_3$ biomineralization during reactive transport in a micromodel: Implications for porosity alteration. *Environmental Science and Technology* 49: 12094–12104, with permission from the American Chemical Society.

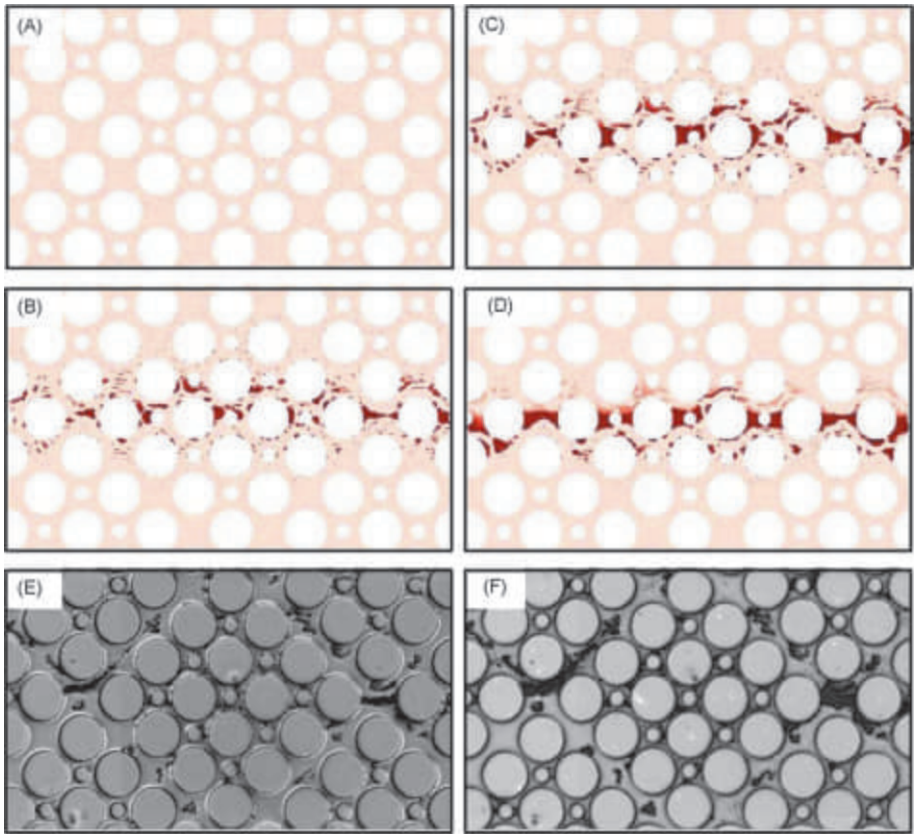

Fig. 6 Simulated (A–D) and experimental (E and F) pore-scale visualization of biofilm distribution in a heterogeneous pore-network microfluidic flow cell. (A) 1st, (B and E) 11th, (C) 16th, and (D and F) 24th day. Reproduced from Tang Y, Valocchi AJ, Werth CJ, and Liu H (2013) An improved pore-scale biofilm model and comparison with a microfluidic flow cell experiment. *Water Resources Research* 49: 8370–8382, with permission from the American Geophysical Union.

Schmidt et al., 2018). While many modeling studies have provided concepts and methods to tackle subsurface porous flow, this study remains one of the very few implemented with groundwater conditions. We will first introduce some complexities about modeling the micro-scale in the groundwater ecosystem in more detail—the following paragraphs apply to all models, but are given here in the context of this "modeling-only" study. The backbone for all groundwater ecosystem modeling is to simulate the flow adequately. Micro-scale approaches need to ascertain either directly or indirectly a parabolic flow profile within a pore with no flow at the pore walls and maximum flow at the largest distance from the pore walls (Benioug et al., 2015), in contrast to the macro-scale Darcy equation which implements pores implicitly only as hydraulic conductivity of a representative volume containing solids and fluids. However, in order to be informative for the whole aquifer, micro-scale models also should provide interfaces for coupling to large scale solutions.

In this third case study, the focus was on how to incorporate biomass that is in a steady state, i.e. neither growing nor decreasing in biomass, while the subsequent section "Additional remark on small scale food web—Fauna grazes on microbes and engineers the environment" discusses the modeling of microbial growth, i.e. increase or decrease in biomass. The steady state is a simplification which might be appropriate in groundwater ecosystem situations that are in (pseudo-)equilibrium, but will not suffice if a pulse of e.g. a contaminant is to be modeled. As mentioned above, in many observational studies representing groundwater ecosystem situations, and by many methods, heterogeneous distribution of microorganisms on the micro-scale has been demonstrated. Thus, models that consider biomass to be homogeneously distributed like in Fig. 7A, seem inappropriate, but are still used.

Modeling the biomass as distributed like a film along the wall (Fig. 7B) is slightly more appropriate, since the majority of cells are attached and the proportion of active cells is higher among the attached ones than among the suspended ones (Grösbacher et al., 2018)—thus, most activity takes place along the wall. A cell positioned at the wall is more mass-transfer-limited than biomass or enzymes within the fastest flowing region—diffusion becomes all the more important, the more advection decreases toward the wall (compare flow profile in Fig. 7A). Such film-like distribution was implemented in modeling studies several decades ago (Baveye and Valocchi, 1989; Molz et al., 1986).

However, to derive effective rates in case of heterogeneous colony-like distributions of microbial cells, such as they were observed in e.g. X-ray computed microtomography (CMT; Fig. 2), is more complex. Scheibe and Wood (2003) point out that particles such as microbial cells do not experience zero velocity, when simulated as single cells attached to the wall, because they are

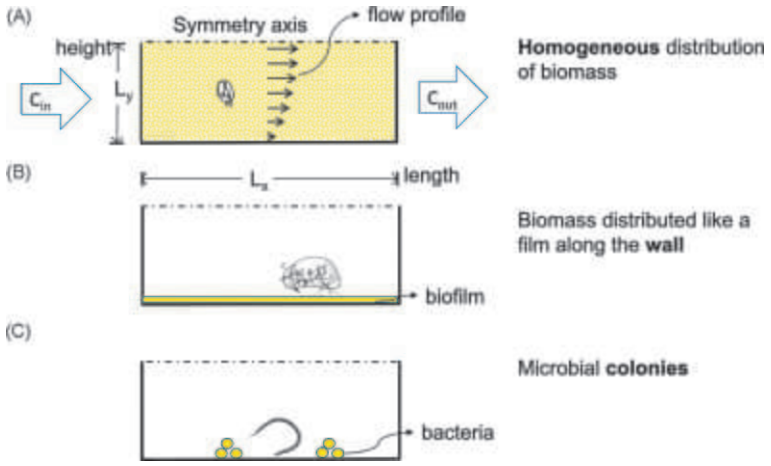

Fig. 7 Three simulation scenarios. Left boundary: laminar flow profile with a set average velocity and fixed concentration; lower boundary: impermeable wall (zero flow (no slip), zero solute flux normal to the surface); upper boundary: symmetry axis; right boundary: set pressure and zero diffusive flux perpendicular to the boundary. (A) Most frequently, biomass is treated as distributed homogeneously in the aqueous phase. The biomass does not oppose flow; (B) distribution of the biomass along the pore wall in a thin film—biomass shows uniform thickness and is often treated as impermeable to flow; (C) the biomass is distributed in discrete colonies built from spherical cells. The colonies are flown through with high viscosity. In the figures, sketches of organisms feeding on microbes are shown, out of scale, to indicate that the bacterial biomass is food for other organisms: (A) protozoon, (B) ostracod (drawing from Dole-Olivier et al., 2000), (C) nematode (photo: Eisendle-Floeckner, pers. comm.); not to scale. Simulating feeding was not performed in the set-up presented here, but is one of the next steps (see also remarks in section "Additional remark on small scale food web—Fauna grazes on microbes and engineers the environment"). Modified from Schmidt SI, Kreft J-U, Mackay R, Picioreanu C, and Thullner M (2018) Elucidating the impact of micro-scale heterogeneous bacterial distribution on biodegradation. *Advances in Water Resources* 116: 67–76, with permission from Elsevier Ltd.

at a physical distance from the wall, either from their own diameter, or due to charges. This means, that already for one single cell attached to the wall, the velocity distribution is truncated. This may also be (one of) the reason(s) for microbial cells preceding inert tracers' pulses (summarized in Dong et al., 2002).

Schmidt et al. (2018) coupled a pore-scale reactive transport model to an IbM code. In this proof-of-principle study, microbes were modeled in pseudo-equilibrium, i.e. they did not grow or decay. One next step, minor changes to the code to implement growth, were later taken and are the basis for further simulations (http://micro-scale-groundwater.online/). In all scenarios, the same biomass was active (200 cells/domain or the equivalent of it in the homogeneous and biofilm case), but it was distributed in different ways. The modeled outcomes for the homogeneous and wall scenarios reflected published results. The substrate was most efficiently degraded in the fictitious situation of microbial enzymes being distributed homogeneously in the fluid (Fig. 7A and top line of Fig. 8). In the also fictitious situation of biomass being distributed continuously along the wall, such as in Fig. 7B and second line in Fig. 8, degradation was shifted toward the wall, but due to diffusion and advection, the substrate was degraded almost as completely as in Fig. 7A. However, if biomass occurred in colonies (Fig. 7C), degradation was decreased all the more, the smaller the number of colonies, into which the biomass was condensed (Fig. 8, third to sixth line). This means that the lowest degradation occurred when all biomass was concentrated in one colony (extreme case of Fig. 7C; third line in Fig. 8). Please note that the apparent degradation upstream, i.e. to the left, of the colony, is due to the pseudo-equilibrium with continuous flux of acetate together with the colony using up more resources than advection and diffusion can replenish toward the pore wall—in the regions upstream of the colony, diffusion toward the bacterial colony results in degradation and no acetate diffuses back upstream, while in regions without colony, diffusion occurs in all directions, and thus also in the upstream direction. The diffusion of acetate toward the colony, and thus loss from the system, outweighs advection and diffusion toward the pore wall (see the flow profile approaching zero toward the pore wall in Fig. 7A). The acetate distribution in the pore would look different in the non-pseudo-steady state where acetate is entering as a pulse. Downstream colonies are shadowed by upstream colonies and the diffusion of substrate from the fast-flowing areas of the pore to the attached cells is a further limitation to the cells.

Fig. 9 shows how the concentration computationally decreased toward a wall-attached colony (down to dash-dot line), because of the decreasing advection and the increasing importance of the slower diffusion. In addition, it shows how the substrate, in this case acetate, decreased within the colony (below point-dashed line) due to the more viscous biomass, which further slows down diffusion. This is in contrast with most models studying biologically mediated reactions, e.g. Bottero et al. (2013) and Tang et al. (2013), who considered biofilms or colonies as impermeable, reactive surfaces. But a model incorporating transport also within the colony is important to study ecological questions such as which colony size is advantageous—as a compromise between the protection against grazing and abrasion within a colony versus receiving less substrate and thus, being the more substrate-limited, the deeper down a cell is located within the colony.

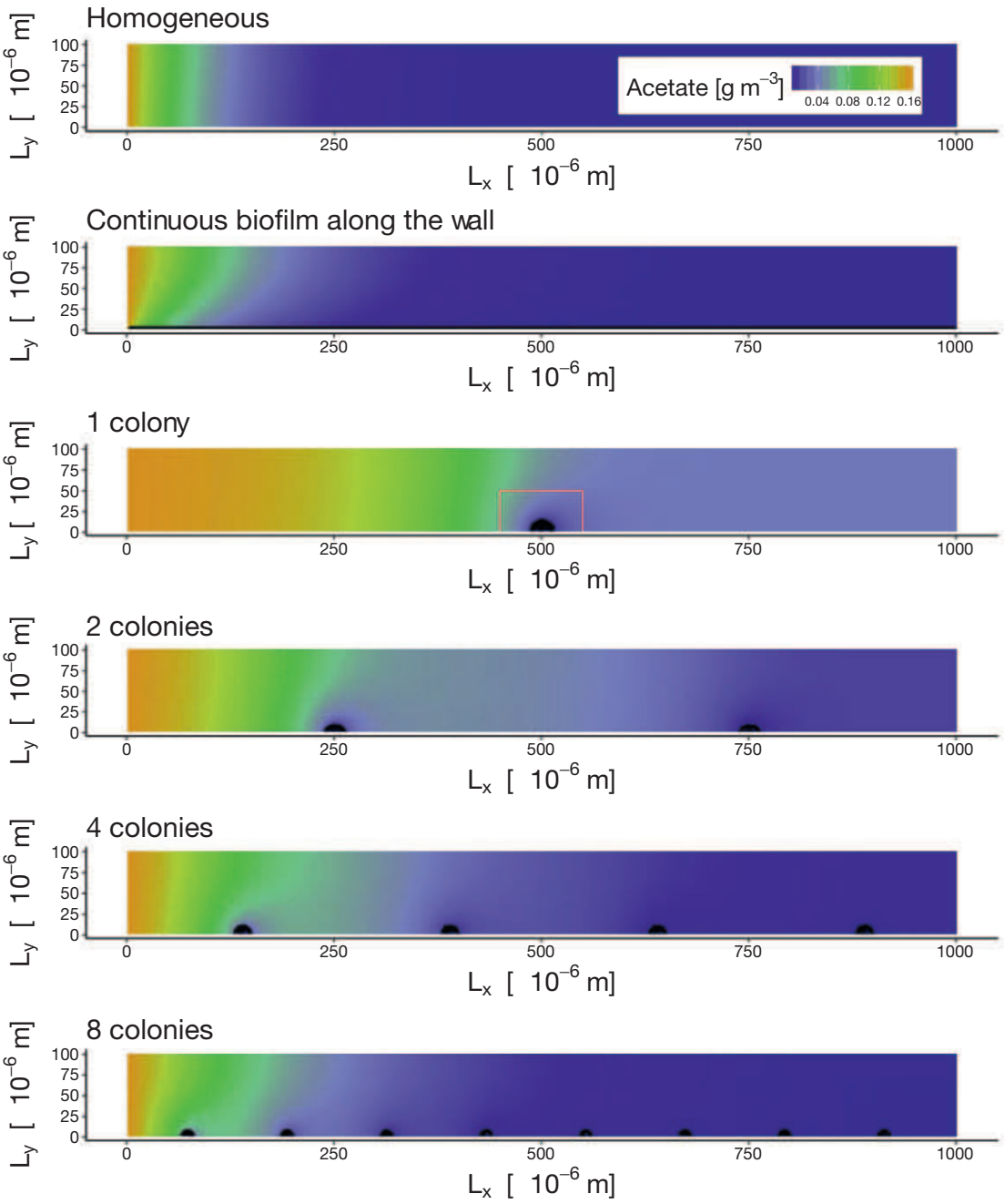

Fig. 8 Computed steady state concentration distributions within a pore channel, for different biomass distribution models. In all scenarios, the same biomass was active (200 cells/domain or the equivalent of it in the homogeneous and biofilm case), but it was distributed in different ways. These 2D simulation results are for the base case scenario (flow velocity 5×10^{-6} m s^{-1}, 200 cells or the equivalent biomass per pore, acetate as substrate). Homogeneous = uniform concentration of biomass suspended in liquid; Wall = continuous biofilm with uniform thickness along the pore wall; Colonies = the same total biomass aggregated into 1, 2, 4, or 8 equidistant colonies, respectively. L_x = length along the *x* axis; L_y = length along the *y* axis. The section within the red box is enlarged in Fig. 9. Modified from Schmidt SI, Kreft J-U, Mackay R, Picioreanu C, and Thullner M (2018) Elucidating the impact of micro-scale heterogeneous bacterial distribution on biodegradation. *Advances in Water Resources* 116: 67–76, with permission from Elsevier Ltd.

Jung and Meile (2019) tested cases of Fig. 7B and C along irregularly shaped pores, but did not clarify whether their scenarios were based on groundwater conditions or not. Like Schmidt et al. (2018), they found that microbial distribution in colonies, instead of in biofilms, decreased bioavailability and thus biodegradation of a substrate. Modeling microbial degradation in setups such as in Fig. 7A and B has thus been confirmed repeatedly to overestimate microbial degradation.

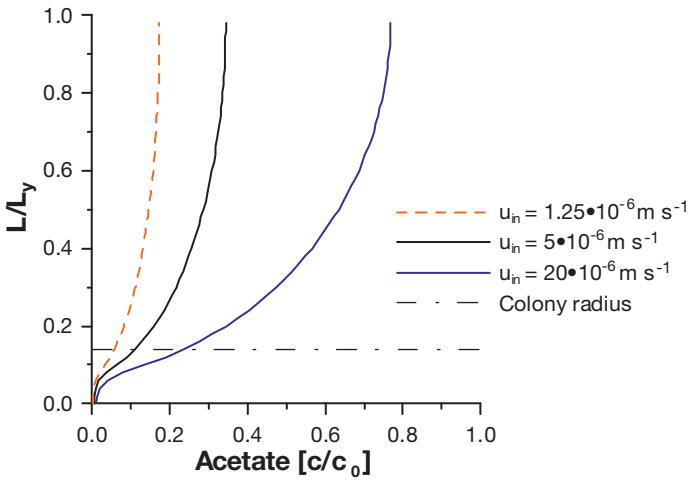

Fig. 9 Computed acetate concentration profiles along L_y ($L_y = 0$ is the wall and L/L_y is the relative distance from the wall with L being the respective metric distance the unit of which depends on the respective set-up) at the L_x position of the center of one colony (line for colony radius marks interface between biomass and pore water) in the base case simulation in Schmidt et al. (2018): one colony comprising 200 cells, with physiological parameters as given in Table 1 in Schmidt et al. (2018), and with three different velocities of the water flowing past the colony. c is the concentration prevailing at the particular point, scaled to the inflow concentration c_0 which is degraded within the colony so that the prevailing concentration can be maximum 1, but is mostly a fraction of the inflow concentration. Modified from Schmidt SI, Kreft J-U, Mackay R, Picioreanu C, and Thullner M (2018) Elucidating the impact of micro-scale heterogeneous bacterial distribution on biodegradation. *Advances in Water Resources* 116: 67–76, with permission from Elsevier Ltd.

Additional remark on small scale food web—Fauna grazes on microbes and engineers the environment

While microbial growth has been studied both experimentally and computationally, as shown in the three case studies above, small scale (impacts of) food webs have been completely ignored so far in laboratory micro-scale experiments and in models. This is despite the role of protozoan grazing on the biodegrading activity of biodegrading bacteria has been suggested decades ago (Mattison and Harayama, 2001). Protozoa are food for metazoa, such as nematodes and crustacea, which are among the most important players in the groundwater food web. Incorporating the food web in observations and modeling is, however, not only important because of the feeding relationships, but also because larger organisms, so far ignored in models, shape the environment through bioturbation—they thus act as micro-engineers (Mermillod-Blondin and Rosenberg, 2006; Hose and Stumpp, 2019).

Since bioturbation is performed mainly by larger organisms, the methods do not always require visual magnification as in microscopy—some phenomena are even visible to the naked eye, e.g. Hose and Stumpp (2019). These authors demonstrated how the burrowing activity of the higher and larger organisms led to bioturbation in mesoscale column experiments, observed through transparent column walls. Metazoa are frequently found in sediments where the porosity would indicate that the pore is too small for metazoa to pass (e.g., Schmidt et al., 2007). Their presence thus indicates secondary porosity not inferable from the grain size distribution alone. That the actual geometry of pore size distributions does often include macropores, e.g. from bioturbation or from decaying roots, has meanwhile been visualized repeatedly, e.g. by axial tomodensitometry (Dufour et al., 2005; Mermillod-Blondin et al., 2003b). Bioturbation results in some pores being widened, while others decrease in size, when the material is relocated. Thus, new micro environments are created. Bioturbation (Fig. 3A), based on sufficient microbial growth (Fig. 3C), lays the foundation for increased spatial and temporal heterogeneity (Fig. 3B and A versus Fig. 3D and E). Bauer et al. (2009) had increased flow pattern diversity by incorporating a lens of coarser substrate grains in their flow cell. The increased degrader activities that they observed, will also apply for situations with bioturbation, but this was not tested yet for the groundwater ecosystem. Indirectly, this effect of increased microenvironment heterogeneity was observed to affect microbial degradation in a study by Mermillod-Blondin et al. (2003a), where denitrification and hydrolytic activity were higher in columns with fauna than in those without fauna. For soils, oligochaete burrows have been described to be clad by an environment of microbially highly active burrow linings, the so-called drilosphere (e.g., Kuzyakov and Blagodatskaya, 2015). They have been shown for different environments to exhibit higher degradation, with more diverse redox situations and thus higher diversity of processes and products (Haas and Horn, 2018). Due to the increased mixing, reaction times are expected to decrease. This will further increase productivity. Similar effects may be expected for oligochaete or crustacea burrows in groundwater sediments, and along root canals where the roots reach into the saturated zone.

Conclusion/synthesis

The micro-scale is so far not at all addressed in field investigations, since adequate techniques are lacking. The importance of the micro-scale for the meso- and macro-scale is only beginning to be acknowledged and it will take more investigations to understand

their interplay more completely, and to gather enough details from which more general patterns can be derived. The distribution of microbial biomass and activity on the micro-scale (pore-scale) is heterogeneous and as such, all investigations and models that assumed homogeneous patterns fail to simulate in situ conditions and processes, in most cases overestimating process rates. As derived from model exercises, organization of sediment attached microbes in discrete colonies (as is indicated by many microscopic studies) instead of homogeneous biofilms (as assumed in most modeling studies) leads to significantly lower process rates, which is more realistic to natural aquifer conditions.

Similar to other habitats (e.g., soils), micro-scale heterogeneity in the distribution of reducing potential (organic matter, reduced inorganic compounds and minerals), electron acceptors, microbial biomass and activities will allow a high diversity of aerobic and anaerobic processes to occur simultaneously, e.g. denitrification and sulfate reduction in a predominately oxic aquifer sediment. Although many processes that are active and detectable at the micro-scale become invisible at the meso- and macro-scale, they nevertheless substantially contribute to the overall transformation and flux of matter. We are (still) at a stage where all disciplines are learning from each other in respect to micro-scale ecology. Studying the micro-scale in groundwater systems is more challenging than studying the micro-scale in the laboratory, in a petri dish at room temperature. This is one explanation why micro-scale investigations in groundwater ecosystems are not much ahead of micro-scale investigations in other ecological settings. However, from the need to understand subsurface processes better, for e.g. CO_2 storage, contaminant degradation to achieve drinkable water, etc., arise studies and results that may help to answer questions for other systems as well.

Understanding micro-scale processes in the groundwater system may thus inform research in other systems, such as the sediment-water interface in lakes (Tankéré et al., 2002), even if the specific experimental tools have to differ. Indeed, micro-scale processes such as studied in a unique laboratory system by Bauer et al. (2009) reflected the results from one of the highest-resolved meso-scale field studies (Anneser et al., 2008). Upscaling from the micro-scale to the meso-scale and from there to local and global scales, is challenging, but is the prerequisite for sustainable water management. Techniques are (at least partly) mature enough to tackle such questions for the groundwater ecosystem, and the near future will see exciting results. Where methods are limited, modeling can provide insights, depending on the chosen framework conditions, and may, via sensitivity analyses, identify potential major drivers which may steer method development.

Knowledge gaps

(a) Conceptual models for groundwater fauna grazing on microbes and impacts on all scales
(b) Qualitative feeding relationships within the food web on all scales
(c) Parameters, i.e. standing stocks, viscosity of microbial colonies on all scales
(d) Rates, i.e. pore-scale flow rates, feeding rates, growth rates, degradation rates, attachment/detachment rates, maintenance rates, reproduction rates, death rates (protozoa and metazoa) on all scales
(e) Conceptual and quantitative models for bioturbation in the groundwater ecosystem and impact for the micro-scale
(f) Generalized upscaling from the micro-scale to the meso-scale and then to larger scales

Important case studies (where appropriate)

There are no field studies on the micro-scale, therefore, here, we focus on laboratory studies and modeling studies. These, however, almost all lack in at least one of the following features: relevant for the groundwater ecosystem, discrete biomass and not just unrealistic biofilm, reactive transport, bacterial growth.

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Relevant websites

http://micro-scale-groundwater.online/.
https://www.sciencedirect.com/topics/earth-and-planetary-sciences/pore-scale.

Trophic Interactions in Subterranean Environments

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Allochthonous Originated from a place other than where it was found.
Biofilm Consortium of microbial organisms able to live on many different surfaces and environments.
Chemoautotrophy The process of obtaining energy through the oxidation of inorganic chemical compounds.
Chemosynthesis The biological production of organic compounds and nutrients by bacteria using chemical reactions (redox reactions) as the energy source, rather than sunlight.
DNA metabarcoding "The automated identification of multiple species from a single bulk sample containing entire organisms or from a single environmental sample containing degraded DNA (soil, water, feces, etc.)" (Taberlet et al., 2012).
Endemism Native to a single defined geographic location.
Fatty acids Carboxylic acids containing long saturated or unsaturated aliphatic chains.
Guano The accumulated excrement of bats and birds.
Hyporheic "The saturated portions of streambeds, banks, and floodplain containing water that originates from a stream and returns to the channel" (Woessner, 2017).
Karst Geological formation derived from dissolution of soluble rocks such as limestone, dolomite and gypsum.
Oligotrophic Refers to an environment with a very low productivity caused by low concentrations of nutrients and carbon sources.
qPCR Quantitative polymerase chain reaction, a technology used for measuring DNA using PCR.
Vadose Relating to or denoting underground water above the water table.

Introduction

The first reported subterranean species dates A.D. 1541 and is a cavefish from the Alugu Cave in the Chinese Yunnan Province, although only formally described in 1993, as *Sinocyclocheilus hyaline* Chen and Yang, 1993 (Borowsky, 2018). Subterranean species have been embedded in folkloric belief and recognized as novelties, but they were subsequently seen as posing challenging issues in evolutionary studies in both aquatic and terrestrial organisms (Racoviţă, 1907).

The solution and fracture cavities that develop in **karst** are large, which is one of the discriminating features between karst and non-karst habitats, the latter having small cavities in the interstitial spaces within gravels and finer grained sediments. Sampling of terrestrial cave fauna (inhabitants as well as transient occupants from the interstices) was initially carried out mostly by hand collection and was limited by the availability of suitable (human-sized) caves as access points to the subterranean habitat. However, the recognition that the subterranean habitat within scree slopes—the *milieu souterrain superficiel* (MSS) of the French Pyrenees (Juberthie, 1983)—could be sampled by means of baited traps buried within them, led to a rapid expansion of such sampling to a broad range of suitable subterranean habitats especially in Europe, United States, and Australia (Culver and Pipan, 2019). Moreover, the ability to sample aquatic habitats remotely, at cave outflows and at springs and wells, has led to a rapidly expanding knowledge in ecological studies during the last 50 years.

Inhabitants of the subterranean lightless world have been defined by many terms—such as cavernicolous, hypogean, stygian, troglobites, troglobionts, stygobionts—and they are typically referred to as blind and translucent (Culver and Pipan, 2019). All categories are recognized by their regressive attributes, especially lack of eyes and pigment in addition to a range of morphological traits that may include vermiform shape, elongate appendages and elaborated extra-optic sensory structures (Figs. 1 and 2).

According to their life cycles and ecological niches they occupy, subterranean fauna can be broadly separated into two categories: stygofauna and troglofauna. Stygofaunal specimens—e.g., amphipods, syncarids, ostracods, cavefishes (Fig. 1), etc.—are obligate aquatic species inhabiting interstices and voids within the groundwater matrix. Troglofauna comprises organisms such as spiders, scorpions and millipedes (Fig. 2) that live in caves, cavities and fractured rocks between the water table and the superficial soil layer. Both groups play a key role in regulating the nutrient cycles and energy flows shaping groundwater ecosystems (e.g., Simon et al., 2003; Venarsky and Huntsman, 2018; Saccò et al., 2019a and references therein) (Fig. 3). However, while the diversity and global

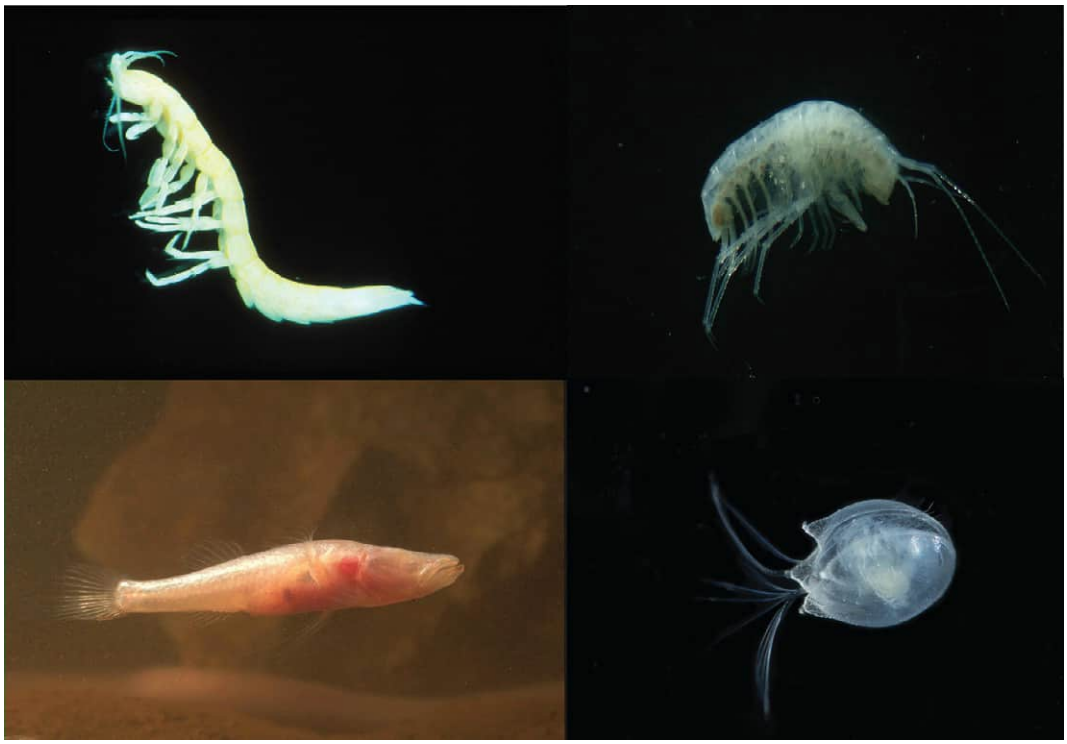

Fig. 1 Photos of some stygofaunal specimens. Upper left: isopod—*Tainisopus napierensis* Wilson and Ponder, 1992 (©George Wilson), upper right: amphipod—*Scutachiltonia axfordi* King, 2012 (©Mattia Saccò), lower left: fish—*Milyeringa veritas* Whitley, 1945 (©Douglas Elford, Western Australian Museum), lower right: ostracod—*Humphreysella baltanasi* Kornicker, 2009 (©Greg Anderson).

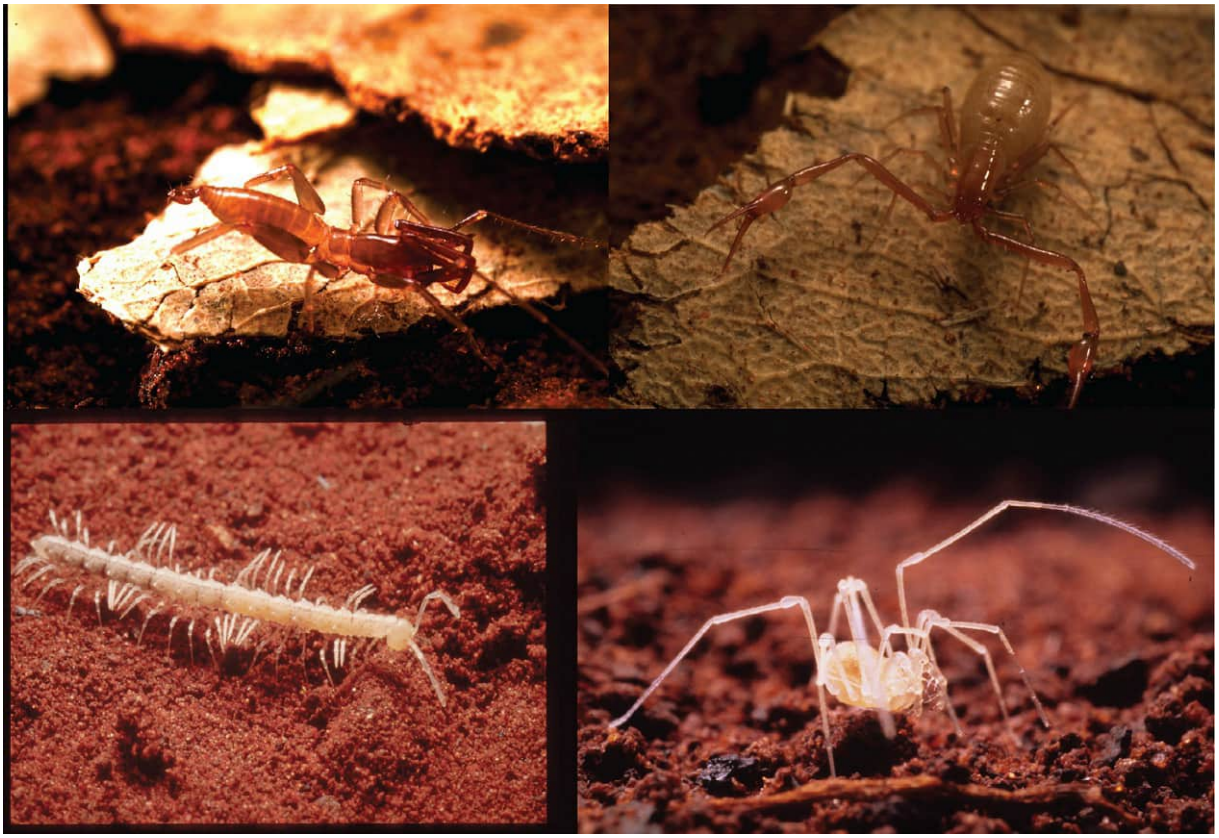

Fig. 2 Photos of some troglofaunal specimens. Upper left: spider—*Draculoides brooksi* Harvey, 2001 (©Patrick Baker, Western Australian Museum), upper right: pseudoscorpion—*Indohya humphreysi* Harvey, 1993 (©Patrick Baker, Western Australian Museum), lower left: millipede—*Stygiochiropus communis* Humphreys and Shear, 1993 (©Bill Humphreys, Western Australian Museum), lower right: opiliones—*Glennhuntia glennhunti* Shear, 2001 (©Patrick Baker, Western Australian Museum).

occurrence of subterranean species was recognized early, studies of subterranean habitats as functional ecosystems developed much later. It is now recognized that subterranean systems are comparable in complexity to surface ecosystems (Gibert et al., 1994) but with a truncated trophic structure owing to the lack of primary producers, except in the special case of **chemosynthesis** (Brankovits et al., 2017). Globally, it is only in the last decades that the magnitude of biodiversity present in subterranean waters has been recognized and given prominence (e.g., Danielopol et al., 2000).

The aim of this article is to report the current knowledge on groundwater trophic dynamics. First, we describe the key ecological mechanisms sustaining aquatic (stygofauna) and terrestrial (troglofauna) subterranean biota. Next, we illustrate the current analytical techniques employed to unravel energy flows and food web interactions of subterranean systems. Finally, we explore future research avenues that will hopefully allow the incorporation of new holistic approaches within the small but rapidly growing field of groundwater ecology.

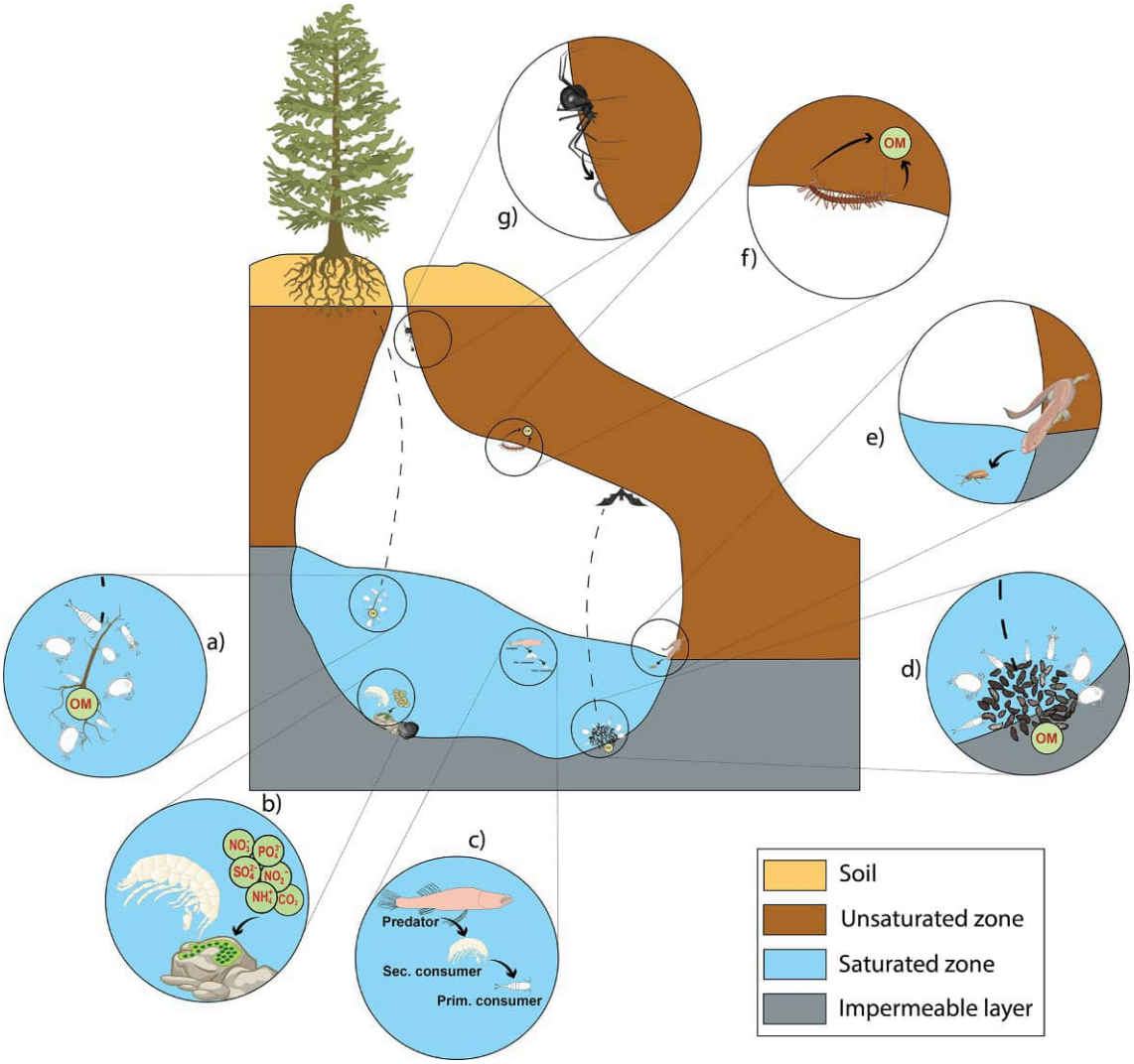

Fig. 3 Diagram showing the main trophic players within the stygofaunal (A and D: primary consumers copepods and ostracods, B: secondary consumer amphipod, C: schematic food web diagram involving cavefish (top predator), amphipod (secondary consumer) and copepod (primary consumer)) and troglofaunal (E: predator salamander, F: millipede processing organic matter and G: predator spider targeting a worm) communities.

Main topics

Stygofauna: Shaping the subterranean aquatic framework

Energy flows and ecological patterns in groundwaters

Groundwaters are crucial components within the global water cycle and also play a vital role in providing services to nature, society and industry (Griebler et al., 2014). However, subterranean environments host challenging conditions for life, due to the lack of primary production and the overall shortage of organic sources (Gibert et al., 2009). Organic matter (OM) in groundwaters has usually an **allochthonous** origin, and gets incorporated from the **hyporheic** and surficial aquatic and terrestrial zones *via* water flow, percolation, gravity or animals falling into the aquifer (Humphreys, 2006). The ecological dynamics sustaining these usually **oligotrophic** subterranean ecosystems are therefore directly influenced by the biogeochemical continuum between groundwater and **vadose**/surficial zones. A vast range of these newly incorporated organic components is utilized, mainly in their dissolved state, by microbial communities (Simon et al., 2003; Foulquier et al., 2011). Groundwater microorganisms also display a plethora of highly adapted **chemoautotrophy** metabolisms involving variedly abundant inorganic compounds such as nitrates, nitrites, ammonia, phosphates, sulfates and carbon dioxide (Brankovits et al., 2017) (Fig. 3B).

Stygofaunal communities display functional and morphological traits carved by evolutionary processes, such as high resistance to starvation, omnivorous diets (Humphreys, 2006; Bradford et al., 2014) but also specialized feeding habits (Francois et al., 2016, 2020), that have allowed them to cope with these "extreme habitats" (Danielopol et al., 2000). As a result of these adaptative mechanisms, subterranean aquatic communities characterize high rates of local **endemism** shaping short-range biodiversity patterns (Humphreys, 2006).

Stygofauna also play a crucial role in maintaining the natural conditions within subterranean ecosystems (Humphreys, 2006). They preserve the hydraulic connectivity between groundwater and surface environments *via* sediment bioturbation, burrowing and grazing (Saccò et al., 2019a and references therein). In addition, depuration from the excess of contaminants and nutrients is mediated by stygofaunal communities through their biological cycles, and **biofilm** proliferation is stimulated through their consumption of microbial biomass (Francois et al., 2016, 2020).

Groundwater food web dynamics

Despite their vast array of ecosystemic functions, stygofauna have only recently gained prominence as key drivers in shaping groundwater ecological dynamics (Hancock et al., 2005). In fact, the archetype of short and simplified food chains has been substantially reviewed recently, bringing new crucial perspectives into the food web interactions casting groundwater ecosystems (Francois et al., 2016; Hutchins et al., 2016; Saccò et al., 2019b). We now know that composite pathways for the incorporation and transfer of OM exist in subterranean ecosystems, and groundwater trophic interactions are likely to be shaped by a combination of opportunistic strategies and evolutionary driving forces (Venarsky et al., 2014).

The basal members of the stygofaunal food chains—i.e., copepods and ostracods (Fig. 1), usually referred as meiofauna—play a key role in transferring OM along the food chain. They filter the particulate OM available in water and also graze on biofilm, triggering the vital transition between microbially-derived OM and the higher levels of the food web (Fig. 3A). Bat **guano** —when present and falling in the water column from the top of a cave—can provide an alternative source of OM that is ultimately targeted by subterranean meiofauna (Cruz-Hernández et al., 2002) (Fig. 3D), aquatic nematodes and mites (Fletcher, 1982) as well as vertebrates such as the Ozark cavefish and salamander (Fenolio et al., 2006).

Stygofaunal amphipods (Fig. 1) and syncarids are globally distributed crustaceans and display a broad array of plastic feeding habits including biofilm grazing (Fig. 3B), filter feeding, predation (mainly on copepods and ostracods) and scavenging (Hutchins et al., 2014). Other widely distributed taxa capable of OM processing include gastropods (deposit feeders) as well as isopods and decapods (both filter feeders and biofilm grazers). These groups, together with copepods and ostracods, often shape the energy flows that sustain groundwater biota. The influence of these taxa on energy flows is extremely relevant considering that groundwater communities are usually bottom-up regulated by the availability of OM, a dynamic that can influence trophic cascade effects (Foulquier et al., 2011).

Higher in the trophic chain, predators such as blind dytiscid beetles, flatworms or cave fishes (Fig. 1), among many others, exert the equally important top-down control on their prey, maintaining the delicate ecological balances shaping groundwater ecosystems. However, groundwater predators are often scarce, a characteristic that triggers redundancies in feeding strategies and overlaps between niche occupations of consumers and predators (e.g., Saccò et al., 2020a). In addition, trophic competition at the species level shapes subterranean food webs, with the degree of trophic (dis)similarity among individuals (i.e., intra-population diet variability) being likely to drive the strength of trophic competitions among conspecifics.

Nonetheless, our understanding of the ecological and functional linkages among stygofaunal groups, and their interaction with the microbial community, is still in its infancy (Griebler et al., 2014). However, recent investigations are bringing to light a wide range of complex stygofaunal interactions (i.e., Ercoli et al., 2019; Francois et al., 2020), stressing the need to consider groundwater biota as components of functionally integrated aquatic and terrestrial subterranean ecosystems.

Troglofauna: The cave-dweller inhabitants

The food web processes in terrestrial and aquatic subterranean environments are broadly similar, as both have: (i) communities composed of obligate and non-obligate subterranean species, (ii) chemolithoautotrophic, photoautotrophic or detrital sources of energy that fuel community productivity, and (iii) strong consumer-resource interactions that influence community composition, abundance, and distribution (Venarsky and Huntsman, 2018). However, aquatic and terrestrial communities obviously live in different media, water versus air, and in this section we explore how this difference appears to influence the food web processes in terrestrial subterranean communities.

Microbial activity in terrestrial subterranean environments

Microbes transform dissolved and particulate OM into high quality microbial biomass, which in turn supports the productivity of larger terrestrial subterranean consumers. Similar to aquatic habitats, terrestrial subterranean microbial productivity can be limited by the availability of both carbon and nutrients. Chelius et al. (2009) tracked the response in microbial abundance following a cave amendment experiment using lint (low quality carbon source) and bat guano (high quality carbon source). Microbial abundance increased in both amendments, but the strongest response was found in the combined lint-bat guano treatment, indicating that microbial communities were co-limited by carbon and nutrient availability. However, terrestrial subterranean microbial communities can also be limited by a factor that is omnipresent in aquatic habitats, water availability.

Humphreys (1991) conducted a litter amendment experiment in an arid Australian cave and found that macroconsumer density did not increase until the litter was misted with water. Similarly, in caves that receive large inputs of guano, the abundance of consumers is often reported to be higher on fresh guano deposits compared to older deposits (Ferreira and Martins, 1999). While microbial processing decreases the quality of guano deposits overtime, authors have suggested that the primary reason for lower consumer abundance on older guano deposits is the result of reduced microbial activity due to lower moisture content in older guano deposits (Pellegrini and Ferreira, 2013). While these studies provide indirect evidence for the influence of water availability

on terrestrial subterranean microbial activity, this mechanism is widely reported in surface habitats (Baldrian et al., 2010). Collectively, these studies suggest that terrestrial subterranean microbial communities are co-limited by multiple interacting factors, including carbon-, nutrient-, and water-availability.

Another difference in aquatic and terrestrial habitats that can influence microbial activity is the spatial and temporal variability in environmental characteristics. For example, measures of temperature and pH will likely vary little throughout a cave stream due to the flow of water, while in terrestrial habitats these variables can change in proximity to surface connections (cave entrances, large cracks and fissures) (Kozel et al., 2019). While we are unaware of studies that have explored spatial variability in terrestrial subterranean microbial activity, factors such as temperature and pH are known to influence microbial activity in general, and we suspect similar mechanisms likely influence microbial activity in terrestrial subterranean habitats. Interestingly, spatial variability in substrate pH is known to influence the distribution of terrestrial taxa, which could be interpreted as circumstantial evidence that spatial variability in pH is influencing microbial activity and thus influences where terrestrial subterranean taxa spend time foraging, but more studies are needed to provide more robust support for this hypothesis (Kozel et al., 2019).

Mediation of surface connectivity on terrestrial subterranean food web processes

Terrestrial subterranean environments are composed of networks of cavities ranging in size, length, and depth from the surface (Venarsky and Huntsman, 2018). Ecotones are created when these cavities are close to the surface and environmental factors, such as temperature and humidity, change in relation to surface environmental conditions. Additionally, ecotones can be rich in energy sources, including animal carrion and wind-blown detritus (Moseley, 2009). While these energy-rich areas often attract consumers, the temporal variability in environmental conditions can prevent foraging during certain seasons. For example, during warmer and more humid seasons (spring and summer) many obligate and non-obligate subterranean taxa will forage in these ecotones and then move deeper into the subterranean environment during cooler and drier seasons (winter and fall). These movements are especially prevalent in obligate subterranean species as many have thinner cuticles which increases integument permeability and thus cannot tolerate low humidity environments (Howarth, 1980). The cavities that connect surface and subterranean environments also direct the flow of water across terrestrial subterranean environments. This water delivers dissolved and particulate OM as well as nutrients which support terrestrial microbial and macro-consumer productivity (Fig. 3F). However, this water can also create micro-habitats suitable for chemolithoautotrophic production. Thin layers of slowly flowing water create hygropetric habitats which have very low OM content, but seemingly with sufficient dissolved allochthonous organic carbon to support chemolithoautotrophic bacteria that are fed upon by terrestrial beetles (Paoletti et al., 2011). Thus, while subterranean environments are generally considered to be more stable than neighboring surface environments, environmental conditions in subterranean terrestrial environments can exhibit strong spatial and temporal variability, which in-turn can influence consumer-resource interactions.

Many surface species utilize subterranean habitats for shelter, breeding, and foraging (bats, crickets, salamanders) and the presence of these species can influence terrestrial subterranean community composition through several food web processes (Fig. 3G). For example, cave crickets and bats forage in surface habitats at night and then use subterranean habitats for shelter during the day (Taylor et al., 2007). Guano is an important energy source to terrestrial subterranean food webs, with some terrestrial taxa showing preferences for different types of guano, such as hematophagous (feed on blood) or frugivorous (feed on fruit) bat guano (Zepon and Bichuette, 2017). Additionally, some obligate cave beetles specialize on cave cricket eggs (Studier, 1996). However, surface species not only support terrestrial subterranean communities *via* the input of resource subsidies (sensu Polis et al., 1997), but they can also influence terrestrial community composition *via* top-down mechanisms. For example, invasive fire ants are regularly observed foraging in caves throughout the United States (Pape, 2016). The top-down influence from surface species is not limited to terrestrial subterranean taxa, as adult salamanders use subterranean terrestrial habitats for shelter and will often lay eggs in aquatic subterranean habitats where larval salamanders can have a strong top-down influence on aquatic subterranean taxa (Venarsky and Huntsman, 2018; Manenti et al., 2020) (Fig. 3E).

Current analytical approaches and future research avenues

The analysis of faunal ecological functions in subterranean environments is constrained by the cryptic nature and small size of the species. *In situ* ecological observation is often impossible, while sampling of the ecosystems is dependent on the availability of appropriate access points (i.e., caves, groundwater, wells, etc.). The relatively low abundance of fauna limits the number of individuals and amount of tissue to work with. These challenges collectively explain why the ecological functioning of subterranean systems is understudied compared with surface terrestrial and freshwater habitats.

The analytical approaches applied to subterranean invertebrates can be divided into four groups: morphological analysis of the mouth parts and feeding appendages (e.g., Hutchins et al., 2014); examination of the gut contents (e.g., Saccò et al., 2021); and chemical, primarily isotopic, proxies derived from either bulk tissue (Bradford et al., 2014; Hutchins et al., 2014; Saccò et al., 2019b, 2020c, 2021) or specific compounds (Saccò et al., 2019b, 2021) (Fig. 4).

Mouthpart analysis rests on the morphological assessment of invertebrate feeding apparatus, and the resultant assignment to a feeding niche (herbivorous, predatory, etc.). Mouthpart and accessory feeding apparatus morphology has been widely assessed across multiple invertebrate groups from a range of environments (e.g., Fryer, 1964; Schram and Lewis 1989; Arndt et al., 2005), including groundwater habitats (see Hutchins et al., 2014 and references therein). Key characteristics include the shape of the mandibles relative to the processing of different sized food items, including the possession of cutting blades; the formation of the

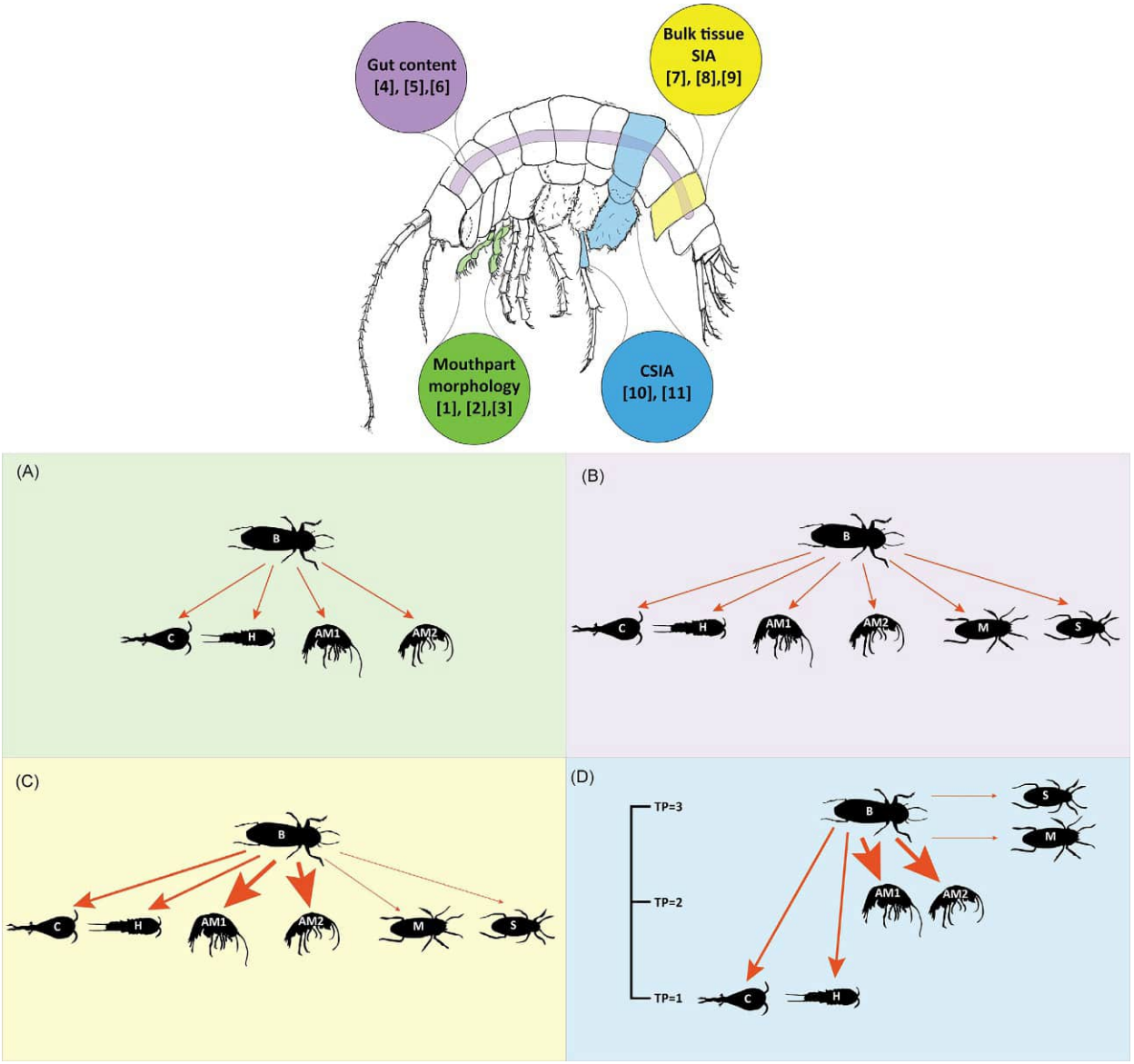

Fig. 4 Analytical techniques currently employed to study subterranean food web interactions (top figure) ([1] Fryer, 1964; [2] Schram and Lewis, 1989; [3] Enghoff, 1985; [4] Humphreys and Feinberg, 1995; [5] Bradford et al., 2014; [6] Weitowitz et al., 2019; [7] Simon et al., 2003; [8] Francois et al., 2016; [9] Ercoli et al., 2019; [10] Saccò et al., 2019b; [11] Venarsky et al., 2018) and schematic representation of the insights provided by each technique (lower 4 graphs): (A) mouthpart morphology studies, (B) gut content analyzes, (C) conventional bulk tissue stable isotope analysis (SIA) studies and (D) Compound Specific Isotope Analysis (CSIA) investigations. The diagrams are based on the empirical data gathered from Bradford et al., 2014 and Saccò et al., 2019b. Beetles—B: *Paroster macrosturtensis* Watts and Humphreys, 2006, M: *Paroster mesosturtensis* Watts and Humphreys, 2006 and S: *Paroster microsturtensis* Watts and Humphreys, 2006; amphipods—AM1: *Scutachiltonia axfordi* King, 2012 and AM2: *Yilgarniella sturtensis* King, 2012; copepods—C: Cyclopoida sp. Burmeister, 1834 and H: Harpacticoida sp. G. O. Sars, 1903. Thicker arrows indicate more marked feeding preferences inferred from the application of each technique. TP: trophic position.

dactylus to allow manipulation of particles; and the morphology of the gnathopods (Arndt et al., 2005). However, while extremely useful for preliminary assessments, this rather descriptive approach provides only indirect evidence of the real feeding behaviors of specimens, and may be biased considering the usually opportunistic trophic habits of subterranean fauna (Fig. 4A).

Gut content analysis is used widely in ecology, and although applied in subterranean fauna (e.g., Humphreys and Feinberg, 1995; Bradford et al., 2014; Weitowitz et al., 2019), it poses specific challenges in the case of smaller invertebrates, especially in terms of obtaining sufficient biomass for analysis. Another unavoidable issue with the use of gut contents alone as a trophic indicator is that they capture only a single snapshot of time. Although reliability can be improved by sampling multiple individuals, unless the food resources within the habitat are very stable, or unless samples are taken across multiple time periods (e.g., seasons, or different levels of rainfall recharge), there is a risk that the results represent a single feeding episode rather than the full range of trophic behaviors (Fig. 4B). Advances in **qPCR** and **DNA metabarcoding** have the potential to improve identification of food items

within invertebrate guts (Saccò et al., 2021), as well as develop estimates of feeding behavior, such as feeding rates (Durbin et al., 2012). Although DNA metabarcoding is increasingly popular in ecology, the application of the approach to subterranean systems is still in its infancy (Saccò et al., 2019a).

The use of stable isotopes in ecology for trophic analysis is well established (see Boecklen et al., 2011 and references therein). The technique rests on the fact that metabolic processes in primary producers create a specific isotopic signature that can either be preserved within the food chain (for example the $\delta^{13}C$ signature of C3 and C4 plants) or amplified with trophic stage (Boecklen et al., 2011). Careful analysis of the ratios of specific isotopes, most commonly carbon and nitrogen, can therefore provide information on both food source and trophic level in specific organisms (Marshall et al., 2019). The focus is most commonly on carbon or nitrogen isotopes, although oxygen, hydrogen and sulfur have also been assessed in surface environments (Vander Zanden et al., 2016).

The analysis of stable isotopes is not without complications (Ishikawa, 2018). Stable isotopic analysis is conventionally undertaken on bulk tissue samples, which in invertebrates may be whole organisms or indeed samples composed of multiple individuals owing to their small mass. This means that the isotopic fractionation within different tissue types is combined, essentially blurring the signal. Additionally, source signal preservation and degree of trophic enrichment varies with organism type. Consequently, interpretation of the results requires both an understanding of the degree of isotopic fractionation occurring with trophic enrichment within the target organism, and a comprehensive isotopic survey of potential food source items.

One way to address at least some of these issues is to use Compound Specific Isotope Analysis (CSIA). This approach uses chemical preparation followed by gas or liquid chromatography to separate out different molecules within the tissue. By analyzing the isotopic ratios within single molecular groups (e.g., specific amino acids or **fatty acids**), it is possible to generate a signal with a closer constraint on their biochemical pathways.

In trophic ecology, a key molecular target for nitrogen isotope analysis is amino acids (see Ishikawa, 2018 and references therein). These are of particular value because some compounds, such as glutamic acid, show isotopic enrichment with each trophic step, while others, such as phenylalanine, retain the value or close to the value of the primary producers in the food web. This essentially means that the data contains an internal isotopic baseline for the system, and that by developing a ratio between the trophically enriched and source value amino acids, taking into account the trophic enrichment factor for the groups concerned, it is possible to calculate a numerical trophic level for the sampled organism (Steffan et al., 2013) (Fig. 4D). Although CSIA has some limitations around sample size and cost, it is recognized as of increasing use in ecology.

The application of stable isotope analysis to subterranean systems has come later than in surface ecosystems, simply because the interest and capacity for studying subterranean functional ecology is a more recent development (Saccò et al., 2019b, 2021). Bulk tissue stable isotope analysis has been most widely used (Fig. 4C), sometimes in combination with other approaches such as the morphological assessment of mouthparts (Hutchins et al., 2014). Although compound specific approaches are likely to give a higher level of precision in trophic estimates (Saccò et al., 2019b), bulk tissue analysis has the advantage of being cheap, and easily accessible. At least some of the complexity deriving from the combined biogeochemical pathways can be resolved by applying Bayesian modeling to the data, incorporating additional geochemical information, or prior information derived from morphology, ecological observation or DNA (Saccò et al., 2020c, 2021).

An important additional geochemical proxy that can be incorporated in modeling to provide a better understanding of energy flows is radiocarbon analysis. Carbon-14 decays with time, so the signal present within the tissues of a modern organism depends partly on the age of the OM providing carbon to the food chain (Larsen et al., 2013 and references therein). This means that detritivores feeding on old or microbially recycled OM will develop an "older" radiocarbon signal than organisms feeding on live or very recently dead plant matter. This approach has been successfully demonstrated in soil and surface freshwater systems (Larsen et al., 2013). It holds particular potential in groundwater systems, as many of these environments offer the opportunity to deconvolute carbon inputs from surface inflow, and those from chemolithotrophic bacteria, or stored older carbon (Saccò et al., 2020b, 2021).

Isotopic analysis and DNA metabarcoding (alone and in combination) have redirected much analysis of trophic behaviors from ecological observations and invasive techniques to small sample tissue analysis, and in many ways have revolutionized methods in trophic ecology (Vander Zanden et al., 2016; Marshall et al., 2019). These approaches are of particular value in cryptic environments such as subterranean systems (Saccò et al., 2019a, 2020c). However, as stressed before, isotopic analysis in particular is not without caveats (Ishikawa, 2018), and each technique—isotopic analysis, DNA metabarcoding, morphology, and gut content analysis—provides only one piece of the picture (e.g., trophic level, feeding niche, dietary composition, energy flows). Therefore, as is frequently the case in studying complex natural environments, one technique alone is less powerful in elucidating the trophic function of subterranean systems than the application of a carefully considered combination, with data from a range of analyzes being integrated *via* robust modeling approaches (Majdi et al., 2018; Saccò et al., 2019a, 2020b).

Knowledge gaps

The field of groundwater trophic ecology is still in its infancy and as a result multiple knowledge gaps still exist (Mammola et al., 2020). Some of the most relevant aspects to be considered in future studies are:

- Expanding our knowledge on the diversity and functional dynamics of subterranean microbial communities
- Untangling the carbon flows and their role within microbial transitions over time and space
- Unveiling the fate of organic matter and unraveling energy flows through the food webs
- Elucidating the food web interactions between stygofauna, troglofauna, epigean fauna and superficial flora
- Understanding the role of invasive species in groundwaters and their effect on food web dynamics
- Widening our understanding on the ethology of subterranean species and bring light to the food assimilation rates of vertebrates and invertebrates in groundwaters
- Unraveling the specific biogeochemical role of the hyporheic zone and its terrestrial inputs (carbon and nutrients) within subterranean food webs
- Understanding the impact of climate change and anthropogenic pressures on the ecological mechanisms sustaining biota underworld

Important case studies

Name of site	*Country*	*Coordinates*	*Main topic*	*Key references*
Sturt Meadows	Australia	28°41′S 120° 58′E	Stygofaunal trophic ecology	Saccò et al. (2019b)
Sturt Meadows	Australia	28°41′S 120° 58′E	Shifts in subterranean trophic niches	Saccò et al. (2020a)
Sturt Meadows	Australia	28°41′S 120° 58′E	Stygofaunal dietary modeling *via* BMM	Saccò et al. (2020b)
Sturt Meadows	Australia	28°41′S 120° 58′E	Rainfall-driven ecological shifts	Saccò et al. (2021)
Organ Cave	United States	NA	Cave food web interactions	Simon et al. (2003)
Hering, Limrock, and Tony Sinks caves	United States	See key reference for details	Energy flows and nutrient cycling in caves	Venarsky et al. (2014)
Bluff River Cave	United States	See key reference for details	OM fluxes in caves	Venarsky et al. (2018)
Jura and pre-Alps (multiple sites)	France	See key reference for details	Stygofaunal trophic specialization patterns	Francois et al. (2016)
Lyon aquifer	France	NA	Surface/groundwater dynamics and stygofaunal patterns	Foulquier et al. (2011)
Edwards Aquifer	USA	NA	Chemoautotrophic flows and stygofaunal shifts	Hutchins et al. (2016)
Prémarie fountain and Bataillé river	France	44°28′N 0° 22′E and 46°10′N 0° 02′E	Trophic niche occupations among the stygofaunal community	Ercoli et al. (2019)
Leeston	New Zealand	43°46′S 172° 18′E	OM flows across stygofaunal webs	Hartland et al. (2011)
Berkshire	England	NA	Amphipods' biofilm grazing and nutrients cycling	Weitowitz et al. (2019)
La Spezia	Italy	NA	Feeding habits of cave salamanders	Lunghi et al. (2020a)
Sardinia (multiple sites)	Italy	NA	Individual diet specialization in cave salamanders	Lunghi et al. (2020b)
Lombardy and Liguria (multiple sites)	Italy	NA	Grazing pressure from salamanders on cave-adapted species	Manenti et al. (2020)

NA, not available; USA, United States of America; BMM, Bayesian mixing models; OM, organic matter.

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Relevant Websites

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Anthropogenic Pressures on Groundwater

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

The following list contains key terms of importance when considering anthropogenic influences on groundwater resources. The definitions are based on Bierkens and Wada (2019).

Consumptive water use Volume of evaporative losses from withdrawn water during the process of utilization (e.g., crop transpiration).

Freshwater withdrawal Extraction of a volume of surface water or groundwater from the environment to meet the water demand.

Groundwater depletion Natural average rate of groundwater recharge is exceeded by withdrawals leading to declining groundwater tables and volumes.

Groundwater mining Almost indefinite depletion of an aquifer due to withdrawals from non-renewable groundwater bodies.

Return flow Withdrawn water that is not lost due to evaporation and thus returns to surface water or groundwater bodies after usage.

Sustainable groundwater use Withdrawals do not exceed natural average groundwater recharge in the long-term, resulting in stable groundwater tables.

Water demand Volume of water requested by a sector (e.g., agriculture) or stakeholder (e.g., farmer) at a certain point in time and space to fulfill their needs.

Water use efficiency Ability to minimize resource use in human water appropriation in terms of volume of water used for unit of process (e.g., irrigation volume per crop unit over time).

Human-groundwater interactions

Globally, groundwater is one of the most important sources of drinking water (IGRAC, 2018), a key resource for food production (Dalin et al., 2017), and characterized by unique biodiversity and essential ecosystem services (Griebler et al., 2014). It is considered as central for human development as aspired in the Agenda 2030 (Velis et al., 2017). At the same time, groundwater bodies are threatened by massive overexploitation (Döll et al., 2014), pollution (Shukla and Saxena, 2018) and increasingly entangled in telecoupling effects (Luetkemeier et al., 2021). In quantitative terms, recent experiences from the prolonged droughts of 2015, 2018, and 2019 in Western Europe have shown how declining groundwater levels limit drinking water production (EurEau, 2020), dry out groundwater-dependent ecosystems (Schuldt et al., 2020) and generate conflicts between cities and surrounding areas. In terms of quality, contamination of groundwater bodies from nitrate and trace substance inputs in many parts of the world (Shukla and Saxena, 2018) lead to human health risks, high costs for drinking water treatment (Uzun and Debik, 2019) and negative impacts on ecosystems (Kløve et al., 2011).

From a natural science perspective, groundwater is stored in the saturated zone of the subsurface, where pores or fractures are filled with water (Domenico and Schwartz, 1998). This storage is replenished by recharge from precipitation, irrigation, and seepage from surface waters (Alley, 2009; Green et al., 2011; Taylor et al., 2013) as a function of local climate, geology and soil, topography, land cover, land use and atmospheric CO_2 concentrations (Green et al., 2011; Taylor et al., 2013; Reinecke et al., 2021). Especially in humid regions, groundwater is discharged into surface waters, such as rivers or springs (Margat and van der Gun, 2013) providing water even during dry periods, which is crucial for habitat quality of river ecosystems (Döll et al., 2014). In comparison, groundwater extracted by wells is a major source of groundwater discharge in semiarid and arid areas, where groundwater is usually the only permanent source of freshwater (Margat and van der Gun, 2013).

While this hydrogeological description of groundwater provides us with the means of studying groundwater theoretically, it often falls short in explaining actual groundwater phenomena as introduced above. In the Anthropocene epoch, the societal dimension becomes increasingly relevant in determining the state of groundwater bodies worldwide (Gleeson et al., 2020), just like for many other Earth System processes. Notions like hydro-social cycle (Budds, 2008), socio-hydrology (Sivapalan et al., 2012) and socio-hydrogeology (Re, 2015) attempt to consider anthropogenic activities not just as external variables, but rather as internal processes that closely interact with hydrological parameters. The idea of close feedback loops between hydrological processes and human activities shapes the way societies interact with water (Pande and Sivapalan, 2017) and groundwater in particular (Castilla-Rho et al., 2015). In this regard, a recent study found that to avoid critical tipping points in groundwater systems, cultural values of stakeholders involved in managing aquifers have to be understood and incorporated into integrated assessment models and actual management (Castilla-Rho et al., 2017).

Against this background, we seek to elucidate how groundwater systems are impacted by human activities in the Anthropocene. We do not claim to review the complex interactions of human-groundwater systems in its entirety, but we intend to highlight core areas and respective pressures that critically affect groundwater bodies. In this regard, we distinguish between "direct" and "indirect" pressures on groundwater. First, we explore the direct interactions in the field of agriculture, domestic uses of water and the industrial sector. Second, we focus on the indirect pressures in the form of the likely impacts of climate change. Finally, we discuss current approaches in groundwater governance and show how these could help to make human-groundwater interactions more sustainable.

Direct pressures: Societal water uses

Societal actors make use of groundwater resources for multiple purposes and with various consequences. Here, we consider the direct anthropogenic pressures on groundwater bodies as the actual processes of quantitative withdrawals and qualitative impairments. Regarding the volumes of groundwater withdrawn from the environment, this trend is increasing globally (Huang et al., 2018) with hot-spot regions being India, China and United States, primarily triggered by a growing population, irrigated agriculture and socio-economic developments (Siebert et al., 2010). Fig. 1 confirms this global pattern by showing modeling results from WaterGAP 2.2b that compare mean annual net abstractions from groundwater (accounting for return flows e.g., from irrigation and surface water infiltration) to the mean annual groundwater recharge rates (Herbert and Döll, 2019). Though, global estimates of groundwater depletion deviate by a factor of three between 113 km^3/year (Döll et al., 2014) up to 362 km^3/year (Pokhrel et al., 2012), current assessments indicate that even the largest aquifers show negative long-term storage trends (Famiglietti, 2014). Groundwater depletion and groundwater mining in particular (Bierkens and Wada, 2019) can lead to consequences such as land surface subsidence, saltwater intrusion in coastal regions and decoupling of groundwater dependent ecosystems (Lall et al., 2020).

Alongside quantitative withdrawals, qualitative contamination is equally important. In this regard, nitrate is the most widespread substance of concern, introduced by agricultural activities. However, other emerging contaminants that originate from residential (waste-) water management and industrial processes of manufacturing or mining are increasingly being focused on (Burri et al., 2019).

As the modeling results in Table 1 indicate, the agricultural sector accounts for about 66% of total water withdrawals, globally. Though, only 25% of this amount is obtained from groundwater, the total volumes outperform those of the other sectors by a factor of three. Groundwater covers about 36% of domestic demands, while for industrial purposes only 8% are withdrawn from groundwater. These global values, however, do only provide a broad and unidimensional illustration of the importance of groundwater since local particularities are essential and can show a completely different picture. Against this background, the following sub-sections will explore the three sectors in more detail and selectively shed light on human-groundwater interactions and the likely feedback processes involved.

Agriculture: Groundwater depletion and pollution

Globally, agriculture is the dominant water consumer, accounting for 88% of total consumptive water use. Irrigation is the major driver behind with 37% of the consumptive water being withdrawn from groundwater (Müller Schmied et al., 2021). Following an increasing trend, today about 114 million hectares of agricultural land are equipped with groundwater irrigation systems, primarily in India, China and United States (Siebert et al., 2010). Respective food production systems are not necessarily driven by local consumer demands, but rather international food trade, which significantly adds to groundwater depletion (Dalin et al., 2017). Irrigation efficiency is an important driving factor in how water use in agriculture contributes to groundwater depletion. However,

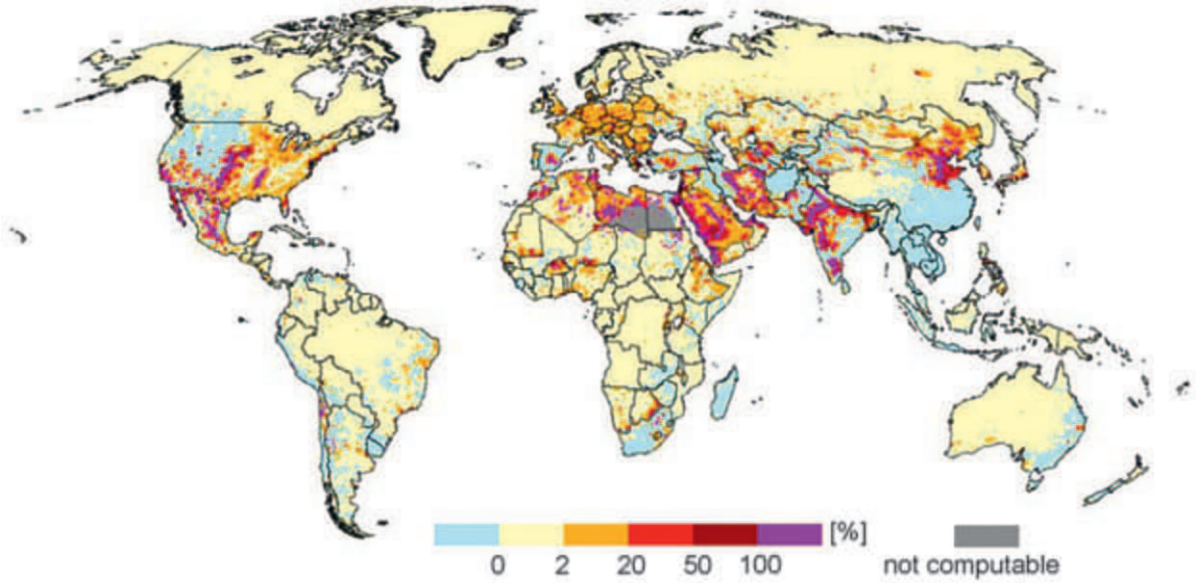

Fig. 1 Groundwater stress spatially depicted as the quotient between mean annual net abstractions from groundwater and mean annual groundwater recharge (WaterGAP 2.2b results). Values of more than 100% indicate groundwater depletion as groundwater withdrawals exceed groundwater recharge. Modified from Herbert C and Döll P (2019) Global assessment of current and future groundwater stress with a focus on transboundary aquifers. *Water Resources Research* 55 (6): 4760–4784. doi:10.1029/2018WR023321, pp. 4768.

Table 1 Withdrawal water use per sector in total volumes and with the share of groundwater therein as simulated by WaterGAP 2.2d for the time period 1991–2016.

Sector	*Water volume withdrawn (km^3 $year^{-1}$)*	*Share taken from groundwater (km^3 $year^{-1}$) (%)*
Agriculture	2392	591 (25)
Domestic	348	125 (36)
Industry	871	73 (8)
Total	**3610**	**789 (22)**

Values provided are results of the WaterGAP 2.2d model and sums can deviate due to rounding errors.
Müller Schmied H, Cáceres D, Eisner S, Flörke M, Herbert C, Niemann C, et al. (2021) The global water resources and use model WaterGAP v2.2d: model description and evaluation. *Geoscientific Model Development* 14(2): S1037–1079. DOI: 10.5194/gmd-14-1037-2021.

simply increasing water use efficiency may not be a sustainable solution as irrigation water was found to act as a significant recharge component for local groundwater bodies via return flows (Lankford et al., 2020). On the other hand, return flows from irrigation mixed with surface water can cause problems such as salinization and the mobilization of pollutants like arsenic (Taylor et al., 2013).

As humans transformed about 55% of the Earth's ice-free land surface for anthropogenic uses, agriculture is today the most area-intensive activity (Ellis et al., 2010) and thus interferes with groundwater bodies the most. Respective agricultural practices are hence critical for both quantity as well as qualitative pressures on the resource. In this regard, three broad types of contaminants can be distinguished that primarily threaten groundwater bodies in a spatially diffuse manner, being fertilizer application (e.g., nitrates and phosphates), crop protection (e.g., pesticides and herbicides) as well as veterinary substances (e.g., antibiotics and hormones) (Burri et al., 2019).

Nitrate is considered the most important and widespread substance of concern. Though, nitrate concentrations of 1–3 mg/L in groundwater can have geogenic origins (Madison and Brunett, 1985; Dubrovsky et al., 2010), the major trajectory for groundwater contamination are anthropogenic activities—primarily agriculture (Shukla and Saxena, 2018). According to the World Health Organization, a threshold of 50 mg/L in drinking water should be targeted (WHO, 2011), which is the current formal benchmark for many regions worldwide. However, in particular North America, Europe, India, China and South-East Asia show critically elevated nitrate levels, being a potential threat to both groundwater dependent ecosystems (e.g., aquatic animals) (Camargo et al., 2005) and human health (Shukla and Saxena, 2018).

Moreover, persistent organic pollutants (POP) remain of concern, despite international agreements (e.g., the Stockholm Convention) to phase out or limit their application. Pesticides (insecticides, rodenticides, herbicides and fungicides) are a major group in POP that enter the soil and groundwater compartment via agricultural application, bio-accumulate persistently (particularly at low concentrations (e.g., Kundu et al., 2019)) and spread across the aquatic environment with severe and partly unknown consequences for ecosystems and human health (Mosharraf et al., 2012). Similarly, the application of antibiotics e.g., in livestock farming (but also in the health care system) can significantly elevate respective concentrations in groundwater bodies. This is likely to support the development and spread of antibiotic resistance among bacteria in the environment. Though, current knowledge is still limited, the ingestion of antibiotic resistant bacteria via drinking or bathing in contaminated water as well as consuming food produced with contaminated irrigation water can pose human health risks (Amarasiri et al., 2020).

Driven by increasing consumer demands and preferences worldwide (e.g., meat consumption), agricultural intensification is critically building up pressures on groundwater resources. Quantitative and qualitative impairments do not just undermine a continued agricultural utilization, but can critically feedback to the consumer via a conflictual competition with ecosystem water requirements and the domestic (drinking) water demand.

Domestic: New peak demands and emerging contaminants

The domestic sector (sometimes referred to as the urban sector) accounts for about 16% of total water volumes withdrawn from groundwater, globally (Table 1). Quantitatively, these volumes are far behind the agricultural sector on a global level but public water withdrawals can locally sum up to significant amounts. In particular, in densely populated regions where irrigated agriculture is less widespread like in Germany, groundwater primarily serves for public drinking water supply (ATT et al., 2015). Qualitatively, major threats to groundwater from the domestic sector can be found in leakages of wastewater and landfills but also from events such as storm water discharge and flooding in urban environments that show a high level of sealing. Especially the exfiltration of substances from wastewater treatment plants and sewer systems is likely a key trajectory for groundwater contamination (Nguyen et al., 2021). In addition, the increasing use of shallow groundwater bodies for geothermal energy (e.g., for heating or cooling of buildings) was found to have major impacts on water chemistry and biodiversity (Griebler et al., 2016).

Public water demand primarily scales with population development but responds to variations in socio-economic and climate conditions (Rinaudo, 2015). During hot and dry seasons, for instance, people tend to use significantly more water, which apparently coincides with a period in which groundwater tables receive less recharge and overall water yield is reduced. Hence, peak demand periods coincide with low availability, potentially creating bottlenecks as happened in the drought years from 2018 onwards in Europe (EurEau, 2020). The societal processes behind water demand patterns are complex as it turned out during lockdown periods of the COVID-19 pandemics with restrictions in public life (Lüdtke et al., 2021).

Urbanization is projected to continue especially in smaller agglomerations as large cities are expected to slow their urban growth (UN-Habitat, 2020). The demand for drinking water will hence continue to increase with pressures on local and distant groundwater bodies (e.g., via inter-basin water transfers) for supplying drinking water. This will trigger conflicts with stakeholders who feel disadvantages and especially the rural-urban divide in water supply will challenge both the urban poor and the rural population (Shi et al., 2021). With growing urban agglomerations (population and area), the transformation of land surfaces due to sealing significantly lowers groundwater recharge rates and thus has a negative effect on the replenishment of groundwater volumes. The change of urban landscapes was found to significantly relocate recharge zones with an overall decrease in recharge rates (Han et al., 2017).

In residential water management, emerging contaminants are a major source of concern. In particular, pharmaceuticals and personal care products (PPCPs) are increasingly being focused on. This group includes substances such as antibiotics, anti-inflammatories, lipid-regulators, and caffeine from wastewater leakages and landfills. Their toxicity is not yet fully known and monitoring schemes are not implemented, yet (Sui et al., 2015). In addition, *per*- and polyfluoroalkyl substances (PFAS) are likewise coming into the focus as they are non-biodegradable and thus highly persistent in the environment. These synthetic organic chemicals can be found in various products and production processes due to their properties of e.g., stability under heat. Hence, a precautionary principal is requested in handling these substances (Cousins et al., 2016).

Domestic water use can be considered as the most direct and apparent interaction between people and groundwater resources, though mediated through infrastructure. In this respect, the recent drought years and qualitative challenges can be conceptually considered as part of an ongoing feedback loop, that might raise awareness of the population for groundwater challenges. This could trigger a more conscious handling of drinking water in the domestic sector and thus contribute to groundwater resources protection.

Industry: Point pollution and localized depletion

The third distinctive sector we consider is industry, which encompasses a wide range of activities from energy production (e.g., cooling of thermal power plants) over manufacturing (e.g., paper, chemistry, machinery, food and beverages) and waste disposal (e.g., dumping sites) to mining activities (e.g., open pit lignite mining) (Flörke et al., 2013). As Table 1 reveals, only 27% of total water withdrawals in this sector originate from groundwater, owing to the fact that the energy sub-sector is the most water-intensive process, which primarily draws on surface water resources (Wada et al., 2016). However, though these values might suggest a lower importance on the global level, industrial water use can have significant effects in terms of lowered quantity and deteriorated quality

on the local scale. With respect to the latter, a wide range of substances can be traced back to various industrial activities like volatile hydrocarbons (e.g., non-aqueous phase liquid (NAPL) like oil), heavy metals and acids (Lall et al., 2020).

The increase in water withdrawals for manufacturing particularly rose in China (Flörke et al., 2013). Researchers found that the increasing number of manufacturing plants (e.g., electronics sector) had significant influence on local groundwater levels (Zheng et al., 2021). Especially the fact that manufacturing plants are increasingly scattered over the country and not concentrated in certain industrial zones of larger agglomerations correlates with falling groundwater tables. Zheng et al. link this development with local governments competing with one another for attracting new companies to invest in certain counties. This results in lowered taxes and environmental standards, which has negative consequences for drinking water supply (e.g., increased costs) as extensive industry-induced well drilling activities create a diffuse pressure on groundwater bodies, lacking adequate monitoring infrastructure (Zheng et al., 2021).

Though, groundwater contamination can have geogenic origins with loads of mobilized arsenic and fluoride (Jadhav et al., 2015) as well as uranium, the mining sector contributes significantly to respective concentrations (Byrne et al., 2021). Mining activities create a massive intervention into natural hydrological patterns (Agboola et al., 2020). As a prerequisite for mineral extraction, lowering groundwater tables for several hundreds of meters via pumping is required to enable personnel and machinery to operate safely. In Germany, for instance, lignite open pit mining strongly altered groundwater conditions in Eastern and Western Germany with depression cones of about 2.100 km^2 like in the case of the Lower Lusatian Region (Koch et al., 2005). The impacts are manifold such as reduced surface water discharge (e.g., drying out of riverbeds), groundwater contamination (e.g., heavy metals) and land subsidence (e.g., damaging buildings) (Agboola et al., 2020). As a consequence from long-term mining activities, the remediation of respective regions affects both people and the ecosystems via rewetting and acidification (Hangen-Brodersen et al., 2005).

Overall, industrial groundwater uses have the ability to strongly interfere with social-ecological conditions due to their intense impact in a certain location. This may be most obvious in the case of mining, as the initiation of a pit fundamentally alters the social-ecological conditions—hydrogeology, ecosystems and communities are fully transformed. This is also true for the abandonment of respective sites when areas are remediated after decades of artificial human influence.

Indirect pressures: Climate change impacts

Climate change is human-induced, but pressures on groundwater due to climate change are rather indirect as they arise from rising temperatures in the atmosphere and changing precipitation patterns. Compared to direct pressures on groundwater from humans, such as the physical extraction of groundwater and the (unintentional) leaching of chemicals into the aquifer, the impacts of climate change on the resource are therefore considered diffuse and uncertain.

Rising temperatures and changing precipitation patterns

Climate change and groundwater have a complex relationship. Changes in groundwater recharge alter groundwater levels and outflows, which affect ecosystems and ecosystem services (Kidmose et al., 2013; Kløve et al., 2014; Griebler and Avramov, 2015). Due to the long residence times of groundwater in the subsurface, ranging from days to tens of thousands of years (Green et al., 2011), the visibility of climate change impacts on groundwater is delayed (Cuthbert et al., 2019; Riedel and Weber, 2020). A variety of climate change impacts on groundwater has already been studied as briefly discussed below.

The Intergovernmental Panel on Climate Change (IPCC) estimates a global warming of 1.5 °C above the pre-industrial global mean temperature until at least 2050 under all emission scenarios (IPCC, 2021). Global warming has multiple impacts on the hydrologic cycle and on groundwater resources. Precipitation and evapotranspiration are the two most important variables for groundwater recharge, yet they are altering due to climate warming (Fallah et al., 2020). Rising temperatures increase the atmospheric vapor pressure deficit of the air and thus, potential evapotranspiration rates, which might decrease groundwater recharge (Vicente-Serrano et al., 2019). However, increasing atmospheric CO_2 concentrations might reduce transpiration of plants due to reduced stomatal conductance, which might lead to increasing groundwater recharge rates (van Roosmalen et al., 2009; Milly and Dunne, 2016) if not balanced by increased leaf area. Moreover, the global warming-induced increasing length of the growing season may increase actual evapotranspiration and thus decrease diffuse groundwater recharge (Ruosteenoja et al., 2016). Rising temperatures and potential evapotranspiration might lead to higher irrigation demand (unless precipitation increases) (Taylor et al., 2013; Riedel and Weber, 2020). Precipitation is likely to increase in many already humid climates, e.g., northern Europe, North America and India, and decrease in many already arid or semi-arid climates, e.g., in the Mediterranean region, South Africa and north eastern Brazil (Anders et al., 2014; Jacob et al., 2014; Spinoni et al., 2020). Simultaneously, household water demand increases due to rising temperatures, especially during hot seasons (Vandecasteele et al., 2014; Simon et al., 2019). Therefore, the combined effect of climate warming and water demand results in "[. . .] amplification of the climate signal by the regional human response" (Lall et al., 2020).

Due to climate change, heavy rainfall events and long-lasting droughts are predicted to increase in frequency, severity and global spatial extent (O'Gorman, 2015; Donat et al., 2016; IPCC, 2021; Mianabadi et al., 2020; Lange et al., 2020). Hydrological droughts and the concomitant decrease of diffuse groundwater recharge may be evident due to the alteration of precipitation rates in combination with increasing evapotranspiration caused by global warming (Hänsel et al., 2019). Such droughts will increase in

regions that already suffer from water scarcity, e.g., the Mediterranean region, southern Africa and southern Australia (Spinoni et al., 2020). However, heavy rainfall events do not automatically lead to an increase in groundwater recharge and water availability (Donat et al., 2016). Depending on the hydraulic conductivity of the soils, heavy rainfall might lead to increased surface runoff, e.g., when the infiltration capacity of the soil is exceeded (Riedel and Weber, 2020). Thus, a smaller proportion of rainfall can recharge groundwater compared to evenly distributed rainfall (ibid.).

Other components that affect groundwater and are caused by climate change, but are not discussed in detail here, include the following: rooting depth of vegetation (deeper roots cause a decrease of groundwater recharge) (Li et al., 2018), forest cover and type (Teuling et al., 2019), snow cover in mountainous areas (Roudier et al., 2016; Bormann et al., 2018), soil moisture (Moeck et al., 2020), and aquifer and soil temperature (Riedel, 2019; Hemmerle and Bayer, 2020).

In addition to the quantitative impacts of climate change, groundwater quality is also expected to respond to changes in climate as groundwater recharge, runoff, and land use affect the groundwater system (Green et al., 2011). Increasing groundwater recharge can lead to quality problems as both geogenic and anthropogenic stressors might be flushed out by the increased recharge, which can increase contaminant transport or mobilize new contaminants and pollute groundwater (Green et al., 2011; Taylor et al., 2013). Increasing irrigation demand due to the reasons mentioned above, might increase recharge under cropland and might affect groundwater quality negatively (e.g., due to infiltration of nitrates, pesticides, fungicides) (Iglesias and Garrote, 2015). Besides quality issues, an increase of groundwater recharge may cause slope instability and landslides (Green et al., 2011).

Alteration of surface water and groundwater interaction

Climate change causes variations in the interaction of surface water and groundwater. Gaining streams (streamflow is recharged by groundwater, Fig. 2A) may turn into losing streams (streamflow infiltrates into the groundwater body, Fig. 2B) caused by changes in groundwater recharge (Green et al., 2011) and hydraulic heads (Jasechko and Perrone, 2021). Hydraulic heads are altered among others by groundwater pumping and may cause quality issues, e.g., groundwater salinization in coastal areas.

Additionally, the process of colmation (clogging) of river channels affects the interaction between surface and groundwater qualitatively. The physical clogging of the heterogeneous interstices affects stream ecology and the biochemical function of interstitial pore water, the hyporheic zone, and groundwater (Nogaro et al., 2010). While still uncertain and in need of further investigation, changing precipitation patterns and increasing temperatures caused by climate change affect the streamflow regime and likely influence this sedimentation (Wharton et al., 2017).

Uncertainties in groundwater recharge under climate change

Groundwater recharge cannot be measured directly, such that observed groundwater recharge rates over large areas or over longer periods are rare (Earman and Dettinger, 2011; Smerdon, 2017; Moeck et al., 2020). Currently and in the recent past, its calculation is based on hydraulic head observations or water-balance calculations (Moeck et al., 2020; Reinecke et al., 2021). However, several sources of uncertainty accumulate in the estimation of groundwater recharge caused by the various water-balance parameters on which groundwater recharge depends, such as evapotranspiration, surface-groundwater connections, or local geology and land use (de Vries and Simmers, 2002; Refsgaard et al., 2016; Reinecke et al., 2021). Thus, groundwater recharge, as part of the hydrologic cycle, is one of the most difficult components to estimate, especially on a global scale (Reinecke et al., 2021).

In addition, significant uncertainties arise in estimating alterations in groundwater recharge in the future due to climate change (Döll et al., 2015; Reinecke et al., 2021). In this process, impact models, such as hydrological models, are combined with climate models. While climate models are rather accurate in projecting temperature increases, they struggle in projecting atmospheric moisture content and thus precipitation (Kent et al., 2015; Fatichi et al., 2016; Fallah et al., 2020). This uncertainty results from complex atmospheric processes and spatial downscaling (Hübner, 2016; Bender et al., 2021). Therefore, both the uncertainty of

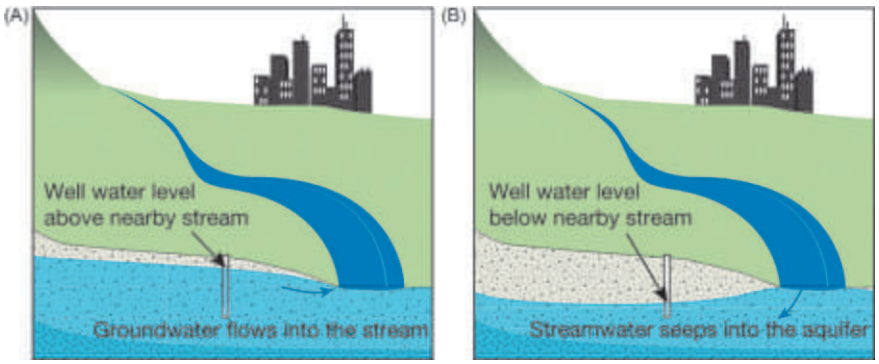

Fig. 2 Cross-section of a gaining (A) and losing stream (B). Gaining streams are prevalent in humid regions of high topographic relief, while losing streams tend to occur in arid climates, flatter topography and in regions of intensive groundwater pumping. Modified from Jasechko, S (2021) Widespread potential loss of streamflow into underlying aquifers across the USA. *Nature* 591.

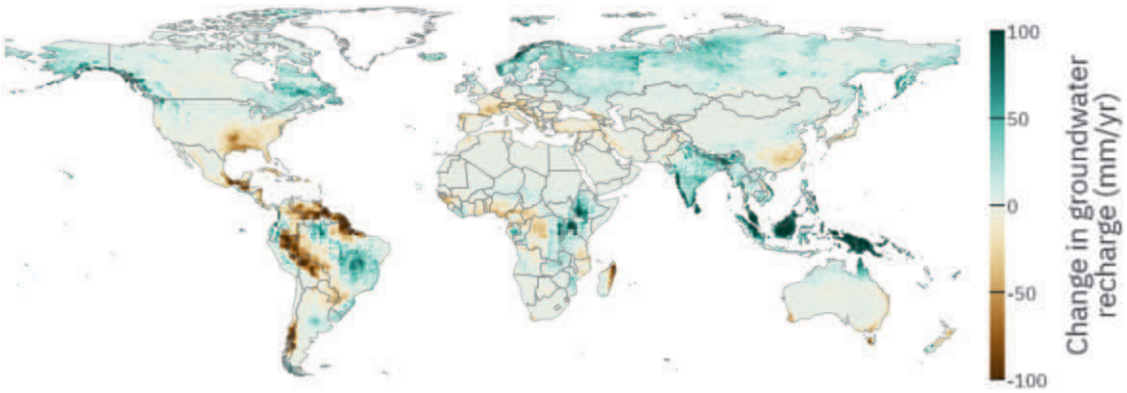

Fig. 3 Mean change in groundwater recharge (in mm/year) between present day warming of the atmosphere of 1 °C and 3 °C (3 °C global warming is projected between 2046 and 2082). Calculation of mean groundwater recharge is based on a multi model ensemble of eight global hydrological models and four global climate models. Reinecke R, Trautmann T, and Müller Schmied H (2021) *How Will Climate Change Impact Groundwater Resources? A Key But Not Yet Fully Resolved Question*. Potsdam Institute for Climate Impact Research. Available online at https://www.isipedia.org/report/how-will-climate-change-impact-groundwater-resources-a-key-but-not-yet-fully-resolved-question/, (Accessed on 13th November 2021).

climate and hydrological models contribute to the overall uncertainty of estimated changes in groundwater recharge (Reinecke et al., 2021). As the annual precipitation and seasonality of temperature have been identified as paramount predictive variables for groundwater recharge rates (Moeck et al., 2020), reliable modeling of future temperature and precipitation changes is crucial to estimate groundwater recharge changes in the future.

As briefly mentioned earlier, another major source of uncertainty in groundwater recharge estimates is the calculation of the effect of increasing CO_2 concentrations and their impact on vegetation transpiration (Milly and Dunne, 2016). Without accounting for active vegetation in global climate models total runoff could be underestimated and groundwater recharge could therefore increase in model output. This might lead to overestimating the decrease in groundwater recharge. As this process is complex and highly uncertain, it is currently neglected in many global hydrological models (Reinecke et al., 2021; Milly and Dunne, 2016).

Groundwater recharge changes due to climate change have been recently simulated between present-day atmospheric warming of 1 °C and 3 °C on a global scale (Reinecke et al., 2021). Despite the aforementioned uncertainties, this simulation showed a statistically significant decrease in groundwater recharge in the central United States, southern Chile, parts of Brazil, and the Mediterranean, and an increase in groundwater recharge in some parts of the Arctic, East Africa, India, and South-East Asia (Fig. 3).

Shaping human-groundwater interactions more sustainably

The challenges from both direct and indirect pressures on groundwater resources require sustainable solutions to prevent critical tipping points in human-groundwater interactions, in particular against the background of global change processes. In the following sub-sections, we briefly explore approaches to manage groundwater resources, take a closer look at groundwater governance and explore potential pathways for adapting current approaches for the future.

Managing groundwater

Being a vital source for potable water supply and food crop irrigation, groundwater is managed through wells, pipes and pumps in most places. Not least because of excessive well drilling, aquifers are affected by salinization and pollution from land and water use above ground (Foster et al., 2013). Aquifer management thus intensely links to land use management—aquifer protection measures include, for instance, land use restrictions (an example are groundwater protection zones in vicinity to groundwater wells for potable water supply). Further practices that interfere with hydrogeological processes such as the discharge of used waters into water bodies are tried to be contained by aquifer protection measures. Monitoring aquifer pollution is an important strategy in managing groundwater quality. Balancing groundwater recharge and abstraction is equally important. One approach to uphold the balance is managed aquifer recharge (MAR) where treated surface water is infiltrated and left to percolate in the ground for eventually contributing to groundwater recharge. Overall, management challenges become more complex where aquifer boundaries transgress administrative ones for which transboundary aquifer management is an important approach (Conti and Gupta, 2014).

However, even where aquifer protection policies exist (e.g., regulating agricultural and other land use), monitoring is often inadequate to detect pollution incidents (Foster et al., 2013). "Safe groundwater exploitation" is commonly misinterpreted, taking the mean recharge rate over 30 years in the past as the reference point, which is untenable under conditions of (global) environmental change (Molle et al., 2018). Groundwater management currently occurs under the framework of Integrated Water Resource Management (IWRM) in hydrologically defined spatial zones (river basins). This management approach potentially collides with the spatial extend of hydrogeological entities. As Foster et al. (2013) argue, "improved integrated groundwater planning" is needed to reduce cross-sectoral and cross-scalar feedbacks that negatively affect groundwater status.

Groundwater governance

Governance refers to "the exercise of authority, by different social actors in a society, through the development and implementation of explicit and implicit substantive and procedural rules to manage resources for the social good" (Gupta and Pahl-Wostl, 2013). Groundwater governance is shaped by multiple rules such as water allocation rights, ownership and rights of use of wells and pumps, land use regulations and pollution rights, that may be written and formalized or not, and that may have been formed "from above" or "from below." As a "common good" that can be found in every country of the world (Conti and Gupta, 2014), groundwater has been used as a case example for studying governance arrangements of natural resources. The work by Elinor Ostrom has been seminal in this regard and is a key reference in subsequent research on sustainable natural resource management (e.g., Ostrom et al., 1994).

Establishing rules in favor of sustainable groundwater management requires knowledge of hydrogeological processes in their interaction with social processes, as well as respective prioritization of managing groundwater sustainably by a multitude of actors involved. However, the field of socio-hydrogeology is only emerging (Re, 2015). Key processes on future developments affecting groundwater are barely understood (Kraemer et al., 2021 and other parts of this chapter). A further barrier to sustainable groundwater governance is the time lag in groundwater deterioration becoming visible and detectable: Because groundwater is hidden underground, changes in quality and quantity become visible only late, for instance when groundwater-dependent ecosystems fall dry or react to pollution. Political attention tends to arise only at this late stage when it may already be too late to take protective measures (Foster and Custodio, 2019). Moreover, concentrations of pollutants in groundwater measured today indicate pollution loads that date back to between 5 and 30 years ago. Accordingly, holding those responsible accountable and implementing the "polluter pays" principle is difficult, as contestations and contradictions between agriculture and water sectors in the implementation of the Nitrates Directive in Europe illustrate (Musacchio et al., 2020).

Against the background of groundwater's "physical vulnerability that has resulted in political invisibility" (Fried et al., 2018), irregular groundwater use and pollution could thrive in most parts of the world. Limited knowledge on relevant biophysical processes, lack of financial and personal resources to monitor groundwater pollution and abstraction, as well as conflicting political interests have been identified as limiting factors in sustainable groundwater governance (Molle et al., 2018). Some countries, such as India for example, even subsidize electricity costs for pumping to encourage greater agricultural productivity at the expense of falling groundwater levels (Shah et al., 2008). In addition, the current governance system in which aquifers fall under diverse jurisdictional entities (608 transboundary aquifers have been listed as of 2014; Conti and Gupta, 2014) implies that multiple legal arrangements govern a single aquifer. This is often linked to contradictory arrangements that spur groundwater over-abstraction. However, when purposefully designed, 'legal pluralism' may also strengthen the protection of groundwater resources, as has been established for the European Union (Conti and Gupta, 2014).

Pathways for the future

While groundwater has long been studied and regulated at local scale, recent publications point to the interlinkages of the resource with other places and scales (Molle et al., 2018; Falkenmark et al., 2019; Luetkemeier et al., 2021). At the same time, the conditions of groundwater bodies are place-specific and locally embedded and therefore difficult to steer at higher levels (Foster et al., 2013). In particular, the definition of "safe yields" for groundwater abstraction has been identified as so complex and riddled with uncertainties that it amounts to a political decision. A series of questions arise in this context, as Molle et al. summarize in the following quote:

> This political question leads directly to an examination of the governance of groundwater development and abstraction. Is the state, as the putative guardian of the public interest, better placed to establish guidelines and policies that offer ways to solve the trade-off? Are the concerned "users," ideally together with the affected constituencies, more likely to be able to address the trade-off? Alternatively, does a form of co-management between the state and citizens have the potential to combine the strengths of the two sides? Is groundwater over-abstraction a local issue or do the spatial (via the hydrologic cycle) or temporal (inter-generational) forms of externality call for its treatment at much larger scales?

(Molle et al., 2018).

Governing groundwater is thus symptomatic of the complexity entailed in sustainable water governance in general that calls for adaptive governance approaches that are flexible in reacting to dynamics and multiple bodies of knowledge on human-water interactions (Pahl-Wostl, 2019). The EU Water Framework Directive and its Daughter Directive on Groundwater are considered a "best practice" example of sustainable groundwater governance, partly because it has been designed in a strong exchange at the science-policy interface. Nevertheless, challenges persist with regard to meeting knowledge needs on complex human-groundwater interactions while also developing and communicating in formats that can be handled by decision-makers (Fried et al., 2018; Foster and Chilton, 2021). Calls for pluralizing groundwater governance research highlight that "there is merit in complementing the current focus on government efforts to better regulate and control extraction, with efforts to document and learn from community initiatives to care for, share or recharge the aquifers they depend on for livelihoods and incomes" (Zwarteveen et al., 2021). Here, adaptive governance approaches are helpful, not least to strengthen the capacity to adapt to change in access to groundwater among those most directly impacted from deterioration and depletion of the resource.

Conclusions

In this chapter, we explored the various pressures humans put on groundwater resources worldwide. We elaborated on sector-specific "direct" impacts in agriculture, the domestic sector and in industrial uses of water. We furthermore looked into the "indirect" effects that stem from climate change, as precipitation patterns and temperature are likely to change. Based on these insights into human-groundwater interactions, we discussed the current state of knowledge with respect to groundwater management and governance and elaborated how respective strategies may contribute to a more sustainable groundwater use.

While departing from a unidirectional notion of anthropogenic stressors on groundwater, the multiple human-groundwater interactions that we have discussed here, and the uncertainties involved in predicting future interactions and trends point to the need for rethinking this clear directionality. As we illustrated at the examples of agriculture, domestic water use and industrial water use, in the Anthropocene, groundwater is thoroughly shaped by dynamic social-ecological interactions. Global trade patterns shape local groundwater (over)use and deteriorations, potentially inflicting with longstanding practices and rules in protecting groundwater in order to enable its use. Climate change impacts alter groundwater ecosystems, the functioning of groundwater-dependent ecosystems and trigger adaptation to new conditions, such as shifting from rain-fed to irrigated agriculture—again reconfiguring groundwater use, directly or indirectly. What is at stake is therefore not so much the protection of groundwater resources from human "pressures." Instead, the politics of establishing a "safe groundwater yield" highlight the need to rethink what the desired condition of groundwater is, who and what has the legitimacy to define this condition, who and what is to be held accountable, and how we understand and govern sustainable human-groundwater interactions in the future.

Against this background, we conclude that for sustainable groundwater use, we need to explicate social-ecological processes—their origins, meanings, purposes and dynamics—to better understand and identify critical trends today and potential traps in the future.

Knowledge gaps

- How can water supply security be ensured under climate change-induced alterations of groundwater recharge and changes in societal water demands?
- How to prevent elevated nitrate concentrations in groundwater bodies against the background of established market-mechanisms (e.g., consumer preferences) in the industrialized agricultural sector?
- How do we incorporate uncertainty attached to data on groundwater availability and demand into decision-making?
- How to account for diverging scales in groundwater management, considering groundwater as a localized resource with complex multi-scalar societal demands?

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https://ourworldindata.org/water-use-stress—Our World in Data on human global water use and stress.
https://www.isipedia.org/—ISIpedia as the open climate-impacts encyclopedia (https://www.isipedia.org/)

From Groundwater to Drinking Water—Microbiology of Karstic Water Resources

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler

Glossary

Biostability The concept of biostability describes the ability to distribute and store water in a distribution system without detrimental quality changes due to microbial growth based on the available substrates (Savio et al., 2018).

Disinfection Inactivation process of microorganisms which causes the loss of their ability to proliferate. Disinfection does not destroy *all* microorganisms but rather reduces the number of disease-causing microorganisms to an acceptable level (Gerba et al., 2003). QMRA can be used to achieve a specified acceptable level of risk.

Epidemiology Epidemiology is the study of the distribution and determinants of health-related states or events in specified populations, and the application of this study to the control of health problems (Last, 2001).

Fecal indicators A group of organisms that indicates the presence of fecal contamination, such as the bacterial groups thermotolerant coliforms or *E. coli*. Hence, they only infer that pathogens may be present (Ashbolt et al., 2001).

Fractured aquifer Often synonymously used for 'karst aquifer' (see below).

Gastrointestinal diseases (GID) Gastrointestinal diseases are those that affect any section of the gastrointestinal tract, from the oesophagus to the rectum, and the accessory digestive organs—liver, gall bladder and pancreas. The term encompasses acute, chronic, recurrent or functional disorders and covers a wide range of diseases, including inflammatory bowel disease and functional dyspepsia (Nature, 2021).

Groundwater vulnerability Groundwater vulnerability is a term used to represent the natural ground characteristics that determine the ease with which groundwater may be contaminated by human activities (European Commission, 2021).

Hydrogeology Hydrogeology is defined as the science of the occurrence, distribution, and movement of water below the Earth's surface (Ravier and Buoncristiani, 2018).

Karst aquifers Karst aquifers form by the chemical dissolution of soluble rock (Goldscheider et al., 2020).

Karst Karst is the term used to describe a special style of landscape containing caves and extensive underground water systems that is developed on especially soluble rocks such as limestone, marble, and gypsum (Ford and Williams, 2013).

Microbial source tracking (MST) Microbial source tracking is an area of research which aims to identify the origins of microbial contamination and so remedial action can be appropriately targeted (Morris et al., 2017).
Microbiome The microbiome is the sum of the microbes and their genomic elements in a particular environment (Ho and Bunyavanich, 2018; Berg et al., 2020).
Perennial spring A spring that continuously discharges water, in contrast to intermittent or periodic springs.
QMRA Quantitative microbial risk assessment (QMRA) is an approach that allows for the quantitative expression of risk in terms of infection, illness or mortality from microbial pathogens (Gerba, 2015).
Standard fecal indicator bacteria (SFIB) Intestinal bacteria used as fecal indicators, for which internationally agreed standard methods are defined (International Standard Organization, ISO).
Water transmissible (intestinal) pathogen Pathogenic microorganisms that are transmitted via water and cause disease (i.e., waterborne disease).

Introduction

Karst aquifers are essential sources for the global supply with drinking water. Most recent estimates state that 15.2% of the global ice-free continental surface area are covered by karstifiable carbonate rock (Goldscheider et al., 2020). In regard to global water supply, latest reports estimated that around 9.2% of the world's population is partly or entirely supplied with freshwater from karst aquifers—accounting for 127 km^3 per year or 13% of the global groundwater withdrawal (Stevanović, 2019b). Only in Europe, six capital cities—namely Podgorica, Rome, Sarajevo, Skopje, Tirana and Vienna—are partly or entirely supplied with drinking water from karst aquifers (Goldscheider et al., 2020). Considering this important role of karst aquifers for global (drinking) water supply, broad knowledge on all factors influencing both quantity and quality of these water resources is needed in order (1) to allow an adequate management of these vulnerable water resources, and (2) to anticipate challenges mankind will likely face in the next decades. When using karst aquifers as drinking water resources, karst water users typically face two potential challenges: (i) temporally variable (i.e., unstable) discharge regimes, and (ii) vulnerability to allochthonous pollution (Fig. 1).

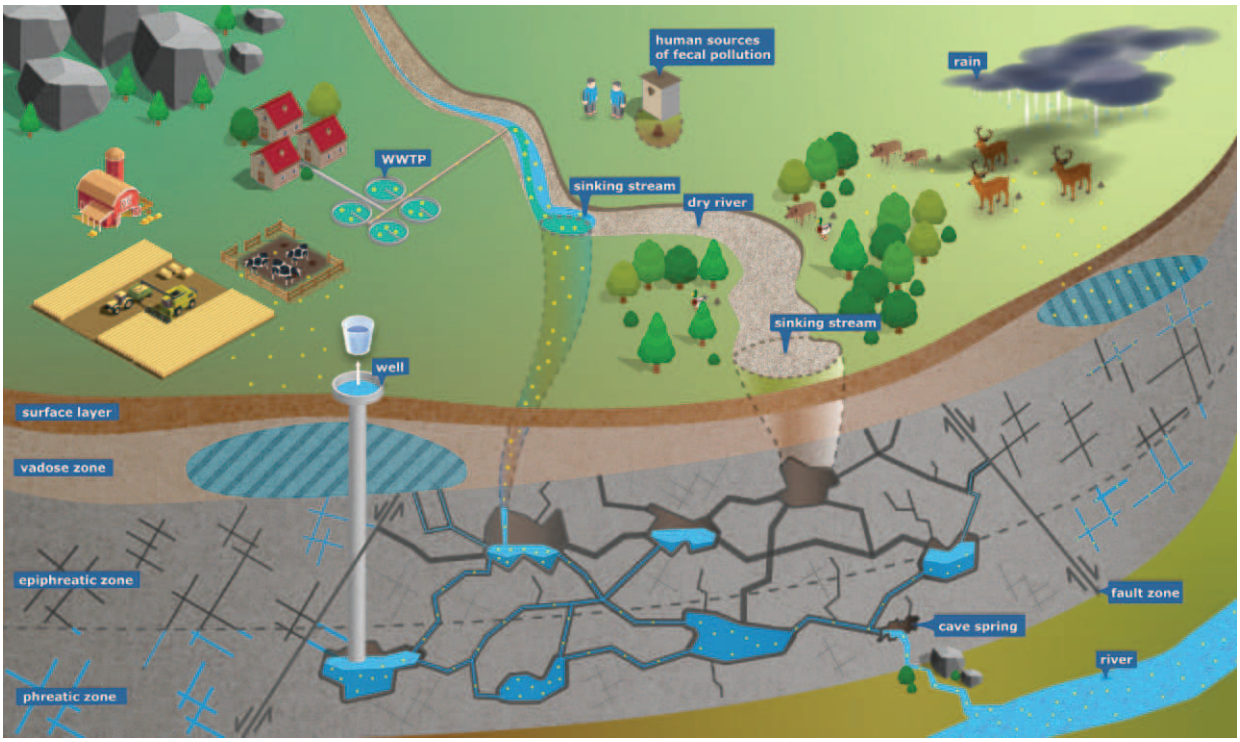

Fig. 1 Schematic illustration of the structure of different karst aquifer types and potential sources and pathways of (fecal) pollution into the groundwater. Aquifers of different geological and weathering status are illustrated: left & right: dense, little weathered karst with small fissures (e.g., dolomite karst); center: highly weathered karst with cave system (e.g., limestone karst); Yellow dots: feces borne pathogens; Potential sources of fecal pollution: wildlife, livestock (cattle), human: open defecation, leaking wastewater infrastructure or its effluent waters, manure application for fertilization.

The hydrogeological setting, the general characteristics of the catchment, as well as the climatic conditions are the most important factors determining the variability in discharge. While the rapid infiltration of (fecally) polluted surface waters in response to (extreme) precipitation events represents a major factor affecting the (microbiological) water quality in the humid regions of the world, water scarcity will likely play an even greater challenge than today in arid regions (Stevanović, 2019a). According to the WHO drinking water guidelines, the greatest risk to public health from microbes in water is associated with the consumption of drinking water that is contaminated with human and animal excreta (World Health Organization, 2017). The majority of outbreaks of waterborne diseases are associated with the inadequate management of water resources and drinking water distribution systems (DWDS), or the insufficient treatment of raw water.

According to data from 2021, worldwide 829,000 people are estimated to die from diarrhea as a result of unsafe drinking-water, lack of sanitation and insufficient hand hygiene every year (World Health Organization, 2019a). The most vulnerable members of our societies—children at the age between 0 and 5 years—suffer from lethal diarrhea in estimated 297,000 cases per year (World Health Organization, 2019a). Only in the year 2010, the United Nations General Assembly declared access to safe drinking water a human right (UN resolution A/RES/64/242). In order to reduce the burden of waterborne disease and deaths, the WHO provides guidelines for drinking-water quality since more than 50 years, and by that a secure basis for national regulations and standards for water safety and public health (World Health Organization, 2017). These include recommendations for contextual hazard identification and risk management through the establishment of health-based targets, catchment-to-consumer water safety plans and independent surveillance.

The aim of this chapter is to give an overview of the current knowledge on the microbiology in karst aquifers, with special focus on factors affecting the health-related microbiology and the sustainable management of karst water resources. Besides a basic introduction on the hydrogeology and catchment settings of karst aquifers, their vulnerability to and common sources and pathways of fecal pollution, and the biogeochemistry of karst aquifers and this also includes an overview of the composition and role of their native microbiomes including their promising potential as biological indicators for the characterization of these aquifers. Main focus of this chapter is on the issue of microbial fecal pollution, the epidemiology of waterborne diseases, and the proper management of karst water resources. In this context, also a recently proposed framework for the comprehensive analysis of microbial pollution with the objective to support the sustainable and high quality management of drinking water resources in accordance with recent World Health Organization guidelines is being introduced. The pollution of karst aquifers with chemical substances is another important issue of global concern, but not in focus of this chapter. Further information on that topic can be found elsewhere (Kalhor et al., 2019; Vesper et al., 2000).

Hydrogeology and catchment characteristics of karst aquifers

The following section provides an overview about the hydrogeology of karst systems based on the reports of Barton et al., 2019, Ford and Williams, 1989, and Taylor and Greene, 2008. For more in-depth information, the reader is referred to the original references.

Basics on hydrogeological characteristics of karst aquifers

A karst aquifer is a hydrological system with a variety of surface and subsurface input, throughput and output flows. Karst aquifers form from the dissolution of soluble rocks such as limestone, dolomite and gypsum by flowing water enriched with carbon dioxide (CO_2) from the atmosphere and produced by biological processes. Karst systems are characterized by underground drainages such as sinkholes, caves (speleogenesis), and conduits (cf. Fig. 1). They typically feature a dendritic or branching network of conduits. The permeability of conduits is interconnected with, but distinctive from the permeability of the bedrock pore matrix and fractures. Due to the complex interplay between the bedrock matrix and the fracture and conduit systems, karst aquifers are characterized by extremely heterogeneous and anisotropic characteristics. Karst *springs* are the natural outlets from the conduit networks (cf. Fig. 1). *Underflow springs* are perennial springs carrying the base-flow discharge of the conduit network. In contrast, so-called *overflow springs* are intermittent, functioning as temporary outlets during high discharge periods. The groundwater is abstracted either directly from springs, or from wells drilled into the aquifer, caves or underground storages (cf. Fig. 1). The spring discharge regime is typically driven by precipitation, snow melt, and may as well be (temporarily) connected to surface water bodies. When precipitation is directly falling on karst terrane, one refers to *autogenic* recharge of a karst aquifer (cf. Fig. 1), if precipitation is falling on non-karstic terrane, one refers to *allogenic* recharge. Moreover, one can distinguish between *concentrated* and *diffuse recharge*. *Concentrated* recharge occurs through the conduits and fractures during heavy rainfall or surface runoff periods. *Diffuse* autogenic recharge is the infiltration through the soil and the unsaturated *aeration zone* (Lehmann and Totsche, 2020), often contributing a considerable part of the recharge of karst aquifers (Taylor and Greene, 2008). *Diffuse allogenic* recharge can be transferred into a karst aquifer from non-karstic aquifers or drains vertically from overlaying layers of non-soluble rocks or sandstone.

Methods to study karst aquifer systems

Besides topography, geological structure and stratigraphy, the following basic information is of relevance for the characterization of karst systems (Taylor and Greene, 2008): (1) the area of the karst catchment, (2) the portion of allogenic recharge, (3) the carrying capacity of the conduit system, (4) the hydraulic conductivity of the matrix and fracture system, (5) the response of the conduit

system over time, (6) the interaction of fractures and conduits and (7) the water budget. Karst springs and cave streams often show highly variable flow rates. For a proper characterization of a karst aquifer, it is therefore important to continuously monitor the spring discharges, surface water inflows as well as climatic variables in the karst catchments. The karst (drainage) catchment (1) is defined by the total area of surface and subsurface drainage contributing to the outlet spring or springs. Its boundaries may vary depending on the groundwater level as well as the geometry of conduits. The most accurate method to identify flow paths (e.g., between sinks or swallow holes and springs) and to delineate karst spring catchments is to conduct tracer tests (Benischke, 2021). The allogenic recharge contribution and conduit carrying capacity (2 & 3) can be evaluated by analyzing the simultaneous measurements of the stream discharges above the recharge locations (e.g., sinkholes/sinking stream as depicted in Fig. 1) and at the spring outlet (e.g. cave spring as depicted in Fig. 1). Conduits and subsurface channels are important groundwater flow paths which can be identified e.g., by geophysical methods applied on the ground surface. They often flow into caves that only in rare cases can be directly accessed—only then allowing direct insights into the channel network. The hydraulic conductivity (4) of the matrix is typically investigated by conventional hydrogeological tools such as laboratory permeability tests of representative soil or rock core samples. The fracture hydraulic conductivity is determined using straddle packer hydraulic tests and borehole flow meters (Sauter, 1991). The integrated matrix and fracture system transmissivity can be measured by time-drawdown, distance-drawdown, or slug tests of the aquifer (Taylor and Greene, 2008). The conventional analytical methods are based on Darcy's law, requiring additional consideration of the presence of turbulence effects (Streltsova, 1988). The response of the conduit system (5) can be investigated by analyzing the time series of spring discharges, such as the ratio between peak and base-flow discharge, by chemical hydrograph separation, or by analyzing the changes in spring discharge and water quality during storm events (hydrological pulse analysis). The partitioning between conduit and non-conduit flow (6) is complex and depends on the hydraulic pressure. The exchanging water volumes can be evaluated by deconvolution of spring discharge time series, comparison of the response of hydrographs during storm events as described by Shevenell (1996), or by analyzing the unit base flow (UBF). Water budgets (7) can be evaluated for different time periods such as a water year, a season, or the duration of a storm event. A conventional water-budget equation reads as follows:

$$I = O + ET + \Delta S,$$

where I is precipitation, O is the discharge at the karst basin outlet, ET is evapotranspiration, and ΔS is the change in groundwater storage (Bassett, 1976). Storm events are often of concern for the spring or well water quality (cf. Section "Fecal pollution in karst water resources and implications for human health" of this chapter). On the event scale, the water budget (i.e., the recharge contribution during a storm event) can be calculated from the change in storage over the time period of an event.

Vulnerability of karst aquifer catchments

Depending on the degree of karstification, karst aquifers are often highly vulnerable to any kind of contaminations from surface-environments (cf. Fig. 1). Contaminants—whether microbiological or chemical—can easily and quickly reach the groundwater and may be transported over large distances via conduits. As stipulated by the Water Framework Directive (Council Directive 2000/60/EC, n.d.), drinking water protection zones in karst systems are delineated based on spring or well intrinsic vulnerability maps. Due to the high heterogeneity and uncertainty that is intrinsic to many karst aquifers, the protection zones often cover the entire catchment of a spring. In the literature, several vulnerability mapping methods have been proposed to assess the vulnerability of karst aquifers (Barton et al., 2019; Marín et al., 2015). Overall, these methods are not universally applicable due to site-specific characteristics of karst terrains. This is especially noticeable on mantled karst areas, where properties of soil cover layers influence the attenuation of contaminants depending on their saturation and hydrological characteristics. Therefore, it is important to account for the site-specific conditions when creating vulnerability maps. *EPIK* is the most widely used method for carbonate media based on multiple criteria to chart the vulnerability (Doerfliger, 1996). The EPIK method accounts for the specific groundwater dynamics of karst aquifers based on the following criteria: (1) development of the epikarst (E), (2) protection efficacy of the surface layer (P), (3) infiltration characteristics (I), and, (4) development of the karst network (K). Newer methods are the so-called *COP* or *COP + K* approaches (Andreo et al., 2009; Vías et al., 2006), the Slovene approach (SLV) (Ravbar and Goldscheider, 2007), and PaPRIKa (Kavouri et al., 2011). COP is based on three main factors: concentration of water flow (C), overlapping layers considering both soil and rock substrate (O), and precipitation (P) (Citrini et al., 2021). The K factor additionally takes into account the development of the karst network. For the protection of groundwater, the attenuation of contaminants is accounted for as a function of soil texture and thickness, lithology, thickness of the unsaturated zone, and the degree of aquifer confinement. The Slovene Approach incorporates and extends several karst-related vulnerability mapping methods and is the only method including risk and hazard maps. PaPRIKa stands for the Protection (P), Infiltration (I), Reservoir (R) and Karstification (K) criteria being used, and is an extension of the EPIK method. PaPRIKa considers both the vulnerability of the resource and the source, by evaluating the transfer speed based on the results of tracer tests. Fig. 2 shows an example for a vulnerability map based on the COP method(Aragão et al., 2019; Tayer and Velásques, 2017). Vulnerability maps of the source are then used for delineating protection zones (Kavouri et al., 2011). The intrinsic vulnerability of karst springs can also be quantified by means of numerical modeling (Butscher and Huggenberger, 2008). Mathematical models can help to better understand the speleogenesis and the flow and transport in karst aquifers, but often involve high uncertainties when delineating well catchment zones or predicting the water quantity and quality of karst springs.

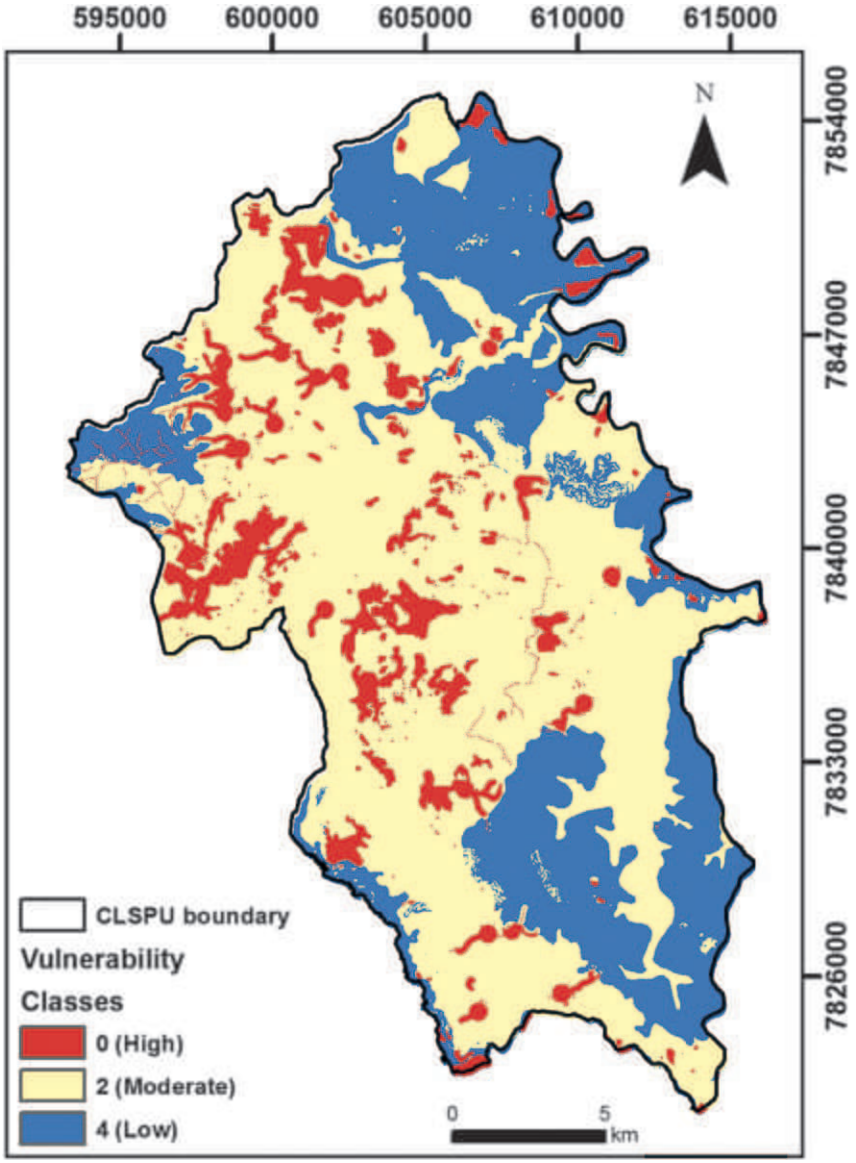

Fig. 2 Example for an intrinsic vulnerability map of the Carste Lagoa Santa karstic region based on the COP method. Adapted from Tayer TDC and Velásques LNM (2017) Assessment of intrinsic vulnerability to the contamination of karst aquifer using the COP method in the Carste Lagoa Santa Environmental Protection Unit, Brazil. *Environmental Earth Sciences* **76**: 445.; Aragão F, Velásquez LNM, Galvão P, De Castro Tayer T, Lucon TN and De Azevedo ÚR (2019) Natural background levels and validation of the assessment of intrinsic vulnerability to the contamination in the Carste Lagoa Santa protection unit, Minas Gerais, Brazil. *Environmental Earth Sciences* **79**: 31.

Microbial ecology and biogeochemistry of karst aquifers

The groundwater habitat and role of the groundwater microbiome

Apart from the potential occurrence of pollution-related, water-transmissible (intestinal) pathogens, karst aquifers also harbor a native microbiome that does not pose a risk to human health. Even the best protected and most pristine groundwaters are far from being sterile (cf. Table 1), and all feature their own characteristic 'signature' in terms of chemistry, physical conditions, and microbiome (Farnleitner et al., 2005). Deep subsurface habitats fascinate microbial ecologists as these habitats harbor the majority of bacterial and archaeal biomass on Earth, with approximately 70 gigatons of carbon (Bar-On et al., 2018). About 60% of all microbial cells of the entire biosphere are estimated to reside in the deep oceanic (4×10^{29} cells) and continental (3×10^{29} cells) subsurface, with an estimated fraction of 20–80% considered to live as single sessile cells or biofilms (Flemming and Wuertz, 2019). About 5×10^{27} cells are globally considered to thrive in groundwaters. While epidemiologically irrelevant to humans, the native subsurface microbiome — comprised of prokaryotes (archaea and bacteria), protozoa, viruses as well as fungi — has positive effects

Table 1 Overview on typically observed prokaryotic cell concentrations (Total Cell Counts; TCC) as reported from different karst aquifers.

Karst system	*Altitude*	*Study site and Situation*	*TCC [$\times 10^3$ cells/mL]*		*Geographic region*	*Method*	*References*
			Mean/Median	*TCC Range*			
Limestone karst	lowland karst	groundwater	–	2.7–380	Hainich National Park (Germany)	EM (SG II)	Opitz et al. (2014) and Herrmann et al. (2019)
	low mountain range	springs (baseflow + rain event)	–	15–650	North western Switzerland	FCM (SG I)	Page et al. (2017)
			57.2–86.8	–	(transition between Folded and Tabular Jura)		Epting et al. (2018)
	alpine	spring	*44.4–63*	25.6–107	Northern calcareous alps (Austria)	EM (AO)	Farnleitner et al. (2005) and Wilhartitz et al. (2009, 2013)
	subsurface cave system (950 m depth)	stagnant rock pools	–	100–520	Bärenschacht cave in Bernese Oberland (Switzerland)	EM (DAPI) & FCM (SG I)	Shabarova and Pernthaler (2010) and Shabarova et al. (2013)
Dolomite karst	alpine	spring	*13.1–14.8*	8–20	Northern calcareous alps (Austria)	EM (AO)	Farnleitner et al. (2005) and Wilhartitz et al. (2009, 2013)
Limestone and Dolomite karst springs	alpine	spring	27	22–34	Northern calcareous alps (Austria)	EM (DAPI)	Wilhartitz et al. (2007)
Karst (not further specified or mixed types)	–	spring (baseflow + rain event)	48.6 (dry season)	$\leq$200 (rain event)	Northeast of Switzerland	FCM (SG I)	Besmer et al. (2017)
	–	(vulnerable) spring	–	140–370	–	FCM (SG I)	Van Nevel et al. (2017)
	subalpine and alpine	spring	–	3–500	Jura Mountains and Alpine Chain (Switzerland)	FCM (SG I)	Sinreich et al. (2014)
	alpine and karst in lower parts	15 springs in 5 eco-regions	23–160	–	Alpine karst (Kamnik-Savinja-Karavanke Alps and Jilian Alps), high Dinaric karst (Trnovo plateau and Ljubljanica karst), low Dinaric karst (Dolenjska karst) (Slovenia)	FCM (SG I)	Opalički-Slabe et al. (2021)

The table is based on a previous publication (Savio et al. 2018) and was updated and extended by more recent studies also including lowland karst systems. For more details, the reader is referred to Derx et al., 2022, in press and the original publications. TCC, Total Cell Counts; EM, Epifluorescence Microscopy; FCM, Flow cytometry; SG, Sybr Green; AO, Acridine Orange.

on the water quality. Anthropogenic contaminations in the form of chemical compounds, nutrients and even water transmissible (intestinal) pathogens, that cannot thrive in groundwater, can serve as carbon and/or energy source for subsurface microbes, finally leading to carbon dioxide and dinitrogen gas. This natural 'self-cleaning' effect is considered of paramount importance to obtain water of high *biostability* and represents only one of many valuable ecosystem services provided by groundwater microbes to humans (Griebler and Avramov, 2015; Van Der Kooij, 1995). Another benefit from the native groundwater microbiome arises from their intrinsic potential to serve as natural biological indicators that can be used to study a variety of questions related to (microbiological) water quality (Derx et al., 2022, in press). For example, Sinreich et al. (2014) proposed a set of microbiological parameters—including the simple parameter of the prokaryotic abundance in the suspended community fraction—in combination with hydrological data for the classification of karst aquifers in respect to the dynamics and the vulnerability of karst springs to (fecal) pollution (Fillinger et al., 2019).

Groundwaters are unique ecosystems, dominated by microbial life, complete darkness that accounts for the absence of light-driven primary productivity, little to no oxygen availability, and nutrient scarcity (Akob and Küsel, 2011; Griebler and Lueders, 2009). Due to the oligotrophic conditions in pristine groundwaters, prokaryotic abundances can be orders of magnitude lower than in aquatic surface habitats like rivers and lakes, and often do not exceed 10^8 cells per liter in groundwater (cf. Table 1). The absence of seasonally varying primary production, low temperature variation, dispersal limitation and limited input of surface-derived, easily available fresh organic matter result in relatively constant living conditions. This lack of periodic or frequent disturbances might explain the sensitivity of the groundwater fauna and microbial communities to anthropogenic impacts. At low levels of disturbances, more competitive organisms will push subordinate species to extinction and, according to the intermediate disturbance theory, dominate the ecosystem (Dial and Roughgarden, 1998). Thus, surface point-source chemical contaminations can have severe and/or long-lasting effects on aquifer community structures and their metabolic activities.

Shallow aquifers are constantly recharged with water from the land's surface. Episodic high-flow events, like those following lasting rainstorms and snow melts, contribute to groundwater flooding (Reiss et al., 2019; Zhou et al., 2012) and the export of suspended organic material from soils into the aquifers (Lehmann et al., 2021). Time-series analyses revealed that also the microbial communities in shallow karstic aquifers vary over time despite the constant living conditions, with groundwater recharge being the driving factor for the observed patterns (Yan et al., 2021). During recharge, not just dissolved and particulate organic matter (DOM and POM), but also soil-borne microbes are translocated via seepage into karstic aquifers (Dibbern et al., 2014; Herrmann et al., 2019; Krüger et al., 2021) (cf. Fig. 1). Specific bacterial taxa can be associated with recharge phases and are responsible for a fraction between 9% and 65% of the groundwater microbiome depending on the surface connectivity (Yan et al., 2020). Surprisingly, the seepage microbial communities do not reflect the soil community, as the susceptibility to seepage-mediated translocation is taxon-specific (Krüger et al., 2021). Especially members of the *Candidatus* Patescibacteria belonging to the candidate phyla radiation (CPR) (Hug et al., 2016) often dominated seepage bacteria with up to 50%, although representing only a tiny fraction of 0.6% in the soil of the studied recharge area (Herrmann et al., 2019).

Challenges affecting groundwater microbiome studies

Today, we know that members of the CPR dominate many groundwaters (Castelle et al., 2018; Luef et al., 2015). These novel lineages have long been overlooked as many pass the widely used 0.2 μm pore-size filters for biomass enrichment due to their small cell size, and their 16S rRNA genes do not amplify well with commonly used universal primers due to mismatches (Schulz et al., 2017). In addition to these ultra-small bacteria, also members of the *Alpha-* and *Gammaproteobacteria* are preferentially mobilized from soil, but with much lower preference than *Cand.* Patescibacteria. This preferential mobilization and transport of specific taxonomic groups must also be kept in mind when focusing on the analysis of microbiological water quality based on fecal indicators whose presence or absence in a particular groundwater sample might not reflect the mobilization and transport behavior of potential fecal-associated pathogens. These considerations highlight just two of the many challenges that groundwater researchers are facing when studying the different aspects of groundwater microbiology. Another very fundamental limitation is that the sessile, biofilm-associated fraction will be missed in most studies if we just focus on the easily accessible water phase (Smith et al., 2018). Nonetheless, this limitation must be accepted as microbial analyses of karstic bedrock need expensive and contamination-free drilling techniques, which contradicts with a high temporal resolution. In contrast to ecological studies focusing on biogeochemical processes and microbial functionality, this limitation is of lesser concern when studying the microbiological water quality which typically focuses mainly on the microorganisms suspended in the water column. In this context, karst springs—as the natural outlet of karst aquifers—are valuable spots for the hydrogeological and microbiological characterization and assessment of the vulnerability of karst aquifers on a larger regional scale (Savio et al., 2018; Sinreich et al., 2014). In contrast, groundwater sampling via well-pumping yield more local information on the groundwater microbial community composition and hydrogeochemical characteristics. As mentioned above, both approaches have in common their limitation to shed light on only the planktonic (free-living) fraction of the groundwater community, and may therefore not adequately represent all members of the microbial subsurface ecosystem that are responsible for biogeochemical cycling and the provision of important ecosystem services.

Groundwater microbiome composition

The hydrogeological settings control subsurface life fundamentally by determining the overall patterns of fluid flow, weathering rates, spatial and temporal distribution of inorganic/organic matter as well as the pH, which is a main driver structuring

subsurface microbial communities and their metabolism (Küsel et al., 2016). A unique feature of karst aquifers is the extreme heterogeneous and anisotropic permeability. Karstic caves, large fractures and fissures alternate with very dense parts of the bedrock matrix (cf. Fig. 1). Thus, both porosity and connected pore space affect not only the water residence time and local geochemical conditions that in turn impact microbial life, but also the vertical and lateral transport of living organisms (Lehmann and Totsche, 2020). Only a fraction of surface derived microbes can thrive or temporarily persist under the oligotrophic conditions in groundwater; the rest will die, with their necromass being recycled, contributing to the DOM pool, or washed out of the aquifer via karst springs.

Microbial communities in karstic aquifers can show high variability even on a local scale. For example, groundwater microbial communities in a multi-storey fractured aquifer system differed substantially even along a 6 km hillslope monitoring transect (Yan et al., 2020). Groundwater collected from surface-near wells is dominated by rare species (here defined as bacterial taxa with a relative abundance of less than 0.01% of the total community), whereas bacteria of the core microbiome (here defined as bacterial taxa present in 80% of the samples collected in the same well over time) increase in downstream direction suggesting increasing environmental selection stress. Local hydrochemical characteristics explain most of the microbial community variation which reflects the importance of local heterogeneity (Yan et al., 2020). The most abundant groups in oligotrophic karstic aquifers are *Cand.* Patescibacteria, *Proteobacteria*, followed by *Nitrospirae*. While *Cand.* Patescibacteria have a fermentative lifestyle (Castelle et al., 2018), many members of the *Proteobacteria* and *Nitrospirae* present in groundwater are shown to be able to assimilate CO_2 with energy derived from reduced sulfur or nitrogen compounds (Wegner et al., 2019). Carbon fixation rates in carbonate aquifers can even reach 10% of the median rates reported in oligotrophic marine surface waters (Overholt et al., 2021).

Similar to shallow karst aquifers, *Cand*. Patescibacteria, *Proteobacteria* and *Nitrospirae* bacteria were also shown to be abundant taxonomic groups in alpine karst systems (Farnleitner et al., 2005; Pronk et al., 2009; Savio et al., 2019). While detailed studies on the assembly mechanisms and origin of the microbes in mountainous karst aquifers are still missing (Savio et al., 2018, 2019), sediments from alpine karst aquifers appear to show a high potential for processes contributing to the self-purification processes in the water. Heterotrophic production rates in the sediments can be significantly higher when compared to the suspended, planktonic fraction (Wilhartitz et al., 2009), and sediment- or surface-associated bacteria might serve as a reservoir contributing cells to the suspended microbial community fraction (Farnleitner et al., 2005; Savio et al., 2018, 2019).

The vast heterogeneity of karst landscapes both on regional and local scale makes it very difficult to propose a universally valid classification system allowing for direct comparisons of karst aquifers. Different systems for mapping the vulnerability of a karst aquifer and its catchment have already been introduced above. As natural spring outlets can generally be viewed as the sum of (suspended) information from an entire aquifer, Stevanović (2015) proposed a classification system of karst springs based on their discharge regime (i.e., 'stable', 'variable' and 'extremely variable'), while Sinreich et al. (2014) proposed a microbiological classification system to characterize karst aquifers in respect to their spring dynamics and vulnerability to fecal pollution. Yet, further studies are urgently needed to gain a deeper understanding on the dynamics and the role of the karstic groundwater microbiomes, which will also enable us to utilize them for water quality indication. In this regard, the recently emerging high-throughput DNA sequencing methods combined with bioinformatics already have, and further will prove as powerful tools to shed light on the highly complex microbiology of karst aquifers.

Fecal pollution in karst water resources and implications for human health

Since more than 100 years, fecal pollution in water is commonly monitored by the detection of so-called 'fecal indicator organisms'. Considering that many commonly applied fecal indicator organisms are bacteria, the term 'standard fecal indicator bacteria' (SFIB) is widely and often synonymously used. This concept aims to detect bacteria (or other microorganisms) that inhabit the digestive system of animals and humans in high abundance. These organisms themselves are not necessarily pathogenic or harmful to human health, but simply *indicate* the presence of fecal pollution influence—and as a logic consequence the eventual presence of fecal-borne *pathogens*—when detected in water. Most widely used indicator organisms today are intestinal bacteria or viruses (often bacteriophages that infect intestinal bacteria). Examples for routinely used bacterial fecal indicators are *Escherichia coli* bacteria or intestinal enterococci (Derx et al., 2022, in press).

Regarding the question of generally observable levels of fecal pollution in freshwater resources, Kavka et al. (2006) proposed a classification system based on SFIB concentration ranges in order to classify surface waters according to their fecal pollution load. In this system, the authors define five classes of fecal pollution, ranging from *little* to *excessive* pollution (cf. Table 2).

Regarding fecal pollution in karst aquifers, a large number of studies has been published that report typically observable SFIB concentrations in karst aquifers with distinct geological and climatic settings (Table 3). While one might intuitively expect rather low (fecal) pollution levels in groundwaters, Table 3 clearly illustrates that karst aquifers globally show an extremely wide range of fecal pollution levels as indicated by SFIB concentrations. These even reach levels usually only detected in highly polluted surface waters, although streams, rivers or lakes in many aspects are not directly comparable with karst aquifers. In regard to their vulnerability to fecal pollution, however, parallels can indeed be drawn. Due to the high porosity of many karst formations, the therewith associated direct connectivity to surface habitats, and in response to precipitation events occasionally low water retention times, fecal material can be rapidly flushed into and through karst aquifers (cf. Fig. 1). The infiltration and retention time of (polluted) surface-water mainly depends on the particular geological settings, the degree of weathering, and most importantly the

Table 2 System for the classification of surface waters in regard to their level of fecal pollution according to Kavka et al. (2006); CFU, colony forming unit.

Classification of fecal pollution						
Pollution class		*I*	*II*	*III*	*IV*	*V*
Fecal pollution level		*Little*	*Moderate*	*Critical*	*Strong*	*Excessive*
Microbiological indicator/parameter [CFU/100 mL]	*E. coli*/fecal coliforms	<100	>100–1000	>1000–10,000	>10,000–100,000	>100,000
	Intestinal enterococci	≤40	>40–400	>400–4000	>4000–40,000	>40,000
	Total coliforms	≤500	>500–10,000	>10,000–100,000	>100,000–1,000,000	>1,000,000

prevailing discharge conditions as a result of precipitation events (cf. Section "Hydrogeology and catchment characteristics of karst aquifers" of this chapter). The lower the water retention time of infiltrated surface water, the higher is the chance for pathogenic microorganisms to reach the groundwater aquifer unharmed and to pose a risk to human health (Allocca et al., 2018; Borchardt et al., 2011; Bucci et al., 2015, 2017; Murphy et al., 2015; Stadler and Skritek, 2003).

Sources and pathways of fecal pollution

In developing countries, the lack or absence of proper sanitation and regionally widespread practice of open defecation still today represents a major source of fecal pollution of groundwaters (GWPP, 2019; UN News, 2019; World Health Organization, 2019b). But also in middle- and high-income countries, fecal pollution originating from human sources represents the main cause in a majority of outbreaks of acute gastrointestinal disease (GID) (Wallender et al., 2014). There, the contaminations typically originate from poorly maintained sewer infrastructure (e.g., septic tanks) or from diffuse or direct discharge of sewage or treated effluent waters from wastewater treatment plants (WWTPs) into rivers (Fig. 1) (Boehm et al., 2018; Holcomb and Stewart, 2020; Kirschner et al., 2009, 2017). When compared to raw sewage, the treated effluent water from WWTPs typically contains significantly lower, but still relatively high loads of fecal associated microbes (Mayer et al., 2016, 2018). In addition to anthropogenic sources—including pollution from livestock farming—also wildlife animals represent a considerable reservoir for human relevant (i.e., zoonotic) pathogenic microorganisms which regularly caused outbreaks of GID in the past and therefore must not be neglected (Wallender et al., 2014).

In conclusion, fecal pollution levels in karst aquifers as indicated by SFIB concentrations can show an extremely wide range, from non-detectable to few colony-forming units (CFU) of *E. coli* per 100 mL in protected or little polluted karst aquifers, to concentrations reaching 10,000 and more *E. coli* CFU per 100 mL in highly dynamic and vulnerable aquifers (cf. Table 3). The main factors determining the extent of fecal pollution are the hydrogeological background of the aquifer, the prevailing or foregoing weather situations and the available sources of fecal pollution in the catchment (cf. Sections "Suggested framework for integrated fecal pollution and health risk analysis" and "Microbial water quality management options for karst water resources" of this chapter and Fig. 1).

Potential infection risks from improperly managed drinking water supplies

The detection of fecal pollution in water based on the enumeration of SFIB is a strong and important indication for the potential presence of fecal-borne pathogens. However, the association between the presence of fecal pollution, the occurrence of infectious pathogens, and an actual risk to human health from the exposure to water depends on many different and case-specific factors (Derx et al., 2022, in press). To gain a general understanding on the specific health-related impact from fecal pollution of karstic drinking water resources, valuable information can be retrieved from epidemiological studies (compare also with site specific QMRA, section "Suggested framework for integrated fecal pollution and health risk analysis"). Although a literature search on available epidemiological studies on acute gastrointestinal disease (GID) outbreaks caused by contaminated karstic drinking water resources revealed only a limited and geographically non-representative number of studies, these clearly highlight the potentially high health risks arising from fecal pollution of these water resources when used for water supply despite improper management, treatment or disinfection.

For the period between 1990 and 2020, we analyzed eight major peer-reviewed epidemiological studies from Europe and North America that reported outbreaks of GID caused by contaminated drinking water from karst aquifers (Table 4).

In these studies, the main GID causing pathogen were human noroviruses, *E. coli* strain O157:H7, *Campylobacter* spp., *Shigella sonnei* and *Salmonella* spp. (Table 4). A leaking septic tank was the only source of pollution in the study on a restaurant-connected outbreak by Borchardt et al. (2011), and one of several suspected sources in a multifactorial outbreak on a highly frequented island in Ohio as reported by O'Reilly et al. (2007). In three of the studies, heavy precipitation or flooding preceding the fecal contamination of the groundwater resources was the suspected trigger of ground and drinking water contamination (Bruce-Grey-Owen Sound Health Unit, 2000; Lawson et al., 1991; O'Reilly et al., 2007). The comprehensive study by Beaudeau et al. (2008) by itself reports four independent GID outbreaks with connection to drinking water abstraction from karst water resources in France in the period between 1998 and 2006. There, the contaminations occurred each two times at the water resource, and two

Table 3 Overview on observed levels of fecal pollution in different karst aquifers and reference environments from around the world as indicated by standard fecal indicator bacteria (SFIB) enumeration.

Continent	*Country*	*Reported concentration range [CFU or MPN*/100 mL]* (median values in italics)				*Study site/aquifer type*	*Study region*	*Studied indicators*	*Suspected (or identified) sources of fecal pollution*	*Study references*
		Total coliforms	*Fecal coliforms*	*E. coli*	*Enterococci (Ent)*					
Europe	Austria	–	–	not detectable	not detectable	deep non-karstic groundwater	North-Eastern Austria	SFIB	–	Steinbacher et al. (2021)
		–	0–128	*177* (event)	*50*	alpine limestone and dolomite karst aquifer springs	Northern European Calcareous Alps	SFIB	wildlife, livestock, human	Farnleitner et al. (2005) and Reischer et al. (2008, 2011)
	Germany	–	–	1–3300*	1–3400*	karst spring *'Gallusquelle'*	Southern Germany	SFIB + genetic bacterial and mitochondrial markers	combined sewer overflow	Heinz et al. (2009) and Stange and Tiehm (2020)
	Ireland	*296* (1–2420) (events)	–	*94* (1–2420) (events)	–	spring in karst grassland catchment	West-central Ireland	TC, SFIB	–	Murphy et al. (2015)
	Italy	–	0–90	0–3000	0–146	karst-fissured aquifers and limestone springs	Apulia, southern & southeastern Italy	TC, SFIB, cultivation based viruses	cattle grazing	Bucci et al. (2015) and De Giglio et al. (2017)
	France	–	< 20,000 (event)	–	< 13,000 (event)	karstic groundwater wells	Lez Basin aquifer, South France	SFIB	primary-treated wastewater irrigation +wastewater treatment plant-impacted surface stream	Mahler et al. (2000)
	Slovakia	*0–7300* (0–100,000)	–	–	–	cave waters in slovak karst	Southern Slovakia	TC	–	Seman et al. (2015)
	Switzerland	*34–134* (14–8,680)	*1* (0–330)	*1–3* (0–648)	*1–2* (0–480)	karst groundwater and springs	Yverdon-les-Bains karst aquifer, Jura Mountains & Alpine Chain, Switzerland	TC, SFIB, cultivation-dependent bacteriophages and genetic bacterial marker	–	Pronk et al. (2009), Sinreich et al. (2014) and Diston et al. (2015)
America	United States	0–12,000	0–200,000	0–31,000	0–≥484	karstic groundwater (springs, wells, caves and cave streams) in different karst settings	Illinois, Wisconsin, Kentucky, Missouri, Ohio, Arkansas, Florida, Tennessee	TC, SFIB, genetic bacterial marker, cultivation-based viruses and phages	Human and animal waste, domestic wastewater, livestock manure, septic systems, land application of septage, land run-off or lake water	Panno et al. (1996), Ryan and Meiman (1996), Peterson et al. (2000), Currens (2002), Neill et al. (2004), Hackley (2007), O'Reilly et al. (2007), Katz and Griffin (2008), Katz et al. (2009), Kelly et al. (2009), Pedersen et al. (2011), Johnson et al. (2011), Reed et al. (2011), Zhang et al. (2014) and Borchardt et al. (2021)

(*Continued*)

Table 3 (Continued)

Continent	*Country*	*Reported concentration range [CFU or MPN*/100 mL]* (median values in italics)				*Study site/aquifer type*	*Study region*	*Studied indicators*	*Suspected (or identified) sources of fecal pollution*	*Study references*
		Total coliforms	*Fecal coliforms*	*E. coli*	*Enterococci (Ent)*					
Asia	Israel	–	≤12,000	–	–	urban karst spring	Gihon Spring, Jerusalem, Israel	SFIB	Extreme pollution event	Amiel et al. (2010)
	Lebanon	0–≥1000	0–534	–	–	coastal limestone karst aquifer	City of Tripoli, Lebanon	TC, *E. coli*	–	El-Fadel et al. (2014)
	Vietnam		100–19,200	–	–	karst springs	Tam Duong karst area in northwestern Vietnam	Thermotolerant coliforms	–	Nguyet and Goldscheider (2006)
River water		–	–	34,500*	>34,600*	Danube River/river water	Europe	SFIB	Wildlife, livestock, human	Kirschner et al. (2009, 2017)
Raw waste water		–	–	∼1.300,000–∼125,000,000	∼200,000–∼800,000	municipal WWTPs in the area of Vienna/untreated sewage	Austria	SFIB genetic bacterial markers	Human or livestock	Mayer et al. (2016)

TC, Total coliforms; Standard Fecal Indicator Bacteria (SFIB): Fecal coliforms, *E. coli*, Enterococci, fecal streptococci, *Clostridium perfringens*; Cultivation-based phages and viruses: coliphage, phage MS2, phage PRD1, enteric viruses (enterovirus, reovirus), Enteroviruses, Noroviruses, Rotavirus, Hepatitis A virus.

Table 4 Overview on the selected epidemiological studies reporting acute gastrointestinal disease (GID) outbreaks as a result of fecal contamination of non-properly managed drinking water supplies from karst aquifers.

Outbreak region	*Outbreak date*	*Reported cases*	*Karst system description*	*(likely) causative OR detected pathogens*	*Site of contamination*	*(likely) contamination source and details*	*Level(s) of treatment*	*Study design*	*References*
Podgorica, Montenegro, Europe	August 2008	1699 reported, 10,000–15,000 estimated	limestone and limno-glacial sediments	detected: Norovirus, Rotavirus, Adenovirus	distribution network	ingress of fecally contaminated water or raw sewage into the drinking water distribution system	chlorination	Case-control	Werber et al. (2009)
Wisconsin, United States	June 2007	229	fractured dolomite	detected: Norovirus	septic system	inflow of sewage into aquifer as a result of a septic tank leak	no treatment; after outbreak: filters + UV irradiation	Case-control	Borchardt et al. (2011)
Upper Austria, Austria, Europe	August 2006	160	limestone	unknown	water resource	introduction of fecal bacteria after heavy rainfalls	no treatment; after outbreak: UV irradiation	Case report	Meusburger et al. (2007)
Miskolc, Hungary, Europe	June 2006	3673	limestone	detected: *Campylobacter* spp., Norovirus, Adenovirus, Cryptosporidium, *Giardia* sp.	water resource	multiple potential sources: illegal communal waste dumps, pit latrines, liquefied manure treatment facilities, treated wastewater	marginal chlorination following increased precipitation	Case study	Dura et al. (2010)
Ohio, United States	August 2004	1450	fractured limestone	detected*: E. coli*, *C. Jejuni*, Norovirus, Salmonella and Giardia species	water resource	application of septage and/or illegal sewage deposition and infiltration into groundwater via a sinkhole	municipal water treatment facility; after outbreak: chlorination + UV irradiation	Case-control	O'Reilly et al. (2007)
Vesoul, France, Europe	September 2003	200	borehole in karst + alluvial aquifer (no geological information)	*Cryptosporidium* sp. + *Campylobacter jejuni*	distribution network	cross-connection with industrial network containing contaminated river water + backflow	filtration + disinfection (chlorine dioxide)	Descriptive + case study	Beaudeau et al. (2008)
Divonne-les-Bains, France, Europe	August 2003	1040	karstic springs + borehole in urban area (no geological information)	*Cryptosporidium parvum* and *hominis*	distribution network	cross-connection with WWTP effluent network + backflow	filtration + disinfection (chlorine)	Descriptive study	Beaudeau et al. (2008)
Gourdon, France, Europe	August 2000	2600	borehole in karst (no geological information)	Rotavirus + *Campylobacter coli*	water resource	polluted river water entering the karstic aquifer + chlorination failure	disinfection (chlorine)	descriptive + retrospective cohort	Beaudeau et al. (2008)
Walkerton, Ontario, Canada	May 2000	1346 reported, >2300 estimated	limestone	*E. coli* O157:H7 + *Campylobacter* spp. (detected in the environment)	water resource	well contamination by surface water after heavy rain and water treatment system failure	water treatment system (not further specified)	case-control	Bruce-Grey-Owen Sound Health Unit (2000)
Se` te, France, Europe	September 1998	>150 children	karstic spring (no geological information)	*Cryptosporidium* sp.	water resource	surface runoff water backflowing into a karstic outlet	disinfection (chlorine dioxide)	descriptive + case study	Beaudeau et al. (2008)
Le Neuville, Switzerland, Europe	August 1998	1607	limestone	detected: *C. jejuni*, *Shigella sonnei*, Norovirus	septic system	pump failure resulting in sewage spill into the groundwater	natural filtration with injection of pure oxygen into the groundwater	retrospective cohort	Maurer and Stürchler (2000)
Arizona, United States	April 1989	110	limestone	detected: Norovirus, *E. coli*, fecal Strepto- and Enterococci	water resource + treatment plant	failure of automatic chlorinator in waste water treatment plant and fully saturated leach fields	chlorination	retrospective cohort	Lawson et al. (1991)

times in the drinking water distribution network (Beaudeau et al., 2008). Another comprehensive study by Wallender et al. (2014) investigated the contributing factors to disease outbreaks that were associated with untreated groundwater (not only karst groundwaters) used for drinking water supply in the United States between 1971 and 2008. These authors report that heavy rainfall or flooding accounted for 21%, rapid pathogen transport through hydrogeologic formations such as karst limestone for 26%, and improper design, maintenance or location of the water source nearby wastewater disposal systems such as septic tanks for 67% of the investigated 248 outbreaks (Wallender et al., 2014). The latter also applied to three of the here presented studies for which the GID outbreaks were associated with mechanical failures at drinking or wastewater treatment plants or in the water distribution network (Lawson et al., 1991; Maurer and Stürchler, 2000; Werber et al., 2009).

Summing up these studies from Europe and North America, there is clear evidence that fecal pollution of karst water resources can have severe impact on public health. Inexistent or ineffective treatment of water may allow pathogenic microorganisms to be transported from the well or spring to the tap, and as a final consequence to cause disease. That contaminated karstic groundwaters may have significant health impacts also in high-income countries highlights the need for an adequate health-risk management including monitoring, protection and treatment (disinfection) of these often highly vulnerable drinking water resources.

From other regions of the world, epidemiological data on acute GID outbreaks resulting from contamination of karstic drinking water resources are limited. This is very unfortunate considering the different societal and behavioral practices in different regions of the world. In particular, in developing, low-income countries, diffuse fecal pollution can be expected to play a much more important role than in Europe or North America. According to estimates by UNICEF from 2015, 13% of the world's population at that time still practiced open defecation, and further 10% had only access to unimproved toilet facilities (Griffiths, 2017, World Health Organization and United Nations Children's Fund (UNICEF), 2017). Numbers from 2004 estimated that globally, 2 billion people did not have access to basic sanitation facilities (Prüss-Üstün et al., 2006).

Water transmissible intestinal pathogens on a global scale

Taking a global perspective, bacterial pathogens such as *Salmonella, Shigella,* pathogenic *E. coli* and *Campylobacter* cause much of the burden of water transmissible diseases (Griffiths, 2017). Further diseases with high impact are infectious hepatitis, norovirus infection, amebiasis, leptospirosis, poliomyelitis, other enteroviruses infections, schistosomiasis, giardiasis, and cryptosporidiosis (Griffiths, 2017; Neil et al., 2018). While deaths from acute, watery diarrhea (such as cholera and rotavirus diarrhea) have declined over the years, increasing attention is paid to the development of antibiotic resistance in many bacterial pathogens that cause dysentery (i.e., bloody diarrhea, often caused by *Shigella*) as well as to emerging pathogens (Griffiths, 2017). Anthroponotic and zoonotic contamination sources have to be considered and are of potential importance (GWPP, 2019; Stalder et al., 2011).

Suggested framework for integrated fecal pollution and health risk analysis

Despite its high relevance for water supply and public health, microbial fecal pollution of fractured groundwater aquifers still today is often considered a "black box" problem. The lack of detailed knowledge on the sources and transport characteristics of fecal pollution hinders a target-oriented and sustainable water quality and safety management. To promote the pro-active and sustainable water quality management of drinking water resources, a new strategy for advanced fecal pollution analysis was recently proposed based on research activities at alpine karst aquifer springs in the Northern Calcareous Alps (NCA) in Austria (Farnleitner et al., 2018). The framework is based on three interacting levels ("3-step approach") that are addressed by the following questions and define the backbone of the concept (cf. Fig. 3): (1) is there a problem with fecal pollution? (2) if yes, what is the pollution source? and (3) what is the actual health risk associated with the fecal source(s) that contribute to the observed pollution? The defined framework can also be viewed as a "bottom-up" approach as one usually starts with the most general analysis (i.e., determination of bulk fecal pollution levels, comprising all potential sources of fecal sources: wildlife, life stock, human, others) and getting more specific towards the top of the approach (cf. Fig. 3). Although suggested for alpine areas, the conceptional approach is also thought to be useful for other types of karstic and fractured groundwater aquifers in order to guide fecal pollution analysis and management. The concept will be briefly outlined in the following steps 1–3.

STEP 1: Detection and monitoring of general microbial fecal pollution

Detection of general microbial fecal pollution can be realized by cultivation-based standardized enumeration methods (Derx et al., same issue, Farnleitner et al., 2010). To achieve robust enumeration, a sound sampling design (e.g., sampling volumes, spatial and temporal resolution) as well as an appropriate selection of fecal indicators (e.g., *E.coli*, intestinal enterococci, *Clostridium perfringens* (spores), somatic coliphages) is essential. In this context, there is an increasing trend towards the combined application of bacterial and viral indicators (bacteriophages) for general fecal pollution. Moreover, to assess the vulnerability of an aquifer to fecal pollution, it is essential to gather knowledge on its hydrological (e.g., discharge dynamics, seasonality) and the pollution dynamics in the catchment (i.e., variability and importance of sources; Reischer et al., 2008, 2011). Time-series analysis during strong thunderstorm events in periods of high levels of fecal pollution in the catchment (e.g., times with maximum numbers of pasturing animals or tourists) can give a good conservative estimate on the overall potential of fecal pollution (Stadler and Skritek, 2003). Information on the aquifer hydrogeology and the microbial ecology of the ground or spring water (e.g., abundance and dynamics of

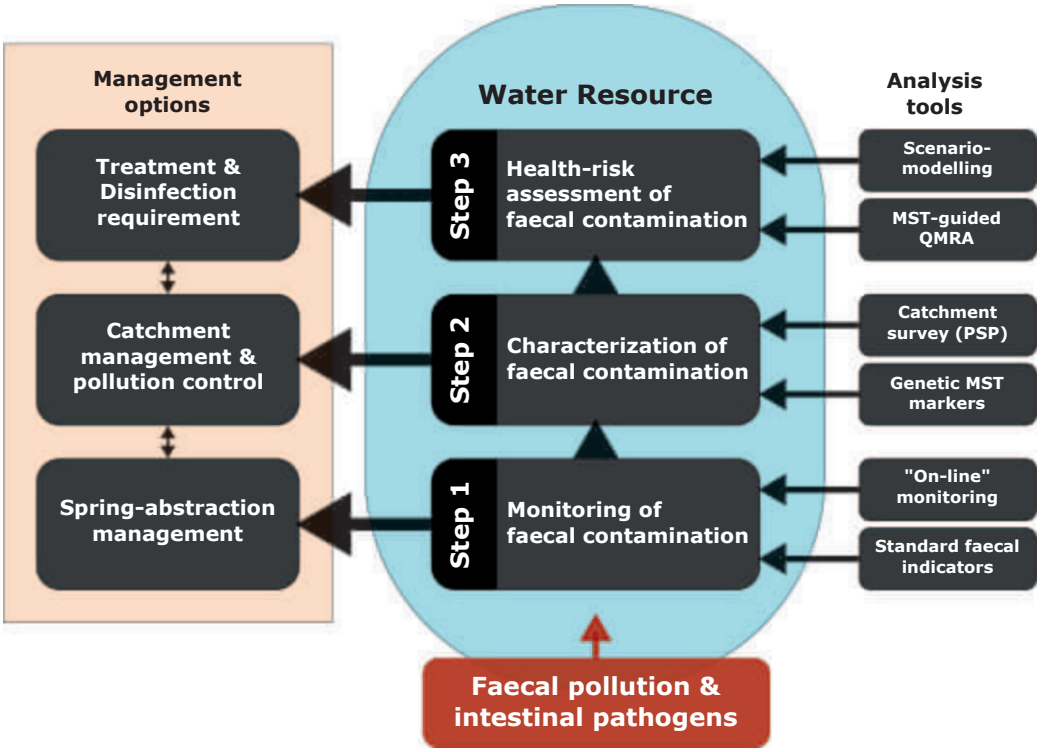

Fig. 3 Overview figure on the proposed "*framework for integrated fecal pollution analysis and management*" to guide sustainable spring water quality management in accordance with World Health Organization criteria as previously suggested by Farnleitner et al. (2018). The three interacting levels ("three-step approach") include (1) the monitoring of fecal pollution levels, (2) the characterization and identification of potential sources of fecal pollution in the catchment, and (3) the assessment of the actual health risk from human exposure to fecal contamination (consumption); MST, microbial source tracking; QMRA, quantitative microbial-risk assessment; PSP, pollution source profiling.

total cell counts, cf. Section "Microbial ecology and biogeochemistry of karst aquifers" and Table 1) are complementing the vulnerability characterization.

For karst water resources with strong fluctuations in fecal pollution levels, it can be very helpful to establish (on-line) automated near-real time measurements to characterize pollution dynamics with sufficient temporal resolution. In this regard, different technical solutions are available. The optimal choice of the respective on-line and/or automatization methodologies thereby depends on the specific question(s) to be answered, and the type and catchment characteristics of the karst aquifer of interest. In general, indications on fecal contamination can be generated either directly or indirectly via proxy parameters. For example, chemo-physical on-line probing to measure discharge, turbidity and spectral absorption coefficient at 254 nm (SAC 254) can be very helpful to generate near-real time information on surface influence and surface water infiltration into the aquifer (Pronk et al., 2007; Stadler et al., 2010). In this context, also on-line flow cytometry was successfully applied by detecting total cell count dynamics (Besmer et al., 2014, 2017). Depending on the aquifer and the specific catchment and pollution characteristics, associations between surface influence and fecal pollution can be observed at least for some periods of time (Stadler and Skritek, 2003). Direct indications on fecal pollution can be obtained either by automatization of standardized approaches for fecal pollution detection (Tryland et al., 2015), or by biochemical/microbiological on-line proxies such as enzymatic glucuronidase activity (Demeter et al., 2020; Ryzinska-Paier et al., 2014). Online and automated fecal pollution detection is a very young discipline, and many activities are currently ongoing to develop reliable and robust solutions for the future (Demeter et al., 2020).

STEP 2: Characterization and source identification of fecal pollution

Cultivation-based enumeration of general fecal indicators such as *E. coli* or somatic coliphages by standardized methods (cf. STEP 1) does not give information on the sources of fecal pollution since these organisms occur in the intestinal tracts of both humans and animals. In contrast, the targeted detection of host-associated or host-specific fecal indicators can give direct information on the sources responsible for fecal pollution, which is the central question of the discipline of *Microbial Source Tracking* (MST). MST indicators can also be combined with information from general fecal indicators to elucidate their origin. First applications of host-associated genetic MST-markers in the NCA catchments could proof that ruminants were the predominant source of fecal pollution in these spring water resources (Reischer et al., 2006, 2008, 2011). Strong statistical associations between general fecal indicators (*E. coli* and intestinal enterococci) and the abundance of ruminant-associated MST markers could be observed especially during periods of increased surface run-off (Reischer et al., 2008, 2011).

Since then, MST technology has also been successfully applied to other karstic water resources. For example, studies available from Midwestern United States and Israel investigated fecal pollution sources in lowland karst aquifers (Ohad et al., 2015; Zhang et al., 2014). The study from Israel reported different MST profiles for three lowland karst springs although these are located in close proximity to each other (Ohad et al., 2015). The study from the US covered a total of 40 springs and wells in four US states (IL, WI, KY and MO) and distinguished between fecal pollution of human, bovine and swine origin (Zhang et al., 2014).

Before applying MST to spring water resources, it is recommended to start with a catchment survey to compile a catchment pollution source profile (PSP, i.e., quantitative estimation of fecal pollution sources). For example, a PSP performed for a certain sub-catchment in der NCA area (Reischer et al., 2011) revealed that wildlife (42.4%) and livestock ruminants (57.6%) together accounted for as much as 99.9% of the total daily *E. coli* cell production in this catchment. Although such a PSP only indicates the daily produced amount of fecal contamination equivalents in the catchment (i.e., the fecal contamination potential) and does not provide information about the quantitative contribution of the respective source to the actual spring water contamination (i.e., the actual transport of fecal sources to the groundwater) a PSP can guide the hypothesis formulation on the relevance of different pollution sources for spring water contamination (Reischer et al., 2011). On that basis, appropriate MST indicators/markers can then be selected and applied to the catchment and spring of interest to evaluate the hypothesis (Linke et al., 2019).

STEP 3: Infection and health risk assessment of microbial fecal pollution

The assessment of the infection or health risk associated with the use of a respective karstic water resource for drinking water abstraction represents the last step of the suggested approach. The drinking water resource can be considered safe or unsafe if the estimated infection risk is below or above the suggested health-based drinking water quality target. Health-based drinking water quality targets (DWQT) are recommended by the World Health Organization (2017) and set to very low levels to ensure a high level of public safety.

The estimation of infection or health risks for individual drinking water resources is suggested by the statistical-mathematical method of quantitative microbial risk assessment (QMRA). On the contrary, epidemiological studies can only be recommended to estimate infection risks (as reported in the previous section) when either the health burden is expected to be considerably high, or the studied populations are very large (World Health Organization, 2017). The principal of QMRA, including the important steps of pathogen exposure assessment and dose-response modelling is described in detail in Derx et al., 2022, in press. QMRA relies on the appropriate choice and quantification of reference pathogens (RP). Commonly used RP include representative pathogens from enteric bacteria, enteric parasites and human enteric viruses. The suggested "bottom-up" approach (Fig. 3) uses information from STEP 2 to guide the selection of appropriate RP for STEP 3 by integrating results from PSP and MST. For example, this approach guided researchers to focus on zoonotic pathogens in the NCA systems where the quantitative occurrence of *Cryptosporidium* sp. and *Giardia* sp. was studied directly in the fecal pollution sources collected in the catchment as well as in the spring water during high-discharge events (Farnleitner et al., 2018). QMRA is currently the least developed part of the suggested 3-step approach for karstic systems (Savio et al., 2018). Practical modelling approaches linking hydrology, microbiology and infection and disease risks—as previously developed for other systems (Demeter et al., 2021; Derx et al., 2021; Schijven et al., 2015)—are increasingly needed. Such simulation tools will not only describe the status quo, but will also allow the evaluation of future scenarios in regard to global change phenomena and challenges.

Microbial water quality management options for karst water resources

Depending on the catchment, the karstic aquifer characteristics, the type of water abstraction system and treatment method, as well as other potentially influencing background conditions, an appropriate and situation-specific set of management measures is required to guarantee a safe and practicable drinking water supply (WHO Regional Office for Europe, 2019; World Health Organization, 2017). Possible management options include spring abstraction management (i.e., spring water abstraction for drinking water production only when raw water quality is appropriate), catchment protection and pollution control (e.g., installation of proper sewage disposal measures), and sufficient treatment and/or disinfection of raw water. In this respect, the suggested framework for microbial fecal pollution analysis and management provides a conceptual basis to select optimal management solutions that are in accordance with the health-based water quality safety criteria at each level of the analysis (Fig. 3) (Farnleitner et al., 2018). The framework also highlights that target-oriented catchment protection and optimized spring water abstraction management helps to minimize the required treatment and disinfection efforts and to keep the final drinking water close to natural conditions for a safe and high-quality drinking water supply. Spring abstraction management can also reduce the input of nutrients and copiotrophic microbes, likely improving the biostability of the water during treatment and distribution. Nevertheless, spring abstraction management requires advanced management efforts, and thus might only be implementable for larger community supplies. However, according to WHO philosophy, highest possible efforts should be put into the protection of the catchment and pollution control, including human and animal fecal contamination sources. In most cases—and especially when direct influence from the surface to the groundwater (such as during rain fall events) is possible—adequate basic disinfection remains an essential requirement to produce safe drinking water and to allow proper infection control for karst spring water. Basic disinfection can be realized by UV-irradiation (Hijnen et al., 2006; Sommer et al., 2008). For a detailed description of water

treatment and disinfection options, the reader is referred to specialized literature (LeChevallier et al., 2004). Finally, it is important to emphasize that the legal requirements in context of the respective national regulations for a safe drinking water supply have to be met. In this context, WHO gives recommendations which are translated into the national legislation by the respective governments.

Conclusion

Karstic drinking water resources can be highly vulnerable to fecal pollution, and in turn pose a direct risk to human health when used for (public) water supply and not properly managed. As shown based on standardized fecal indicator enumeration by a large number of studies, karst aquifers around the world show a wide range of fecal pollution. Available epidemiological studies—mostly conducted in North America and Europa—highlight the high potential of insufficiently protected or treated water from karstic or fractured groundwater aquifers to cause outbreaks of waterborne diseases. The fact that waterborne infections, and gastrointestinal disease in particular, cause a disproportionally higher burden in low- and middle-income countries highlights the existing need for appropriate strategies to provide safe drinking water from these water resources. Several possibilities regarding microbial diagnostics and health risk assessment—including the detection of fecal pollution, pollution source profiling, microbial source tracking (MST), quantitative microbial (infection) risk assessment (QMRA) as well as water quality management methods (e.g., catchment protection, abstraction management, treatment and disinfection)—exist. Depending on the given situation (low vs. high income country, large vs. small supply systems, urban vs. rural impacted catchments, hydrogeology, etc.), the right measures have to be selected in order to guarantee for a safe drinking water supply according to WHO criteria. If fecal contamination cannot be ruled out, adequate basic disinfection constitutes an essential requirement.

Knowledge gaps

- How will expected future changes in climatic conditions and water availability affect microbial water quality of karst water resources both on local and global scale?
- What are the emerging pathogens of potential future concern in karst water resources both on local and global scale?
- What are the epidemiological consequences and societal costs of (diffuse) fecal pollution of karstic drinking water resources worldwide?
- Can high-throughput DNA-sequencing and bioinformatics help us to identify indicator microbes for the future assessment of the vulnerability of karstic groundwater resources?

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https://www.waterpathogens.org/—Global Water Pathogen Project (GWPP).
https://www.who.int/publications/i/item/9789241549950—World Health Organization.
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From Groundwater to Drinking Water – Current Approaches for Microbial Monitoring and Risk Assessment in Porous Aquifers

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Aquifer An aquifer is an underground layer of permeable materials (gravel, sand or silt) or rock that can contain or transmit groundwater.

Dose response model In the QMRA framework, dose response models are mathematical functions that describe the relationship between the risk of infection, illness or death (response) given a known dose of a pathogen for specific pathogens, transmission routes, and hosts (dose) (QMRA Wiki).

Epifluorescence microscopy (EFM) A specialized type of optical microscopy that uses fluorescence and allows to detect fluorescently labeled cells or objects.

Fecal indicator A group of microorganisms that indicates the presence of fecal contamination such as *E. coli*. They indicate that pathogens may be present.

First-order decay A decrease in quantity at a rate proportional to the current value. First-order microbial decay rates depend on the microbial concentration and follow exponential decay (www.wikipedia.org).

Flow cytometry (FCM) A method that allows gathering statistical data on individual cell populations from a heterogenous cell sample by optically analyzing single cells that have been separated prior to analysis.

Fluorescence-activated cell sorting (FACS) A special type of flow cytometry allowing the analysis and physical separation, sorting and isolation of subpopulations of a heterogeneous cell sample. To do so, cells have to be stained with fluorescence dyes prior to analysis and sorting.

Groundwater protection zones Zones around the drinking water abstraction sites in which any type of pollution must be prevented and land use is not permitted. In these zones, groundwater sources are at a certain level of risk from contamination. The closer the contamination source, the greater is the risk (Environment Agency, 2021).

High-throughput DNA-sequencing (HTS) DNA sequencing technologies that are capable of processing massive amounts of DNA sequences in parallel, enabling researchers to decipher full genomes or to resolve the composition of complex microbiomes. HTS methods are often synonymously referred to as "Next-generation sequencing."
Microbiome The microbiome is the sum of microbes and their genomic elements in a particular environment.
Natural isotopes Differing ratios of the oxygen and hydrogen isotopes exist that constitute the water molecule. Isotopes such as deuterium, tritium or $_{18}O$ are hydrogen or oxygen atoms that have a different number of neutrons in their nuclei. The water molecules carry distinct fingerprints based on differing proportions of the hydrogen and oxygen isotopes.
Quantitative Microbial Risk Assessment (QMRA) A tool for estimating human health risks from exposure to pathogens via any route such as food, water, air, and the environment.
Surrogate A particle or solute that serves as a substitute for pathogens for studying pathogen treatment and transport characteristics, experimental tracer tests, analytical and numerical transport models and QMRA.

The WHO approach for safe drinking water in the 21st century

To achieve safety of drinking-water, the World Health Organization (WHO) recommend a risk assessment and risk management approach called water safety plan (WSP) (Davison et al., 2005). This approach includes all steps in a water supply from catchment to tap and includes water resource protection (Fig. 1). To implement such a plan is an interdisciplinary challenge, requiring the expertise from many different fields. The national strategies for protecting drinking water serve as input to the WSP. In many countries, groundwater protection in the vicinity of drinking water wells are based on a water travel time of 50–60 days from the borders of the protection zones. These travel times were historically adopted based on die-off rates of *E.coli* (Knorr, 1937). The parameter *E.coli* is an important representative of the standard fecal indicator bacteria (SFIB) used in water regulations worldwide e.g. (EU, 2020). Many pathogens, especially viral and protozoan representatives, can survive considerably longer than bacteria. However, information about their quantitative occurrence in water resources is very limited. Alternative water quality indicators and methods to estimate the pathogen transport and required treatment have therefore been proposed for a long time (Gyllenberg et al., 1960). The conceptual framework for implementing the WHO guidelines for safe drinking water include health-based targets, the WSP, and a system of independent surveillance that verifies the proper operation (WHO, 2017). The health-based targets can be defined either as maximum tolerable infection risk (maximum number of infections per person and year) or as maximum tolerable illness risks which are often expressed as disability adjusted life years (DALYs). Models and planning tools are needed for quantifying the potential sources and transport pathways of fecal-borne pathogens and the pathogen treatment reduction by soil

Fig. 1 Microbial fate and transport processes in a risk assessment for water supply according to water safety plans (WSP) (Davison et al., 2005).

passage and subsequent disinfection steps. Such tools can be also useful for investigating the impact of future changes such as in climate or wastewater management and thus support the sustainable water safety management (Demeter et al., 2021; Okaali et al., 2021). Climate change, together with population growth, increasing urbanization and increased water demand, is expected to present an additional burden to water supply. Increasing insight into impacts of global change phenomena and required adaptation initiated some shift towards global and climate resilient water safety planning (WHO, 2017).

How do microbial pathogens move through groundwater?

When microbial pathogens enter subsurface environments from land discharges of human and animal fecal matter, how do they move through the underground water systems called aquifers? Pathogens are bio-colloids ranging in size from nanometers to micrometers. Once pathogens enter aquifers, they can be transported with the groundwater through pores in the aquifer media that are larger than them and they disperse towards low concentration areas, they can attach to the surfaces of the aquifer matrix, to the air-water interface, or they can be strained out by pores that are smaller than them. Some immobilized pathogens can remobilize if the water flow or its chemistry changes. Pathogens become inactivated and non-infectious over time.

Depending on the degree of aquifer heterogeneity and the rates of attachment and detachment processes, the average speed of pathogen transport in groundwater can be faster or slower than that of non-reactive solutes which do not adsorb or desorb (Sen, 2011; Ginn et al., 2002). In heterogeneous aquifers, pathogens tend to move through larger pores and cracks where water moves more quickly, because they are excluded from small pores where water moves relatively slowly. Thus, if their attachment rate is slow or their detachment rate is fast, the average speed of pathogen transport in heterogeneous aquifer media with large pores, for example, alluvial gravel, karst and fractured rock aquifers, can be faster than that of non-reactive solutes (Schijven et al., 2017; Sen, 2011; Ginn et al., 2002). Such aquifers are therefore particularly vulnerable to contamination such as from fecal-borne pathogens (Savio et al., 2021). Conversely, the average speed of pathogen transport in groundwater can be slower than that of non-reactive solutes in uniform fine-grained aquifers, such as coastal and river sand, or if the pathogens are very strongly attached to the aquifer matrix.

In summary, the attachment and detachment to and from soil particles, straining, detachment, and inactivation are the most important transport mechanisms of colloids on top of the convection and dispersion (Sen, 2011; Ginn et al., 2002). The degree of pathogen attenuation and transport in groundwater is largely determined by the properties of the aquifer media and pathogens, groundwater chemistry (such as redox conditions, cf. Section "Modelling pathogen transport in surface water and groundwater") and flow conditions. Pathogen transport and survival in groundwater are favored by coarse-grained heterogeneous porous media with preferential flow paths, highly negatively charged and hydrophilic pathogens, high flow velocities, high pH values, low ionic strengths, high dissolved organic carbon levels, low dissolved oxygen levels and low groundwater temperatures (Schijven et al., 2017; Sen, 2011; Ginn et al., 2002). These environmental factors enhance pathogen transport by increasing the quantities of pathogens travelling through and/or by releasing pathogens previously retained by the aquifer media.

Pathogens can associate with other colloids (such as clays, metal oxides and organic matter) in effluent and environmental waters, and, thus, they can hitch rides on other colloids when they travel through aquifers. Colloids play a dual role in pathogen transport. Mobile colloids that travel through large pores and cracks increase the pathogen transport velocity and facilitate the transport of colloid-bound pathogens. Conversely, immobile colloids with pathogens bound to them reduce the quantities of pathogens travelling through the aquifer (Sen, 2011; Ginn et al., 2002). Which of these two processes dominate depends on the number of large pores available for the transport of colloids and colloid-bound pathogens. Understanding how microbial pathogens move through groundwater and the dual role of colloids in transporting pathogens have important implications for risk analysis and remediating contaminated sites.

Observational methods in surface water and groundwater

Hydrological and physical-chemical parameters and monitoring design

The groundwater flow, and its recharge via precipitation or adjacent river water strongly control the microbial transport. It is therefore important to monitor the levels and the geochemical status of the groundwater and river water from a network of observation wells surrounding the area of interest. Loggers recording continuous datasets are immensely valuable in this respect, as the conditions commonly vary along rivers. Standard physical and chemical parameters include e.g. the temperature, pH, electric conductivity (EC), and oxygen content (Stuyfzand et al., 2006). The monitoring design is aligned to the type of drinking water abstraction site. Managed aquifer recharge systems, such as riverbank filtration, are among the most widely used treatment systems for drinking water production (Regnery et al., 2017). In case of riverbank filtration, the flow mechanisms are either driven by pumping or are periodically changing such as when the flow direction reverses during receding flood events (Derx et al., 2010). Suspended particles tend to infiltrate deep into the sediments of the gravelly river bed and riverbank. A clogging layer can drastically reduce the groundwater flow velocity and strongly enhance the removal of pathogens (Blaschke et al., 2003). It is therefore important to monitor the groundwater quantity and quality in wells that are situated within the first meters of soil passage from the river towards the well. Fig. 2 shows an example of such a well setup at the Danube riverbank, where piezometer pipes are installed underneath the river bed and in the riverbank.

Fig. 2 Groundwater piezometers located underneath the Danube river bed and bank in Vienna, Austria, to monitor the groundwater quantity and quality in wells that are situated within the first meters of soil passage from the river towards the well.

Microbiological characterization of surface water

Fecal indicators and genetic fecal markers

The concept of fecal indicators was developed over a hundred years ago and is still successfully applied worldwide and are an obligate part of guidelines and legislation (WHO, 2017; European Union, 2020). Required properties for a suitable fecal indicator are that it is universally present in large numbers in the feces of humans and animals, readily detected by simple methods, not able to proliferate in natural waters and soils as well as having a persistence in water and resistance to water treatment comparable to other waterborne pathogens. However, there is no one single fecal indicator which can serve as a surrogate for all different waterborne pathogens. Depending on the aim of the investigation, a set of indicators has to be selected. The most important fecal indicator organisms (FIO) used as microbiological parameters are described below. Standard detection methods for these indicators are based on cultivation, meaning that the organisms detected are capable of proliferation, which is the prerequisite of pathogens to be infective.

Escherichia coli (*E. coli*) and enterococci bacteria normally live in the intestines of humans and animals. Most *E. coli* are harmless and actually are an important part of a healthy human intestinal tract. However, some *E. coli* strains are pathogenic, meaning they can cause illness, either diarrhea or illness outside of the intestinal tract. *E. coli* and enterococci have proven sensitive and reliable general fecal indicators in alpine mountainous water resources (Farnleitner et al., 2010). *E. coli* is the most prominent member of the coliform bacteria group. In contrast, coliform bacteria cannot be seen as reliable indicator for fecal contamination, as they represent a very heterogeneous group, also including environmental species, which are even capable to proliferate in water (Stevens, 2003).

Clostridium perfringens has been successfully used to detect fecal pollution in the aquatic environment in various geographic areas (Fujioka and Shizumura, 1985). *C. perfringens* is able to form spores that allow prolonged detection of fecal contamination in the environment. In contrast, the fecal indicators *Escherichia coli* and enterococci are considered to be short-lived in aquatic systems and not representative for the behavior of the more resistant pathogens, including viruses and parasites. Monitoring of spores of *C. perfringens* has shown to be useful to assess the water quality during the stages of natural and technical water treatment. The spores can serve as surrogates for protozoan cysts and oocysts of *Giardia lamblia* and *Cryptosporidium* (Ryzinska-Paier et al., 2011; Vierheilig et al., 2013; Payment, 1991).

(Bacterio)phages are viruses that infect prokaryotic cells. Phages are more persistent and resistant than fecal bacteria and can serve as surrogates for human pathogenic viruses (Mesquita and Emelko, 2012). Coliphages (somatic and F-specific coliphages) are fecal viral indicators using *E. coli* as host (Jofre et al., 2016). A European study on surface bathing water quality revealed the high abundance of somatic coliphages and its usefulness as fecal viral indicator (Contreras-Coll et al., 2002). Regulatory authorities are therefore beginning to implement coliphages as parameter of water quality (European Union, 2020).

The enumeration of cultivation-based fecal indicator bacteria described above still represents the gold standard for the investigation of fecal pollution of water sources. However, due to their ubiquity in both human and animal fecal sources, source determination without further analysis is not possible (Farnleitner et al., 2010; Ishii and Sadowsky, 2008; Ahmed et al., 2015). Today, molecular techniques are available which enabled the development of methods for source identification (e.g. discrimination between human and non-human sources), referred to as Microbial Source Tracking (MST) (Hagedorn et al., 2011). Many of these approaches are library-independent DNA-based methods, most commonly targeting the 16S rRNA gene of highly abundant

host-associated intestinal bacteria (Hagedorn et al., 2011). These library-independent methods are opposed to library-dependent methods which require the development of a so-called catchment-specific library, i.e. a dataset of characteristics of the target microorganisms from relevant source hosts (Mott and Smith, 2011).

Detection of MST parameters usually involves enrichment of cells by filtration, followed by DNA extraction and finally detection of the specific DNA target sequences by (quantitative) polymerase chain reaction (PCR). Currently, a plethora of methods targeting fecal contamination of human and animal sources, including traditionally used fecal indicator bacteria, are available (e.g., Reischer et al., 2013; Bernhard and Field, 2000; Boehm et al., 2013; Wuertz et al., 2011; Roslev and Bukh, 2011; Harwood et al., 2017). Besides of methods targeting host-associated intestinal bacteria, also methods targeting viruses as MST tools become increasingly available (e.g., Rusiñol et al., 2014; Rusiñol et al., 2016; Ahmed et al., 2020; Farkas et al., 2020). Finally, also molecular methods targeting mitochondrial DNA of both humans and different animal species are emerging. These methods have the advantage of enabling the assignment of a contamination source with certainty since the mitochondrial DNA sequence is unique to a species (Schill and Mathes, 2008; Malla and Haramoto, 2020). However, there is contradictory information here if meat consumption, either by humans or predators, can cause carryover of mitochondrial DNA from the consumed meat source possibly resulting in false positive signals (Schill and Mathes, 2008; Malla and Haramoto, 2020).

The use of such molecular markers is a good complement to the use of traditional fecal indicators, especially when applied to surface waters and waste- or stormwater impacted areas where genetic marker concentrations are high and sample volumes of 200–500 mL are sufficient for reliable detection and quantification. By the application of such MST methods, for example, the dominance of human fecal impact in the River Danube could be proven (Kirschner et al., 2017). In ground water environments however, much lower concentrations of these genetic fecal markers are observed. Here, tracer tests can aid in estimating the fate and transport (cf. section "Natural and artificial pathogen surrogates to characterize transport in groundwater").

No matter to which water source they are applied to, it is necessary to properly evaluate the methods used. Most of these procedures have been developed and used in temperate latitudes. However, it could be shown that geographical differences in the composition of the gut flora of humans and animal groups exist (Reischer et al., 2013). A direct transfer of such procedures to other regions might therefore not always be straightforward and have to be evaluated (e.g. temperate zones versus tropics) (Reischer et al., 2013; Boehm et al., 2013; Odagiri et al., 2015; Mayer et al., 2018).

Pathogens

Fecal-borne pathogens are pathogens that are introduced into aquatic systems by animal or human point or non-point fecal pollution, e.g. by discharge of human sewage or washing in by rain events (GWPP, 2015), and transmitted by water to the human (or animal) target. Infectious fecal-borne pathogens include bacteria and viruses as well as protozoa and helminths (Leclerc et al., 2002; Ramírez-Castillo et al., 2015; Aw, 2018). Considering the large number of different fecal-borne pathogens known today, it is practically impossible to target all of them to assess the microbiological water quality and estimate risks. Unless there is no specific reason (e.g. epidemic occurring), pathogen detection is therefore focused to so-called reference pathogens. These are representative members of each of the microbial groups mentioned (Ashbolt, 2015; Stalder et al., 2011b). Ideally, a reference pathogen provides a conservative estimate of risk by representing a bad to worst-case combination of high occurrence, high concentration and long survival, low removal and/or inactivation during treatment, and high pathogenicity. Detection methods, preferably standardized cultivation-based or equivalent methods capable of testing for viability and infectiousness, must be further available (Health Canada, 2019). Reference pathogens include norovirus, rotavirus, adenovirus, *Cryptosporidium sp.*, *Giardia lamblia*, *Campylobacter spp.*, *Salmonella enterica spp.*, and *E. coli* O157:H7 (USEPA, 2010; Soller et al., 2010; Stalder et al., 2011a,b). Sound water safety management measures have to be based on carefully and appropriately chosen reference pathogens. The aim is to ensure sufficient protection from fecal-borne pathogen infections and diseases based on conservative assumptions.

In contrast to host-associated intestinal bacteria used for MST applications, fecal pathogen concentrations are often very low in water resources simply due to dilution effects. However, they show higher persistence and resistance to environmental conditions which is why they may be transferred into groundwater systems and might be further distributed (cf. Section "Quantitative microbial risk assessment (QMRA) and required treatment barriers"). For pathogen detection their very low abundance often represents a great challenge. Large sample volumes and complex procedures for target enrichment and concentration might precede detection (Ramírez-Castillo et al., 2015; Bofill-Mas and Rusiñol, 2020). Although culture-dependent detection methods are the gold standard for detection and identification of many bacterial and viral pathogens (Haramoto et al., 2018; Maurya et al., 2020; McKee and Cruz, 2021), molecular methods such as (quantitative) PCR methods are increasingly used. Culture-based methods are often time consuming. However, they provide evidence of the presence of viable/infectious pathogens (Girones et al., 2010). Because pathogens can also exist in the environment in a viable but nonculturable state, culture-dependent methods can lead to an underestimation of risk (Girones et al., 2010; Law et al., 2015). Molecular methods, on the other hand, cannot distinguish between viable and nonviable pathogens, so these methods tend to overestimate potential risk (Girones et al., 2010; Knight et al., 2013; Farkas et al., 2020; McKee and Cruz, 2021). Therefore, a combination of different methods like integrated cell culture and molecular detection can be useful, as for example for the detection of viruses (Farnleitner et al., 2018; Savio et al., 2018). Representative estimates of the reference pathogen concentration in the considered water resource are an essential prerequisite to support QMRA (cf. Section "Modelling pathogen transport in surface water and groundwater").

Microbiological characterization of groundwater

Molecular tools for the characterization and vulnerability assessment of groundwater

As discussed in the above sections, the direct detection of pathogens in groundwater is challenging in many respects. The most important limitations are related to low pathogen concentrations in the environment, insufficient sensitivity and high limits of detection (LOD) of the respective methods – constraining their usefulness for health risk assessments. To overcome these limitations and to address more specific issues related to water quality, efforts were made to discover additional indicators. In this context, the natural water microbiome has been considered a valuable, but hidden treasure since many years.

Even the most pristine ground waters harbor an abundant and often highly diverse microbiome (Karwautz and Griebler, 2021). These microbial communities comprise autochthonous and – depending on the vulnerability and type of the respective aquifer – also allochthonous, transient microorganisms (Savio et al., 2018; Farnleitner et al., 2005; Pronk et al., 2009; Sinreich et al., 2014; Smith et al., 2018). These microorganisms carry an intrinsic potential to serve as natural indicators (or 'biomarkers') for characterizing aquifers or studying the water quality. For example, autochthonous surface water bacteria could serve as alternative tracers for tracking infiltrated surface water through the aquifer (Harvey et al., 2018; Savio et al., 2019). On top of that, bacteria may serve as indicators for the general ecological water quality and stability of the aquifer (Korbel et al., 2017; Fillinger et al., 2019). Recent progress in molecular and optical methods such as High-throughput DNA-sequencing (HTS) or fluorescence-activated cell sorting (Bonner et al., 1972) (from hereon abbreviated as FACS) will fuel the efforts towards discovering novel indicators (Tan et al., 2015; Vartoukian et al., 2010; Kurm et al., 2019; Ben-Amor et al., 2005; Cichocki et al., 2020).

The analyses of the compositional community dynamics are advanced in terms of morphology and physiology. Epifluorescence microscopy (EFM) and automated flow cytometry (FCM) are additionally used to study the dynamics of the bulk microbial community abundance at high temporal resolution (Besmer et al., 2014, 2016). The *total prokaryotic numbers* – also referred to as *total cell counts* (TCC) – for example can reveal valuable information on the stability and vulnerability of a (ground) water resource (Sinreich et al., 2014; Fillinger et al., 2019; Retter et al., 2021). TCC have therefore potential as early warning parameter for water quality deficiencies (Besmer et al., 2014, 2016).

Novel HTS methods have proven extremely valuable by opening the 'black boxes' of the diverse aquatic microbiomes and aiding in identifying novel indicator microorganisms (Newton et al., 2013; Mclellan and Eren, 2014; Tan et al., 2015). In combination with FACS, specific subpopulations can even be physically separated prior to genetic analyses based on morphological or physiological characteristics or taxonomy (Müller and Nebe-von-Caron, 2010). The search for an alternative indicator generally starts by looking for a specific taxonomic group (e.g. genus, species or strain) whose abundance (or physiology) is directly related to temporary changes in hydrological conditions or physico-chemical water quality (Savio et al., 2019). Since the advent of HTS methods, such correlations between the dynamics of specific taxonomic groups and environmental parameters can be identified (Ramette, 2007; Buttigieg and Ramette, 2014; Savio et al., 2019; Tan et al., 2015). The causality of these correlations, however, is in most cases not understood.

Once identified, novel alternative indicator organisms can be detected by a variety of molecular or optical methods, including DNA-based methods such as qPCR and digital PCR (dPCR) or EFM and FCM in combination with fluorescence in situ hybridization (FISH). Different taxonomic groups can inform about different water quality aspects such as potential (fecal) pollution-related health risks, the deterioration of the ecosystem status (e.g. toxigenic algae/cyanobacteria), or the influence of surface water in an aquifer (e.g. prokaryotic or eukaryotic photoautotrophs).

Natural and artificial pathogen surrogates to characterize transport in groundwater

Pathogen removal in groundwater can be investigated either by monitoring indicator organisms which are present in the infiltrating water (as a consequence of fecal pollution, Section "Fecal indicators and genetic fecal markers") or by conducting classical injection tracer tests. Indicator organisms are part of the infiltrating water mass and often occur in moderate concentrations (Table 2). Common surrogates include bacteriophages for viruses (e.g. enteroviruses in the Netherlands), *E. coli* for bacteria such as *Campylobacter*, and anaerobic spores such as *C. perfringens*, which are commonly used as indicators for protozoa such as *Cryptosporidium* and *Giardia* (Section "Fecal indicators and genetic fecal markers"). Thus far, MST markers have rarely been used for groundwater protection studies. This is because, in groundwater environments, these genetic fecal markers occur in low concentrations due to low persistence and resistance of the target organisms to environmental conditions and due to filtering effects of soils (e.g. retention due to sorption on soil particles) (Krauss and Griebler, 2011). MST markers, however, have been used for the characterization of karst springs (Diston et al., 2018; Reischer et al., 2011). Therefore, it could be demonstrated for the first time that ruminants, rather than human sources, were the cause of fecal contamination (Reischer et al., 2008, 2011; Savio et al., 2018).

To study microbial transport in groundwater, tracers can be added on purpose in high concentrations (artificial surrogates or lab strains of fecal indicators, Table 2). The classical tracer test in the field is with a conservative salt or dye tracer that is injected upstream of a well or piezometer where samples are taken. Tracer tests can be performed with a natural gradient (between piezometers) or with a forced gradient created by a pumping well. From the breakthrough curve of tracer concentration over time, one can calculate different parameters analytically or numerically, such as the dispersivity, pore velocity and hydraulic conductivity (cf. Section "How do microbial pathogens move through groundwater?"). A tracer can also be introduced into a surface water body and monitored in groundwater, to determine the extent of surface-groundwater interaction.

Examples of common solute tracers are the dyes uranine (also known as fluorescein) (Buzady et al., 2006) and rhodamine WT (Pang et al., 1998), or chloride and bromide salts (Harvey et al., 1989), as well as naturally occurring isotopes such as deuterium,

tritium or ^{18}O (Mali et al., 2007). A disadvantage of the dye tracers is that transport may be retarded due to sorption, depending on the dye and type of aquifer matrix (Kasnavia et al., 1999). High seasonal variation in the background concentration of chloride may confuse results; conversely, low natural background concentrations of bromide make it a favorable tracer. Synthetic DNA tracers are promising as a way to detect connections between surface water and groundwater (Ptak et al., 2004; Pang et al., 2017). These tracers can be applied as free molecules or encapsulated in microparticles, and therefore acting like colloids, which usually travel faster than a conservative tracer through heterogeneous aquifers (Pang et al., 2020).

Potential pathogen transport in groundwater can be estimated or predicted using tracer tests with pathogen surrogates and numerical modelling (Schijven et al., 1999) (cf. Section "Modelling pathogen transport in surface water and groundwater"). A pathogen surrogate is usually a synthetic colloid or another microorganism that is not dangerous to humans or the environment and comparable in its behavior to pathogens. Aspects that need to be considered when searching for an appropriate surrogate are: inactivation, adsorption to soil material, chemical reactions (geological chemistry), size, surface electrical charge, hydrophobicity, and biological interactions.

Due to their small size, bacteriophages, such as MS2, PRD1 and φX174, are commonly used as surrogates for viruses (Schijven and Hassanizadeh, 2000). Spores, such as *Bacillus subtilis* (Pang et al., 2005) and *Clostridium perfringens* (Hijnen et al., 2005), as well as harmless *Escherichia coli* strains (Sinton et al., 1997), have acted as surrogates for pathogenic bacteria (Table 1). Examples of synthetic colloids are silica or polystyrene nanoparticles or microspheres that have a similar density to a pathogenic microorganism. These surrogate particles can have carboxyl surface functional groups (Bales et al., 1995) or other coatings to mimic the surface charge of the pathogen in question. For example, it has been found that glycoprotein-coated microspheres imitated the transport of the protozoa *Cryptosporidium parvum* better than carboxylated microspheres of the same size (Pang et al., 2012; Stevenson et al., 2015). Likewise, DNA-labeled-protein-coated silica nanoparticles were found to have outperformed MS2 in mimicking rotavirus attenuation in coastal sand (Pang et al., 2014), organosilane coated silica sand (Farkas et al., 2015) and silt loam over gravels dosed with onsite wastewater (Clemens et al., 2020). The transport of pathogen surrogates in the field can be compared to column tests in the laboratory, using the aquifer material taken from drilled boreholes. In this way, it is possible to compare the transport of the surrogate and corresponding pathogenic microorganism in the column (usually 10–100 cm one-dimensional transport) and the surrogate transport observed at the field site (Hijnen et al., 2005; Weaver et al., 2013).

Observational data uncertainty

A critical aspect of interpreting quantitative microbial data is that concentrations of pathogens or other target microorganisms in water are not measured directly; they are estimated from raw data such as analyzed sample volumes (that may reflect only a portion of a collected sample) and microscopic counts, colony counts, arrays of presence-absence data, or numbers of PCR cycles. This estimation can be relatively straightforward for enumeration-based methods, and it may involve more elaborate statistical methods such as most probable number (MPN) estimation or standard curves in detection-based methods and quantitative molecular methods, respectively (Cochran, 1950; Rutledge and Côté, 2003). Microbial concentration values reported by commercial laboratories or in research investigation are often perceived as exact measurements. In fact, they are estimates and therefore reflect some degree of uncertainty that may impact or even mislead interpretation or decision-making.

Quantitative microbial methods inherently feature random variation (i.e., error), as may be evidenced by repeated analyses yielding variable results—even when samples and methods are controlled to be as identical as possible. When evaluating the microorganism concentration in a source, random error adds variability to observed data and conversely adds uncertainty to concentration estimates obtained from raw data. As a result, all microbial concentration estimates are uncertain, though some are more precise than others. Selecting a sample size leading to observation of at least 10 microorganisms where possible is a useful target for reducing this uncertainty (Emelko et al., 2008). Of course, lower counts remain valid but they do yield concentration estimates with greater uncertainty. Ignoring the effect of random error in microbial concentrations presumes that it is trivially small in relation to the spatial or temporal variability among samples (Emelko et al., 2019), which can be quite incorrect in some environmental analyses.

Beyond basic uncertainty, concentration estimates also may be biased if losses in the analytical methodology are ignored or incorrectly quantified. For some types of methods (e.g., plating, MPN) and/or microorganisms, it is common to implicitly presume that there are no losses. For others (e.g., enumeration-based methods for waterborne protozoa), substantial losses are widely recognized (Reynolds et al., 1999; U.S. EPA, 2005). Analytical recovery studies are designed to quantify these losses. Recovery is evaluated by spiking samples with known quantities of microorganisms and may vary among water matrices and labs. Analyses in matrix water must account for background quantities of target microorganisms using split samples or spiked microorganisms that are distinguishable from native microorganisms. Correcting concentration estimates through division by recovered fractions is a common practice, but this may introduce substantial bias when recovery values are small (Schmidt et al., 2013).

In settings with low numbers of target microorganisms, non-detects may be prevalent. It is common practice to regard non-detects as concentrations below some limit of detection, but this practice is fundamentally flawed and is known to lead to biased data analysis (Chik et al., 2018). Instead, the result may be reported as a concentration estimate of zero, recognizing that all concentration estimates—not only non-detects—are uncertain. Availability of raw data is particularly critical to the interpretation of non-detect data. Limits of detection in microbiology may have value in communicating the capacity of a method to detect low concentrations, but they are not thresholds partitioning reliable and unreliable data.

Table 1 Overview of different groups of organisms and exemplary naming of explicit procedures (cultivation - and molecular based techniques) for assessing microbiological water quality.

Organism group	*Target organism/ population*	*Fecal specificity*	*Often used detection and example methods*	*Additional characteristic*	*Example references*[a]
Bacteria	*Escherichia coli*	general	Cultivation, qPCR methods (e.g., EC23S857, *uidA*405, *rodA*984)	Indicates recent pollution event, not persistent in the environment, might occur autochthonous and replicate in the environment under certain conditions	ISO (2001a) and Chern et al. (2011)
	Enterococci	general	Cultivation, qPCR methods (e.g., ENT)	Indicates recent pollution event, ENT more persistent than *E. coli*	ISO (2000b) and Haugland et al. (2005)
	Clostridium perfringens	general	Cultivation, qPCR methods	Produces persistent spores, very conservative indicator	ISO (2013), Chern et al. (2009), and Maheux et al. (2013)
	intestinal *Bacteroidetes*, *Firmicutes*	Human associated	HF183/BacR287, BacHum, Lachno3,	Detects human associated gut bacteria, more persistent compared to *E. coli*, detects DNA and cannot distinguish between living and dead organisms or free environmental DNA	Green et al. (2014), Kildare et al. (2007), and Feng et al. (2018)
	intestinal *Bacteroidetes*, *Firmicutes*	Ruminant/cattle associated	BacR, BacCow, BoBac	Detects ruminant/cattle associated gut bacteria, more persistent compared to *E. coli*, detects DNA and cannot distinguish between living and dead organisms or free environmental DNA	Reischer et al. (2006), Kildare et al. (2007), and Layton et al. (2006)
	intestinal *Bacteroidetes*, *Firmicutes*	Pig associated	Pig2Bac	Detects pig associated gut bacteria, more persistent compared to *E. coli*, detects DNA and cannot distinguish between living and dead organisms or free environmental DNA	Mieszkin et al. (2009)
Viruses	Bacteriophages, somatic, F-RNA, *Bacteroides fragilis*	general,	mainly cultivation based methods, some qPCR assays recently developed (e.g., CPQ056)	More persistent in the environment compared to bacteria, culture methods detect viable particles, qPCR assays detect DNA only and cannot distinguish between living and dead particles or free environmental DNA	ISO (2000a, 2001b), USEPA (2001a, b), European Committee for Standardization (1995), Jebri et al. (2017), and Stachler et al. (2018)
	Virus	specific, human	NoV, HAdV, HPyV,	More persistent in the environment compared to bacteria, culture methods detect viable/infectious particles, qPCR assays detect DNA only and cannot distinguish between infectious and dead particles or free environmental DNA	Rusiñol et al. (2014), Kirs et al. (2016), Ahmed and Harwood (2017), and Farkas et al. (2020)
		Specific, Ruminant/cattle	BAdV, BPyV	More persistent in the environment compared to bacteria, culture methods detect viable/infectious particles, qPCR assays detect DNA only and cannot distinguish between infectious and dead particles or free environmental DNA	Wong and Xagoraraki (2010), Hundesa et al. (2010), Ahmed and Harwood (2017), and Farkas et al. (2020)
		Specific, pig	PAdV	More persistent in the environment compared to bacteria, culture methods detect viable/infectious particles, qPCR assays detect DNA only and cannot distinguish between infectious and dead particles or free environmental DNA	Hundesa et al. (2009), Ahmed and Harwood (2017), and Farkas et al. (2020)
	Enteroviruses	human	Cell culture	Mainly poliovirus and Coxsackievirus B serotypes are detected, they replicate and form plaques in BGM cells, only infectious viruses can be analyzed	CEN (2005)
Protozoa	*Giardia lamblia*	general	Direct laboratory methods mainly, some qPCR assays	Very persistent in the environment, form resistant cysts	ISO (2006) and Guy et al. (2003)
	Cryptosporidium sp.	general	Direct laboratory methods mainly, some qPCR assays	Very persistent in the environment, form resistant cysts	ISO (2006), USEPA (2005), Fayer et al. (2000), and Hassan et al. (2020)

Abbreviations: BAdV: bovine adenovirus, BPyV: bovine polyomavirus, HAdV: human adenovirus, HPyV: human polyomavirus, NoV: norovirus, PAdV: pig adenvirus.

[a]Please note that only a few examples of methods currently used are given here. Furthermore, MST procedures for sources other than humans, cattle, and swine also exist in the literature.

Table 2 Concentration ranges of representative culturable or synthetic microbial indicators naturally occurring in water and artificial pathogen surrogates that can be injected into groundwater during tracer tests.

Fecal pollution indicators available in the environment		*Laboratory strains of indicators or synthetic surrogates*	
Escherichia coli	n.d./100 ml (groundwater) – 10^8/100 ml (raw sewage)	Phages, bacteria and spores (e.g. *Bacillus subtilis*), synthetic particles, synthetic DNA tracers	Total amount per tracer test (number per amount injected): 10^{10}–10^{12}
Clostridium perfringens	n.d./100 ml (groundwater) – 10^5/100 ml (raw sewage)		
Somatic coliphages	n.d./100 ml (groundwater) – 10^7/100 ml (raw sewage)		

Modelling pathogen transport in surface water and groundwater

To encompass the full pathway of pathogens from the fecal sources towards the drinking water well, it requires models for the microbial overland transport, infiltration via the unsaturated zone into groundwater, in-river transport, and transport via river-groundwater exchange (Bradford et al., 2013; Drummond et al., 2018). Microbial transport models in rivers or lakes generally account for mixing, dilution and microbial decay (Derx et al., 2016; Demeter et al., 2021). Flow velocity is described by the Manning formula for open channel flow (Manning, 1891) or by hydrodynamic modelling (Tolouei et al., 2019). To validate such models, data of fecal indicators, host-associated genetic fecal markers or pathogens in the wastewater source and surface water can be used (Derx et al., 2016).

The actual pathogen treatment reduction by attenuation towards the abstraction wells can be estimated using groundwater flow and microbial transport models. As for conservative tracers and solutes, the microbial transport in groundwater is described numerically by the advection – dispersion equation (ADE). Advection refers to the movement of solutes as a function of groundwater flow velocity. Diffusion is the result of the thermal motion of individual molecules or particles. Mechanical or hydrodynamic dispersion results from solutes or microbial particles moving at different rates than the average velocity in groundwater. This causes spreading of the contaminant plume in the porous media. Dispersion is a function of the dispersivity coefficient and groundwater flow velocity. The dispersivity relates to the aquifer grain size distribution and generally increases with the travel distance (Gelhar et al., 1992). Microbial subsurface transport is most commonly coupled with attachment – detachment and first-order decay (Schijven et al., 2002). Attachment and detachment lead to immobilization and remobilization of microbial particles to and from the solid matrix. In order to account for heterogeneity of the geochemical soil properties, two-site attachment – detachment rate models can be used in groundwater (Schijven et al., 2002; Yang et al., 2019). Dual-porosity or dual-permeability approaches can be used to account for the enhanced microbial transport in groundwater via preferential flow paths (Šimůnek et al., 2003).

The attachment of microbial particles can be described by the colloid filtration theory (Yao et al., 1971), as the product of two probabilities: the collector and the collision efficiency. The former is the probability that microbial particles collide with soil particles when approaching the soil particle surface. The latter is the probability that they attach during the collision (Auckenthaler and Huggenberger, 2003). The virus and microbial attachment and detachment rates are influenced by the soil geochemical properties and changes in hydraulic flow conditions, as shown in soil laboratory column experiments (Sadeghi et al., 2011). If applying the removal rates derived from laboratory experiments at the field scale, this can lead to strong underestimations of the risks from groundwater contamination. It was therefore proposed to compare laboratory with field-site experiments (Stevenson et al., 2021). Some of the uncertain parameters shown to affect microbial transport at pore scale may become irrelevant in complex hydrological and porous systems at field scale. For instance, bacterial inactivation, straining, size of the bacterial cells, and the permeability of the clogging layer with bed sediments (influencing the residence times) were found to determine the bacteria transport during riverbank filtration at field scale (Knabe et al., 2021). The hydraulic and microbial transport parameters are commonly obtained from fitting the models to the observed breakthrough concentrations at the observation wells. At a more general level, studies relied on literature values, e.g. for providing recommendation guidelines. Blaschke et al. (2016) used a wide range of reported hydraulic and virus transport parameters to model the virus removal by soil passage in the unsaturated and saturated soil zone. They modelled safe setback distances for drinking water at on-site disposal sites of biologically treated wastewater for different scenarios and types of aquifer media.

Quantitative microbial risk assessment (QMRA) and required treatment barriers

This chapter describes QMRA for drinking water, and specifically, how it is conducted in the Netherlands, because, since 2005, the Dutch drinking water companies are obliged by law to demonstrate that less than 1 per 10,000 persons per year (health based target; WHO (2011)) acquire an infection by consumption of unboiled drinking water (Schijven et al., 2011). To that aim, a guideline

document (Ilent, 2020) and computational tools (Schijven et al., 2010, 2011) have been developed. The drinking water companies – producing drinking water from surface water and vulnerable groundwater sites – conduct QMRA of index pathogens (enterovirus, *Campylobacter*, *Cryptosporidium*, *Giardia*, and occasionally other relevant pathogens) based on the reduction of indicator organisms (bacteriophages for enterovirus, *E. coli* for *Campylobacter* and anaerobic spores for the (oo)cysts of *Cryptosporidium* and *Giardia*) to determine treatment efficiency (Ilent, 2020). The risk of infection is estimated as follows:

$$C_{drw} = C_{raw}/S * Z \tag{1}$$

$$D = C_{drw} * V \tag{2}$$

$$P_{inf} = f(D, drpars) \tag{3}$$

Where C_{drw} is the drinking water concentration, C_{raw} is the raw source water concentration of the index pathogen, S is the sensitivity (or recovery efficiency) of the detection method and Z is the fraction of pathogens able to pass treatment. $Log_{10}Z$ is the log removal by treatment. Commonly Z entails a sequence of treatment steps (multibarrier principle). Indicator organisms (cf. Section "Natural and artificial pathogen surrogates to characterize transport in groundwater") are used as proxy for removal of the corresponding index pathogens. Dose D is the number of pathogens ingested by consuming V ml of unboiled drinking water. P_{inf} is the infection risk for a given D as a function of dose response with parameters *drpars*.

The QMRA is repeated every 4 years. QMRA*spot* is the computational tool that is available to conduct the QMRA, entailing fitting of the data to distributions, computing the risk using Monte Carlo simulations and dose response models including variability and uncertainty (Schijven et al., 2011).

The drinking water companies - producing drinking water from groundwater - have to protect the groundwater source. If adequately protected, additional treatment of the collected water to remove pathogens is not necessary. Basically, Z in Eq. (1) has to be sufficiently small so that the probability of infection will not exceed the health based target. For a sufficiently small Z, the setback distance between a fecal source of contamination and the groundwater production well must be large enough to enable removal of pathogens by attachment to soil particles and/or inactivation and die-off of pathogens. The QMRA for groundwater is mainly identical to the QMRA for surface waters, although limited to virus as index pathogen assuming that if virus removal is sufficient, this applies to other pathogens too (Schijven et al., 2017). Even though this assumption is valid for homogeneous sandy aquifers commonly found in the Netherlands, bacteria and protozoa may be likewise of concern in heterogeneous soil and sediment. As described in the guideline document (Ilent, 2020), the risk analysis for a groundwater production site assumes no problems with wellhead integrity. It also states that vulnerable groundwater aquifers require a QMRA to demonstrate compliance to the legal infection risk of less than 1 in 10,000. To assess vulnerability, groundwater production sites are ranked from high to low in terms of vulnerability, followed by QMRA of the most vulnerable sites. The vulnerability of a site (geohydrologic system) for pathogens is determined by the intrinsic properties that affect survival of an index pathogen on its way from the contamination source to the production well. A site is less vulnerable if confining (clay) layers are present, permeability is lower, the aquifer is thicker and deeper, the well screen is deeper, the sand is finer, there is less heterogeneity and preferential flow paths are absent, anisotropy is higher, the vadose zone is thicker and the groundwater has a higher ionic strength, lower pH, higher temperature, and conditions are anoxic (Ilent, 2020; Schijven and Hassanizadeh, 2000).

Based on QMRA, the size of the protection zone is determined using a standard contamination scenario. A risk assessment is needed if a contamination source is found within the protection zone. A monitoring program of 4 years is required if the determined protection zone is larger than the protected zone. If fecal contamination is detected, the source needs to be found and, if possible, to be removed. The QMRA required to determine the protection zone is based on a standard contamination scenario of 100 enteroviruses per liter leak at $Q_{leak} = 1$ m^3/day from a sewage pipe, and the following conditions of the aquifer: a groundwater temperature of 10 °C–12 °C and under anoxic conditions virus inactivation is 0.01 per day on a $\log_{10}$-scale and attachment of virus is conservative (sticking efficiency 10^{-5}), resulting in a removal rate coefficient $\lambda = 0.030$/day (0.013 $\log_{10}$/day). If (sub)oxic, then virus attachment is 100 times higher and $\lambda = 1.1$/day (0.49 $\log_{10}$/day). The virus source concentration must be reduced by 8.5 $\log_{10}$ for an infection risk of <1 per 10,000 persons per year. Log_{10} reduction by dilution of the source by the pumping at the production well, Q_{well}, and by dilution of the water from a single production well by the water from the complete well field, Q_{total}, are included. Virus removal in the unsaturated zone is set at 0.5 $\log_{10}$ per meter unsaturated zone. Following the standard scenario, a protection zone can be computed using a numerical hydrologic model that includes first-order decay (λ), or using a hydrological model to compute groundwater travel times to determine the size of the zone that provides enough travel time for the required virus removal, or by using computational model QMRA*well*, with an empirical formula specifically developed for this purpose (Schijven et al., 2010). The required travel time T can be computed as follows:

$$T = [8.5 - log_{10}(Q_{well}/Q_{leak}) - log_{10}(Q_{total}/Q_{well}) - log_{10} unsat]/\, log_{10}\lambda \tag{4}$$

The computational model QMRAcatch (Schijven et al., 2015; Demeter et al., 2021; Derx et al., 2021) calculates the microbial concentrations in rivers and the needed pathogen reduction treatment during drinking water production. It allows integrating data of fecal indicators, MST markers and reference pathogens and to evaluate future scenarios to pro-actively determine robust and sustainable water safety management options. Please also refer to the overview documents on QMRA by Teunis and Schijven (2019) and WHO (2016).

Conclusion

A number of analytical and modelling methods exist to estimate suitable and required catchment protection and drinking water treatment measures. The pathogen fate and transport processes in rivers and groundwater towards drinking water wells are subject of ongoing research. A good understanding of these processes is needed to model the fecal microbial flow and transport and predict the concentrations in raw water resources. Based on health-related water quality targets one can determine the status of drinking water safety and for deriving required infection barriers.

Current knowledge gaps

- Interaction between microbial pathogens and diverse environmental surfaces, a multitude of physical, chemical, and microbiological factors, and (emerging) contaminants in aquifers
- Upscaling tracer transport from the column scale to the field scale
- Tracer testing in heterogeneous material with preferential flow paths
- Identification of taxonomic groups from the water microbiome that can be used such as for the assessment of fecal pollution sources, or as indicators for biostability, eutrophication, biofilm-formation, pipe corrosion, and surface water infiltration
- Dose response models for specific genotypes of pathogens such as protozoan cysts and oocysts of *Giardia lamblia* and *Cryptosporidium* spp.
- Standardization of approaches for reporting non-detects and associated data needs to quantify uncertainty in microbial count data
- Extension of quantitative description of uncertainty in microbiological data to next generation sequencing approaches

Further reading

- Schijven et al. (2017) provides an overview of tracers and surrogates for studying the transport of pathogenic microorganisms, describes the major transport processes in terms of governing equations, lists typical removal rates of microorganisms (mainly bacteriophages and fecal indicator bacteria) during soil passage.
- Sen (2011) and Ginn et al. (2002) reviewed the processes of pathogenic biocolloidal contaminant transport in saturated and unsaturated porous media.
- Allaire et al. (2009) reviewed different tracer techniques to quantify preferential flow in soil.
- Chik et al. (2018) reviews approaches and provides guidance regarding approaches for reporting non-detects in microbial count data.
- The Global Water Pathogen Project (GWPP) is a knowledge resource on pathogens supporting sanitation and safe water and promoting quantitative information via monitoring of sewage, fecal sludges and freshwaters to inform public health measures (www.waterpathogens.org).
- The QMRA Wiki (http://qmrawiki.org) is a community portal for current quantitative information and knowledge developed for QMRA. It is an evolving knowledge repository intended to be the go to reference source for the microbial risk assessment community.

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The High Plains Aquifer, USA—A Case Study

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Baseflow The contribution of groundwater to a stream, often expressed as a percentage.
Ephemeral A term indicating that a body of surface water, such as a stream or pond, does not contain water year-round.
Hydraulic conductivity The ability of a rock or sediment to transmit (conduct) water.
Perennial A term indicating that a body of surface water, such as a stream or pond, contains water year-round.
Playa lake A depressional feature that collects rainwater from a small surrounding area, and is inundated for only part of the year.
Recharge Water that travels from the land surface to the saturated zone, replenishing groundwater.
Specific yield The proportion between the volume of water withdrawn and the dewatered volume of the aquifer, often expressed as a percentage.
Spring A location where groundwater naturally discharges to surface water, due to the intersection of the water table and the land surface.

Introduction

The High Plains Aquifer—often referred to as the Ogallala Aquifer—is one of the largest and most heavily developed groundwater resources in the United States (McGuire, 2017; Scanlon et al., 2012; Dennehy et al., 2002). The vast majority (about 97%) of all water withdrawn from the aquifer is used for irrigation, mostly of corn, soy, and cotton (Gurdak et al., 2009; Sahoo et al., 2017). Although it is a vital resource, it is most famous for its declining water levels (Smidt et al., 2016; Gleeson et al., 2012). The High Plains Aquifer is often used as a poster child for unsustainable water withdrawals, but this only applies to some areas of the aquifer. The aquifer is very large—the High Plains comprises roughly 452,000 km^2 of land area (Qi, 2010)—and if the entire volume of water in the High Plains Aquifer were collected into a lake, it would be close to the volume of Lake Huron (Fig. 1; Haacker et al., 2016). Therefore, generalizations about the aquifer usually fail to describe many of the aquifer subregions.

Physical geography

Many people believe that groundwater is found in underground lakes, but an aquifer is more like a gigantic stone sponge. The body of rock that makes up the largest part of the High Plains Aquifer is called the Ogallala Group (Gutentag et al., 1984). The Ogallala Group is a series of geologic formations that were deposited across the Great Plains as sediment eroded from the Rocky Mountains, mostly during the Miocene Epoch, from about 19–5 million years before present (Joeckel et al., 2014). Other formations, such as the Brule Formation and Arikaree Formation in western Nebraska and unconsolidated gravels in central Kansas, have distinct geologic histories and hydrologic properties, but exchange groundwater with the Ogallala Group (Gutentag et al., 1984).

Climate is a major factor determining groundwater resources. The High Plains has a north-to-south gradient in temperature, with colder temperatures in the north, and an east-to-west gradient in precipitation, with drier average conditions in the west. This means that the northeast corner of the aquifer gets the most precipitation relative to the evaporative demand, while the southwest corner receives much less precipitation, and has much greater potential evaporation. This balance between precipitation and evaporation helps to determine how much water can percolate past the root zone and eventually recharge (replenish) the aquifer. The climate

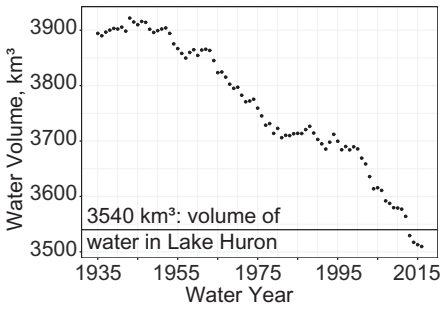

Fig. 1 A graph of water volume in storage over time in the High Plains Aquifer, from predevelopment to 2016. The volume of water in the modern aquifer is close to the volume of water in Lake Huron, one of the US Great Lakes. The methods for this figure are described in Haacker et al. (2016).

also affects the availability of alternative water sources (Crosbie et al., 2013). In the Texas portion of the High Plains, where the climate is hot and dry, groundwater is the only truly reliable source of water for agriculture. On the other hand, in eastern Nebraska, where the climate is cooler and wetter, much of the irrigation water supply can be sourced from surface water. Surface water irrigation and transport of water in unlined canals can induce additional recharge to the aquifer, which in a few locations has caused the water table to rise almost to the land surface (Cherry et al., 2020; Sueltenfuss et al., 2013).

Both the land surface and the base of the High Plains Aquifer have an elevation gradient, tilted from the west to the east (Houston et al., 2013). Major streams tend to run west-to-east, and the natural movement of groundwater tends to parallel stream gradients, even in places where the surface water has a somewhat different direction of flow. This is not a coincidence; springs can encourage erosion (Lapotre and Lamb, 2018). The box valleys in the Southern High Plains are likely features of groundwater erosion. Erosional features also cut through the aquifer materials of the High Plains in several locations, such as the Canadian River Valley in Texas, and the Republican River in Kansas and Nebraska. When rivers erode through the aquifer to expose the rock below, which is unable to transmit water as efficiently, groundwater cannot effectively flow across these barriers from one side of the river to the other. This means that the High Plains Aquifer does not circulate water across its entire extent, and could not, even if regional gradients were more conducive to north-south flow. The idea that it would be possible to contaminate the entire aquifer from a chemical spill in one location, or similarly drain the entire aquifer as a result of pumping in one region, is one of the most common misconceptions about the High Plains Aquifer. At the same time, this lack of flow throughout the region is one of the many factors that make it difficult to generalize science and policy across the aquifer. Hrozencik et al. (2017) showed that even within a relatively small area, a given groundwater management policy will not have the same effect for every farmer that is using water from the High Plains Aquifer (Fig. 2).

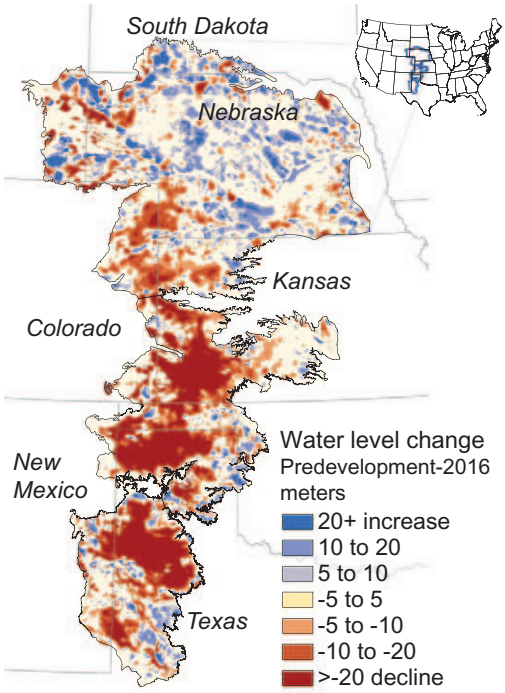

Fig. 2 A map of water level change from predevelopment to 2016, in meters. The top right shows the location of the High Plains Aquifer with respect to the conterminous United States. The methods for this figure are described in Haacker et al. (2016).

Groundwater is the primary source of irrigation water in most of the High Plains. As a result of irrigation withdrawals, saturated thickness (the distance from the top of the saturated zone to the base of the aquifer) has declined by more than 50% in a few places (McGuire, 2017). Overall, the aquifer has lost roughly 360 cubic kilometers of water in storage, representing about 10% of its total water volume (Haacker et al., 2016). However, most of that loss has occurred in places without alternative reliable water resources. The uneven distribution of water in the High Plains Aquifer has meant that close to 20% of the land area of the High Plains overlies a portion of the aquifer that can no longer efficiently sustain pumping for irrigation (Haacker et al., 2016). This is particularly important for irrigation, because declines in the water table can lead to lower well capacities, making it more difficult for farmers to irrigate effectively (Rad et al., 2020).

Hydrogeology

The High Plains Aquifer is primarily an unconfined aquifer. This means that the water table is the top of the saturated zone (Freeze and Cherry, 1979). In other aquifers, and in a few parts of the High Plains Aquifer, there is a confining unit of rock with low permeability that affects both the supply of water to wells and the connection between groundwater and surface water. The water table is the theoretical surface at which the pressure between sediment particles is equal to atmospheric pressure. Pore spaces above this surface might not contain air—only water—but the water is held against the force of gravity, due to capillary action. If a well is drilled into the aquifer, the water level in the well will be equivalent to the water table elevation in an unconfined aquifer.

The characteristics that govern the movement of water in the subsurface include hydraulic conductivity and specific yield, among others. Hydraulic conductivity describes how effectively a geologic material can transmit water (Freeze and Cherry, 1979). Hydraulic conductivity varies widely across the High Plains Aquifer, but values are highest in the Sandhills of central Nebraska, where there is a thick deposit of sand that transmits water very rapidly (Gutentag et al., 1984). Most of the water volume in the High Plains Aquifer is stored in this portion of the aquifer (Haacker et al., 2016).

Specific yield is the amount of water that can be extracted from a unit volume of the aquifer, often expressed as a percentage. If one cubic meter of the High Plains Aquifer is drained, one might expect to derive 0.15 cubic meters of water, meaning that the specific yield is roughly 15% (McGuire et al., 2012). Like hydraulic conductivity, specific yield is difficult to measure, and may change significantly over short distances. The idea that one cubic meter of water withdrawal will only dewater one cubic meter of aquifer material is another common misconception about aquifers.

Natural water quality in the High Plains Aquifer tends to be good (Gutentag et al., 1984). Some parts of the aquifer have high nitrate concentrations resulting from agricultural applications (Juntakut et al., 2019). The water quality of the Northern High Plains, where the depth to water is much shallower, is at greater risk than the areas of the Central and Southern High Plains, where water travels longer distances through thick unsaturated zones to reach the water table (Juntakut et al., 2020).

History of development

Prior to widespread displacement of Native American tribes, springs originating in the High Plains were an important water source (Wood et al., 2002). These springs were fed by groundwater where the water table intersected the land surface.

In the 1800s, ranchers installed windmills that pumped water from the High Plains Aquifer into stock tanks for livestock. As well technology developed and pumping became cheaper, more wells were installed for irrigating vegetables, particularly in the Southern High Plains where flood irrigation from surface water sources was not an option (Green, 1981). Irrigation remained highly labor-intensive for much of the 1900s. Center pivots were invented in Nebraska in the late 1940s and became widespread in the decades that followed (Ashworth, 2006). Satellite images of the High Plains show the now-ubiquitous "crop circles" that distribute groundwater across farm fields; recently, scientists have begun mapping the irrigation on the High Plains using remote sensing and machine learning techniques (Deines et al., 2017). Modern irrigation technology continues to improve, from more efficient pivot attachments such as drop nozzles that deliver water closer to the soil surface, to complex variable-rate irrigation equipment (Barker et al., 2018).

Aquifer management

As water levels in the aquifer decline, calls for management have increased. Much of the groundwater management of the High Plains Aquifer has been relegated to management areas within states. These management areas have widely different goals, styles, and histories. Many of them were implemented for the purpose of protecting irrigators' interests, which did not always include prolonging the life of the aquifer (Green, 1981; White and Kromm, 1995). Nevertheless, most local management areas have now adopted conservation goals, and farmers in the region are increasingly committed to groundwater conservation (Lauer et al., 2018).

Haacker et al. (2019) found that there was a slight positive effect in water within 10 years of establishment of a local groundwater management area in the High Plains Aquifer, but the effects of climate variability and crop prices were much more significant. It is also possible that management districts were systematically established after drought years, and that the positive effects were the result of rebound associated with wetter conditions.

Groundwater-surface water connections

In the Northern High Plains, in the states of Nebraska, South Dakota, and Wyoming, the High Plains Aquifer supplies a substantial proportion of water to surface streams. This baseflow ensures that the streams run all year, and helps maintain beneficial ecosystem features such as relatively cold summer water temperatures. The water table also intersects with the land surface to create wet meadows, particularly between dunes in the Sandhills region of Nebraska (Shrestha et al., 2021).

In contrast, the Central and Southern High Plains Aquifer is less well-connected with surface water. These areas had numerous springs prior to widespread development, but many of these streams have disappeared as the water table elevation declined. Some formerly perennial streams have become ephemeral. Ephemeral streams in the southern Great Plains show an overall increasing trend in zero-flow days, meaning that there are more days that the streams are not flowing (Zipper et al., 2021).

In the Southern High Plains, and to some extent in the Central High Plains, playa lakes are a primary source of groundwater recharge (Scanlon and Goldsmith, 1997). Playa lakes are ephemeral features that are fed by rainwater. The collection of surface water creates a strong enough gradient to push water through the root zone. Water that is absorbed by the soil between playa lakes is generally evaporated or extracted by plant roots before it can reach the deep unsaturated zone. There are also locations in the Southern High Plains where groundwater is discharged to lake basins. However, these basin lakes are saline, as a result of evaporative concentration of salts in the water (Wood and Jones, 1990).

Lifespan of the High Plains Aquifer

Several researchers have forecast the expected lifespan of the High Plains Aquifer, if current rates of pumping continue (Scanlon et al., 2012; Haacker et al., 2016; Steward et al., 2013). The expected lifespan varies across the Southern, Central, and Northern High Plains, with depletion expected in parts of the Southern High Plains within the next few decades (Deines et al., 2020). It is worth noting that as the aquifer declines, it is unlikely that pumping can be sustained at historic rates (Foster et al., 2014). When the water table drops close to the base of the aquifer, then pumping becomes less efficient, in addition to the increased cost of lifting the water from the saturated zone to the land surface (Rad et al., 2020). This may slow the depletion of the aquifer, extending its lifespan. However, this will also limit the usefulness of the aquifer for irrigation, and potentially create tension between economic and environmental sustainability goals (Young et al., 2021).

The High Plains Aquifer is rightfully famous for its unsustainable use, but this is a complex problem that will require tailored solutions in different parts of the High Plains. Lamb et al. (2021) demonstrated that water policy, local hydrology, weather, agricultural practices, and economic factors are all significant in determining irrigation demand in the Kansas High Plains, showing that there is no simple answer to decrease groundwater pumping. Conservation efforts for the High Plains Aquifer tend to focus on areas where the water table has declined substantially. Although this is an intuitive approach, it centers the needs of irrigators, and therefore economic and community goals. Water tables are relatively stable in most of the Northern High Plains (Haacker et al., 2016; Sahoo et al., 2017), but this region is also the last major region of the aquifer that sustains surface habitats through natural groundwater discharge. If the water table in this region were to drop, or if water quality declines substantially, the environmental consequences would be significant. There is no single policy or practice that can ensure future generations of irrigated agriculture on the High Plains, but lawmakers, researchers, and farmers are working toward local solutions in all of the states that share this vital resource.

Knowledge gaps

- How can irrigation and environmental demand be balanced in the short term and long term?
- How will communities be sustained when certain parts of the aquifer can no longer sustain irrigation?
- What is the role of soil health in groundwater conservation for agriculture?

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www.ogallalawater.org—The Ogallala Water Coordinated Agricultural Program.
www.hydroshare.org—CUAHSI HydroShare.

Techniques for Sampling and Monitoring of Groundwater Fauna

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Christian Griebler.

Glossary

Aquifer An *aquifer* is a body of rock or unconsolidated sediment whose porosity allow the storage and transport of groundwater.

Environmental DNA (eDNA) metabarcoding *Environmental DNA (eDNA) metabarcoding* allow to determine the presence of species in an environmental sample, e.g., water or sediment, and is therefore a suitable method for biodiversity research. Since the organisms themselves do not have to be collected directly, as is the case with DNA metabarcoding or morphologically based species identification methods, *eDNA metabarcoding* allows representative sampling of aquifer water. Thus, species that occur in only low individual densities can be recorded. Furthermore, as a molecular tool, it allows for detection of cryptic species in contrast to morphological approaches.

Hyporheic zone The *hyporheic zone* is the transition zone between surface water e.g., streams and a nearby aquifer. This transition zone is characterized by a mixing of surface water and groundwater. As a result, organisms from surface water, stream sediment and groundwater commonly occur in this habitat.

Piezometers *Piezometers* are monitoring wells used for groundwater level measurements and sampling.

Quantitative sampling For ecological studies of groundwater communities, the data must be at least *semi-quantitative*. *Quantitative sampling* also allows calculating individual densities. For this, the sampled water volume must be known. Sampling methods where the sampled water volume can only be approximated, such as net samplers, are therefore referred to as *semi-quantitative*, while pumping aquifer water allows to determine the water volume. *Qualitative sampling*, i.e., recording the presence and absence of species, is often sufficient for biodiversity research.

Representative sample A *representative sample* reflects the community composition and diversity of the sampled habitat. For this, groundwater must be taken directly from the aquifer. This is done, for example, in representative sampling for microbiological or hydrochemical analyzes. Here, groundwater is pumped from the aquifer until key physical-chemical parameters such as the electrical conductivity are stable. In terms of groundwater fauna, eDNA for metabarcoding can be collected in a similar way to study its diversity.

Introduction

Groundwater ecosystems are dimensionally extremely large and therefore, difficult to access which is why most ecological research initially focused on related ecosystems such as springs and caves. Moreover, aquifers are highly heterogeneous in structure and hydrologically complex habitats, where faunal species are patchily distributed and often occur in low numbers of specimen

(Griebler et al., 2010; Hahn, 2006). This, in combination with the difficult access to most groundwater ecosystems, place special demands on sampling strategies and methods, and is one reason why basic ecological information, such as species distribution pattern and population sizes, are largely unknown for many aquifers worldwide. This knowledge is urgently needed for an adequate risk assessment, biomonitoring, and the development of sustainable concepts for the management and protection of these ecosystems (Gibert and Culver, 2009; Boulton et al., 2003b).

Since the onset of groundwater ecology, more than 100 years ago, various methods have been developed for the collection of groundwater fauna. The choice of an appropriate sampling method strongly depends on the objectives of the research. For example, some sampling methods aim to record species diversity as comprehensively as possible, while others allow for a repeated and reproducible sampling, qualitative data comparability and statistical analyzes.

In biodiversity research the goal is to document the overall repertoire of species at a site. The PASCALIS project (Protocols for the Assessment and Conservation of Aquatic Life In the Subsurface) made an important contribution by developing first standardized sampling procedures and methods for biodiversity assessment already 15 years ago (Gibert et al., 2005; Malard et al., 2002). The project focused on recording the European biodiversity in groundwater and related ecosystems, including shallow aquifers, springs, cave waters and the hyporheic zone of rivers and streams (Malard et al., 2002). Key findings, among others, included large scale biogeographic distribution patterns. Moreover, it revealed that groundwater fauna (stygobionts) is characterized by a high proportion of endemic species (Gibert et al., 2005; Dole-Olivier et al., 2009). A manual summarizing standardized sampling procedures and methods for assessing the faunal biodiversity of groundwater ecosystems has been published by Malard et al. (2002). However, modern approaches for the assessment of aquatic fauna biodiversity, such as selected molecular tools, i.e., environmental DNA (eDNA) and metabarcoding, may require different sampling methods than the classical approaches compiled in Malard et al. (2002). In fact, molecular approaches ideally complement traditional efforts in biodiversity research as they allow for the bridging of taxonomic knowledge gaps and the discovery of further cryptic species.

Community ecology studies aim to understand biotic and abiotic dynamics. For example, information is collected on spatial and temporal distribution changes. It is necessary that sampling is reproducible and representative of the corresponding habitat, i.e., the surrounding aquifer, (DVGW, 2018; Guderitz and Hahn, 2012). However, access points to the groundwater ecosystems may differ in kind, e.g., monitoring wells and large farm wells. This raises questions about the representativeness of one sampling method for all. It is also necessary to clarify how many sampling events and at what spatial resolution are needed to capture the heterogeneity of these habitats.

The goal of this chapter is to describe common sampling methods for the collection of groundwater faunal communities suitable for ecological studies, taking into account taxonomic analyzes by comparative-morphology and molecular tools. Their accuracy, efficiency and applicability will be discussed in terms of potential application areas in biodiversity and community ecology research. Groundwater related or dependent ecosystems others than shallow aquifers are not considered here.

Study design for representative sampling

Species occurrence depends largely on the hydrogeology and history of the region, the type of aquifer, and other habitat characteristics such as depth below the water table and sediment properties (Hutchins and Orndorff, 2009; Hancock and Boulton, 2009; Dole-Olivier et al., 2009). In consequence, groundwater faunal biodiversity and distribution patterns are characterized by a high spatial and temporal heterogeneity and variability (Gibert, 2001; Griebler and Mösslacher, 2003; Hahn and Matzke, 2005; Dole-Olivier et al., 2009; Hahn and Gutjahr, 2014). This is a real challenge for representative sampling needed for ecological studies (Hahn, 2006) raising questions about (1) the required number of sampling sites and their spatial distribution, (2) timing and frequency of sampling, (3) the type and condition of available access points, (4) and the dedicated analysis of the sample, e.g., fauna, hydrochemistry, eDNA, among others.

Spatial variability

Assessing species distribution patterns requires sampling at different spatial scales and depths (Hahn and Fuchs, 2009). For choosing appropriate sampling sites, basic hydrogeological information such as groundwater catchment boundaries, flow direction, temporal dynamics of oxygen concentration and temperature dynamics as well as potential surface water intrusion and land use patterns should be considered. Malard et al. (2002) recommend a set of criteria for the selection of regions and sites. For groundwater ecological studies on a small spatial scale, we would propose a minimum number of 5 to 10 sampling sitesto be required (Thulin and Hahn, 2008). Other studies suggest sampling at least six sites at once in order to determine absence or presence of stygofauna and individual species (Hutchins and Orndorff, 2009; Eberhard et al., 2009; Hahn and Gutjahr, 2014).

Temporal variability

Species composition and abundance have also been found to vary seasonally (Hutchins and Orndorff, 2009; Dole-Olivier et al., 2009). An Australian study revealed that new taxa were still being collected in the fourth sampling event (seasonal samples), indicating that there is a need for repeated surveys that account for temporal variability (Hancock and Boulton, 2009). Gutjahr et al. (2013) showed that the success of sampling is the result of both sampling efficiency and stability of the populations

investigated. Another challenge in assessing basic ecological parameters such as community structure and biodiversity is that many stygobionts tend to be rare and patchy distributed. Overall stygobiont densities are often low, making difficulties for the collection of sufficient specimens (Hancock and Boulton, 2009). In addition, particularly rare and endemic species that occur only in small ranges could easily be overlooked. Therefore, to account for temporal variability and to minimize the risk of missing rare species, sampling effort (i.e., number of sites and sampling events) should be increased (Dole-Olivier et al., 2009; Hancock and Boulton, 2009).

At least semi-annual sampling up to quarterly sampling per site is highly recommended in order to uncover spatio-temporal faunal community distribution patterns (Eberhard et al., 2009; Avramov et al., 2022). Well-studied sites that do not show a pronounced seasonal variation in abundance and species composition, as well as in key environmental parameters such as temperature and oxygen content, allowing for an annual sampling routine. In case sampling at a site takes place several times a year, there should be a minimum break of 4 weeks in between to allow the site to recover (Avramov et al., 2022).

In order to assess the entire faunal diversity at a site, published species accumulation curves indicate that at least 10–12 sampling events are needed (Hose and Lategan, 2012), however, these estimations are largely dependent on the spatial and temporal heterogeneity present at a site and the specific research purpose. For example, with the study of groundwater-surface water interaction need an extra high spatio-temporal resolution of faunal sampling (Bork et al., 2009a).

Access to groundwater ecosystems

Direct natural access to groundwater ecosystems is in most cases limited. Thus, taking a sample, i.e., collecting a representative water volume from the aquifer, is challenging. However, good access is often provided via groundwater monitoring wells, large farm wells and piezometers. In addition, research has already early focused on springs, caves and the hyporheic zone (Malard et al., 2002). However, faunal communities found in these habitats may differ significantly in composition from those in the aquifer (Matzke, 2006).

Groundwater monitoring wells are suitable sampling sites that allow direct access and are typically well distributed in most countries worldwide. Thus, existing groundwater networks of water authorities and waterworks are frequently used for ecological studies, especially on a larger scale. However, monitoring wells are designed for a hydrological and physical-chemical monitoring and therefore the chosen sites and their distribution may not be ideal for recording groundwater species composition and distribution patterns (Thulin and Hahn, 2008; Hahn and Fuchs, 2009).

In order to allow an easy entry of groundwater fauna into wells the well-screening should have a filter slot width ≥ 0.5 mm. Furthermore, wells should ideally tap the shallow aquifer (max. depth 40 m), especially in porous aquifers. For fauna to occur, an oxygen concentration ≥ 1 mg/l on the long term was found a basic requirement. Moreover, high amounts of iron hydroxide precipitation (ocher) and/or a high proportion of very fine sediments (e.g., silt), impair the colonization by groundwater invertebrates (Avramov et al., 2022).

Standing water sampled in monitoring wells or large farm wells is not always considered a representative sample of the adjacent aquifer (Korbel et al., 2017). However, a qualified comparison of different sampling sites to each other is still possible if the same sampling methods are used. Groundwater is routinely sampled from monitoring wells via pumping, having replaced the well water volume three times and when electrical conductivity, temperature and pH in the withdrawn water is stable. However, the representativeness of a faunal sample taken from the pumped aquifer depends strongly on the type of the pump and type of aquifer and hence selective filter effects of the surrounding rocks or unconsolidated sediments.

Many Groundwater species accumulate at the bottom of monitoring wells or large farm wells feeding on detritus and sediment (Hakenkamp and Palmer, 1992; Hahn and Matzke, 2005). As a result, samples collected from the well bottom show elevated densities (Bork et al., 2008). Whether the faunal community found in monitoring wells is representative for the community of the adjacent aquifer is still poorly investigated. Wells represent microhabitats that are selective to the species that congregate there, depending on feeding and habitat preferences or pipe design (Eberhard et al., 2009). However, individual studies found that (besides of varying densities), species composition from the well was representative for the adjacent aquifer (Hahn and Gutjahr, 2014; Hahn and Matzke, 2005; Matzke and Hahn, 2002) if the surrounding sediment shows a high hydraulic conductivity (Bork et al., 2008).

Another study by Korbel et al. (2017) found similar results for wells. Total abundance of invertebrates per liter was higher in wells than in surrounding aquifer water. The same taxa occurred in both standing water of the well and aquifer water, except that amphipods were not found in the aquifer samples. Thus, the proportion of individuals per taxa differed between well and aquifer water. Korbel et al. (2017) suggest selection of the sampling techniques depending on the research question. With ecological studies that investigate the species community dynamics (abundances, proportions of species), Korbel et al. (2017) recommends sampling water from the aquifer. Several sampling events may be necessary over a longer period of time in order to capture all species present.

Sampling requirements for different species identification methods

Species can be identified morphologically or by using molecular tools, i.e., metabarcoding and eDNA metabarcoding. The main difference between these three methods lies in the source of sample material (see Table 1). In order to identify species morphologically or to perform metabarcoding, it is necessary to take a faunal sample. For a morphological analysis, the organisms have to be well preserved. The identification of juvenile or damaged organisms is often not possible. The eDNA, on the other hand, is composed of DNA from organisms or parts of them (e.g., faunal sample) as well as free, accumulated DNA. It can also be extracted

Table 1 Comparison of different species identification methods in ecological and biodiversity research.

	Morphological analysis	*eDNA metabarcoding*	*Metabarcoding*
Sample source	Faunal sample	Aquifer water & sediment samples	Faunal sample
Representative sampling of aquifer water	Uncertain	Yes	Uncertain
Data	Number of individuals per species (quantitative)	Number of species (qualitative)	Number of species (qualitative)
Application areas	Ecological research and biodiversity research	Biodiversity research	Biodiversity research

from water or sediment samples that are routinely used for microbiological or hydrochemical analyzes (Creer et al., 2016). Thus, for a representative analysis of groundwater fauna to be obtained, a water sample of the aquifer is possible when applying the eDNA approach (Siemensmeyer et al., 2019). The same is true for microbiological sampling, in contrast to faunal samples from standing water or pumped aquifer water which are affected by selective filtering effects of the matrix.

Molecular tools allow to detect cryptic species (Pfenninger and Schwenk, 2007). Thus, studies comparing molecular biological and morphological approaches, found that molecular biological methods reveal more species, if appropriate references are available (Elbrecht et al., 2017). Although new molecular approaches are rapidly being developed, estimation of organisms abundances, often needed for empirical, ecological studies, is still hardly possible (Elbrecht and Leese, 2015). For this, it is still necessary to identify the species also morphologically.

Sampling techniques and equipment

Depending on the access to groundwater and the depth of the groundwater table, different sampling techniques and materials are applied to access faunal communities. An overview of sampling methods is provided by Malard et al. (2002), Pospisil (1992), Griebler and Mösslacher (2003), Hahn (2002), Bork et al. (2008), and Hose and Lategan (2012). Guderitz and Hahn (2012) also provide detailed suggestions for the application of sampling methods (i.e., piston pumps, net sampler and unbaited traps).

Collecting samples for microbiological and molecularbiological analysis

For microbiological or molecular biological investigations of water or sediment samples, it is particularly important that the sample is not contaminated. Therefore, sterile material should be used if possible and samples must be taken carefully. It must be ensured that the sampled area is representative of the surrounding aquifer. This is ensured by pumping aquifer water. The well water should not be sampled for this purpose. Additional faunal samples collected by net samplers from the well bottom can be taken prior to pumping of water for micro- or molecular analysis (Guderitz and Hahn, 2012).

Collecting faunal samples

In general, there are three techniques to sample groundwater fauna either for morphological or metabarcoding analysis: (1) net samplers (2) pneumatic piston pumps with or without double packers and Bou-Rouch pumps and (3) unbaited traps. A summary of the characteristics of sampling methods to collect groundwater fauna is provided in Table 2. Comparative studies of all three mentioned sampling techniques did not reveal significant differences in community composition but higher densities found in traps and at the bottom of monitoring wells sampled by net sampler (Dumas and Fontanini, 2001; Matzke, 2006; Scarsbrook and Halliday, 2002; Boulton et al., 2003a; Hahn, 2005; Hahn and Matzke, 2005; Allford et al., 2008; Bork et al., 2008). It is important for ecological studies that the chosen methods allow representative sampling and leave the surrounding substratum largely unchanged (Guderitz and Hahn, 2012). The chosen sampling method should also leave the animals as intact as possible to allow subsequent taxonomic and molecular biological analysis (Guderitz and Hahn, 2012).

Net sampler

A net sampler (also phreatic or haul net) is used to collect faunal samples from the bottom of groundwater monitoring wells and large farm wells (Schmidt et al., 2004; Dumas and Fontanini, 2001). It is a combination of a plankton or Cvetkov net that is used in lakes (Cvetkov, 1968) and a net used for sampling springs (Noll, 1939). The net sampler consists of a plankton net (mesh size 74–100 µm, diameter 49 mm) which is connected to a sample vial (50 ml) via a closure with a filter system. It is suitable for sampling monitoring wells with a diameter $\geq$5 cm (Guderitz and Hahn, 2012; Hahn and Fuchs, 2009). The net sampler is lowered into the groundwater monitoring borehole e.g., with the help of a winch or a fishing rod (DVGW, 2018). By pulling the net sampler up quickly (approx. 1 m) and letting it fall onto the bottom, the sediment in which the animals are located is stirred up. This process is repeated 10 times in a standardized manner in order, and also to detect rare species (Dumas and Fontanini, 2001; Malard et al., 2002; Guderitz and Hahn, 2012; Avramov et al. 2022; Eberhard et al., 2009). Hence, the net sampler collects fauna, sediment and detritus from the bottom of the monitoring borehole or well.

Table 2 Comparison of sampling methods for groundwater fauna (Guderitz and Hahn, 2012)[a].

	Pneumatic piston pump with double packers	*Bou-Rouch pump*	*Net sampler*	*Unbaited trap*
Application area	stratified sampling of existing monitoring wells and wells	small-scale investigations with high spatial resolution, repeated sampling	High number of monitoring wells and wells, large-scale investigations, repeated sampling	stratified sampling of monitoring wells, small-scale investigations with high spatial resolution, repeated sampling
Representativeness	good	Good	Good	Good
Stratified sampling	restricted, only together with double packer	very good	No	very good
Depth limitation	50–60 m	Groundwater levels lower than 2 m	Theoretically none, unproblematic up to 200 m	Groundwater level lower than 8 m
Effects on surrounding substrates	moderate[b]	Moderate	No	No
Costs	high	Low	Low	Moderate
Work effort	high	Moderate	Low	Moderate

[a]Submersile pumps can damage the organisms, thus are not appropriate sampling methods for groundwater fauna and not further specified here.
[b]Guessed, no studies available according to Hahn (2002).

The net sampler method is time saving and cost efficient for sampling many monitoring borehole and thus suitable for large-scale studies (Bork et al., 2009a; Guderitz and Hahn, 2012). Stratified sampling is not possible unless specific monitoring sites are sampled at different depths (Bork et al., 2009a). A quantitative sample to calculate species densities and thus be able to compare different samples, can only be taken if the sampled water volume is known. Thus, net samplers are considered semi-quantitative sampling methods. Due to the fact that the filtered water volume can only be estimated roughly and samples from groundwater monitoring wells show increased densities (trapping effect), no conclusions can be made about the total abundance of stygobionts in the aquifer. However, the method allows a comparative and representative assessment of species diversity and community composition at different monitoring wells (Hahn, 2005; Bork et al., 2008).

An Australian study found differences in sampled community composition between net sampler and pump, suggesting that pumping larger volumes of water multiple times reflects species abundance and the proportion of different taxa better than the net sampler which would underestimate species richness (Hancock and Boulton, 2009). Another study suggested a combination of net hauls and pumps when sampling stygofauna (Eberhard et al., 2009). Allford et al. (2008) considers haul nets (phreatic nets) as an efficient sampling method in terms of the number of taxonomic groups and abundance of individuals. In this study, the haul net captured all taxa which were subsequently also collected by pumping. They propose haul nets as a useful method for long-term monitoring focusing on the occurrence of different species and changes in the proportion of taxa, since it is cost-efficient, easy to use and allows taking multiple samples in a short time (Allford et al., 2008) (Fig. 1).

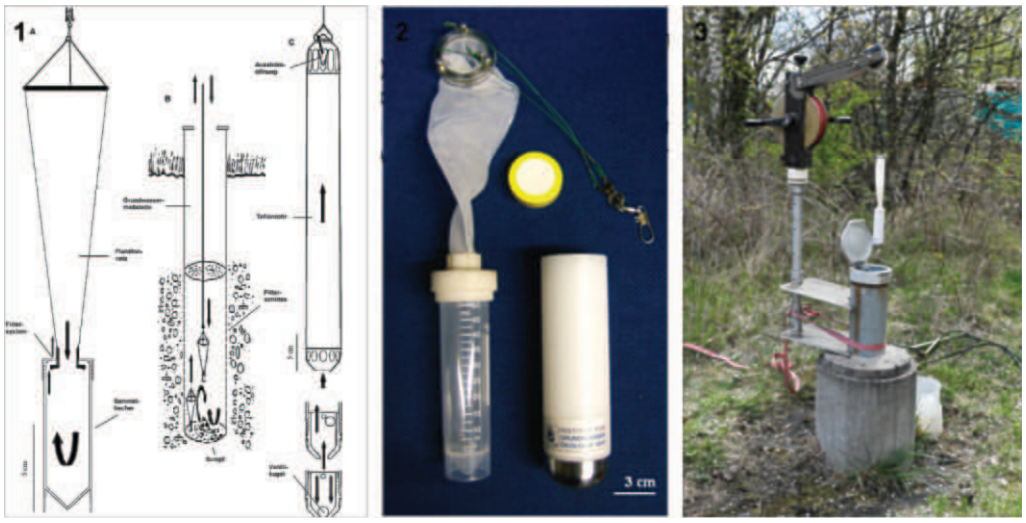

Fig. 1 **1** Net sampler and sampling vessel (A); Use of the net sampler (B); (C) Setup of the Aqua sampler © (Fuchs, 2007). **2** Photo of a net sampler with attached sampling vessel at the lower end of the net, in which the sampled groundwater fauna is collected (Avramov et al., 2022). **3** Sampling of a groundwater monitoring well. In this example, the net collector is moved up and down with the help of a winch (Avramov et al., 2022).

Pumps

Faunal samples can also be taken by using pumps, e.g., piston pumps with or without packer systems and simple piston (Bou-Rouch) pumps (Malard et al., 2002). In order to calculate the pumping rate, the time it takes to fill a container of known volume is measured. A difficulty in using pumps is to ensure that animals are not collected from multiple microhabitats. This depends largely on the pumping rate and matrix permeability (Allford et al., 2008). Repeated sampling is necessary to capture all species at a site over time (Hancock and Boulton, 2009). Pumping can alter sediment structure in the direct surrounding of a well, i.e. with repeated pumping high portions of fine sediment and detritus is removed (Guderitz and Hahn, 2012; Hahn, 2003). Especially in aquifers composed of fine sediments, mobile and small species are over represented relative to larger species in the samples due to the filtering effect of sediments (Boulton et al., 2004; Dumas and Fontanini, 2001; Fraser and Williams, 1997; Scarsbrook and Halliday, 2002). Representativeness can be improved by turning the pump off and on (approximately 30–60 s) so that organisms that have clung to the substrate during pumping can be captured more easily (Guderitz and Hahn, 2012).

The *pneumatic piston pump with double packers* is lowered into the well at the depth of choice. At least a volume of 20–1000 l should be pumped (Hakenkamp and Palmer, 1992). Malard et al. (2002) recommends pumping a minimum of 50 l. The pumped water is filtered through a plankton net. This allows the groundwater animals to be transferred to a sampling vessel. The pump does not harm organisms during sampling (Sinton, 1984; Malard et al., 2002). Since it is time consuming and labor intensive, the piston pump is a suitable method to sample deep (<70 m), but fewer measuring sites (Malard et al., 2002; Guderitz and Hahn, 2012). However, they seem less suitable for exploratory sampling.

The pneumatic piston pump with double packers allows for stratified sampling at discrete depths by inflating the double packers with compressed air. However, this method is time and labor consuming and it is recommended to take only a small sample volume (50 l) at a time (Guderitz and Hahn, 2012).

Standards for e.g., sampled water volume, pumping frequency, do not yet exist, and thus variations in the application of this method occur. Uniform standards are needed because abundance and species composition change as sample volume and pumping rate vary (Hunt and Stanley, 2000; Dumas and Fontanini, 2001; Boulton et al., 2004) (Fig. 2).

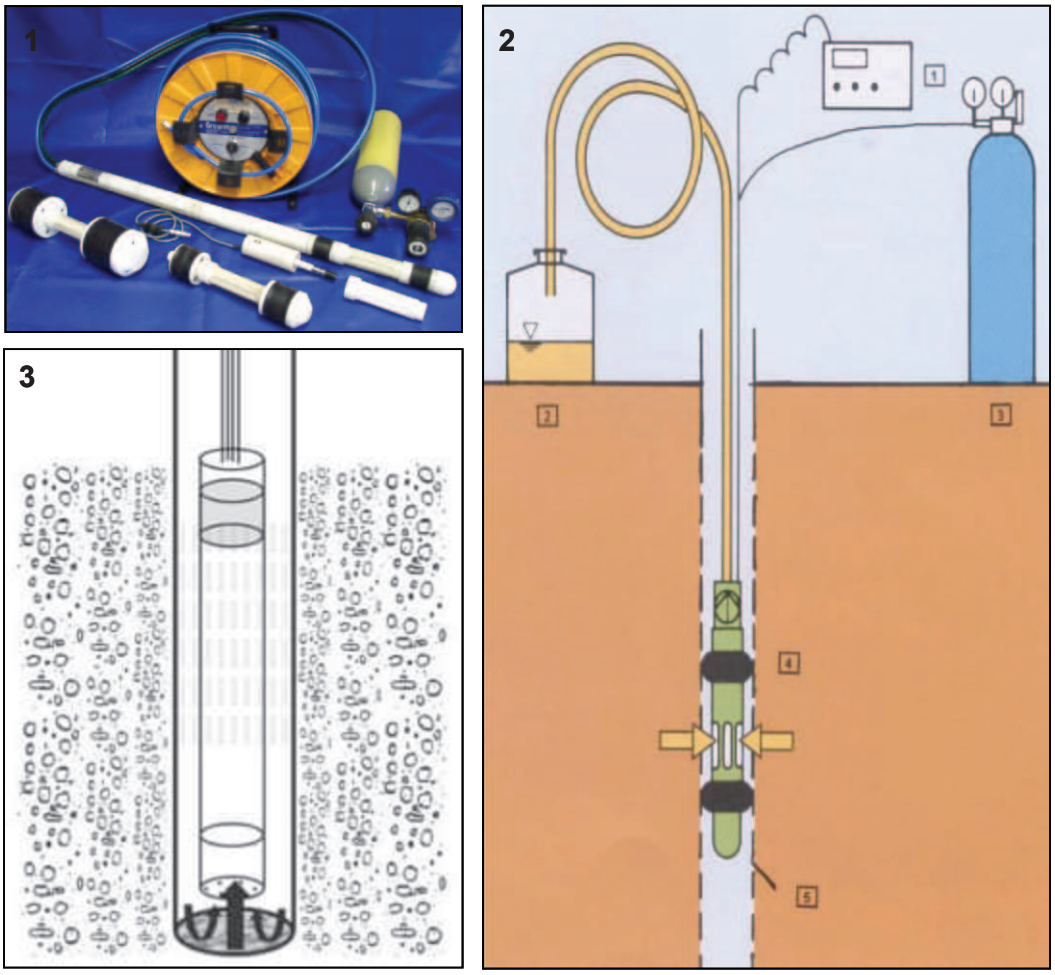

Fig. 2 **1** Pneumatic piston pump with double packers (Umwelt und Wissenschaftstechnik (UWITEC, Niederreiter). **2** Pumping of aquifer water. **3** Pumping of standing water in monitoring well.

The *Bou-Rouch pump* is a hand operated piston pump that can be used to sample groundwater close to the surface (down to 1.5 m) or the hyporheic zone (Bou and Rouch, 1967; Griebler and Mösslacher, 2003; Malard et al., 2002).

For this purpose, a pipe, a galvanized iron tube, which is perforated at the tip, is inserted into the sediment to a desired depth. The pipe should ideally be inserted days before sampling, as the process disturbs the faunal community and the sample might not be representative. When installing the pipe, channels can form that attract water from different depths, which is why in such a case, an assignment of the sample to a discrete depth would no longer be possible (Griebler and Mösslacher, 2003). If a pipe is sampled multiple times, it should be noted that pumping might alter the sediment structure in its surrounding (Griebler and Mösslacher, 2003). Thus, with this method only qualitative data of community composition can be obtained. If the pipe is installed beforehand and sampled once only, then a representative sampling for ecological studies is possible (Griebler and Mösslacher, 2003).

The Bou-Rouch pump is placed on top of the pipe. The pump maintains an interstitial flow by which floating organisms as well as organisms from the surrounding sediment are brought up into a 10 l sampling vessel (Malard et al., 2002). The sample should be thoroughly rinsed with filtered water so that the organisms are washed out of the sediment (Malard et al., 2002). Malard et al. (2002) recommend collecting a maximum of 5 l of water since these typically contain 76–100% of the taxa found in 10 l. Boulton et al. (2003a) recommend to pump between 1 and 10 l.

Submersile pumps are generally not suitable for sampling groundwater fauna, because they damage the animals, making their proper morphological identification impossible. Many wells used for drinking water supply or irrigation have a permanently installed submersile pump. Malard et al. (2002) state that sample intensively used wells is not recommended.

Unbaited traps

Unbaited traps can be used to collect fauna in groundwater and in the hyporheic zone (Hahn, 2003, 2005, 2006; Bork et al., 2009b). Baited traps are selective and therefore not suitable for ecological studies whose aim is estimating invertebrate abundances and community composition. However, baited traps are an effective sampling method when specific species are targeted for collection (Hutchins and Orndorff, 2009).

The groundwater inhabiting organisms accumulate at the bottom of the trap and can be brought up with a suction pump and transferred into a sterile, preferably wide-necked sample vessels consisting of acrylic glass (Bork et al., 2009a). The traps consist of vessels with a diameter of 98 mm and a height of 150 mm (Guderitz and Hahn, 2012). The organisms can enter through vertical rows of holes (diameter 15 mm) and accumulate at the bottom, where there is another row of holes closed with a plankton net (63 µm), from which the animals cannot escape and a hydrochemical gradient is prevented (Guderitz and Hahn, 2012). Top and bottom sealing rings enable connection to the groundwater monitoring well (diameter 100 mm). The traps allow for stratified sampling to a maximum depth of 8 m below groundwater table due to technical limitations of the suction pump (Bork et al., 2009b). Traps are applied for instance to investigate surface-groundwater interactions (e.g., bank filtration) (Bork et al., 2009b). They are often used for repeated measurements and where high spatial resolution is needed. Sampling is not time expensive but it needs special wells to be equipped with traps since the traps stay in place for some time (Guderitz and Hahn, 2012). Similar to the net sampler, the samples collected with traps show a higher density of invertebrates than with pumping methods, but the community structure can be recorded in high spatial and temporal resolution representative for the aquifer or hyporheic zone (Hahn, 2005; Bork et al., 2008) (Fig. 3).

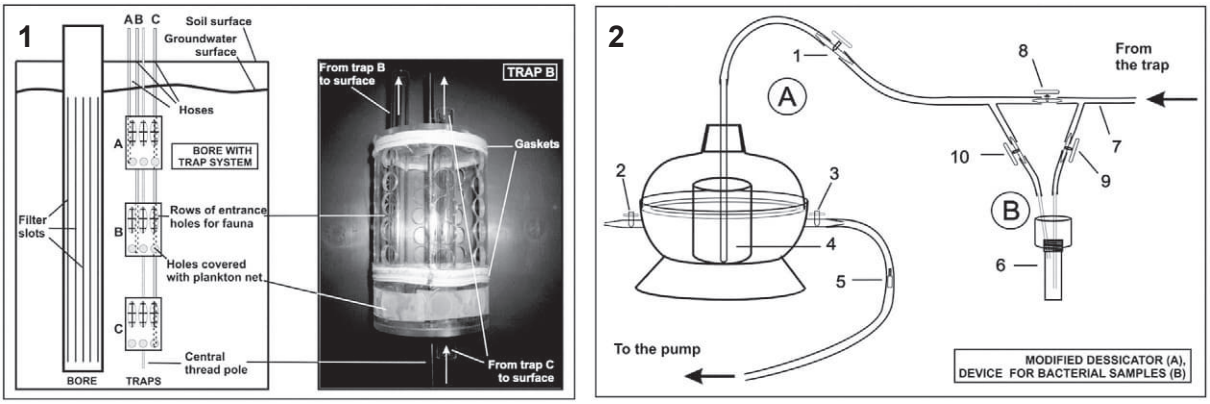

Fig. 3 **1** Bore with unbaited traps for taking stratified samples. **2** Desiccator with vacuum pump for taking samples from a trap. Institute of Groundwater Ecology (IGÖ GmbH).

Karaman-Chappuis method

Another sampling technique is the Karaman-Chappuis method, where a hole is dug into the loose sediments of the river bank or a gravel bar. The incoming water during digging takes with it organisms from the subsurface (Malard et al., 2002). The water is then collected and filtered to collect the organisms (Chappuis, 1942).

Sample processing and analysis

Microbiological and molecular biological samples (eDNA and metabarcoding analyzes)

Once the sample is taken, it is important that the chemical-physical conditions remain the same. Otherwise, changes in the DNA and RNA or in the composition of the microorganisms can occur quickly. Thus, the sample needs to be transported and stored in opaque insulated containers under cool and dark conditions (5 ± 3 °C, according to DIN EN ISO 19458). The analysis should be done as soon as possible. Microbiological samples can also be preserved with aldehydes (10–20 g/l formaldehyde or 10 g/l glutaraldehyde). However, only if the organisms are not required alive for the subsequent investigation, such as for culture experiments or metabolic activity studies (Guderitz and Hahn, 2012).

Organisms dedicated for later molecular biological analysis can be preserved in Ethanol 100% (Creer et al., 2016). They can be stabilized by adding ammonium sulfate or tetradecyltrimethylammonium oxalate for eDNA samples (also called Catrimox-14) (Guderitz and Hahn, 2012).

The collected DNA and RNA will be extracted and stored at −70 °C to −80 °C. For molecular analyzes the DNA and RNA will be amplified and sequenced. In order to identify the species of a faunal community, the sequences are then aligned with a reference database (Creer et al., 2016; Shaw et al., 2016).

Faunal samples for morphological analysis

After taking the sample, the plankton net is thoroughly rinsed with filtered tap water until the entire sample is transferred into the sample vial. The sample should be stored cold (10 °C) and in the dark for transport, and then washed and fixed as soon as possible (same day). If the organisms should stay alive, they must be kept under the same conditions, i.e., at a cool place, protected from light and in the same water from which they were sampled (Griebler and Mösslacher, 2003).

Later, samples are carefully washed with filtered water through a sieve (63–100 µm) in order to separate the organisms from the sediment for improved examination (Guderitz and Hahn, 2012; DVGW, 2018; Avramov et al., 2022; Malard et al., 2002). Following this, sediment type and quantity can be estimated which allows a "qualitative" classification (Hahn, 2006). A quantitative assessment can be made by using several sieves with different mesh sizes to assess sediment quantity and particle size distribution. The smallest sieve must have a mesh size equal to or smaller than 150 µm (Malard et al., 2002).

Faunal samples are preserved in Ethanol 70% or 96% (Malard et al., 2002; Guderitz and Hahn, 2012) in order to store the sample until taxonomic identification of organisms which is especially recommended for high sample numbers or high animal densities. Please consider fixation methods for specific taxonomic groups (see Table 3). After fixation, the sample is stained by adding Eosine B (1%) or Bengal red for at least 24 h in order to stain the organisms for a better distinguishing from other organic and inorganic particles (Malard et al., 2002; Guderitz and Hahn, 2012). Note, the use of Bengal red conflicts with later genetic analyzes.

Table 3 Fixation and preservation procedures for morphological species identification according to different taxonomic groups.

Taxonomic group	*Fixation and preservation procedures*
Cyclopoida, Harpacticoida	Ethanol (96%) with glycerol Ethanol (80%) with CaCO
Ostracoda, Gastropoda, Bivalvia	No glycerol (Guderitz and Hahn, 2012) Fixation and preservation in ethanol (70%) (Griebler and Mösslacher, 2003), no higher concentrations since it can dry out and make shell brittle
Acari	Koenike's fluid, a mixture of Glycerol (50%), acetic acid (10%), and water (40%) (Guderitz and Hahn, 2012; Griebler and Mösslacher, 2003), 70% Ethanol
Oligochaeta	Ethanol (80%) with 3 drops formol
Nematoda, Rotatoria, Copepoda, Cladocera, Bathynellacea	Formol (4%), glycerol for preservation
Insecta	Ethanol (70%)
Turbellaria	Fixation with Bouin's fluid and preservation with ethanol (80%)

For molecular biological analysis only ethanol (96%) should be used.

Morphological species identification

Samples are sorted under the binocular or microscope (magnification of at least 20 times). Small quantities of the sample are transferred to a Petri dish. A grid facilitates orientation when viewing the sample cell by cell. The organisms are sorted into taxonomic groups, counted and transferred with forceps into small vials filled with ethanol (70%). A sorting sheet is provided by Malard et al. (2002), which simplifies the taxonomic identification later on.

Conclusions

The choice of the appropriate sampling method and effort depends as much on the research objectives, i.e., biodiversity or ecological research, and field conditions, as on its efficiency and accuracy. Both influence the sampling success and must be considered for data interpretation and comparison with results from other studies using other sampling methods. Because groundwater ecosystems are highly heterogeneous habitats and species are often rare, endemic, and occur at low individual densities, sampling effort must be adapted to this situation (Dole-Olivier et al., 2009; Eberhard et al., 2009; Hancock and Boulton, 2009; Hutchins and Orndorff, 2009). Access to groundwater ecosystems is often limited to farm wells or monitoring wells. However, these reflect well the species that occur in the surrounding aquifer. However, abundances, proportions of certain taxa, and individual densities may differ from the total numbers in the adjacent aquifer (Hahn and Matzke, 2005; Korbel et al., 2017). Assessment approaches of the ecological status of an aquifer based on abundances or proportions of taxa within a community may therefore be biased should only water from monitoring wells or large farm wells be sampled (Korbel et al., 2017; Korbel and Hose, 2017). Faunal samples which are needed for morphological species identification or metabarcoding are difficult to obtain by representative sampling of the aquifer water. In contrast, the eDNA approach allows for a representative sampling of the aquifer. Thus, for the first time it is possible to look for groundwater in the same water sample that is dedicated to microbiological and hydrochemical analysis.

The most common sampling methods each have advantages and disadvantages for sampling groundwater fauna. Net sampling is a cost-efficient method to collect many samples from near-surface aquifers that reflect species diversity and community composition of the surrounding aquifer (Hahn, 2005; Bork et al., 2009a). Thus, it is well suited for exploratory sampling or for biomonitoring (Allford et al., 2008). Pumping is more cost and labor intensive than net sampling, but is advantageous for sampling deeper aquifers (Allford et al., 2008). In combination with a double packer it allows for stratified sampling at discrete depths in screened wells and collection of quantitative data (Guderitz and Hahn, 2012). The Bou-Rouch pump is especially useful to take samples from the shallow aquifer close to the surface or the hyporheic zone (Bou and Rouch, 1967; Griebler and Mösslacher, 2003; Malard et al., 2002). Unbaited traps are particularly useful because of their efficiency and ability to collect fauna from discrete depths.

Several studies show that molecular approaches offer promising applications for biodiversity research and monitoring (Elbrecht et al., 2017; Keck et al., 2018; Valentini et al., 2016). Currently even though approaches are under development to estimate the abundance of individuals, this is to date not possible with the eDNA approaches in place (Elbrecht and Leese, 2015). In the next few years, molecular tools such as eDNA metabarcoding will gain in importance, so that sampling techniques might be further adopted. Environmental DNA metabarcoding together with microbiological and hydrochemical analyzes allow a representative sampling of the faunal community directly from a common aquifer water sample. A combination of both, morphological and molecular biological species identification can complement each other well to meet the requirements of monitoring aquatic ecosystems (Harvey et al., 2017).

Some suitable sampling methods are available, and important progressive steps have already been taken toward standardization of sampling methods (Malard et al., 2002). However, further research is needed to better evaluate the ability of sampling methods

to representatively and quantitatively record adjacent aquifers and their faunal communities. For this, it is also necessary to investigate the sources of spatial and temporal heterogeneity affecting species communities (Dole-Olivier et al., 2009; Gutjahr et al., 2013).

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Knowledge Gaps, Obstacles, and Research Frontiers in Groundwater Microbial Ecology

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Glossary

Allochthonous Material and organisms that are from outside the (eco)system; have been introduced from outside.
Autochthonous Material and organisms that are from inside the (eco)system; have its origin in the system.
Chemolithoautotrophy Microorganisms that gain cellular energy from converting inorganic compounds—such as hydrogen, reduced iron, nitrite, or hydrogen sulfide—and fix inorganic carbon into organic carbon.
Ectosymbiotic Form of symbiotic relationship in which one partner lives on the body surface of the host (other partner).
Endosymbiotic Form of symbiotic relationship in which one partner lives inside the body of the host (other partner).
Syntrophic Species of organisms that live in a metabolic relationship in which one species depends on the nutrients, growth factors, or substrates provided by the other partner.
Ultramicrobacteria Bacteria that are smaller than 0.1 μm^3 or less than 0.3 μm in diameter in active state.

Summary

Groundwater ecology, and groundwater microbial ecology in particular, are comparably young disciplines that have gained momentum in recent decades. Nevertheless, groundwater ecosystems still belong to the least explored environments worldwide and as such there are more open questions than we have answers. The aim of this chapter is to critically highlight existing knowledge gaps, obstacles, and research frontiers in groundwater microbial ecology. Without doubt, a major issue is the difficult accessibility of the subterranean habitats. Analyzing microbial communities in groundwater that is withdrawn from observation wells or collected at springs and in caves, we deliberately ignore the vast majority of microbes that live attached to the aquifers' sediment and rock matrix that are inaccessible with routine sampling methods. Only recently, we learned that active members of the microbial community have been overlooked because of their small size ($\leq$0.2 μm). Moreover, there is increasing evidence that chemoautotrophic primary production does play an important role in carbon cycling of aquifers that have so far been perceived as solely heterotrophic domains. Overall, our knowledge about carbon pools, fluxes and transformation in the subsurface is still extremely poor and needs rapid improvement. Similarly, our ideas about groundwater food web interactions and the link between microbes and fauna is immature. Modern molecular tools in combination with the analysis of groundwater fauna microbiomes open new doors to study micro-meio-macro relationships. In light of the anthropogenic pressures on groundwater ecosystems, it is necessary to study the resistance and resilience of microbial communities and their key ecosystem functions that provide essential ecosystem services, i.e. purification and storage of drinking water. From the perspective of basic research, it is timely to test established ecological concepts and principles for their validity in groundwater ecosystems.

Introduction

The discipline of groundwater ecology started to develop late in the 19th century with natural history observations about organisms living in subsurface habitats accessible to humans. During the first part of the 20th century, naturalists targeted subterranean habitats in order to sample strictly stygobiotic animals. Our current knowledge of the unique attributes of groundwater environments and its inhabitants, such as (i) the extreme oligotrophy of many cave water habitats, (ii) the relative thermal stability of the subsurface, (iii) the reduced organismic diversity, and (iv) for some species, their reduced abundance, date back to this period (Danielopol and Griebler, 2008). While groundwater fauna ecology already had some momentum in the 1950s, microbiological research was just beginning. Interest in subsurface microbial life was initially related to drinking water quality from aquifers and the corrosion and clogging of oil production pipes. The effective birth of subsurface microbiology involved the development of aseptic sampling techniques in the beginning of the 1970s (e.g., Dunlap et al., 1977). Since then, the ubiquitous presence of microbes in the subsurface, as well as their intimate involvement in biogeochemical cycles and ecosystem services has been well established. Today, groundwater microbial ecology is a modern sub-discipline within limnology and environmental microbiology. However, the difficulties accessing subsurface habitats, with its hidden heterogeneity, and invisible ecosystem boundaries is a major reason why knowledge of groundwater microbial ecology still lags behind that in surface fresh and marine waters. Groundwater ecosystems are among the most unexplored habitats in the world, with entire regions, even continents (e.g. Africa) that have not been extensively studied.

The biologically active terrestrial subsurface extends several kilometers below the land surface (Ghiorse, 1997). Although there are records of the occurrence of fauna in caves and aquifers deeper than 2000 m (Borgonie et al., 2011; Sendra and Reboleira, 2012), deep aquifers, particularly in porous systems, are anoxic and do not support higher organisms. Even in shallower and oxic subsurface zones, microbes dominate in terms of numbers, biomass, and activity. Microbes are the drivers of all biogeochemical cycles. They are responsible for cycling nutrients, the biodegradation of organic contaminants, the (im)mobilization of metals, and the formation of minerals. Most of our knowledge on microbial processes come from controlled laboratory experiments, while in situ measurements and field studies are exceptionally rare (Schroth et al., 2001; Mailloux and Fuller, 2003; Fischer et al., 2006). The limited accessibility of the subsurface is a major hurdle to making observations in situ. Costly drilling is possible only in exceptional cases, and the installation of the many groundwater observation wells worldwide have not been accompanied by microbiological investigations.

In many areas groundwater ecological research is still dominated by observational studies that focus on biotic distributions and taxonomic description, rather than hypothesis-testing, mechanistic understanding, and delineation of general principles. Larned (2012) pointed out critical obstacles that limit the progress of the discipline. These include the structural and hydraulic heterogeneity of the subsurface, the lack of physical habitat templates and classification schemes for groundwater habitats, but opportunities include emerging molecular methods that will, in combination with traditional morphological methods, improve our taxonomic resolution. Finally, he advocates laboratory and field experiments to quantify ecological relationships and test hypotheses. Although Larned (2012) did not specifically focus on groundwater microbial ecology, all of the presented arguments are transferable also to this sub-discipline.

Recent 'horizon scanning' identified the highest priority research questions in subterranean ecology (Mammola et al., 2020). These research questions covered six subject areas, i.e. (1) adaptation, (2) origin and evolution, (3) community ecology, (4) macroecology and biogeography, (5) conservation ecology, (6) microbiology and applied topics. Rather than repeating knowledge gaps already identified in previous works (Larned, 2012; Mammola et al., 2020), we will complement their list of research questions with respect to microbial ecology. We provide below 10 topics where there is an urgent need for microbiological research in groundwater.

Free swimming vs. matrix associated microbes in aquifers – Informed overlook?

The majority of microbial cells in aquifers live attached to rock or sediment surfaces as single cells, in small colonies (Fig. 1), or occasionally in thin biofilms (dense biofilms are usually absent). The number of surface-attached cells can be 10–10,000 higher than are suspended in an equal volume of groundwater (Pedersen and Ekendahl, 1992; Alfreider et al., 1997; Lehman et al., 2001; Griebler et al., 2002; Smith et al., 2018). In addition to being more abundant, surface-attached microbial cells are generally bigger and have higher metabolic activity (Fig. 1) (e.g. Kölbel-Boelke and Hirsch, 1989; Wilhartitz et al., 2009), and assemble into communities that are taxonomically different and more diverse than planktonic communities (e.g. Flynn et al., 2008, 2013; Zhou et al., 2012; Fillinger et al., 2018). Moreover, the colonization of mineral surfaces and particles by microbes from the surrounding groundwater is determined by selective forces (Fillinger et al., 2018; Graham et al., 2017), causing not only differences in community composition between surface-attached and planktonic communities, but also heterogeneous distribution of microbes across different aquifer zones (Bennett et al., 2000; Rogers and Bennett, 2004; Grösbacher et al., 2016).

The difficulties of observing and sampling microorganisms from the subsurface apply even more so to surface-attached cells. Drilling is generally prohibitively expensive and rarely an option. As such, most research on microbial communities and their functionality in groundwater environments ignore 90–99% of the present microbial cells. The 1–10% that reside as planktonic cells may not be fully representative of their attached counterparts in terms of community composition, function, or in situ process rates.

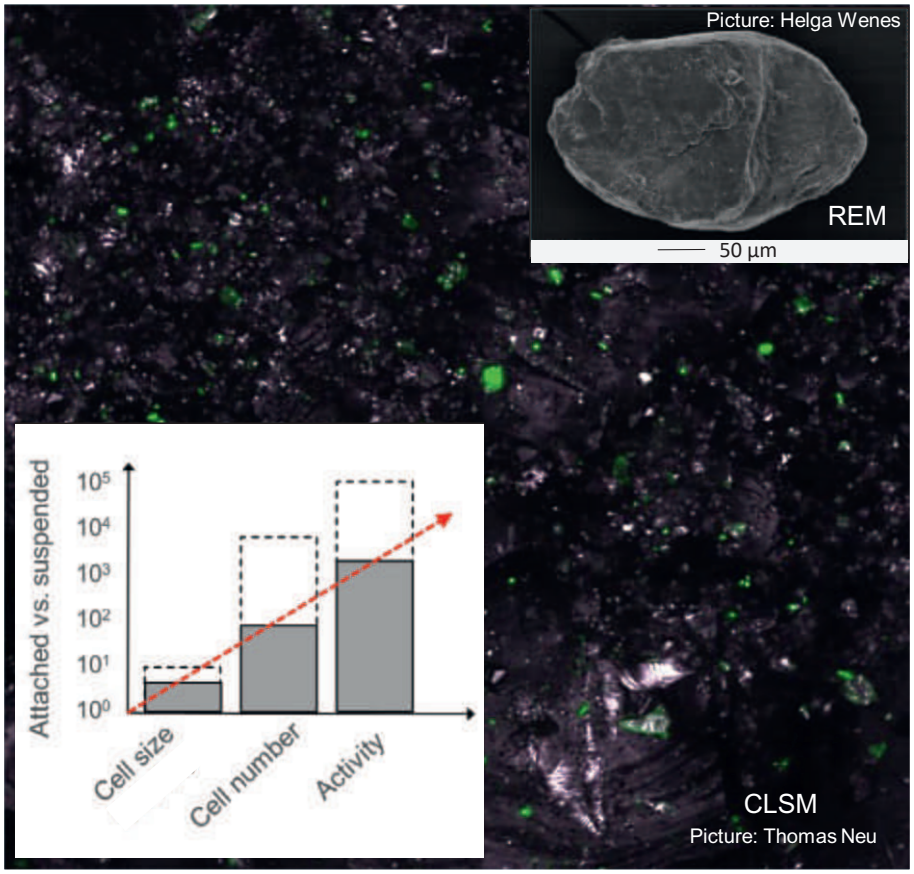

Fig. 1 Surface-attached microbes dominate in aquifers in terms of cell size, cell numbers, and activity (bottom right). A raster electron microscopy (REM) picture of a quartz grain is shown in the top. The left lower CLSM (confocal laser scanning microscopy) picture depicts the distribution of microbial cells over the particle surface made visible by the fluorescent stain SYBR Green.

In terms of community functions, the differences between surface-attached and planktonic communities are less well understood. Anantharaman et al. (2016) found functional redundancy in processes involved in the cycling of carbon, sulfur, nitrogen, hydrogen, and iron in both attached and planktonic communities in a shallow porous aquifer. However, other studies found individual groups of microbes, such as those associated with iron reduction or methanogenesis, to dominate in either the attached or planktonic communities (Flynn et al., 2008, 2013). Similarly, the microbial degradation of hydrocarbons can be differently associated with sediments or groundwater in contaminated aquifers, depending on the partitioning of contaminants between sediments and water (Anneser et al., 2010). To partly overcome this bias, various substrata have been incubated in groundwater observation wells for microbial colonization for a re-creation of natural attached microbial communities (Hirsch and Rades-Rohkohl, 1990; Alfreider et al., 1997; Griebler et al., 2002; Stelzer et al., 2006; Fillinger et al., 2018), accepting new constraints (e.g. artificial substratum, well water conditions). In fact, considering the striking differences in terms of abundance, activity, and composition between surface-attached and planktonic microbes in groundwater, the implications on a functional level and overall impact on biogeochemical processes is certainly a key focus for future research.

Occurrence of ultra-small prokaryotes

For a long time, prokaryotes smaller than 0.2 µm have been overlooked in the aquatic environment and largely ignored in microbial ecology (Velimirov, 2001). The so-called 'ultramicrobacteria' (UMB) or 'nanobacteria' (nanobes) were originally perceived as starving and dormant states of cells (Lappin-Scott and Costerton, 1992). UMB are now considered ubiquitous and to constitute a significant fraction in terms of cell numbers and active members of the microbial community (Hahn, 2004; Wang et al., 2009). Not surprisingly, UMB are also found in groundwater ecosystems (Castelle et al., 2015; Miyoshi et al., 2005; Luef et al., 2015; Herrmann et al., 2019; Nazina et al., 2020). Described as the 'minimalists' by Herrmann and Taubert (2022), these organisms are characterized by a minimalistic strategy, having reduced genomes and, as a consequence, restricted metabolic capabilities. Members of the bacterial Candidate Phyla Radiation (CPR) and archaeal DPANN phyla, which are often present in high abundance in groundwater habitats (Liu et al., 2018; Herrmann et al., 2019), are prime examples of this strategy (Rinke et al., 2013). Lacking pathways for

synthesis of essential amino acids and nucleotides, these organisms likely exhibit a symbiotic lifestyle (Nelson and Stegen, 2015). Taking into account that the nanobes are quite robust to stress (Liu et al., 2018) and can be transported widely through the subsurface (Lappin-Scott and Costerton, 1992), their ecological role is of fundamental interest. The minor switch from using 0.1 μm instead of 0.2 μm filters when collecting microbial biomass from groundwater will definitely extend our common understanding of groundwater prokaryotic communities.

Primary production in the subsurface – Importance in carbon cycling and the groundwater food web

It has long been believed that microbes in the terrestrial subsurface are predominantly heterotrophic, and therefore depend on the import of organic matter originating from photoautotrophic primary production at the surface. However, chemoautotrophic prokaryotic microbes do exist in groundwater, such as sulfidic cave waters and springs (Sarbu, 2000; Sarbu et al., 2000; Engel et al., 2003; Hutchins et al., 2016; Engel, 2019).

Inorganic carbon (carbon dioxide, hydrogen carbonate and bicarbonate) is typically available in excess in groundwaters, with the exception of highly alkaline systems. A basic requirement, however, is a chemical gradient that offers a sufficient flux of an electron donor (H_2, NH_4^+, NO_2^-, HS^-, S^0, $S_2O_3^{2-}$, CO, Fe^{2+}), and an electron acceptor (O_2, NO_3^-, SO_4^{2-}, S^0, $S_2O_3^{2-}$, Fe^{3+}, CO_2) in an appropriate combination to gain energy for CO_2 fixation. There is limited knowledge of how frequently these requirements are met in aquifers and cave water bodies.

The fixation of inorganic carbon consumes ATP and thus is energetically costly. In the absence of light, insufficient energy gain from redox reactions often limits growth of chemoautotrophs in groundwater. However, there is a diversity of pathways among prokaryotes for CO_2 fixation in the dark, which increases the chance that primary production in the subsurface is more important than traditionally expected. However, its importance and contribution to the subsurface carbon cycle may vary substantially from site to site.

In aquifers below agricultural land that receive regular pulses of ammonium derived from fertilizers, chemoautotrophy may play a particularly important role. Here, ammonium can fuel the activity and growth of nitrifying bacteria, and although abundances of these chemoautotrophs can be lower than heterotrophs, they may contribute significantly to the total gene expression in a microbial community (Jewell et al., 2016; Wegner et al., 2019). Recent studies of an oligotrophic limestone aquifer found that up to 17% of the microorganisms relied on autotrophic growth via denitrification coupled to the oxidation of reduced sulfur compounds or hydrogen, or aerobic ammonium oxidation in oxic zones (Herrmann et al., 2015; Kumar et al., 2018; Wegner et al., 2019). Interestingly, metazoan predators occurred at sites with elevated abundances of microbial genes associated with chemolithoautotrophy (Herrmann et al., 2020), suggesting that chemoautotrophic primary production has a role in sustaining trophic interactions in groundwater ecosystems (Taubert et al., 2021).

Another important yet frequently overlooked aspect in the carbon cycle is heterotrophic CO_2-fixation. Virtually all heterotrophic organisms—from microorganisms to humans — incorporate CO_2 via a variety of pathways involving carboxylases in the central and peripheral metabolism (Erb, 2011; Spona-Friedl et al., 2020). Up to 10% of the carbon biomass in heterotrophic prokaryotic microorganisms may derive from these reactions and in cases where the organic substrate degraded by prokaryotes is more reduced than their own biomass, then the contribution from CO_2 fixation can be even higher. For example, in methanotrophs it is up to 50% of the cell carbon. However, in contrast to photosynthesis and chemolithoautotrophy, the overall ecological role of heterotrophic CO_2 fixation remains unclear (Braun et al., 2021).

Carbon cycling in groundwater ecosystems

Whereas there are comprehensive estimates of the carbon pools and fluxes into and from major ecosystems of the world (e.g. Ciais et al., 2013), estimates for the subsurface mainly refer to remaining stocks of fossil fuels (coal, oil, gas) in the deep subsurface. Data for groundwater ecosystems are scarce and have not been compiled in a systematic way. For a fundamental understanding of groundwater ecosystems and its communities, we need a better knowledge of the carbon cycle from the local to the global scale. Below, we provide first simple estimates of carbon stocks in the subsurface compared to data from inland surface waters.

Based on estimates by Drake et al. (2018), inland waters receive about 5.1 Pg (10^{15} g = giga tons) of terrestrial carbon per year, of which 0.6 Pg $year^{-1}$ are stored in sediments, 3.9 Pg $year^{-1}$ are emitted to the atmosphere, and 0.9 Pg $year^{-1}$ are exported to the sea. Only about 0.3 Pg of organic carbon result from photoautotrophic production. Referring to these numbers, we may address a few open questions. (1) How much carbon enters and leaves groundwater ecosystems, and where does the exported carbon go? (2) How much carbon and what kind of carbon is stored in aquifers? (3) How much carbon is processed in aquifers, and (4) is the subsurface a sink or source for carbon and under what conditions?

Aquifers contain about 30% of all freshwater on earth, while 69% is stored in ice and snow, and less than 1% is stored in inland surface waters (Danielopol et al., 2003). Most of the groundwater is old and not involved in what we would call a modern hydrological cycle. Modern (≤50 years) and young (≤100 years) groundwater, as calculated by Gleeson et al. (2015), accounts for only 1.5% and 2.8% of the total groundwater, respectively, which still is 3.5 times and 6.3 times the volume of surface water. Downing and Striegl (2018) estimated turnover times of 10 years for groundwater to a depth of 25 m below land surface and 350 years to a depth of 100 m; the latter equals 3.1% of the total groundwater (8–23.4 million km^3). In consequence, the putatively

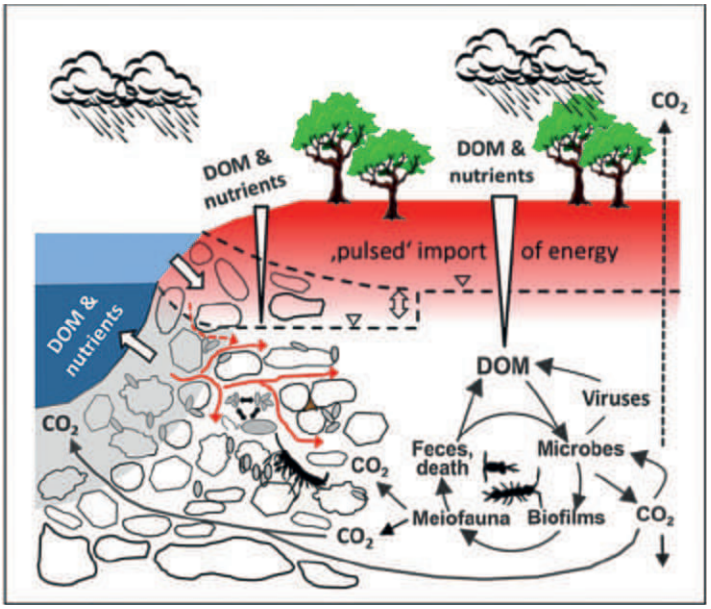

Fig. 2 Carbon cycling in groundwater ecosystems.

large stock of carbon in the subsurface (e.g. Whitman et al., 1998; McMahon and Parnell, 2014; Bar-On et al., 2018; Magnabosco et al., 2018) only partly participates in the 'modern' carbon cycle.

Import of organic matter (OM) into the subsurface is facilitated by precipitation and high water levels in rivers and streams. As such, influx of OM often occurs in irregular pulses (Fig. 2). Estimates of global groundwater recharge range from 5 to 497×10^3 km^3 year^{-1} (Gleeson et al., 2015). If we assume that seepage water that passes through soils and the vadose zone contains 1–2 mg dissolved organic carbon (DOC) L^{-1} and 30–40 mg dissolved inorganic carbon (DIC) L^{-1}, then 0.005 to 1 Pg DOC and 0.15 to 20 Pg DIC are entering aquifers each year. Downing and Striegl (2018) estimated that the global mass of carbon in groundwater (down to 2000 m) is about 145 Pg, which is about the same as all marine sediments and about one-sixth of the carbon in the ocean. Modern and young groundwater contains 2–9 Pg carbon. These values ignore any carbon in the sediments and rocks, which may account for several thousand peta gram. Magnabosco et al. (2018) assume 4–13 Pg biomass carbon in the terrestrial subsurface (to a depth of several kilometers). Although around 80% of the water discharged (exported) from aquifers comes from the top 40 m and 99% from the upper 100 m of the subsurface (Downing and Striegl, 2018), the overall transport of carbon into surface waters via groundwater discharge is estimated to be 0.68 Pg carbon year^{-1}, which is similar to that exported to the sea via river discharge. If we acknowledge that subterranean groundwater discharge to the oceans is 3–4 times that of rivers (Kwon et al., 2014), significant amounts of carbon from aquifers are exported to surface waters every year.

While the values provided here are broad estimates, dynamic changes of carbon pools and fluxes may be expected along with global and climate change. Here, one final example may highlight the immense gaps in knowledge of groundwater geochemistry we are facing. Groundwater is typically super-saturated in CO_2 and may contain significant amounts of methane (CH_4) (Bell et al., 2017) and dinitrogen oxide (N_2O) (Laini et al., 2011; Jurado et al., 2017). The quantitative contributions of greenhouse gases contained in groundwater to surface waters and into soil air, as well as its emission at springs or during irrigation of arable land with groundwater, have never been estimated in detail (e.g. Macpherson, 2009).

It is not only the quantity and flux of organic carbon into and through the subsurface that matters for our improved understanding of carbon cycling. Crucial are also the factors that determine the degradability of OM, such as composition, quality, and element stoichiometry. To date only a few studies have addressed the fate of OM in groundwater and its link to microbial carbon use efficiency and overall prokaryotic production (e.g. Baker et al., 2000; Shen et al., 2015; Hofmann and Griebler, 2018; Hofmann et al., 2020). Connected to that, all of our current ideas about the interactions within the groundwater microbial food webs are based on experience from surface waters, but have rarely been tested for groundwater.

Microbial loop and viral shunt – Bottom-up versus top-down control

Microbes are an integral part of groundwater food webs (Fig. 3). The available resources (e.g. organic matter and nutrients) and the biomass of primary producers (i.e. autotrophs) form the 'bottom' of the trophic pyramid, above them may be several trophic levels leading up to the highest order consumers at the 'top'. Ecological theory predicts two opposing, but co-existing forces occur in food webs: "top-down" control via predation/parasitism and "bottom-up" control via availability of resources regulating the number of trophic levels, the biomass in each level, and ecosystem productivity. The overall structure and dimensions of a food web are determined by the diversity of resources and environmental constraints.

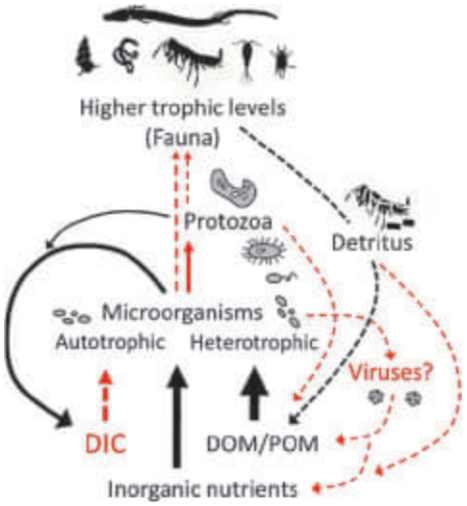

Fig. 3 Groundwater food web with a focus on putative interactions within the microbial food web.

Without doubt, in terms of functionality, aquifers are run by microbes. Ignoring chemoautotrophic primary production (discussed above), heterotrophic prokaryotes rely on DOC and are grazed by heterotrophic protozoa (flagellates, ciliates, amoeba) as well as being infected and lysed by bacteriophages (Fig. 3). In surface waters, top-down control by protozoa and viruses each removes 20–50% (in total 40–100%) of the daily prokaryotic biomass production. However, prokaryotic cell numbers in groundwater are 10–100 times less than in surface waters (Griebler and Lueders, 2009). This dramatically lowers the probability for predators to find their prey. As a consequence, the expected ratios of bacteria-to-protozoa (BPR) of 100 and virus-to-bacteria (VBR) of 10 in surface waters are not generally valid for groundwater and top-down control seems questionable (Karwautz et al., 2022; Schweichhart et al., 2022), with the exception of organically contaminated aquifers (e.g. Zarda et al., 1998; Kinner et al., 2002).

Natural groundwater ecosystems are most likely bottom-up controlled (Figs. 3 and 4) with prokaryotic production always limited by the amount of bioavailable DOC and/or co-limited by individual nutrients like phosphorus (Hofmann and Griebler, 2018). Within the microbial food web, heterotrophic nanoflagellates are the main grazers of prokaryotic cells; however, at a PBR of >500 (Zarda et al., 1998; Sintes et al., 2004; Karwautz et al., 2022). Production of prokaryotic cells and lytic phages seem decoupled (Schweichhart et al., 2022). Whereas in top-down controlled systems a predator or parasite maintains the biomass of prey below the carrying capacity of the system (Konopka, 2006), microbial biomass in groundwater may well reflect the system's carrying capacity (Fig. 4). However, many details remain unclear. As mentioned above, most studies to date have overlooked the importance of sediment-attached microbes, which is relevant here given that protozoa in aquifers are mainly sessile, while for viruses, adsorption to particles and surfaces may lead to (temporal) inactivation. Studies dissecting interactions in groundwater microbial food webs are without doubt urgently needed.

Research on microbes and fauna in groundwater ecosystems are still generally conducted separately, with only a few exceptions of studies in karstic environments in which a tight connection between microbial biofilms and stygo- and troglofauna has been

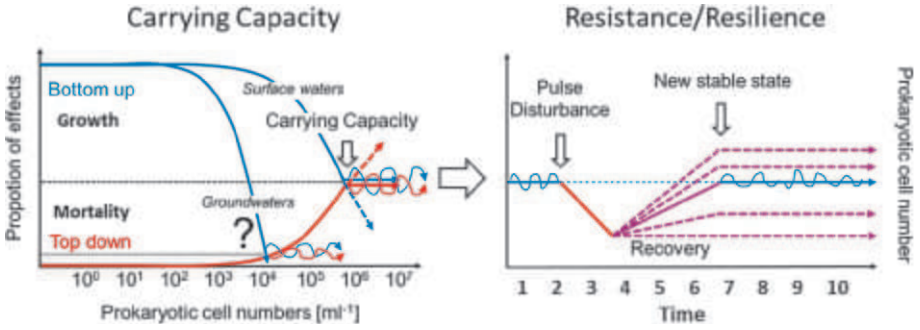

Fig. 4 Conceptual proposal for the microbial carrying capacity and the resistance and resilience of groundwater ecosystems. In comparison to surface waters, the microbial carrying capacity in groundwater is low and almost exclusively bottom-up controlled (left picture). Whereas in top-down controlled systems a predator or parasite maintains the biomass of prey below the carrying capacity of the system, microbial biomass in groundwater may well reflect system's full carrying capacity, taking into account multiple limitations. Environmental fluctuations are dampened in the subsurface causing only little fluctuation in microbial abundances (thin blue line). Microbial communities adapted to living in low-energy systems like groundwater can be expected to have low resistance to environmental changes and perturbations. A pulse disturbance changes community composition and functions (right picture). With time, a new stable state establishes, often with a new community composition and functions. Functions regularly fully recover when the disturbance (pollution) disappear. Community composition often do not return to ints original composition.

shown (Sarbu, 2000; Sarbu et al., 2000; Simon et al., 2003; Cooney and Simon, 2009; Hutchins et al., 2016; Saccò et al., 2019; Weitowitz et al., 2019). Such relationships have been suggested to exist also in sedimentary environments (Barlocher and Murdoch, 1989), but are not yet supported by empirical data. Taking into account that the microbial biomass in natural pristine aquifers is low and dense biofilms are largely absent, a detritus-based food web is more likely than a food web based on microbial production alone.

The 'missing link' between microbes and fauna

Animals are a hot spot of organic carbon and nutrients and provide a habitat for microorganisms. Early investigations on the microbiome of aquatic invertebrates have mainly focused on marine environments (Harris, 1993). A lack of concepts, process-oriented studies and the persistent interest in the role of microorganisms in the physiology of their hosts has propelled this research topic in the recent past (Petersen and Osvatic, 2018). In particular, the development of molecular tools and the start of the "omics era" have enabled research into eco-evolutionary dynamics and processes. A prominent example is the hologenome theory, based on the hypothesis that selective forces act on the collective genomes of the organism (e.g. host) and its associated microbial community (Zilber-Rosenberg and Rosenberg, 2008). In nature, some tight connections between the host and the gut microbiome are known (Engel and Moran, 2013; Ceja-Navarro et al., 2019), while some organisms seem to be unaffected by the often transient microbial communities (Hammer et al., 2019).

The strength and specificity of host-microbe interactions may vary with time. For example, microbes that colonize the exterior will be shed during molting, intestinal bacteria may be released with feces, and different microbial communities are involved in the degradation of dead host biomass (Tang et al., 2010) (Fig. 5). Moreover, host microbiomes can be specific to different life stages (Reis et al., 2020). However, the influence of environmental factors, ontogenetic and evolutionary time scales, and life history traits on these symbiotic interactions remain largely unknown in nature (Leung and Poulin, 2008). Studying host-microbe consortia and interactions may give new insights on the fitness (e.g., reproduction, longevity, nutrient scavenging, parasites) of groundwater fauna. For example, syntrophic relationships between ectosymbiotic bacteria and groundwater amphipods provide the bacteria with mobility, an active dispersal mechanism, and access to favorable conditions as the host seeks its own nutrient resources. The bacteria provide the crustaceans a ready food source and detoxification (Dattagupta et al., 2009; Smith et al., 2016). Additionally, endosymbiotic prokaryotes can use a host as a refugium against environmental stress (Fig. 5). This trojan horse hypothesis is well established and typified by the interaction of pathogenic *Legionella* sp. inside amoeba and ciliates (Taylor et al., 2009). Certainly, all stygobionts constitute niches and opportunities for the interaction with microorganisms, and may act as important bioreactors, and stores of energy and resources (Fig. 5).

The gastrointestinal tract and hemolymph appear to be the preferred organs for endosymbiotic colonization in aquatic invertebrates. So far, the bacteria have been the focus of microbiome studies, but it is well known that viruses, protozoa, and fungi may also be involved (Anderson and May, 1981). Several important, yet unanswered research questions relate to the trophic specialization of groundwater invertebrates and their associated microbiome. How are the microbiomes transmitted? How are the invertebrates, microbes and viruses interacting? Symbiotic relationships are now investigated in the light of network interactions between the host, the endosymbiont, and the wider microbiome, which are all affected by the environmental conditions (Brinker et al., 2019). These interspecies relationships are likely to be dynamic. Consequently, many symbioses do not fit into the traditional categories of mutualism, commensalism, or parasitism.

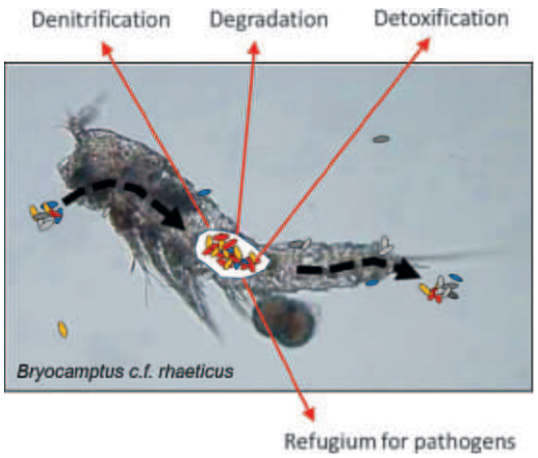

Fig. 5 The microbiome of groundwater invertebrates as hotspot of key processes.

Resistance, resilience and vulnerability

Pristine aquifers are generally characterized by relatively stable environmental conditions and low levels of nutrients and energy compared to surface environments (Gibert et al., 1994). These constraints have a large impact on microbial community composition by selecting for organisms that are adapted to living and competing in such stable, oligotrophic environments. Coping with environmental stress consumes energy and can reduce the metabolic flexibility of microorganisms as well as their ability to compete for nutrients (Ferenci and Spira, 2007). Hence, microorganisms adapted to living in groundwater can be expected to have low resistance to environmental changes and perturbations. Indeed, low resistance of microbial communities in situ and in experimental aquifer meso- and microcosms have been demonstrated with respect to sudden contamination with high loads of hydrocarbons (Herzyk et al., 2017; Ma et al., 2015a, b; Zhou et al., 2014), micropollutants such as herbicides (Mauffret et al., 2017) and antibiotics (Haack et al., 2012), or surface water intrusion (Fillinger et al., 2021). A common pattern that has emerged from those studies is that changes in microbial community composition is driven by loss and replacement of resident taxa following perturbations. To date, few studies have investigated microbial community resilience, i.e., the ability to recover to their original state in terms of composition and functions once a perturbation has ceased. However, there is evidence suggesting that changes in community composition caused by perturbations can persist for long periods of time, if not permanently, even if the initial stressor is removed (Herzyk et al., 2017; Ma et al., 2015a, b; Zhou et al., 2014). Recovery of functions may take place in more reasonable time scales (weeks to months).

The link between microbial community composition and function is not always clear, and loss of resident taxa following a perturbation may in some cases be compensated on a functional level through immigration of functionally similar taxa (Konopka et al., 2015). However, there are examples of low functional resistance and resilience of groundwater microbial communities (Ma et al., 2015b; Zhou et al., 2014). Nevertheless, overall understanding of the resistance and resilience of groundwater microbial communities, and the role of functional redundancies remains limited.

Besides the need for a better understanding of the impact of perturbations on community functioning, we still lack a more nuanced approach to investigating microbial community resistance and resilience with regard to different types and intensities of perturbations. For instance, short-term perturbations occurring as pulses (e.g. pulses of surface water during a flood) may affect communities differently to persistent pressures occurring over longer time scales (e.g. chronic exposure to contaminants; increasing groundwater temperatures resulting from climate change, urbanization, or heat discharge) (Fig. 4). Applying ecological frameworks of community resistance and resilience to targeted studies of press versus pulse disturbances will be key to understanding the responses of groundwater microbial communities to environmental pressures, identifying tipping points, and designing countermeasures (Shade et al., 2012).

Finally, the ability to buffer the loss or inactivation of resident taxa in a microbial community following a perturbation critically depends on the recruitment of microorganisms from surrounding unaffected areas via dispersal (Comte et al., 2017; Ferrenberg et al., 2013; Székely and Langenheder, 2017). Therefore, the integration of theoretical concepts from metacommunity ecology (Langenheder and Lindström, 2019; Leibold et al., 2004) and microbial community coalescence (Mansour et al., 2018; Rillig et al., 2015) as well as tools such as community assembly models (Stegen et al., 2013) and microbial source tracking (Knights et al., 2011; Shenhav et al., 2019) are valuable means to assess the potential of microbial communities to be recolonized following perturbations.

Biodiversity and ecosystem functioning

Understanding how microbial community composition and diversity (e.g. taxon richness) relate to ecosystem functioning is one of the central questions in microbial ecology in general (Antwis et al., 2017), which, however, has rarely been addressed in groundwater ecosystems. Although functional redundancy and horizontal gene transfer may blur this relationship in certain cases (Martiny et al., 2015), microbial taxonomic richness is often positively correlated with functional diversity, for example, in soil and sea water (Fierer et al., 2013; Galand et al., 2018). Moreover, experiments with lake water microbial communities have shown that increasing taxon richness can enhance respiration rates and broaden the spectrum of carbon sources that can be degraded by a community (Zha et al., 2016). Considering these findings, it is reasonable to assume that high microbial diversity at least bears the potential to increase functional diversity and accelerate biogeochemical processes. However, the actual effect of diversity may vary depending on the process in question (Graham et al., 2016) as well as substrate availability and microbial interactions (Langenheder et al., 2010).

Especially in anoxic groundwater, microbial diversity and the interaction between different functional microbial guilds appear to be essential for key processes such as the turnover of organic matter and electron acceptors. Different stages of nutrient and energy cycles are driven by metabolic handoffs between different microbial taxa that would be unable to conduct the complete cycle in isolation (Anantharaman et al., 2016; Wrighton et al., 2014). Similarly, anaerobic hydrocarbon degradation is driven by syntrophic interactions between primary degraders and terminal electron-accepting species (Kleinsteuber et al., 2012; Lueders, 2017; Lueders and Táncsics, 2022). Reductive dehalogenation of chlorinated organic contaminants also relies on interactions between fermenting organisms that provide suitable electron donors and cofactors for specialized dehalorespiring organisms (Weatherill et al., 2018; Yan et al., 2013).

The examples above suggest that at least a certain microbial diversity is necessary to sustain important ecosystem functions in groundwater. However, we still lack information on whether functional diversity scales with taxonomic richness as shown for other environments (Fierer et al., 2013; Galand et al., 2018). Apart from biogeochemical processes, diversity is also important for ensuring community stability in response to environmental fluctuations and disturbances. Here, organisms that may be rare or dormant at a given time or under certain conditions, may play a critical role in maintaining long-term community functioning under changing conditions (Jousset et al., 2017; Lennon and Jones, 2011; Shade et al., 2014). However, the role of conditionally rare taxa and their contribution to microbial community diversity and function in groundwater are still largely unexplored (see discussion on 'ecological laws' below).

Biogeography in microbes – Where do they come from – Everything is not everywhere

Aquifers are hydrologically connected to the surface, even though exchange times may vary strongly depending on depth and geology. At a coarse taxonomic resolution (e.g. phylum, class, order, genus), microbial communities in groundwater often contain organisms that are common in surface freshwaters or soil (Akob and Küsel, 2011; Griebler and Lueders, 2009). However, the characteristic environmental conditions in groundwater act as an environmental filter that only allows a fraction of the microorganisms derived from the surface to colonize and establish in aquifers (Fillinger et al., 2021; Graham et al., 2017; Herrmann et al., 2019). Consequently, at a finer taxonomic resolution, microbial communities in groundwater can be distinct from other habitats (Smith et al., 2012) and markedly different even from communities in connected surface waters or overlying soil (Fillinger et al., 2021; Graham et al., 2017; Herrmann et al., 2019).

Microbial communities in groundwater not only differ from communities in other habitats, but they can also show distinct compositions between different aquifers. So far only a few studies have compared microbial communities across geographically distinct aquifers, mainly based on 16S rRNA gene amplicons (Ben Maamar et al., 2015; Danczak et al., 2018; Fillinger et al., 2019; Korbel et al., 2022), but also species-level comparisons based on MAGs (He et al., 2021). These studies unanimously showed little overlap in microbial community compositions between aquifers. While differences in environmental conditions and microbial interactions likely were the primary factors that selected for distinct organisms at each site in those studies, neutral processes like dispersal limitation across aquifers and ecological drift can be significant contributors to observed differences in microbial community composition (Danczak et al., 2018; Fillinger et al., 2019).

The fact that dispersal limitation does affect microbial community composition across aquifers (particularly shallow aquifers as cited above), is an indication that "everything is not everywhere". We expect that this must especially be true for microorganisms in aquifers at depths of several kilometers with water residence times of millions of years (Chivian et al., 2008; Lin et al., 2006; Nyyssönen et al., 2014). These environments have been habitable for ~1 billion years and were likely colonized by microorganisms from the surface via rock fissures in the ancient past (Drake and Reiners, 2021). While reasoning would suggest that evolutionary drift should play a strong role in the diversification of microbes across different deep subsurface zones, recent evidence suggests that this might not necessarily be the case. Evolutionary rates in the deep subsurface may be extremely slow, leading to the conservation of microbial lineages in different parts of the globe over geological timescales (Becraft et al., 2021).

While we are starting to better understand the factors that determine microbial community composition within as well as across aquifers, several biogeographic patterns of species diversity that are frequently observed in classical ecology, such as species-area relationships, gradients of species richness along latitude, altitude, and depth, or richness-productivity relationships, still await being assessed in groundwater microbial ecology. In addition, we are still lacking insight into the global distribution of individual taxa in groundwater. To tackle this issue, studying microorganisms at a sufficient taxonomic resolution is key. We now know for microorganisms in surface environments that similar habitats in different regions can harbor distinct microbial ecotypes with virtually identical 16S rRNA genes but different environmental optima and metabolic properties (Chase et al., 2018; Choudoir and Buckley, 2018; Hahn et al., 2016; Larkin and Martiny, 2017). However, only a few studies to date have looked into the diversity and distribution of microorganisms in groundwater at the species or sub-species level using genome-resolved analyzes, for instance based on MAGs or single-cell genomics (He et al., 2021; Probst et al., 2018), leaving room for further exploration in the future.

Ecological concepts and laws

Several prominent scientists stated that microbial ecology lags behind macroecology in terms of a conceptual framework, with general principles and ecological laws missing (e.g. Konopka, 2006; Prosser et al., 2007). However, there are a number of theories and principles that have been established in microbial ecology, in some cases their origin indeed is in macroecology. One of the few universal laws in ecology (Lawton, 1999) is the relationship between species richness and habitat size. Data supporting this taxa-area relationship (Fig. 6) are available for bacteria in surface waters (Reche et al., 2005) and salt-marsh sediments (Horner-Devine et al., 2004), but so far not for groundwater ecosystems (Griebler and Lueders, 2009). Microbial phylogenetic and functional diversity was suggested to peak at intermediate intensities or frequencies of disturbances (Ibekwe et al., 2002; Fierer et al., 2003). Today, the intermediate disturbance hypothesis (Connell, 1978) is controversially discussed in particular in aquatic ecology (Moi et al., 2020). Disturbances in aquifers can be the result of multiple concurrent stressors, including hydrological events and pollution (e.g. Bugnot et al., 2019). Although there are numerous studies focusing on microbial communities in disturbed

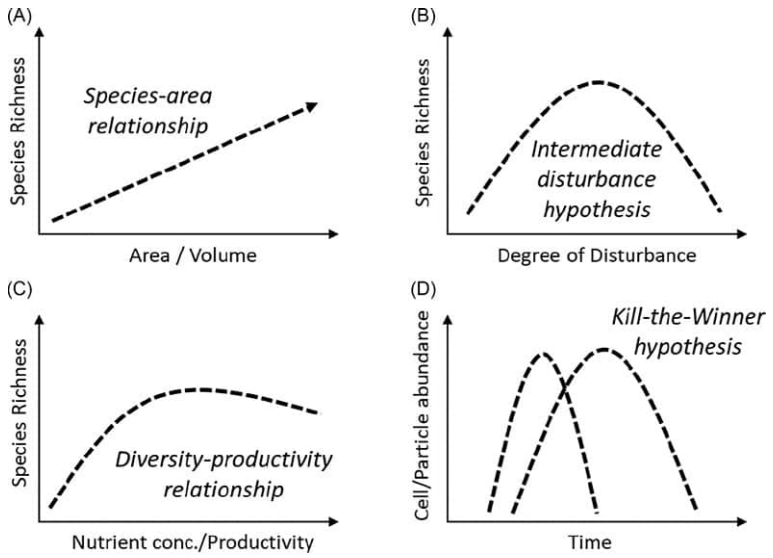

Fig. 6 Ecological principles and laws that await to be tested in different groundwater ecosystems.

groundwater systems, only a few have addressed ecological concepts such as the intermediate disturbance hypothesis, the functional redundancy concept (Allison and Martiny, 2008), and the insurance hypothesis (Baho et al., 2012; Awasthi et al., 2014). In the same way we may mention the diversity-productivity relationship (Smith, 2007) and the Kill-the-Winner hypothesis (Winter et al., 2010). In conclusion, repeating the lines of Larned (2012), tests of causal hypotheses, which characterize more mature branches of ecology, are rarely undertaken in groundwater ecology. Many principles and patterns established in other fields of ecology await testing in groundwater ecosystems (Griebler and Lueders, 2009).

Conclusions

Microbial ecology is a rapidly evolving discipline, perhaps more than other branches of ecology, as new technologies and declining costs are transforming our ability to characterize communities and identify and quantify their functions. While the discipline moves forward, there remain a suite of key research questions that are specific to groundwater ecosystems that require urgent further research. The often stable and simplified groundwater environment provides a unique test bed for experimentation and observation, and provides opportunities for progressing deep-seated ecological theories.

Addressing the questions discussed here will undoubtedly progress understanding of microbial and groundwater ecology, but will also have immense social and economic benefits given the importance of groundwater microbes to water quality and the delivery of ecosystem services on which the majority of earth's population relies.

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SECOND EDITION

Encyclopedia of INLAND WATERS

VOLUME THREE

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ACADEMIC PRESS
An imprint of Elsevier
elsevier.com/books-and-journals

Set ISBN
ISBN 978-0-12-819166-8
9 780128 191668

Vol ISBN
ISBN 978-0-323-99122-3
9 780323 991223

Encyclopedia of INLAND WATERS

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Library of Congress Cataloging-in-Publication Data
A catalog record for this book is available from the Library of Congress.

British Library Cataloguing-in-Publication Data
A catalogue record for this book is available from the British Library.

ISBN 978-0-12-819166-8

Publisher: Oliver Walter
Acquisition Editors: Priscilla Braglia
Content Project Manager: Paula Davies
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Klement Tockner is an internationally leading freshwater scientist, in particular in the research domains biodiversity, ecosystem science, and environmental management. He has published about 250 scientific papers including 180 ISI papers. He was editor-in-chief of the journal *Aquatic Sciences* (2005–2014) and is subject editor of the journal *Ecosystems*. He has published about 250 scientific papers including 180 ISI papers. In 2009, he edited a comprehensive book on European Rivers (Rivers of Europe, Elsevier; 2nd Edition in 2021). He is elected member of the Austrian Academy of Sciences and the German Academy of Sciences, Leopoldina.

Photo credit: David Ausserhofer

Thomas Mehner is vice director and senior researcher at the Leibniz Institute of Freshwater Ecology and Inland Fisheries in Berlin, Germany. He is limnologist and fisheries biologist by training, and has got his Diploma and Ph.D. at the University of Rostock (formerly East Germany) in 1992. In 1999, he had received his habilitation and venia legendi in limnology, which allowed him to start teaching as Privatdozent at universities. Since 1997, he has been working at IGB in several positions. He has published about 170 ISI papers, with primary focus on fish communities, lake food webs, and species interactions. However, his topical interests are broader, and he has authored and co-authored several publications on freshwater fisheries management, fish population genetics and evolutionary and behavioral ecology of aquatic organisms. He has been Handling Editor of the journals "*Aquatic Ecology*" and "*Freshwater Biology*" for several years, and he is currently member of the Editorial Boards of "Global Change Biology" and "Limnologica." Since spring 2018, he has been the president of the International Society of Limnology (SIL), the oldest and most international scientific society devoted to the study of inland waters. Thomas Mehner has taught M.Sc. courses at universities on limnology, fish ecology, fisheries management, and behavior and evolution. His one-week course on "Scientific Writing" for Ph.D. students has been run at 3 universities and in total 18 times, with >120 international students participating. He has trained many M.Sc. and Ph.D. students and supervised their theses, and he is actively mentoring undergraduates, graduates, and post-doc researchers.

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Damien Bouffard is leader of the aquatic physics lab at Eawag (Switzerland). He holds a Ph.D. from EPFL (with Ulrich Lemmin). After his Ph.D. he worked in Canada with Leon Boegman (Queen's U.), Ram Yerubandi (Environment Canada), and Joe Ackerman (Guelph U.) before returning to Switzerland as first assistant at EPFL with Alfred (Johny) Wüest. He has published over 70 peer-reviewed papers in aquatic physics and serves as associate editor for JGLR, AS, and HESS. His program research is focused on two axes: (i) linking the small-scale turbulence to the large-scale forcing with today a special interest in convective processes in lakes and (ii) aquatic physics as a tool to understand lake ecosystems. The later includes the use of 1D and 3D operational hydrodynamic models such as simstrat.eawag.ch or meteolakes.ch. Bouffard is also involved in promoting multidisciplinary and high-tech research on lakes, notably as member of the steering committee of the LéXPLORE floating research platform in Lake Geneva and in promoting open science in limnology with the web platform Datalakes-eawag.ch.

Debbie Chapman as a graduate of the University of London, Deborah Chapman started her research career as limnologist at the Freshwater Biological Association in the English Lake District. She subsequently became interested in monitoring the impacts of disposal of sewage sludge on aquatic organism and the potential for human health impacts from aquatic pollution. In 1986 she joined the United Nations Environment Programme's (UNEP) Monitoring and Assessment Research Centre (MARC) in London, participating in the international monitoring and assessment activities of UNEP and the World Health Organization (WHO), and assisting in global environment assessment programs. In 1988 she became the deputy director of MARC and took responsibility for the developing country workshops and training program, and global environment data review and compilation. After moving to Ireland in 1990, she worked as a freelance Environmental Consultant engaged mostly on international and developing country projects for WHO, UNEP, and other international organizations. She has assisted with the compilation of State of the Environment reports and has contributed to, edited, and produced more than 20 books on water resources and environmental management, including the internationally successful *Water Quality Assessments: A guide to the use of biota, sediments and water in environmental monitoring.*

In 1998 she joined UCC becoming the first lecturer in Environmental Science and then Head of Environmental Science in 2013. In recent decades her research interests have focused on water resources management, especially recreational and amenity lakes and reservoirs, developments and current practice in design and implementation of water quality monitoring programs, and human health risk assessment in relation to the use of freshwater resources and wastewater disposal. Drawing on 30 years of international experience, in 2015 she established the UNEP Global Environment Monitoring System for Water (GEMS/Water) Capacity Development Centre at UCC. This center delivers capacity development activities in water quality monitoring and

assessment worldwide for UNEP, including support for the Sustainable Development Goal indicator for good ambient water quality. She retired as director of the center in June 2021 and now acts in an advisory role and as an independent consultant.

Photo by Blythe White

Kendra Spence Cheruvelil is professor of limnology and co-director of the Data-intensive Landscape Limnology Laboratory at Michigan State University (MSU) in the Department of Fisheries and Wildlife (https://www.canr.msu.edu/fw/). She is also serving as Interim Dean of the Lyman Briggs College, which is MSU's residential college for studying the sciences and maths within their societal and global contexts (www.lbc.msu.edu). Kendra co-established the discipline of landscape limnology (https://bigdatalimno.org/research-themes/landscape-limnology/) and co-leads the LAGOS research program that is creating the research infrastructure to conduct big-data research on U.S. lakes (https://lagoslakes.org/). This large, collaborative, and interdisciplinary research program has been funded by the U.S. National Science Foundation and seeks to understand how global changes such as climate change and land use intensification affect lakes across regions and continents and through time. Dr. Cheruvelil also pushes the boundaries of how to conduct limnology research by using data-intensive science, science of team science, and open science approaches, tools, and perspectives to answer complex scientific questions. She also has an active research program to advance diversity and inclusion in the sciences (https://ee-stem.weebly.com/) and serves as an associate editor for the journals *Limnology & Oceanography Letters* and *Frontiers in Ecology & the Environment*. Prior to joining MSU, Dr. Cheruvelil was a faculty member in the Purdue University system. She has a dual Ph.D. from MSU in Fisheries & Wildlife and Ecology, Evolution, & Behavior (2004).

Photo by Shayenna Nolan

Catherine Febria is a Tier 2 Canada Research Chair in Freshwater Restoration Ecology and assistant professor at the Great Lakes Institute for Environmental Research (GLIER) & Dept. of Integrative Biology at the University of Windsor. Her research focuses on the ecology and restoration of small streams and wetlands in human-impacted landscapes, and the role of small waterways in supporting good ecosystem health in the Laurentian Great Lakes. She launched her lab—the Healthy Headwaters Lab—in 2019 and also wears multiple hats as co-director of the GLIER Organic Analysis & Nutrients Laboratory (a central research facility), associate director of FishCAST (an NSERC CREATE graduate student training program in Canada), co-chair of the International Science Advisory Panel for New Zealand's Biological Heritage National Science Challenge, coordinating editor with the journal *Restoration Ecology* and alumni fellow and contributing author with the Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services (IPBES). She previously held a postdoctoral role at the University of Maryland's Chesapeake Biological Laboratory (USA), the University of Canterbury (Aotearoa New Zealand). Her research has been published in the *Science*, *Nature Geoscience*, *Canadian Journal of Fisheries and Aquatic Sciences*, *Environmental Science & Technology*, and *Frontiers in Microbiology*, *Restoration Ecology*, *Proceedings of the Royal Society*, to name a few. She is co-founder of the Kindness in Science global initiative, and contributes actively to actions, scholarship and mentorship to advance justice, equity, diversity, and inclusion in academia.

Christian Griebler is full professor and head of the Limnology unit at the University of Vienna, Austria. He is a dedicated groundwater ecologist with core expertise in microbial ecology and biogeochemistry.

Kenneth Irvine has a broad range of multidisciplinary experience working on aquatic ecology, ecological assessment of surface waters, especially lakes and wetlands, and policy and related policies and management. After gaining a Ph. D. in 1987 at the University of East Anglia (U.K.) for a study on trophic ecology of shallow lakes, he worked for the U.K. Nature Conservancy Council, before moving to study ecosystem structure of Lake Malawi in Africa. He moved to Trinity College Dublin in 1994 Ireland. There, he continued work on the African Great Lakes, as well as building a research group working on ecological assessment in support of the EU Water Framework Directive. In 2011 he moved to IHE Delft Institute of Water Education, the Netherlands, as chair of Aquatic Ecosystems. Current work focusses on wetlands and capacity development in Sub-Sahara Africa. Recent work also includes a review of hydromorphology and links to policy. He currently sits on the Board of the Board of the *African Center for Aquatic Research and Education* (ACARE) and on the Scientific Advisory Board of the *Leibniz Institute of Freshwater Ecology and Inland Fisheries* (IGB), Berlin.

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Krantzberg is professor and lead for the engineering and public policy in the School of Engineering Practice and Technology at McMaster University offering Canada's first master's degree in engineering and public policy. Gail completed her M.Sc. and Ph.D. at the University of Toronto in environmental science and freshwaters. She worked for the Ontario Ministry of Environment from 1988 to 2001, as coordinator of Great Lakes Programs, and senior policy advisor on Great Lakes. Dr. Krantzberg was the director of the Great Lakes Regional Office of the International Joint Commission from 2001 to 2005. In 2007 she was appointed as an adjunct faculty member of the United Nations University Institute for Water and Environmental Health and participated in the twinning of the Laurentian and African Great Lakes (principally Lake Victoria). She has co-authored and edited 9 books and more than 200 scientific and policy articles on issues pertaining to ecosystem quality and sustainability and is a frequent speaker to media and the public. Her research interests include investigating Great Lakes governance capacity, analyzing interjurisdictional co-management arrangements internationally for application to the Great Lakes regime, and methods to better integrate science and engineering in policy formulation and decision-making.

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She is also involved in promoting high-tech research on lakes, notably as a member of the steering committee of the LéXPLORE floating research platform in Lake Geneva, and in connecting science and management through a transdisciplinary network involving National Parks in France. She has published over 75 peer-reviewed papers and serves as associate editor for WIRES Water.

N. LeRoy Poff is professor of biology at Colorado State University and holds a partial appointment as distinguished professor at the University of Canberra, Australia. Since receiving his Ph.D. in 1989, his research has focused on understanding how natural and human-caused hydrologic variability regulates the interactions among species and the structure and function of riverine ecosystems. By developing techniques to quantify streamflow variability in ecologically meaningful terms and using species (functional) traits as generalized, mechanistic response variables, he has been a leader in advancing the field of hydroecology. Through his interdisciplinary and collaborative work, he has contributed fundamentally to the development of the field of "environmental flows," which aims to support sustainable management of streams and rivers at local to regional to global scales in the face of growing human water demands. His current interests are on developing better conceptual frameworks and decision support tools for science-based management of streams and rivers in our current period of rapid climate and ecological change.

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Stuart Warner works with the United Nations Environment Programme with a focus on helping countries to monitor and assess their freshwaters. He was born in England, he moved to Ireland in 2001 to work at University College Cork. Stuart has published in the areas of water quality monitoring and assessment and citizen science approaches to data collection. He has written reports on the capacity of countries to understand their freshwaters which highlight the challenges faced in different world regions. Recent efforts have focused on the development and implementation of a global water quality indicator, and the delivery of capacity development targeted at improving freshwater management. His professional interests include using both traditional and innovative approaches to understand and protect freshwater ecosystems.

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His research focuses on neotropical wetlands, with special interest in biogeography, plant species distribution, species diversity, forestry and sustainable management, remote sensing, biomass and primary productivity, and botany and vegetation ecology. Actually, he teaches at the Institute for Geography and Geoecology of the Karlsruhe Institute for Technology, Germany, and in the post-graduate program of Tropical Ecology—Botany at the National Institute for Amazon Research—INPA, Manaus, Brazil. He supervised numerous M.Sc. and Ph.D. students and published more than 150 peer-reviewed publications, including several books and book chapters on Amazonian wetlands.

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CONTENTS OF VOLUME 4

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Overview of section

Human pressures leading to degradation of inland waters are multiple, widespread, interacting and increasing (Dudgeon et al., 2006; Tickner et al., 2020; Vörösmarty et al., 2010). Pressures occur across a range of scales from global to extremely local, and arise from drivers that can occur far removed (distal) from a water body or close to (proximate) where the impact occurs (van Asselen et al., 2013). The chapters of this section of the Encyclopedia address *Human pressures and Management of Inland Waters* and have been generally organized so that an overview of a particular human pressure is followed by a chapter elaborating some key issues, and a chapter of either illustrative case studies or an important associated topic. The topics covered mostly reflect those pressures that are of current and known concern. For some of these, such as agriculture, the level of understanding is quite advanced while for others, such as emerging chemical micropollutants and microplastics, research is still identifying potential and real impacts.

The first series of three chapters is concerned with Measuring Impact, with a focus on how assessment is based on a comparison with estimated reference states (Irvine, 2022), followed by the use of biotic indicators and rapid assessment through use of citizen science (Simaika et al., 2022). The application of citizen science and underlying philosophies and methodology is a growing discipline involving greater understanding of the motivation of citizens and how measurement taken by citizens can help with environmental monitoring and co-management. This is covered by Wehn (2022).

Agriculture is a major pressure on inland waters; an overview is provided by Vero and Fenton (2022) and best practices for the protection inland waters are illustrated by Pacioglu et al. (2022). A series of case studies addresses different pollutant risks and their management (Vero et al., 2022). Potential impacts from agriculture can also involve a number of physical modifications that affect the rate of transfer of water and material from land to water, and modification of, especially, river channels. The effects of such *hydromorphological* alterations are an increasing topic of importance for the management of land and water, and across scales from that of the catchment to individual parts of water bodies. An overview of hydromorphology and the impacts of human pressures on it, focusing mainly on rivers, is provided by Sandin and Kemp (2022), and Miler, 2022) discusses how hydromorphological alterations affect different habitats and interact with other pressures. Case studies from individual water bodies to whole catchments are described by Porst (2022), identifying many of the challenges that these changes have for management. The hydromorphology theme is highly relevant to the next three sub-themes on Hydropower and Dams, Mining Impacts, and Sediment Extraction; illustrating how so many human pressures on inland waters are interconnected. Management of these can be addressed by strong sector regulation, but are often bedeviled by multisectoral interests and diverse groups of stakeholders, operating within formal or informal institutions (Cleaver and De Koning, 2015).

An overview of the evolving perspectives on hydropower, focusing on the need to balance societal benefits and environmental aspects is given by Bradley (2022). This is followed by a case study on the Danube River by Bradley and Habersack (2022), illustrating some of the difficulties posed by hydropower on large rivers with many international interests in their catchments. Hayes et al. (2022) highlights hydropeaking (an important but understudied hydromorphological pressure) and its consequences for balancing ecosystem needs and energy generation from dams. These are complemented by a chapter on case studies in hydropower sustainability by Ulibarri et al. (2022), including the improvements that are being made to small hydropower schemes. At the other end of the scale is the mega hydropower development of the Three Gorges dam in China, which also has associated impacts on the water quality of the impounded reservoir and its tributaries, described by Zhang (2022).

Impact from, and management of, mining is covered by an overview by Wolkersdorfer and Mugova (2022) and case studies addressing different mining operations by Wolkersdorfer et al. (2022). In-between, a chapter by Esterhuse et al. (2022) focuses on environmental damage and future risks from hydrocarbon extraction. The extraction of sediment from water bodies is of increasing concern. Despite being widespread, it has not had the attention, or global management, that this pressure requires. Like some mining practices in the world, it is often executed by an informal sector, often involving illegalities and criminal enterprises.

An overview by Juez and Franca (2022) outlines the key issues, followed by a policy perspective by Bussettini and Schmidt (2022). Both chapters demonstrate that the knowledge base to effectively manage sediment extraction (often referred to as sand mining) is lacking basic principles of sediment movement in rivers, and is not properly considered in environmental planning and management. Clear recommendations of good practice and licensing processes are, nevertheless, available and implemented in some countries. The case studies by Franca et al. (2022) illustrate the dramatic consequences when there is insufficient attention to principles of hydromorphology and sediment mobility. While sediment extraction may not be new phenomenon, there are also many new or recently emerging pressures on inland waters, and for which management approaches and policies to address the problems are still developing. Emerging organic contaminants are covered by Bacci and Campo (2022), and microplastics, a topic that is very much building in global awareness, by Jansen et al. (2022). These pressures are still a matter of much ongoing research into their detection, distribution and potential impacts on freshwater ecosystems and on human health, in order to effectively monitor and manage them and to support policy development and the necessary policy interventions.

Man-made constructed wetlands can play an important role in mitigating impacts from contaminants in freshwater systems, as well as enhancing semi-natural and biodiversity networks in both urban and rural settings. Rousseau et al. (2022) provide an overview of the use of constructed wetlands in the urban environment, and Hatvani et al. (2022) discuss how constructed wetlands can be used to mitigate agricultural pressures on inland waters. These complementary chapters are followed with a series of case studies using wetlands to treat point and non-point pollution sources in very different settings by Bhomia et al. (2022).

While the chapters described above are largely focused on the effects of physical and chemical pressures, the next six chapters consider more explicitly those arising from biotic exploitation and species translocations. In many parts of the world, fisheries are a major source of livelihoods, not just for food but also for recreation and therefore require careful management. The first of three chapters on fisheries addresses fisheries management in relation to their need to sustain livelihoods (Elliot, 2022a,b), while the second chapter considers the implications of climate change on fisheries and some of the knowledge gaps that have implications for fisheries management (Kelly et al., 2022). The third chapter presents a suite of case studies viewed from different perspectives of the use and management of inland fisheries (Elliot, 2022a,b). The exploitation of fish has also involved the effects of species introductions, which is the topic of the following three chapters. The first of these by Jeschke et al. (2022a,b,c) provides an overview of biological invasion and the conditions needed for the establishment and spread of invasive species. This is followed by more details on the impact and management options for invasive species (Jeschke et al., 2022a,b,c) and a concluding case studies chapter under this theme (Jeschke et al., 2022a,b,c). The final chapter in the section on *Human pressures and Management of Inland Waters* demonstrates how the concept of water retention can be used for city water management in so-called Sponge cities (Fu et al., 2022). This is also an emerging topic of considerable interest and importance for sustainable cities and, like constructed wetlands, employs Nature Based Solutions for water management (WWDR, 2018).

Sustainable development

The chapters in this section of the Encyclopedia are all connected with the idea of managing water resources and the pressures in them in a sustainable way, and how knowledge and understanding of processes can be best employed to provide evidence informed management (Adams and Sandbrook, 2013; Haddaway and Pullin, 2013; Sutherland and Wordley, 2017). This is a common tenet of environment management and the policy cycle of adaptive management (Kingsford et al., 2021; Owens, 2009; Pahl-Wostl et al., 2007). Nevertheless, for many pressures using knowledge to design effective monitoring and management (Lovett et al., 2007) is not sufficient to adequately protect inland waters. There are many reasons for that, but it is also clear that more concerted efforts employing multiple sectors and stakeholders are urgently needed (Carpenter et al., 2009).

The threats to, and degradation of inland waters and other habitats on Earth have been recognized for decades:

- The 1972 UN Conference on the Human Environment (World Commission on Environment and Development, 1987) identified the choices required for human development without major impact on life-supporting ecosystems;
- The international Convention on Wetlands (www.ramsar.org) dating from 1972 (UNESCO, 1994) provided an international Agreement on the protection of wetlands;
- The 1992 Rio Earth Summit (United Nations, 1992) highlighted the need for sustainable development; the 2002 Johannesburg Declaration on Sustainable Development (United Nations, 2002), (re)affirmed the interdependence of natural, economic and social pillars;
- The Millennium Ecosystem Assessment (2005) placed an emphasis on the importance of ecosystem services for human well-being;
- The Aichi targets of the Convention on Biological Diversity (CBD, 2012) fed into the first stage targets of the UN Sustainable Development Goals;
- Agenda 2030 (https://sdgs.un.org/2030agenda) set a plan of action for people, planet and prosperity based on 17 Sustainable Development Goals (https://sdgs.un.org/) (Fig. 1) for which there are 169 targets with between 1 and 3 indicators used to measure progress for each target.

The call for urgent action has also been sounded for a long time, and endorsed by world governments. Paragraph 13 of the Johannesburg Declaration (United Nations, 2002) could hardly have been clearer:

Fig. 1 Outline of the SDGs, attributed to where the goals fit within societal support systems. From: https://revistaidees.cat/en/biodiversity-time-for-action/.

The global environment continues to suffer. Loss of biodiversity continues, fish stocks continue to be depleted, desertification claims more and more fertile land, the adverse effects of climate change are already evident, natural disasters are more frequent and more devastating, and developing countries more vulnerable, and air, water and marine pollution continue to rob millions of a decent life.

Since 2002, the loss of habitats and their species, particularly high in inland waters, have continued (Tickner et al., 2020) and the term 'crisis' is an increasingly familiar adjective, not only for inland waters but across other sectors and biomes (Groves et al., 2002; Irvine, 2018; Kamp et al., 2021). Addressing the pressures and impacts does not occur because of good intent, or even strong and legally binding policies (Carvalho et al., 2019; Hering et al., 2010), but through environmental management to reduce pressures and mitigate impacts. National or international policies do not necessarily lead to local action (Egoh et al., 2012). That there is overall so little international protection of aquatic and other ecosystems raises fundamental questions about society and the choices made for environmental protection (Ellis, 2018).

While the SDGs together represent the ambition for an integrated approach to sustainability, there is also fragmentation within the structure for policy coherence (OECD, 2019). Nevertheless, the SDGs are probably the best current opportunity to steer the globe towards sustainable management of resources, including inland waters. It is not a clear path, but one that involves considerable challenges and inevitable conflicts between goals and their targets. The section on *Human pressures and Management of Inland Waters* connect to a number of the SDGs. For an overview of interrelationships across the SDGs see Miola et al. (2019).

The key goal for water is SDG 6, with six targets, and two supplementary ones. Each Target has a series of Indicators (Table 1). SDG 6 needs to connect with all other SDGs, but is particularly closely connected with the other so-called 'Biosphere Goals', SDGs 14, 15 and 16. In particular, SDG target 6.6 (protect and restore water-related ecosystems) is intertwined with SDG 15 (halt biodiversity decline) and to the Aichi Biodiversity targets under the Convention on Biological Diversity (CBD, 2012; Coates, 2018). The timetable for SDG Target 6.6 and the Aichi targets not only had overly ambitious timelines of 2020, ahead of other targets, but which cannot ever be met without a dramatic change in how ecosystems are considered and valued in decision making (Irvine, 2018). This requires a greater focus on holistic and systems thinking across sectors and society at large (Darwall et al., 2018; Tickner et al., 2020; van Rees et al., 2020). The chapters on Fisheries and Biological Invasions in the Section on *Human pressures and Management of Inland Waters* connect strongly with SDG 15. For the other SDG 6 Targets we focus here on SDG indicators 6.3.2, 6.6.1, and both of these indicators link with SDG 6.5.1.

Management of Inland Waters is strongly related to water quality. Even within well structured processes such as that required by the EU Water Framework Directive (Council of the European Communities, 2000), meeting environmental quality objectives with reliable connection between indicators and quality status can be problematic (Poikane et al., 2020). Across the overall policy network of the EU, with its myriad of environmental legal protections, difficulties in cross-compliance demonstrate the importance and need for a better 'systems thinking' approach (Nilsson et al., 2012; Voulvoulis et al., 2017).

Table 1 Sustainable Goal 6 targets and indicators.

Targets	*Indicators*
6.1 - By 2030, achieve universal and equitable access to safe and affordable drinking water for all	**6.1.1** - Proportion of population using safely managed drinking water services
6.2 - By 2030, achieve access to adequate and equitable sanitation and hygiene for all and end open defecation, paying special attention to the needs of women and girls and those in vulnerable situations	**6.2.1** - Proportion of population using safely managed sanitation services, including a hand-washing facility with soap and water
6.3 - By 2030, improve water quality by reducing pollution, eliminating dumping and minimizing release of hazardous chemicals and materials, halving the proportion of untreated wastewater and substantially increasing recycling and safe reuse globally	**6.3.1** - Proportion of wastewater safely treated **6.3.2** - Proportion of bodies of water with good ambient water quality
6.4 - By 2030, substantially increase water-use efficiency across all sectors and ensure sustainable withdrawals and supply of freshwater to address water scarcity and substantially reduce the number of people suffering from water scarcity	**6.4.1** - Change in water-use efficiency over time **6.4.2** - Level of water stress: freshwater withdrawal as a proportion of available freshwater resources
6.5 - By 2030, implement integrated water resources management at all levels, including through transboundary cooperation as appropriate	**6.5.1** - Degree of integrated water resources management implementation (0–100) **6.5.2** - Proportion of transboundary basin area with an operational arrangement for water cooperation
6.6 - By 2020, protect and restore water-related ecosystems, including mountains, forests, wetlands, rivers, aquifers and lakes	**6.6.1** - Change in the extent of water-related ecosystems over time
6.A - By 2030, expand international cooperation and capacity-building support to developing countries in water- and sanitation-related activities and programs, including water harvesting, desalination, water efficiency, wastewater treatment, recycling and reuse technologies	**6.A.1** - Amount of water- and sanitation-related official development assistance that is part of a government-coordinated spending plan
6.B - Support and strengthen the participation of local communities in improving water and sanitation management	**6.B.1** - Proportion of local administrative units with established and operational policies and procedures for participation of local communities in water and sanitation management

Modified from https://www.unwater.org/publications/sdg-6-indicators-tiering-system.

Outside of countries with a history of legally mandated environmental objectives, the situation is more acute and accentuated by gaps in data collection and limits of institutional capacities (Irvine et al., 2016a). A key to the implementation of the SDGs, is the capacity to monitor and manage inland waters, and the known disparity between high, middle and low-income countries was highlighted in stark terms in the most recent progress report on *Global Indicator 6.3.2 Updates and Acceleration needs* (UNEP, 2021). In 2020, those countries at the lower end of the income spectrum used a fraction of the number of water quality measurements compared with wealthier countries, and often, the classification method applied was performed with little insight into natural conditions of these water bodies. This is supported in a review of the progress with the SDG 6 on water and indicator 6.3.2. Kirschke et al. (2020) found a negative relationship between the global human development index (HDI) that aggregates a small set of metrics on health, knowledge and standard of living (UNDP, 2016) and capacity challenges that need to be met to monitor water quality and to report on SDG indicator 6.3.2.

Integrated water resource management (IWRM) as a process for management of freshwater resources is considered within the SDG framework under indicator 6.5.1. This indicator requires country surveys to be completed that provide a broad overview of water-related policy, institutional arrangements and activities in countries. The most recent information available makes clear that huge improvements are needed in many countries. For example, approximately 50% of countries report limited management instruments for pollution control, and these are ad hoc, spatially limited and are rarely enforced (UNEP, 2021). On a positive note, this same report identified that with targeted efforts, rapid improvement is possible, but also that a "business as usual" approach is not an option.

The SDGs offer an important mechanism to take stock of the global capacity to monitor and assess the quality of inland waters and make clear the capacity gaps that urgently need to be filled. Many countries are near the start of this journey, but it is an essential one if there is to be any conclusion on whether the SDG targets have been reached by 2030. Target 6.3 is about improving water quality, but for those countries without suitable monitoring systems in place that struggle to collect information on their inland waters, it will be impossible to know whether this target has been reached. Putting the appropriate systems in place is becoming increasingly urgent given climate change and the predicted population growth in regions such as sub-Saharan Africa (UNDESA Population Division, 2019) and the associated increased pressure on water resources that come with it.

Looking forward for effective environmental water management

As pressures continue and are amplified by climate change (Moss, 2015), meeting the management challenge requires much more than the metaphor of Alice In Wonderland running faster to stay still (Carroll, 1865), but increased and concerted global efforts. The

challenges for environmental management in the global south are particularly daunting (Irvine et al., 2016a), stemming from a combination of increasing pressures to meet economic and food security and capacity to meet those challenges (Kirschke et al., 2020; Zimmerer, 2000). There are, however, powerful economic and business arguments for conservation of inland waters (Costanza et al., 2014; Russi et al., 2013), and greater employment of nature based solutions (Green et al., 2015; Vörösmarty et al., 2021; WWDR, 2018) that can support on-going economic needs and development (Lucas et al., 2013; van Asselen et al., 2013). It is also abundantly clear that progress in addressing multi-layered environmental challenges requires better alignment of economic, environmental and educational policies. The need to address these challenges so as not to sleep-walk into an environmental catastrophe is clearer now than at any other time in human history. The SDGs provide a mechanism to do that. From the science perspective this requires effective monitoring and common understanding of what the data are indicating (Lu et al., 2015). But this is not enough, and can only be at best a supporting mechanism, albeit an essential one. The real means to a more sustainable management of inland waters is the application of knowledge, as illustrated for a number of pressures in the following chapters and elsewhere in this Encyclopedia, connected and supported by policy mechanisms and political will. There is no doubt that achieving effective trade-offs between development and economic objectives and the ecological health and integrity of inland waters is a major challenge. Although national economies and local livelihoods ultimately depend on ecosystem services and benefits, public and political acceptance of this, although building, is not yet so clear and accepted, as Tickner et al. (2020) call for to "bend the curve" of aquatic ecosystem declines.

Solutions will not lie in the attempted preservation of designated 'protected areas', especially in the tropics where scientifically valid conservation planning can collide with social and historical realities (Adams and Hutton, 2007; Naughton-Treves et al., 2005; Sarkar and Montoya, 2011), and where protected areas do not necessarily safeguard river ecosystems and related livelihoods because of the influence of upstream impacts (Abell et al., 2007; Castello and Macedo, 2016; Feld et al., 2011; Nel et al., 2009). Throughout the world, accommodating human social structures for water management is crucial (Nel et al., 2007; Norgaard et al., 2009). Transitioning from traditional 'top down' authority to local management of resources is also not an assurance of better management (Etiegni et al., 2020; Lane and Corbett, 2005), or where poor design of new governance structures fails to meet community expectations (Kahmann et al., 2015).

Governance structures provide the setting for effective and sustainable resource management and practice (Pahl-Wostl et al., 2007), but even high quality evidence does not guarantee that decisions are made by rational actors. Sustainable development requires skills that can communicate across institutional structures (Irvine et al., 2016b). Effective environmental management requires the necessary investment in human and financial resources. The model employed with some success, but still with quite some variability, in more developed countries has relied on technically competent scientists producing verifiable information, reported and acted upon to develop and implement policy. While the value of long-term monitoring is well known(Lovett et al., 2007), in many parts of the world monitoring networks have declined over recent decades (Houghton-Carr and Fry, 2006). At the same time, the global agenda should interrogate how hidden assumptions, implicit biases and structural obstacles are built into 'best practice'. Collecting representative data of water and ecosystem quality needs effective institutional structures, and can be greatly assisted by the involvement of locally empowered communities in the monitoring and reporting of their own resources (Aceves-Bueno et al., 2015; Fritz et al., 2019). Engagement of this type with citizens can also provide an important bridge between the formal and informal institutions (Cleaver, 2012).

Ultimately achieving sustainable development, and effective protection and management of inland waters within that framework, will almost certainly need a re-assessment of dominant extractive economic models. The use of GDP as an indicator of societal wealth and successful growth has been recognized as a key obstacle to sustainability since the 1960s. GDP disregards the wealth of human capacity and the loss of natural capital (Perez-Carmona, 2013; Steffen et al., 2007). A shift from the outdated economic paradigm towards more equitable social systems may become a necessity rather than an ideological choice, but one that will bring considerable societal challenges, and likely conflict. It comes down to the capacity and willingness to adapt to change and new collective understanding (Figueroa et al., 2002; Pahl-Wostl et al., 2008).

In the face of difficult choices, environmental protection, and the management needed to achieve that, seems often to be viewed as a dispensable luxury. Yet, the evidence is clear and stark that insufficient environmental safeguards lead to more costly options and a diminishing of human well-being. Environmental degradation has been defended with the logic of the Environmental Kuznets Curve (EKC) (Grossman and Krueger, 1991). This supports a policy that allows environmental degradation in the interests of economic growth, and that the clean-up can come later (Azadi et al., 2011). While de facto this has occurred throughout global North, where attention to environmental protection becomes sequential, not simultaneous, with industrial development, the EKC has not stood up well to critical analysis (Mills and Waite, 2009; Rudi et al., 2012). In the sayings of the wise, the idea that "prevention is better than cure" is a much more logical and critical path (Spears et al., 2021).

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Measuring Impact, Overview and Reference Conditions

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Baseline syndrome The tendency to judge change based on a view constrained by experience or life-span of an individual. A similar phenomenon can occur at the collective, or policy dimension.
Designated beneficial use A numerical or narrative statement identifying maximum concentrations of various pollutants compatible with its use.
Driver A policy or economic demand that leads to a change in human activities that have the potential to change the structure and function of an ecosystem.
Ecosystem service The goods and benefits that humans derive from an ecosystem.
Impact The consequence of a pressure or stressor that leads to observable and measurable change in the structure and function of an ecosystem, affecting the use or value of the ecosystem.
Indicator A component of an ecosystem that can be measured and which provides a surrogate of the extent of change from defined pressure(s) or impact. An indicator can be a single measurable metric, or a combination of metrics that are assessed together to form a multi-metric.
Palaeolimnology The study of the history of a waterbody through the examination of the sediment that enables a reconstruction of environmental conditions over time.
Pressure This results from the driver, and usually applies to the input of a harmful chemical, alteration of physical condition, or the activities of an invasive species. Pressures can occur in isolation or in combination.
Reference State The character and quality of an ecosystem against which changes, usually from human activities, can be compared.
Response A policy or management action that is intended to reduce pressures, stressors or mitigate impact or improve the state of an ecosystem.
State The character of an ecosystem.
Stressor Sometimes used as a more precise descriptor of a factor that can have a direct effect on components of the ecosystem.

Introduction

The aim of this chapter is to introduce an overview of the environmental assessment of water bodies and how the concept of Reference Condition is a fundamental part of that. The chapter outlines the commonly used DPSIR model for managing impact. Establishing a baseline is essential for measuring the current state of the ecosystem, and the Reference State provides a means of comparison for judging the health of an ecosystem, for setting targets of what might be the limits of acceptable change, or to guide ambitions for restoration.

The driver (D), pressure(P), state (S), impact (I) and response (R) model

Measuring impact on an ecosystem depends fundamentally on the expectation of change as a result of something that can lead to that change. For environmental management, that something arises from a "Pressure" that leads to an increase of a "Stressor," resulting in a change of the environmental condition, or "State." This idea is captured in the now commonly used drivers, pressures,

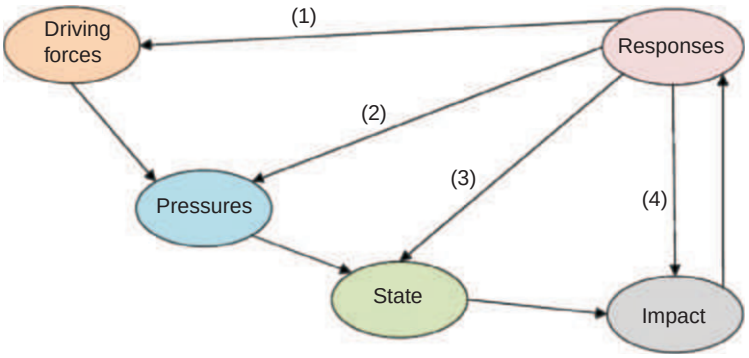

Fig. 1 Conceptual links between drivers, pressures, state, impact and response proposed by Smeets and Weterings (1999). In the diagram a separate Response can be effected to address each of the other components. See text for further details. Diagram adapted from www.eea.europa.eu.

state, impact, response (DPSIR), originally proposed by Smeets and Weterings (1999) to support environmental assessment and decision making, and using environmental indicators that:

1. "supply information on environmental problems, in order to enable policy-makers to value their seriousness;
2. support policy development and priority setting, by identifying key factors that cause pressure on the environment; and
3. monitor the effects of policy responses."

The DPSIR model (Fig. 1) that supports these objectives is conceptually straightforward, can be applied across a wide spectrum of environments and circumstances, and can incorporate multiple sectors.

The use of the DPSIR model is very common, used as both a means to communicate information of the state of the environment to stakeholders and interested parties (van Asselen et al., 2013) and to frame major environmental policy such as the EU Water Framework Directive (Council of the European Communities, 2000). An overview of definition and interpretations of the DPSIR model are:

Driving forces: The underlying causes/origins of pressures on the environment. These are normally considered to be human induced (anthropogenic) and brought about by social, demographic and economic change and developments, although some authors include natural drivers of change in their definition. Distinction can be made between Direct Drivers, usually manifest at local scales, and Indirect Drivers, resulting from wider policy, economic decisions or circumstances. For example, political decisions to promote or regulate a commodity for export in one part of the world can lead to environmental pressures in another.

Pressures: The outcomes of the driving forces, which influence the current/future environmental state. Pressures can be considered as potentially damaging to the environment, or demonstrably damaging, the latter suggesting that there are thresholds below which the e.g., emission of a pollutant or a change in land use is not of concern. A potential misgiving of this approach is that it is very susceptible to particular political or stakeholder interests. The term stressor is sometimes used to illustrate when an individual pressure, such as increased nutrient emissions to water are likely to cause an impact (see below).

State: The physical, chemical or biological condition of the environment, often described by physical or chemical variables, or single or a combination (multi-metric) of physical-chemical, biotic or even socio-economic indicators. State has also been defined in terms of vulnerability and risk of damage (Fassio et al., 2005). Generally speaking the state can be measured, either directly (e.g., extent of a wetland; or by in situ environmental sampling of key variables) or judged by expert opinion or perceptions of interest groups. This can lead to contradictions. A productive fishery may be viewed as being in a good state, even though chemical and other biological measurement may indicate some impact from pressures.

Impact: The effect of changes of a state on human population, economy or ecosystem in terms of damage (or benefit) to ecosystem functions and services. This could be, for example, in terms of biodiversity loss or changes, reduced flood regulation capacity, lower fish yields, or reduced quality of water supply. It can also be from a socio-economic perspective, and considered as a negative (the more common), neutral or positive effect. The combinations of these perceptions can be viewed in terms of a utilitarian view of ecosystem services (Millennium Ecosystem Assessment, 2005). Maxim et al. (2009) identified that "it is clear that different disciplines are dealing with different aspects of Impacts, and are addressing different things with this same concept." The view of impact can be in the "eye of the beholder."

Responses: These are mechanisms put in place at a political or societal level to remove or reduce drivers, ameliorate pressures, improve a state or mitigate an impact. Response can comprise e.g., a policy instrument, commercial incentives, educational awareness program, or on-site management measures. Any given response can target any, or several, of the drivers, pressures, state or impact. Policy responses can reverse previous policy decisions that were instrumental in promoting the relevant drivers in the first place. By way of example, applying the notations in Fig. 1 to nutrient enrichment of waterbodies from dairy production could be: (1) trade agreements that reduce incentive for high local cattle numbers that rely on an export market of dairy products; (2) national regulations that reduce spreading of slurry and fertilizer so to maintain concentrations of soil phosphorus below permissible levels; (3) maintenance of riparian vegetation that reduces nutrient loss from land to water, or provides shade to reduce temperature and light intensity on the waterbody; and (4) manipulation of fish stocks in a lake to remove small fish that feed

preferentially on those species of plankton that can efficiently remove algae, so that concentration of nuisance algae are reduced. In this example, the likelihood of the response being successful reduces along the D-P-S-I chain.

It can be seen that while the DPSIR framework provides a useful structure for the description and evaluation of the environment and impacts on it from pressures, there are a number of features open to interpretation, and even contradiction. Uncertainty inherent in natural systems can influence its use (Maxim et al., 2009). It is for this reason that clarification of meaning and use of the terminology in each circumstance is advisable. This applies in some way to all components of the DPSIR model, but is of particular importance for defining and measuring state and impact. This becomes more difficult when considering the effect of a combination of pressures, leading to multiple stressors that can lead to combined, and often unpredictable, effects on the character of an ecosystem. Impact from multiple pressures can be additive, synergistic, or neutralizing (O'Toole and Irvine, 2006).

Judging impact

Measuring an impact on an ecosystem requires making a judgment of the condition in the absence of pressures. It is often easy, even for the untrained eye, to see when a waterbody is grossly polluted. Anyone looking into the Bagmati River flowing through Katmandu (Image 1) would be hard pressed not to recognize that discolored water, an assortment of rubbish, even dead cattle on the banks, its use as a crematorium site and the pungent odor as unmistakable clues that this was an unhealthy river. However, even where a waterbody may look like it is in good condition, or where water policy standards have been set to define acceptable water quality, this does not equate necessarily to no impact. Making a judgment about environmental impact requires two, not necessarily compatible decisions. First, what would be the state of the waterbody in the absence of a stressor? Second, what is the acceptable threshold of water quality or ecosystem health? Answering the first question is often technically challenging. Answering the second question reflects a societal, often governmental, choice.

Inland waters have been disturbed by humans since the Neolithic. Early impact would have arisen from alterations of the landscape, notably forest clearance, and the subsequent mobilizing of sediment loss to waters. As humans congregated into larger communities, adjacent waterways became the conduits of human waste, with urban rivers noted for their pungent smells and, increasingly, associated with fevers from unseen pathogens (Image 2). Global industrialization of the 18th and 19th centuries led to further emissions of pollutants. These included toxic substances such as heavy metals in effluent entering waterbodies; and aerial deposition of pollutants from factory chimneys, carried by the wind and polluting waterbodies even at considerable distance from their origin.

Recent, and projected, changes in climate patterns can profoundly affect the physical structure of waterbodies, and their ecological response to pressures and stressors. These include single or combined pressures from e.g., nutrient enrichment, alien species, reductions of large mammals, and patterns of fish migrations through over exploitation and obstructions to fish movements (Moss, 2015; Penk et al., 2015; Zarfl et al., 2015). Climate mediated changes in the structure of ecosystems and their response to pressures raises the question if it is even reasonable that reference state is a valid concept in a rapidly and profoundly changing Anthropocene (Kopf et al., 2015). The answer depends on what an estimate of a reference value is used for and, hence, the purpose of having one.

Image 1 The Bagmati River flowing through Katmandu. https://www.flickr.com/photos/philcilcain/with/5249028642/Attribution-NonCommercial-ShareAlike 2.0 Generic (CC BY-NC-SA 2.0).

Image 2 Caricature published in Punch at the time of the "Great Stink." The River Thames introduces his children—diphtheria, scrofula and cholera—to the city of London, showing some understanding that the river was a danger to health. John Leech—Punch 35: 5. 1858. Wikimedia Commons, the free media repository.

Setting reference conditions

Assessing the state of a waterbody requires a judgment based on expectation compared with a defined baseline condition. Early monitoring of rivers in the US and Europe focused on measurements of pathogens and assessment of biota downstream of public sewerage outfalls as an indicator of river pollution (Hawkes, 1998; Hynes, 1960). The presumed, if often unstated, reference value was the conditions upstream of an organic-rich point source of pollution from an outfall of sewage or organically rich industrial emission.

Modern views of reference state are much more encompassing than the previous upstream-downstream comparisons, with wider reaching considerations of what would be the condition of a waterbody in the absence of human pressures. Assessment of surface waters in the US is often based on "Designated Beneficial Use," outlined in the U.S. Clean Water Act (1972), and supported by quantitative or qualitative descriptors (Davies and Jackson, 2006; Goldfarb, 2020).

A healthy ecosystem would be expected to support a diversity of life compatible with natural background water quality and hydrology, intact habitats and a low level of human disturbance. The idea of naturalness provides a very simple mental picture of the baseline or reference state. It is along these lines that a number of national water policies, including the very comprehensive EU Water Framework Directive (Box 1), are predicated on.

Under the WFD, each waterbody "type" is defined in terms of broadly recognized character (e.g., lakes, rivers), physical features (e.g., size, depth), geography (e.g., ecoregion, high altitude, low altitude), and background water chemistry (e.g., acid neutralizing capacity). The principle is that waterbodies with similar natural geological and landscape settings are compared with each other. As waterbodies lie across multidimensional continua, it is clearly a compromise between the practical need to keep the number of types as low as possible and maintaining the power to discriminate between natural variability and human impacts.

The seemingly simple and attractive idea is that each waterbody type has an expected natural composition of plants and animals, and when that composition is minimally disturbed it can provide an anchor (or reference state) with which to evaluate changes to the waterbody brought about through human activities. The environmental quality of any waterbody can then be assessed along a

Box 1 General definition of the upper tier (High Status) of a waterbody type under undisturbed conditions from Annex V of the EU Water Framework Directive (WFD, 2000).

"There are no, or only very minor, anthropogenic alterations to the values of the physico-chemical and hydromorphological quality elements for the surface waterbody type from those normally associated with that type under undisturbed conditions. The values of the biological quality elements for the surface waterbody reflect those normally associated with that type under undisturbed conditions, and show no, or only very minor, evidence of distortion."

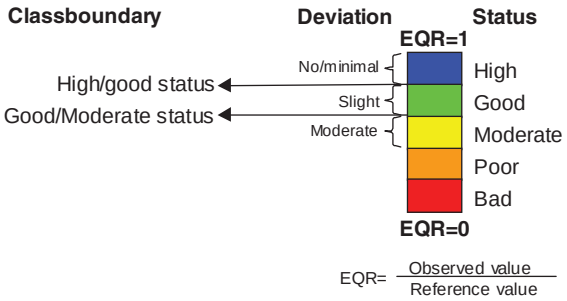

Fig. 2 The five-category classification of the EU Water Framework Directive. Waterbody status is derived for a measurement of critical biological and supporting chemical and hydromorphological elements. Source www.epa.ie.

five-category scale (Fig. 2) based on departure from reference state, and measured by an "Ecological Quality Ratio" derived for each of a number of biological "elements" appropriate to the waterbody type being assessed. Since its ratification by European Member States in 2000, the WFD has generated multiple official guidance documents and thousands of reports and publications. A good overview of the early progress is provided by Hering et al. (2010). More critical reflections are provided by Moss (2008) and Bouleau and Pont (2015). For many aquatic ecosystems where habitats are complex and subject to stochastic changes such as vegetated wetlands, the description of a reference condition can seem an elusive concept (Beuel et al., 2016).

Variations in meaning and interpretation of the reference state concept are widespread (Gibbons et al., 2008; Stoddard et al., 2006; Verdonschot, 2000), including: "totally or nearly totally undisturbed conditions" (WFD, 2000); "best available" (Clarke et al., 2003), "least disturbed" (Davies, 2000; Reynoldson et al., 1997; USEPA, 2002; Wigand et al., 2010); "best attainable" (Harrison and Whitfield, 2006); sites with low pressures (Lougheed et al., 2011); "relatively undisturbed biological communities" (Logan and Taffs, 2011); departure from full ecological integrity (Fennessy et al., 2004); and "historical condition" (Nijboer et al., 2004; Young and Sanzone, 2002).

Reference conditions are commonly understood to refer to sites in near-natural conditions at one end of an ecosystem health continuum. It is clear, however, that perception of reference condition, on which assessment of impact must logically be based, is anything but straightforward. The difference between expert subjective opinion and objective verification can be marked (Nõges et al., 2009; Oberdorff et al., 2001). In Ireland, a test using diatom records preserved in sediment cores on the validity of expert opinion, showed that only 11 out of 35 candidate lakes were verified as being in reference condition (Leira et al., 2006). All had mean water column concentrations of total phosphorus (TP), a measure of nutrient status, of less than 20 μg L^{-1}. Misperceptions of water bodies considered as having no or minimal impact from human pressures can lead to errors in classifying a site along a gradient of impact (Oberdorff et al., 2001). Guidance documents from the EU (European Commission, 2003) recommended that pressure criteria be used to screen for potential reference because the reference community is expected where there is no or only very minor human induced disturbance. Nevertheless, natural variability can sometimes mimic an impact (Hartnett et al., 2011), and, in a type-specific approach to the setting of reference state, can have a large effect on the perceptions of the biotic composition of average reference state.

Type-specific reference (Bailey et al., 2004) assumes concordance of biotic communities among similarly-typed water bodies, or influenced similarly by natural changes within a regional reference network (Bates Prins and Smith, 2007). Nevertheless, even in similar types of waterbodies, there can be a distinctiveness among individual sites. Given that separate water bodies have their own character, this is not surprising. While this does not invalidate the idea of assessing type-specific waterbodies to detect overall patterns of change, it does raise questions about the validity of the approach. This led to the view among a number of workers involved in the implementation of the EU WFD, that "site-specific" estimates of "true" reference state is the most valid approach (Carvalho et al., 2009; Jyväsjärvi et al., 2009); so that the ecological health of a waterbody site is only compared with itself over temporal scales and not across a network of albeit similar sites. However, this approach necessitates long-term monitoring, or use of robust site-specific mathematical models (Aroviita et al., 2009; Cardoso et al., 2007; Carvalho et al., 2009; Clarke et al., 2003).

Estimates of reference state

For pollutants, such as aromatic hydrocarbons, pesticides and herbicides, pharmaceutical residues and plastic particles, natural background concentrations can be considered as zero. Detecting these in water samples indicates pollution of some degree. The extent that this is viewed as an environmental problem depends on establishing a relationship between concentrations and effect, as for all other stressors, but there is little doubt the site is not at reference state unless concentrations of the pollutants are considered to represent trace background amounts. Some pollutants have dispersed through the atmosphere to the most remote parts of the globe. For many pollutants, establishing reference state can be also very uncertain. Heavy metals, for example can be common in many soils and, hence, contained in the runoff to waterbodies. Many metals occur naturally at concentrations that can pose a risk to public health. Water quality standards for such toxicants are derived from toxicity studies rather than the use of reference values discussed here. Reference state for invasive alien species might be considered as zero presence, although that raises interesting questions on the status, and our views of species that may have been introduced by humans centuries ago, and are now considered as naturalized.

The EU WFD defined Reference State as synonymous with High Status, but raised further discussion if reference should be anchored at the upper, higher quality, end of the High Status category (Pardo et al., 2010). This has intuitive value, otherwise the

reference bench mark will be set where minor impact has already occurred. However, it is difficult to separate the top of the range from others in the same quality category (Erba et al., 2009). Similarly, it is difficult to reliably distinguish ecological boundaries between successive status classes (Ellis, 2006; Hering et al., 2010; Irvine, 2012).

The WFD allows type-specific reference conditions to be "either spatially based or based on modeling, or may be derived using a combination of these methods. Where it is not possible to use these methods, EU Member States may use expert judgment to establish such conditions. In defining high ecological status in respect of concentrations of specific synthetic pollutants, the detection limits are those which can be achieved in accordance with the available techniques at the time when the type-specific conditions are to be established."

Guidelines provided for similar purpose in Australian/New Zealand (ANZECC/ARMCANZ, 2000) are that reference conditions can be derived from: (i) historical data collected from the site being assessed; (ii) spatial data collected from sites or areas nearby that are uninfluenced by disturbance; or (iii) data from other sources if there are neither suitable historical data nor comparable reference sites nearby. The South African River classification scheme (Roux et al., 1999) evaluates river health across four categories, the highest quality of which is "negligible modification of instream and riparian habitats and biota."

Irrespective of the method used to set a reference value, its purpose is to provide a fixed point for which monitoring can be used to assess change, and thereby enabling classification of a waterbody across a continuum or among categories of quality. The principle is more straightforward than the practice. In northern Europe, for example, widespread changes to catchment have occurred since the Neolithic period, but using that as a baseline has little merit for modern day water management. More recent comparison with a time before industrialization or intensive agriculture have greater appeal, but is susceptible to unfounded assumptions. A reference date of ca 1850, and prior to establishment of major 19th century industrialization, may be appropriate for the United Kingdom, but in nearby Ireland this period coincided with high impact to lake water quality from an increasing human population in the century leading up to 1850, and followed by a major de-population caused by the Great Irish Famine (Donohue et al., 2010). In other parts of Europe, major changes to water quality were associated with the introduction of the plough, as shown for Danish lakes (Johansson et al., 2005).

The Irish and Danish records mentioned above were based on the historical record captured in the sediment (Image 3). This enables quite an accurate reconstruction of the state of many lakes when samples can be collected from relatively undisturbed sediment. Inputs of materials from the catchment and the residues of internal production that settle out of the water column can be used to trace the history of geological events, landscape changes, industrial production and climate shifts. The study of the sediment of lakes (or "palaeolimnology"), developed over the first half of the 20th century (e.g., Pennington, 1943, 1947), but came to widespread attention in the 1980s in the investigation of lake acidification (Flower and Battarbee, 1983; Renberg and Hellberg, 1982), and

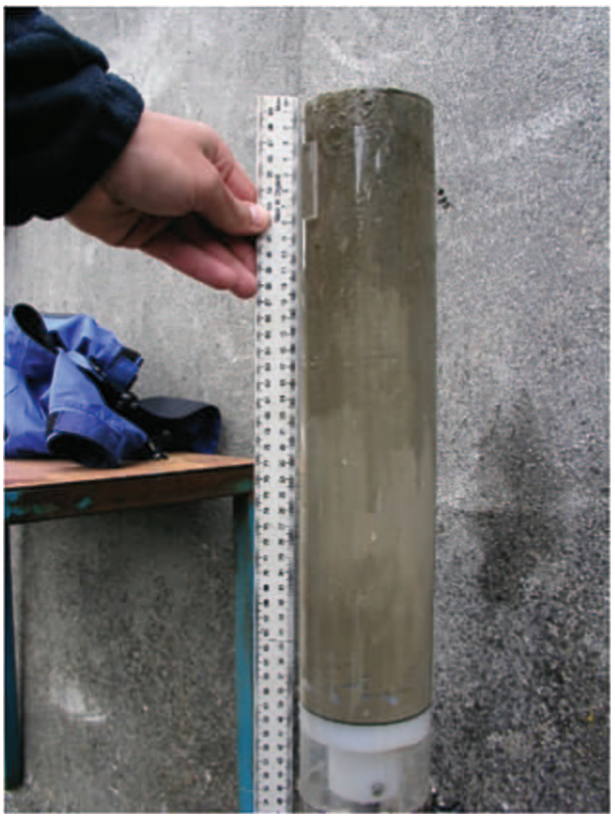

Image 3 A core of sediment extracted from a shallow lake contains an historical record from chemistry and remains of biological organisms. Photo credit: David Taylor.

supported by the development of accurate dating from the radioactive decay of ^{210}Pb in the sediment. Dating of sediment is important because rates of accumulation of material raining down from the water column is neither constant within or across lakes. Other signals that assist in the accurate dating of sediment profiles are ^{137}Cesium-137, from nuclear weapons testing, or other locally applicable events that relate to a specific period, including volcanic ash and carbon deposits, related to e.g., 19th century industrialization. Palaeolimnology is now a standard technique used for reconstructing the history of lakes from the recent or distance past. For a very readable overview see Smol (2008).

For some slower flowing rivers, sediment deposits can provide a sufficiently readable historic record, but generally speaking palaeolimnology is not suitable for rivers because of dynamic hydrology and frequent disturbance of the river bed. In marshes and swamps, sediment profiles have been used successfully to trace shifts and historical development of agriculture, largely from pollen analysis (Lejju et al., 2006), although of limited use is assessing a true reference condition relevant to contemporary wetland management. Assessing quality of swamp or marsh like habitats often uses contemporary observation of wetland ecological structure and function against perceived, or theoretical reference state, to assess current wetland health (Brinson and Rheinhardt, 1996; Kotze et al., 2020).

For dynamic systems, such as vegetated wetlands and rivers, direct in situ measurements as a means to estimate what might be considered as true reference state is not possible. Additionally, the lack of suitable reference sites in some regions (Bennion et al., 2004; Borja et al., 2007) has led to selection of "least impacted" or "best available" as description of reference sites. This is not the same as reference state (O'Toole and Irvine, 2006), although it is a view that can influence (we could say distort) policy decisions (Dodkins et al., 2005). Selecting best available sites as the reference value is, at best, ecologically useful if based on the assumption that these sites are subject to low pressures (Erba et al., 2009). A notable example where comparison with a reference network of sites with a similar nature has been used to set the reference anchor is the River Invertebrate Prediction and Classification System (RIVPACS) (Clarke et al., 2003) and the Australian River Assessment System (AusRivAS) (Davies, 2000). In RIVPACs, the condition of a sampled site (the Observed site) is compared with that of the "expected" metric from the reference network. Reference state in this sense is not un-impacted per se. In some countries long-term monitoring that has coincided with widespread decline of water quality serves as a reasonable baseline, with those sites originally classified in the top tier of quality a reasonable estimate of reference state (White (née Ní Chatháin) et al., 2014).

Baseline syndrome and users' perception

Over the last several decades, water quality objectives have been developed as a means to safeguard surface and ground waters from impact considered detrimental either to human or ecosystem health. Criteria for protecting human and ecosystem health are not necessarily the same. The World Health Organization (WHO) estimates of safe limits of nitrate of 50 mg L^{-1} in drinking water provides allowance for a concentration of nitrate an order of magnitude higher than that which would have an ecological effect, through stimulating primary production, in surface water. Across a range of toxicants there can be different national standards for the protection of human and ecosystem health (Lijzen et al., 2001).

In some jurisdictions, such as under the US Clean Water Act (CWA) 1972, quality standards that represent "beneficial use" (see above), designations for public water resource and quality consider a water's assimilative capacity for pollutants, based in an assessment of total maximum daily loads (TMDLs). Highest quality waters can be designated as "Outstanding National Resource Waters" nominated by stakeholders. This level of public participation in identifying high quality waters introduces a very interesting level of public perception of local value in ecosystem water management. It raises questions such as "What does a "healthy" river mean, and for whom does it have benefit?" This very much relates to utilitarian ideas of ecosystem services, and the goods and services that humans derive from ecosystems (Millennium Ecosystem Assessment, 2005). It also evokes questions of human perception and decision making of what merits protection and at what cost? Technically justified ecosystem standards may or may not be in-line with local views and needs. Fishing for species of coarse (a general term applied to non-salmonids in United Kingdom) fish commonly found in canals and moderately polluted waterbodies is an extremely common recreational activity in the United Kingdom (for overview of recreation fishing in United Kingdom see Winfield (2016)). Formal evaluation of the state of United Kingdom surface water bodies by Carvalho et al. (2019) shows widespread degradation, but many of these degraded waters provide very suitable habitat for coarse fish and extensive recreational benefit. If a society's desire was to catch more fish on a Sunday afternoon, then investment in the restoration of the coarse fishers' hobby location may not be popular. However, perceptions of the quality of the habitat will almost certainly be influenced by the experience and memory of those who use it.

Shifting baseline syndrome (SBS) is when perception of worth, be it water quality or anything else, is determined by individual or collective memory (Soga and Gaston, 2018). If the perception of ecosystem health is compared by succeeding generations based on life-time experience, motivation or restoration or higher degree of protection are reduced (Ainsworth et al., 2008; Campbell et al., 2009; Pauly, 1995). Perceptions of quality can transcend to estimation of reference state, and can be particularly troublesome for views of regional water quality. A scientific career working in shallow lowland eutrophic lakes with high pressures from nutrient loadings provides a very different baseline perception compared with those working on similar lakes subject to much lower intensity of human pressures. For management, SBS can erroneously set targets of high quality for what in truth are degraded habitats (Humphries and Winemiller, 2009). Examples that apply to the EU WFD are the association of high nutrient concentrations with Good Status (Moss, 2008), not considering alien invasive species in ecological assessment (Irvine, 2009), and misperceptions of contemporary ecological state compared with putative reference state (Leira et al., 2006).

If professional expert judgment is susceptible to SBS, the risks for other stakeholders are likely to be greater. The increasing engagement of citizen and community science and of institutions such as River Trusts and other interest groups in water and ecosystem assessment, raises important issues of how perception affects management goals and the democracy of water quality objectives.

Decision making

It is common for national water quality assessment schemes to depend on categories of quality, typically comprising four or five quality classes, such as occurs under the EU WFD (Fig. 2). While the anchor point is implicitly or, preferably, explicitly based on a reference state with defined characteristics, successive boundaries separating quality classes are in effect also applying criteria of baselines between adjacent classes. Very often these classes have legal meaning and are used to define a quality class and need for water quality improvements, raising some crucial considerations for management and environmental compliance (Howarth, 2006).

In any management plan, it is important to identify minimally impacted sites, and decide if these represent a true baseline (as discussed in "Setting reference conditions" section) or the best available, least disturbed, sites. This is important for setting management targets. In many situations, setting targets for "best attainable condition" (BAC) may be the more reasonable approach (Stoddard et al., 2006) while appreciating that it is not the same as a true reference state. Targets are only achievable if there is sufficient understanding of the link between pressure and impact to be able to set relevant indicators for monitoring (Lovett et al., 2007). In assessing quality, the closer a metric score is to a class boundary, the greater the statistical probability of misclassification (Clark, 2002; Ellis, 2006). Uncertainty can be reduced with more sampling effort, and, for biota, targeting representative habitats, although that loses information on e.g., total species richness. Resource limitation also prevents more detailed sampling effort. In any case, appreciating uncertainty in ecological assessment can liberate the over-reliance on using fixed-boundaries for waterbody classifications (Irvine, 2012). Uncertainty in all stages of water quality management can be reduced through quality assurance at all stages of the process, from sampling to reporting. Communicating uncertainty to stakeholders improves transparency and makes for better decision making. Adopting a philosophy of no-deterioration and continuous reduction of risks to water quality, checked by periodic monitoring, is recommended.

For water quality and ecological management, it is impossible to ignore that assessment of quality depends on monitoring, and the interpretation of monitoring results depends on understanding of the link between pressure and impacts (Fig. 1). This guides the selection of relevant indicators to be monitored (Lovett et al., 2007). Attributes for a successful indicator (http://www.epa.gov/bioindicators/html/about.html) are that "the indicator is objective; the indicator is transparent and reproducible; the underlying data are characterized by sound collection methods, data management systems to protect their integrity, and quality assurance procedures; data are available to describe changes or trends; the data are comparable across time and space, and representative of the target population; and the indicator used is relevant for the system(s) studied." The reliability of the indicator is influenced by natural and operation variability. Natural variation, is inherent in all ecosystems, and if monitoring fails to account for that, reliability of results, and hence policy relevance, is reduced (Irvine, 2004).

Naturally, the use of any indicator of water quality is part of a cycle of environmental management, within which water quality monitoring is just one, albeit crucial, part. Many representations of the monitoring cycles can be found, but the purpose is to put in place a well-structured series of connected processes designed to detect, report and act on changes of water quality (Timmerman et al., 2000) (Fig. 3).

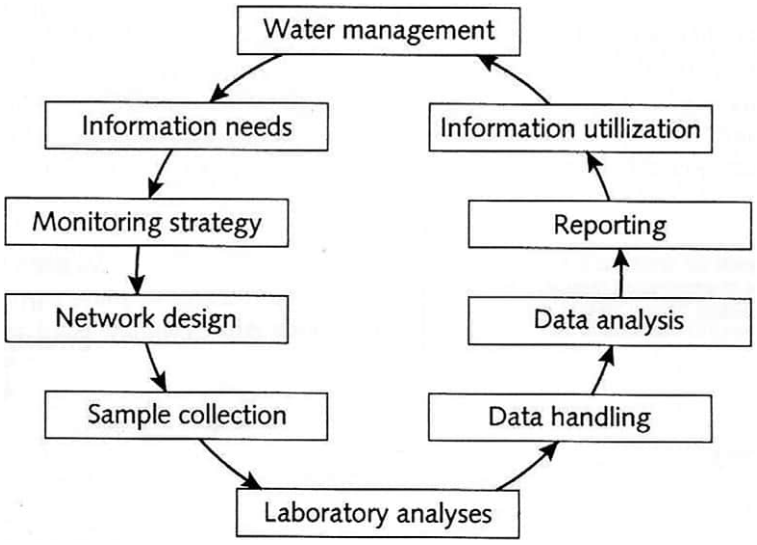

Fig. 3 An example of the monitoring cycle. Laboratory analysis can be for any physical, chemical or biotic variable, including those measured in situ in the water body. After Chapman D (ed.) (1996) Water Quality Assessment—A Guide to the Use of Biota, Sediments and Water in Environmental Monitoring. London: E & FN Spon.

Connecting the components of water management is an ongoing process of planning, setting objectives compatible with relevant policies, monitoring, reporting and reviewing. Adapting to new circumstances and development of knowledge maintains the relevance of management objectives (Pahl-Wostl, 2009). However, no matter what the adaptive capacity entails, assessing the current state of a waterbody compared with a robust description of reference state should remain an essential element of the process.

Conclusion/Synthesis

Key points covered in this chapter are:

(i) An assessment of anthropogenic impact of a waterbody requires an estimate of the State of environmental condition in the absence of, or subject to only minimal, disturbance. This Reference State enables a judgment on how far an ecosystem has departed from no or minimal impact. It aids decisions in protecting remaining high quality sites and setting realistic restoration targets where impact has occurred. Estimating the true reference state, can however be difficult. In contrast, relying on the best available condition as a reference point, concedes the acceptability of an ambition limited to lesser quality sites and increasing the risk of further biodiversity loss and diminished ecosystem services.

(ii) Measures of ecological quality range from simple metrics of quality derived from expert opinion to complex multi-metrics techniques developed across waterbody types. However, all quality metrics reflect some agreed view of quality, involve some uncertainty, and are ultimately subject to the judgments of scientists, policy makers, and citizens.

(iii) Whatever the approach adopted, descriptions and rational of reference state and how this is used to assess ambient ecosystem quality should be clearly outlined in relevant policy and management plans. The use of a natural (no impact) or historical reference using available data from the past, is recommended, but it may be necessary to consider reference condition from the commencement of monitoring, or other well-defined criteria This can include the use of mathematical modeling that predicts the ecological state commensurate with minimal impact.

(iv) Adopting a philosophy of no-deterioration and continuous reduction of risks to water quality, checked by periodic monitoring, is recommended. This follows an Environmental Management approach where the goal is to prevent ecosystem deterioration or work towards continuous improvement.

Knowledge gaps

(i) Estimating reference state and incorporating uncertainty in both the initial estimate and departure from it, are poorly understood and controversial. Even when applied within a systematic typology, establishing baseline/reference conditions can be controversial, with varying definitions and interpretations potentially legitimizing the lowering of targets and baselines.

(ii) The setting of reference conditions for policy compliance remains a significant challenge. There are largely unresolved discussions of what is natural or how to include invasive alien species in the assessment of reference state.

(iii) Estimating probabilities around quality class designation provides a more realistic, and in the longer-term, useful approach for management compared with dependence on fixed-boundary schemes. It remains challenging how to apply these in data-poor situations and considerable further work is required to link uncertainty to boundary conditions.

(iv) Because there are various views of reference conditions, as described in this chapter, there is a need for greater consistency in the terminology. Reference condition can be used as a term to depict the naturalness of the structure and function of ecological communities. Further discussion and resolution is needed in describing minimally disturbed condition (MDC), historical condition (HC), least disturbed condition (LCD) and best attainable condition (BAC) following Stoddard et al. (2006).

(v) It remains challenging how to apply classification boundaries in data-poor situations, as now required for the global implementation of water quality assessment for the Sustainable Development Goals (UN Environment, 2018).

See Also: Human pressures and management of Inland Waters: Biological Invasions: Introduction, Establishment and Spread; Biological Invasions: Case Studies; Biological Invasions: Impact and Management; Citizen Science for Co-monitoring and Co-managing Impact on Ecosystems and Inland Waters; Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment

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Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Allochthonous organic material Organic material (e.g., leaves, twigs, pollen) that enters a freshwater ecosystem.
Autotroph An organism, such as an alga or green plant, that fixes inorganic carbon using light energy in the process of photosynthesis.
Beta diversity A measure of compositional heterogeneity between two sampling points.
eDNA (environmental DNA) Genetic material from organisms present in sediment and water which can be used to detect biota.
Hydromorphology A subfield of hydrology (the scientific study of water in the environment) which is concerned with understanding the change in the physical structure of waterbodies, and their water content, over time.
Meso-habitat A distinct habitat type in a habitat patch, such as a river reach with pools, runs or riffles. The presence of these habitat types increases the compositional heterogeneity of the habitat patches, which in turn leads to an increase in biological diversity.
Metabarcoding A method of identifying species based on a genetic sequence unique to that species (the barcode). In the process a sample of e.g., macroinvertebrates is homogenized, the genetic material of interest isolated and amplified. The amplified genetic barcodes are then read, and the species in the homogenized sample identified suing a database of known species barcodes.
Ordination An analytical method used in statistics, also known as gradient analysis, that orders objects along axes based on the similarity of their character values. Once plotted, similar objects will appear to cluster together, while dissimilar objects will be further apart.

River reach A short stretch of a river with similar hydrological conditions.
Taxonomic classification A hierarchical system in which organisms are classified into groups based on their physical similarities. There are eight main ranks in the system, from the general Domain rank, to the specific Species rank, they are: Domain, Kingdom, Phylum, Class, Order, Family, Genus, and Species.
Trophic guild A guild is a grouping of species based on similarities in function or feeding. A tropic guild is a group of species that feed on the same food (e.g., planktonic, algae-eating herbivores).

General introduction

The ecological impacts of pressures on freshwater environments are typically assessed by evaluating the extent to which conditions deviate from "reference conditions" (i.e., the conditions we expect to find in the absence of significant anthropogenic influence (Bennion et al., 2011; Stoddard et al., 2006). These can be defined in a variety of ways, including (a) analysis of historical data; (b) space-for-time substitution, in which conditions from similar unimpacted systems are taken to represent nearby reference conditions; and (c) expert judgment (in cases where data is absent) (Wallin et al., 2003). In order to assess the extent of impacts on freshwater systems, modern policies such as the EU Water Framework Directive (WFD) (2000) and the U.S. Clean Water Act (CWA) of 1972, require that methods be developed to assess, interpret and report on the ecological state of surface waters in relation to their reference conditions. These policies require both methods and data for defining baseline conditions against which past or future change can be assessed.

The assessment methods that have been developed for surface waters are diverse. Most rely wholly or in part on measurements of various freshwater biota that respond to general pressures, or more precise stressors. In this chapter we focus on the biota, discussing how impacts are reflected in various different taxonomic groups. We present case studies of methods that can be used to measure impacts based on monitoring of algae, macrophytes, invertebrates, and fish. We then discuss challenges associated with acquiring data, and show examples of some novel techniques that can be used to fill spatial and temporal data gaps.

Policy relevance for monitoring

Policies such as the EU Water Framework Directive (WFD) (2000) and the U.S. Clean Water Act (CWA) of 1972 require that methods be developed to assess, interpret and report on the ecological state of surface waters. The assessment methods developed for surface waters are diverse, and most rely on the different taxonomic groups discussed in this chapter, as well as information on water chemistry and hydromorphology. The bioassessment protocols developed for the WFD and CWA are comprehensive, making use of several indicator groups to assess the ecological state of a system. Across Europe, countries have for historical reasons, developed their own assessment methods. Still, these needed to be harmonized, meaning that conflicting or redundant standards had to be minimized, in order to report on the ecological status of European water bodies. Many of the biologically-based national methods are now intercalibrated (Poikane et al., 2014).

Freshwater biota as indicators of impact

Freshwater ecosystems are remarkable in that they cover a tiny 0.01% fraction of the Earth's surface, and at the same time are home to nearly 10% of its genetic diversity (WWF, 2018). The vast majority of faunal diversity is represented by the invertebrates (86%) and the rest by vertebrates. The most diverse animal taxon are the insects, followed by crustaceans, arachnids and mollusks. The least diversified groups are the rotifers, annelids, nematodes and platyhelminths (Balian et al., 2007). Freshwater algal diversity may well exceed 100,000 species when taking into account taxonomic uncertainty and the fact that many species in freshwater ecosystems still await discovery and taxonomic description (Balian et al., 2010). Many major taxonomic groups have been used for the assessment of water quality and ecological status, including bacteria, protozoans, algae, macrophytes, benthic macroinvertebrates, fish and birds (Moog et al., 2018). The most commonly used groups are the algae, macrophytes, invertebrates and fish. For use as indicators of ecosystem health, each organism group has distinct advantages over the others, and used for different purposes. Indeed, there is a general proliferation of bioassessment methods, with nearly 300 ways to assess surface waters in Europe alone (Birk et al., 2012).

Algae occur anywhere where there is enough light, moisture and nutrients. For monitoring in the short-term or to measure the effects of sudden changes, algae are ideal indicators in lakes and rivers, because they have short lifespans and high reproductive rates, leading to high community turnover. The turnover in the algal communities, benthic algal communities in the case of rivers and planktonic algal communities in the case of lakes, can be used as an indicator of impact (Ortiz et al., 2020). Also, as long as there is some water, algae are relatively insensitive to extreme hydrological conditions (e.g., high water velocity), which helps to reduce the number of variables that need to be considered when evaluating the status of an ecosystem.

Macrophytes, like algae, are autotrophs and thus respond to changes in available light and nutrients in both surface water and sediment, but are longer-lived and have lower reproductive rates. Responses to changes take longer as macrophytes respond to changing conditions over longer timespans. They are, therefore, ideal indicators of longer-term changes in the prevailing nutrient regimes of both rivers and lakes. Unlike algae, macrophyte sensitivity to hydromorphology is useful in ecological assessment (Hering et al., 2006).

Invertebrates, particularly benthic macroinvertebrates, are by far the most commonly used indicator group in freshwaters (Moog et al., 2018). They are visible to the naked eye, and mostly readily identified at least to the broad taxonomic classification of family. Invertebrates are an ubiquitous and diverse group, and taxonomically relatively well known. The tolerance across different invertebrate groups to reduced oxygen caused by organic pollution has provided the underlying mechanism for their use in early monitoring schemes (Resh and Jackson, 1993). The relatively long lifecycle of benthic macroinvertebrates allows for the analysis of temporal disturbances (DeWalt et al., 2010). Although mobile, macroinvertebrates generally stay close to their local habitats and thus are also sensitive indicators of spatially-dependent disturbances, such as hydromorphological alterations.

Fish are present in most surface waters and because of their large sizes their identification is relatively easy, at least in temperate waters. Their taxonomy, life-histories and environmental requirements are largely well-known. Fishes can be categorized according to their feeding preferences (Sánchez-Hernández, 2020) into detritivores, herbivores, planktivores, piscivores, benthivores and omnivores. There is a close relationship between what a fish eats and its shape. For example, bottom-feeders like catfishes tend to be chunky, while predatory fish like salmon are streamlined. Fishes are highly mobile, and thus are affected by hydromorphological changes on the meso-habitat and reach-scale. Lateral and longitudinal connectivity play a huge role for both fishes (Shao et al., 2019) and macroinvertebrates (Wang et al., 2020), although the latter are less well-documented.

In the following sub-sections, the uses of major taxonomic groups, the algae, macrophytes, macroinvertebrates, and fishes, in surface water assessment are discussed and case-study examples presented of common group-specific assessment methods.

Case study: Algae

Algae are major primary producers in freshwater systems and, along with bacteria and allochthonous organic material, form the base of the aquatic food chain. The disruption to natural algal assemblages by addition of nutrients such as nitrogen and phosphorus, which typically limit primary production, can lead to ecological cascades with negative implications for ecosystem structure and the human use of water bodies for a wide range of purposes. Increased concentrations of the nutrients that normally limit algal growth can lead to alterations of algal community composition and increased biomass. The water industry has long had an interest in the algae that inhabit water supply reservoirs, and the problems they can cause particularly at high biomass, because of the direct risks to potable water supplies through clogging of filters (Henderson et al., 2008), taste and odor problems (Perkins et al., 2019), and cyanobacterial toxins (Carvalho et al., 2011). The risk of cyanobacterial toxins can limit the use of water for recreational uses (Carvalho et al., 2013) and increase the cost of water treatment, while deoxygenation of nutrient enriched waters can affect the viability of commercial fisheries (Gerdeaux et al., 2006). Algal blooms are particularly acute in lakes and reservoirs (Harper, 1992), where most primary production is due to suspended algae (phytoplankton). However, in recent years, interest has also extended both to benthic habitats in lakes (Vadeboncoeur et al., 2002, 2003) and to rivers. Phytoplankton blooms can also develop in slow-flowing rivers (Moorhouse et al., 2018) but the focus in rivers is more typically on attached benthic algae.

Lakes and other standing waters

There is a long history of the use of chlorophyll *a*s a proxy for the quantity of algae present in lake water. In 1982, terms such as "oligotrophic," "mesotrophic," and "eutrophic" were defined in terms of nutrient and chlorophyll concentrations (OECD, 1982) and this provided a basis for many subsequent trophic classification schemes. However, chlorophyll concentrations alone give little indication of the types of algae present and are, therefore, of limited value for estimating risks from cyanobacterial blooms. For these more detailed insights, estimation of taxonomic composition is required. A standard working procedure using inverted microscopy has existed for some time (Lund et al., 1958) and has, more recently, been standardized (Comité Européen de Normalisation (CEN), 2015a). Results are commonly expressed as biovolume of each taxon present—calculated from the cellular dimensions as measured during the analysis and standard formulae for each of the many shapes and forms of phytoplankton (Comité Européen de Normalisation (CEN), 2015b). This gives an indication of the relative proportion that each taxon makes to overall primary productivity, which means that contributions of key species can be evaluated and risks computed (Carvalho et al., 2011). Calculation of biovolume is, however, time-consuming and World Health Organization guidelines for managing toxic cyanobacteria are expressed in simpler terms (World Health Organization (WHO), 1999): the numbers of cyanobacterial cells per milliliter, with 20,000 cells/mL representing a threshold above which there is a low probability of adverse health effects, and 100,000 cells/mL representing the threshold for a "moderate probability" of adverse health effects.

Assessment of chlorophyll concentrations, nonetheless, provides either adjunct information or, in some situations, a viable alternative to enumeration and identification. Procedures for analyzing chlorophyll are well-established and the lower cost means that higher frequency sampling is possible, and is more commonly used than full enumeration and estimation of biovolumes. Long-term trends in chlorophyll provide evidence of the benefits of reducing nutrient inputs to lakes (e.g., Reynolds et al., 2012).

Rivers and streams

Assessment practices in flowing waters differ in two significant ways from that in lakes: algal assemblages are assumed to be vulnerable to a wider range of stressors than just nutrients and applied analyzes focus particularly on one group of benthic algae, the diatoms. Nutrients are one of a number of simultaneous stressors in rivers, and several metrics also capture toxic effects of ammonium-N, deoxygenation, heavy metals and salinity/conductivity, often referred to collectively as "general degradation."

Most of the metrics used to assess ecological health in rivers use diatoms as proxies for the entire algal community (Fig. 1), either to indicate general degradation (e.g., Indice de Polluosensibilié Specifique, IPS, Coste in CEMAGREF, 1982) or eutrophication (e.g., Trophic Diatom index, Kelly and Whitton, 1995). In addition, a few metrics have been developed to assess acidification (Juggins et al., 2016), and a few focus on soft-bodied algae rather than diatoms (e.g., Schneider and Lindstrøm, 2011). As for phytoplankton in standing waters, the type of water body has an effect on the observed communities, which then needs to be compared against an estimated reference condition (Kelly et al., 2020; Charles et al., 2021) provide a summary of all the benthic algae metrics used in the European Union and the United States.

Implications for the assessment of freshwaters using algae

If algal-based tools are to detect long term trends of change, then forward and backward compatibility of data is essential. For diatoms, in particular, this can be achieved by archiving slides to give the option of re-analyzing samples as taxonomic knowledge increases. A second important criterion is that methods are harmonized and, where possible, conform to national and international standards (Comité Européen de Normalisation (CEN), 2014a,b). This provides confidence that comparisons focus on the environmental "signal" rather than on "noise" introduced by sampling and analytical differences. Thirdly, most algae-based methods depend on the identification of groups of highly diverse organisms, but that often appear to be morphologically similar, and whose differentiation therefore depends on working at the limits of optical microscopy. Awareness that cryptic and semi-cryptic species both exist (Kahlert et al., 2019),and have differences in ecological profiles that may influence classifications (Kelly et al., 2015), raises questions about the potential for microscopy-based methods in the future. There are two plausible alternatives: first, to aim for a simpler generation of metrics based on traits that link to ecosystem functioning rather than simply aiming to maximize correlations with water chemistry and, second, to shift to alternative means for identifying and quantifying algae, such as metabarcoding (Kelly et al., 2020).

These observations reflect a general poor level of awareness among policy makers and managers of the important roles that algae play in freshwater ecosystems. Algae predominate media headlines when they cause problems. Yet, the time-consuming nature of

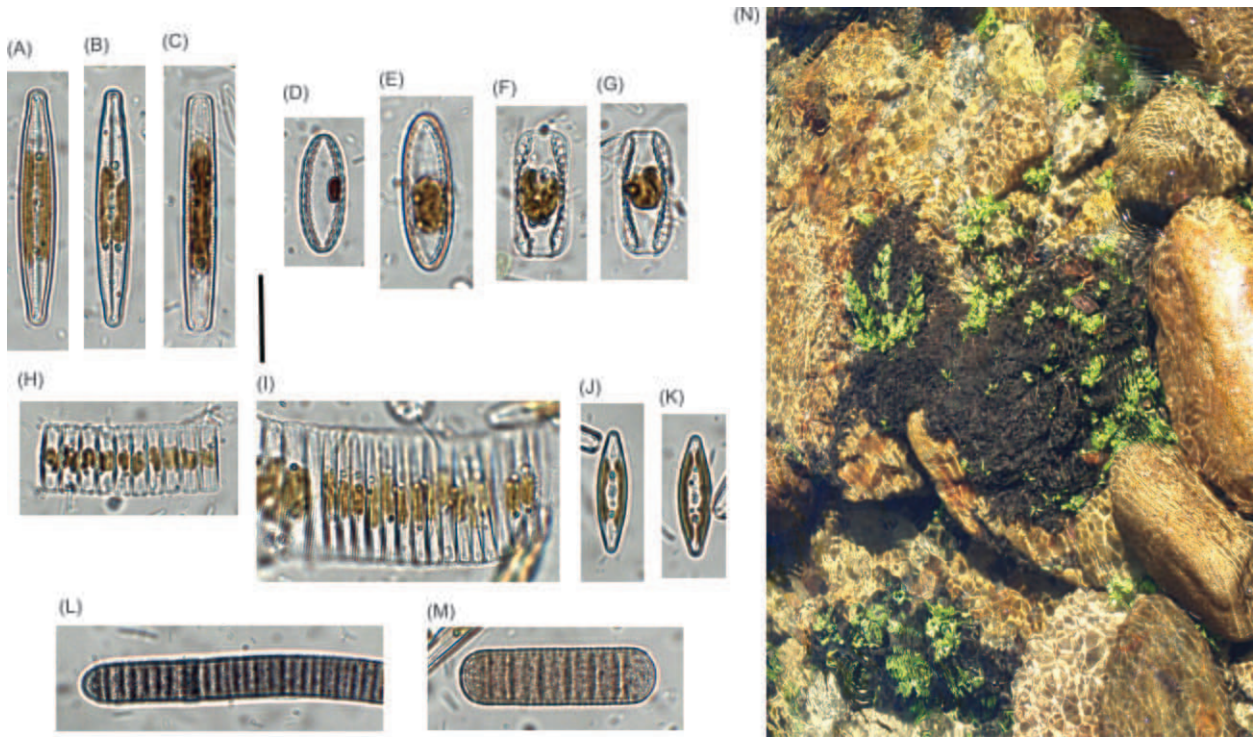

Fig. 1 Diatoms and other algae collected from mosses in a stream in the Sierra de Estrela, Portugal. (A–C) *Navicula angusta*; (D–G) Surirella cf. roba; (H and I) two different chain-forming Fragilaria sp.; (J and K) Navicula cf. cryptocephala; (L and M) Oscillatoria sp.; (N): a view of the moss habitat. Scale bar: 20 μm (=1/50th of a millimeter). Photo credits: Martyn Kelly.

the analyzes required is often regarded as an extravagance in light of budgetary constraints that state regulators have to work with. Moreover, expanding the ecologist's toolkit to include sensitive organisms such as diatoms more often than not increases the number of water bodies that fail to meet regulatory standards, therefore requiring investment, with costs borne by consumers and other stakeholders. This could be a potential barrier to political will.

Case study: Macrophytes

In healthy ecosystems, aquatic macrophytes (Fig. 2) play an important role as primary producers, as habitat for benthic algae, invertebrates and fish, and in nutrient and carbon cycling (Carpenter and Lodge, 1986). In shallow lakes, macrophytes also provide resilience to ecosystem-wide shifts towards algal dominance in cases of nutrient enrichment by providing habitat for algal-grazing fauna (Jeppesen et al., 1998). Given their important structuring and functional roles, any human impacts from eutrophication, climate change, acidification, alien species introductions, and other pressures that lead to reduced macrophyte diversity and abundance can also lead to knock-on impacts across the aquatic ecosystem (Chambers et al., 2007). Changes in macrophyte species composition are, therefore, a key indicator that pressures lead to, or have the potential to, cause significant ecological change.

Important influences on macrophyte species composition and distribution are often locally-driven and include water and sediment nutrient concentrations, organic carbon availability, light, temperature, and water flow (Alahuhta et al., 2021). Most commonly, changes in macrophyte species composition are used to monitor changes in (a) hydrology/morphology, and (b) trophic status as a result of eutrophication or, sometimes, acidification (Birks et al., 2005). As a result of the EU Water Framework Directive, a large number of different multi-taxon macrophyte indices have been developed and used across Europe to assess trophic impacts and deviation from reference conditions in both rivers and lakes. These are based on a number of different approaches, including total species or functional group richness, relative abundances of "sensitive," "tolerant," and "indifferent" species, and Lake Trophic Rank score approaches based on individual species responses to eutrophication (Penning et al., 2008). Examples include LEAFPACS, which has been applied to monitor eutrophication in both rivers and lakes (Willby et al., 2012), the Macrophyte Biological Index for Rivers (IBMR), which has been used to detect organic pollution (Furse et al., 2006; Szoszkiewicz et al., 2006), and the German macrophyte-based assessment for lakes, which has been used to assess deviation from reference condition in lakes across Germany (Stelzer et al., 2005). Beyond Europe, the development and use of macrophyte indices has been limited to site-specific

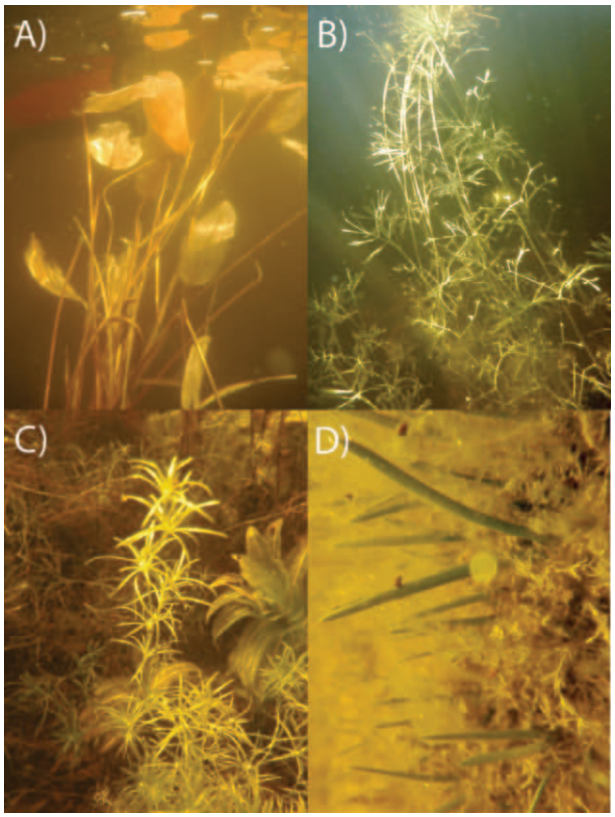

Fig. 2 Underwater images of (A) Floating-Leaf Pondweed (*Potamogeton natans*); (B) Lesser Marshwort (*Apium inundatum*); (C) Slender Naiad (*Najas flexilis*); and (D) left-rotated image of Shoreweed (*Littorella uniflora*). Photo credits: Isabel Bishop.

applications. Examples include the use of a wetland macrophyte index to detect water quality impacts on fish habitats in the Great Lakes (Croft and Chow-Fraser, 2007), and a submersed macrophyte index used to assess pollution in the Upper Mississippi River (Moore et al., 2012).

One of the most common critiques of the use of macrophyte community change as an indicator of environmental impact is the fact that relationships between plant species composition and specific environmental conditions are ambiguous (Demars et al., 2012). On a global scale, the factors that define macrophyte beta diversity (i.e., the ratio between regional and local species diversity) are understood now, and are strongly linked to habitat heterogeneity (Alahuhta et al., 2017a,b). Because of this, recent attempts to monitor macrophyte responses to environmental impacts have often taken a multi-indicator approach. In the EU Water Framework Directive, for example, macrophyte indices are often combined with algal indices to give an overall assessment of the status of primary producers (Cellamare et al., 2012; Kelly et al., 2020). Palaeoecological studies focussing on macrophytes typically also use multiple proxies, including the remains of crustacean cladocerans, diatoms, and pollen (Bishop et al., 2020; Salgado et al., 2010; Smol, 2008).

Implications for global assessment of freshwater systems using macrophytes

Historically, data on macrophyte abundance and species composition was difficult to obtain, and aquatic macrophytes were relatively poorly studied compared with other freshwater taxa (Alahuhta et al., 2021). However, new techniques for monitoring species and/or functional composition offer opportunities to increase global coverage of macrophyte data. These include both image-based survey techniques, such as satellite, aerial, or automated autonomous vehicle (AUV) surveys (e.g., Visser et al., 2015), and hydroacoustics (Spears et al., 2009).

If these advances in monitoring and availability of new data are to be used to assess changes in macrophyte species composition on a large scale, further research must be done into the macroecology of macrophytes. Alahuhta et al. (2021) identify a number of limitations to the current understanding of large-scale macrophyte responses to global environmental change, including: (a) excessive focus on local patterns and processes, (b) lack of temporal studies, and (c) few studies focussing on biotic interactions. This lack of macroecological understanding is reflected in the wide array of different macrophyte indices that are currently applied in different circumstances around the world. If these challenges can be overcome, macrophytes have the potential to act as indicators for whole-ecosystem responses to a wide variety of pressures (O'Hare et al., 2018). This potential has yet to be fully realized.

Case study: Invertebrates

The ecological and economic importance of invertebrates cannot be overstated. Invertebrates are functionally vital to aquatic ecosystems and can directly or indirectly affect human health and well-being. Invertebrates play major roles in the regulation of rates of primary production, decomposition, water clarity, thermal stratification, and nutrient cycling in lakes, streams and rivers (Strayer, 2006). Aquatic invertebrates are the primary food source for most fish species and many vertebrate species that live in or around freshwater. Some species, particularly in the Mollusca and Decapoda, are harvested from the wild or farmed, supporting regionally important fisheries. Some invertebrates are intermediate hosts or vectors of disease, such as malaria, schistosomiasis, and river blindness. Recent analyzes of long-term monitoring data reveal the ongoing decline in insect biodiversity, which is higher in freshwaters than other ecosystem types (WWF, 2018).

Cairns and Pratt (1993) offer a detailed history on biological monitoring with an overview of the differences in the European and North American traditions. The European tradition has its roots in saprobity (the degree of pollution) measured in rivers from the severity of organic enrichment (sewage) and its related decrease in dissolved oxygen. The presence and absence of pollution intolerant organisms is the basis on which the Saprobien system functions. The North American tradition started in the 1870s. This work focussed on the indicator value of benthic fauna. Further developments were made in the mid-1900s in which stream conditions were assessed using community indicator groups. Surveys were then adapted based on new and refined concepts about functional feeding groups and species assemblages and stream gradients.

Multi-taxon indices: Benthic invertebrates

Traditionally, water quality monitoring relies on multi-taxon indices, such as the Biological Monitoring Working Party (BMWP) (Hawkes, 1997) and an adaptation of that method, the South African Scoring System version 5 (SASS5) (Dickens and Graham, 2002). The advantage of multi-taxon indices is that they are relatively rapid assessments, as they usually operate at a coarse taxonomic resolution (family-level). The indices include multiple functional feeding groups, which have different tolerances to stressors. These advantages also lead to significant limitations. In the multi-taxon scoring system, sensitivity to pollution scores are set at the family level, and taxa identified to the family level. This ignores taxonomic and ecological sensitivities to stress at the taxonomic genus and species levels that make up a family. Secondly, these methods do not account for the sensitivity of individual functional feeding groups (e.g., shredders which feed of leaf litter, grazers which feed on periphyton, or predators which in turn feed on the grazers and shredders and other predators). An alternative, therefore, might be to use a single-taxon assessment method instead. The next section focusses on the use of a group of invertebrate predators in rivers and wetlands (dragonflies), but there are some notable uses of single-taxon approaches, for example using Chironomidae (Nicacio and Juen, 2015) in other habitat types including lakes.

Single taxon approach: Dragonflies

Dragonflies and damselflies (Odonata) are frequently identified as bioindicators (Samways and Simaika, 2016; Simaika and Samways, 2011, 2012), and are considered ideal candidates for medium to long-term monitoring (Oertli, 2008). The use of dragonflies as indicators for riverine ecological integrity is widespread (Chovanec et al., 2015; De Marco Júnior et al., 2015; Silva et al., 2010). They have also been used as indicators of wetland quality (Kutcher and Bried, 2014; Rosset et al., 2013), shallow lake restoration (D'Amico et al., 2004), and climate change in lakes and ponds (Fennessy et al., 2007; Rosset et al., 2010).

The Dragonfly Biotic Index (DBI) provides a measure of ecological integrity for both lotic and lentic freshwater systems (Simaika and Samways, 2008, 2011). It is a weighted measure based on the quantitative assessment of three sub-indices of: species distribution, threat status (i.e., IUCN Red List assessment) and sensitivity to disturbance. The total DBI of a river or stream reflects the total dragonfly assemblage, thus enabling water bodies to be compared and restoration success monitored.

The DBI, being based on the incidence of adult dragonflies at a monitoring site, has the advantage that it operates at the species level, and makes use of only one functional group, the predators. In comparing the performance of SASS with the DBI, a comparative assessment found that the DBI performs equally well to SASS and that dragonflies as a single taxon from a single functional group at the species level respond more clearly to habitat changes than multiple taxa from multiple functional groups (Simaika and Samways, 2011). Additionally, the value of adult dragonflies is their dependence on the overall "health" (ecological integrity) of both the terrestrial and aquatic parts of their habitat (e.g., Dolný et al., 2013). Lastly, practitioners do not need to enter the water, that can present safety concerns, and constraints to accessibility to sites.

Multivariate systems

Multivariate systems of macroinvertebrates are complex models that predict the aquatic community composition of a site based on the environmental conditions at that site. The multivariate model can be used to predict which taxa will be present at the site under given undisturbed environmental conditions. The site is then assessed based on the deviation between the observed and expected (reference or other baseline) condition. In order to be effective at prediction, multivariate systems require large amounts of data on the taxa used in the assessment. Taxa need to be well sampled and their spatial and temporal distributions and variability well documented. Similarly, the environmental parameters chosen to predict the presence of the taxa need to be relevant. Few such systems are in use, the most notable one is RIVPACS (Wright et al., 2000) developed in the United Kingdom. Similar systems have been developed in Australia, Canada, Czech Republic, Sweden and some states of the United States (see Paisley et al., 2014).

Implications for the globalization of freshwater invertebrate assessment approaches

Many nations have clear policies that call for the protection of biodiversity and ecosystem resources. Implicit to these policies is that appropriate indicators are used, or created where they do not exist (Stephenson et al., 2020). In terms of the DBI, this means that national DBIs need to be established. In terms of cross-country monitoring and co-operation, a pan-African DBI already exists (see Vorster et al., 2020). In Africa, the challenge is similar for the South African Scoring System, adaptations of which have been developed for Tanzania (TARISS) (Kaaya et al., 2015) and Zambia (ZISS) (Dallas et al., 2018). In many countries, the development of multivariate systems is not an option yet because of the enormous amounts of data required to build response models. It is more likely that where multi-taxon approaches exist, they will be supplemented with environmental DNA (eDNA) surveys. Where multi-taxon approaches do not exist, it is likely that traditional methods will give way to modern monitoring methods like eDNA, acoustics and remote sensing.

Case study: Fishes

Fish span multiple trophic levels, and the general public has an emotional connection to fishes. In Europe, there are at least 24 fish-based ecosystem assessment methods in use by 21 different countries for lakes alone (Ritterbusch et al., 2022). The situation is a bit different in North America (the United States and Canada), which has settled on a single method, the fish index of biotic integrity (IBI). In the 1980s in the United States, Karr (1981) developed a preliminary IBI framework. The12-metric IBI considered species composition and richness, and ecological factors such as abundance, trophic guild (group of species with similar diet), and condition of the fish. The multimetric IBI calculates a final score that reveals the integrity of the sampled site ranging from "very poor" to "excellent" (Minns et al., 1994). Integrity is defined as "the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region" (Karr and Dudley, 1981).

How do fish communities reflect habitat integrity?

Fish species vary in their tolerances to environmental change. The most common metric when calculating the biotic integrity of a site using fishes is the presence and abundance of intolerant species (Ruaro et al., 2020). Fish species intolerant of human-induced changes in their environment cease to persist at a site or occur at very low numbers. Intolerance can be classified as a sensitivity to

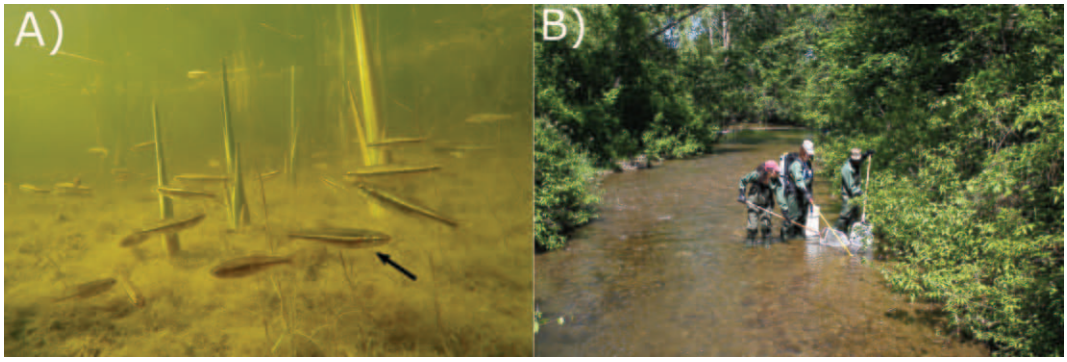

Fig. 3 (A) Underwater image of Redside Dace (*Clinostomus elongatus*, indicated by a black arrow) among several other fish species at a restored site; (B) sampling fishes using a backpack electrofishing unit in a wadeable stream. Photo credits: R.A. Castañeda.

one or multiple human-induced stressors, depending on the stressor(s) of interest of the biotic integrity study. In many cases, intolerant species are more likely to be endangered or imperiled as these fishes are the first to disappear with habitat degradation. For example, in Canada, an endangered minnow, the Redside Dace (*Clinostomus elongatus*), is considered to be a positive indicator of stream water quality as it is sensitive to loss of canopy cover, and increasing turbidity and water temperatures. These stressors are often associated with urbanization (COSEWIC, 2017) (Fig. 3). Other positive indicators of biotic integrity include species richness, endemic taxa richness, and the presence of piscivores (top predators) and habitat specialists (Ruaro et al., 2020).

Some species are very tolerant to changes and as a result would be considered negative indicators of biotic integrity. Other negative indicator criteria include the presence and high abundance and biomass of generalists, omnivores, hybrids, and non-native species; and the number of individuals with signs of failing health (Hughes et al., 1998). The presence of non-native species, for example Round Goby (*Neogobius melanostomus*) in Canada (Raab et al., 2018) and Largemouth Bass (*Micropterus salmoides*) in South Africa (Weyl et al., 2015), is a strong negative indicator of ecosystem integrity because of their often destructive impacts on local biotic communities and environment (Kennard et al., 2005).

Context- and region-dependence of the IBI

Karr (1981) cautioned that each region will need to create its own index based on fundamental ichthyological knowledge of the region, i.e., the index is context- and region-specific. For example, a fish community in a Canadian river is inherently different from, and less speciose than, a fish community in a river in the Amazon basin. As such, different information on species tolerances and diversity are needed to populate the IBI variables. Additionally, assigning species to the metrics for the IBI score should be specific to the type of waterbody, e.g., lakes, wetlands, rivers, streams, and at the appropriate scale (Bacigalupi et al., 2021). Further, knowledge on fish species natural distributions and on the identification of hybrids and trophic guilds for each region is necessary to accurately score the integrity of a study site.

Fish sampling approaches to inform IBI scores

Given that the most used metric is the presence of intolerant species, conventional sampling methods are being restricted to mitigate the impacts of stress and mortality that may result from using these gear types, for example, seine nets and electrofishing (Castañeda et al., 2020). The use of underwater cameras and eDNA, methods that do not require physical handling of fishes, are becoming increasingly popular for detecting fishes in temperate and tropical waterbodies, especially in remote areas (Ellender et al., 2012). Nevertheless, rigorous replicable sampling protocols still need to be developed. Lastly, investigations on the optimal number of sampling sites is needed to ensure variance in IBI scores is not an artifact of non-fish related parameters (Kindree et al., 2020).

Using the fish IBI is a useful and practical method to assess the health of a waterbody, however, as highlighted in this section careful attention is needed when used. Reference conditions need to be defined, and detailed relevant regional ichthyological knowledge and sampling protocols need to be established and tested to ensure comparability between sites and to ensure that differences in indicator scores are due to human-related impacts and not just natural variability (Ruaro et al., 2020).

Global assessments of impact using freshwater biota: Filling data gaps

Sizeable gaps remain in the availability of data describing freshwater taxa and their habitats, both geographically (e.g., sub-Saharan Africa) and for specific groups (e.g., freshwater mollusks) (Tickner et al., 2020). Furthermore, datasets covering periods of decades or longer are rare, despite the fact that many pressures are active over these timescales (Sayer et al., 2010). Both spatial and temporal data are vital for defining reference conditions and measuring changes in state. Gaps in data also have implications for applying the bioassessment methods described above (see discussion).

Several techniques for filling these data gaps have already been discussed in this chapter and elsewhere. In the specific context of measuring deviation from reference state, the best approaches are those that seek to provide continuous data over long timescales

(Roberts et al., 2020). Paleoecology is often used both to define reference conditions (e.g., Bennion and Simpson, 2011) and to investigate the extent of ecological impacts on lakes (e.g., Bishop et al., 2020; Salgado et al., 2010). New technologies can also help to increase the spatial resolution of available data in the present day. Analysis of the genetic material present in water and sediments (i.e., environmental DNA or eDNA) is increasingly being used as a biomonitoring technique that allows rapid detection of biota (Díaz-Ferguson and Moyer, 2014).

Image-based surveys (Spears et al., 2009) also show promise. However, most of these techniques rely on the use of proxies to detect species presence. The most promising means of increasing the spatial resolution of in-situ observations exists in the rapidly-growing field of citizen science.

Case study: Collecting data from across the world using citizen science

Citizen science (i.e., the involvement of non-scientists in scientific research) is increasingly being cited as a potential source of data to fill the gaps that exist in global descriptions of freshwater taxa and habitats (Turak et al., 2017). Given careful consideration of methodological design, data management, and volunteer training, well-designed citizen science projects can collect high quality data (Fig. 4; Anhalt-Depies et al., 2019; Wehn et al., 2021). Citizen science can also be used to harness and interpret local and indigenous knowledge, and to provide contextual information about observed impacts and their associated drivers, pressures, and appropriate management responses (Danielsen et al., 2019). Through their involvement in citizen science, volunteers can be encouraged to become more active participants in freshwater ecosystem management (van Noordwijk et al., 2021).

Citizen science bioassessments and impact monitoring

There exist a huge variety of citizen science monitoring schemes that can be used to measure impacts on freshwater ecosystems. Perhaps the most well-known are the many biodiversity recording schemes that exist around the world and allow volunteers to record species sightings (Chandler et al., 2017). From a public engagement perspective, species monitoring schemes that focus on a single charismatic species can be particularly effective. For example, single species of dragonflies have been used to raise conservation awareness in citizen science, e.g., the Amani Flatwing (*Amanipodagrion gilliesi*) in Tanzania has been used as a symbol of conservation and good water quality, and has at the same time been used as a tourist attraction at a local village (Clausnitzer et al., 2017). Crowdsourcing platforms like iNaturalist allow data from multiple projects to be uploaded and accessed in one place, meaning that data are available for use in bioassessments (Matheson, 2014).

Where citizens are involved in monitoring impacts more directly, simplified bio-indices are a common approach. Perhaps unsurprisingly, they most commonly use invertebrates as a bioindicator. In the United Kingdom, the Angler's Riverfly Monitoring Initiative (ARMI) has created a simplified version of the BMWP score based on eight easily-recognizable taxa, and volunteers use this score to detect biological responses to pollution (Brooks et al., 2019). SASS5 has also been adapted for use by citizen scientists

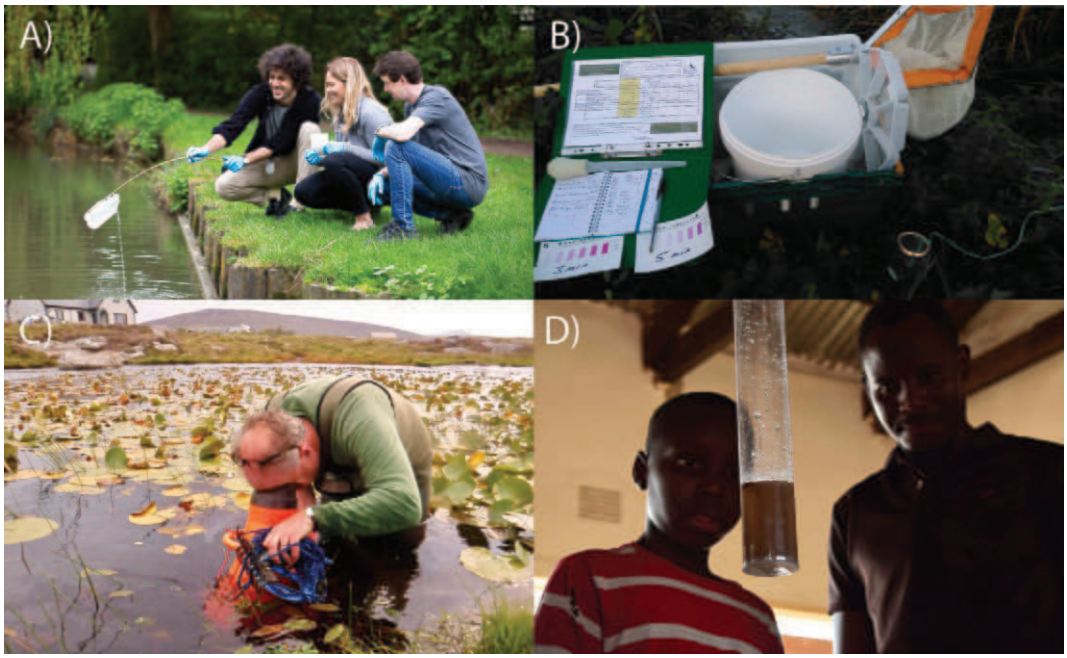

Fig. 4 Citizen scientists, professionals and in practice (A) FreshWater Watch volunteers sampling for water quality with a water bottle on a stick, (B) water quality and macroinvertebrate sampling equipment and appropriate forms for filling-in; (C) professional macrophyte survey using a double-sided rake grapnel and bathyscope; and (D) demonstration of water quality assessment using a turbidity tube to school children and staff in Zambia. Photo credits: (A) John Hunt, (B) John Pratt, (C) Isabel Bishop, and (D) WWF Zambia.

(Graham et al., 2004). The DBI has not yet been explicitly employed in citizen science, but its development has benefitted from citizens compiling distribution maps of dragonflies across Africa (Clausnitzer et al., 2012).

Algae are relatively easy for citizen scientists to collect, but identification is challenging, particularly without access to a microscope. This puts taxonomy-based algal assessments beyond the reach of all but the most specialist citizen scientists. Recent innovations in sensor technology allow citizen scientists to easily measure either chlorophyll *a* fluorescence or hyperspectral water color as a proxy for chlorophyll using low cost sensors or smartphones (Busch et al., 2016; Friedrichs et al., 2017). Less high-technology approaches involve asking citizen scientists to report visual algal blooms or to observe changes in water color over time. Both of these approaches have been used to successfully quantify phytoplankton increases in systems that have an impact from nutrient enrichment (Castilla et al., 2015).

Fish populations can be monitored using angler catch data. Often, these datasets extend over long time periods and it is, therefore, possible to assess long-term community responses to ecological pressures (e.g., Snyder et al., 2019). Other approaches have mostly focused on single species of conservation interest and/or invasive species, allowing them to use targeted trapping (e.g., monitoring movement of the European Eel (*Anguilla anguilla*) (Pecorelli et al., 2019)). The development of eDNA methods that can be used by citizen scientists offer future opportunities for more complete bioassessments to be carried out by volunteers beyond the angling community (Biggs et al., 2015).

Citizen science programs that assess changes in macrophyte community structure as an indicator of impacts on freshwater systems are rare. One exception is the global citizen science project FreshWater Watch (see below), which asks volunteers to record the presence of submerged, emerging, and floating leaved plants as part of the standard method. This information has been used to assess differing responses of macrophyte- versus phytoplankton-dominated ponds to nutrient inputs (Scott and Frost, 2017).

Considerations for global implementation

There is a huge variety of different types of citizen science projects, each of which has different characteristics and different volunteer motivators (Ceccaroni and Piera, 2017; van Noordwijk et al., 2021). Typically, citizen science projects that are successful in engaging volunteers over a longer time period are strongly place-based, often tapping into participants' vested interest in environmental impacts that directly affect themselves or their communities (Jollymore et al., 2017). While short term or highly localized projects are often best suited to volunteers, they are less well-suited to gathering information about impacts on freshwater systems on regional or global geographic scales.

A solution to this challenge is to link local or short-term clusters of citizen science activity to a more extensive global network of freshwater volunteer monitoring. This is the approach taken by the FreshWater Watch project (https://freshwaterwatch.thewaterhub.org/). FreshWater Watch volunteers use a globally consistent core protocol to monitor the state of freshwater systems worldwide. This protocol is built around the basic building blocks of freshwater systems, and includes simple observations of hydrology, ecology at family level, and land-use context, as well as measurements of turbidity and nutrient concentrations (Thornhill et al., 2018). This method has been applied to investigate localized issues, such as phytoplankton dynamics in urban watercourses in Brazil (Cunha et al., 2017). Uniquely for a freshwater citizen science project, it has also been used to assess the ecological impacts of nutrient enrichment in both lotic and lentic waters on a global scale (Loiselle et al., 2016). Because of this globally standardized approach, FreshWater Watch is now being explored as a potential tool that can be used to monitor global progress towards the Sustainable Development Goal 6 indicator for ambient water quality, indicator 6.3.2 (Bishop et al., 2020; Quinlivan et al., 2020).

Conclusion/Synthesis

The use of organisms for measuring the impact of human activities on inland waters is important and has found application globally. It makes sense to measure the condition of organisms and the composition of assemblages and communities to assess the state of ecosystems to get a measure of their "health" over time, and to use water chemistry as complementary information, rather than to rely on water chemistry alone. However, an enormous variety of assessment methods exists, many with similar goals (Birk et al., 2012).

In order to manage and reverse the effects of increasing pressures on the freshwater environment, comprehensive monitoring and evidence gathering is necessary on a global scale (Winfield, 2014). A key recommendation for safeguarding freshwaters for the future is to fund and implement globally standardized monitoring strategies (van Rees et al., 2020), and to more explicitly include freshwater ecosystems across the UN Sustainable Development Goals framework. This means including freshwater ecosystems not only as part of SDG 6 "Clean Water and Sanitation," but also SDG 15 "Life on Land" and SDG 14 "Life below Water." In addition to this, individual nations and regions have implemented their own policies that include specific requirements for monitoring impacts on freshwater systems, such as the European Union's Water Framework Directive. Assessment methods, therefore, need to be fit for purpose not only within their local and national context, but also on international scales. This means that methods need to be harmonized and underpinned by national and international standards (Comité Européen de Normalisation (CEN), 2014a,b), to give confidence that comparisons focus on the environmental "signal" rather than on "noise" introduced by sampling and analytical differences. Across Europe, countries have for historical reasons, developed their own assessment methods. In practice, only a few methods have become standard methods used at national levels. Still, these needed to be harmonized, meaning that conflicting or

redundant standards had to be minimized, in order to be able to communicate clearly on the ecological status of water bodies using a continental-scale European standard. Indeed, this has been achieved, and the different national methods are now intercalibrated (Birk et al., 2013), albeit critical issues remain (Poikane et al., 2014).

Data are fundamental to measuring impact, not only because they allow us to understand the current state of the environment relative to reference conditions, but also because they underpin our ability to develop harmonized bioassessment protocols. Bioassessments require, by nature, a fundamental understanding of the responses of individual taxa and/or functional groups to defined pressures. Often, multiple interacting pressures are involved, each of which acts on different spatial and temporal scales. This means that bioassessment methods are often location-specific, and the availability of protocols varies globally in accordance with the availability of data. For fish, region-specific IBIs have been developed worldwide (Ruaro et al., 2020), in North and South America (Moncayo-Estrada et al., 2015; Petesse et al., 2014), Europe (Aparicio et al., 2011), Asia (Jia et al., 2013), Africa (Kamdem Toham and Teugels, 1999), and Oceania (Joy and Death, 2004). For invertebrates, national DBIs need to be established. In terms of transnational monitoring and co-operation, a pan-African DBI already exists (see Vorster et al., 2020). In Africa, the challenge is similar for the South African Scoring System, adaptations of which have been developed for Tanzania (TARISS) (Kaaya et al., 2015) and Zambia (ZISS) (Dallas et al., 2018). The development of multivariate systems is not an option yet in many countries, and thus transnational protocols are a far way off also. Historically, data on macrophyte abundance and species composition was difficult to obtain, and aquatic macrophytes were relatively poorly studied compared with other freshwater taxa (Alahuhta et al., 2021). This has led to a limited understanding of macrophyte ecology and response to global change. As a result, macrophyte-based indices are currently under-utilized outside of Europe. Algae present a specific challenge because they are highly diverse, often morphologically-plastic organisms for which differentiation depends on working at the limits of optical microscopy. Awareness that cryptic and semi-cryptic species both exist (Kahlert et al., 2019) and have differences in ecological profiles that may influence classifications (Kelly et al., 2015) raises questions about the potential for microscopy-based methods in the future. Possible solutions are to work out simpler metrics or to shift to more modern methods in species identification, such as metabarcoding (Kelly et al., 2020).

We now know that freshwater environments are under pressure from a huge number of stressors, on both local and global scales (Tickner et al., 2020). The differences in sampling protocols and sampling effort make comparisons across methods difficult. There is therefore a need to identify which protocols yield the most information across local, regional or continental scales, keeping in mind also that many waterbodies cross several national boundaries, and water authorities have to, in order to effectively manage waterbodies, communicate consistent information with each other, preferably based on standardized sampling protocols. While in Europe there have been efforts to harmonize sampling protocols, these have also presented some challenges in consistency across national and biogeographical boundaries. There is an important need to develop agreed protocols globally and for greater use of biotic indicators. This can particularly assist in the progress towards the assessments needed for the implementation of the internally agreed Sustainable Development Goals (sdgs.un.org/goals). As a result of this, the importance of cross-sector collaborations cannot be underestimated. Involving multiple stakeholders in monitoring impact, for example using citizen science, will facilitate this consistent communication, as well as opening up opportunities to harness new sources of knowledge and involve wider populations in waterbody management.

An example of good practice is the Freshwater Biodiversity Observation Network (FWBON, geobon.org/bons/thematic-bon/freshwater-bon/), a volunteer network of freshwater practitioners, researchers, citizen scientists, and decision makers. It is the aim of FWBON to globally harmonize monitoring sampling protocols that can be used to measure and analyze changes in the abundances of taxa, which is particularly useful for tracking climate change. At the same time, FWBON has also recognized the need to standardize assessment protocols for better management of aquatic ecosystems and ecosystem services. Ideally, a globally harmonized monitoring network would function on top of a globally harmonized ecosystem assessment network, thereby collecting information about the state of the ecosystems, while at the same time delivering important information on changes in the richness, abundance and phenology of key species.

Knowledge gaps

- Aim for a simpler generation of metrics based on traits that link to ecosystem functioning.
- Shift to alternative means for identifying and quantifying algae, such as metabarcoding.
- Further research must be done into the macroecology of macrophytes.
- Development of eDNA methods that can be used by citizen scientists.
- Implement globally standardized monitoring strategies.
- Development of assessment methods for multiple pressures on aquatic ecosystems.

See Also: Human pressures and management of Inland Waters: Biological Invasions: Case Studies; Biological Invasions: Impact and Management; Biological Invasions: Introduction, Establishment and Spread; Citizen Science for Co-monitoring and Co-managing Impact on Ecosystems and Inland Waters; Measuring Impact, Overview and Reference Conditions

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Citizen Science for Co-monitoring and Co-managing Impact on Ecosystems and Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Citizen science The involvement of members of the public in data and knowledge generation.
Co-management Involves the sharing of power and responsibility between government and local resource users (Berkes, 2009).
Co-monitoring The involvement of citizens and communities in measuring the status of ecosystems, and/or monitoring the effects of policy responses.
Knowledge co-production Different constellations of scientists, members of the public, decision makers, industry and other stakeholders collaborating in the generation of data and knowledge in line with the scientific method.
Participation The practice of involving members of the public in agenda setting, decision-making, and policy-forming activities of organizations/institutions responsible for policy development' (WeObserve glossary).
Stakeholder All persons or groups who can affect or can be affected by a project, program or organization.

Introduction

This chapter introduces citizen science as a means for co-monitoring and co-managing impact of ecosystems and inland waters and explains what comes into play when implementing citizen science. In essence, citizen science constitutes the involvement of members of the public in data and knowledge generation. Citizen science has been used, for example, for inland water quality assessment (Malthus et al., 2020), for hydrological monitoring and ecosystem services management (Njue et al., 2019; Assumpção et al., 2018), and for comparing temperature difference between air and inland waters and its link to global warming (Weyhenmeyer et al., 2017).

This chapter focuses specifically on citizen science as an approach to the management of ecosystems and inland waters. This can entail identifying driving forces (especially direct drivers at local scale) and pressures (e.g., increased nutrient emissions to water), measuring the status of water bodies (e.g., in terms of pollution) as well as impact (e.g., changes in fish yields) and results of policy responses (targeting drivers, pressures, state and/or impact).

Over the past three decades, co-monitoring and co-management of the environment, including ecosystems and inland waters, have been recognized in, and encouraged by, international policy guidelines, e.g.:

- Principle 10 of the Rio Declaration on Environment and Development: "Environmental issues are best handled with participation of all concerned citizens, at the relevant level" (UNGA, 1992).
- Two articles of the Aarhus convention: "public participation concerning plans, programs and policies relating to the environment" (Article 7), "public participation during the preparation of executive regulations and/or. . .legally binding instruments" (Article 8) (UNECE, 1998). In 2021, recommendations adopted by the Parties of the Aarhus Convention explicitly state citizen science as ways to collect and imprvove accessibility of environmental data, and to implement effective public participation in decision making in environmental matters (UNECE, 2021).
- Article 14 of the Water Framework Directive: "Member States shall encourage the active involvement of all interested parties in the implementation of this Directive, in particular in the production, review and updating of the river basin management plans" (EC, 2000).

- Target 6b of the Sustainable Development Goal #6: "Support and strengthen the participation of local communities in improving water and sanitation management" (2030 Agenda for Sustainable Development, adopted by the United Nations in 2015).

The body of literature on what is citizen science and what works well when implementing citizen science (and what does not) is steadily evolving. As citizen science requires the involvement of people, paying attention to their motivations, skills and resources, constraints and expectations provides the basis for sound and successful implementation. The aim of this chapter is to introduce different forms of citizen science and what comes into play when involving citizens in co-monitoring and co-managing inland waters, i.e., the practicalities and key challenges involved when implementing citizen science.

Definitions and typologies of citizen science

The term citizen science is often used to refer to the involvement of the public in data collection for scientific purposes or other steps of the scientific method (Shirk et al., 2012), not least to fill data gaps. Others consider citizen science as a novel form of stakeholder engagement to address societal challenges (Fritz et al., 2019), democratizing science and policy (Irwin, 1995), and improving transparency, equity, inclusiveness and justice (e.g., Wehn et al., 2021a,b; Cooper et al., 2021).

Owing to the diversity of contexts and applications of citizen science as a concept, there is no single agreed definition for citizen science (see also chapter by Latimore and Lowry, 2022, in press) Haklay et al. (2021a) identified more than 30 definitions and argued that while definition of citizen science center around the notion of public participation in scientific research, most definitions lack precision and hence can be interpreted in different ways. The chosen definition should fit the context, aim and purpose of use.

De facto, by now citizen science has become an "umbrella term" for a wide range of activities and interactions related to data and knowledge co-production among different constellations of scientists, members of the public, decision makers, industry and other stakeholders (Fig. 1).

Fig. 1 Illustration of stakeholders and their interactions in citizen science, the Ground Truth 2.0 project. Source: Wehn U, Alfonso L, Lobbrecht A, van de Giesen N, van der Kwast H, Joshi S and Masó J (2015) Ground Truth 2.0 – Environmental Knowledge Discovery of Human Sensed Data, Horizon 2020 Project, Description of Action.

Wiggins and Crowstone (2011) created a typology focused on project goals and their use of technology, based on an examination of a variety of project characteristics across 32 projects and clustering, resulting in five mutually exclusive and exhaustive types of projects:

(1) **Action**—Action-oriented citizen science projects encourage participant intervention in local concerns, using scientific research as a tool to support civic agendas. They are most commonly grassroots or "bottom-up," are not conceived or planned by scientists, and usually involve long-term engagement in local environmental concerns.
(2) **Conservation**—Conservation projects support stewardship and natural resource management goals, primarily in the area of ecology; they engage citizens as a matter of practicality and outreach, and they tend to be regional in scope.
(3) **Investigation**—Investigation projects are focused on scientific research goals requiring data collection from the physical environment. Education is frequently a strongly valued but unstated purpose, and task structures often support ongoing learning. These projects range from regional to international in scope, and can achieve very large scales of participation.
(4) **Virtual**—Science-oriented Virtual projects are ICT-mediated with no physical elements whatsoever, they are formed through top-down organizing by academics, and most projects' affiliations are exclusively academic.
(5) **Education**—Education projects make education and outreach their primary goals, with relevant aspects of place. They can be split into those focusing on informal compared with formal learning opportunities, and are sometimes explicitly designed to permit cumulative learning experiences.

Shirk et al. (2012, p. 4) distinguished five models of citizen science, based on the degree of participation of citizens and communities in scientific research:

- "*Contractual* projects, where communities ask professional researchers to conduct a specific scientific investigation and report on the results;
- *Contributory* projects, which are generally designed by scientists and for which members of the public primarily contribute data;
- *Collaborative* projects, which are generally designed by scientists and for which members of the public contribute data but also help to refine project design, analyze data, and/or disseminate findings;
- *Co-Created* projects, which are designed by scientists and members of the public working together and for which at least some of the public participants are actively involved in most or all aspects of the research process; and
- *Collegial* contributions, where non-credentialed individuals conduct research independently with varying degrees of expected recognition by institutionalized science and/or professionals."

What these five models of citizen science (the so-called 5C) imply for the involvement of the public in each step of the scientific method is illustrated in Fig. 2 by Haklay (2019) partially based on Cooper et al. (2007).

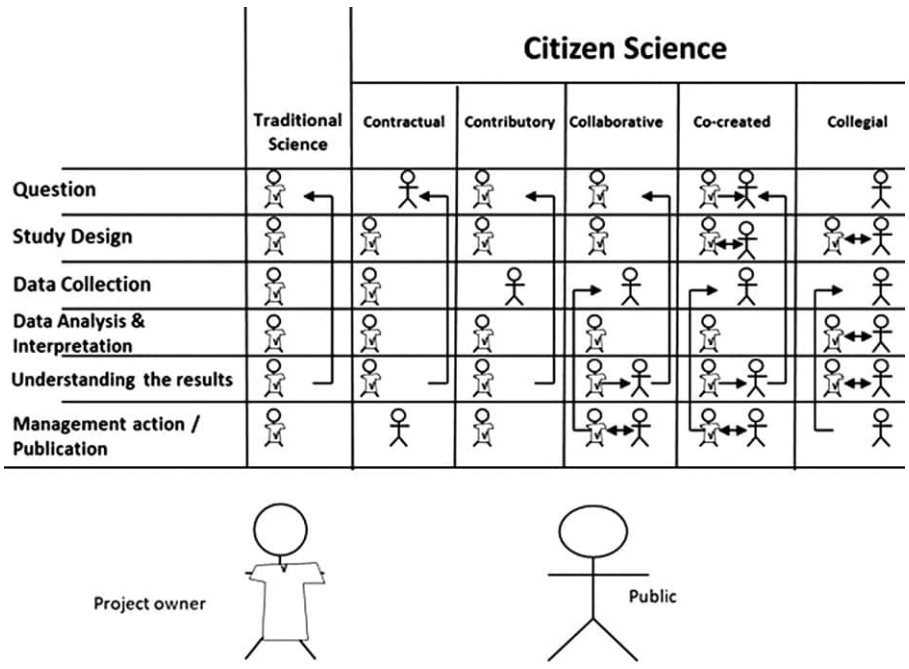

Fig. 2 Illustration of the five citizen science types. Source: Extracted from Haklay MM (2019) Introduction to Citizen Science & Scientific Crowdsourcing, Lecture Notes, UCL., partially based on Cooper C, Dickinson J, Phillips T and Bonney R (2007) Citizen science as tool for conservation in residential ecosystems. *Ecology and Society* 12 (2).

This categorization highlights that the roles of citizens and communities, on the one hand, and scientists (including those in public agencies), on the other hand, can differ substantially when engaging in citizen science in terms of "who takes the lead" and "who invites whom." This is often also distinguished more simply as either "top down" (science-driven or authority-driven) and "bottom up" (community-driven) initiatives.

Combining both aspects—the goals of projects and the degree of participation—Schäfer and Kieslinger (2016), based on Bonney et al. (2009), Shirk et al. (2012) and Wiggins and Crowston (2011), mapped citizen science projects that differ in terms of the main knowledge "producers" (citizens compared with scientists/researchers) and in terms of the project aims (answering a scientific question compared with implementing interventions in the socio-ecological system) (Fig. 3).

This illustrates that a range of different knowledge co-production activities can be considered citizen sciencei.e., pursuing civic agendas related to local environmental concerns; creating learning opportunities and awareness raising). It also positions the role and application of the produced knowledge in terms of its contribution to either science (answering a scientific question) or policy and local action (intervention in socio-ecological systems).

Co-monitoring and co-management via citizen science

Co-monitoring and co-managing ecosystems and inland waters entails the involvement of citizens and communities in measuring the status of ecosystems, monitoring the effects of policy responses, and/or setting targets for limits of acceptable change or ambitions for restoration. Citizen science projects and initiatives can contribute to co-monitoring and co-managing ecosystems and inland waters, albeit to differing degrees (see case studies Table 1).

Some argue that community-based monitoring encompasses the activities and relational dynamics of both, community-based "monitoring" and community-based "management" (Conrad and Hilchey, 2011). Specifically, Whitelaw et al. (2003) define community-based monitoring as "A process where concerned citizens, government agencies, industry, academia, community groups and local institutions collaborate to monitor, track and respond to issues of common community concern" (p. 410).

The distribution of both rights and responsibilities related to a particular resource appears to be pivotal to different definitions of co-management (Plummer and Fitzgibbon, 2004), e.g.:

- Co-management involves "the sharing of power and responsibility between government and local resource users" (Berkes et al., 1991, p. 12).
- "Co-management can be thought of as a spectrum of institutional arrangements in which management responsibilities are shared between the users (who may or may not be community-based) and government" (Yandle, 2003, p. 180).

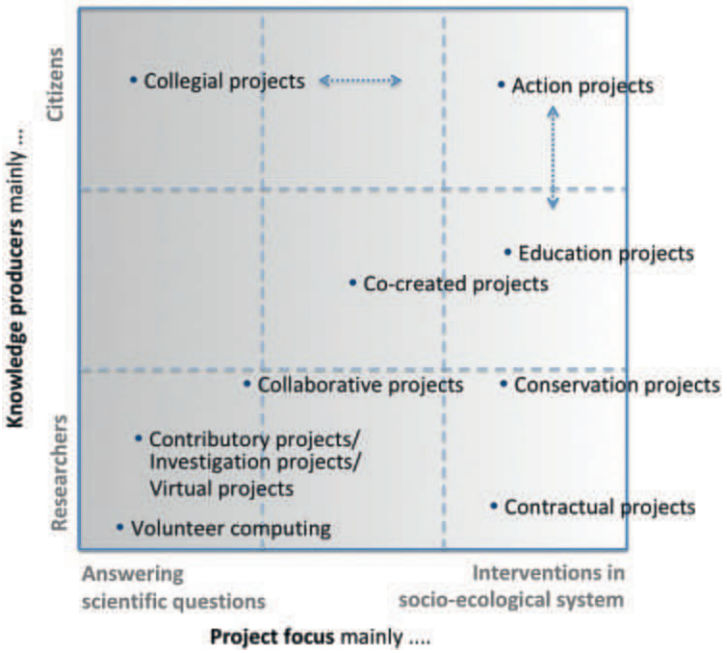

Fig. 3 Types of citizen science projects. Source: compiled by Schäfer T, Kieslinger B (2016) Supporting emerging forms of citizen science: A plea for diversity, creativity and social innovation. *Journal of Science Communication* 15(2): Y02, based on Bonney et al. (2009), Shirk JL, Ballard HL, Wilderman CC, Phillips T, Wiggins A, Jordan R, McCallie E, Minarchek M, Lewenstein BV, Krasny ME, Bonney R (2012) Public participation in scientific research: A framework for deliberate design. *Ecology and Society* 17(2): 29. doi:10.5751/ES-04705-170229 and Wiggins A, Crowstone K (2011) From conservation to crowdsourcing: A typology of citizen science. In Proceedings of the Forty-fourth Hawai'i International Conference on System Science. Koloa.

Table 1 Overview of selected Citizen Science projects related to water quality monitoring.

Name of citizen science initiative	*Country/region*	*Coordinator*	*Main topic covered*	*Description*	*Key reference*
Drinkable Rivers	Various European countries (hubs)	Drinkable Rivers (organization)	Monitoring and managing water quality	Education approach. Engage people to experience their rivers by doing citizen science on water quality using measurement kit and help track progress towards drinkable rivers.	https://drinkablerivers.org/
Outfall Safari	United Kingdom	Zoological Society of London & The Rivers Trust	Locating and assessing the impact of, and reporting on polluted surface water outfalls	Contributory approach. Citizen-based systematic surveying of outfalls (pollution pouring directly into greater London rivers via drains) and direct reporting to Thames Water and Environment Agency.	https://www.zsl.org/conservation/regions/uk-europe/londons-rivers
Vatten Fokus citizen observatory	Sweden, Malarendalen region	University of Stockholm	Water quality management in socio-economic systems	Co-created with local stakeholders. It supports all stakeholders to collaborate in the governance and action of the aquatic ecosystems by collecting data, sharing knowledge, making data accessible and complements established governmental initiatives.	https://vattenfokus.se/
Rio Quiroz Catchment	Peru, Peruvian Andes	Consortium for Sustainable Development of the Andean Ecoregion, CONDESAN	Monitoring the catchment to identify hydrological impacts of land-use change, and benefits of restoration activities in Rio Quiroz catchment	Bottom-up initiative emerging from local awareness about the need for better information on ecosystem services. The monitoring is performed by citizen scientists, operated by CONDESAN, in close collaboration with the upland municipalities	Buytaert et al. (2014) Capdevila et al. (2020)
miniSASS (mini stream assessment scoring system)	South Africa, others	GroundTruth	Monitoring water quality in rivers and stream through macroinvertebrates	Low tech, scientifically reliable and inexpensive participatory tool. miniSASS scores can be uploaded onto the miniSASS website	http://www.minisass.org/en/ Graham and Taylor (2018)
Alabama Water Watch	USA	Auburn University Water Resources Center	Monitoring of water quality in streams, rivers, lakes and coastal waters.	Contributory approach to conservation projects. Citizens are trained to monitor and evaluate physical, chemical and biological features of water. Data used for advocacy to upgrade waterbodies to higher classification or designation.	https://aaes.auburn.edu/alabamawaterwatch/ Deutsch and Ruiz-Cordova (2015)
Swim Drink Fish	Canada	Swim Drink Fish (organisation)	Citizen science monitoring hubs of water quality used for recreation. Using technology to connect people with water and nurture the next generation of water guardians	Bottom-up approach to connect people and communities with water, collect and share data, and restore swimmable, drinkable, fishable water for all.	https://www.swimdrinkfish.ca/
Fresh Water Watch	Global	Earthwatch	Monitoring quality of inland waters	Contributory approach. Guided by professional researchers, citizen scientists measure nutrients with easy-to-use nitrate and phosphate field kits with a relatively low minimum detection threshold.	https://earthwatch.org.uk/get-involved/freshwater-watch
Eye on Water	Global	Eyeonwater.org	Monitoring of inland and coastal water quality through smartphone application (water colour and water clarity).	Contributory approach to generate data for calibration of satellite information, and a synoptic overview of rivers, lakes and coastal water quality for natural resource management.	https://www.eyeonwater.org/ www.citclops.eu

The power-sharing arrangements and institutional relations are conceived as differing degrees of role sharing between government and resource user communities (Molle and Closas, 2019). Some suggest to not get stuck on the specific institutional arrangements, but consider co-management as a "continuous problem-solving process" (Carlsson and Berkes, 2005, p. 65). In this sense, co-monitoring has been proposed as a strategy to facilitate or improve co-management (Berkes, 2009), involving local partners and stakeholders in deciding what is to be monitored and including local traditions of reading and interpreting environmental signs (Kofinas, 2002; Mutimukuru et al., cited in Berkes, 2009). The long-standing tradition of community science, linked to social action for improving environmental injustice, protecting of human rights and addressing public health issues, has even been regarded to "elevate local experts and place-based issues above scientific experts and publication-driven research agendas" (Cooper et al., 2021, p. 1387).

The use of citizen science in co-monitoring and co-management enhances and changes existing forms of public participation (Wehn et al., 2015b): this varies depending on who is selected to participate in decision making (including in decisions on what data to collect); how participants interact in decision making (e.g., spectator compared with negotiator) and when and how citizen-generated data and knowledge are included; and how and by whom the generated knowledge and insights are acted upon and turned into formal decisions. It thus still holds that the precise definition of co-management should be considered in context- and application-dependent (Berkes, 1994), including—or especially—the role of citizen science. Similarly, the changes resulting from co-monitoring and co-management via citizen science are also location-specific and locally-shaped (Wehn et al., 2015a).

Overall, the role of citizen science in co-monitoring and co-management can be grouped into three, partially overlapping, categories (Fig. 4) Wehn et al. (2019a), all of which entail some form of community-based monitoring: (i) environmental monitoring via implicit and explicit data collection by citizens; (ii) cooperative planning via stakeholder engagement and interactions, including among citizens, communities and decision makers, in consultation, feedback and discussions; and (iii) environmental stewardship, i.e., communities, authorities and other stakeholders jointly taking care of the environment via fully realized dialogs and shared responsibility for natural resource management.

Moreover, the role of citizen scientists in co-monitoring and co-management is not necessarily fixed and can—and is even intended to—evolve over time: their initial awareness of and involvement in water health may be raised, for example via personal interest as in the Swim Drink Fish initiative in Canada or the Drinkable Rivers initiative in Europe (Table 1); this can then evolve into stewardship of waterbodies, using citizen science data and influence to advocate and negotiate for upgrades of their local waterbodies to higher classification and designation.

In Europe, efforts to seize the opportunities presented by the increasing popularity of citizen science and the rapid diffusion of Information and Communication Technologies (ICTs), for co-monitoring and co-management purposes have led to the emergence of citizen observatories (COs) for a wide range of thematic issues (Fig. 5) (WeObserve, 2021), including water quality and the health of ecosystems.

As a particular form of citizen science and community-based monitoring schemes, from the outset and very directly and deliberately, COs seek to foster citizen and community participation in environmental management and to contribute to policy

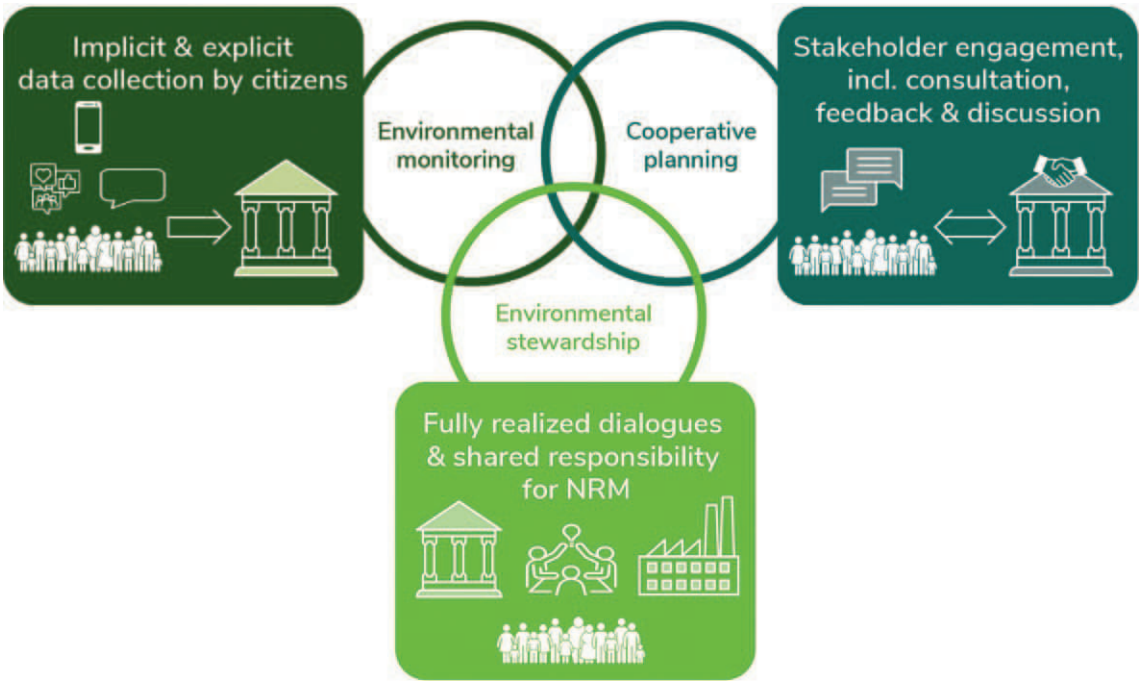

Fig. 4 Different roles of citizen science in co-monitoring and co-management. Source: Wehn U, Pfeiffer E, Anema K, Joshi S, Vrancks S, van der Kwast H, Giesen R, Masó J, Gil-Roldàn E, Ceccaroni L, Almonani A, and Gharesifard M (2019a) Co-designing Local Knowledge Co-Production for Sustainability: The Ground Truth 2.0 Methodology, Presented at the ASSIST-UK Conference (Association of Science, Technology and Innovation Studies UK), 9–10 September, University of Manchester.

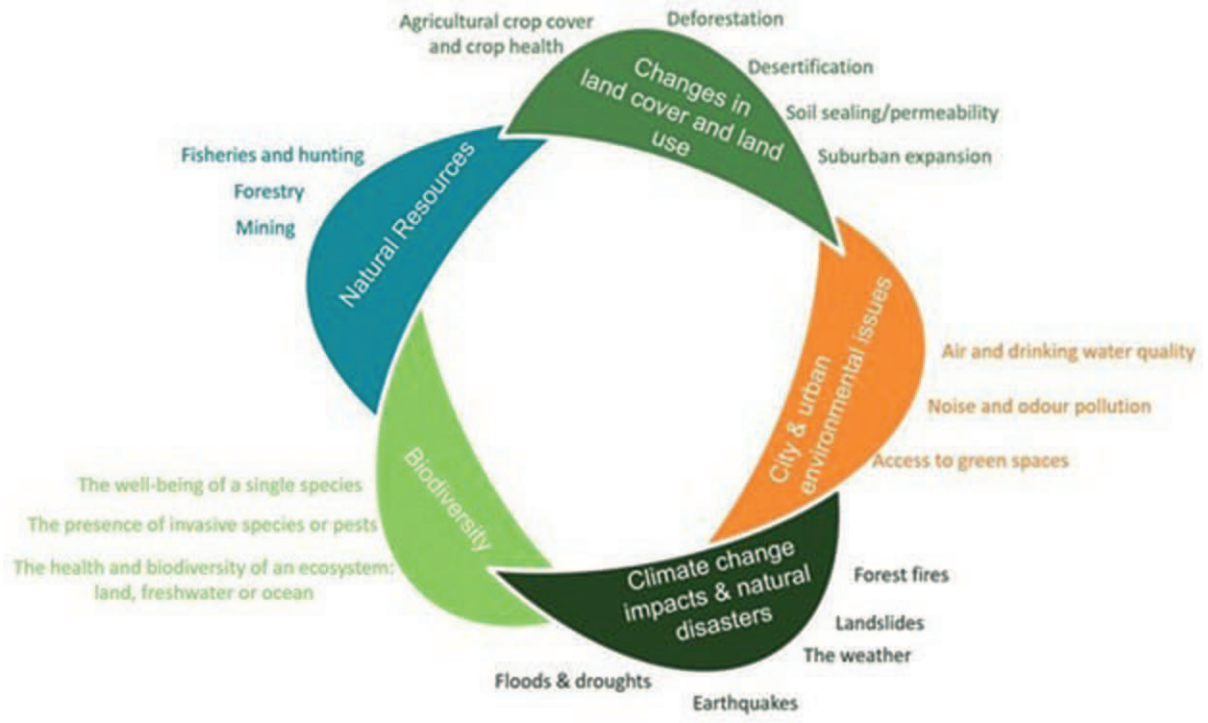

Fig. 5 Examples of thematic issues monitored by citizen observatories. Source: WeObserve consortium (2021). WeObserve Cookbook: Guidelines for creating successful and sustainable Citizens Observatories, www.weobserve.eu/weobserve-cookbook.

and decision making, ideally beyond the project lifetime (Wehn et al., 2015a). In essence, COs consist of a set of stakeholders, interactions and a platform: citizens, decision makers and scientific experts (and other stakeholders) are interacting to improve natural resource management, using a technical platform to facilitate their interactions (Wehn et al., 2019b). In such an information ecosystem for citizens and communities (Mazumdar et al., 2016), tailored ICT infrastructure serves to support joint monitoring activities, communication, data and information flows (Liu et al., 2014) and place-based actions (Ciravegna et al., 2013) to improve the local environment (see also illustration in Fig. 6). Nevertheless, deliberate and substantial efforts are required to set up,

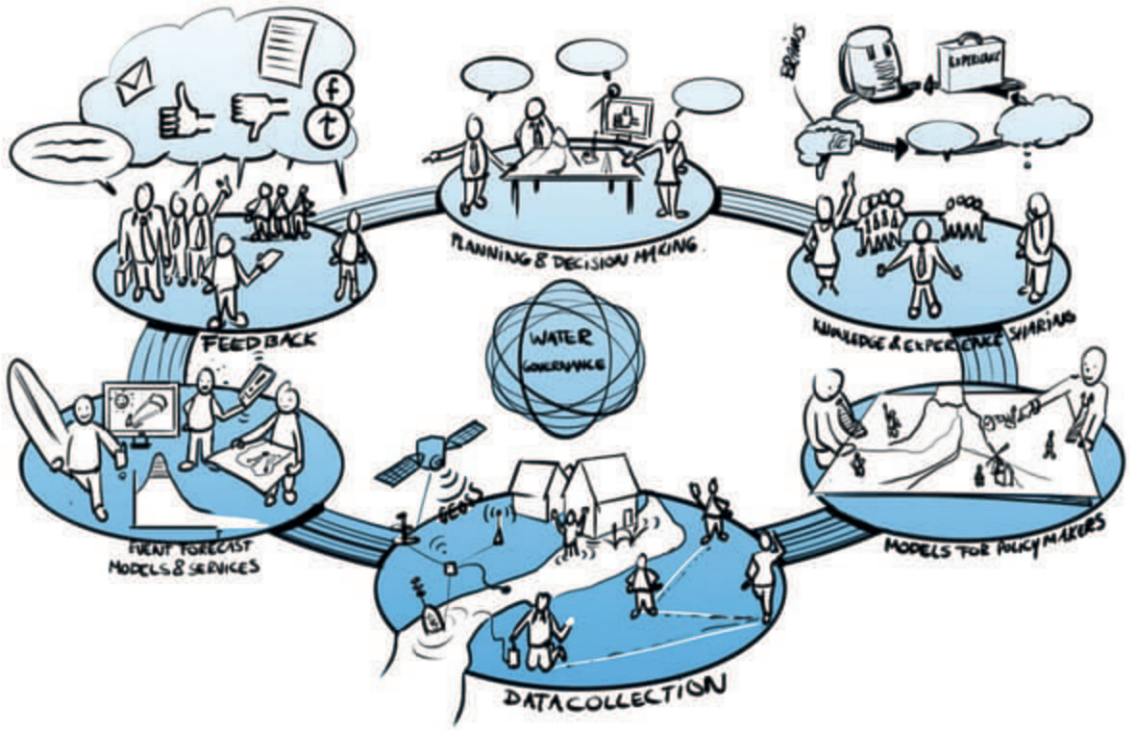

Fig. 6 Citizen observatories according to the WeSenseIt project. Source: wesenseit.eu.

implement and sustain COs (Hager et al., 2021); and achieving the envisaged institutional changes to citizen participation in environmental management is typically outpaced by much faster technological changes (Wehn et al., 2015a).

In summary, the mere intention to implement citizen science, in whatever form, is not sufficient to result in meaningful co-monitoring and co-management of impact on ecosystems and inland waters. Careful attention needs to be paid to the context in which citizen science is used, the process by which it is implemented, who is involved when and how, and how the expectations of different stakeholders can be managed and met. These aspects are addressed in the next section.

Practicalities and challenges of co-monitoring and co-management via citizen science

The increasing use of citizen science in co-monitoring and co-management of inland waters and ecosystems is resulting in a growing experience base with this practice, including evidence of the actual practicalities and challenges. The systematic review of water-related citizen science initiatives by Walker et al. (2020) identified the wide range of benefits (Table 2). It also specified distinct and salient negative impacts, specifically related to livelihoods and disempowerment that have been experienced and reported in the literature.

The set of "demotivational impacts" in fact refers to issues with the implementation of such water-related citizen science initiatives (e.g., boring nature of some tasks for participants or mismatches in the goals of citizen science organizers and participants). This in turn can lead to high dropout rates of participants and reduce the chance of improving the physical environment (e.g., water quality, health of ecosystems) as well as the governance mechanisms. A core difficulty in maintaining participants' interest and motivation stems from the inherent delays involved in manifesting impacts such as improvements in the state of inland water and ecosystems and changes in policy. In the case of the long-standing Alabama Water Watch, a water quality monitoring program established in 1992 covering all of the major river basins of the state of Alabama (United States), this lead to disillusionment and "volunteer fatigue" (Deutsch and Ruiz-Córdova, 2015; see Table 1).

Experience has shown that the success of implementing citizen science depends on the careful consideration of five dimensions of citizen science (Fig. 7) and their interactions.

- ***Thematic, geographic & temporal dimension of citizen science:*** citizen science is composed of the characteristics and priorities (of stakeholders) in a specific geographic area, the thematic focus (e.g., water, biodiversity) and the timing of the resource/object/issue observed.

Table 2 Summary of benefits and negative impacts of water-related citizen science initiatives.

Benefits	*Negative impacts*
Inferred benefits[a]	**Livelihood impacts**
▪ Awareness raised	– Overburdening the public, especially low-income areas (e.g., farmers)
▪ Reduced disaster risk	– Health and safety issues (flooding, water quality)
▪ Environmental stewardship	– Decreased self-reliance and damage to existing community institutions (post funding)
▪ Educational (knowledge gained, increased scientific literacy, social learning)	– Increased sensitization to hazards (over pre-occupation)
Observed benefits[b]	**Disempowerment**
▪ Enhanced capacity	– Process-based exclusion (reinforcement of existing power structures; continued marginalization)
▪ Democratization of science	– Technology-based exclusion (affordability, adoption issues)
▪ Combination of raised awareness, increased scientific literacy, social capital leading to behavior change and decreased risk/improved health	– Relinquished responsibilities by authorities (substitute labor)
▪ Empowerment to contribute to mitigation action, e.g., combat water pollution	– Conflict creation (selective acceptance of citizen science data)
▪ Livelihood improvements and conflict reduction	– Data privacy (identification, location of participants)
Investigated benefits[c]	**Demotivational impacts**
▪ Appreciation and elicitation of local knowledge	– Time consuming, boring, difficult tasks, leading to high drop out rates/low participation
▪ Human and social capital, personal and leadership skills	– Mismatched goals between organizers and participants
▪ Knowledge gained of socio-ecological systems, water quality and ecosystem services	– Disappointment if lack of or delayed impact
▪ Science literacy	– Erosion of confidence, trust and social capital
▪ Increased political participation	– Problems caused by financial incentives
▪ Trust, community building and recognition; networking	
▪ Empowerment of indigenous/disadvantaged communities	
▪ Decreased risk, changes toward more environment friendly behavior	
▪ Fun and learning	

[a]Benefits inferred based on reports but not investigated.
[b]Benefits provided based on specific observations.
[c]Benefits based on research of outcomes.

Source: compiled from Walker D, Smigaj M, Tani M (2020) The benefits and negative impacts of citizen science applications to water as experienced by participants and communities. *WIREs Water* 8: 1488.

Fig. 7 Dimensions of citizen science implementation. Source: the author.

- ***Socio-political dimension of citizen science:*** the social dimension of citizen science encompasses the involvement of non-experts in knowledge co-creation, with differing perceptions, motivations, expectations, capacity, priorities and local, traditional and/or indigenous knowledge backgrounds; citizen science is also a political multi-stakeholder process in terms of who decides what is measured by whom, how and when; what data (and how) are included with respect to reporting requirements, monitoring objectives and decision-making processes;
- ***Scientific dimension of citizen science:*** in terms of scientific discipline, citizen science needs to be integrated with, and validated for, specific scientific/knowledge fields; in terms of scientific method, citizen science constitutes a change to the traditional scientific paradigm—from providing merely a new data source for scientific enquiry, to fully involving citizens and communities in the scientific method;
- ***Technological dimension of citizen science:*** the technological dimension of citizen science entails new (inexpensive) sensors; the use of new or adaptation of existing interaction platforms; and citizen science data access, interoperability, compatibility, complementarity and integration with standard data sources;
- ***Economic dimension of citizen science:*** this dimension of citizen science pertains to the influence of financial resources on the scope, success and sustainability of citizen science activities, as well as to the economic benefits derived from generated citizen data, e.g., for the public good and/or for the benefit of private sector actors from value-added services.

The need to consider these different dimensions of citizen science and their interactions highlights that citizen science is not a "one size fits all" plug for co-monitoring and co-management; rather, citizen science requires careful implementation to serve agreed environmental and institutional purposes and impacts in a given bio-physical context. Fundamentally, since citizen science requires the involvement of people, paying attention to their motivations, skills and resources, constraints and expectations provides the basis for sound and successful implementation. Extensive guidance is available in various online resources on how to address these practicalities and challenges of implementing citizen science, such as dedicated toolkits, a "cookbook" and MOOCs (see resource section) that bring together and synthesizes experience from a range of citizen science project implementations in Europe and beyond.

Fig. 8 Reinforcing success cycle for citizen science initiatives. Source: Hager G, Gold M, Wehn U, Ajates R, See L, Woods M, Tsiakos C, Masó J, Fraisl D, Moorthy I, Domian D, Fritz S (2021) Onto new horizons: Insights from the WeObserve project to strengthen the awareness, acceptability and sustainability of citizen observatories in Europe. *JCOM* 20 (06), A01. doi:10.22323/2.20060201.

Moreover, the WeObserve project (H2020, 2017–2021) investigated overarching issues encountered by citizen science projects across the board and found that the key challenges facing citizen science projects and COs are awareness, acceptability and sustainability:

- **Awareness**: Citizens are often unaware of opportunities to address and help monitor environmental issues. Likewise, public authorities, SMEs and NGOs are often unaware of the potential of COs to support decision making and create business opportunities.
- **Acceptability**: COs and citizen science are often assumed to lack the required quality standards to generate insights for decision making and environmental governance. Public authorities are hesitant to accept data from citizen science efforts to complement authoritative data.
- **Sustainability:** Although local and continent-wide projects have shown great promise, the existing processes, infrastructures, measures of success, and legislation are currently insufficient to sustain or scale-up citizen science projects across various sectors. Deficiencies in transition governance, funding systems and standards of data preservation and data interoperability are limiting the long-term potential of citizen science and COs (Hager et al., 2021, p. 5).

The WeOberve project demonstrated that these challenges are closely interlinked. If they are addressed as such, a cycle of positive reinforcement can be created, whereby progress with addressing one issue can likely trigger improvement of the others (Fig. 8).

The WeObserve project found that it is critical to:

(1) build awareness and engage established, place-based communities and facilitate exchange across stakeholders;
(2) foster data quality and trust in data and technologies within context and for their intended use and deploy methods that ensure data quality as well as the use and accessibility of data;
(3) continuously demonstrate impact through impact stories and create value for all stakeholders;
(4) consider initial project funding as seed-money and establish sustainability elements in the project design with the aim to establish the COs longer-term (Hager et al., 2021, p. 18).

Conclusion/synthesis

This chapter has introduced different conceptualizations of citizen science and the challenges and practicalities for implementing citizen science as a means for co-monitoring and co-managing ecosystems and inland waters. The field of citizen science—both in terms of its theory and its practice—is still evolving. Citizen science is a fast expanding field of study in itself: how we define citizen science, how we implement citizen science in different ways and what this means in terms of impact of the respective initiatives for the health of ecosystems and inland waters as well as individual citizens, communities and society at large.

Knowledge gaps

- The field of citizen science is evolving—so are terminology, definitions and even the name itself (Haklay et al., 2021b; Cooper et al., 2021) The plurality and diversity of interpretations of citizen science in terms of definitions, typologies and descriptors need further attention (Haklay et al., 2021b).
- Important challenges for citizen science, and for citizen observatories in particular, consist of awareness, acceptability and sustainability of these initiatives (Hager et al., 2021) as well as inclusivity and process (Cooper et al., 2021).

- Cases that present sound evidence of positive environmental changes in local ecosystems monitored by citizen scientists need to be compared in order to distill factors for their success (Conrad and Hilchey, 2011).
- Experiences with the implementation of citizen science are accumulating and increasingly well-documented in the academic literature as well as in online resources; however, measuring the impact of these initiatives in sound and comparable ways is lagging behind and suffering from conceptual and methodological inconsistencies (Wehn et al., 2021b). This is particularly the case with respect to claims and ambitions of citizen science to serve for behavior change toward sustainable lifestyles.
- Moreover, limited understanding by citizen science practitioners of policy needs and processes means that communication about the impacts of citizen science remains challenging (Wehn et al., 2021a).
- There is a danger of re-inventing the wheel in citizen science: existing insights and sound scientific practices from relevant behavioral science disciplines are being disregarded and therefore re-invented (often in inferior ways), for example, when examining and addressing the motivations, attitudes, incentives and challenges for stakeholder participation (Wehn and Almomani, 2019).

Important case studies

Citizen science as an approach for co-monitoring and co-management of inland waters is becoming increasingly popular and has been implemented across the globe, as illustrated by selected case studies (Table 1).

See Also: Emerging methods and topics: Citizen Science, Crowdsourcing, and Social Media Advance Our Understanding and Conservation of Inland Watersaters

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Relevant websites

https://cseol.eu/cseol-csdk/—CSEOL Citizen Science Development Kit.
https://www.weobserve.eu/weobserve-cookbook/—WeObserve Cookbook.
https://www.futurelearn.com/courses/weobserve-the-earth—WeObserve MOOC.
https://www.weobserve.eu/toolkit/—WeObserve Toolkit.

Agricultural Pressures on Inland Waters

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This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

The agricultural landscape

Agriculture is a dominant land use and economic activity worldwide (Chen et al., 2018), occurring on every continent barring Antarctica (Fischer et al., 2001). It accounts for approximately 42% European Union (Castillo et al., 2019), >50% Asia (Zhao et al., 2016), 52% United States (Bigelow and Borchers, 2017), 38% Africa (Food and Agriculture Organization of the United Nations, 2020) and 58% Australia (Australian Collaborative Land Use and Management Program, 2016) land areas, respectively. Agricultural systems vary widely depending on location. This reflects resource availability, climate, soil type, market orientation, and history. Consequently, the nature and intensity of farming impacts the magnitude of the pressures exerted upon local watercourses. Production of meat, dairy, crops, and non-food produce including fuel and fiber is a crucial activity for human survival. It is estimated that 42% of world population is employed in agriculture (Anzar-Sánchez et al., 2019). Agriculture could be reasonably considered to be the primary and most important enterprise without which our population could not be sustained. While we cannot do without agriculture, and benefit from it economically and culturally, it does exert pressures on water bodies which impacts their capacity to supply adequate drinking water and to sustain aquatic life (Vitousek et al., 2017). Agricultural land delivers and impacts, to varying degrees, multiple ecosystem services (ES): food/fiber/fuel production; habitat; carbon sequestration; nutrient cycling; and water storage and purification (Schulte et al., 2010). While synergies exist between some of these ES (for example, recycling of nutrients from livestock can replenish soil stores and support plant growth), there are also trade-offs in which freshwater quality and quantity can be negatively affected (Rodríguez et al., 2006).

Under national and international legislation, frameworks have been set for attainment of water quality, for example the Water Framework Directive (WFD; EC, 2000) in the European Union (EU) or the Clean Water Act (CWA; United States Congress, 1972) in the United States (USA). Identification of the activities which are impacting watercourses at a local or regional scale allows appropriate management plans to be designed. Taking the WFD as an example, section 1.4 of that directive stipulates that member states must identify the type and magnitude of anthropogenic pressures to which water bodies in each river basin distract are subject, via both diffuse and point sources. Pressures are categorized into urban, industrial, agricultural, and other, and must be accompanied by characterization of land use. The 2018 report on the status and pressures influencing WFD attainment indicated that agriculture is the primary driver of diffuse source pollution, with 38% of surface waters failing to reach targets as a consequence. At the time of writing (2020) results indicate that 29% of EU groundwater (by area) exhibits poor chemical status as a result of agriculture with 9% impacted by abstraction, primarily for irrigation (European Environment Agency, 2018).

Agricultural pressures

Nutrients

Application of organic and inorganic fertilizers is crucial for maintaining the fertility of agricultural soils and sustaining plant growth. Organic fertilizers include livestock manures and slurry, biosolids, composts, and seaweeds. Synthetic or 'chemical'

fertilizers include refined or processed nutrients which are extracted from mineral resources held within rock reserves (e.g., phosphorus) or converted from other forms (e.g., transformation of gaseous to mineral nitrogen (N) via the Haber-Bosch process). There is an increasing emphasis to use organic wastes from a variety of sources, as this reduces reliance on finite, mineral stores and allows recycling of agricultural and processing by-products. However, research is needed into the agronomic availability and environmental footprint of organic sources, as well as technical and infrastructural supports. Ideally, nutrients would be applied at times and in quantities which allow them to be completely utilized by the growing plant, whether that is a crop which will be harvested for anthropogenic use or grass/forage which will be grazed by livestock and recycled within a closed agricultural system. Such systems are considered to be 'balanced' (Fig. 1). Achieving this balance, however, is rarely simple. Inefficiencies in the utilization of applied nutrients by plants, processes of attenuation and immobilization in soil, rainfall patterns, and hydrologic pathways all reduce the balance of the system and allow nutrients to be lost to water or the atmosphere. Furthermore, poor nutrient management by the farmer, including both over-application and mis-timing of fertilizers relative to crop requirements or weather patterns can encourage greater losses. While plants require a variety of nutrients, it is N and phosphorus (P) are in greatest demand, but which also present the most significant pressures to water quality. However, it is not only terrestrial plants which flourish in response to abundant nutrients. Enrichment of surface-waters with nutrients is known as 'eutrophication'. Under such conditions and in the presence of sufficient light, algal blooms can proliferate, leading to anoxic conditions, reduced vertebrate and invertebrate life, out-competing of desirable plant species, impaired taste and portability, and negative impacts on amenity use.

Pollution of watercourses by nutrients within agricultural settings can be organized within the nutrient transfer continuum framework (Haygarth et al., 2005; Wall et al., 2011). This framework identifies four tiers: sources, mobilization, delivery, and impacts. Sources represent inputs to the system; in this case, chemical or organic fertilizers such as manures, seaweeds, or biosolids. At catchment scale there are several co-occurring nutrient sources (e.g., diffuse agricultural, point agricultural, domestic, and industrial) and discrete transport pathways operating simultaneously. Ascertaining the contribution of agricultural components, independently of other factors, relies largely upon source apportionment models used to evaluate the contribution of various pressures. These models may utilize statistical approaches to disentangle hydrochemical data from monitoring stations or may utilize conceptual, physical, or empirical data to quantify catchment hydrology. Apportionment models range in the complexity of their approach (Yuan et al., 2020) which has concomitant demands on the level of skill of the operator and of data requirements. Notably, many (though not all) models focus on non-point agricultural sources (diffuse runoff and subsurface pathways), excluding point sources. However, point-source models may be coupled or integrated with diffuse models. As with all modelling, selection of the appropriate model can be challenging due to the wide variety of options. Factors including desired outputs, data requirements and availability, spatial scale, and budget should all be considered (Yuan et al., 2020). Nutrient source apportionment is applied as an investigative tool to identify priority areas/issues for mitigation, in the design of agricultural best management practices, and to forecast and trial potential future scenarios.

Mobilization is the initial separation of nutrients from their source. For example, P sorbed to soil may become solubilized, or may be physically detached by erosion. Delivery refers to the physical transport of the nutrient through surface (overland flow) or subsurface (leaching—vertical movement through the unsaturated zone, lateral flow, or groundwater) pathways to a receptor. Delivery is subject to hydrologic and biogeochemical time lags (Schulte et al., 2010; Fenton et al., 2011; Hamilton, 2011; Chen et al., 2019) which confound the direct relationship between management practices and water body response, subject to delays. The distinct transport pathways operate within agricultural catchments simultaneously. This is due to the topography of the landscape, presence or absence of barriers which disrupt overland connectivity, and distribution of soil types, depths, and geology.

Finally, impacts are the 'change or perturbation' (Haygarth et al., 2005) in the water body receiving the nutrient input. These changes are primarily chemical, but this in turn has consequences for the portability and ecology of the water body. The two principal nutrients which are of concern as agricultural pressures, P and N, will be discussed hereafter. These are summarized according to the nutrient transfer continuum in Fig. 2.

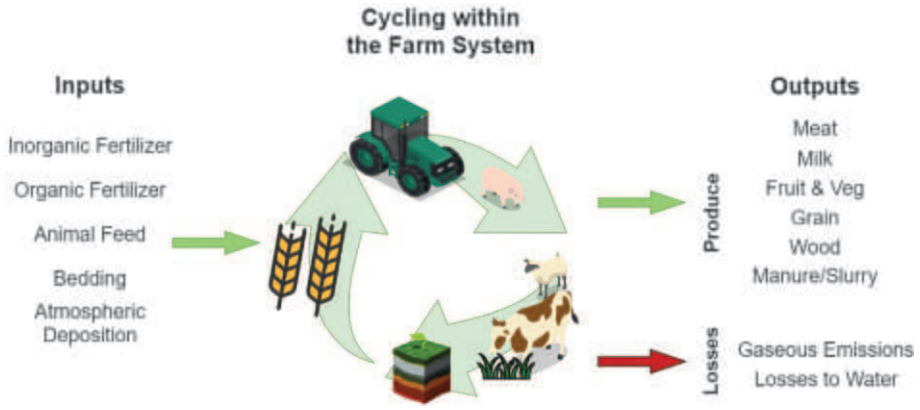

Fig. 1 Conceptual balance of farm nutrient inputs/outputs.

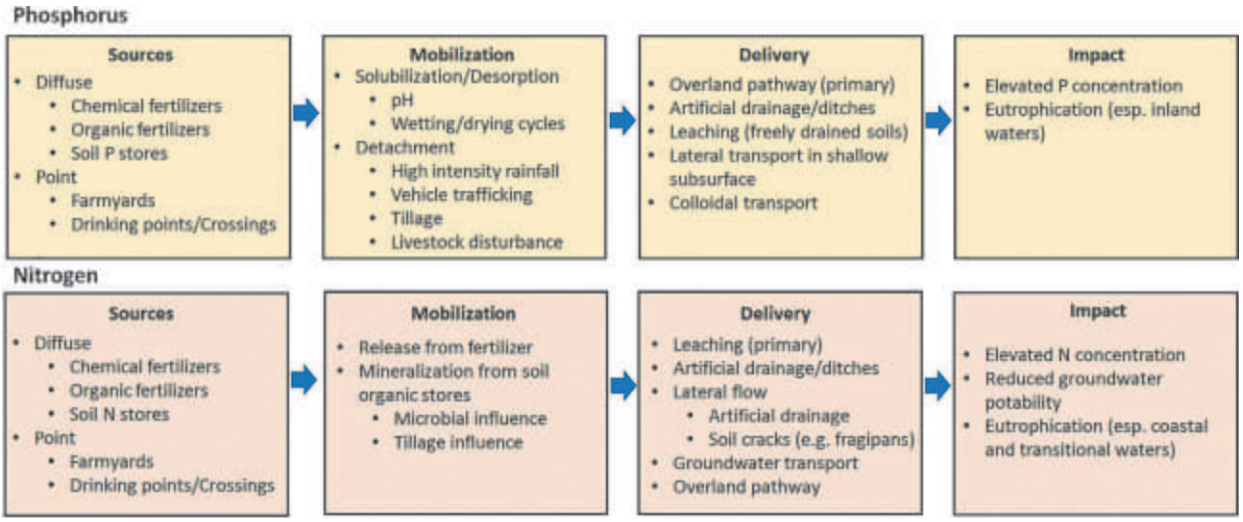

Fig. 2 Stages of the nutrient transfer continuum as relates to phosphorus and nitrogen.

Phosphorus

Phosphorus is frequently considered to be the limiting nutrient for freshwaters, particularly rivers, although nitrogen limitation or co-limitation does also occur especially in headwater streams (Jarvie et al., 2018). It's propensity for attenuation to soils and sediments means that reduction in losses can only be achieved subject to time lags driven by soil chemistry. Schulte et al. (2010) modelled soil P decline from high to moderate agronomic indices, which are also considered to indicate risk of loss to watercourses (Daly and Casey, 2005). Declines to optimal indices were estimated to range between 7 and 15 years; however, significant variability was observed with worst-case scenarios exceeding 20 years. Subject to these prolonged lags, diffuse losses of P from the soil to watercourses will continue if not abated by crop uptake. P stores within the soil may also become solubilized or desorbed subject to changes in pH (McDowell et al., 2001), or due to wetting and drying cycles (Turner and Haygarth, 2001; Pezzolla et al., 2019) which influence microbial activity. This P may be vulnerable to accelerated transport as drying processes create cracks, particularly in clay-rich soils, through which preferential transport may occur. Overland flow is typically the main pathway for delivery of P (either dissolved or particulate) to watercourses. However, leaching may also occur in freely-drained soils (Dupas et al., 2017) or those in which preferential pathways such as artificial drainage or naturally occurring macropores are present (King et al., 2015). While the focus of environmental research is frequently on inorganic P forms due to their bioavailability, dissolved organic P may also leach, and subsequently become available at a later date (McDowell et al., 2021). High levels of soil organic matter exhibit low sorption capacities, meaning that applied P tends to stay in solution in pore water (Daly et al., 2001). This P is at greater risk of loss during either runoff or leaching events, compared with mineral soils. There is also a diversity of agricultural point sources of P. Overland flow from farmyards includes relatively uncontaminated runoff from rooftops and clean collecting areas, but also highly contaminated effluents created during silage production (Gebrehanna et al., 2014), cleaning of dairy parlours (Minogue et al., 2015), and the collection and storage of livestock slurry and manures if these factors are not managed correctly. Other common point sources in agricultural landscapes are septic tanks, as rural dwellings tend not to be connected with municipal waste processing. While the loads contributed by these discharges tend to be relatively small in the context of overall losses, they have been observed to have a disproportionate impact on water quality during low-flow river conditions (Arnscheidt et al., 2007; Macintosh et al., 2011). From a catchment management perspective, it is important that these non-agricultural point sources which are nested within the rural landscape are recognized as a separate and distinct factor.

Nitrogen

Since the advent of chemical N fertilizer resulting from the development of the Haber-Bosch process in the early 20th century production has increased exponentially supporting a vastly enlarged population (Smith et al., 2019). This was facilitated by an increase in synthetic N fertilizer from 12 Tg N $year^{-1}$ in 1960 to 110 Tg N $year^{-1}$ by 2013 (Battye et al., 2017; Peoples et al., 2019). As a conservative nutrient it tends not to attenuate to soils and sediments but rather, is highly mobile and dynamic within the environment. Although some nations do not specify threshold criteria for N in lakes and rivers based on the premise that P is the limiting nutrient, research has shown that N is a factor in eutrophication of inland waters, particularly when it co-occurs with anthropogenic P (Lewis Jr. et al., 2011). Poikane et al. (2019) and Dodds and Smith (2016) recommended that both nutrients should be considered in assessing the ecological status of water bodies. The source of N which is vulnerable to loss has increased, and inefficiencies in balancing inputs vs outputs are a financial and environmental challenge. The increase in N load translates to an increase in N surplus, where crop offtake is not equivalent to inputs from fertilizers, manures, and atmospheric deposition. Surpluses vary depending on landuse type, cropping system, management practices and climate (Lord et al., 2006). These surpluses

represent the N which is vulnerable to transport, however the magnitude of surpluses correlates poorly to both groundwater and surface water N concentrations, due to the complexity of transport and transformation processes (Rosário Cameira et al., 2021).

The sub-surface pathway is generally dominant in N transport and large N loads may accumulate as a result of antecedent management practices. Stores of nitrate (NO_3^-) in the vadose zone (soil and unsaturated bedrock) have been estimated to range between 605 and 1814 Tg worldwide (Ascott et al., 2017). This load is subject to two issues which render the impact of agricultural practices on water body N complex to unravel. Firstly, N cycles dynamically within the soil, shifting between occluded forms within soil organic matter, gaseous forms which can be emitted to the atmosphere (ammonia (NH_3), dinitrogen (N_2), nitrous oxide (N_2O)), and soluble forms which may be transported hydrologically (ammonium (NH_4^+), NO_3^-, nitrite (NO_2^-)). This cycle is mediated by microbial activity and a variety of influencing factors, including soil saturation, nutrient inputs, pH, temperature, etc. (Bingham and Cotrufo, 2016). Consequently, the understanding of this cycle is constantly evolving. The second confounding factor is the issue of time lag. Time lag is the delay in response of water bodies to changes in management practices including delays in implementation, effect, delivery, response, and finally in measurement within the water body (Meals et al., 2010). Hydrologic time lag refers exclusively to the time taken for physical transport of NO_3^- through vertical (leaching) or lateral subsurface pathways (including fractures and artificial drainage) (Fenton et al., 2011). Total hydrologic lag (t_T) can be divided into two portions: unsaturated zone (t_U) and groundwater (t_S) (Sousa et al., 2013). The duration of t_U is controlled by soil physical characteristics (porosity, conductivity, etc.), moisture regime, and depth to the water table (Fenton et al., 2011; Vero et al., 2017). The t_S component, being constantly saturated, is dictated by distance to the watercourse. Duration of t_T varies widely within agricultural landscapes, but evidence from Europe (Vero et al., 2017; Granlund et al., 2005; Kim et al., 2020), United Kingdom (Wang et al., 2013), North America (Van Meter and Basu, 2015), Asia (Wu et al., 2020) and Oceania (Wilson et al., 2014) (amongst other references to exhaustive to list here) all indicate decadal scale responses. Consequently, the expected timeframes for water quality improvements (such as those prescribed under the WFD in Europe) should be set based on biophysical limits, rather than timeframes which are politically oriented (Ascott et al., 2021).

Nutrient impacts

The impact of nutrients on ecology and water quality depends not only on the gross quantities delivered to the watercourse, but on the degree of dilution and on their timing with respect to season. Regarding dilution, rivers vary in their rate of discharge over time and consequently, a certain load of N or P may result in a greater or lesser concentration depending on the time at which it is delivered to the watercourse. Low-flow conditions offer the least dilution and incidental transfers due to flashy storms (Jordan et al., 2012) have potential for high impact. Furthermore, persistent point sources such as nutrient-laden washings from farmyards (Edwards and Hooda, 2008), domestic septic tanks (Arnscheidt et al., 2007; Macintosh et al., 2011), animal drinking points or stream crossings (O'Callaghan et al., 2019) can become pronounced. These low-flow inputs may reflect a small proportion of total annual fluxes (Arnscheidt et al., 2007) and may be relatively small at each delivery point. However, the cumulative effect of multiple such sources across entire river networks can result in increasing concentrations moving from headwater to outlet (Vero et al., 2019).

Regarding timing, stream ecology is subject to ecologically sensitive periods corresponding to the lifecycles of aquatic species. These periods may also align with periods of high risk of eutrophication during summertime, when flow is often lower due to limited precipitation, and sunlight hours are greatest. These conditions promote photosynthesis of harmful macroalgae and are difficult to influence in many cases. This may force ex-situ measures to control nutrient inputs to be emphasized (i.e., those which limit nutrient sources such as caps on fertilizer application rates, and those which disrupt the transport pathway such as buffer strips), over in- or near-stream measures. However, some options do exist. For example, shading of streams by encouraging riparian cover has been observed to significantly lower gross primary production in-stream even in the presence of elevated nutrient concentrations (Nebgen and Herrman, 2019). Such approaches may have utility where time lag or orientation of highly productive agricultural catchments makes reductions in nutrient loading challenging in the short to medium term.

Certain aquatic species show particular sensitivity to eutrophication and thus act as indicators for the pollution status of the water body. Other, more resilient species may inhabit even degraded waters. The individual taxa which reflect good or poor water body status varies geographically, and for the purposes of assessment individual criteria and indices are determined regionally. Generally, there is a preference for fish and macroinvertebrate species as indicators (O'Brien et al., 2016), likely because they can be easily identified, compared to algae, biofilms, and bacteria. Similarly, high status water bodies and those existing in environmentally sensitive or conservation areas are least tolerant to additional nutrient inputs and require rigorous efforts in order to avoid declines in status. A feature of agricultural wastes, particularly effluents originating from silage production or manure storage, is a high biochemical oxygen demand (BOD). This is the quantity of oxygen which is required by micro-organisms to break down organic matter at a specific temperature. Regarding water quality, this is observed over five-day assays, and so BOD_5 is a reference measurement, although longer observations are also possible. As organic matter decays, oxygen in the water column is depleted. Hypoxic conditions are unsuitable for both vertebrate and invertebrate species. For this reason, effluent discharges are particularly associated with sudden fish kills. These discharges may result from persistent point sources (e.g., leaky effluent tanks or silos) but also from accidents such overflows of storage, pipe failures, or tanker spills.

Sediment

Erosion and deposition of sediments from stream banks are a fundamental process controlling the dynamics and evolution of surface water bodies; as is the translocation of soil particles from the landscape to the watercourse. As a consequence, the

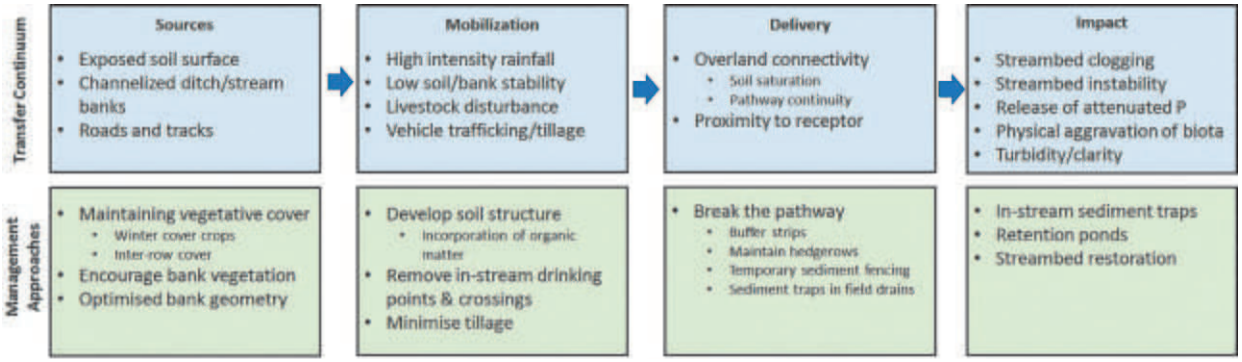

Fig. 3 Conceptual framework of sediment transfer to water bodies. Adapted from Haygarth et al., (2005) The phosphorus transfer continuum: Linking source to impact with an interdisciplinary and multi-scaled approach. *The Science of the Total Environment* 344: 5–14.

hydromorphology of rivers and the topography of the surrounding landscapes changes with time which can impair agricultural productivity and cause declines in ecosystem health (both in terrestrial and freshwater systems). Concurrently, erosion causes loss of soil and nutrients and therefore affects primary productivity and crop production. It has been estimated that tolerable rates of erosion not exceeding rates of soil formation are (in Europe) at maximum 1.4 t ha year^{-1} (Verheijen et al., 2009). In reality, rates of erosion are often much higher, and rates of both soil formation and erosion vary widely both worldwide and even between nearby catchments. Similar to nutrient pollutants, factors influencing sediment deposition in watercourses can be understood using the source to impact framework (Fig. 3) described by Haygarth et al. (2005). This framework was originally used to understand P transport.

Sediment sources

Exposed soils are vulnerable to erosion during high intensity rainfall, trafficking by livestock, and during cultivation. Sediment fingerprinting using distinctive inorganic properties such as radionuclides has been used to apportion sediments arising from various sources within agricultural catchments (Sherriff et al., 2019; Lamba et al., 2014). Sources within individual catchments include both arable (crop) and grassland (or other forage used for livestock grazing), public roads (a non-agricultural source nested within agriculturally dominated catchments), tracks used by livestock and agricultural vehicles, riverbanks and beds which have become disturbed by livestock accessing the watercourse to drink or to cross (Sherriff et al., 2015, 2019; Lamba et al., 2014; Lefrançois et al., 2007). The proportion of total sediment load derived from each of these sources varies by location, depending on their land use, hydrology, soil type, and management.

Mobilization and delivery

Land use affects the mobilization of sediments from the soil surface. The conventional understanding is that arable land typically exports greater sediment loads to watercourses than equivalent grassland areas. This is due to the greater proportion of exposed soils, more frequent tillage, large field areas, and fewer hedgerows (i.e., boundaries consisting of shrubs or trees) in arable land. However, some grassland catchments, exhibiting high surface connectivity as a result of low soil infiltration capacity as well as prolonged saturation, have been documented to yield greater loads of sediment to receiving water bodies than more freely drained arable catchments (Sherriff et al., 2015). This is a function of the hydrology of the catchment. Reduction in the extent of hedgerows due to intensification of agriculture and merging of small fields into larger, single units (White and Roy, 2015; Sheridan et al., 2011) has increased the surface connectivity via overland flow pathways. This allows sediment, once it has become detached from the soil surface, to be transported to receiving water bodies, rather than being retained at the field margin.

Impacts of agricultural sediment on watercourses

Suspended sediment within the water column is a feature of natural waters (Vercruysse et al., 2017) however, excessive sediment poses several problems which constrain the desired functioning of watercourses. Accumulation of sediment in the streambed may destroy the habitat of freshwater biota. The freshwater pearl mussel (*Margaritifera margaritifera L.*), for example, requires a stable, aerated gravel bed with <20% fine sediment (particles measuring <1 mm) constituents (Denic and Geist, 2014). Deposition of fine sediment arriving from outside the watercourse or from upstream reaches has been documented to choke gravel streambeds. This renders these beds uninhabitable for pearl mussel (Österling et al., 2010; Niraula et al., 2017) and other sensitive species such as trout (Lange et al., 2013), salmon (Walling et al., 2003), amphibians (Schmutzer et al., 2008; Muenz et al., 2006), and macroinvertebrates (Davis et al., 2019; Beerman et al., 2018). Considering the variability of bed substrates both across regions and along individual watercourses, it is difficult to set qualitative thresholds for sediment accumulation. Macroinvertebrates are a common indicator of water quality. They are subject to multiple ecosystem stressors, making it difficult to disentangle the influence of any one factor. In a recent mesocosm study mimicking instream ecosystems, manipulated nutrient and sediment dynamics (Davis et al., 2019) sediment was the most influential stressor, negatively impacting the total abundance of sensitive taxa and the

diversity of species. Sediment also interacted with P concentrations; however, this could occur in either a synergistic (exacerbating the impacts of P on ecological status) or an antagonistic (reducing the impacts) fashion. The nature of the interaction may be related to the P sorption capacity, such that additional sediment may in some cases bind soluble P from the water column.

In other scenarios, sediment arriving from agricultural land may bring high quantities of P sorbed to the surface of particles, as a legacy of antecedent fertilizer application. In-stream P reserves may be released to the water column via desorption, precipitation and dilution, and advection and diffusion processes (Withers and Jarvie, 2008). The characteristics of the sediment itself influences release, with low Ca/P ratios facilitating P mobilization (Shore et al., 2016). The indeterminate timing of P mobilization from transported sediment adds uncertainty to interpretations of agricultural impacts on water quality.

Emerging agricultural contaminants

Within the agricultural setting, emerging contaminants include those that have only recently become a concern due to their increased use in line with intensification, and pollutants which have only recently been developed or identified. Emerging contaminants from agriculture include veterinary medicines, biocides, steroids, disinfectant residues, and metals (Snow et al., 2012). Veterinary medicines may be excreted by livestock to which they have been administered. Runoff contaminated by contact with these manures may consequently carry dilute concentrations (Sinclair et al., 2007). Antibiotics (Bailey et al., 2015; Wei et al., 2011), hormones (Boxall, 2012), and anti-coccidials (Mooney et al., 2020) have been observed in the surface- and groundwater bodies of agricultural catchments. While absolute loads and concentrations may be extremely small compared to nutrients, the impact on aquatic species may be significant even at trace exposures. Concentrated animal feeding operations have been correlated to high river concentrations of veterinary medicines, due to the reliance on treatments in these systems and the high density of animals (Burkholder et al., 2007).

Biocides including herbicides and insecticides are widely recognized emerging contaminants. Impacts on aquatic species has been a factor in regulation of the industry including withdrawal of high-risk active ingredients (e.g., the herbicide atrazine in the United Kingdom (Stuart et al., 2012)). These have high acute toxicity and/or chronic effects on aquatic species. For example, exposure to atrazine has been observed to reduce egg production by 17–39% in fathead minnow (*Pimephales promelas*) with significant reductions occurring by day 20 even at concentrations observed in agricultural settings (Tillitt et al., 2010). The neonicotinoid variety of broad-spectrum, systematic insecticides has been widely observed in surface and groundwaters, due to its high solubility and mobility (Morrissey et al., 2015). These insecticides are common in tillage production however, they have well-established toxic effects on aquatic macroinvertebrates. Multiple treatments can act synergistically and furthermore, their lethality varies between affected non-target species making hazard and impact assessment challenging (Morrissey et al., 2015). Biocides may also have secondary poisoning effects, wherein predators consuming contaminated species in-turn become exposed (Hinck et al., 2009), particularly for contaminants which bioaccumulate in tissues. Legislation such as the EU Sustainable Use Directive (European Parliament, 2009) outline structures to mitigate risks posed by biocides. These rules include use of low-drift applicators, avoidance of watercourses and drainage networks, and directions regarding handling, storage, and disposal. A central feature of biocide regulation is requirements to implement integrated pest management (IPM), which gives preference to non-toxic measures to control weeds and invertebrate pests. While there are several approaches to IPM, they typically emphasize preventative rather than reactive measures. This prioritizes monitoring, encourages mechanical and biological controls, and promotes chemical controls only as necessary and at minimum.

Notably, not all emerging contaminants now recognized within the agricultural system are a de facto feature of farming itself, but rather, originate elsewhere within the circular bioeconomy. Personal care products (PCPs) and pharmaceuticals for the treatment of humans have been identified in landspread biosolids recycled from domestic wastewater treatment (Clarke and Cummins, 2015; Healy et al., 2017). The objective of landspreading is to utilize nutrients within biosolids and sludges, thereby limiting their loss to watercourses. The extent of this recycling is likely to increase subject to legislation such as the European Union's Urban Wastewater Treatment Directive (Clarke and Cummins, 2015). However, emerging contaminants within these biosolids exhibit similar ecological hazards as those originating from livestock or crop production; specifically, high persistence in soils and sediments, bioaccumulation in aquatic organisms, and frequently, chronic toxicity to exposed species. However, the risks associated with biosolid application can be reduced through pre-treatment and application method. Decisions surrounding use of these fertilizers should be supported by analysis of the potential risks and benefits, with strategies imposed to offset risks.

Land drainage and abstraction

The primary impact of agriculture on hydromorphology is via artificial drainage and the modification of rivers and streams. Artificial drainage improves the suitability of land for production and is a hallmark of agricultural production. Valipour et al. (2020) documented the long history of this practice in civilizations worldwide, citing evidence from Iran dating as early as c. 4000 BCE, though the modern phase of land drainage could be considered to have developed first in the Netherlands during the 16th Century (Harris, 2017). While it is difficult to estimate the extent of artificially drained land worldwide due to limited records and differences in approach, Schultz et al. (2007) estimated it to be av. 13%, ranging from 3% in least developed countries to 25% in developed countries. Climate and soil type influence the extent of artificial drainage, with drained area as a percentage of cropped area being 29%, 8% and 4.5% for temperate-humid, arid/semi-arid, and humid/semi-humid areas, respectively (Zimmer et al., 2005). It should also be recognized that funding and resources also play a role in the degree of investment in drainage (Schultz et al., 2007).

While artificial drainage in itself is not a pressure on water quality, it does provide an accelerated pathway for contaminant transport (Lowrance et al., 1984). Review of the literature indicates strong consensus that nitrate loss is particularly amplified in artificially drained soils due to hydrologic connectivity (Castellano et al., 2019). This may be exacerbated by a concomitant reduction in storage time and consequently, in denitrification (Jahangir et al., 2012; Rivas et al., 2020). There is a trade-off between the beneficial implications of land drainage, which increases the area available for agriculture and improves the productivity of existing farmland versus negative impacts on habitat, species, and on flood mitigation.

On a positive note, by creating greater storage and infiltration capacity within the vadose zone artificial drainage may reduce runoff during peak flows from saturated soils (Gramlich et al., 2018). This will influence the timing and type of nutrients lost, and potential for attenuation and transformation prior to reaching a water body. As a consequence of reduced runoff, sub-surface drainage has also been observed to limit erosion on mineral soils (Gramlich et al., 2018). However, erosion may still occur along the banks of open drains. The cross-sectional profile of the open drain influences its capacity to slow the flow of water and allow sediment to drop out before reaching the main watercourse. In Ireland, Shore et al. (2015) identified three classes of sediment retention potential for open drains (Table 1), although crucially, soil type will affect the stability of side slopes (Tuohy and Fenton, 2013). Furthermore, the chemistry of ditches influences their potential to either attenuate or mobilize P (Shore et al., 2015; Moloney et al., 2019) (Table 1). Similar research has been conducted in New Zealand (Nguyen and Sukias, 2002) and elsewhere. Correct design and management of ditches can be used to moderate their role as a nutrient pathway to receptors (Sharpley et al., 2007) while retaining their intended function of removing water from the landscape. Efforts to retain sediment will reduce particulate P reaching watercourses. Indeed, two-stage ditches and sediment traps have been developed to amplify this effect (Davis et al., 2015). A major advantage of in-ditch mitigation measures is that they offer potential solutions without reducing farmed area.

Modification of rivers and streams is an intrinsic element of artificial drainage. More rapid delivery of soil water to the surface watercourse as a result of subsurface drainage creates greater discharge in the watercourse itself. This discharge exerts force, causing erosion of banks and straightening (or 'channelization') of the profile of the river. Aerial photography of watercourses has revealed significant channelization over decades (Hajdukiewicz and Wyzga, 2019; del Tánago et al., 2016). As a consequence, water travels with greater energy which increases the erosion of riverbanks. This sometimes contributes to flooding of downstream reaches. Increased flow as the result of channelization can lead to streambed instability, decreased habitat variability, and consequently decreased fish assemblage (Lau et al., 2006). Excessive or prolonged low flows as a result of abstraction may impair the migration of fishes upstream which is critical for the reproductive cycle of certain species (Ohlberger et al., 2018).

The area of land under irrigation has expanded worldwide, from 151 M ha in 1961 to 284 M ha in 2014 (Pellegrini and Fernández, 2018). This expansion has been greatest for 12 countries heavily dependent upon irrigation: Bangladesh, Chile, China, Egypt, India, Italy, Japan, Nepal, The Netherlands, Pakistan, Peru, and South Korea, which together account for an expansion of 64 M ha within that timeframe. Along with drainage, irrigation has been a core factor in bringing uncultivated land into production. Abstraction of surface and groundwater resources for irrigation is common, along with rainwater harvesting in some regions. It should be recognized that geographic regions have a natural predisposition for certain types of agriculture, which reflects water availability inter alia (Rijsberman, 2006). For example, the water footprint (WF) (indicating the direct and indirect consumption or use of water) per kg beef produced under the Irish pasture-based system has been estimated at 8,391 L kg (the majority of which is 'green water'—utilized rainfall, as opposed to 'blue water'—abstracted ground- or surface waters) (Murphy et al., 2017). Conversely, the WF of beef produced in Brazil in either grazed of mixed systems exceeds 20,000 L kg (Gerben-Leenes et al., 2013). This calls into question the equitability of importing produce from less water-efficient to more efficient systems. This 'offshoring of pollution' (Li and Zhou, 2017) has occurred in other industries where production is shifted to low-wage or low-regulation countries, rather than those which are the most efficient or where the goods are actually consumed. While the goods and money exchanged may be displaced, the pollution remains in situ (Hoekstra, 2010). This is not restricted to water pollution, but to other environmental aspects such as habitat and biodiversity loss (Dalin and Rodríguez-Iturbe, 2016).

Table 1 Drainage ditch characteristics and sediment and nutrient transport potential.

Sediment Retention Potential	*Ditch Slope*	*Phosphorus Retention Potential*	*Calcareous Soils Al/P[a] Ratio*	*Non-Calcareous Soils Ca/P[a] Ratio*
High	≤2%	High	>11.7	≥74
Moderate	2–5%	Low	<11.7	≤74
Low-Moderate	≥5%			

[a]Mehlich test.

Adapted from Shore M, Jordan P, Mellander PE, Kelly-Quinn M and Melland AR (2015) An agricultural drainage channel classification system for phosphorus management. *Agriculture, Ecosystems and Environment* 199: 2017–215; Shore M, Jordan P, Mellander PE, Kelly-Quinn M, Daly K, Sims JT, Wall DP and Melland AR (2016) Characterisation of agricultural drainage ditch sediments along the phosphorus transfer continuum in two contrasting headwater catchments. *Journal of Soils and Sediments* doi: 10.1007/s11368-015-1330-0.

Summary

The effects of agriculture on inland waters are significant, widespread, and diverse. While it is beyond the scope of this chapter to exhaustively document all scenarios, priority issues and processes have been outlined. Agriculture is a pivotal activity, underpinning and supporting human populations and societies. Therefore, there is a need to balance its essential, positive consequences (food and material production, employment, secondary industries, land stewardship, etc.) with its detrimental impacts. The challenge of agriculture is to balance the food production required to support the current and expanding population against environmental protection and the provision of other ecosystem services (Falkenmark et al., 2007). Best management practices can mitigate contaminant losses and impacts; however, sufficient time and investment are required to allow them to have full effect on waterbodies.

Knowledge gaps

- What mitigation measures will be most effective for individual pollutants, watercourses, and landscape scenarios?
- What are the trade-offs between agricultural production, the delivery of other ecosystem services, and pollution and abstraction of water?
- How will changing agricultural practices and demands impact on water bodies?
- What are the time frames by which improvement in water quality can be expected subsequent to interventions?
- How can water use efficiency be improved for various livestock and crop systems?
- How should the costs of water quality and the delivery of water-related ecosystem services be reflected in food and fiber prices?
- How do we achieve a balance between the positive (e.g., food production) and negative impacts (e.g., pressures on waterbodies) of agriculture?

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The Best Management Practices in Agriculture for Protection of Inland Water Ecosystems

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Best management practices Proposed methods that are most effective for reducing non-point source pollution to attain inland waters' quality goals. Such practices include measures to prevent and mitigate pollution.

Conservation management of buffer zones Efficient implementation of multilayer plant based structure between grasslands or crops and water bodies, aiming for diminishing the nutrients, pesticides and fine sediment runoff into aquatic habitats.

Conservation management of crop nutrients A mixture of traditional and more recent methods that optimize nutrients (i.e., N, P and K) cycling in crops, aiming for a healthy balance between their demand by crops and inland water eutrophication.

Conservation management of irrigation waters Efficient irrigation methods that aim to diminish salts, pesticides and nutrients release into inland waters and efficient water transportation from the aquatic source to crop, as such as to limit water losses.

Conservation pest control management A complex package of measures for the prevention of pest issues and reduction of pesticides usage. Such measures comprise a combination of biological control of pests, cultivation of pest-tolerant plant varieties and crop rotation, as well as the monitoring of pests evolution.

Conventional tilling Comprise various sequences of soil tillage, such as ploughing and harrowing and the removal of most of the previous crop. This practice is opposed to conservation tillage (definition provided in text).

Management of grazing activities Proposed package of measures to diminish the impact of livestock on aquatic habitats through their permanent fencing, alternative water sources, controlled grazing and supplemental feeding.

Management of intensive animal feeding operations Methods employed for limiting the quantity of manure release into inland waters, by limiting its ground application rate and through off-farm diverting toward pelletization industry, power factories, as well as through changes of animals' diet.

Introduction

Globally, intensive agricultural practices have a substantial impact on inland waters. The array of stressors with detrimental effects for freshwater habitats is multiple: fine sediments, nutrients, pesticides and emergent pollutants acting alone or in synergy (Yates et al., 2007). Both point and diffuse types of pollution, mixed with improper land usage (e.g., tilling, nutrients leaching or overgrazing) can affect all types of freshwater habitats in the proximity of agroecosystems (Meals et al., 2010).

In the attempt for reconciliation between most intensive agricultural practices and aquatic ecosystems degradation, a variety of structural and management conservation practices have been proposed, generally named Best Management Practices (hereafter BMP's, Haas et al., 2017; Liu et al., 2017; Napier and Bridges, 2003). One of the aims of these practices is to minimize the release and impact of stressors from agriculture on inland waters.

This article introduces the basic types of agricultural practices that are suitable for reducing the detrimental impact on water quality and ecological status, and which can be applied as part of an overall watershed approach. Categories include the management of:

- Tillage: activities that leave in place the vegetal remains following crop harvest as such as to reduce runoff, soil erosion, nutrients and pesticides leaching through soil (Fig. 1);
- Crop nutrients: the assessment of proper nutrient concentrations to maintain a healthy balance between crop needs and water eutrophication (i.e., enrichment of surface and groundwater ecosystems with nutrients such as nitrogen and phosphorus);
- Pests: the trade-off techniques between the use of pesticides and alternative methods involved in the control of invertebrate pests, plant disease agents and weeds and inland waters' pollution issues (Fig. 2);
- Buffer zones: techniques that ensure the efficient functionality of aquatic and riparian vegetation working as buffers in capturing pollutants and to impede livestock's direct access to water bodies (Fig. 3);
- Irrigation: techniques to reduce surface and groundwater pollution within irrigation systems;
- Grazing: techniques to minimize the impact of livestock grazing on aquatic ecosystems (Fig. 3); and
- Animal feeding operations: techniques to control the impact of animal feeding activities and waste discharge within inland water habitats (Fig. 4).

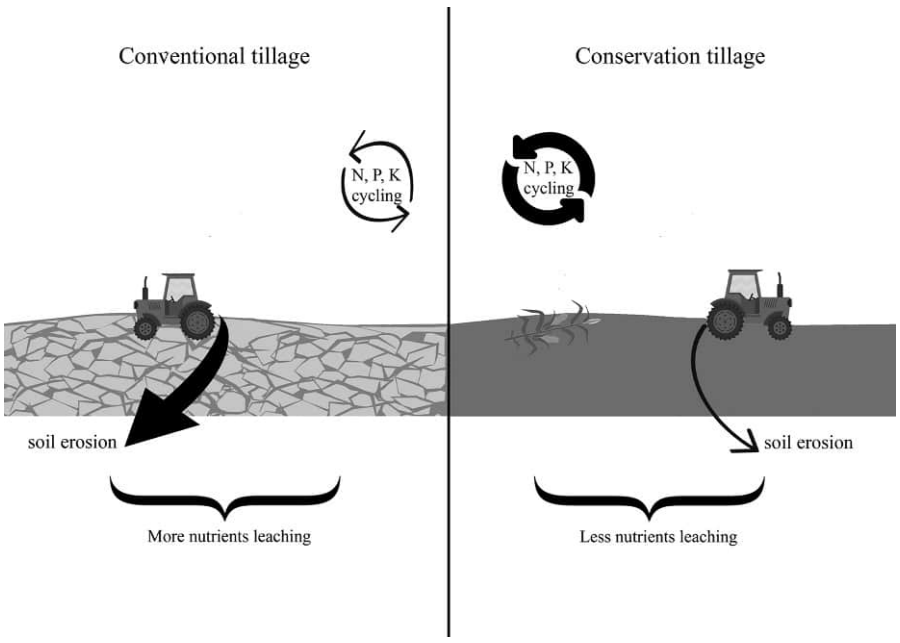

Fig. 1 Example of effects produced by conventional (left panel) versus conservative (right panel) tillage techniques on the magnitude of cycling rate of nutrients (i.e., N, P and K) at air—soil interface, as on soil erosion and nutrients leaching in a water body situated in the vicinity of an arable crop. The tractor symbolizes the tilling techniques and the corn the crop. The magnitude of the cycling rate at air—soil interface, soil erosion and nutrients leaching rate in the recipient water body is represented by arrows of different widths.

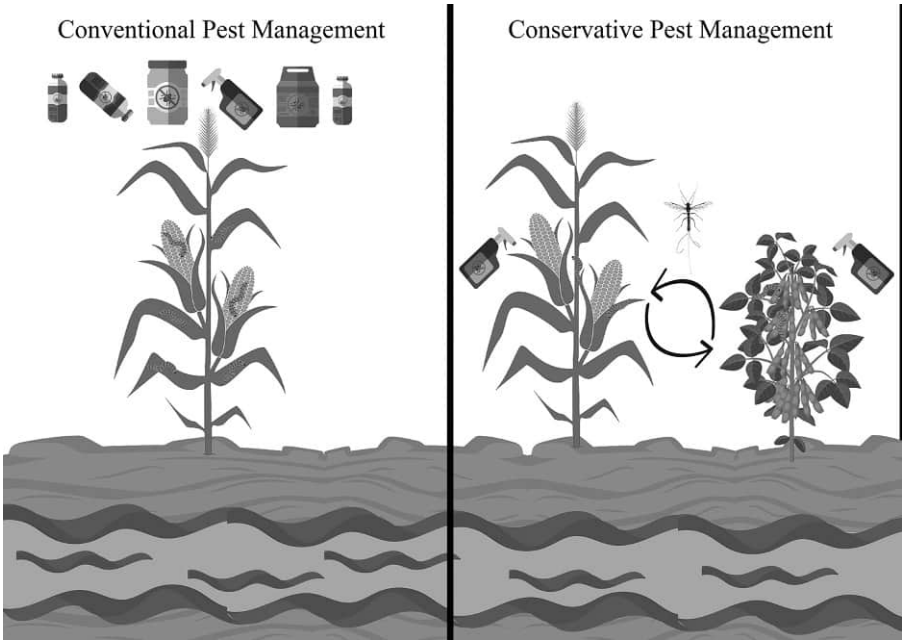

Fig. 2 Example of effects produced by conventional (left panel) versus conservation (right panel) pest management techniques and their effects on watersheds. The conventional techniques involve heavy application of pesticides that end up in the watercourse, threatening the health status and biodiversity. The conservation techniques, whilst not excluding the application of pesticides, albeit used at a lower rate, comprise additional environmental-friendly methods, such as the biological control of pests (in this example with the aid of parasitoid wasps) combined with crop rotations that interrupt the life-cycle of species-specific pests.

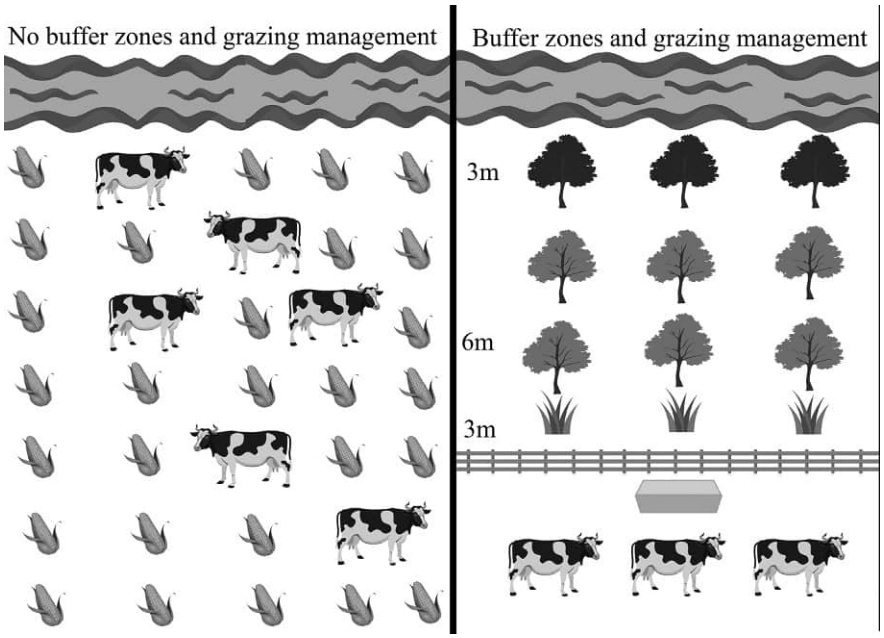

Fig. 3 Example of combination of conventional (left panel) versus conservative (right panel) buffer zones and grazing management techniques. The design of an appropriate buffer zone comprises a three-layer structure (sensu Christen and Dalgaard, 2013): a first layer (3 m wide) comprising grass (e.g., reed canary grass), followed by two layers of riparian tress (6 m wide layer of green alder and another 3 m wide strip of black alder trees). The grazing is mainly rotational and less intense, complemented sometimes with permanent fencing of livestock, and provided with supplementary water sources (e.g., trough) as compared to traditional management practices.

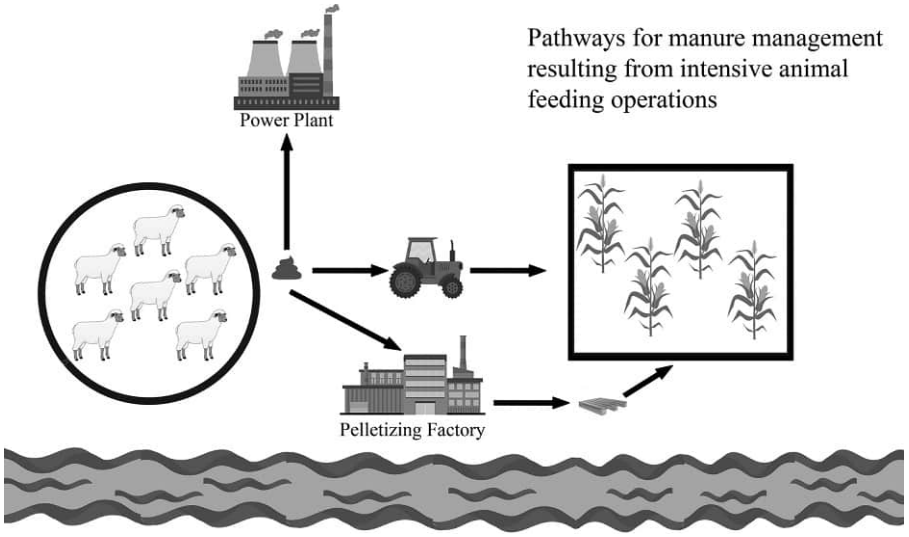

Fig. 4 Example of best management techniques for intensive animal feeding operations. Whereas the usual practice is ground application of untreated manure in crop fields, the alternatives are either the pelletizing technology or their usage as fuel for power plants.

Conservation tillage

Conservation tillage is broadly defined as any tillage technique with at least a third of the previous crop's residues remaining on the soil surface after seeding and represents one of the most popular BMPs that have been promoted around the world (Lal, 2003). However, its efficiency is strongly dependent on local characteristics of soil and climate; hence, it is paramount to understand how these factors interact whenever recommending conservation tillage measures to reduce and control nutrients and sediment export (Fig. 1). Conversion to conservation tillage has been shown to reduce the annual export of suspended sediments (considered as an indicator for sediment export) situated in the vicinity of crops by up to 65% compared with classic tillage systems (Seta et al., 1993; Tiessen et al., 2010; Reicosky, 2015). However, its efficiency depends strongly on local climate conditions. In the northern hemisphere, where snowmelt often exceeds rainfall runoff over the year, the efficiency of conservation tillage on sediment export is stronger during winter and spring compared with summer season, because snowmelt is usually less erosive, due to lower available kinetic energy than raindrops and occurs when the soil is frozen (Rekolainen et al., 1997). However, snowmelt in spring increases runoff significantly, hence increasing nutrient leaching. With respect to nutrient budgets, the results are conflicting, but with a general acceptance that overall, the proper implementation of site-specific tillage measures is effective in reducing nutrients leaching to water bodies (Fig. 1). As such, the situation of nitrogen (N) and phosphorus (P) retention is very much case-dependent. In the case of N export, its reduction was explained through a combination of diminished rainfall-induced runoff and effective tillage measures (Power et al., 2001). Other important factors involved in N retention could be the differences in its mineralization rate (i.e., the conversion of organic nitrogen to inorganic forms) as induced by proper implementation of conservation tillage. As a result of tillage, N mineralization can increase, leading to the build-up of nitrates in the uppermost soil layers of 0–15 cm (Campbell et al., 2008).

With respect to P retention and more specifically, various fractions of P-bound chemical species, conservation tillage can have mixed effects. The particulate phosphorus export in runoff can be directly dependent on the total export of eroded sediments and local runoff events (e.g., strong precipitation summer events), hence expectedly to be highly correlated to the amount of suspended sediments in the nearby water bodies (Sharpley et al., 2008). If the conservation tillage measure is effective, then this form of particulate P export should be equally diminished. However, the export of dissolved fraction of phosphorus in runoff is directly related to its fraction in soil and chemical reactivity (Tiessen et al., 2010). Previous investigations showed that the fraction of dissolved P can be higher in soils after implementation of conservation than under conventional tillage (Jennings et al., 2003; Selles et al., 1999).

The management of crop nutrients

The modern concept of crop nutrient management represents a mixture between old and new methods into a complex package of measures that is both environmentally friendly and economically sustainable. These management methods optimize most aspects of nutrients (i.e., N, P and K) cycling, aiming for synchronizing their demand by crops whilst diminishing their release in nearby water bodies (Kassam et al., 2011).

Barren fields and rotation crops

Barren fields left as gaps between crops represent both an economic and environmental issue. The replacement of such arable fields with other crops is considered nowadays one of the basic, but crucially important aspects for an efficient management of crop nutrients (Drinkwater and Snapp, 2007). The crop covering can reduce nitrate leaching up to 70% and avoids supplementary associated environmental risks (Howarth, 2005). Moreover, it was observed that the vegetal residues left in the field following crop harvest were followed by the increase of both N and P mass through the addition of organic matter used by the following crops (Howarth, 2005). Such an impact on microbial communities alters the timing of carbon (C) input and increases its conversion into microbial biomass (Jans-Hammermeister et al., 1998).

The introduction of legumes in crop rotations is seen as a viable means of reducing current dependence on synthetic N-fertilizers (Wu and Ma, 2015). This method has been proven to be highly influential in changing N cycling among soil, plants and atmosphere. The efficiency in N cycling is attained due the ability of legumes to fix atmospheric N_2 through symbiosis with bacteria and greater rate of residues turnover due to their biochemical composition (Plaza-Bonilla et al., 2015). Leguminous residues increase soil mineral N availability as a consequence of their turnover and accelerate the decomposition of soil organic matter (Wu and Ma, 2015). In order to avoid nitrogen losses, such as nitrate leaching and/or nitrous oxide emission to the atmosphere, the introduction of legumes needs to carefully consider the N balance between plants' requirements and its chemical availability in soil (Plaza-Bonilla et al., 2015).

In tropical systems, where P is often a major limiting nutrient easily lost in runoff in nearby water bodies, alternative environmentally friendly solutions represent an operative method. Experimental plots of various crops indicated that in such environments, the mixture of legumes lupin (*L. albus*) and pigeon pea (*C. cajan*) enhanced P availability for maize crops (Abawi and Widmer, 2000). The classic long-term experiments combining grass and legumes in pastures indicated larger P pools available compared with any of these two families of plants cultivated alone (Oberson et al., 2001). Moreover, by increasing plant diversity, the arthropod community is diversified, leading to enhanced number of natural biological top-consumers for various pests and decreasing the costs for herbicide or pesticide application and abundance of weeds (Abawi and Widmer, 2000).

Plantation of winter crops

The plantation of winter crops can be highly beneficial for crop nutrient management. Winter crops can reduce nitrate leaching into groundwater during winter and spring seasons, when highest infiltrations into soil tend to occur. Winter crop plantations reduced nitrate loss by three-fold compared with barren soils in a study undertaken in Maryland, United States (Staver and Brinsfield, 1998).

Application of fertilizers only when the time needed

A still very common practice among farmers from the northern hemisphere is to apply fertilizers, otherwise a very cheap product, during autumn, when the farmer has time. Because of this, much fertilizer (comprising various forms of N-related compounds) is leached into groundwater, leading to often serious degradation of water quality, given the long-term time period necessary to naturally remove these compounds from these water bodies. The optimal time to spread fertilizers is, however, during spring and summer. Autumn applications of fertilizers have been shown to increase N leaching into groundwater by 30–40% compared with spring and summer applications (Randall and Mulla, 2001).

The management of pests

Such measures comprise a holistic approach for the prevention of pest issues and reduction of pesticides usage that may adversely affect the inland water bodies (Barzman et al., 2015). Rather than simply decreasing the usage of pesticides, several complementary methods have been suggested in order to reduce detrimental effects on aquatic environments:

Pest-tolerant plant varieties and closely monitoring of their efficiency

The use of pest-tolerant and resistant crops helps decreasing dependence on pesticides in arable crops (Fig. 2). However, for efficient pest management this should be combined with the monitoring of pathogens carrying resistance genes (Haverkort et al., 2008).

Crop rotation

Crop rotation represents one of the most efficient alternatives to pesticides use (Fig. 2). Alternating winter and spring-summer crops is highly recommended, since this action breaks the life-cycle of many pests more efficiently than the classic rotation with winter or summer crops (Bartoli et al., 2014). Another example is the one of legumes used either for leaf products or root. However, the usage of crops within the same family is highly discouraged, since the selection for pathogens can increase in such conditions. Therefore, this method is efficient solely for those species-specific pathogens; others, with a broad spectrum of hosts (e.g., the bacteria *P. syringae*) may require alternative solutions (Lamichhane, 2014). The rotation of maize with soybeans is another example applicable on large scale in United States, in order to discourage the invasive Western corn rootworm (*D. virgifera virgifera*) to complete its life-cycle (Vasileiadis et al., 2011).

Monitoring

Besides crop rotation and cultivating pest-resistant varieties, another complementary method is the monitoring of pests at regular intervals or upon issue of local warnings. In European countries such as Denmark, Germany, France and Switzerland such systems are operational and provided good results for local farmers and landowners (Barzman et al., 2015). The changes that occur naturally in weed populations create favorable conditions to generate predictive models with their forecasted geographic distribution (Samietz et al., 2011). This way, the monitoring can prove a useful BMP method in pest control.

Alternative protective methods, excluding the application of chemical solutions

Soil solarization and biological control of pests represent an alternative to the usage of pesticides; however, their availability and efficacy varies considerably. One of the most widespread techniques is pheromone-based mating disruption. This technique has been shown effective in controlling the population size of several insect pests, with success of up to 50% in apple orchards and 60% in vineyards and reducing the usage of synthetic pesticide use by two thirds (Samietz and Höhn, 2010). The use of live natural enemies represents another important tool in pest management (Fig. 2). A very successful example is the application of *Trichogramma* sp. against the European corn borer *O. nubilalis* (Barzman et al., 2015). Therefore, although applied with variable success, this environmentally friendly approach represents a desirable method in the control of insect pests.

For the management of weeds, alternative methods to pesticides application exist. One such approach considers the differential vertical distribution of seeds in the soil and has the potential to affect weeds emergence and population dynamics, upon the application of complementary BMP's, such as appropriate tillage techniques (Chauhan et al., 2010). Another approach involves weeds' seeds consumption by granivore fauna, such as ants and other insects. Seed predation could be an important BMP in agricultural crops where newly produced weed seeds remain on the soil surface, for example, in no-till systems (Chauhan et al., 2010). When combined with other methods of weed control, seed predation may help to minimize the usage of herbicides (Chauhan et al., 2012).

The management of irrigation waters

The main environmental concerns related to irrigation waters are the discharge of salts, pesticides and nutrients into inland waters (Ramos et al., 2011). Appropriate management practices for irrigation need to take into consideration several aspects, such as arable terrain slope, soil moisture and the water necessities of plants (Najafi and Vatanfada, 2011). Additionally, the chemical characteristics of the soil and the quantity and quality of the irrigation water should determine whether this technique represents a sustainable BMP or not (Schaible and Aillery, 2012). Very often, the irrigation waters are overused, being delivered in higher quantities than needed by a particular crop, mostly because of processes such as evaporation, runoff, wind drift and percolation losses (Benfetta and Ouadja, 2020). Additionally, in arid regions, salinity represents another environmental issue, requiring usage of additional water to flush the soil (Niyazov et al., 2012). The accumulation of salts in excess in the root zone of plants leads to the partial or complete loss of soil productivity, hence compromising the crop (Benfetta and Ouadja, 2020).

We consider that five important steps and priorities of any irrigation-related BMP should be considered prior and during their implementation:

1. Appropriate timing for irrigation. This measure should consider carefully the overexploitation of water resources as such as to minimize the impact on the source itself, usually an inland water habitat. Prior knowledge on minimum humidity level of soil for each crop and the amount of water applied to the field to support a feasible yield is helpful (Irmak et al., 2000).
2. Irrigation water application efficiency. Such aspects should consider the suitable water usage and distribution, bearing in mind potential detrimental impact on the environment, and finally on the recipient water body (Smith et al., 2005). Minimizing surface runoff or deep percolation toward the phreatic layer and soil erosion represent targets for any BMP of irrigation water (Howell, 2001).
3. Irrigation water transport efficiency. The technical measures applied in water transport from source to crop should be designed and managed as such as to minimize water evaporation and seepage from irrigation canals (Wriedt et al., 2009). The technical solutions, beyond the aspect of this article, should consider the improvement of the transportation systems (e.g., lining of canals and ditches, pipes).
4. Irrigation water re-use efficiency. Surface runoff is sometimes re-used for irrigation of crops. This method is very practical, since it reduces the amount of water lost from irrigation systems, and simultaneously diminishes the quantity of dissolved pollutants or suspended sediment in the recipient aquatic ecosystems (Budd et al., 2009). Therefore, this practical measure should be considered as a must in any appropriate BMP package of measures tackling the irrigation water issue (Robinson et al., 2003).
5. The management of drainage water. Complementary BMP's, such as buffer strips, tillage works and crop nutrients (see above) should be considered to minimize the detrimental aspects of current irrigation practices on aquatic ecosystems. Moreover, surface (i.e., ditches to collect excess water in field) and subsurface (i.e., pipes installed beneath the ground collect drainage water) drainage systems should be applied appropriately in irrigation strategies (Malash et al., 2008).

The management of buffer zones

Buffer zones on agricultural land are generally acknowledged to be effective in protecting inland aquatic habitats by reducing soil erosion and diffuse nutrients pollution (Christen and Dalgaard, 2013). The implementation of this method is still limited to date, but the increasing demand for efficient measures in the vicinity of agriculture fields or grasslands calls for improved solutions (Irvine and Ni Chuanigh, 2011; Mayer et al., 2007).

Out of all potential suggested designs for buffer zones situated nearby agricultural fields, one of the most efficient is a three-zone structure comprising: a zone with grass and shrubs, followed by a second zone with trees where the main maintenance activities are forestry rotation and coppice and finally, a third component comprising permanent and intact woody vegetation along the water banks (Christen and Dalgaard, 2013, Fig. 3).

The first layer (i.e., grass and shrubs strip, Fig. 3) decreases runoff speed, filters sediment and halts soil erosion, and helps significantly in nutrients bioaccumulation in vegetal tissues and enhances denitrification (Liu et al., 2008). Moreover, the grass can be easily harvested, used further as hay or grazing site for livestock. The second component is efficient in retaining suspended sediment particles and dissolved pollutants, enhancing the bioaccumulation of nutrients and denitrification processes from the first component (Schultz et al., 2004). The third component mainly reduces bank erosion, and has an important role in mitigating flood effects and continues the buffering capacity of the previous two sectors (Zhang et al., 2010). Moreover, it plays a direct beneficial role in maintaining the aquatic habitats' wellbeing, through shading (that prevents overgrowth of macrophytes and algae) and addition of woody debris and litter (fuelling basal resources for aquatic food webs) (Hefting et al., 2006; Seitzinger et al., 2006, see Fig. 3).

If the cropland is flat, as it occurs in most agricultural areas worldwide, the buffer strip can comprise fast growing species of grass (e.g. reed canary grass (*P. arundinacea*), see Fig. 3), followed by a narrow strip of fast growing and cheap to maintain riparian trees, such as willow (*Salix sp.*), poplar hybrids (*Populus* sp.) and alder (*Alnus* sp.) (Uri et al., 2008). The grass strip may be replaced by a ditch, acting as sedimentation basin depending on local conditions. If the slope is of medium- to high gradient, the buffer zone is essentially of the same structure, but with different species of choice (Schultz et al., 1995). On steep slopes, however, the scope of the buffer strips is rather shifted toward erosion prevention and particularly P loss in runoffs (Dorioz et al., 2006). Hence, the first layer could comprise rather scattered trees with light foliage over stiff stemmed grass, to maximize infiltration capacity. Moreover, tree species should be different in such particular case, such as oak (*Quercus* sp.), black locust (*R. pseudoacacia*) or maple (*Acer* sp.) (Vidon et al., 2010).

The management of grazing activities

The management of grazing activities should primarily focus to adjust the intensity and duration of livestock presence in the water body vicinity, as the animals' movement control (Papanastasis, 2009).

Permanent fencing

One of the best known radical measures is the permanent fencing and the restriction of livestock from entering waterways (Fig. 3). The effects of this practical measure comprise the removal of animals' movement in adjacent aquatic habitats, the maintenance of riparian buffer zones (see above), given reasonable length of fencing from the targeted water body, hence reducing soil and vegetation damage by trampling (Mosley et al., 1997).

However, alternative solutions, of less drastic nature, have been proposed, with variable success (Fig. 3).

Alternative water sources for livestock

Such measures include providing alternative water sources (i.e., trough) to improve the nearby targeted water body's quality (Fig. 3). Applied with variable success, researchers noticed changes in animals' behavior upon the instalment of troughs. Cattle changed their behavior, rather preferring the closer water source (Kaucner et al., 2013). Moreover, depending on how humid the season was, horses rather preferred to consume less water, given wet pasture conditions (Mosley et al., 1997).

Controlled grazing

Continuous grazing degrades aquatic habitats adjacent to pastures or meadows (Gassman et al., 2006). Up to 60% increase in sediment loss was registered in water bodies experiencing both summer grazing and winter-feeding compared to those that supported only the former type of livestock impact (Gassman et al., 2006). Whereas such measures maximize the profit for a farmer, the impact on aquatic habitats, mainly as leached nitrates, besides sediment loss, is significant (Agouridis et al., 2005). The alternative solution is the rotational grazing, which was already proved efficient in reducing stream banks erosion, fine sediment delivery in river channels, as better functionality and status of buffer zones, when applicable (Lyons et al., 2000).

Supplemental feeding

This represents a complementary method that goes well with alternative water supplies that can reduce significantly the impact of livestock on nearby aquatic habitats. However, both methods, when used, changed significantly the amount of time spent by cattles in the water body vicinity, hence with a positive aspect on the manure quantity and nutrients leaching in the adjacent freshwater bodies (Agouridis et al., 2005).

The management of intensive animal feeding operations

One of the most pressing detrimental effects stemming from intensive animal feeding operation units has its source in the amount of manure produced (Fig. 4). The detrimental effects of manure on aquatic ecosystems are multifaceted and are intimately associated with the array of contaminants they provide, essentially a cocktail of nutrients (e.g., nitrogen and phosphorus), pathogens, growth hormones, antibiotics, chemicals used to clean equipment, animal blood and copper sulfate used in footbaths for cows (Government Accountability Office, 2008).

Large intensive animal operation unit manure production can surpass the waste production of big cities (Ribaudo et al., 2003). Instrumental is the example of a feeding operation with 800,000 pigs which produces over 1.6 million tons of waste a year, one and a half times more than the annual sanitary waste produced by the city of Philadelphia in the United States (Government Accountability Office, 2008). Annually, it is estimated that livestock animals in United States produce each year somewhere between 3 and 20 times more manure than people produce (Environmental Protection Agency, 2003). Such huge amounts of manure do not benefit from treatment plants, as human waste usually does, threatening all types of freshwater bodies in the vicinity of such large farms (Government Accountability Office, 2008).

The handiest management solution for untreated manure, the ground application (due to its low cost) can equally prove cumbersome for the environment, given the aforementioned array of detrimental pollutants it contains (U.S. Department of Agriculture, Natural Resources Conservation Service, 2000). Currently, nutrient management policies recommend the use of a dual approach: nitrogen and phosphorus standards. Manure application rates that are based on a nitrogen standard would supply all the nitrogen recommended for the crop. Manure applied at a nitrogen standard will usually result in overapplication of phosphorus. Alternatively, when using the phosphorus standard, the environmental policies allow the application of phosphorus equal to the amount contained in the biomass of multiple years of crops grown on the site, provided that the nitrogen recommendation rate for the first year is not exceeded (Ribaudo et al., 2003).

Alternatives solutions to spreading manure on land are currently used (Fig. 4). Such technologies redirect the manure off-farm toward industrial use. Several processes have been developed to make the nutrients and organic matter in manure more uniform, manageable, and marketable (Lichtenberg et al., 2002). An example is offered by the pelletizing technology and process developed by companies that converge the raw litter into organic fertilizers (Fig. 4). The final product comprises a pasteurized organic fertilizer, with an optimal nutrient (N: P: K ratios), specially designed for agriculture (Government Accountability Office, 2008).

Alternatives for reducing nutrients concentration in manure comprise the modification of animals' diet. However, so far, the lack of economic and regulatory incentives leads to little advances on this direction (Council for Agricultural Science and Technology (CAST), 2002). Such approaches focus toward developing the appropriate nutrients requirements of animals by gender and growth phase, developing ways to increase feeding efficiency and for minimizing the usage of phytase and synthetic amino acids for alternative ration components (Ribaudo et al., 2003).

Summary

This article comprises an overview on the main Best Management Practices required for reducing the direct or indirect detrimental human impact on inland waters' quality and ecological status. For each proposed management measure the positive and negative aspects were highlighted, suggesting that, when applicable, they should consider site-specific characteristics for crop needs, climate and land use intensity. This proposed package of measures, if properly applied, can be more efficient compared with conventional techniques and comprises a set of recommendations that should be considered carefully by environmental scientists, stakeholders, farmers and land-owners alike.

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Agricultural Case Studies

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Abstraction Removal of water from waterbody for irrigation, drinking or other use.
Adsorption Accumulation of molecules to a solid surface. Adsorption is usually reversible (desorption) and typically occurs until an equilibrium is reached.
Aquifer A saturated body of groundwater held within sub-surface porous rock or soil.
Baseflow Index The proportion of river discharge coming from groundwater.
Cambisol A soil group which is in the early stages of development and differentiation into distinct horizons. Cambisols are the second most abundant soil group worldwide.
Colloidal A mixture of insoluble, microscopic particles suspended in a fluid. Soil colloids are organic and mineral particles <0.0001 mm, which have large surface area and may carry adsorped nutrients.
Cross-border Referring to a geographic area such as a river catchment that includes land in two or more countries.
Deltaic sediments Sediments derived from where the mouth of river intersects with an estuary.
Derogation An exemption or relaxation of regulations. In the context of Irish water quality, it refers to permission to exceed the standard upper threshold for application of nitrogen fertilizers (from 170 to 250 kg ha).
Dredging The excavation of sediment from a river, harbor or ditch.

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[§]This author contributes to case study 3.
[¶]This author contributes to case study 4.

 https://doi.org/10.1016/B978-0-12-819166-8.00095-5

Ecological indicator species A species whose presence or absence reflects the conditions of a habitat. Ecologically sensitive species are vulnerable to pollution or other pressures, whereas insensitive species are tolerant and may be present even in degraded environments.
Eutrophication Excessive plant or algal growth in watercourses due to the presence of available nutrients and exposure to sunlight.
Extensive With reference to grassland or grazing, this means that fertilizer inputs are low and only small animal numbers are grazed on the area. Extensive grasslands are frequently less productive than other systems but offer a harbor for biodiversity and add esthetic value to the landscape.
Fluvial Relating to rivers. Fluvial sediments are deposited by rivers or streams.
Intensive With reference to grassland or grazing, this means that the system relies on high fertilizer inputs to drive productivity and usually entails high livestock stocking rates. Additional feed may also be significant to maximize the productivity of animals in intensive systems.
Mineralization In relation to nitrogen, mineralization is the process by which organic forms are converted to inorganic forms (ammonium and nitrate) which can be used by growing plants.
Nitrates Directive (ND) Irish legislation introduced in 1991 that aims to protect water quality through good agricultural practices.
Podzol Soils with high organic matter typically developed under forestry.
Potable Water which is safe for human consumption.
Pyrite A sulfide mineral that is common in the geology of the Bengal basin and which often co-occurs with arsenic.
Recharge The mechanism by which water percolates through the soil and bedrock to refill the aquifer.
Redox Chemical reaction involving electron transfers which is responsible for the release or retention of molecules such as arsenic or phosphorus, in the case studies presented here.
Time Lag The delay in contaminant transfer from a source to a receptor, such as a watercourse.
Unconsolidated aquifer A body of rock or sediment which has high porosity, such as gravel or sand.
Water framework directive (WFD) Overarching European legislation introduced in 2000 that commits member states to achieve good ecological status within fixed timelines.

Introduction

Agriculture is intrinsically linked to water quality and availability, as discussed in chapters 6004 and 6005. The demands exerted on waterbodies due to production type and intensity vary widely and considering the reliance of modern societies on either subsistence or commercial agriculture, some impacts are to be expected although management practices are implemented in many regions to mitigate some of the harmful effects. Presented here are examples of regional water quality issues resulting from agriculture and the management approaches implemented in response to those pressures. It is beyond the scope of this chapter to provide a comprehensive overview of agriculture and waterbody interactions, but the case studies discussed herein demonstrate priority issues in diverse regions of the world.

The four case studies presented here are:

- Nutrient pressures in an intensive grassland catchment in the Republic of Ireland,
- Groundwater abstraction and arsenic contamination in the Bengal Basin, India,
- Herbicide impacts on freshwater in Northern Ireland, United Kingdom,
- Sediment and nutrient dynamics arising from wetland conversion in Rwanda.

Case study 1: Nutrient pressures in an intensively managed grassland catchment

Overview of the catchment

The south-west of Ireland is dominated by highly productive grassland agriculture, particularly emphasizing grass-based dairy production (Fig. 1). It represents an important area of permanent grassland within Europe (Kempen et al., 2011). The Timoleague study catchment (Fig. 2) is a 7.6 km^{-1} river catchment, predominated by dairy production (51°38′59 N, −8°45′59 W). Land use is 77% grassland, and 11% arable, with the remainder in non-agricultural use. The catchment reaches its greatest elevation at 120 m a.s.l., and the stream drains into Courtmacsherry bay. The geology of the area is old red sandstone and mudstone, overlain by freely drained brown earth soils, ranging between 0.5 and 10 m in depth. A small area of gleyic brown alluvial soil is present bordering the stream. Average annual rainfall is c. 1120 mm. The stocking rate of the catchment is among the highest in the country at 1.9 livestock units per ha, and 54% of the land in derogation (2010–18) to the EU Nitrates Directive (European Commission, 1991). This derogation allows application of fertilizer ≥ 170 kg N ha^{-1}. The freely drained nature of these soils encourages a long growing season and grazing throughout much of the year, including early turnout of housed cattle to grass in spring. Diffuse nitrate loss is

Fig. 1 The Timoleague catchment in Southwest Ireland is a highly productive grassland dominated by dairy production.

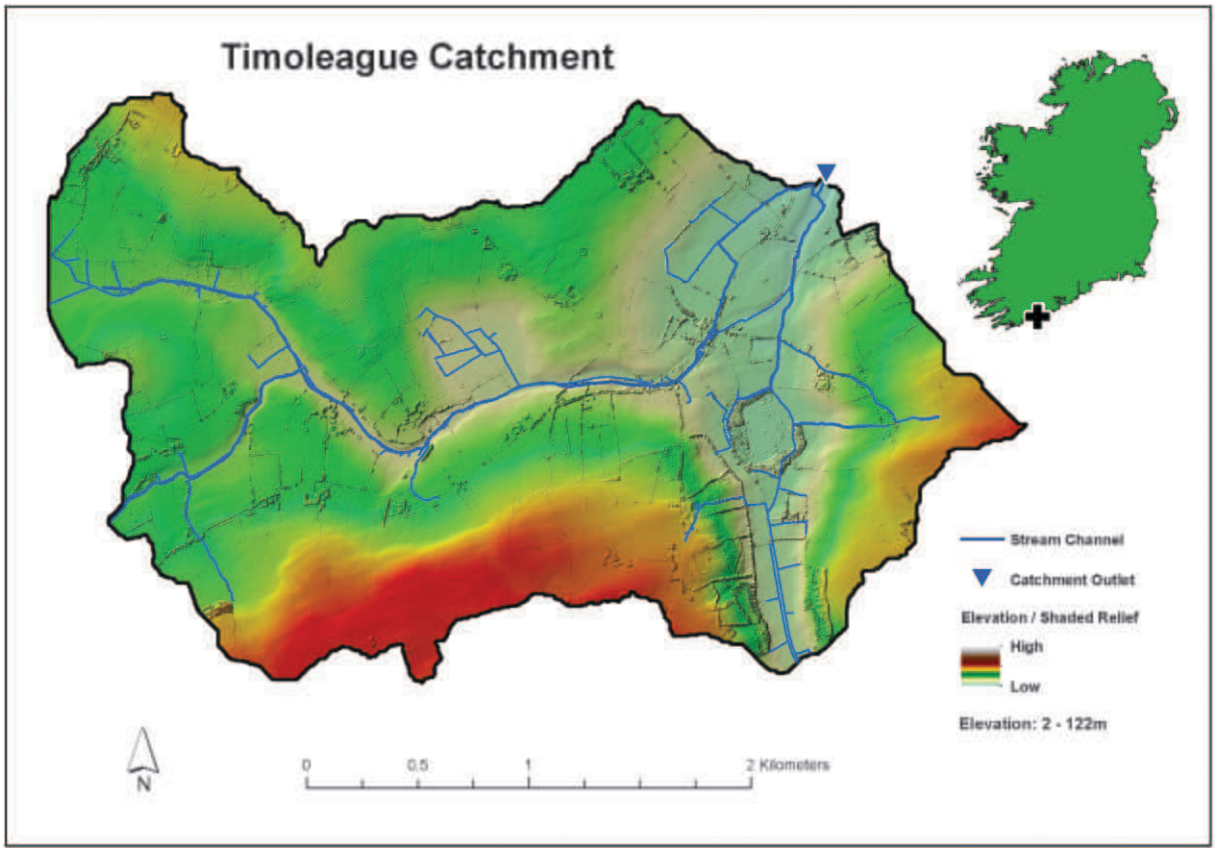

Fig. 2 Map of the Timoleague grassland catchment in Ireland.

potentially the highest nutrient risk to water quality in this setting, as a result of (a) high loading and (b) presence of a sub-surface pathways. The catchment exhibits a high baseflow index (73%), indicating a substantial proportion of streamflow contributed by groundwater (McAleer et al., 2017).

Nutrient pressures and pathways

Monitoring at the outlet of the watercourse has shown that nutrient loss to water is an issue in the catchment. The annual average NO_3-N concentration (2009–19) was 6.1 mg L^{-1} which is lower than the Water Framework Directive (WFD) (EC, 2000) drinking

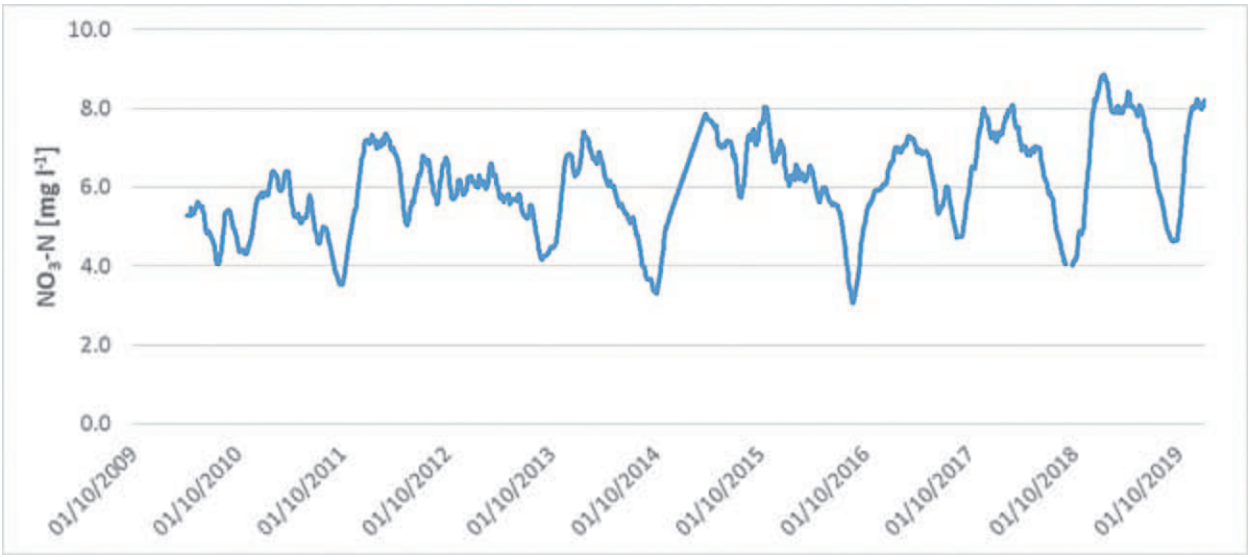

Fig. 3 Nitrate fluctuations over time (10-min sampling resolution) as measured at the catchment outlet (2009–19).

water standards (11.3 mg L^{-1}) but substantially higher than the NO_3-N concentration considered to be commensurate with good ecological status (2.6 mg L^{-1}) (Fig. 3) (S.I. 272). The annual average total reactive phosphorus (TRP) concentration was 0.066 mg L^{-1} which is above the Water Framework Directive target value for rivers (0.035 mg L^{-1}) (Fig. 4) (S.I. 272). There were large temporal variations in both NO_3-N, TRP, and total phosphorus (TP) associated with both natural temporal variability and changes in hydrometric, biogeochemistry and agronomic conditions. There has been an increase in the NO_3-N concentration over the monitored period (2010–20), particularly during the last 3 years. The organic nutrient load has increased during the period and changes in weather patterns has likely enhanced nutrient loss, with warmer and drier summers reducing the plant nutrient uptake and enhancing mineralization, together with more large rain events in autumn and winter allowing for nutrient flushing (Mellander et al., 2018). In-stream vegetation in parts of the catchment is high at times, particularly during peak growing conditions during summer months (Shore et al., 2017). Nitrate (NO_3^-) loss does occur through the vertical pathway in this catchment, with subsequent delivery to the watercourse via groundwater (McAleer et al., 2017). Decadal time lags of NO_3^- through the soil and groundwater components delay observation of the full effect of programs of measures intended to reduce nutrient emissions under the Water Framework Directive (Vero et al., 2017). The impact of past nutrient management, therefore, continues to impact NO_3^- loads delivered to the watercourse. However, prolonged transit through anoxic groundwater does provide opportunity for denitrification, thus reducing overall loads to surface waters (McAleer et al., 2017). Spatial variability in NO_3^- removal capacity is observed across the catchment, influenced by water table depth, conductivity of the bedrock, and presence of denitrifying bacteria and substrates. McAleer et al. (2017) observed a 43% reduction in groundwater compared with stream NO_3^- concentrations. While offsetting NO_3^- loads by denitrification to water is a benefit from an aquatic ecological perspective, there are trade-offs as the end products (N_2O) is a potent greenhouse gas. This pollutant swapping is important to consider for the agricultural landscape. Not only are there direct emission from agricultural soils but also indirect emission of N_2O from groundwater to the atmosphere (Jahangir et al., 2012) and both must be accounted for in accordance with International Panel on Climate Change (IPCC) protocols.

Elevated baseflow concentrations of dissolved reactive phosphorus (DRP) measured using a Phosphax automated analyzer had mean values across the catchment exceeding the Water Framework Directive threshold for good ecological quality (0.035 mg L^{-1}) during summer but declining to concentrations below the threshold specified under Irish legislation (SI 272, 2009) over autumn and winter as dilution predominates (Fig. 4) (Vero et al., 2019). During low-flow periods, diurnal fluctuations in DRP concur with typical timings of morning and evening milking of cows. This indicates recurring point discharge of soiled dairy wastewater, which is obscured during high-flow periods. The importance of multiple agricultural (e.g., farmyards, livestock crossings) and rural-domestic (single house septic tank and group wastewater treatment facilities) point sources is crucial, as their cumulative loads supplement diffuse losses, and their impact may be under-estimated. While P loss in agricultural landscapes is most frequently attributed to the overland pathway, monitoring of groundwater wells and concentrations in stream baseflow indicate high sub-surface loads arriving in this catchment. Soils in Timoleague are rich in iron and have high P concentrations (~50% soils at Index 3 or 4 (Thomas et al., 2016)), favoring mobilization of P into soluble forms with potential for leaching particularly during saturated conditions (Mellander et al., 2016), or movement in colloidal form in areas of the catchment with cambisol or podzol soils (Fresne et al., 2020). While the catchment might not be identified as being of particularly high risk of P loss compared with landscapes with a greater propensity for runoff, evidence from long-term monitoring and an abundance of peer-reviewed publications indicates that it is indeed a threat to the ecological status of the catchment. Indeed, runoff is frequently considered to be the chief pathway for P loss, however, leaching is increasingly recognized as an important pathway (Smith et al., 2021). Declines in legacy P in soil stores have been estimated to take decades to reach agronomic and environmentally optimal ranges (Schulte et al., 2010) and so mitigation of losses from soil requires commensurate timescales.

Impacts

Following removal of Irish national milk quotas in 2015, the productivity of the Irish dairy sector has increased over recent decades, a trend typified by expanding herd numbers, reduction in small farms, expansion of large farms, and increasing number of farms availing of derogation (Kelly et al., 2020), The proportion of grazed grass in the cows' diet has a close relationship with cost of milk production per liter, meaning that dairying in this region is likely to remain an attractive land use. National agricultural plans predict a 65% increase in primary agricultural productivity by 2025 (Department of Agriculture, Food and the Marine, 2017). The updated goals described in FoodVision 2030 (Department of Agriculture, Food and the Marine, 2021) emphasizes reduction of nutrient losses, increases in efficiency, and overall improvements in sustainability. This suggests that intensity of production, which naturally is accompanied by nutrient loads which must be effectively managed, is unlikely to reduce in this catchment, and others like it.

The Courtmacsherry bay into which the Timoleague catchment discharges has not improved from poor ecological status over the 2010–18 period. Nevertheless, modeling of the bay has indicated that flow-load relationships of dissolved inorganic N and dissolved inorganic P suggest improvement in agricultural practices between 2010 and 2016, particularly the retention of inorganic P within the catchment by breaking hydrologic pathways (McGovern et al., 2017). That study suggested that amounts of the green macroalgae genus *Ulva* (indicative of eutrophic growth) in the bay would have increased from 380 t wet weight in 2016 to 1391 t if the 2010 flow-load relationships prevailed. While this suggests a positive effect of integrated catchment management practices organized by local authorities and agricultural advisors, sustained adherence to best practices by farmers as regards diffuse pollution and suppression of point sources are crucial to achieve future targets, particularly under intensified production scenarios. Best practices must be designed for specific land uses and landscapes and there is no one-size-fits-all approach. Consequently, selection of measures for maintaining and improving water quality should be on a case-by-case basis. Certain measures such as use of buffer strips to break the runoff pathway or use of cover crops, are promoted by agri-environmental schemes and as research develops, newer novel methods will likely arise. High temporal water quality monitoring and improved quantification of land use, characteristics, and management has allowed clearer elucidation of trends and patterns in watercourses and to connect those with both agricultural and non-agricultural activities.

Case study 2: Groundwater abstraction and arsenic contamination in the Bengal Basin, India

Overview of the catchment

The Bengal Basin is a 200,000 km^2 catchment in West Bengal, India and Bangladesh, and home to some ~120 million people, approximately 2% of the world's population. The catchment is drained by three major rivers: the Ganges (2510 km), the Brahmaputra (2900 km), and the Meghna (270 km), flowing ultimately into the Bay of Bengal, and is sometimes referred to as the Ganges-Brahmaputra-Meghna basin. The supply of potable water is largely dependent upon groundwater abstraction. Increasingly, this resource is also utilized for irrigation of cropland. The Bengal basin is a low-lying landscape (~1.8 masl) of meandering channels, meander scrolls, and natural levees formed by the river and its tributaries. The geology of the basin consists of Holocene sand, silt and micaceous clays deposits. The aquifers are composed of sandy unconsolidated Pleistocene to Holocene fluvial and deltaic sediments. Shallow groundwater is largely relied upon for drinking water supplies, despite recommendation that deeper reserves (>150 m bgl) are less likely to be contaminated (Chakraborty et al., 2015).

Arsenic (As) contamination is believed to affect up to 90% of drinking water wells in some districts (Chakraborty et al., 2015), particularly in low-lying regions. Districts at greater elevations are relatively unaffected. Arsenic presents a significant health threat; causing arsenicosis, characterized by impaired childhood development, skin disorders, cancers, and a variety of chronic organ conditions. The threshold concentration for drinking water is set at 50 $\mu g\ L^{-1}$ and exceedances have been estimated present a health risk to c. 30–35 million and 15 million people in the Bangladesh and West Bengal, respectively (Chakraborty et al., 2015). Still greater numbers rely upon sources which exceed the World Health Organisation (WHO) threshold of 10 $\mu g\ L^{-1}$ with 42% of wells in Bangladesh exceeding this concentration. While contamination of drinking water is frequently associated with industrial production, in this case, the scientific consensus identifies geologic origins of As contamination. Young groundwater is moderately oxygenated but undergoes reducing conditions in the subsurface, facilitating microbial degradation of iron compounds within the sediments. Dissolution of ferric oxyhydroxides releases sorbed As to the groundwater, which may then be abstracted. Although As is naturally occurring within certain sediments, abstraction of groundwater with high As concentrations for agricultural irrigation causes adds to the pollution of surface waterbodies.

Irrigation as a pathway for geogenic arsenic

Although widespread use of groundwater abstraction wells began during the 1960s (Burgess et al., 2010), abstraction is not restricted to drinking water. Contamination of drinking waters with As escalated significantly during the 1990s along with a surge in abstraction of groundwater for irrigation (Kinniburgh et al., 2003). By 2001, over 1 million irrigation wells were installed in Bangladesh, with a further quarter of a million in West Bengal (Michael and Voss, 2009). These pumps abstract water at a 10 times greater rate than traditional or drinking-water wells. Irrigation has facilitated increases in crop production essential to support the growing population, and agriculture represents the largest employment sector nationally. Despite negligible expansion in the area

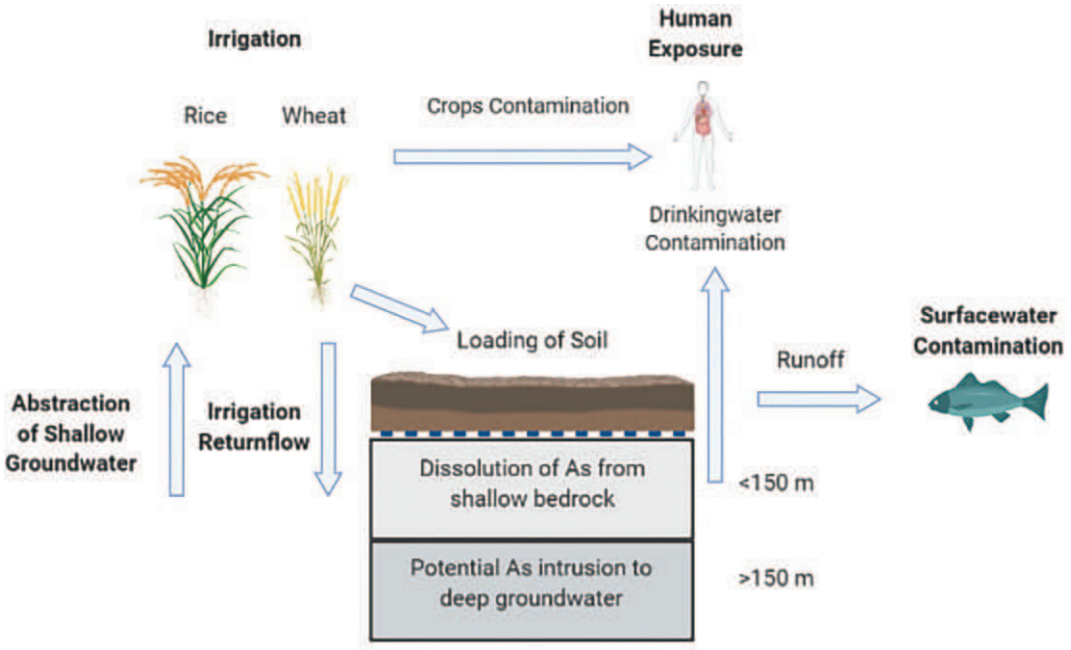

Fig. 4 Conceptual diagram of arsenic mobilization and circulation.

under cultivation, irrigation has been responsible for an increase of 70–80% of rice and wheat production between 1970 and 2004 (Zaveri et al., 2016). The increase in abstraction was supported by government subsidy schemes during the 1980s (for deep tube wells), superseded by a later preference for shallow, less expensive, tube wells.

The pyrite-reduction hypothesis suggests that not only does agricultural abstraction transport As contaminated water to the surface, but may also promote mobilization from pyrite stores in the bedrock due to oxidization as the water-table is lowered (Hossain, 2006). This creates a potential feedback in which abstraction of contaminated shallow groundwater leads to contamination of the previously higher quality deeper aquifers over decades. It must be noted that this is one hypothesis, and there is not yet consensus whether this is the only action contributing to the As problem and multiple processes may simultaneously contribute to mobilization (Chakraborty et al., 2015). A conceptual model of this hypothesis is presented in Fig. 4. Correlation of As-related disease with patterns of irrigation suggests a relationship, although data for the region is incomplete prior to the 1990s (Ravenscroft et al., 2005). It also seems likely that there are other concurrent mechanisms of geochemical release of As.

Irrigation return flow recirculates irrigation water within the hydrologic system. Enhanced recharge mechanisms (including injection and percolation) are, in particular, used to accelerate the return of contaminated water, both replenishing the vadose zone and eventually deep groundwater aquifers. The exchange rates of As between vadose and groundwater zones is still not fully explored and is likely to be spatially and temporally variable. Return flow is frequently charged with various elevated ions, in this case As, which presents a hazard to drinking water supplies abstracted from the shallow aquifer where maximum recharge occurs. In this way, As which would otherwise be occluded within the subsurface is mobilized by initial abstraction that creates a change in redox stability in the aquifer, and then brought into circulation within the agricultural and surface-water systems.

Impacts

The abstraction of groundwater has been, and continues to be, crucial for continued agricultural production in the region. Depletion of accessible groundwater reserves is a concern, with depth to the water table increasing, however, there is also an acute threat to human health as irrigation mobilizes As-rich water to the environment. Besides contamination of otherwise potable water, As bio-accumulates within crops, particularly rice grains, providing a further mechanism of exposure to humans. Furthermore, the application of contaminated groundwater has increased soil As concentrations (Saha and Ali, 2007), reaching 40 mg kg^{-1} in some areas (Chakraborty et al., 2015). Mobilization of soil particles during storm events may result in sediment-bound As being transported to surface-waters as a result of erosion. Similarly, during the monsoon period saturated top-soils which have become laden with As may release bound P into solution and transported to rivers (Chakraborty et al., 2015). This is due to the process of

competitive adsorption. Where soils which are rich in phosphate also have a considerable proportion of adsorbed arsenates, under saturated conditions P may be released along with As. This may deliver a combination of both As and nutrient enriched leachate to groundwater.

In addition to the direct impacts on human health from consumption of As-contaminated food and water, there is an ecological impact. Freshwater fish species such as pangasius have shown acute response (lethal concentration - LC_{50} 28–34 mg L^{-1}) to As which is exacerbated at elevated temperatures (>38 °C) (Kumar et al., 2019), as well as bioaccumulation within tissues during sub-acute exposure. Sub-lethal exposure also has damaging effects upon the gills of freshwater mollusks, which are key ecological indicator taxa (Chakraborty et al., 2010).

Shifting towards abstraction of deeper groundwater may offer an alternative to continued utilization of unsafe shallow groundwaters, however, aquifer depletion and indeed, intrusion by contaminated water are potential risks associated with this approach (Burgess et al., 2010). Indeed, over-abstraction of the deep aquifer for irrigation purposes may effectively eliminate this resource as a source of safe drinking water (Burgess et al., 2010). An integrated approach to planning involving national and international policymakers, agricultural representatives, and scientific expertise is therefore essential to protect the future of the hydrologic basin, and the communities living there.

The abstraction-irrigation-contamination cycle demonstrated in the Bengal Basin is an example of an indirect pressure on water quality as a result of agriculture. Although elevated As concentrations are a natural characteristic of the area based on its geology, the agricultural system and intensity of rice and wheat production exacerbates the associated impacts on both of surface and groundwater resources.

Case study 3: Herbicide impacts on freshwater in Northern Ireland, United Kingdom

Overview of the catchment

The Derg catchment (54 N°40′, 7°42′W) is a rural catchment straddling the border between Northern Ireland (UK) and the Republic of Ireland. The area has a maritime climate, with a mean annual temperature of 9.0 °C and mean annual rainfall of approximately 1800 mm. The main uses of water in this catchment are the supply of drinking water and agricultural uses. The drinking water catchment, which is the focus of this case study, is 384 km^2 (Fig. 5) (Morton et al., 2021). The river headwaters originate in the highlands of County Donegal, Ireland, and flow eastward from Lough Derg and Lough Mourne as the River Derg and Mourne Beg River, respectively. These rivers are joined by a multitude of minor tributaries, and converge just west of Castlederg, Northern Ireland, the catchment's main town with a population of around 3000 people.

The rolling upland hills in the west of the catchment are dominated by peat soils, with blanket bog and coniferous forestry plantations covering most of this area and together comprising nearly half (47%) of the land use within the catchment. While the river channels are composed of sand, silt and alluvium, the soils in the lower eastern part of the Derg catchment and the broad valley bottom comprise mainly brown earths and brown podzols. Rough grazing (unmanaged grassland) and extensive grassland (lightly managed with low stocking rates) border the bogs and forestry plantations, with agriculture intensifying to permanent pastures and hay and silage meadows towards the catchment outlet. These permanent pastures are more heavily managed and often grazed year-round. Similarly, the silage meadows are subject to intensive management and mowing. Arable agriculture covers only 0.2% of the catchment, mainly in the east of the valley. Sheep are grazed mostly on the more extensive grassland, while cattle (both beef and dairy) occupy the more intensive (heavily managed) grassland in summer and are usually housed indoors during winter.

Description and use of MCPA

MCPA (2-methyl-4-chlorophenoxyacetic acid) is a phenoxyalkanoic acid herbicide. This group of chemicals simulates the action of auxins, which are plant growth hormones. For herbicide applications, MCPA is usually supplied in a salt form, although chemical ester formulations are also used. While the formulation plays little role in the efficacy of MCPA, it affects the volatility and solubility, with esters being more volatile than salts and salts being much more soluble than esters. As a selective herbicide, MCPA is used mainly to control broad-leaved weeds such as wild mustard, docks, volunteer oilseed rape and thistles in arable, horticultural and grassland settings.

MCPA can also be used to treat rushes (*Juncus* spp.) (Fig. 6). Rushes, particularly soft rush (*Juncus effusus*), are common across Ireland, occurring most prevalently on waterlogged ground in the west and north. MCPA is one of the few herbicides that is effective against rushes. Even so, rushes are only moderately susceptible to MCPA, with treatment tending to reduce the spread of rushes and kill most of the aboveground portion of the plant. However, rushes produce thousands of seeds which can remain dormant yet viable for over 60 years in the soil (USDA NRCS Plant Materials Program, 2002) until brought to the surface or exposed to light (Moran, 2015). This means that, even if the rushes were not allowed to reach flowering stage the previous season, farmers with rush problems typically spray annually (or biannually) between March and September to prevent the returning rushes from out-competing the grass.

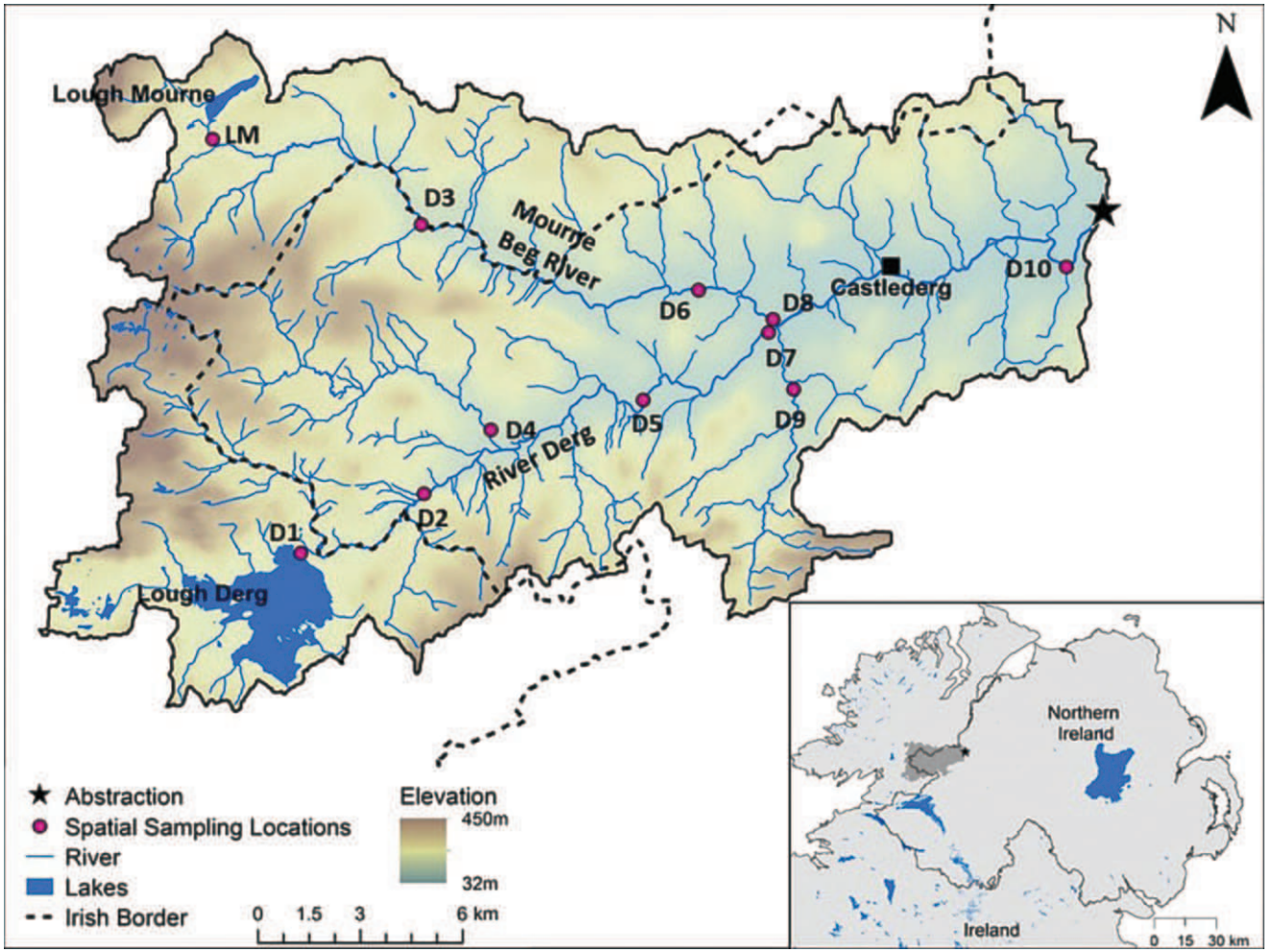

Fig. 5 Map of the Derg catchment, with the inset showing its cross-border location on the island of Ireland (gray shaded area). The two main tributaries, the River Derg and the Mourne Beg River, and their minor tributaries are shown with spatial sampling locations. The main town of Castlederg is on the River Derg after the confluence. The drinking water abstraction point is also the catchment outflow and the location of the temporal sampling. Reproduced from Morton PA, Cassidy R, Floyd S, Doody DG, McRoberts WC and Jordan P (2021) Approaches to herbicide (MCPA) pollution mitigation in drinking water source catchments using enhanced space and time monitoring. *Science of The Total Environment* 755: 142827.

Fig. 6 MCPA is boom-sprayed to treat rushes (seen in the foreground) in grassland. Photo credit: Steven McDowell

Impacts

In the European Union (EU), MCPA is only licensed for use in a boom sprayer (Fig. 6). This can create spray drift, particularly in windy conditions, which can deposit MCPA droplets directly into watercourses (Kreuger, 1998). However, while only small quantities of the applied MCPA are likely to reach non-target areas via spray drift, far greater quantities can be lost via runoff and sub-surface flow. This is because MCPA is highly soluble, with up to 866 g of MCPA salt able to dissolve in a liter of water (Hornsby et al., 1996), and has low adsorption to soil (log K_{OC} 1.73–2.07) (Mackay et al., 2006). Areas with a high prevalence of MCPA use, high rainfall and low soil permeability are, therefore, most at risk of MCPA transfer to watercourses.

The Derg catchment fits all three of these criteria: MCPA is frequently used throughout the catchment, annual rainfall can be in excess of 1800 mm annually and is well distributed across the seasons, and soils across the catchment are poorly-drained and often waterlogged. An intensive (7-hourly to daily) sampling program demonstrated that concentrations in the main river at the catchment outlet reached 4.3 μg L^{-1} (Fig. 7) and a spatial sampling program found concentrations up to 9.0 μg L^{-1} in one of the tributaries (Morton et al., 2021). To put this into perspective, legally, drinking water in EU countries must not contain more than 0.1 μg L^{-1} of any single pesticide or more than 0.5 μg L^{-1} of all pesticides combined (Council of the European Commission, 1998). Additionally, the World Health Organisation recommends a maximum of 2 μg L^{-1} of MCPA in drinking water (World Health Organisation (WHO), 2017). The intensive sampling programme found that 25% of the samples taken from the river between April 2018 and April 2019 contained more than 0.1 μg L^{-1} of MCPA, 6.5% contained over 0.5 μg L^{-1} and 1.3% contained over 2 μg L^{-1} (Fig. 7) (Morton et al., 2021). As the Derg catchment is the drinking water source for about 30,000 people, these MCPA concentrations present a major problem for drinking water quality. Treatment options, such as granular activated carbon filters or ozonation, are available are available—with the former used in the Derg water treatment works—but these are costly and energy-intensive solutions. Furthermore, with such high concentrations in the river, it is not always possible to remove all of the MCPA from the treated water, or even a high enough proportion to bring concentrations below the EU limits, even with treatment options in place.

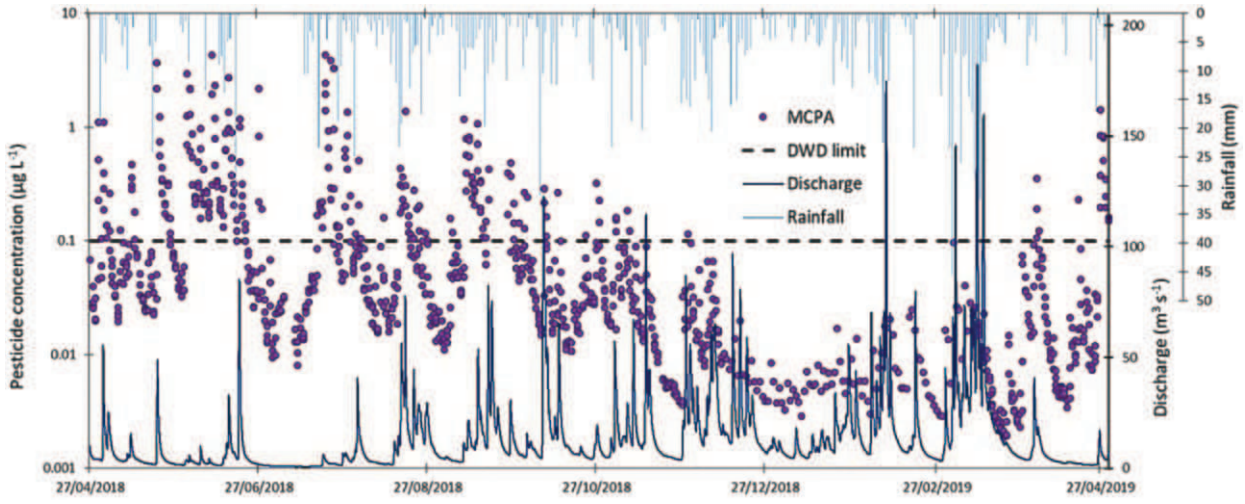

Fig. 7 Concentration of MCPA in the River Derg at the catchment outlet and abstraction point, the River Derg discharge 7 km upstream of the monitoring point at Castlederg, and Malin Head daily rainfall between 27/04/18 and 30/04/19. The single pesticide drinking water limit for treated water is shown for reference as a dashed line. Note that the pesticide concentrations are shown on a log scale on the left y-axis. Reproduced from Morton PA, Cassidy R, Floyd S, Doody DG, McRoberts WC and Jordan P (2021) Approaches to herbicide (MCPA) pollution mitigation in drinking water source catchments using enhanced space and time monitoring. *Science of The Total Environment* 755: 142827.

Due to the short term nature of many studies, there is very little evidence on long-term health effects of drinking water containing MCPA nor on whether there are any potential interactions between MCPA and other common compounds found in drinking water sources (Morton et al., 2020). However, public health limits tend to be very conservative, with considerable safety margins built in, as evidenced by the 20-fold difference between the EU drinking water limits and the WHO recommendation for MCPA, thus the MCPA concentrations allowed by the drinking water limits are well below any thought to pose a risk to human health. Similarly, ecotoxicology studies for other organisms indicate that the MCPA concentrations found in the Derg catchment are unlikely to have ecological implications but the majority of these studies were of the effects of just MCPA on single organisms tested under laboratory-controlled conditions and were relatively short-term (Morton et al., 2020).

The short-term nature of most toxicological tests means that there still could be potential ecological consequences over longer periods of time. The degradation half-life of MCPA has been reported as between 5 and 78 days (European Commission (EC), 2008), depending on the conditions, and therefore it tends to be assumed that concentrations would be very low or negligible outside of the spraying season. However, in the Derg catchment, concentrations did not fall below the limit of detection (0.0005 μg L^{-1}) at any point during the year of intensive monitoring and concentrations over 0.1 μg L^{-1} occurred up to the end of November (Fig. 7) (Morton et al., 2021). Not only did this indicate that the MCPA was not degrading as quickly as expected, but also that heavy autumn rainfall did not flush all MCPA from the catchment. This is possibly due to the high organic content of the soils in the Derg catchment, that increases the retention of MCPA (Hiller et al., 2012) and the waterlogging of these same soils reduces the oxygen available to pesticide-degrading organisms (Vink and van der Zee, 1997). As a result, aquatic organisms in the Derg catchment are exposed to MCPA throughout the winter, albeit mostly at low concentrations. The effects of long-term, multi-generational exposure are unknown.

Wider context

MCPA has been found in both surface water and groundwater in countries around the world, usually at low concentrations but occasionally above the highest recorded in the Derg catchment (e.g., EPA, 2017; Loos et al., 2017). However, most monitoring of MCPA to date is by local authorities or governmental organizations and is thus relatively infrequent. Therefore, the finding that a high proportion of concentrations in the Derg catchment that were above 0.1 μg L^{-1} indicates a more significant problem than was previously recognized here. This could also be the case elsewhere, where similar monitoring regimes are in place. Further monitoring is needed to determine whether the Derg catchment is representative of other locations throughout Ireland and across the world. Furthermore, it is not known whether MCPA is detectable in other waterbodies in Ireland throughout the non-spraying period. Given that these winter detections are likely due to the highly organic and waterlogged soils in the catchment, the Derg catchment is probably representative of a significant number of catchments on the island of Ireland and possibly some in other countries.

Regardless, there are alternative measures to costly water treatment processes that may help to reduce MCPA concentrations in the river. One such measure being trialed in the Derg catchment is to discourage farmers from boom spraying MCPA. Instead, they are incentivized to apply glyphosate using weed-wipers to get rid of rushes, thus greatly reducing the total pesticide used. Weed-wipers are devices mounted on off-road vehicles which apply herbicides directly to the surface of the plant. This prevents spray-drift and allows far smaller volumes of chemical to be used. Other potential measures mainly focus on discouraging rush growth through adding lime to fields to increase the pH, cutting rushes and draining waterlogged areas, as well as controlling grazing so as to encourage grass growth. Less soluble pesticides may also act to prevent the growth of unwanted plant species whilst also reducing the amounts of pesticide reaching waterbodies.

Case study 4: Sediment and nutrient dynamics due to wetland conversion in Rwanda

Overview of the region

Rwanda, known as the Country of a Thousand Hills, and located in central Africa just south of the Equator (2°00′S 30°0′E), has the highest population density in Africa (415 inh/km^2; National Institute of Statistics of Rwanda (NISR), Ministry of Finance and Economic Planning (MINECOFIN), 2012). Most of its landscape is high altitude at 950 m, with a peak at 4507 m. The climate is temperate tropical humid with a moderate average temperature of 20°C and annual precipitation between 1000 and 1400 mm. Peak rainfall occurs in November and April, and a dry period in June–August. Water covers c. 8% of the Rwandan territory (210,000 ha), including 100 lakes (128,000 ha), 861 rivers (7260 ha) and wetlands (77,000 ha) (MINAGRI, 2017). A wetland inventory in 2008 showed that about half of Rwandan wetlands were covered by natural vegetation (often dominated by *Cyperus latifolius* or *Cyperus papyrus*), and the other half were converted to rice paddies or fishponds (REMA, 2009). These freshwater resources provide essential ecosystem services (e.g., drinking water provision, biodiversity) and offer high potential to support irrigation and fish farming (Millennium Ecosystem Assessment (MEA), 2005).

Agriculture in Rwanda is predominantly small-scale, subsistence, rain-fed, and highly vulnerable to climate variability, but represents the primary occupation of c. 70% of the population (Niyagaba and Peng, 2020). On average, a single household cultivates 0.6 ha, with c. 80% of farm households practicing traditional farming and 70% located on steep (5–55%) slopes (MINAGRI, 2017). This results in dramatic soil degradation and erosion with annual soil losses estimated between 20 and 150 t ha^{-1} (MINAGRI, 2017). The national average fertilizer application has increased steadily, from an average of about 4 kg ha^{-1} in 2006 to 30 kg ha^{-1} in 2013 and 46.42 kg ha^{-1} in 2019/2020 and is projected to reach 75 kg ha^{-1} in 2024 (MINAGRI, 2014, 2020).

Fig. 8 Conversion of valley-bottom wetlands to rice farming in Migina catchment, southern Rwanda. Photo: Anne van Dam.

Recently, valley-bottom wetlands have attracted the attention of the Government of Rwanda as fertile lands with high water availability that can contribute to national food production, mainly rice, fish and vegetables. With government policies aiming to convert up to 80% of these wetlands, large areas of natural wetland have been converted to agriculture, thereby expanding the national farmed area fourfold between 2006 and 2020 (MINAGRI, 2009, 2010a). Wetlands are also drained for land reclamation, settlement, urbanization, industrial development, and road construction (e.g., Nhapi et al., 2011; Usanzineza et al., 2011). Wetlands converted to agriculture are used mostly for rice production, but also for other crops such as sugarcane, maize, beans, vegetables and for subsistence-level pond aquaculture (MINAGRI, 2009, 2010a). Due to its high productivity compared to other crops ($\geq$7 t ha^{-1}), rice was regarded as one of the most appropriate crops in Rwandan inland valleys (MINAGRI, 2010b). Strategies to increase rice production include increasing the area under cultivation (with vast areas of valley bottom wetlands converted into rice farms; Fig. 8), the use of modern inputs such as seeds, fertilizers, pesticides, and the construction of small dams and ponds to support irrigation and fish production. Rice farming area increased from <4000 ha in 2000 to c. 35,000 ha in 2018 and is expected to reach c. 51,000 ha by 2024 (MINAGRI, 2013, 2018). Similarly, aquaculture production of 4038 Mt. in 2007 (Mwanja et al., 2011) is expected to reach 90,000 Mt. by 2020/2021 (MINAGRI, 2018).

Agricultural pressures

Wetland conversion to agriculture and intensification of production have become the preferred options for increasing food security and economic development under the government's Strategic Plans for the Transformation of Agriculture (PSTA) and the Rwanda Irrigation Master Plan (MINAGRI, 2009, 2010a, 2013). However, expansion may also result in negative environmental impacts due to the alteration or destruction of wetland ecosystems and biodiversity, and disruption of regulating ecosystem services, particularly water purification and hydrological regulation (flood control). The valley-bottom wetlands of many headwater catchments in the region have been converted to agriculture. Consequently, the original natural wetland vegetation has almost disappeared, and valley-bottom land cover changes from bare soil immediately after hoeing to a densely cultivated crop canopy at the end of the season. Farming practices including plowing, fertilizer application, and weeding make the soil more vulnerable to runoff of soil particles and nutrients, whereas wetland vegetation, a dense established crop, or ponds and reservoirs facilitate attenuation within the catchment (Dabney, 1996; Dabney et al., 2001). Like in many farming systems in sub-Saharan Africa, the peak of activity coincides with the beginning of the rainy season, when valley bottoms are most vulnerable to the loss of sediment and nutrients. At the onset of high rainfall, loose material from the plowed soil and built-up material accumulated during the dry season are mobilized and exported (Uwimana et al., 2017). Similarly, effluent discharge from reservoirs and fishponds during periods of water release, or when ponds are drained for fish harvesting or dredging, is a major loss pathway of sediments and nutrients. The loss of the nutrient retention function of wetlands has consequences for both local (e.g., surface water quality, drinking water production) and downstream ecosystem services (e.g., eutrophication in Lake Victoria, impacts on fishery).

Wetland conversion research in the Migina catchment

The effects of wetland conversion to agriculture on the sediment and nutrient retention of valley bottom wetlands in the Migina catchment, located in the Southern Province of Rwanda and one of the uppermost catchments of the Akagera river, the largest tributary of Lake Victoria in the Nile Basin has been the subject of recent research. The landscape is mountainous with small valley bottom wetlands, streams, and rivers (Fig. 9; Centre for Geographic Information Systems & Remote Sensing, 2008). In the upper catchment, the hillsides are dominated by urban areas and settlements. The valley bottoms are dominated by rice cultivation, vegetables (maize, beans, potatoes, carrots, tomatoes), clay, silt and sand mines, grassland, and fishponds and dams (standing water), with some patches of natural wetlands.

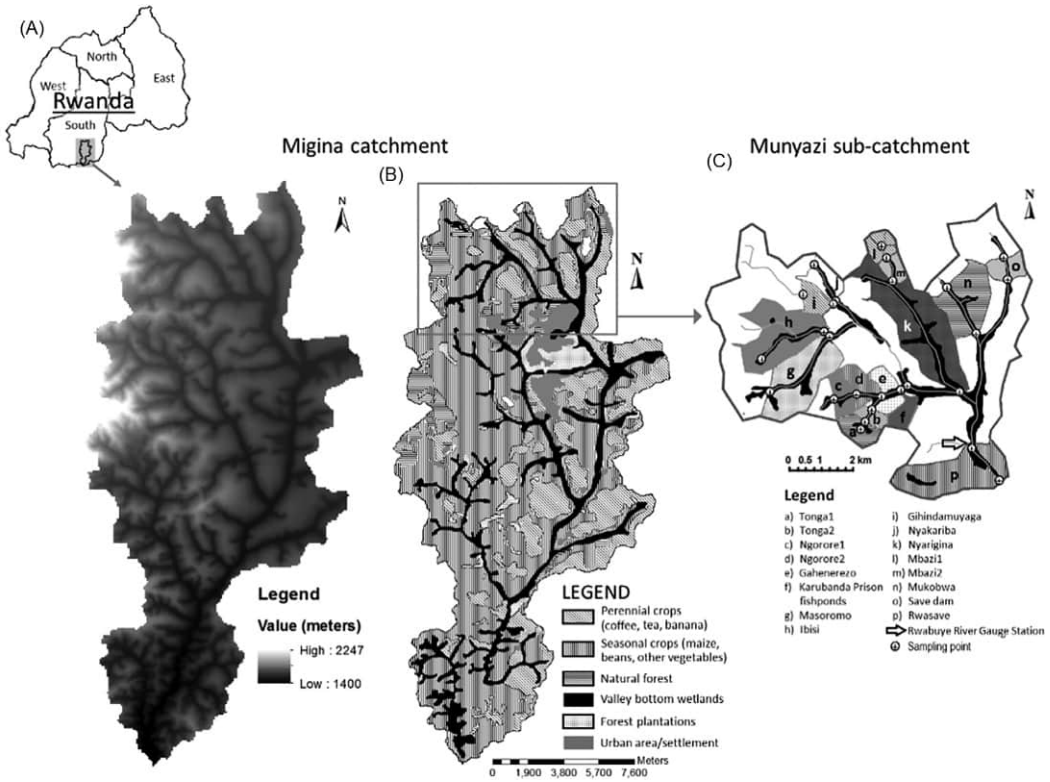

Fig. 9 The Migina catchment: (A) Digital Elevation Model; (B) land use; and (C) 16 reaches of the upper Migina River in the Munyazi sub-catchment, southern Rwanda. (A) From: Centre for Geographic Information Systems & Remote Sensing (2008) University of Rwanda).

The study used landscape-scale synoptic surveys to study relationships between land use and land cover (LULC: farms, fishponds/dams, forest, wetlands), stream discharge and water quality parameters (nitrogen, phosphorus, suspended solids). A Digital Elevation Model (DEM) with LULC information helped to identify the hydrological network, river reaches and land use (Fig. 9). Rainfall and stream discharge data were collected from May 2009 to December 2011 from rain and river gaging stations in the whole Migina catchment (Fig. 9). Water quality was measured during two storm events that started during field sampling on 23 March 2013 and 5 April 2013. More detailed field surveys were conducted in 16 reaches of the Munyazi sub-catchment in the period May 2012–May 2013, using a combination of visual estimates and GPS measurements/mapping to classify LULC into five groups (plowed land, rice farming, vegetable farming, grass/forest, and ponds/reservoir). Monthly net yields of nutrient loss were calculated from measurements of discharge, total suspended solids (TSS), and total nitrogen (TN) and phosphorus (TP) upstream and downstream of reaches with different LULC. Full details of the study are described in Uwimana et al. (2017, 2018).

Impacts

The results of catchment scale surveys showed that farming activities coinciding with heavy rainfall and high flows mobilize high concentrations of TSS, TN, and TP. During the dry season N and P accumulate in the catchment, then are washed into the water courses during the early stages of the higher flows, with subsequent lower concentrations at the end of the rainy season due to dilution. Human activities such as plowing, weeding, fertilizer application, fishpond drainage, and dredging of canals were the main source of sediments and nutrients in water when these activities coincided with high flow. The study estimated that 93%, 60% and 67% of the annual loads of TSS, TP and TN, respectively, were transported during 115 days with rain (Uwimana et al., 2018).

In the 16 reaches, the net yields of water, TSS and nutrients were different among LULC types and varied seasonally. Overall, reaches with plowed soil or dominated by rice and vegetable farming showed negative net yields, while reaches dominated by ponds/reservoir and grass/forest had positive net yields of sediment and nutrients (Fig. 10; Uwimana et al., 2018). Differences in net yield among LULC types were more pronounced during periods of high stream flow (in May 2012, November 2012 and April–May 2013), with higher exports of especially sediment and P in the agricultural reaches (plowed, vegetables and rice) and higher retention in reaches with ponds/reservoirs and natural land cover. Over the whole experimental period, mean net yields of sediment and nutrients were positive in reaches with standing water or natural land cover, and negative in reaches with agricultural land uses (Table 1).

The observed variation in water quality parameters with discharge in the Migina catchment can be interpreted as a "build-up, washout and dilution mechanism" (Uwimana et al., 2017). During base-flow conditions, urban and agricultural areas, wetland grass and ponds or dams act as sinks for sediments and nutrients, which are subsequently released (flushed out) during the early stages of high flows. The more detailed study in stream reaches with different land uses confirmed that sediment and nutrient

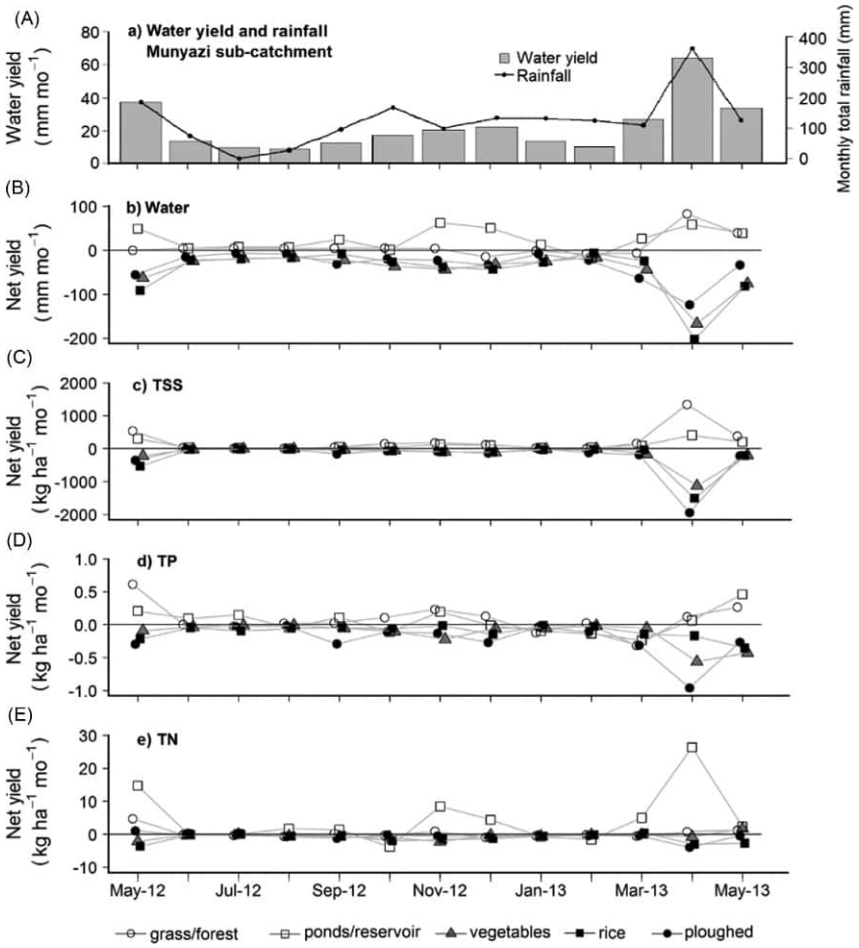

Fig. 10 Seasonal dynamics of water, sediment, and nutrients in Munyazi sub-catchment, Rwanda: (A) water yield at the outlet of Munyazi sub-catchment, and rainfall at Rwasave station; (B–E) Net yields of water (B), total suspended solids (C: TSS), total phosphorus (D: TP) and total nitrogen (E: TN) in 16 reaches of the Migina River (Munyazi sub-catchment), southern Rwanda. Data are means of reaches ($n = 3$–5) with different land use/cover, estimated monthly between May 2012 and May 2013.

retention are strongly related to both land use and water flow. Generally, reaches converted to farming exported, whereas reaches with grass/forest cover or water bodies (ponds or reservoirs) retained TSS and nutrients. These differences were fairly consistent throughout the year, although some individual reaches could shift from being a source to a sink. The more pronounced differences and higher exports during periods of higher rainfall and streamflow ("washout") emphasize the importance of preventing erosion and nutrient runoff during these periods. This could be done by responsible irrigation management and land preparation, including accounting for rainfall in land preparation and irrigation and various erosion control measures such as e.g., mulching, minimum tillage, contour-strip cropping, and terracing (FAO/IWMI, 2018). Other options include land use arrangements that make use of the different retention capabilities, with LULC types with high retention placed downstream (as buffer zones) from LULC types that export sediment and nutrients. In this way, runoff to downstream systems can be reduced. Quantitative data from studies like these can support the design of more sustainable land use configurations in highland valley systems like the Migina catchment.

Table 1 Net yields of water, total suspended solids (TSS), total phosphorus (TP) and total nitrogen (TN) in reaches of the Migina River in the Munyazi subcatchment in southern Rwanda with different land uses.

Land-use category	*Net yield*							
	Water (mm month^{-1})		*TSS (kg ha^{-1} month^{-1})*		*TP (kg ha^{-1} month^{-1})*		*TN (kg ha^{-1} month^{-1})*	
Grass/forest	−1.87	ab	224.8	b	0.0503	b	0.408	ab
Ponds/reservoir	28.1	b	117.0	ab	0.0940	b	4.638	b
Rice	−60.5	a	−246.9	a	−0.108	ab	−1.368	a
Vegetables	−27.6	ab	−91.6	ab	−0.0861	ab	−0.516	a
Plowed	−34.5	ab	−269.1	a	−0.240	a	−0.564	a

Numbers are means of 13 monthly net yield estimates in 3–5 river reaches (total $n = 16$). Means within a column with different superscript letters were significantly different ($P < .05$; repeated measures ANOVA).

Concluding statement

The case studies presented are just four examples of the diverse relationships which agriculture has with waterbodies in various geographic regions. Many other issues surrounding the use of water and impacts of agriculture on waterbodies exist. For example, depletion of groundwater in areas depending on irrigation for intensive crops, runoff and leaching of veterinary products from feedlots, and straightening of river channels due to re-routing and excessive land drainage are among the scenarios in which agricultural needs must be balanced against the pressures they exert upon waterbodies. Crucially, both the waterbodies themselves and the hydrologic catchments in which they are located, deliver multiple ecosystem services and trade-offs and synergies must be explored in light of all of these.

The solutions to these problems will necessarily be specific to the pollutant in question and to the agricultural, geographic, and climatic contexts. Approaches to these problems can be broadly divided into implementation of best management practices and mitigation measures, legislation and regulation to co-ordinate response to serious and eminent public health issues, and basic research into the underlying mechanisms of pollutant transport and impacts. In many cases, some element of each of these three approaches is needed. Strong scientific evidence provides the basis for agri-environmental legislation, which in turn specifies measures implemented to bring about the desired improvements. As research more clearly identifies the factors driving pollution, legislation and measures may change. In all cases, a concerted effort of these three approaches is required, with the involvement of multiple actors and crucially, balancing the trade-offs and synergies with different types of pollution and with the other services required of agricultural land such as food and fiber production, provision of habitats, and cultural values.

Knowledge gaps

- The types and impacts of pollution on inland waters is diverse and no one-size-fits all approach to management is likely to be successful in mitigating declines in quality.
- Nutrient pressures largely arise from agriculture. Better understanding is needed regarding how to use fertilizers with less environmental impact and how to balance the need for increased productivity while protecting water and biodiversity.
- Pollutants such as arsenic that are native to certain environments present hazards to drinking water supplies, particularly where large demands are exacerbated by the need for irrigation or in some cases, to support industry. Greater investigation of geology and hydrology are needed in these basins and policy design should reflect the natural risks implicit in certain environments.
- The effects of emerging contaminants such as pesticides are only now becoming apparent. Increased research is required to understand the dynamics of these chemical in the environment. These new formulations may require different and novel application methods to ensure their safe and effective use and further research and technological innovation is needed in this area.
- The conversion of land to agriculture fundamentally changes the hydrologic dynamics of those basins, with consequences for habitats and ecology. The consequences of land conversion as regards trade-offs and benefits need to be explored.

Acknowledgments

The authors thank the editors and reviewers for their constructive and helpful comments. The Teagasc Agricultural Catchments Programme is funded by the Irish Department of Agriculture, Food and the Marine (Case Study 1). This work was funded by the Source to Tap project (project reference IVA5018—www.sourcetotap.eu). The Source To Tap project (Case Study 3) is supported by the European Union's INTERREG VA Programme (project reference IVA5018—www.sourcetotap.eu), managed by the Special EU Programs Body (SEUPB). The views and opinions expressed in this document do not necessarily reflect those of the European Commission or the SEUPB.

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Hydromorphology: Overview and Assessment Methods

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This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Anabranching River divided into a branching network of smaller channels divided by vegetated, longer-lived islands.
Bar A depositional sediment feature, usually made of cobbles, gravel and/or sand, which occurs on the inside of bends, at the side of the channel, or mid-channel.
Biological Indicator An indicator based on the function, population, or community of organisms that can reveal qualitative status of the environment.
Braided rivers A network of river channels separated by, often dynamic, bars.
Confinement The degree to which a river is constrained by its valley. A wide valley has low confinement and a v-shaped valley has high confinement and the river has little opportunity for lateral movement.
Connectivity The connectedness of different parts of a system (e.g., a river). Can refer to longitudinal connectivity, for example, sediment connectivity or migratory fish passage, but also to connection with floodplain.
Dynamic equilibrium All processes are in balance leading to no net change in the system.
Hydrograph A graph showing the change in flow (discharge) in relation to time at a specific point in a river etc.
Hydromorphology The hydrological and geomorphological elements and processes of waterbody systems.
Hyporheic The water-filled spaces within and along the bed of a river or stream where stream water and local groundwater mix.
Interstitial The spaces between individual sand, gravel and stone etc. grains within the aquatic sediment.

Introduction

This chapter focuses on hydromorphology and the assessment of hydromorphological change in running water ecosystems with some references also to lake ecosystems. The term hydromorphology stems from soil science (Vogel, 2011) but was 'appropriated' with the implementation of the EU Water Framework Directive (WFD) to mean "the hydrological and geomorphological elements and processes of waterbody systems" (European Commission, 2000) and has been defined as 'the suite of hydrological and geomorphological processes and forms that occur within catchments and their river systems' (Gurnell et al., 2015). Hydromorphology links hydrology and geomorphology, with physical stream characteristics and processes at the center of management and restoration (Belletti et al., 2015). Orr et al. (2008) defined hydromorphology as the physical habitat constituted by the flow regime (hydrology and hydraulics) and the physical template (fluvial geomorphology) of rivers, whereas a wider definition states that hydromorphology is the: "science that deals with problems relating to the structure, evolution, and dynamic morphology of hydrologic systems over time" (Vogel, 2011). Rivers and lakes have been, and are increasingly, physically modified, degraded and exploited by humans through e.g., regulation, river channelization and straightening, flood-defence engineering, damming, urbanization, water abstraction, land-fill, reclamation, and dredging (e.g., Malmqvist and Rundle, 2002; Ostendorp et al., 2004) (Fig. 1).

 https://doi.org/10.1016/B978-0-12-819166-8.00199-7

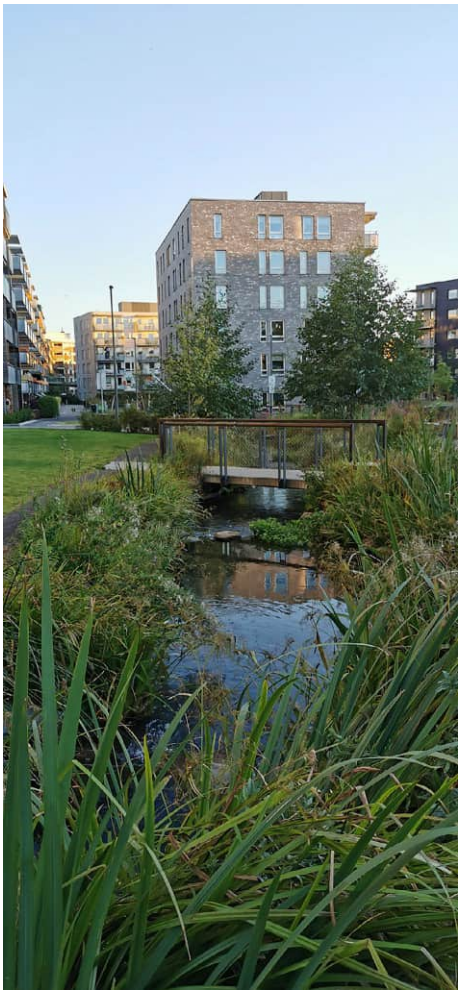

Fig. 1 Hovindbekken—a reopened stream channel in Oslo city, Norway.

Within the WFD, the hydromorphological components of rivers are divided into: hydrological regime; river continuity (quantity and dynamics of flow and connection to groundwater) and morphological conditions (depth and width variation, structure and substrate of the river bed, and structure of the riparian zone). In lakes they consist of: hydrological regime (quantity and dynamics of flow, residence time, connection to the groundwater) and morphological conditions (depth variation, quantity, structure and substrate of the lake bed, structure of the shore). In the WFD the hydromophological status of rivers and lakes underpins their 'ecological status,' with 'high' hydromorphological status of rivers defined as: "Channel patterns, width and depth variations, flow velocities, substrate conditions and both the structure and condition of the riparian zones correspond totally or nearly totally to undisturbed conditions" (European Commission, 2000).

Human activities affecting physical and hydrological aspects of freshwaters

Interrelatedness of hydrology and morphology

Human activities affect the hydromorphology of rivers and lakes in profound and numerous ways, creating a complex web of impacts and multiple feedbacks (Newson, 1994). It has become increasingly clear that understanding the interlinkages within and between these ecosystems are of great importance to better understand and manage freshwater ecosystems (Lamberti et al., 2010). Hydrological alterations are caused by activities that change the natural run-off and flooding pattern of a catchment, the flow regime of a river or the water circulation and retention in a lake. These hydrological changes cause morphological changes to waterways, as the amount of water and the height and duration of flood pulses and low-flows change. Humans then cause further impact by directly modifying the physical shape and material structure of river and lake morphology. Indirect hydrological changes and direct human alterations change the physical shape, sediment composition, dynamics, patterns of erosion and deposition, depth and velocity patterns of waterbodies. Changes to waterbody morphology can then cause hydrological changes, for example by reducing time that floodplains are flooded and, therefore, decreasing soil moisture content, changing water retention times or even altering local weather patterns (Collow et al., 2014).

Any change in land use away from its natural state will change the pattern and velocity of runoff. It can even influence the total amount of precipitation falling on the catchment, as some ecosystems, forests in particular, cause and create rainfall, both locally and further afield (Ellison et al., 2017). In general, complex vegetation, such as natural forests, tends to slow the speed at which water reaches waterways and can help rainwater penetrate the ground, leading to the slower, subterranean recharge of rivers. Floodplains can have an important moderating affect too. A natural floodplain acts to store water and release it slowly, giving a smoother hydrograph.

Human alterations across catchments, such as plantation forestry or clearing and/or draining of land for grazing or crops often increase the rate at which rainwater or snowmelt reaches waterways, which can increase the flood peaks and make rivers more 'flashy,' with higher high-flows and lower low-flows. Farming often causes soil compaction and topsoil erosion, which also exacerbate these effects. No till farming, in contrast, helps to reduce compaction and erosion and increases soil-water retention. Urbanization is an even more direct and obvious cause of rapid runoff, with hard, impermeable surfaces and drainage systems providing a direct pathway to waterways (Rhoads, 2020).

Water withdrawal

Water is removed from rivers, lakes, reservoirs and groundwater for myriad purposes. At the global scale, agriculture, mostly irrigation, is the largest use (about 70%) and is, in many cases, unsustainable, especially as it is most useful during periods and in areas, of low rainfall. Industrial use comprises 20% of water consumption (3/4 of which is used for power production), and domestic use comprises 10% (Boretti and Rosa, 2019). About 30% of world freshwater is groundwater (Hendriks et al., 2015). Overexploitation of aquifers can be thought of as 'groundwater mining,' taking water out of the ground faster than it is replaced. In some aquifers ancient 'paleowater' is being mined. In Libya, for example, the groundwater taken by the Great Man-Made River dates from the last ice-age, with no hope of replenishment (Kuwairi, 2006). At the global scale, around 15% of groundwater abstraction was non-renewable between 2000 and 2009 (Döll et al., 2014).

Forecasts of water demand compared with water availability are truly alarming. Global water demand is about 4600 km^3 a year and estimated to increase by 20–30% by 2050, due to population and economic growth. About half of the world's population already live in areas that suffer water scarcity for at least 1 month a year and almost a third of humans live in potentially severely water-scarce areas. Worldwide, clean freshwater is decreasing and the timing and pattern of its availability is changing (Boretti and Rosa, 2019). The damage water abstraction does to surface waters ranges from drying of wetlands and lakes, drying, shrinkage and low-flow in rivers, to salinization and coastal saline intrusion and even land subsidence (Boretti and Rosa, 2019). The reduction of wetted-channel width of streams causes a decrease in ecosystem processes, such nutrient uptake and organic matter breakdown. Low-flow velocities decrease biofilm biomass and activity as the boundary layer gets larger, decreasing diffusion rates (Arroita et al., 2016).

Morphology and dynamic equilibrium

River morphology is affected by hydrology, sediment, riparian and instream vegetation as well as direct, physical alteration of river channels. Changes to the hydrograph alter channel morphology. Higher and more frequent peak-flows means a greater water power to rework the channel, potentially causing increased erosion and deposition, changes to channel shape and dimensions, and even to channel type (Knighton, 1998). Lower low-flows bring their own problems, for example, sediment deposition, clogging of hyporheic interstitial spaces, organic matter deposition, overgrowth of vegetation, less aeration of water, increase in water temperature, and increase in water retention time. Humans directly impact river morphology in many ways, including straightening, deepening, widening, removal of vegetation or other flow obstructions, reinforcement, embankment and damming. These tend to be carried out to increase flood conveyance, drain and reclaim land, improve navigation, and for impoundments of water for water storage and/or hydropower. Rivers are often constrained to a single, convenient, straight and unmoving channel (Knighton, 1998).

The knock-on effects of these modifications can be less obvious. Actions that diminish natural processes of a river often require regular intervention to be maintained. Consequences can be serious, unintended and unpredictable. A river is not just a flow of water, but also a flow of sediment and organic matter, and often of woody material. Understanding the physical and ecological processes within a river is crucial to predicting how a river will respond to alteration and mitigating any adverse effects. Many natural rivers maintain a state of dynamic equilibrium, meaning that the channel form is adapted to its hydrograph, with balanced sediment transport, erosion and deposition (Knighton, 1998; Wampler, 2012). Rivers in dynamic equilibrium range from being relatively stable to highly mobile, depending on the type of river. If dynamic, then they are predictably so and retain a characteristic morphology and are considered to be geomorphologically stable (Shields et al., 2003).

Being cognizant of dynamic equilibrium, it is then easy to understand how artificial modifications can trigger disequilibrium. A sinuous river actually has a lower bed slope than a straight river. Think of a road of hairpin bends winding down a steep hill. Making the road a straight line down the hill would be much too steep. As river gradient is directly linked to energy of the water, a straightened river means that the water has more power to erode the bed and banks. Straightening a section of river can create a knick-point at the upstream end, due to the abrupt change in bed slope, and this will erode the bed and the knick-point will move upstream (fast or gradually), mobilizing more and more bed sediment. The sediment can then travel all or part of the way through the straightened section (with increased flow velocities) and deposit downstream, thereby creating another problem that needs solving. The banks may also slump in the straightened section, adding further material to the downstream sediment dump (Knighton, 1998).

Water flow down a straight channel does not 'obediently' go in a straight line, but tends to swing from bank to bank, meaning that without reinforcement or structures such as weirs to use up the water's energy, the river will tend to return to a more sinuous condition (Knighton, 1998). In lowland environments widened, deepened, and straightened channels can be relatively stable as the low channel slopes mean the stream has little power to re-shape its channel (Urban and Rhoads, 2003; Grabowski and Gurnell, 2016). They do, however, tend to fill up with silt, sand and gravel and may suffer from excessive plant growth. In such systems coarse sediment can be scarce and dredging can cause long-term loss of riffle-pool morphology and cobble and gravel habitat causing negative effects on e.g., fish populations (Freedman et al., 2013).

Dams that hold back water, also block sediment transport, causing downstream channel incisement and ultimately, coastal erosion. Loss of delta areas is not just loss of their associated ecosystems but as landform features they can mitigate sea level rise (Warrick et al., 2019). Wampler (2012) captures the idea of sediment-starved water *consuming* the river-bed and banks below impoundments with the term 'hungry water.' Given that many dams are relatively new and that channel adjustment may take over a hundred years, many rivers worldwide are currently actively suffering the consequences (Knighton, 1998).

Biogeomorphology

Instream, bankside and riparian vegetation influence and control geomorphological processes through their physical structure. The effects vary according to biogeographical area and hydromorphological type (Gurnell et al., 2014a). The presence and type of vegetation is itself controlled by substrate type, water availability (soil and groundwater) and the river flow regime (reliability and disturbance) (Gurnell, 2014). The river Tagliamento in Northern Italy demonstrates well the interplay between vegetation and hydromorphology. The river has both braided and anabranching sections (both types have multiple channels, but anabranching channels are more stable and more likely to form islands). Large woody debris such as tree trunks is crucial to the formation of islands and it is predicted that simple changes in the water table could completely change the character of sections of the river by altering the vegetation. A fall in the water table could trigger a change from anabranching to braided due to changes in woodland structure and a reduction in the supply of wood to the channel. In contrast, a rise in the water table could cause more pronounced anabranching and even a change to a single-thread, sinuous river. Numerous activities could potentially trigger such changes, e.g., flow regulation, abstraction, gravel mining, tree cutting and removal of wood from the channel (Gurnell et al., 2014a).

Animals themselves also have their own impacts on hydromorphology; from the direct ecosystem engineering of beavers (Levine and Meyer, 2019) to the indirect and unforeseen impact of wolves. Attributed to the reintroduction of wolves to Yellowstone National Park, United States, are changes to the behavior and grazing pattern of their prey, rocky mountain elk, leading to taller riparian willows, narrower, less incised and more flood-prone creeks (Beschta and Ripple, 2019); although Marshall et al. (2013) suggest that this may be an oversimplified interpretation.

Burrowing activities of native mammals are sometimes considered a nuisance when they threaten dams and embankments (Harvey et al., 2019). Non-native species are another significant human-mediated impact on river morphology. Non-native burrowing animals are a global problem and include mammals (e.g., *Myocastor coypus*), reptiles (e.g., *Iguana iguana*), and fish (e.g., Loricariidae) and various invertebrates (Harvey et al., 2019). Invasive crayfish (*Pacifastacus leniusculus*) in the river Thames catchment directly excavated an estimated 2 L of fine sediment per meter of affected bank and bank collapses caused by the burrows will also have greatly added to this sediment load (Faller et al., 2016). Non-native plants are also implicated—Himalayan Balsam (*Impatiens glandulifera*) may cause increased erosion along European rivers, due to seasonal die-back leaving unprotected banks (Greenwood et al., 2018). Modelling colonization of an invasive plant, based on Japanese Knotweed (*Reynoutria japonica*), van Oorschot et al. (2017) found that the effects of high propagule pressure on morphology could be profound, including preventing colonization of trees and other native vegetation, reduced summer erosion rates and increased winter erosion rates and higher autumn water levels.

Magnitude of anthropogenic impacts

Anthropogenic impacts on river systems are often extreme. Worldwide, 87% of wetlands have been lost since 1700 (Boretti and Rosa, 2019). Numerous large lakes are shrinking, drying, becoming more saline and disappearing. Lake Chad, once the fourth largest in Africa, has shrunk to 1/20 of its former size and is forecast to disappear by 2030. The causes are a reduction in rainfall due to deforestation, irrigation, overgrazing and global climate change. Hydromorphological alterations have been estimated to affect 38% of all lakes by lake area in the European Union (Poikane et al., 2019). In the drought-prone Murray-Darling, Australia's largest river basin, 69% of its water was abstracted during the 2000s, causing severe and probably irreversible ecological damage, including to its 16 Ramsar wetlands (Overton and Doody, 2012).

One of the major driving forces of change in river systems are dams as they fragment rivers and alter their flows (Aguiar et al., 2016). This is especially true for rivers with dams built for hydropower production (Renöfält et al., 2010) (Fig. 2). Hydropower can have huge ecological impacts based not only on changes to water volumes, but also through changes to water temperature and gas saturation, for example, by causing oxygen saturation levels high enough to kill fish and invertebrates (Demars et al., 2021). There are an estimated 2.8 million dams with reservoir areas $>10^3$ m^2 worldwide and only 37% of rivers longer than 1000 km are completely free-flowing, the majority of these being in the Arctic, the Amazon and the Congo (Grill et al., 2019). Large dams (walls higher than 15 m) are estimated to have a combined storage capacity equivalent to one-sixth of the total annual river flow into the

Fig. 2 Harsprånget hydropower plant in Stora Lule river, Sweden.

oceans (Mulligan et al., 2020). More than 800,000 dams world-wide obstruct approximately two-thirds of the fresh water flowing to the oceans and over 70% of the large rivers of Europe, North America and the former Soviet Union are strongly regulated (Giller, 2005) (Fig. 3).

Lack of data prevents an estimate being made for the number of barriers in smaller rivers on the global scale (Grill et al., 2019), but in Europe there are an estimated 1.2 million instream barriers (a density of 0.74 barriers/km) with 68% of these structures being small (less than two meters in height) (Belletti et al., 2020). The largest impoundment in the world, the Three Gorges in China, has caused deadly landsides (Tang et al., 2019), massive sediment problems, drought, hydromorphologically-mediated ecosystem damage and downstream saline intrusion (Zhang et al., 2016). Large dams can alter weather patterns (Degu et al., 2011) and the Three Gorges dam has caused earthquakes (Tang et al., 2019) and is even calculated to slow the speed of rotation of the earth (JPL, 2005).

Forty percent of European rivers have been estimated to be affected by hydromorphological pressures (Buijse, 2016): and 23% and 16% affected, respectively, by changes in hydrology and morphology (Lemm et al., 2021), and this was the most common reason rivers failed to reach "good ecological status", as required by the WFD (Kristensen et al., 2018). A huge proportion of the rivers worldwide have been straightened, which has resulted in a drastic loss of river length and hydraulic complexity, and consequently habitat and biodiversity (Zhou and Endreny, 2020). A hydromorphological assessment of Europe's second-largest river, the Danube, categorized it as 0% nearly natural, 40% slightly modified, 28% moderately modified, 29% severely modified and 3% totally modified. The banks were 17% nearly natural, 22% reinforced in small sections, 40% reinforced in large sections, 18% continuous bank reinforcements and 3% totally reinforced (Liška et al., 2008).

Increases in stream power after straightening of a river channel can be dramatic. Guzelj et al. (2020) calculated that stream power had increased by 13.3 times, based on a sixfold increase in stream slope and a more than doubling of bankfull discharge, in a formerly meandering lowland river. This meant that the erosive power of the water was such that attempts to move back towards the historical reference by creating a partially meandering river would be unsuccessful as the river would be too active. Designing restoration projects that aim for an imagined past or static reference state is flawed thinking. For example, in many countries in Europe, 100–200 years ago, sediment delivery to rivers was much higher than now because of active deforestation and expanding agriculture (Rinaldi et al., 2015b).

Aiming for a combination of processes, which could be a set of reference dynamics, can be ideal if the situation allows, but in other situations a more practical approach is needed (Dufour and Piégay, 2009). Much of the loss of wet habitats worldwide (lakes, ponds, wetlands, oxbows, side channels) comes from damage and draining of floodplains. Tockner and Stanford (2002) describe cultivated floodplains in Europe and North America as "functionally extinct," with a view that up to 90% of European and North American floodplains are like that. The SOER report (EEA, 2019) agrees with this assessment for Europe. Damage to floodplains in the developing world is accelerating.

Although the European Water Framework Directive (European Commission, 2000) requires the quantification of hydromorphological and ecological damage to waterbodies, many of these former habitats are simply gone, drained or constrained, sometimes hundreds of years ago and are not included, or possible to be included, in current statistics. The ecological assessment of rivers tends to focus entirely on the instream sampling of, usually, single channel rivers, which ignores the vast array of other habitats within an undamaged river (Peacock, 2003). With the WFD monitoring approach it is clear that it does not include the riparian zone vegetation, therefore hydromorphological alteration will be greatly underestimated as there is an intimate relationship between in-stream physical and biological conditions and riparian zones (Gurnell, 2014). A proper definition of a river includes the width of its floodplain, which needs to be an integral part of hydromorphological and ecological assessment. Floodplains are a hotspot for biodiversity, with far more species living there than in any other type of landscape unit in most regions of the world (Tockner and Stanford, 2002). Mismanagement of floodplains is literally killing people, with over half of people who died as a result of natural disasters in recent decades, dying in floods (Habersack and Schober, 2020).

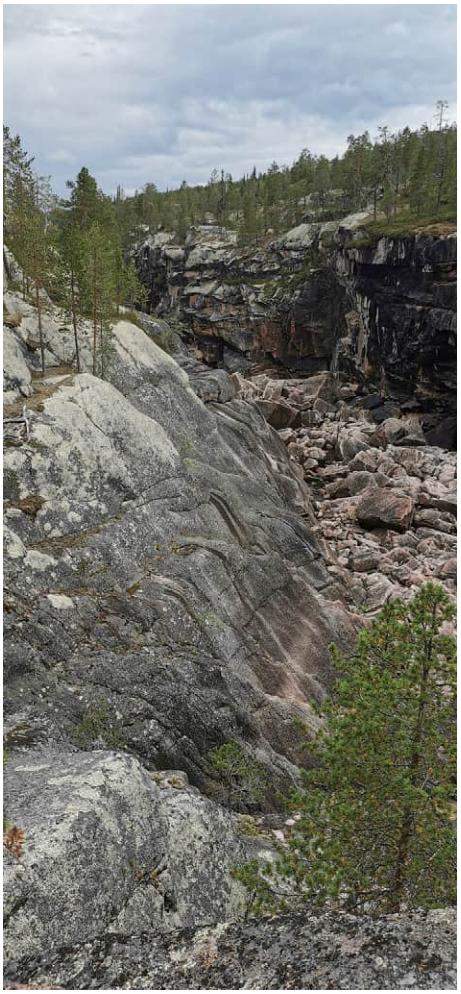

Fig. 3 Harsprånget, a former river stretch in the Stora Lule river which used to have a discharge of 268 $m^3 s^{-1}$ now the water is diverted to the hydropower station.

Assessing human induced hydromorphological alteration

Hydrological, physical and geomorphological state

There are three basic strands to the assessment of hydromorphological condition of waterbodies: hydrological, physical morphological (including riparian/floodplain), and geomorphological process. Gathering such data relies on field measurements and surveys, as well as map-based, historic, paleo- and remote-sensed information, each having benefits and drawbacks (Gurnell et al., 2014b). Techniques range from recording habitat types, to describing and quantifying processes and using mathematical models for predicting change. Assessment methods vary greatly in scale, from reach or lake-scale to catchment or region, and from instream up to riparian and floodplain zones. Most methods look at the smaller scales, with a tendency to focus on physical habitat, riparian habitat and morphology; while underlying physical processes have often not been considered, partly because they are more difficult to assess rapidly (Belletti et al., 2015).

The EU FP7 funded REFORM project undertook a thorough evaluation of current practices (Rinaldi et al., 2013). They proposed a process-based, hierarchical, flexible and open-ended framework to guide future hydromorphological assessments (Rinaldi et al., 2015b). This helps the practitioner think about every scale and factor, including oft-ignored dimensions, such as catchment-scale variables and a consideration of geomorphological adjustment over different timescales. The hierarchy of scales is: region, catchment, landscape unit, segment, reach and geomorphic units/hydraulic units/river elements (Rinaldi et al., 2015c). Suggested information to be gathered includes geology, topography, hydrology, land use, vegetation cover, river morphology, lateral confinement, channel dimension, river energy, hydraulics, bed and bank sediments, flow regime, floodplain, groundwater—surface water interactions (based on valley confinement, substrate character, geology and climate), riparian and aquatic vegetation. See tables 3.2 and 3.3 in Rinaldi et al. (2015b), see Rinaldi et al. (2015c) for an exhaustive list of indicators.

Drivers of physical processes such as sediment sources (e.g., landslides, soil erosion, bank erosion) should be identified and recruitment of large wood examined. Physical controls on the pattern of channel morphology and floodplain features should be

understood, including the physical pressures and human impacts on river processes and morphology (such as structures altering longitudinal and/or lateral continuity, flow regulation, dredging, mining, other structures, reinforcement, instream and riparian vegetation removal, embankments, riparian buildings and infrastructure).

Given the complexity of interacting factors on a river and the wide range of physical environments found globally, it is a useful simplification to define river types, by looking at the characteristics of their morphology, flow regime and floodplain. Knowing river type helps to predict its behavior. Rinaldi et al. (2015c) suggest using three typologies to encompass morphology, flow regime and floodplain character.

Morphological typology: an extended river typology (Rinaldi et al., 2015c, 2016) with 22 morphological types, based on confinement—whether lateral movement of a river is constrained by its valley (confined, partly confined, unconfined), dominant bed material caliber—how coarse or fine its substrates are (bedrock, boulder, cobble, gravel, sand, silt), and planform—the pattern it makes in the valley when viewed from above (straight-sinuous, meandering, pseudo-meandering, wandering, braided, island-braided, anabranching).

Flow regime typology: based on intermittency, river-aquifer interaction, prevailing type of river-flow source.

Floodplain typology: based on river energy and cohesive or non-cohesive floodplain sediments (Rinaldi et al., 2015c; Nanson and Croke, 1992). An additional useful method, published after the REFORM project, is the floodplain evaluation matrix (FEM) (Habersack and Schober, 2020) focusing on floodplain functionality and damage, and considered from a flood-mitigation and hydrograph smoothing perspective.

Assessing hydromorphological change trajectories

It is not enough simply to look at the condition of a river on the day of survey. Many factors affecting hydromorphology are not constant over time, even without human impacts, and hydromorphologically damaged rivers are often in a prolonged non-equilibrium state. Thinking in terms of longer and shorter timeframes can be helpful as the trajectory of change in each case can be opposite (e.g., long-term incision, with recent aggradation). Another important question is whether a river is in a state of dynamic equilibrium or instability. A river is in dynamic equilibrium if its average properties (width, depth, slope, sediment input and output) remain stable over 10 years or more. Such a river can still be highly dynamic (Rhoads, 2020).

Instability of a river's hydromorphology is caused by changes to water or sediment inputs or outputs and can be progressive (e.g., climate or land use change), impulsive (floods), transient disturbance—(e.g., sediment mining) or long-term (e.g., by dams). Particular attention should be paid to rivers close to geomorphic thresholds, where even a small change to pressures can trigger a dramatic change in the state of the river (e.g., from a multi-thread to a single-thread channel).

When critical reaches or reaches of particular interest have been identified, their hydromorphological condition can be assessed in detail. Four types of assessment are useful:

Hydrological assessment: to understand changes compared with previous or unaltered conditions. Methods are based on "Indicators of Hydrologic Alteration," developed by Richter et al. (1996) and Olden and Poff (2003).

Morphological assessment: this is different to a simple physical habitat assessment as it considers processes, change over time and impacts. A number of methods tackle this, including the MQI (Morphological Quality Index) (Rinaldi et al., 2015d), which is applied at the river reach scale (reaches are fairly morphologically homogeneous and usually stretch over kilometers—whereas physical habitat surveys are usually carried out at a smaller scale). MQI uses 28 indicators based on channel forms, processes, sediment and wood fluxes, vegetation, channel mobility, channel adjustment, historical and future changes, dynamic equilibrium (reference condition) to evaluate the reach in terms of: (1) geomorphic functionality; (2) artificiality and (3) channel adjustments (morphological changes indicating instability due to human impacts).

Riparian vegetation assessment: as vegetation is fundamental to hydromorphological processes, it must be included (e.g., RQI Riparian Quality Index (González et al., 2011)). Among other vegetation features, vegetation processes, such as age diversity and plant regeneration are assessed.

Geomorphic unit assessment: assesses the presence and diversity of physical habitats, thereby linking hydromorphology with biology (using e.g., GUS—Geomorphic Units survey and classification System (Rinaldi et al., 2015a)).

Using hydromorphological assessment in restoration planning

In restoration planning, it is vitally important to understanding *if* and *how* rivers will change under different scenarios (Rinaldi et al., 2015b). Predicting the response of a river to geomorphic change can be used to determine an appropriate restoration strategy. In a river where there is little potential for re-establishing natural processes, as can be the case in lowland, low-slope environments, 'morphological reconstruction,' physically re-building lost habitat features such as riffles, bars and meanders may be most appropriate. The more sustainable and often cheaper option is to use the river's own dynamics, processes and energy to re-shape habitats. Working out the sensitivity of a river to geomorphic change relies on many of the assessments previously described. River type gives a good, first clue. In general, channels in confined valleys with large substrate size and low-gradient, lowland rivers are not highly sensitive to change. Whereas a multi-thread, high power river on mobile substrate in a wide valley is highly sensitive (Reid and Brierley, 2015).

Detailed geomorphological sensitivity can be used to work out, for example, conditions under which bed material starts to move, bank stability and thresholds of channel-pattern change (Rhoads, 2020). Understanding geomorphic thresholds and

anticipating state changes is particularly important as sensitive rivers can dramatically change character with only small changes to the pressures. A river which is highly sensitive to geomorphological change can be more easily nudged to change its morphology than a stable one, but more care will be needed to avoid unforeseen consequences (Schumm, 1979).

Biological indicators

The importance and influence of river physical habitat on freshwater ecological response is widely recognized (e.g., Maddock, 1999; Urban and Daniels, 2006). Bunn and Arthington (2002) identified four key principles that form the link between the flow regime and the biota: instream flow conditions determine habitat and therefore biota, the lifestyles of the biota have evolved to live in synchrony with the natural flow regime, longitudinal and lateral connectivity (floodplain) is necessary for undamaged communities, and disturbances to natural flow regimes create opportunities for non-native species. A number of conceptual frameworks have been developed that emphasize these links, for example biotic and ecological integrity (Karr and Dudley, 1981) and ecological health (e.g., Karr (1999)). It is clear that biota utilize specific habitat types and these are relatively well understood in terms of hydrological and hydraulic habitats and to some extent micro-morphological habitat, particularly for fish (e.g., Moir et al., 2004; Chovanec et al., 2003). There is also evidence that larger scale morphological habitats determine biotic response (e.g., Montgomery, 1999; Pess et al., 2002).

Many attempts have been made to find biological indicators that give a useful measure of hydromorphological impact, but this has proven challenging in both lakes (Poikane et al., 2019) and rivers (Poikane et al., 2020; Friberg et al., 2013). This partly reflects the problems inherent in coming up with any type of impact-specific biological indicator, in that organisms respond to the entire range of natural and anthropogenic effects at work in their ecosystem and different impacts working together sometimes have surprising and additive, synergistic or antagonistic effects (Ormerod et al., 2010). One of the most basic and popular river biological index for benthic invertebrates, Average Score Per Taxon (ASPT) (Hawkes, 1998; Armitage et al., 1983), responds strongly to poor water quality (organic pollution, its target impact), but is also affected by other anthropogenic impacts such as nutrients, toxic pollution, hydromorphological damage, as well as by the full range of natural variation such as climate and river type. Many therefore also consider ASPT to be a general indicator of river health (Eriksen et al., 2021) and Friberg et al. (2016) found it to be just as responsive to hydromorphological damage as some indices designed specifically to measure hydromorphological impact. While it is often possible to find significant correlations between impacts and biological responses over large datasets (Göthe et al., 2015), using the biological community found at one site to give an accurate and impact-specific assessment of that site is difficult and unreliable (Demars et al., 2012; Sandin and Johnson, 2004), and indeed based on outmoded ideas according to Woodward et al. (2013).

Assessing effects of hydromorphological alterations can be particularly difficult, as it is very clearly not a single impact but a complex web of interactions (Göthe et al., 2019). A damaged community at one site may resemble a more natural community at another. Floodplain and riparian damage cannot be readily detected by instream sampling. Contraction in wetted area of a river (resulting from hydropower for example) may not give a strong biological signal if the remaining smaller stream still has a good habitat and only the wetted area is sampled. The quest for biological indicators of river health has generally been at the level of organism groups, usually algae (phytoplankton—lakes, phytobenthos—rivers—often only diatoms), macrophytes (including macroalgae and bryophytes), macroinvertebrates and fish (Furse et al., 2009). Within these groups various aspects are considered, with metrics belonging to four general types: (1) composition/abundance; (2) richness/diversity; (3) sensitivity/tolerance metrics; and (4) functional. Across these categories, literally hundreds of metrics exist (Birk et al., 2012). Examples of the more widely applied macroinvertebrate hydromorphology-specific indices in rivers include PSI (Turley et al., 2016)—designed to target fine-sediment impacts and LIFE (Extence et al., 1999)—targeting low-flow impacts. Efforts have also been made to combine existing indices into multi-metrics, in an effort to synthesize different facets of hydromorphological impacts into one measure (Hering et al., 2006).

Examining biological ecosystem processes (functional indices) is another way to assess impacts on ecosystems. These can either be species-trait based or involve other measurements of biological processes (Sandin and Solimini, 2009). Indices based on traits still require the taxonomic determination of the organisms present but can give information about ecosystem functioning; for example, by looking at how the dominant lifestyles change in relation to hydromorphological damage. Traits also have the benefit of being independent of biogeography. Friberg et al. (2016) looked at the future potential for using both taxa-based and species-trait based indices in the different organism groups to detect hydromorphological impact in rivers. They found diatom communities to be more strongly related to nutrient impacts than hydromorphology, except in the case of fine sediment impacts, where they showed potential. Macrophyte traits showed potential as indicators, but macrophytes are likely to be useful in only a subset of river types (e.g., lowland, macrophyte dominated). Macrophytes should also be a focus of attention, however, as aquatic and riparian vegetation are key drivers of hydromorphological processes. Although hydromorphological impacts on invertebrates are well known, these authors did not find any community or trait-based measures that did not also respond to other stressors. Some fish are very sensitive to hydromorphological stress and offer the potential for successful development of metrics. In river types having naturally low diversity, then other factors such as community size-structure would need to be considered (Friberg et al., 2016).

It is also possible to measure or infer biological processes such as stream metabolism without looking directly at the organisms. No such biological hydromorphological indices have yet been developed, although existing studies suggest that it could be a fruitful direction to follow. For example, Kupilas et al. (2017) found that river restoration increased ecosystem metabolism. Li et al. (2010)

see the future of river biomonitoring as involving a range of functional indicators, potentially including microbial enzyme activity, bacterial luminescence, photosynthesis, respiration, locomotory activity, fluctuating asymmetry, community metabolism (primary productivity and respiration), nutrient uptake and spiraling, and secondary production.

Management of hydromorphology

Both rivers and lakes provide many benefits for humans (Postel and Carpenter, 1997). As hydromorphological factors and human-induced changes have strong impacts on rivers and lakes, the understanding of these variables and their interactions are crucial for freshwater management and restoration (Del Tánago et al., 2016). There are a large number of hydrological and geomorphological processes that occur across spatial and temporal scales in freshwater ecosystems. Processes at smaller spatial and temporal time scales are nested within larger scales (Frissell et al., 1986). This, together with the interaction between hydromorphology and ecology needs to be taken into account in freshwater management, especially with a changing climate, as this will affect both the physical template and biological response in these systems (Vaughan et al., 2009). Climate change also means management targets need to be adapted. In many areas, rainfall is predicted to become more extreme, causing intensified flooding and an increased demand for hydropower is expected, which will negatively affect rivers and lakes and their hydromorphological status (SOER, 2019). These more powerful high flows will shape larger channels, increase sediment transport and could change the dynamics and character of the channel, leading to channel instability for example (Shrestha et al., 2020).

Planning is key for accomplishing targets in hydromorphological management of freshwater ecosystems (Angelopoulos et al., 2017). There are several relevant management guidelines for running waters (Beechie et al., 2008; Gurnell et al., 2015), but in many instances parts of these guidelines are not taken into account and investments in river restoration and management over the last decades have failed to halt declines in habitat quality, ecosystem function, and biodiversity (Bernhardt et al., 2005; Almond et al., 2020). One major aspect that needs to be better taken into account is the improvement of monitoring and evaluation of management and restoration actions (Jansson et al., 2007; Palmer et al., 2010). These are integral parts of management and restoration programs. The management program also needs to include quantitative predictions of outcomes and setting appropriate targets and expectations for the magnitude and response of management actions (Beechie et al., 2010). Understanding the limitations of potential management actions and evaluating earlier efforts are key to improving guidance and execution of future efforts (Angelopoulos et al., 2017). This is especially true in the Anthropocene with changing hydromorphological conditions affecting multiple aspects of management and restoration in freshwaters (Downs and Piégay, 2019; García et al., 2021) where e.g., increased intensities of peak flows or drought could have strong negative effects on fish habitat restoration (Battin et al., 2007).

At the international level, the UN Sustainable Development Goal 6.6 (Protect and restore water-related ecosystems) focuses on protecting and restoring water-related ecosystems to ensure they continue to provide sustainable social and economic services and benefits to society. The aim of target 6.6 is to halt ecosystem degradation and destruction and to assist in recovering already degraded water-related ecosystems (United Nations, 2018). The United Nations conclude in the report that there is insufficient data to satisfactorily measure progress towards the SDG target on water and sanitation (SDG 6) but the data that does exist shows that artificial waterbodies (often related to hydromorphological pressures on natural ecosystems) such as dams, reservoirs and rice paddies have increased across the globe. One available dataset is on large dams, known as GOOD (GlObal geOreferenced Database of Dams) includes c. 58,000 large dams worldwide with a total storage capacity about as large as one-sixth of the total annual river flow into the oceans (Mulligan et al., 2020). Most of these dams have been built in the last 60 years and about 50% of the dams have been built for irrigation.

It has become evident that 'hydromorphic limits' are becoming important factors restricting the ecological quality of freshwater ecosystems (Vaughan et al., 2009). In the European Union, the legally binding Water Framework Directive (WFD) (European Commission, 2000) has highlighted the importance of hydrological processes and the morphodynamics of river channels and floodplains and their effects on ecological status and management actions (Rinaldi et al., 2016). The aim of the WFD is to achieve 'high status' (reflecting totally, or nearly totally, undisturbed conditions) with an environmental objective of at least 'good status' and no deterioration of classes in water bodies (rivers and lakes) corresponding to unaltered hydromorphological and physico-chemical conditions in comparison to type-specific reference states. In the European Union 40% of the water bodies do not reach 'good ecological status' because they have been affected by hydromorphological pressures for centuries. On the global scale, the United Nations decade on Ecosystem Restoration (2021–2030) will increase the momentum on freshwater ecosystem restoration. Within the European Union, the EU Green Deal and The EU 2030 Biodiversity Strategy (BDS 2030) call for urgent action to restore damaged aquatic and terrestrial ecosystems with a specific target to establish at least 25,000 km of free-flowing rivers by 2030.

Evaluating the physical characteristics (in terms of hydrology and morphology) of rivers and lakes is important to fulfill the requirement in public policies such as the EU Water Framework Directive, the US Clean Water Act, the Swiss Water Law, the Australian National Strategy for Sustainable Development, the New Zealand Resource Management Act, the Canadian Environmental Protection Act, and the National Water Act (NWA) in South Africa. To implement such policies and water management initiatives, guidelines are needed, such as the one developed by UNEP, the International Water Quality Guidelines for Ecosystems (IWQGES) (UN Environment, 2018). This guide contains a cyclical step-by-step process to ecosystem assessment in freshwaters, which includes: (i) agreeing on a vision and setting objectives, (ii) assessing ecosystems, formulating guidelines, monitoring, reporting, evaluating successes and weaknesses, and (iii) identifying future management goals, before the cycle begins anew.

The IWQGES includes physical, chemical, biological, and hydromorphological indicators applicable to different freshwater ecosystem types, and methods to define water quality targets and threshold values that are appropriate depending on context.

Conclusion

Hydromorphological components in river systems include: hydrological regime, river continuity (quantity and dynamics of flow and connection to groundwater), and morphological conditions (depth and width variation, structure and substrate of the river bed, and structure of the riparian zone), whereas in lakes it consists of: hydrological regime (quantity and dynamics of flow, residence time, connection to the groundwater) and morphological conditions (depth variation, quantity, structure and substrate of the lake bed, structure of the shore). Rivers and lakes are increasingly physically modified, degraded and exploited by humans and hydromorphology in freshwaters links hydrology and geomorphology with physical characteristics and processes and are thus at the center for management and restoration of these ecosystems. In order to assess and manage lakes and river systems from a hydromorphological perspective, data from field measurements and surveys, map-based, historic, paleo and remote-sensed data and information are needed. There are three basic strands to such assessment of hydromorphological condition of waterbodies: hydrological, physical morphology (including riparian/floodplain), and geomorphological process. It has been challenging to find appropriate biological indicators to measure the degree of hydromorphological impact in freshwaters, but a fruitful direction might be the development of functional and ecosystem process-based indicators for hydromorphological management and restoration.

The importance and influence of the physical habitat (hydromorphological condition) on freshwater ecological response is widely recognized and there are a number of conceptual frameworks that have been developed to assess these links. There are several such management guidelines available for running waters, but in many instances parts of these guidelines are not taken into account and investments in river restoration and management over the last decades have failed to halt declines in habitat quality, ecosystem function and biodiversity. Both rivers and lakes need to be managed for a multitude of purposes as they provide many different benefits for humans. As hydromorphological factors and human induced changes have strong impacts on river and lakes, the understanding of these variables and their interactions are crucial in freshwater management and restoration. Evaluating the physical characteristics of rivers and lakes is thus important to fulfill the requirement in public policies, and guidelines are also needed to guide such policies and water management initiatives, such as the UNEP, the International Water Quality Guidelines for Ecosystems (IWQGES) (UN Environment, 2018).

Knowledge gaps

- The fundamental and theoretical understanding of hydrological and geomorphological processes are generally well developed. The important gaps are between the specialists and those that actually take the practical, everyday decisions about land and water management.
- The difficulty of bridging this gap is that hydromorphological science does not provide an easy set of prescriptive steps for decision-making, there is not a one-size fits all solution and apparently sensible actions can have unforeseen and dramatic consequences.
- Easy to use methods for predicting the outcomes of catchment management decisions and physical interventions are lacking.
- The understanding that the general public have of land-use effects on watersheds and river dynamic processes is close to zero and this extends, to a greater or lesser extent, to those with decision-making power, from the politician giving the green light to floodplain development to the landowner who wants “their” river to be “tidy” and go in a straight line.
- This knowledge gap can extend to those funding and executing improvement measures, with many projects undertaken considering only habitat improvement, without considering whether these habitats are appropriate and sustainable over time.
- The science of river restoration is in its infancy, with a shortage of geomorphologically-trained specialists with practical experience. Many projects have been driven by ecologists, with an understanding of organisms and habitats, but without support from those with the knowledge of the processes that create and maintain these habitats.
- Even specialists need to change mindsets, as current monitoring strategies treat rivers and floodplains as separate entities and the Water Framework Directive, the single most important piece of legislation for hydromorphology, does not consider floodplain habitats such as wetlands, or the fundamental role of riparian vegetation in shaping rivers.
- Currently available ecological indicators are inadequate for assessing hydromophological impacts on lakes and rivers. Future developments may focus more on ecosystem functioning and developments in molecular ecology.
- Many or even most restoration projects fail to carry out adequate pre- and post-project physical and ecological monitoring, meaning that lessons are learnt more slowly than they should be.
- Change is coming, with many strong example projects appearing across the world. The number and experience of practitioners is going up and funding is rising in many countries. Process-based restoration is to be treasured as the standard method at the EU level.
- This general positive trend is not spread evenly across the globe, however. In many countries hydromorphological restoration does not exist and old mistakes are being repeated, destroying natural systems that many, more developed, countries are now struggling to recreate.

See Also: Human pressures and management of Inland Waters: Hydromorphology: Case Studies

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Relevant websites

https://amber.international/—The Amber project.
https://www.reformrivers.eu/—The Reform project.
https://damremoval.eu/—Dam removal Europe.
http://globaldamwatch.org/—Global dam watch.
https://www.eea.europa.eu/—European Environment Agency.

Hydromorphology—Interactions and Habitats

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Connectivity in streams

- Longitudinal connectivity: linear connectivity along the entire length of a stream, with the physical gradient changing from source to mouth and chemical systems and biological communities shifting and changing in response (see also Vannote et al., 1980).
- Lateral connectivity: floodplain connectivity, i.e. the periodic inundation of the floodplain and the resulting exchange of water, sediment, organic matter, nutrients, and organisms.
- Vertical connectivity: connection between the atmosphere and a stream via (1) precipitation falling onto land and then flowing over land or percolating through the groundwater (the hyporheic zone, i.e. the zone below the stream bed) to the stream and (2) transfer of water from the streambed itself to surrounding aquifers.
- Temporal connectivity: connectivity of continuous physical, chemical, and biological interactions over time; occurs on several scales, e.g. seasonal, multiyear, generational.

CWD (coarse woody debris) Fallen dead trees and the remains of large branches (snags) in rivers and lake littoral zones, mostly originating from the riparian zone.

Rip-rap Erosion-resistant layer of large, loose, angular stones or chunks of concrete at a lake shore or river bank, often on an artificial embankment.

Xylophagous macroinvertebrate taxa Macroinvertebrate taxa feeding on or boring into wood and having a close association with coarse wood debris in lakes and rivers.

Effects of morphological degradation on macroinvertebrate, macrophyte and fish communities

Aquatic ecosystems worldwide are influenced by human alterations of their hydrological and morphological environmental conditions. These are often described and assessed together as hydromorphological alterations and have manifold impacts on biotic communities, for example on macroinvertebrates, fish and macrophytes (Leps et al., 2015; Noges et al., 2016; Strayer and Findlay, 2010). With respect to morphological degradation in lakes and ponds, human activities often reduce the overall diversity of littoral mesohabitats available for biota. This can occur through a replacement of natural habitats by anthropogenic structures, such as retaining walls and rip-rap (Fig. 1), recreational beaches (Fig. 2), docks and marinas (Fig. 3) and boat houses (Brauns et al., 2011; Strayer and Findlay, 2010). Physically complex habitats such as CWD (coarse woody debris), tree roots, submerged and emergent macrophytes often have a low relative frequency of occurrence at degraded lake shores (Brauns et al., 2007b; Francis and Schindler, 2006; Miler et al., 2015; Ostendorp et al., 2020). Submerged and emergent macrophyte stands are impacted by anthropogenic wave action via boat and ship traffic, which is amplified by retaining walls (Gabel et al., 2017; Ostendorp et al., 2020). At recreational beaches, submerged and emergent macrophytes are either cut back by controlled removals or negatively impacted via mechanical stress (trampling) by swimmers (Johnstone, 1986; Liddle and Scorgie, 1980; Ostendorp, 1989).

Hydromorphological degradation can occur in a floodplain/catchment and affect the entire lake basin. The presence of a functioning riparian zone with trees and shrubs provides the littoral zone with CWD and other organic material as well as submerged tree roots as a living organic habitat (Brauns et al., 2007b, 2011; Francis and Schindler, 2006; Miler et al., 2015).

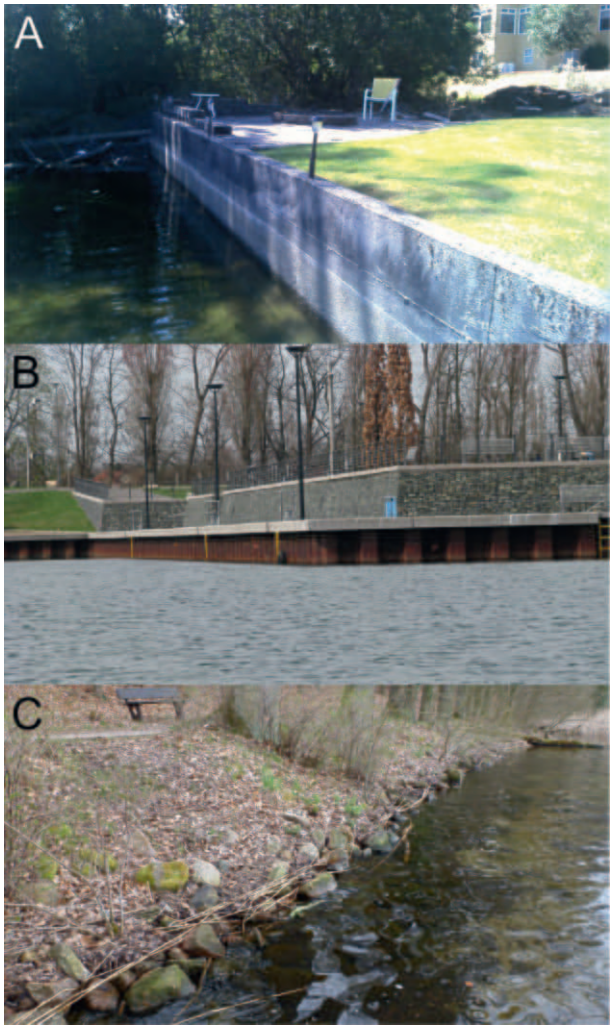

Fig. 1 Examples of hard shore modifications: (A) concrete wall in Fivemile Lake, Washington State, United States of America, (B) retaining steel wall in Lake Goitzschesee, Sachsen-Anhalt, Germany, (C) rip-rap in Lake Arendsee, Sachsen-Anhalt, Germany.

Consequently, if the native riparian vegetation is absent or diminished in its spatial extent, composition and functioning due to residential, commercial and industrial uses, this will affect the occurrence of physically complex habitats such as CWD, CPOM (coarse particulate organic matter) and tree roots and the biota inhabiting these, including xylophagous macroinvertebrate taxa (Brauns et al., 2007b; Christensen et al., 1996; Czarnecka, 2016; Francis and Schindler, 2006). Furthermore, shoreline urbanization has been shown to significantly reduce the input of terrestrial insects inhabiting riparian vegetation to the water where they serve as a food source for fishes (Francis and Schindler, 2009).

In streams and rivers, how morphological degradation manifests itself depends on scale. Large rivers often exhibit types of shore degradation characteristic for lakes, such as docks, retaining walls and recreational beaches (Noges et al., 2016). With decreasing stream width, the importance of the riparian vegetation for a stream increases, providing essential habitats for the adult stages of aquatic insects, buffers from terrestrial runoff and sources of shade and organic matter input for aquatic organisms (Death and Collier, 2009; Harrison et al., 2000; Harrison and Harris, 2002). In small and mid-sized streams, impacts on the channel morphology as well as sedimentation and other types of stream bed modifications have been identified as major morphological stressors on physical habitat quality (Gieswein et al., 2017; Piggott et al., 2012; Townsend et al., 2008).

Effects of hydrological degradation on macroinvertebrate, macrophyte and fish communities

The hydrology of lakes is frequently affected by modified water levels and/or regulations of the seasonal regime of water level fluctuations (Evtimova and Donohue, 2016; Mjelde et al., 2013; Smith et al., 1987; Wilcox and Meeker, 1991). Artificial water-level fluctuations alter the taxonomic and trophic structure of benthic consumers (Evtimova and Donohue, 2016) and reduce benthic algal biomass and the density and taxonomic distinctness of benthic invertebrate assemblages (Carmignani and Roy, 2017; Evtimova and Donohue, 2014). Furthermore, high water-level fluctuations reduce the cover and density of macrophytes and

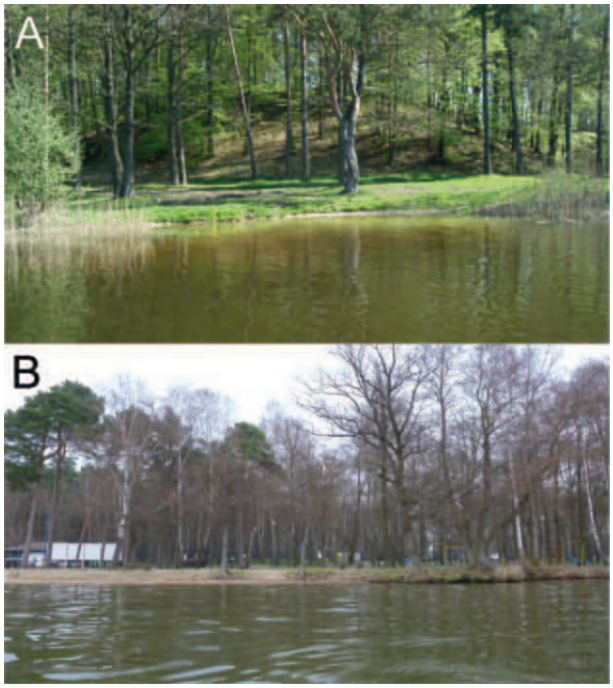

Fig. 2 Examples of soft shore modifications: (A) Recreational Beach in Lake Bystrzyno Wielkie, Poland, (B) Recreational Beach in Lake Arendsee, Sachsen-Anhalt, Germany.

Fig. 3 Examples of docks and marinas: (A) Docks in Lake Süßer See, Sachsen-Anhalt, Germany, (B) Docks in Lake Arendsee, Sachsen-Anhalt, Germany.

change the taxonomic composition of macrophyte communities by adversely affecting submerged macrophyte species propagating mainly via rhizomes, e.g. *Myriophyllum spicatum* and *Nuphar lutea*, and species sensitive to ice scour, e.g. isoetids (Carmignani and Roy, 2017; Hellsten and Mjelde, 2009; Mjelde et al., 2013; Smith et al., 1987). Stands of the reed *Phragmites australis* showed severe declines in area and vitality after an extreme flood in Lake Constance in 1999 (Ostendorp et al., 2003).

Another aspect of hydrological degradation in lakes, riverine lakes and large rivers, including many navigable water ways, is the presence of anthropogenic wave action. This is caused mainly by recreational and commercial boat and ship traffic and results in

increased mechanical stress on macrophyte, macroinvertebrate and fish communities, similar to the effects of human activities at recreational beaches (Gabel et al., 2011b, 2017; Weber et al., 2012). Increased wave action has been shown to decrease the time for feeding and to increase energy expenditures of benthic invertebrates and fish (Gabel et al., 2011a,b; Stoll et al., 2008). These effects tend to be more pronounced for native compared with non-native species, as shown for benthic invertebrates by Gabel et al. (2011a). High mechanical stress caused by anthropogenic wave action can lead to aquatic macrophytes either getting uprooted or parts of plant stems and leaves breaking off (Riis and Biggs, 2003; Schutten et al., 2004, 2005), thereby reducing macrophyte densities and influencing species composition.

Flow regulation structures, such as dams and weirs, are placed in many streams and rivers, with consequences for the hydrologic connectivity of lotic ecosystems (Bellmore et al., 2019; Dynesius and Nilsson, 1994; Fullerton et al., 2011). The loss of longitudinal, but also lateral, vertical and temporal, connectivity in streams has detrimental effects on many biota and their metapopulations, especially freshwater megafauna and fish species, impeding fish migrations and reducing genetic and taxonomic diversity (Fullerton et al., 2011; He et al., 2018; Turgeon et al., 2019). Furthermore, human alterations of the flow regime, i.e. changes in magnitude, frequency, duration, rate of change, and timing of flow, which are frequently measured via indicators of hydrological alteration (IHAs) (Olden and Poff, 2003; Schmutz and Sendzimir, 2018) can have significant impacts on macroinvertebrate, fish and aquatic plant community composition, population dynamics and food web structure (Bunn and Arthington, 2002; Haslam, 2006; Meißner et al., 2019; Mims and Olden, 2013; Palmer and Ruhi, 2019).

Types of multiple stressor interactions

Hydromorphological alterations are often accompanied by other stressors, leading to multiple stressor interactions affecting the population dynamics, diversity and food web structure of freshwater biota. In general, multiple stressors can interact in additive (sum, i.e. the simple addition of the effects), synergistic (i.e. larger than the sum of the effects) or antagonistic (i.e. smaller than the sum of the effects) ways (Cote et al., 2016; Jackson et al., 2016; Piggott et al., 2015). While freshwater ecosystems often integrate environmental effects over several scales and are hence sensitive to multiple stressors, only in recent years have increased efforts been made to comprehensively and systematically quantify these (Jackson et al., 2016; Lemm and Feld, 2017; Noges et al., 2016). How multiple environmental stressors interact in their effects on freshwater communities and how these can be optimally assessed for ecosystem management decisions are important fields of ongoing research (Craig et al., 2017; Noges et al., 2016). Ecological assessments based on biota must be calibrated based on well-defined stressor types, which can be single stressors, such as eutrophication or hydromorphological degradation, or alternatively multiple stressors (Hering et al., 2006; Karr and Chu, 1999). Hence, understanding the effects of specific stressors on metrics, i.e. assessment relevant characteristics of ecological communities, is vitally important to precisely describe stressor-response relationships and to develop statistically robust assessment tools (Johnson et al., 2018; Lemm et al., 2019; Miler and Brauns, 2020).

Interactive effects of hydromorphological degradation and other stressors on lake biota

In lentic ecosystems, eutrophication together with hydromorphological degradation are considered as the major ecological stressors (Miler and Brauns, 2020; Noges et al., 2016; Wetzel, 2001). The relative effects of eutrophication and hydromorphology on benthic invertebrates vary between the depth zones of a lake (Bazzanti et al., 2012; Pilotto et al., 2012; Saether, 1979; Wetzel, 2001). Invertebrates inhabiting the profundal zone, especially chironomids, strongly react to eutrophication pressures and have been used for several decades to reliably indicate eutrophication (Pinder, 1986; Saether, 1979; Wiederholm, 1980), with several early studies having established the ecological relationships between oxygen content and profundal invertebrate community composition (Brinkhurst, 1974; Lenz, 1925; Thienemann, 1918). The influence of hydromorphology relative to eutrophication increases from the profundal over the sublittoral to the eulittoral/infralittoral zone (Bazzanti et al., 2012; Pilotto et al., 2012).

Anthropogenic stressors have been shown to act on eulittoral invertebrate communities in a hierarchical manner and can be ranked according to their importance (Johnson et al., 2018; Miler and Brauns, 2020; Pilotto et al., 2015). In a study on 14 Italian lakes, Pilotto et al. (2015) identified that morphological alterations explained approximately 2.5 times more of the variation in eulittoral macroinvertebrate composition than eutrophication. Similarly, Miler and Brauns (2020) found a significantly higher influence of hydromorphological alterations compared with eutrophication on eulittoral macroinvertebrates. Previous studies on lakes in Finland, Germany and Ireland have found substantial effects of trophic state on eulittoral macroinvertebrate composition (Brauns et al., 2007a; Donohue et al., 2009; Tolonen et al., 2001; Tolonen and Hämäläinen, 2010). However, the focus of these studies was on hydromorphologically undisturbed sites and did not include sites with hard or soft shore modifications, in contrast to Pilotto et al. (2015) and Miler and Brauns (2020). Furthermore, Pilotto et al. (2015) and Miler and Brauns (2020) distinguished in their analyses between shared and unique variation and also used composite macroinvertebrate samples comprised of several meso-habitats that were representative of the overall habitat composition at a site (as opposed to habitat-specific samples in the other studies).

Habitat-scale effects (hydromorphological degradation) on eulittoral macroinvertebrate communities are often more significant than larger scale effects, e.g. effects at the catchment scale (eutrophication) (Johnson et al., 2004; Johnson and Goedkoop, 2002; McGoff and Sandin, 2012). This highlights the importance of scale for analyzing multiple pressures and their effects on biota.

Trophic effects on eulittoral macroinvertebrate communities have been shown to be nested within meso-habitats, i.e. they are more influential when analyses are stratified by habitat types such as stones, sand, macrophytes etc. (McGoff and Sandin, 2012; Tolonen et al., 2001; Tolonen and Hämäläinen, 2010).

Acidification is another important stressor for lake biota, especially in regions with granite rock geologies, for example in Scandinavia and the United Kingdom (Johnson et al., 2018; Muniz, 1990; Schartau et al., 2008), Canada and the Northeastern United States (Keller et al., 1999; Lacoul et al., 2011; Schindler et al., 1989) and in former mining pits in Germany (Klapper et al., 1996; Nixdorf, 1999; Nixdorf et al., 2005). Depending on lake geology, acidification can become the dominant stressor for macroinvertebrate communities and can interact with other stressors, e.g. hydromorphological degradation and eutrophication (Johnson et al., 2018).

Interactive effects of hydromorphological degradation and other stressors on stream biota

Noges et al. (2016) have argued that in rivers and streams, hydromorphological stress is a more important stressor than eutrophication due to high benthic-to-pelagic habitat ratios, and low water retention times and directional flows. The presence of flowing water reduces the environmental impacts of nutrients (and other chemical substances), while it increases the importance of hydraulic stress (Noges et al., 2016; Wetzel, 2001). While hydrological stressors are highly localized in lakes, for example at wind-exposed shore-lines, the nature of uni-directional flow in rivers strongly affects geomorphological processes, e.g. erosion and sedimentation, along the whole lotic system (Lampert and Sommer, 2007; Strayer and Findlay, 2010; Wetzel, 2001). The higher benthic-to-pelagic habitat ratios in rivers compared with lakes lead to a higher influence of morphological stress on biota in rivers than in lakes (Noges et al., 2016). This also explains the need to stratify stressor analyses in lakes by water depth, with for example macroinvertebrates only reliably indicating hydromorphology in the eulittoral zone (Bazzanti et al., 2012; Pilotto et al., 2012).

Overall, the total impacts of stressors (indirect and direct) act hierarchically on stream biota, depending on spatial scale (Frissell et al., 1986), and can be ranked in their importance as decreasing from watershed over stream and reach to habitat scales (Dahm et al., 2013; Meißner et al., 2019; Villeneuve et al., 2018). Catchment land use often comprises a varied mix of stressors, such as agriculture and urbanization, and hence encompasses and overrides more specific stressors at finer spatial scales, e.g. hydromorphology (Dahm et al., 2013; Leps et al., 2015; Meißner et al., 2019). A study of mountain streams in Germany found total (i.e., direct and indirect) effects on macroinvertebrates decreasing from catchment-scale land use over stream-scale hydrology and reach/local-scale physical habitat structure to local-scale physico-chemistry (Meißner et al., 2019). However, focusing on the direct (unique) effects, hydrology had the largest influence on macroinvertebrate metrics (Meißner et al., 2019). The effects of site-scale stressors on macroinvertebrate communities can also differ between stream types: Villeneuve et al. (2018) showed that in hard water (lime stone) streams hydromorphology (and land use) constituted major stressors for macroinvertebrate assemblages compared with physico-chemical variables, whereas physico-chemistry was the dominant stressor in soft water streams.

Interacting effects of multiple environmental stressors on benthic macroinvertebrates have been determined in lotic mesocosm experiments (Beermann et al., 2018; Elbrecht et al., 2016; Matthaei et al., 2010). Using experimental streams, the effects of sediment addition and flow reduction on benthic macroinvertebrates and algae were twice as common as nutrient enrichment, with additive effects of the former two stressors (Matthaei et al., 2010). Similarly, fine sediment addition was identified to be a more significant stressor than nutrient enrichment for macroinvertebrates, with both stressors acting in additive, antagonistic as well as synergistic ways on macroinvertebrates, depending on the respective analyzed metrics and traits (Townsend et al., 2008; Wagenhoff et al., 2011). Elbrecht et al. (2016) found "triple" additive effects of nutrient enrichment, sediment addition and reduced flow velocity on several disturbance-sensitive stream macroinvertebrate taxa. Field survey data from European lowland rivers show that additive interactions of hydromorphological, physico-chemical and land use stressors on benthic macroinvertebrates prevailed with 80% of the studied interactions (Lemm and Feld, 2017). Antagonistic and synergistic interactions were, in accordance with Noges et al. (2016), approximately equally common (Lemm and Feld, 2017). Ortho-phosphate and fine sediment addition were the most commonly found interactions and most of these were synergistic in nature (Lemm and Feld, 2017). Mechanistically, sediment addition affects macroinvertebrate communities more directly, whereas the effects of nutrient enrichment are indirect, via an increase of the stream phytobenthos biomass (Doledec et al., 2006; Wagenhoff et al., 2011; Yuan, 2010). Since the latter is also impacted by a multitude of other environmental factors, the relative strength of both stressors and their interactions can display considerable variability (Lemm and Feld, 2017; Wagenhoff et al., 2011; Yuan, 2010).

Invasive species

Invasive species influence and modify the effects of hydromorphology on aquatic biota in several ways. Firstly, in many lakes and streams, invasive macroinvertebrates and macrophytes often constitute a major component of biotic communities and often significantly modify native biological structures and impact the ecological functioning of aquatic systems (Magliozzi et al., 2020; Schultz and Dibble, 2012; Strayer, 2010). For the biotic assessment of stressors, such as hydromorphology, usually the determination of the reference condition of a specific water body type is required (European Commission, 2000; Karr and Chu, 1999). This complicates the biotic assessment of hydromorphology in more densely populated regions impacted by human pressures, where water bodies are connected by navigable water ways or where vessels carrying invasive species are routinely transported between water bodies (Leuven et al., 2009; Panov et al., 2009; Rothlisberger et al., 2010).

Secondly, invasive macrophyte species can constitute littoral or in-stream habitats or form part of the riparian zone at lake shores and stream banks (Haslam, 2006). The condition of the riparian zone (together with the eulittoral zone) is generally considered when assessing hydromorphological degradation (Miler et al., 2015; Strayer and Findlay, 2010). In Europe and North America, knotweeds (*Reynoutria* spp.) are widely distributed invasive plants colonizing the riparian zone and have been shown to be catalysts for streambank erosion and to negatively impact plant and arthropod species richness in riparian zones (Colleran et al., 2020; Gerber et al., 2008). In North America, the European subspecies of the reed *Phragmites australis* is an aggressive invader that grows more densely than the North American subspecies and has replaced native vegetation in many regions (Kettenring et al., 2012; Schultz and Dibble, 2012). The effects on aquatic fauna are however less clear and negative as well as beneficial effects have been reported (Holomuzki and Klarer, 2010; Kettenring et al., 2012). The invasive benthic zebra mussel (*Dreissena polymorpha*) has been shown to increase the physical complexity of bottom substrates in lakes and rivers and consequently influences benthic invertebrate community composition (Burlakova et al., 2012; DeVanna et al., 2011; Ward and Ricciardi, 2007). In addition, the biodeposition of feces and pseudofaeces by *Dreissena polymorpha* affects the structure of benthic invertebrate communities and provides a food source for example for Amphipoda (DeVanna et al., 2011; Gergs et al., 2011; Mörtl and Rothhaupt, 2003). Furthermore, many floating and submerged aquatic macrophytes outcompete native vegetation and can form dense stands or floating mats, thereby changing the hydromorphology of the littoral zone and the conditions for other aquatic biota, such as macroinvertebrates (Kovalenko et al., 2010; Schultz and Dibble, 2012; Stiers et al., 2011). In streams, the presence of macrophytes is controlled by water velocities, discharge and sedimentation, but macrophytes also modify these feedback relationships (Franklin et al., 2008; Haslam, 2006; Miler et al., 2012; O'Hare, 2015). Consequently, the establishment of dense and dominant invasive macrophyte stands, such as *Myriophyllum aquaticum* (Kuehne et al., 2016) and *Egeria densa* (Collier et al., 1999; Yarrow et al., 2009) can change macrophyte community composition, impede water flow and cause flooding events (Franklin et al., 2008; Yarrow et al., 2009).

Restoration projects

Stream hydromorphology restoration efforts in recent decades often consisted of geomorphic restructuring that reconfigures the shape of the channel and depends on stream corridor and watershed form, e.g. straight/meandering/braided/anastomosing streams, sinuosity (establishment of meanders) and stream-type appropriate cross-sections and depth to width ratios (Palmer et al., 2014; Poppe et al., 2016). This also includes changes to in-stream structures, e.g. the creation of riffle-pool sequences, coarse woody debris addition, diversification of bed materials and elevation patterns, and the re-structuring of the stream bank to a natural slope, height, shape, riparian vegetation and substrate composition (Harrison and Harris, 2002; Kail et al., 2007; Poppe et al., 2016). There is an increasing trend toward process-based river restoration that aims to reestablish natural flow and sediment regimes which in turn affect the environmental conditions, ecosystem structures, as well as the biotic and ecosystem processes in rivers (Beechie et al., 2010; Booth et al., 2016; Palmer and Ruhi, 2019). According to the current literature, the majority of river hydromorphology restoration projects worldwide has been conducted in Europe, the United States, Canada, Australia and Japan (Brierley and Fryirs, 2009; Friberg et al., 2016; Nakamura et al., 2006; Palmer et al., 2007; Pike et al., 2010). Lake shore restoration projects are increasingly conducted in recent years, but studies are still rare compared with stream hydromorphology restoration efforts (Ostendorp et al., 1995, 2020).

Restoring hydromorphological connectivity by removing dams, weirs, culverts and other obstacles impeding the free flow of water and sediment is another major component of the restoration of hydromorphological functioning (Bellmore et al., 2019; Palmer and Ruhi, 2019). These restoration efforts have primarily occurred in Europe and North America, with only few projects conducted in Africa, Asia and South America (Al-Zankana et al., 2020; Koebel et al., 2014; Palmer et al., 2014). In North America, there has been a focus on dam removal projects in recent years with the removal of larger dams, for example in the Pacific Northwest, such as the Elwha river dams (East et al., 2015; Morley et al., 2020) and the planned removal of the Klamath river dams, but also smaller dams all over the United States (and to a lesser extent in Canada) that are now obsolete remnants from previous industrial activities (Bellmore et al., 2017; Foley et al., 2017a,b). In contrast, worldwide, but largely concentrated in Africa, South America, Southern Asia, the Mediterranean and the Middle-East, there is an ongoing dam construction boom (Zarfl et al., 2015). Additionally, the monitoring and evaluation of the effectiveness of restoration efforts is often insufficient (Al-Zankana et al., 2020; Kail et al., 2007; Roni et al., 2008; Stoll et al., 2014). For the evaluation of the success of stream hydromorphology restoration projects, the most common criticisms are (1) the frequent absence of Before–After–Control–Impact (BACI) study designs, (2) sampling often only for one season, (3) infrequently applied multi-habitat sampling and (4) rare inclusion of macroinvertebrate metrics other than taxa richness and diversity (Al-Zankana et al., 2020). This observed lack of a proper methodology to assess effectiveness might contribute to the reported highly variable success of stream restoration efforts on fish, benthic invertebrates, and macrophytes that has been attributed to confounding stressors, e.g. nutrient pollution, or the characteristics of the regional species pool (Al-Zankana et al., 2020; Haase et al., 2013; Kail et al., 2015; Stoll et al., 2014).

Conclusions

In summary, hydromorphological stressors affect freshwater macroinvertebrates, macrophytes and fish in a multitude of ways, depending on the water body type (lotic/lentic), size and morphology (e.g. shallow lakes, deep lakes, ponds, rivers, streams, creeks etc.) and other environmental characteristics (Fig. 4). Interactions between hydromorphology and other environmental stressors,

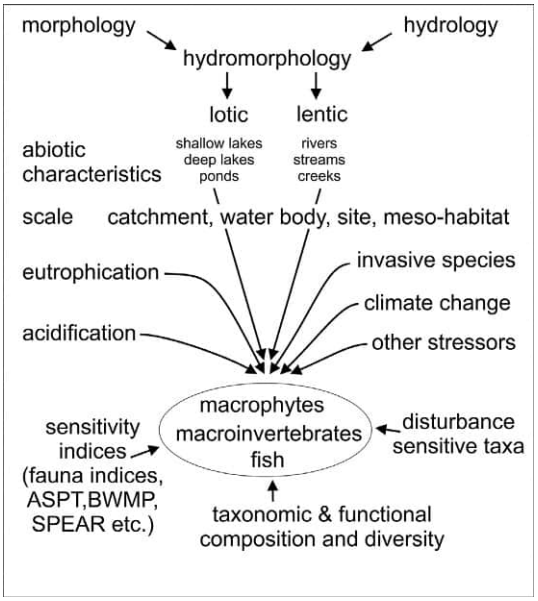

Fig. 4 Schematic overview of hydromorphological and other pressures acting on lake and stream biota and their assessment.

most importantly eutrophication/nutrient enrichment, are specific to the studied biota and water bodies. The scale at which the environmental stressor acts (eutrophication: catchment scale, hydromorphology: meso-habitat scale) is important as well as the type of interaction (additive, synergistic, antagonistic). Invasive species can constitute an important component of hydromorphological degradation, e.g. as riparian or aquatic vegetation. In addition, they can modify the effects of hydromorphological degradation or complicate its assessment. Numerous hydromorphological restoration projects have been conducted to date, but their scope and geographical location has been comparatively limited so far (mainly to Europe, the United States, Canada, Australia and Japan). Furthermore, the monitoring and evaluation of the effectiveness of restoration projects needs to be further improved. With a world-wide increasing human population, hydromorphological degradation will remain an important stressor for freshwater biota and interactions with multiple other stressors are receiving increasing attention and will most likely increase in importance, for example in the context of global anthropogenic pressures such as aquatic invasions and climate change.

Knowledge gaps

- Effectiveness of restoration projects, especially of lake shores, but also streams and rivers
- Better disentanglement of the effects of multiple stressors (hydromorphology, eutrophication, acidification etc.) and quantification of unique and shared variation of stressor effects on macroinvertebrates, macrophytes and fish especially in lakes, but also streams and rivers
- Increased and more specific incorporation of functional metrics and functional diversity in the assessment of hydromorphological stress with macroinvertebrates, macrophytes and fish
- Better quantification of the relationships between physical habitat survey parameters and biotic assessment metrics (macrophytes and macroinvertebrates), especially in lakes

See Also: Human pressures and management of Inland Waters: Hydromorphology: Overview and Assessment Methods; Hydropower: Case Studies in Sustainability

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Relevant websites

https://www.gewaesser-bewertung-berechnung.de and https://www.gewaesser-bewertung.de—Biotic freshwater assessment systems in Germany (in German).
https://professionnels.ofb.fr/en/node/654 and http://www.river-restoration.onema.fr/content/physical-restoration-rivers—Collections of river hydromorphology restoration examples in France.
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Hydromorphology: Case Studies

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This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Anthropogenic Man-made; relating to, or resulting from the influence of human beings on nature.
Biodiversity Biological diversity in an environment as indicated by numbers of different species of plants and/or animals.
Channelization Method of river engineering that widens or deepens rivers to increase the capacity for flow volume at specific sections of the river.
Dam A barrier constructed to hold back water and raise its level, forming a reservoir used to generate electricity or as a water supply.
Flood plain An area of low-lying ground adjacent to a river, formed mainly of river sediments and subject to flooding.
Hydromorphological modification Change to the physical habitat, and/or a water bodies' natural functioning (i.e. water flow dynamics).
Invertebrate Any animal that lacks a vertebral column, or backbone, in contrast to the cartilaginous or bony vertebrates.
Irrigation The artificial process of applying controlled amounts of water to land to assist in production of crops.
Littoral zone Part of a lake, river or stream that is close to the shore and is illuminated.
Riparian zone Interface between land and a lake, river or stream.
Water abstraction The process of taking water from any source, either temporarily or permanently for irrigation, industry, recreation, flood control or treatment to produce drinking water.
Wetland Distinct ecosystem that is flooded by water, either permanently or seasonally.

Introduction

Inland waters worldwide are subject to major modifications, such as morphological alterations, straightening and canalization, the disconnection of flood plains, water abstractions and water flow regulations by dams, weirs, sluices or locks. The aim of this article is to exemplify a range of hydromorphological pressures under a series of case study headings and illustrated by a variety of key examples, highlighting the different pressure types comprising the array of main physical alterations of water bodies modifying their shores, riparian and littoral zones, water level and flow on a global scale. It also provides examples for possible and already implemented restoration measures for hydromorphologically altered waters.

Case study 1: Morphological alterations of shore zones

Freshwater shores have been modified by humans in a variety of ways over the last centuries (Strayer and Findlay, 2010). While these zones typically are highly diverse in terms of habitats and consequently provide shelter for many faunal communities, this heterogeneity and high biodiversity is typically diminished or even lost when these zones are altered morphologically (Brauns et al., 2011; Christensen et al., 1996; Elias and Meyer, 2003).

Modifications of shore structures, such as the construction of erosion control measures, are usually accompanied by massive reductions or even clear-cutting of natural habitats, such as removal of shoreline vegetation, littoral macrophytes and reed belts. A typical feature of anthropogenically altered shore sites is the absence of riparian woodland, which leads to a reduction of coarse woody debris (CWD) and tree roots within the lake (or river) and thus a loss of important habitats and ecosystem processes

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(Brauns et al., 2011; Porst et al., 2012). These changes in habitat structure, which accompany morphological alterations in shore zones, affect different parts of the freshwater community, both fauna and flora, in different ways.

In a study by Christensen et al. (1996) on 16 north temperate lakes in the area of Wisconsin, United States, the relationships among coarse woody debris, riparian vegetation, and shoreline residential development was assessed. This study related the density of CWD within lakes to the tree density and thus the density of residential housing along the shore, with lakes situated in less populated areas showing higher densities of woody remains in lake shore zones. The observed loss of important habitats such as tree roots, tree branches and leaves in turn has direct effects on littoral faunal communities in lakes subject to residential development (Brauns et al., 2011).

Several studies carried out in lakes across Europe acknowledged the negative effect of morphological alterations in littoral shorelines on their macroinvertebrate communities (Brauns et al., 2007; McGoff et al., 2013; Porst et al., 2019). In a pan-European study across 51 European lakes situated in Denmark, Finland, Germany, Italy, Ireland, Sweden and Great Britain, comprising a gradient of nutrient states, macroinvertebrate biodiversity was detected to decline drastically when lake shore zones were altered (Porst et al., 2019). Types of modifications at lake shores investigated ranged here from "hard alterations," comprising retaining walls, rip raps or boulders to "soft alterations," such as recreational beaches and riparian clear cutting or grassland (Fig. 1). These hard and soft modifications were compared with lake shores, which showed a (near) natural state, such as unmodified shore stretches, at each lake under investigation. The observed decline in macroinvertebrate biodiversity, which was apparent across all four European demographic regions, was shown to be a result of the reduced variety of habitats in morphologically altered shore types and here especially the loss of complex habitats such as macrophytes. While at natural lake shores a great number of habitat types such as macrophytes, sand, stones, woody debris or tree roots is usually present, morphologically altered shores are typically characterized by one to two habitats only (Elias and Meyer, 2003; Radomski and Goeman, 2001).

In altered lake shores, both soft and hard, structurally complex habitats such as macrophytes or tree roots are typically replaced by structurally less complex habitat types like sand or stones (Miler et al., 2015; Porst et al., 2012, 2019). At soft altered shores such as beaches or grazing pastures/grassland, the most dominant or often only available aquatic habitat sand is quite unfavorable for many macroinvertebrate species, as it cannot provide many ecological niches or shelter from predators or wave-action and does not offer a great variety of food-sources. This structurally very simple habitat, which has been shown to be the most dominant at most morphologically altered shorelines across European lakes, is often dominated by only a few taxa groups (e.g., in the pan-European study: fly larvae and oligochaetes). While this decrease in biodiversity is quite dramatic, it is furthermore accompanied by extremely high densities of fewer species in altered lake habitats (McGoff et al., 2013; Porst et al., 2012, 2019). More sensitive macroinvertebrate groups such as caddisflies, crustaceans, dragonflies, gastropods and mayflies typically get reduced in their densities and diversity or might be even totally absent from modified shorelines (Porst et al., 2012, 2019). Morphological shore alterations consequently also have a strong influence on macroinvertebrate food-webs, by changing their structures and trophic basis (Brauns et al., 2011). The comparatively low diversity of food sources and associated consumers at morphologically altered shorelines leads

Fig. 1 Shore embankment (retaining wall) at Lake Müggelsee, Berlin, Germany.

to a reduction of the number of trophic links in macroinvertebrate food webs of up to one order of magnitude lower at morphologically altered shorelines when compared to natural lake shores (Brauns et al., 2011).

Using a subset of the European lakes studied by Porst et al. (2019) for the study mentioned above, McGoff et al. (2013) found clear evidence, that macroinvertebrate communities of European lakes are being homogenized by lake shore development on a whole lake-level. The study showed that morphological alteration of lakeshores and near shore, and the surrounding habitats have an even greater effect on macroinvertebrate community diversity than nutrient enrichment.

Fish assemblages seem to be equally negatively affected by anthropogenic alterations to shore zones (Lewin et al., 2013), as further demonstrated in a study of 17 north temperate lakes in the area of Wisconsin, United States (Jennings et al., 1999). The study, which compared littoral fish assemblages of lakes subject to extensive residential and recreational development, found that different types of erosion control structures such as riprap and retaining walls had a strong influence on fish biodiversity in the shore zone, similar to the studies on macroinvertebrates (McGoff et al., 2013; Porst et al., 2019).

As described above, anthropogenic shoreline alterations have a strong effect on lake ecology, including lake fauna and flora and, thus, lake ecosystem state. In order to restore morphologically altered lakes and lake ecological status, conservation should focus on preserving the structural integrity of littoral zones. Potential restoration measures, as for example demanded by the EU Water Framework Directive (EEC, 1992) in order to reestablish good ecological state of lakes in the European Union, include the re-establishment of coarse woody debris, reed stands and root habitats in lake shores. These lake restoration measures have already proven to be a cost-efficient method to improve degraded lakeshores (Sondergaard and Jeppesen, 2007) and consequently the ecological state of lakes.

Case study 2: Channelization of running waters

During the last 2000 years, many rivers and streams have been subject to engineering measures, which typically include manmade morphological changes to their course, their river features, or flow regime, with the purpose to result in some defined benefit (Brooker, 1985; Hohensinner et al., 2018). Channelization of rivers or streams usually has the purpose of either diverting water for irrigation, draining wetlands/floodplains for agriculture, increasing "usable" land, improving river channels for navigation or preventing flooding (Brookes, 1985). These hydromorphological changes to natural river courses and their floodplains, however, have wide implications on their ecology (Brooker, 1985). General environmental effects of river channelization include the alteration of the natural flow regimes, habitat loss and loss of habitat complexity within the river or stream, loss of floodplains and associated wetlands and consequently the decline of natural biodiversity (fauna and flora) within the river system (Wilcock and Essery, 1991). While many rivers and streams were still actively engineered and channelized during the last century, in recent decades the focus has shifted towards restoring previously channelized running waters to their natural state as free flowing rivers or streams (Brookes, 1990; Koebel Jr et al., 2014).

One impressive example of a river, which has been subject to substantial channelization measures, with the purpose to prevent extensive flooding, is the Kissimmee River located in Central Florida. The river, which belongs to the Kissimmee Basin forming the headwaters of Lake Okeechobee and the Everglade (the Kissimmee-Okeechobee-Everglades (KOE) system), formerly meandered freely over a stretch of about 166 km from Lake Kissimmee to Lake Okeechobee (Koebel Jr, 1995). Its natural floodplains reached a width of up to 3 km in the past and were inundated for long periods of time during times of heavy seasonal rainfall (Toth et al., 1998). In its natural state, diverse animal and plant communities characterized the river and its floodplains, which included at least 39 species of fish and 38 species of water birds (Koebel Jr, 1995). Prolonged flooding of the Kissimmee basin and surrounding residential areas in the late 1940s (caused mainly by hurricanes), lead to a public outcry demanding flood protection measures in the area.

Consequently, between 1960 and 1971, this once beautiful meandering river was transformed into a 90 km-long, 10 m-deep and 100 m-wide canal, known as the C-38 canal, to provide flood control for central and southern Florida. While these measures controlled the flooding well, about 60% of the rivers' wetland habitats were lost and its natural hydrological cycle was greatly modified, with the river placed under stage-fluctuation management (Harris et al., 1995). This led to a dramatic decline of the river systems natural biodiversity in terms of vegetation, invertebrates, fish, wading birds and waterfowl (Harris et al., 1995; Koebel Jr, 1995). Studies reported a 90% decrease in waterfowl and a 70% decrease in Bald Eagle (*Haliaeetus leucocephalus*) populations in the Kissimmee River Basin (Koebel Jr, 1995). Biologists predicted the devastating ecological consequences of the channelization project already while the engineering measures were still in progress. Their concerns have since been confirmed, and there is wide consensus that the channelization project has damaged the river and its floodplains greatly, which among other things led to major environmental problems in the Kissimmee Valley and Lake Okeechobee.

After the Florida Legislature passed the Kissimmee River Restoration Act in 1976, three major restoration and planning studies were carried out, which resulted in a dechannelization plan (Koebel Jr, 1995), and finally the Kissimmee River Restoration Project. The main purpose of the project is to restore ecological integrity to the Kissimmee river-floodplain ecosystem (Koebel Jr et al., 2014). After an extensive planning phase, the Kissimmee River Restoration Project began in 1999 by backfilling about 14 km of the C-38 canal, with the purpose to restore the river's natural flow patterns. Today, three restoration phases have been finalized, and near natural water flow has been re-established to about 65 km of the meandering Kissimmee River. As a result, seasonal rains and changing flow patterns once again periodically inundate the floodplains in the restored area. The Kissimmee River Restoration Project is expected to restore the flow conditions to about 70 km of the historic river channel and to reestablish about 104 km^2 of

Fig. 2 The Kissimmee River was straightened to drain surrounding swampland and control the flooding within the region (left before and right after restoration). Found at: https://www.npr.org/2014/10/19/356647396/the-kissimmee-a-river-recurved—Courtesy South Florida Water Management District.

the rivers' floodplain ecosystems (Fig. 2). This will include 11,000 ha of wetland habitat, which is expected to benefit over 320 species of fish and wildlife (Koebel Jr, 1995).

The Kissimmee River clearly illustrates the change from a pure flood-controlled management of a river system to a management taking into consideration conservation issues such as ecological integrity and biodiversity protection.

Case study 3: Dams and weirs

Together with channelization of rivers and streams, damming is one of the most common hydromorphological alterations found in river systems around the world (McCartney, 2009; Van Looy et al., 2014). Worldwide, more than 45,000 large dams exist and more are meant to be built in the future (McCartney, 2009).

Dams and weirs are usually built to support water supply, particularly for irrigational purposes, to generate hydropower, control floods or for navigational purposes. However, the construction of firm, solid walls built across a river valley or catchment to block the flow of the river, leads to a great variety of negative effects, such as landslides, a great deal of ecological problems, together with a general decline in water quality within the river systems and floodplains. While each dam's environmental impact is very unique and dependent on the dam's structure, the characteristics of the resident biota, the local climate and geomorphology, a variety of negative effects of the construction of these very sturdy structures within a river system cannot be denied (McCartney, 2009). Dam construction has severely altered rivers and their wetlands around the world, which has global implications on river and, especially, wetland biodiversity (Nilsson et al., 2005). Dams always alter the flow regime of a river greatly. The robust structure prevents the movement of sediments and nutrients downstream and causes slower flows upstream, which in turn leads to increased settling of sediments in this part of the river and is accompanied by more unpredictable flows downstream of the dam (Wu et al., 2019). Additionally, annual flood-pulses are also disturbed by dams or weirs, which severely interrupt the exchange of nutrients between the river and its floodplains (Benke et al., 2000; Wu et al., 2019). Other negative effects of dams are the interruption of fish migration within the river system, the loss of many foraging and spawning habitats within the river floodplains and a general change in plant and animal communities, often resulting in lower biodiversity below the dam (McCartney, 2009; Wu et al., 2019).

The Yangtze River, the largest river in East Asia and the 3rd longest in the world, is the most important river in China, on which more than 400 million people depend (Kaifeng et al., 2013). To facilitate irrigation, to generate hydropower, to store water and to manage flooding in the area, between 1950 and 2010 more than 50,000 dams have been built in the Yangtze River basin (CCYRA, 2006, Yang et al., 2011). Since 2012, the Three-Gorges-Dam (TGD), located in the Yangtze River, is presently the largest dam and hydropower project in the world (Fig. 3). The benefits and costs of this huge dam have been under debate since the planning stage and have continued since the dam became fully functional (Zhang et al., 2012). Especially the environmental and ecological effects of the TGD on the ecosystem of the Yangtze River and here especially its biodiversity, have been of increasing concern in recent years (Wu et al., 2004, 2019). The construction of the dam and its reservoir has implications on the entire river system, both upstream and downstream (Fu et al., 2010), as well as associated wetlands, floodplains and terrestrial systems (Wu et al., 2004). Quite a number of studies have been carried out looking at the environmental effects of the TGD on its faunal communities. Research observing the implications of the changed hydrological regime and movement of sediments and nutrients along the river in the TGD reservoir region, for example indicated an increase in densities/biomass together with a decrease in biodiversity of many macroinvertebrate taxa downstream of the TGD (Wu et al., 2019), similar to the effects of morphological lake shore alterations.

Very devastating effects were, furthermore, found for many fish species inhabiting the Yangtze River. The main reasons for the observed dramatic changes in different fish populations are explained by the obstruction of migratory routes, with no effective mitigation through construction of fish passes (Shi et al., 2015), habitat fragmentation, changing from lotic to lentic water in

Fig. 3 In this picture released by China's Xinhua News Agency, water flows out from sluiceways at the Three Gorges Dam on the Yangtze River near Yichang in central China's Hubei Province. Fount at: https://thehimalayantimes.com/world/china-blasts-dam-to-release-floodwaters-as-death-toll-rises—China's Xinhua News Agency—Wang Gang/Xinhua via AP.

impounded areas, and changes in hydrological flow regimes, especially in downstream reaches (Wu et al., 2004, 2019; Zhang et al., 2012). An example for these adverse effects of the construction of the TGD on fish populations is the drastic decline of catches of the four "major carps" (known as grass carp *Ctenopharyngodon idella*, silver carp *Hypophthalmichthys molitrix*, black carp *Mylopharyngodon piceus* and bighead carp *Aristichthys nobilis*), which naturally inhabited the middle and lower stretches of the Yangtze River. These commercially very important species grow and mature in the Yangtze River floodplains and migrate into the river between April and July to spawn, when temperatures increase and water levels rise during the flooding season. Larvae and juveniles enter the nursery areas in the flood plains again when transported downstream by the river flow (Zhang et al., 2012). Through the construction of the TGD, most of the natural spawning areas of the carps were lost and temperature and flow conditions changed, which resulted in a dramatic decline of the juvenile carp that had drifted into the floodplain below the TGD (Xie et al., 2007; Zhang et al., 2012). Negative effects of the changed hydrological regimes associated with the construction of the TGD were furthermore described for plant communities in the drawdown area of the dam (Wang et al., 2014). As a consequence of the hydrological alteration in the area, the number of vascular plant species in the Three Gorges reservoir declined noticeably from 175 to 127 after the full impoundment (Wang et al., 2014). The Yangtze River Dolphin (baiji; *Lipotes vexillifer*) was declared extinct in 2007 probably because of pollution, unsustainable fishing and a high shipping pressure in the river. The Three Gorges Dam is assumed to have added an additional pressure to the already highly endangered species, by further reducing its natural living space through the alteration of river flow downstream, and facilitating an increase in ship traffic along the Yangtze River (Wu et al., 2019).

Additionally, the impoundment of the 660 km long reservoir behind the TGD has almost certainly led to an increase of seismic activity in the region (Tang et al., 2019). After the filling of the reservoir in 2003, the number of earthquakes per year increased from approximately two per year to approximately 14 earthquakes per year after full impoundment of the reservoir in 2008, together with hundreds of landslides (Tang et al., 2019).

Despite providing water for drinking, irrigation and electricity, the TGD shows impressively the implications the constructions of dams and weirs can have on rivers, streams and associated floodplains. Dams are one of the most noteworthy anthropogenic interventions in the hydrological cycle (McCartney, 2009) and have (had) severe impacts on freshwater systems through the disruption of physicochemical and biological processes worldwide. Plans for new large dams continue, especially in tropical regions (Vörösmarty et al., 2010; Zarfl et al., 2015). In the planning and design of most already existing dams, potential environmental issues did not play a major role, but environmental awareness has led to more holistic planning and management of dams in recent decades in order to decrease the most damaging effects of dams. These should include, among other things, the implementation of effective fish passages in the design of all dams (big or small) to ensure river connectivity and migratory fish conservation.

Case study 4: Water level changes

Many lakes worldwide are experiencing changes or fluctuations in water levels, which severely affect their hydrological regimes and consequently their inherent natural faunal and floral communities (Baumgartner et al., 2008; Wantzen et al., 2008). Changes in water levels can be caused by actively abstracting water from the lake, for example for irrigational purposes or drainage. These anthropogenic changes to lake hydrology can be augmented further by temperature changes or other climate change effects (Coe and Foley, 2001; Coops et al., 2003). Excessive water abstraction from lakes together with changes in regional hydrological budgets will especially affect shallow and/or groundwater-fed lakes, as their hydrological budget is directly dependent on changes in groundwater levels.

A dramatic example of the influence of increased water consumption for irrigation and drainage and a grown water demand of a growing population on water levels is Lake Chad (Fig. 4). The Lake Chad Basin is a large, hydrologically closed drainage system in West Sahelian Africa (Coe and Foley, 2001). For the states of Chad, Cameroon, Nigeria, Niger, the Central African Republic and Libya the Lake Chad Basin signifies an important area both economically and environmentally, as it contains vast pasture and arable land together with rich fish stocks. The water levels of Lake Chad largely depend on the inflow from rivers, particularly the Chari/Logone River from the south and, seasonally, the Komodugu-Yobe River from the northwest, together with smaller tributaries and groundwater discharge (Lemoalle et al., 2012). Lake Chad and the Chari/Logone river system, which transports 90% of the runoff generated in the Lake Chad Basin, are significant water resources for the local multi-ethnic population of about 38 million people (GIZ, 2015). The lake itself is shared by Chad, Cameroon, Nigeria and Niger. It is situated 250 m above sea level and has an average depth of only 7 m. Owing to its natural monsoon climate and variable rainfall patterns together with its shallowness, Lake Chad has experienced natural seasonal and inter-annual water level fluctuations in the past. However, the warming climate and a general expanding desertification in the Sahel region have led to a dramatic decrease in minimum lake area of only 1350 km^2 compared with former average dry season extent of about 10,000 km^2 (Coe and Foley, 2001). Since the early 1960s the Northern Africa Sahel region has faced several devastating droughts, as prolonged rainfall events such as the monsoon rains, which typically occur between June and August, have decreased substantially (Coe and Foley, 2001). As the region becomes drier, the use of water, particularly for irrigation, is increasing (Coe and Foley, 2001). While agricultural water use has dramatically increased as a response to a drier climate and the discharge from the Chari/Logone river system has decreased by almost 75%, water levels of Lake Chad have been reduced enormously. Consequently, Lake Chad has shrunk in size by about 90% since the 1960s. The study by Coe and Foley (2001) on human and natural impacts on the water resources of the Lake Chad Basin suggested that, while climate variability controlled the fluctuating water inflow to the Basin and Lake Chad, water abstraction for irrigational purposes and drainage accounted for about 50% of the decrease in lake area since the 1960s/1970s. With a drier climate, the problem is expected to worsen in the years to come as the population within the Lake Chad Basin is growing and the water demand for irrigational use is increasing.

As a response to the ever-worsening situation in the Lake Chad Basin, in 1964 the intergovernmental organization Lake Chad Basin Commission (LCBC) was founded by the lake's bordering states Chad, Cameroon, Niger and Nigeria. The Republic of Central Africa joined the organization in 1996 and Libya was admitted to join the LCBC in 2008. The commission's main aim is to regulate the use of the waters of Lake Chad and the Lake Chad Basin for irrigational, farming and drinking water purposes and with regard to fisheries. It has the mandate to conserve natural resources, monitor and coordinate cross-border water projects, regulate and control water use and resolve disputes in the Lake Chad Basin region. As a part of this, the LCBC has also attempted to find ways to reverse the drastic decline in the size of the lake. Its mandate also includes advising member states on dealing with the effects of climate

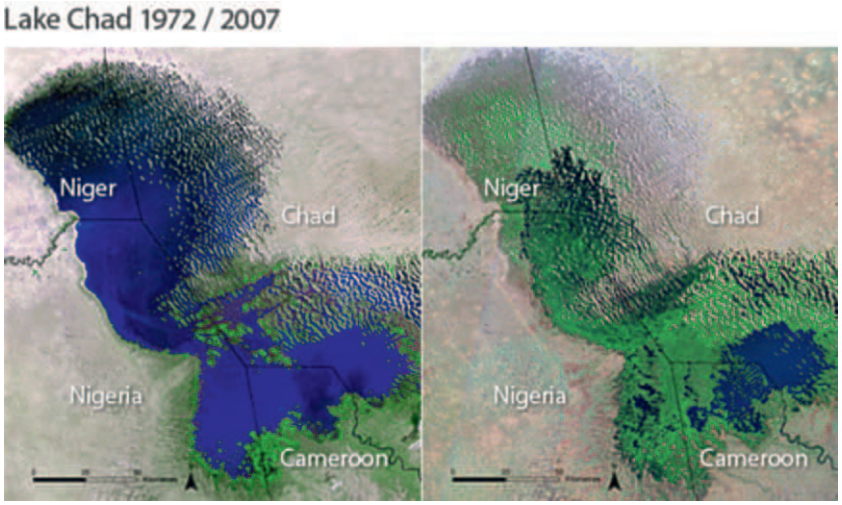

Fig. 4 The pictures show the area covered by Lake Chad in 1972 (left) and 2007 (right). Found at: https://ourworld.unu.edu/en/sucking-dry-an-african-giant—UNEP Atlas of Our Changing Environment.

change, particularly with regard to agricultural development (food security). There are several projects and action plans coordinated by the LCBC, which have the aim to conserve Lake Chad and its basin on different levels. The current "Lake Chad development and climate resilience action plan" aims at a climate-resilient, integrated ecosystem-based management of the Lake Chad Basin through implementation of intergovernmental policy, legal and institutional reforms, and investments that will improve the water quality and quantity of Lake Chad and protect its biodiversity, while sustaining livelihoods of the resident population (Lake Chad Basin Commission, 2016). Future management of the Lake Chad Basin under the LCBC should include proper assessment of further wetland conversions in the area. This should include the development of more integrated techniques for assessing ecosystem services across diverse stakeholder groups. This holistic management approach should ideally be accompanied by a total economic value assessment (Russi et al., 2013).

Conclusions

The examples of hydromorphological alterations described in this article affect inland waters in a variety of ways and occur globally. Consequences of hydromorphological alterations can be generalized as changes to the structure of surface waters, such as modification of shore structures, sediment/habitat composition, alterations of natural flow and discharge regimes by channelization or dams and changes in water levels through water abstraction, damming or climate change. As described above, altering the physical condition of surface waters can cause detrimental damages to ecosystems and has the potential to negatively impact the water's ecological status. In order to maintain the ecological integrity, biodiversity and quality of inland waters, a sustainable, holistic, ecosystem-based management is required to ensure the protection of freshwaters and their biodiversity worldwide.

See Also: Human pressures and management of Inland Waters: Hydromorphology: Overview and Assessment Methods; Hydromorphology—Interactions and Habitats

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Evolving Perspectives on Hydropower: Balancing Societal Benefits and Environmental Impacts

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Diadromous fish Fish that migrate between freshwater and marine environments.
Diatom Photosynthesizing algae with a siliceous shell.
Gigawatt (GW) Unit of power equal to 1000 MW (MW).
Hydropeaking Artificial water level fluctuations due to electricity generation at times of peak electricity demand.
Pumped storage plant Hydropower plant in which water is released from an upper reservoir to generate electricity during times of peak electricity demand; and water is pumped back to the upper reservoir using off-peak electricity.
Run-of-river Hydropower plant which raises upstream river levels slightly but does not significantly impede river flow.

Introduction

Over the past century free-flowing rivers on every continent have been progressively impacted by hydropower developments seeking to utilize a river's potential to generate renewable energy. Hydropower has become an increasingly important source of energy, enabling a reduction in fossil fuel use and reducing the costs of energy generation. Global installed hydropower capacity has been estimated at 1330 GW in 2020, with an increase of 21 GW over the year mainly in SE Asia (IHA, 2021). While only 22% of the world's total hydropower potential is thought to be currently utilized (Zarfl et al., 2015), hydropower developments have progressively impacted individual river basins with widespread environmental, social and economic consequences (Moran et al., 2018). This chapter summarizes the chronology of hydropower developments and reviews recent work that emphasizes the need to balance the potential benefits of new hydropower developments, against their environmental and socio-political impacts. This is a somewhat contested area: some argue that further developments of potential hydropower sites are essential if we are to achieve a significant reduction in greenhouse gas emissions and reach net zero. However, individual hydropower developments differ widely in their potential benefits and in the associated social and environmental impacts. Hence hydropower schemes require careful scrutiny to determine whether the benefits of individual schemes exceed the environmental and societal costs.

Currently, one third of all countries globally rely on hydropower for >50% of their energy requirements and hydropower contributes ~20% of total energy supply (IHA, 2021). These developments have made a substantial contribution in reducing fossil fuel use, but the environmental impacts include increasingly fragmented river catchments (Nilsson et al., 2005), reduced sediment transport (Habersack et al., 2016), changing river regime (Hecht et al., 2019), and loss of biodiversity. The effects on local communities are also difficult to quantify: in some cases surrounding areas have benefited from infrastructure improvements, employment and security of energy supply. However, Richter et al. (2010) suggest that between 40 and 80 million people have been directly displaced by dams (not solely hydropower), with as many as 472 million people affected downstream. While these estimates are more than 20 years old, and are for dams generally, they illustrate the need to consider impacts throughout the river catchment, where a succession of small or moderate dams or hydropower plants (HPPs) can have a cumulative impact comparable to that of a single large development. In many cases, this wider, holistic, perspective has been lacking. However, this is an opportune time to (re)consider the case for hydropower. Many plants, which were constructed during the peak years of hydropower development in the mid- 20th Century, now require upgrading and refurbishment, and elements of their design and operating procedures can potentially be revised to reduce their environmental impact and increase their efficiency.

A hydropower chronology

Current hydropower schemes are but the latest developments in a >2000 year process of harnessing water to generate power (Table 1). In Europe, one of the main legacies of the Greco-Roman empire was the water mill. These were used to produce flour, cut wood and stone, and iron working. While this was generally at a small scale, Passchier et al. (2020) describe a complex of 16 water mills at Barbegal, S France, with 2 lines of 8 mills arranged in parallel, and fed by a complex water distribution system (Fig. 1). This development, in the second century CE (Common Era), was not exceeded in scale until the 16th Century. More widely, throughout Europe, small free-flowing rivers were increasingly harnessed for water power: >5000 water mills were recorded in England in the Domesday Survey of 1086. These primarily used mill-stones to grind corn, but from the 12th Century onwards, they were used increasingly for industrial purposes: for wool and metal processing (fulling; lead smelting). The culmination of these developments were the large industrial complexes of the Derwent Valley Mills, Saltaire and New Lanark in the British Isles. Technology was imported from Italy to throw silk (1721) and Richard Arkwright harnessed water power for cotton production in a series of mills in the Derwent valley (Derbyshire, England) constructed between 1777 and 1782. These industrial developments were soon replicated in other countries, where conditions allowed, in (inter alia) North America, Germany, France and the Czech Republic.

While water power was soon superseded by other sources of energy in the industrial revolution, hydro-electric developments transformed river catchments globally through the 20th Century as engineering advances enabled larger rivers to be impounded, and with run-of-the river and pumped storage schemes providing more opportunities to generate electricity. One of the earliest hydroelectric power (HEP) developments, albeit on a relatively small scale, was at Cragside, N. England, where in 1879–1882 a Newcastle industrialist, William Armstrong, generated electricity using a small stream flowing through his estate. The first

Table 1 Historical timeline of hydropower developments.

Year	
300	Romans major water-powered mills
1000	Water mills widespread in Europe
1500	Water: major source of power for food processing (flour; corn), textile (fulling) and manufacturing (iron works)
1800	Water: drives the Industrial Revolution supporting urban and industrial development in upland valleys
1880	First Hydroelectricity schemes (Cragside, NE England; Salmon Leap Falls, N. Ireland)
1900s	Development & operation of hydropower scheme on the Niagara Falls with power transmission to urban centers (e.g., New York)
1930s	First 'mega' hydropower developments (e.g., Hoover Dam on the Colorado River)

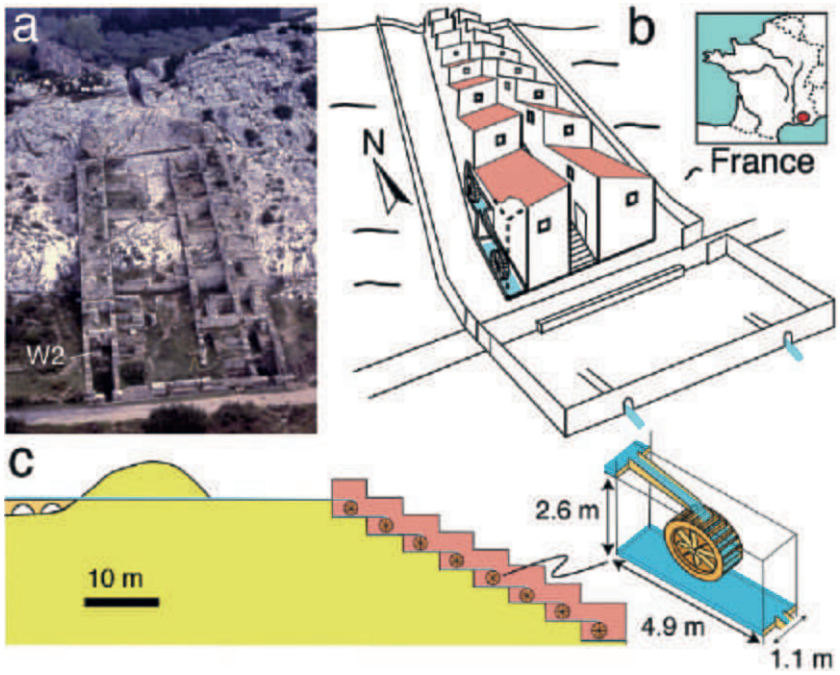

Fig. 1 The Barbegal water mill complex: (A): ruins of the mill complex; (B): reconstruction of the site; and (C) cross-section through one train of mill wheels. From Passchier, CW, Bourgeois M, Viollet PL, Surmelihindi G, Bernard V, Leveau P and Spotl C (2020) Reconstructing the hydraulics of the world's first industrial complect, the second century CE Barbegal watermills, France. *Scientific Reports* 10: 17917. https://doi.org/10.1038/s41598-020-74900-5.

Table 2 Selected 'mega' hydropower projects developed over the past century.

Year	*Dam*	*River*	*Generating Capacity*
1928	Hoover	Colorado R	2080 MW
1937	Bonneville	Columbia R	1242 MW
1942	Grand Coulee	Columbia R	6809 MW
1961	Volga GES	Volga	2671 MW
1964	Aswan High	Nile	2100 MW
1969	Guri	Caroni R	10,235 MW
1972	Iron Gates I	Danube	2281 MW
1976	Tarbela	Indus R	4888 MW
1984	Itaipu	Parana	14,000 MW
1984	Tucurui	Tocantins R	8370 MW
2008	Three Gorges	Yangtze	22,500 MW
2013	Xiluodu	Yangtze	13,860 MW
2016	Belo Monte	Xingu R	10,621 MW
2022	Baihetan	Jinsha	16,000 MW
?	Inga Falls	Congo	40,000–70,000 MW

commercial HEP station was commissioned soon afterwards, at Salmon Leap on the River Bush in N Ireland in 1883, which powered a local tramway. However, the Niagara Falls HEP scheme in N. America, developed between 1890 and 1910, was on a much larger scale and included long-distance transmission of the power generated to the city of New York >550 km away.

The Niagara development was the precursor to the hydroelectric power (HEP) 'mega-projects' which transformed many river catchments in the 20th Century (Table 2). These included a suite of HEP schemes developed by the Tennessee Valley Authority, and the construction of large dams on the Colorado, notably the Hoover Dam. These developments in the United States, were matched in the Soviet Union, by large HEP schemes on the Rivers Don, Dneiper and Volga as HEP developments were seen as providing opportunities to support and encourage economic development, and manage water availability with benefits for irrigation, flood control and drinking water supply (Zarfl et al., 2015). While the geographical distribution of these large HEP developments has changed in recent years (e.g., to China with the Three Gorges Dam on the Yangtze), the primary motivation for these schemes is largely unchanged, although the scale is much larger, and could be dwarfed by proposals to construct a series of 7 HEPs on the Congo River at the Inga Falls which could potentially generate between 40 and 70 GW of electricity.

Environmental impacts of hydropower

The proliferation of hydropower plants of varying scale has had widespread environmental impacts on physical, chemical and biological processes both within catchments, but also in coastal deltas and seas. While it may be difficult in some cases to attribute problems solely to hydropower development (given the many interacting anthropogenic modifications to rivers and catchments) in many rivers, the physical impacts extend throughout the basin, and >40% of global river volume is either moderately or severely impacted by fragmentation (Grill et al., 2019; Hoeinghaus, 2018) and 6% of European surface-water bodies have been affected by hydropower barriers (Schwartz, 2019), to the extent that only five free-flowing river reaches remain on the Danube (Habersack et al., 2016). Hydrophysical disturbances below impounded reaches are highly variable, depending upon the individual site, the catchment context, and the type of HPP (i.e., pumped storage, barrage, or run-of-river; Fig. 2; Lumbroso et al., 2014) but include the introduction of an artificial flow regime downstream (typically lower peak flows, reduced flow variability), hydropeaking (sharp increases and falls in river levels as storage plant release water during times of high energy demand), the interruption in sediment transfer and changing channel dynamics with evolving process-form relationships as described below (Petts and Gurnell, 2005). Individual reaches below dams may experience sediment starvation, leading to river bed incision, while there may be periods of aggradation elsewhere (e.g., during reservoir construction) due to reduced channel capacity and ability to transport sediment. For example, on the Yangtse, river reaches immediately below the Three Gorges Dam experienced increased channel erosion, due to reduced suspended sediment concentrations and the increased frequency of high flows; mid-channel bars downstream have been eroded, with lower water levels at low discharges (Li et al., 2019). These process-form relationships are complicated by wider changes in riparian vegetation and in the lateral connectivity between river and floodplain.

The hydromorphological implications of HPPs are widely evident in basins where hydropower developments are relatively mature (in Europe and N. America), but the potential implications of a similar density of HPPs in tropical catchments in S. America (the Amazon), SE Asia (the Mekong) and Africa (the Congo) have been highlighted only recently. Proposed hydropower dams in the Andean headwaters of the Amazon will impact the sediment, water and nutrient fluxes to the main stem of the river. In 2018, there were 142 hydropower plants (largely <50 MW) operating in the Andean tributaries, but a further 160 were in different planning stages, including several >100 MW (Anderson et al., 2018). The effects are likely to be particularly marked on riparian

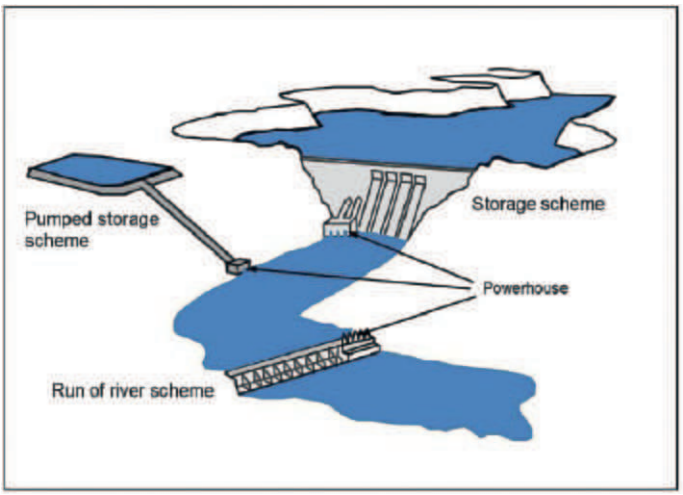

Fig. 2 Schematic illustrating the three main types of hydropower scheme. From Lumbroso, D, Hurford AP and Winpenny J (2014) Synthesis report: Harnessing hydropower. *Evidence on Demand*. Institute of Development Studies, p. 80. https://doi.org/10.12774/eod_cr.september2014.lumbrosoetal2.

forests in nutrient-poor catchments (i.e., igapó forest communities) downstream due to changing river flow dynamics and particularly any reduction in high river flows which would affect the annual flood pulse (Latrubesse et al., 2017). Similarly in SE Asia, 141 HPPs have either been constructed or planned on the Mekong (Hecht et al., 2019) resulting in reduced high (flood) flows which had formerly been responsible for the majority of river flow and sediment transport. If planned HPP proceed as anticipated, it is suggested that suspended sediment fluxes might fall by as much as 96% from their pre-development total of an estimated 160×10^6 t/year which could affect the rate of coastal and deltaic accretion downstream (Kondolf et al., 2014). The total volume of water storage within the basin is currently estimated as approaching 60 km^3 (Hecht et al., 2019) with substantial evaporative loss and modification to the catchment water balance.

Nutrient flows are similarly impacted by HPPs with nutrient retention through sedimentation above the dam, or gaseous emissions which may offset some of the environmental benefits of hydropower. The latter is particularly serious in tropical climates where emissions of greenhouse gases may be as much as 22 times higher than before dam construction, due to deforestation (Fearnside, 2015). Reductions in nutrient loads (N, P, Si) are facilitated by longer water residence times (Maavara et al., 2020), generally with P eliminated preferentially and with N:P ratios increasing in proportion to residence time. However, in catchments with residence times <50 days, Si may be eliminated by enhanced diatom activity. While reduced nutrient fluxes may be beneficial in eutrophic rivers, changing biogeochemical cycles can have widespread implications (Friedl and Wüest, 2002) with impacts on freshwater and marine food webs. In the Danube, for example, dam construction throughout the catchment led to a >60% reduction in Si transported to the Black Sea which led to a change in plankton species in the Black Sea and more frequent harmful algal blooms (Humborg et al., 1997) and a dramatic decline in what was formerly (<1970) a very productive marine fishery.

The consequences of hydropower development and limited connectivity are particularly marked for diadromous fish, such as sturgeon, houting, shad, and salmon, which migrate between freshwater and marine ecosystems (Duarte et al., 2021). Historical records indicate that there was a 90% decline in salmon stocks in NW Europe from the Early Middle Ages (450–900 CE) to Early Modern Times (~1600), with reduced fishing yields that tracked the development of vertical water mills on major rivers (Lenders et al., 2016). The salmon fishery was particularly impacted due to the degree to which water mills affected stream oxygenation, flow velocity, water depth and substrate. Cumulative declines of <99% in the salmon fishery have been suggested over this period, illustrated by the annual salmon catch at Montchaton, Normandy, France, falling from 300 to 350 in the 14th Century to 3–4 by the end of the 15th Century, and with an annual biomass loss across the Rhine catchment estimated to be >230,000 t (Lenders et al., 2016). More recently, in the Danube, the sturgeon has been particularly impacted by hydropower developments on the main stem of the river (Bănăduc et al., 2016) and even run-of-the river plants have the potential to impact local fisheries significantly (Bilotta et al., 2016).

In tropical catchments proposed hydropower developments have the potential to impact freshwater fish diversity: particularly species that are morphologically adapted for fast flowing, high gradient streams, which generally are amongst the first to be developed for hydropower. In the upper reaches of the Amazon, a decline in fish diversity has been linked to catchment fragmentation due to hydropower development (Anderson et al., 2018) as migrating fish are impacted by a combination of physical barriers, artificial fluctuations in flow and changing thermal regime. In such cases it is difficult to isolate the effects of changes in hydrology (due to hydropower operations) from the effects of reductions in suitable habitat and wider environmental degradation emphasizing the importance of holistic, basin-wide, approaches to assess the individual and in-combination consequences of hydropower developments.

The societal context of hydropower

The many environmental consequences of hydropower development are complex, often inter-related and site specific, but should not be considered in isolation from the societal benefits that these developments potentially offer (Biswas, 2004, 2012). Through much of the 20th Century hydropower offered a vision of tamed rivers, with improved infrastructure, increased (low cost) electricity production and improved flood control (Schulz and Adams, 2019). Many OECD countries have benefited from the availability of low-cost energy, which has enabled socio-economic development, and was considered (with dams) as one of 'the most essential aspects of man's attempts to harness, control and improve his environment' (Smith, 1971). Trefon (2016), for example, summarizes the potential for hydropower developments in the Congo to foster economic growth, notwithstanding problems with siltation and maintenance at the Inga I and II plants, constructed in 1972 and 1982. However, more recently perspectives on hydropower have been increasingly polarized with economists and engineers focusing on the economic benefits and development opportunities while environmental scientists highlight the negative impacts summarized in the previous section (Schulz and Adams, 2019). There are also concerns with social capital and the negative impacts on displaced people: 400,000 people are thought to have been affected directly in Africa (United Nations World Water Assessment Programme (WWAP), 2014) and the food security of many communities below HPPs have also been impacted by, for example, reduced fish or farming yields due to the effects of hydropower operations on water and sediment fluxes (Intralawan et al., 2018).

These problems, together with wider questions over the costs and benefits of individual hydropower developments, led to the development of the Hydropower Sustainability Assessment Protocol (HSAP) which summarizes best practice in balancing environmental, social, technical and economic elements in hydropower projects (IHA, 2018). The protocol provides key criteria that can be used to assess the sustainability of HPPs: from planning, through to implementation and operation. The funding landscape has also changed, as a result of lobbying by pressure groups, the need for detailed cost-benefit analysis and full environmental impact assessment. While some developments can circumvent these requirements, there is a widely recognized need for improved stakeholder engagement and social inclusion to ensure that the benefits of improved infrastructure and energy availability are realized. However, this pre-supposes that it is possible to balance objectively the environmental impacts of hydropower against the benefits that hydropower potentially offers to society. Here it helps to look separately at perspectives in countries where the technology is relatively 'mature', i.e., in North America and Europe, and in developing countries where there is unfulfilled hydropower potential, recognizing that in both cases innovative approaches to hydropower may reduce environmental impacts and/or increase the benefits to society.

Basins with a 'mature' level of hydropower development

In basins with a long history of hydropower development, there are relatively few free-flowing reaches, whether due to individual 'mega-projects' or chains of smaller plants. In these rivers, the challenges include: (i) how can the existing hydropower infrastructure be operated to maximize the opportunity to supply green energy; (ii) Is it possible to upgrade existing facilities to reduce environmental impacts; and (iii) Where relatively old HPPs come to the end of their operational life, is it possible to upgrade the facility, or is decommissioning potentially viable.

Hydropower is widely assumed to be central in our transition to a low carbon society, and Wagner et al. (2019) argue that pumped storage plants make a particularly important contribution in providing energy at times of peak demand. This requires more research on technologies, and operating procedure, to ensure environmental sustainability, and to manage the problems posed, for example, by hydropeaking. At the same time, there is a strong argument for systematic basin planning and integrated water resource management to look at basin-wide impacts of hydropower operations and their vulnerability to climate change (e.g., the potential for energy generation to be compromised by reduced water availability during drought). Where possible, environmental flows may also be prescribed to mitigate specific environmental impact [cross-reference to another chapter in the volume].

The potential to upgrade current HPPs so they conform to current standards is also a promising area to explore. This could include improved hydropower designs to allow fish passage, recognizing the limitations of current designs (e.g., of fish ladders; Fig. 3) which may not be as effective as originally intended (Moran et al., 2018). More fish friendly solutions are needed (e.g., Quaranta et al., 2020) to improve fish passage and hence fish biodiversity and abundance. In many cases, however, there may be no easy solution to enable continued hydropower operations and in recent years ~5000 dams have been removed in Denmark, Estonia, Finland, France, Germany, Italy, Portugal, Spain, Sweden, Switzerland and the United Kingdom. While the financial costs of dam removal may be considerable, it is generally accepted that these dams are either too expensive to upgrade, or are associated with unacceptable environmental problems, and dam removal provides the opportunity for river restoration.

Hydropower in less economically developed countries LEDCs

There may still be considerable potential for new hydropower developments on rivers in many LEDCs, which could potentially address the very real problems of limited availability of energy and water in some regions (e.g., the household electrification rate in Sub-Saharan Africa is the lowest in the world, averaging 42% in 2016) (O'Brien et al., 2021). However, there are many challenges including: (i) maintaining and upgrading current HPPs to ensure continued operation; (ii) assessing proposed new developments

Fig. 3 A fish ladder in SE Alaska. © Prof. Sandy Milner.

to ensure that their environmental and social impacts are fully quantified; and (iii) Exploring the potential to take advantage of new technologies to provide energy for local communities in remote areas with little environmental impact. Here, the difficulties are how to balance the opportunities provided by improved energy availability, with protecting the environment and ensuring that the development benefits (and costs) of hydropower are shared equitably.

It has been suggested that the projected benefits of many large dams were overly optimistic (World Commission on Dams, 2000) and HPPs require ongoing maintenance and investment to ensure that individual plants remain operational. The two operational dams on the Congo: Inga I and II were constructed in 1972 and 1982 respectively, with a generating capacity of 351 and 1424 MW, but both dams are only generating a fraction of their potential, because of maintenance and sedimentation problems, to the extent that half the turbines are inoperable (Trefon, 2016, p. 79). A wider review of the case to support the development of 12 large dams in Africa, including the Inga III dam on the Congo and the Grand Renaissance Dam on the Blue Nile, argues that the benefits of large dams in the past had been undermined by substantial cost over-runs, illustrated by costs to construct Inga I and II which totaled $1.1 billion, against an initial estimate of $250 million (International Rivers, 2015). While the 12 dams could potentially generate 15 GW of electricity, as many as 100,000 people would be directly affected, and key ecosystem services lost: the Fomi Dam in the Guinea highlands would impact the Inner Niger Delta wetlands in Mali; and the Congo Plume (freshwater discharged by the Congo to the Atlantic Ocean) would be impacted by the Inga III Dam on the Congo. There are also questions over the extent to which local communities would benefit, as the Inga III scheme envisages energy export to S. Africa and E. Congo with the construction of >3000 km of transmission lines. Accordingly, where hydropower developments do proceed, this should be within the context of basin-wide planning and taking stakeholder views into account, with an integrative assessment of environmental and social impact (O'Brien et al., 2021).

While there are questions over the costs and benefits of large hydropower schemes, smaller chains of HPPs may be equally problematic. Chaudhari et al. (2021) have highlighted the potential to use in-stream turbines harnessing the river's kinetic energy to generate power, suggesting that these systems could be used to generate ~63% of the energy supplied by HPPs on the Amazon. While this technology is still likely to have an ecological impact (Moran et al., 2018), it is more environmentally benign because it removes the need for water storage with its associated loss of riparian and floodplain habitat, thereby potentially stabilizing greenhouse gas emissions. There are wider opportunities though, to explore the use of small-scale hydropower plants, i.e., the so-called pico-hydro schemes generating <5 kW, operated by independent power producers. These have the potential to provide energy for remote communities, because they have relatively little environmental impact and do not require significant infrastructure and transmission lines. Pico-hydro schemes are particularly appropriate in mountain basins which, outside Europe such as in the Himalayas, have been described as one of the last frontiers for hydropower (Lord et al., 2021).

Knowledge gaps

- How can the existing hydropower infrastructure be managed most efficiently?
- How feasible is it to upgrade existing facilities to reduce their environmental impact.
- How can recent advances in hydropower technology be utilized to provide energy in remote areas with minimal environmental impact?

Conclusions

Hydropower has a relatively long history and has made a significant contribution to reducing the use of fossil fuels and greenhouse gas emissions. However, the scale and extent of hydropower developments over the past century has had widespread environmental and social impacts. These impacts are, to a large extent, site- and basin-specific. However, it is essential that the benefits and impacts of hydropower are fully quantified, to determine the extent to which we can continue to generate hydropower and satisfy stakeholder concerns, whilst preserving vulnerable ecosystems.

See Also: Human pressures and management of Inland Waters: Hydromorphology: Case Studies; Hydromorphology: Overview and Assessment Methods; Hydropeaking: Processes, Effects, and Mitigation; Hydropower: Case Studies in Sustainability

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Relevant websites

https://www.hydrosustainability.org/hs-council—The Hydropower Sustainability Council
https://www.damremoval.eu—Dam Removal Europe (DRE)

Hydropower in the Danube River Basin: Current Status and Emerging Challenges

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Free flowing reaches A river reach that is not impacted by downstream impoundments.
Hydrogeomorphology The inter-disciplinary study of the links between on the interaction between hydrological processes and landforms.
Hydropeaking Artificial water level fluctuations due to electricity generation at times of peak electricity demand.
Run-of-river Hydropower plant which raises upstream river levels slightly but does not significantly impede river flow.

Introduction

In this case study chapter, we summarize the current state of hydropower developments on the River Danube and the wider Danube River Basin (DRB). Over the past century, a widely distributed network of hydropower plants has been constructed throughout the Danube River Basin in response to a societal pressure to increase the proportion of energy requirements that are satisfied by renewable energy. Currently, across most of the DRB (with the exception of Germany, Hungary and Moldova), hydropower is the most important component of renewable energy production, contributing ~45% of the total electricity generated within the catchment (ICPDR, 2013a). However these developments, in association with river management, and wider climatic and environmental changes in the DRB, have contributed to a suite of impacts on the Danube, its tributaries and on coastal environments downstream. The situation is further complicated in the DRB by the wider political context. The basin is the most international river basin globally with a catchment that spans 19 countries.

The scale and complexity of the basin are such that the DRB exemplifies the difficulties in managing catchments sustainably: by ensuring water security and flood protection, whilst conserving biodiversity, and enabling navigation and electricity generation. While it is difficult to look at one of these pressures (i.e., hydropower) in isolation, the cumulative effects of hydropower developments have been the progressive loss of free-flowing river reaches, and the lack of continuity from the basin headwaters, along the main stem of the Danube and its tributaries, down to the Danube Delta. Over time, this has substantially changed the hydromorphology of the Danube and its tributaries, impacting the biodiversity of the river corridor (Hein et al., 2017), and contributing to reduced water and sediment fluxes to the Danube Delta and Black Sea downstream (Habersack et al., 2016; Panin and Jipa, 2002). Resolution of these problems requires new approaches to inter-disciplinary river science that consider the whole basin and encourage stakeholder engagement and knowledge exchange to identify realistic and sustainable solutions to current problems.

Hydropower in the Danube River Basin

Before summarizing recent hydropower plants developments in the DRB, it is essential to understand the wider geography of the basin which provides the context within which these developments have occurred. The River Danube is 2857 km long: flowing east from the Black Forest Mountains and discharging into the Black Sea where its mean annual discharge is ~6550 m^3/s (Sommerwerk et al., 2009). River flow fluctuates seasonally, reflecting variations in annual precipitation across the basin ranging from ~3000 mm in the West to ~500 mm in the East. The DRB extends over more than 800,000 km^2 of Central and South-Eastern Europe (Fig. 1). One third of the DRB is mountainous extending from Piz Bernina (4052 m asl) in the West and Peak Krivan (2496 m asl) in the North. The Danube flows through a series of basins and gorges: below the confluence of the Danube and the Morava, the river enters

Fig. 1 The Danube River Basin (Sommerwerk et al., 2009).

the Devin Gate below which the Danube forms an internal delta as it crosses the Pannonian Plain. Here the Danube is joined by the Drava, Tisza and Sava rivers which rise in the Southern Alps, the Western Carpathians, and the Julian Alps respectively. As a result, the flow of the Danube is strongly supported by flows generated in alpine areas. Prior to regulation, the Danube used to experience two floods in a typical year: the first in early spring due to snow-melt, and the second in early summer, reflecting peak runoff. Downstream the Danube flows through the 117 km long Iron Gate gorge in the Southern Carpathians before the river crosses the Romanian and Bulgarian lowlands and flows through the Danube Delta to the Black Sea.

The River Danube and its tributaries have been progressively managed from the 16th century onwards for navigation, flood protection, and increasingly over the last century, for hydropower (Habersack et al., 2016), and to the extent that today there is an extensive network of 44 hydropower plants on the Danube with a further 1610 plants on the Danube's tributary rivers (Hein et al., 2017). This includes ~646 hydropower plants in catchments of tributaries of the Danube in Bosnia and Herzegovina, Croatia, Montenegro, Serbia and Slovenia, and currently >1000 additional plants are planned, mainly along the Sava River (Huđek et al., 2020). Over the course of the 20th century, and following construction of the Kachlet dam on the Danube in Germany in 1927, there has been a rapid expansion in engineering works that sought to harness the potential of the basin for hydroelectric power. The consequence of these relatively recent developments is that hydropower plants are now widely, but unevenly, distributed across the basin reflecting the hydrological and geomorphological potential for hydropower in the DRB, as well as the recent political and economic history of countries within the basin (Fig. 2). Hydropower plants of ~100 MW capacity account for between 50% and 80% of the total installed capacity in Austria, Bosnia-Herzegovina, Serbia, Slovakia, and Romania (ICPDR, 2013b), while plants smaller than 1 MW make a relatively small contribution to the total installed hydropower capacity (<10% for Austria, Germany, Croatia, Bosnia-Herzegovina, Moldova, Romania, Serbia, Slovakia, and Ukraine).

The ongoing development of hydropower, coupled with extensive channel re-engineering for navigation and flood control, have extensively modified the river course and floodplain connectivity to the extent that at present >1100 km of the length of the Danube is impounded by 78 barriers, the majority of which are situated at points where there is the greatest change in channel gradient (Fig. 3A). In Austria and Germany, chains of hydropower plants impound 269 km of the Danube (77% of the Austrian Danube). The largest hydropower scheme, at the Iron Gates, is situated at a point where there is a step change in channel elevation: Iron Gates I impounds 310 km of the Danube up to the city of Novi Sad (11% of the total length of the Danube; Fig. 4) and the two Iron Gates plants (I and II) together have an installed capacity of ~2840 MW. Further large hydropower plants are situated progressively upstream on the Danube: Gabčíkovo (720 MW) which impounds 17 km of the middle Danube downstream of Bratislava and Freudenau (172 MW) a run-of-the-river plant on the Danube at Vienna.

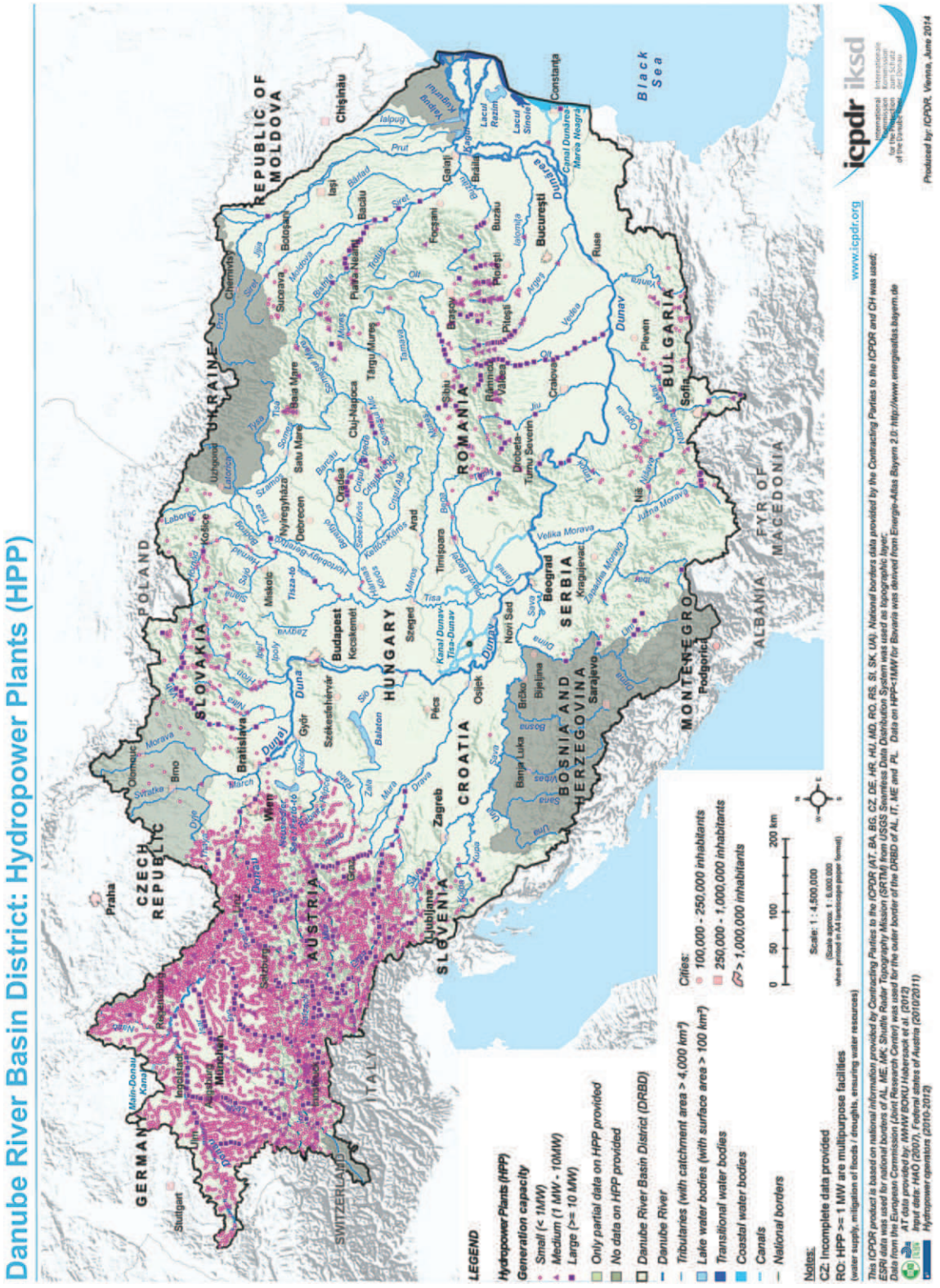

Fig. 2 Distribution of hydropower plants in the Danube River Basin (ICPDR, 2013b).

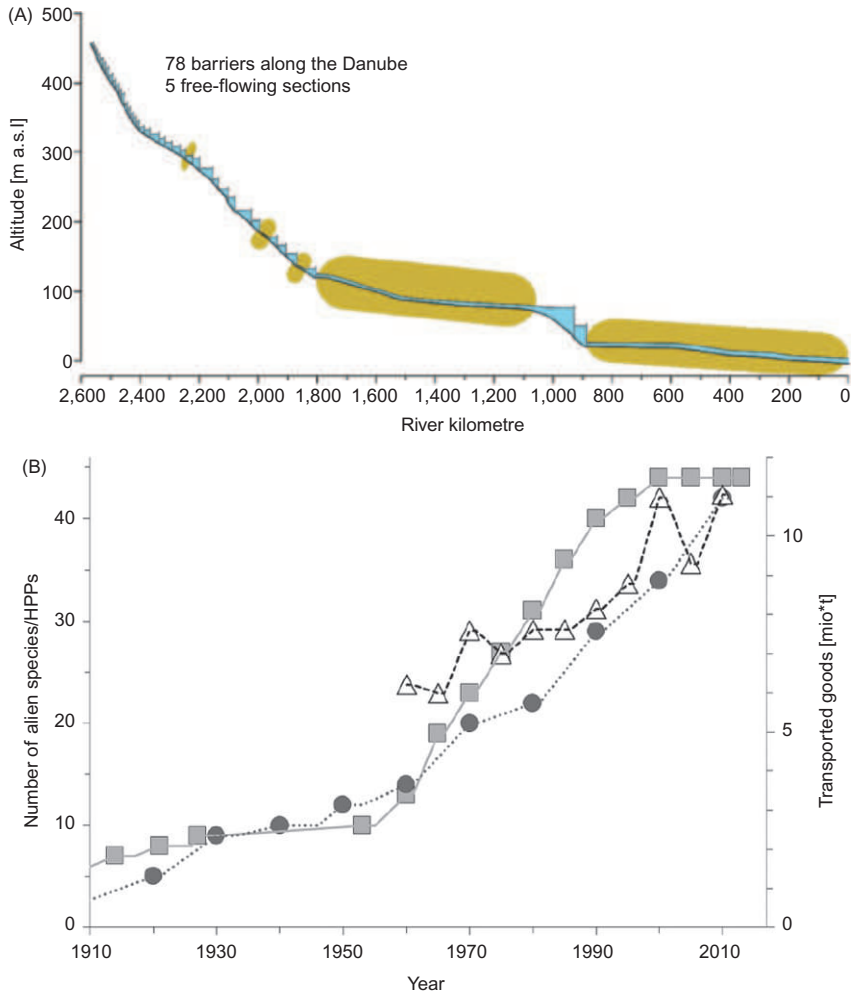

Fig. 3 (A) Long profile of the River Danube showing impoundments and free-flowing sections. (B) No of alien species (gray dots) hydropower plants (HPP, filled squares) and goods transport (open triangles) in the middle Danube. (A) From Habersack H, Jager E, and Hauer C (2013) The status of the Danube River sediment regime and morphology as a basis for future basin management. *International Journal of River Basin Management* 11(2): 153–166, Habersack H, Hein T, Stanica A, Liska I, Mair R, Jager E, Hauer C, and Bradley C (2016) Challenges of river basin management: Current status of, and prospects for, the river Danube from a river engineering perspective. *Science of the Total Environment* 543: 828–845, (B) from Hein T, Funk A, Pletterbauer F, Graf W, Zsuffa I, Haidvogl G, Schinegger R, and Weigelhofer G (2017) Management challenges related to long-term ecological impacts, complex stressor interactions, and different assessment approaches in the Danube River basin. *River Research and Applications* 35: 500–509.

Environmental implications of hydropower schemes

While the increasing potential to generate renewable energy has been beneficial, these hydropower developments have had many environmental consequences in the DRB. The extensive chains of dams along the Danube and its tributaries have wide-ranging hydromorphological consequences including changes in runoff, in the water balance, sediment transport and river morphology.

Over the period 1950–80, 69 reservoirs were constructed in the DRB with an estimated total storage volume of 7300×10^6 m^3 (Habersack et al., 2013). The Danube itself is now split into many impounded reaches and only five free-flowing river reaches remain on the main stem of the Danube. The longest of these extends from the Iron Gates 2 hydropower plant to the Black Sea coast and the second longest free-flowing reach lies in the Hungarian Plain. In Austria only two free-flowing reaches remain: 48 km between Vienna and Bratislava and 33 km in the Wachau area, while in Germany the last free-flowing reach on the Danube is between Straubing and Vilshofen. Impounded reaches which are affected by dams downstream typically experience increased water temperatures, a decrease in dissolved oxygen and sediment deposition (Grill et al., 2019). Below dams, hydropeaking (described by the ratio of Q_{max} to Q_{min} over a given time period) may be problematic. Hydropeaking is associated with an increase in hydraulic stress downstream, with impacts on benthic fauna. At least 44 water bodies in the DRB are affected by hydropeaking, in some cases with daily river level changes of >1 m (ICPDR, 2013a).

The impoundments have significantly affected water and sediment fluxes through the basin: with increased sedimentation in impounded reaches, and changing sedimentary composition downstream. Coarse sediment, derived from alpine headwaters is progressively lost through sedimentation in impounded reaches, to the extent that in the Danube below Budapest, there is relatively

Fig. 4 The Iron Gates (I) dam on the River Danube(© www.all-free-photos.com).

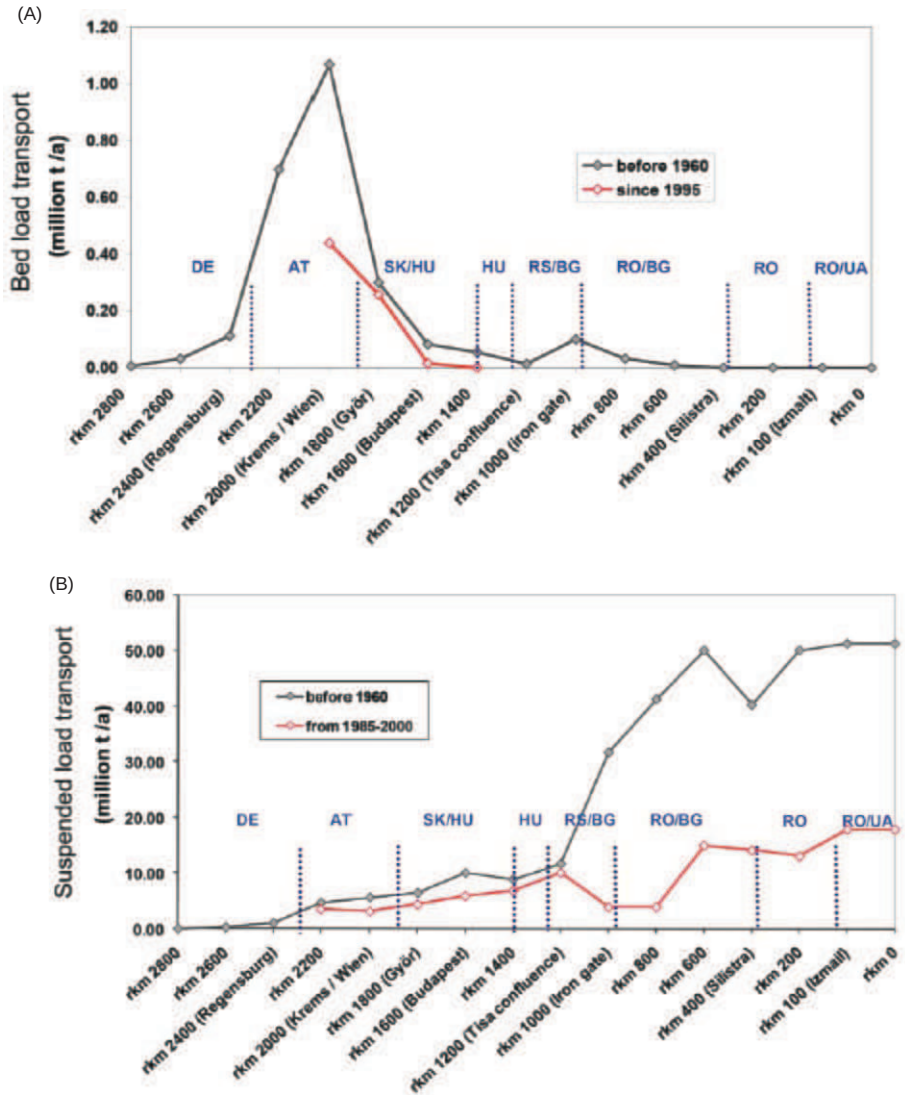

Fig. 5 Bedload (A) and suspended sediment (B) transport in the Danube River: prior to 1960 and from 1985 to 2000. From Habersack H, Jager E, and Hauer C (2013) The status of the Danube River sediment regime and morphology as a basis for future basin management. *International Journal of River Basin Management* 11(2): 153–166.

little coarse sediment transport (e.g., gravel), unless contributed by major tributaries. This is illustrated dramatically by reductions in sediment fluxes in some of the upper tributaries of the Danube. In Austria/Germany, for example, sediment fluxes on the River Lech at its confluence with the Danube have fallen from 180,000 t/year prior to hydropower development, to effectively zero, and at the Danube's confluence on the River Inn, from 540,000 to c. 180,000 t/year (Habersack et al., 2013). Elsewhere, on the Drava River over the period 1918–1967, hydropower developments have contributed to reductions in sediment fluxes from 9.5×10^5 to 4.1×10^5 t/year, primarily due to the trapping of bed-load, with extensive hydrogeomorphological changes as discussed below (Kiss and Andrasi, 2017). The sedimentary load of the Danube has also fallen from an estimated 1.7×10^6 t annually at the beginning of the 19th century, to about 300,000 t in 1995 (Schwarz et al., 2008), with marked changes in bedload and suspended sediment transport (Fig. 5A and B). Sedimentation in impounded reaches upstream of dams accounts for between 25% and 30% of the sediment load of the Danube that would formerly have been transported to the Danube Delta and the Black Sea.

In the Lower Danube, the suspended sediment load is estimated to have fallen from 876 kg/s (1971–1984) to 790 kg/s (1950–1971) and then 311 kg/s (1985–2000) (Bondar and Teodor, 2008). These trends are, at least partly, due to the construction of the Iron Gates I and II dams. Iron Gates I was completed in 1972, and is estimated to retain >30% of the total sediment input from upstream, and as much as 44% of the suspended sediment, with sediment retention over the 22 years from 1972 to 1994 of 325×10^6 t by the Iron Gates I dam alone, filling an estimated 10% of the reservoir capacity (Klaver et al., 2007). With an approximate capacity of 2.1 km^3 (2.1×10^9 m^3) this suggests that the indicative volume of sediment stored within this impounded section alone is $\sim 2 \times 10^8$ m^3, which is likely to include some sedimentary units with high concentration of, inter alia, Al, Cr, Fe & Mg from historic mining, industry, and sewage (Szabo et al., 2020), as well as micro-plastics. The consequent reduction in sediment transport downstream has led to channel incision in sediment-starved reaches immediately below dams, and increased coastal erosion on the Black Sea coast where the Danube Delta is experiencing rates of coastal retreat in some areas that is approaching 20 m/year (Panin and Jipa, 2002). In addition to changes in the volume of sediment transported annually in the DRB, the timing of sediment fluxes has also changed: during floods a strong remobilization of sediment from reservoirs occurs, whereas previously sediment transport was more evenly distributed through the year (Nachtnebel et al., 2004).

Throughout the DRB, river management has led to progressive hydromorphological changes at different scales: ranging from the whole catchment, to the individual river reach/section, and extending down to the characteristics of specific sites. The observed changes reflect changes in the equilibrium between hydraulic processes and the fluvial morphology with multi-dimensional impacts that extend throughout the basin. These include changes in instream structures: with the loss of gravel bars in upstream river reaches, above HPPs, and changes in the form of sand bars downstream. On the Drava, below HPPs, Kiss and Andrasi (2017) noted changes in flood dynamics, decreasing river stage, and hydropeaking (for example, with 1–1.2 m high flood peaks in reaches below the Donja Dubrava hydro-electric power plant). Since the 19th century the river has evolved from a state in which the river was characterized by a multiple channel system in its upper reaches (either braided or anastomosing) and a single, meandering, channel downstream, to a predominantly single thread river characterized by river incision below impoundments.

Over the period of rapid hydropower developments, the DRB experienced widespread ecological changes and a decline in biodiversity. While these may, in part, reflect wider anthropogenic impacts (pollution, navigation, flood control), there are recorded instances of biological invasions tracking hydropower developments in the DRB (Fig. 3B; Hein et al., 2017). This illustrates the complexities of biotic and abiotic interactions following dam construction, which are difficult to quantify and manage. There has been widespread morphological degradation (less variability in flow, increased sedimentation) although it is difficult to attribute specific ecological changes that have been observed to a single cause (such as hydropower developments) given the extent to which the basin is responding over different time-scales to multiple stresses. However, anadromous (migratory) fish, such as the sturgeon, have been particularly affected because they live in saltwater, but return to freshwater to spawn (Bănăduc et al., 2016). Rheophilic fish (living in flowing waters) have also been impacted by river regulation, the loss of floodplain habitats in impounded reaches, and the disconnection between rivers and floodplains (Waidbacher et al., 2018). These problems highlight the need for improved understanding of ecosystem functioning, but there are also challenges in how to enable fish migration (for example by retrofitting fish bypass structures to impoundments), maintaining river bed substrate (for spawning), and determining appropriate ecological flows to mitigate the effects of artificially stabilized flows in impounded reaches. In response, the Sturgeon 2020 action plan calls for no new hydropower plants in river reaches where sturgeon may have been present in the past. Environmental Impact Assessments of any new hydropower plants are also required to take account of sturgeon migration and habitat requirements (Sandu et al., 2013).

The future of hydropower in the DRB

These challenges illustrate some of the wider problems in how to reconcile the benefits of increased renewable energy generation by hydropower (such as reduced greenhouse gas emissions), with the resulting environmental problems. A report by the ICPDR on sustainable hydropower in the DRB highlighted the need for holistic and basin-wide assessment of hydropower development with appropriate mitigation of past engineering works (ICPDR, 2013b). This requires a balance between environmental, social and economic impacts, but in some parts of the DRB the potential for hydropower is already fully realized. Attention should, therefore, be focussed on specific problems, such as how to improve sediment management, and on investigating the potential to apply new technical solutions, such as using hydrokinetic energy conversion systems, that are environmentally more benign, as well as on fish bypass structures (Quaranta, et al., 2020). ICPDR (2013b) indicate that where the development of new HPPs is permitted, there

should be strict criteria for minimum ecological flows, limited hydropeaking, and in-stream structures should be designed in order to maintain upstream/downstream continuity.

At present, hydropower developments in the DRB include work on existing power plants to increase capacity: for example, 68 MW of additional capacity was installed on the run-of the river Iron Gate I plant on the Danube in 2017, and currently there are proposals to extend the Iron Gates II plant from 270 to 320 MW. However, throughout the basin as a whole, there are only limited opportunities for new HPPs, except in the Balkans and in some headwater reaches on tributaries of the Danube. In Serbia, hydropower generation is currently c. 10,000 GWh/year against a potentially feasible total of 17,000 GWh/year (Panic et al., 2013). The focus is on construction of small hydropower plants (<10 MW), potentially re-using sites of former water mills. However, in some cases, construction costs are high, and there are constraints in minimizing environmental impacts downstream. Elsewhere in the DRB, in Romania for example, 26% of the electricity generated is from hydropower, with the first (small) plant constructed in 1884 at Peles Castle (Nastase et al., 2017). A total of 115 HPPs were constructed over the period 1950–90 but, as in Serbia, the focus is on small scale HPPs with a total, estimated, micro-hydraulic potential of 1600 MW. However, a chain of 19 HPPs have been developed, largely since the 1960s along the Olt River, a south-flowing tributary of the Danube with headwaters in the Carpathian Mountains (Dragomirescu, 1993). There are also proposals to develop new HPPs that would impact Natura 2000 sites at Defileul Jiului National Park and Rastolita.

Ultimately, the extent to which future hydropower developments are allowed to proceed will depend upon political and social factors. Hydropower remains an essential component of the energy mix as part of the transition to a lower carbon society, and on-going research is seeking to reduce the environmental impacts of individual developments. For example, hydro-kinetic energy conversion systems (HKEC), such as the Strom-Boje turbine on the Austrian Danube, have the potential to generate electricity from free-flowing waters without impounding a river (Wagner et al., 2019). Some HPPs, particularly pumped storage schemes, also have considerable potential to store energy, and thereby alleviate problems of fluctuating energy demand and supply. However, a supporting economic justification is essential, given potential cost overruns on large projects, including pumped storage facilities. Aside from questions related to unexploited HEP potential, which is relatively low across much of the DRB, more work will be needed to assess old HPPs as they approach the end of their operational life and to determine whether to remove or renew individual plants. Inevitably however, improvements in sediment management will be required whether at a catchment-scale (to reduce erosion and hence sedimentation in impounded reaches), in reservoirs (sediment removal) or in relation to flow hydraulics and sedimentation immediately above dams (Hauer et al., 2018).

Additional areas of concern include the impacts of climate change and increasing water use (Lehner et al., 2005) which will affect the functioning and efficiency of HPPs. For example, a severe drought in 2003 substantially reduced hydroelectricity generation in Austria, leading to the lowest annual HEP production since 1955. HEP generation in the DRB is subject to additional uncertainties relating to climate change: Koch et al. (2010) suggest that, under the IPCC A1B scenario, hydropower generation in the basin may potentially decrease by 2% between 2011 and 2035, and by as much as 11% between 2036 and 2060. These estimates largely reflect changes in precipitation, and flow regime through the basin. The impacts will be compounded by changing sediment dynamics, possibly with increased fine sediment deposition. Hence the benefits of operating HPPs, and their further development, must be balanced against potential environmental impacts as "with every new dam, additional environmental challenges emerge, and there are often contradictory energy and environmental targets" (Wagner et al., 2019). This illustrates the need to look at new ways to advance the scientific base for river basin management, and to ensure that the individual and cumulative effects of current developments are fully quantified.

Conclusion

The Danube River has been progressively impacted by hydropower developments that extend throughout the basin. At present only five free-flowing reaches remain on the Danube itself and hydromorphological processes have been impacted throughout the basin. While the basin is now relatively "mature" with respect to hydropower, many small hydropower plants have been proposed in the South and East of the DRB, and there are questions over how the basin might be managed to reconcile the need for continued hydropower generation, with the individual and cumulative environmental impacts of HPPs, throughout the basin.

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Relevant websites

https://www.icpdr.org/main—The International Commission for the Protection of the Danube River.
Recent EU projects
https://amber.international/—AMBER.
https://www.reformrivers.eu/—REFORM.

Hydropeaking: Processes, Effects, and Mitigation

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Flexibility (of the power system) The extent to which a power system can modify electricity production or consumption in response to expected or unexpected variability.

Hydraulic stress The measure of the internal force per unit area acting on liquids. In hydropeaked rivers, flow ramping leads to an increase of hydraulic stress for aquatic organisms, often facilitating involuntary downstream displacement (drift) or encouraging them to colonize shoreline areas in the ramping zone that will later fall dry, leading to stranding if organisms are not capable to follow receding water levels.

Hydropeak diversion power plant A hydropower plant that aims to prevent artificial flow fluctuations from occurring in the residual flow stretch created by the construction of a diversion weir.

Hydropeaking The discontinuous release of turbined water due to fluctuations of energy demand. Synonyms include *flow ramping*, *rapid flow fluctuations* or *artificial (sub-)daily flow alterations*.

Pumped-storage power plant Storage power plant which, in addition to turbines, also has electric pumps that enable energy storage by pumping up water to a higher reservoir for later hydropower use.

Ramping zone River area that is exposed to periodic wetting and drying due to fluctuations in water level caused by hydropeaking.

Re-regulation or compensation basin An artificial reservoir below the hydropower plant that retains turbine outflows to reduce hydropeaking intensity in the downstream river section.

River morphology The morphology of a river refers to the patterns and changes in river channel size, shape and bed material over time. It depends on the composition and erodibility of the bed and banks, the availability of sediment, the transport rates in relation to flow intensity, and riparian vegetation. Human activities such as hydropower affect river morphology by altering one or more of these elements and processes, and the equilibrium between them.

 https://doi.org/10.1016/B978-0-12-819166-8.00171-7

Run-of-river hydropower plant Hydroelectric power plant with limited water storage capacity where water is released at roughly the same rate as the natural flow of the river.
Sediment transport The movement and transfer of solid particles (from clay and silt to sand, gravels, and boulders) reacting to the shear forces exerted by a fluid (i.e., water) on the earth's surface, in particular regarding particle mobilized from the erosion areas (catchment's headwaters, river bed, slopes, landslides, etc.) through the fluvial network until distal deposition zones (deltas, estuaries, coasts).
Storage hydropower plant Hydroelectric power plant that stores water in a reservoir and converts the energy of the water into electricity when needed.

Introduction

The energy production scheme inducing 'hydropeaking' was first described in the 1930s in Europe (Vibert, 1939), and is now found throughout the world. Hydropeaking operations are defined as rapid and frequent changes in river flow to optimize hydropower operation (Widén et al., 2021). This rapid operation mode is closely linked to energy markets, which can exhibit quick shifts between production and demand, even changing at sub-daily scales. Fluctuations in energy availability and demand, therefore, directly translate into changes in turbine outflows to ensure grid stability, while generating highest profits (Olivares et al., 2021).

Hydropeaking comes with environmental costs, causing high variability of river flows on a daily or sub-daily basis in the receiving waterbodies. Hence, hydropeaking operations transform a river's hydrological signature and modify morpho-sedimentary dynamics, typically altering the downstream river ecosystem—to an extent that hydropeaking is regarded as one of the most significant impacts downstream of hydropower plants (Hayes et al., 2019).

The ecological effects of hydropeaking have been examined in a growing body of literature, and mitigation options, including dam operational changes and structural arrangements, are considered. This chapter builds upon the current knowledge to provide an overview of hydropeaking processes, effects, and mitigation. In particular, it aims to illustrate how the drivers of peaking-power production and the associated pressures are linked to river ecosystem structure, function and integrity, with a focus on hydro-ecological relationships. Finally, the chapter seeks to provide a process-based overview of mitigation measures from a river- and energy-grid-specific perspective (Fig. 1).

Drivers and pressures of hydropeaking: From a rising demand for renewables to artificial flow fluctuations

Pressing issues such as climate change, fossil fuel resources depletion and decommissioning of nuclear power plants call for an energy transition towards a low-carbon economy. Within this context, hydropower construction is on the rise (Zarfl et al., 2015). Indeed, hydropower is the only system that currently exists to store energy effectively, making up 99% of the global electricity storage capacity (World Energy Council, 2016). Also, hydropower is considered a mature technology that contributes to climate change mitigation by constituting a fundamental building block of today's energy systems. The last decade saw a sharp rise in renewable energy production, with wind and solar sources being increasingly developed (Berga, 2016). Energy production through wind and solar technologies is, however, very variable, but combined with storage hydropower, it can balance out irregularity in the system and supply peak load. These renewable energy sources complement each other well, particularly considering that hydropower from large reservoirs is to date the only reliable method of flexibly producing electricity—besides fossil fuels (Fig. 2).

At the hydropower facility, hydropeaking operations respond to market demands by quickly turning their turbines on (start of production) and off (stop of production). Start-stop operations can occur within minutes and they are difficult to predict in today's de-regulated energy market. In the future, hydropower production will have to increasingly buffer the inevitable energy grid

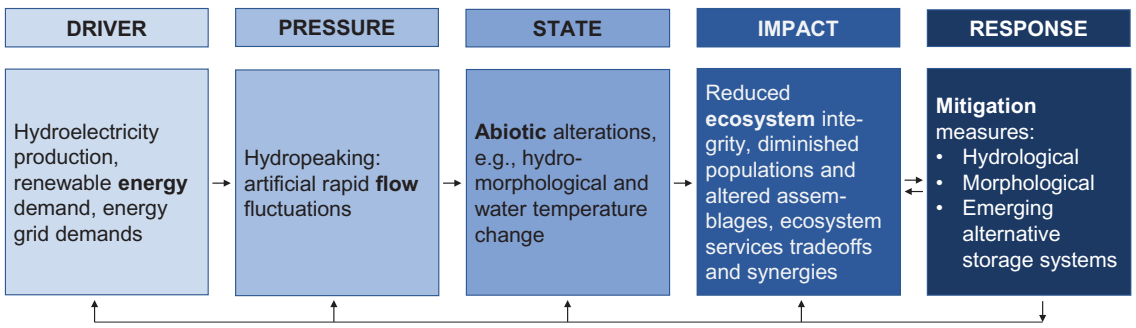

Fig. 1 A conceptual Driver-Pressure-State-Impact-Response (DPSIR) framework for hydropeaking research and management showing causal links and feedback loops.

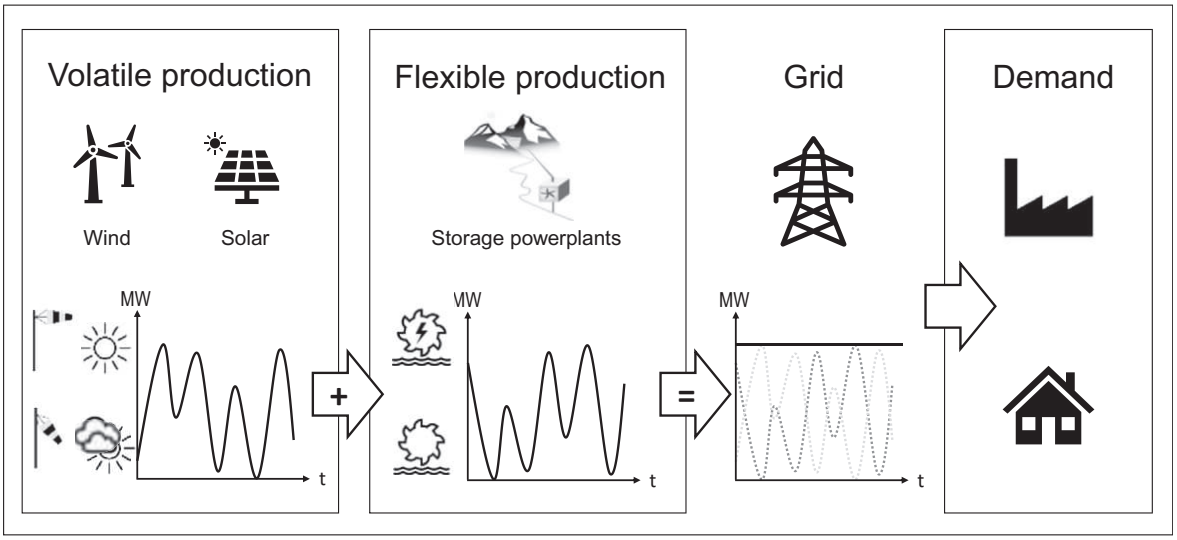

Fig. 2 Hydropeaking power production plays a key role in energy systems with increasing shares of renewables. Due to its flexibility, storage hydropower plants (and other flexible sources) can buffer volatile or intermittent energy sources such as wind and solar, thereby ensuring grid stability and security of supply—a systematic sketch.

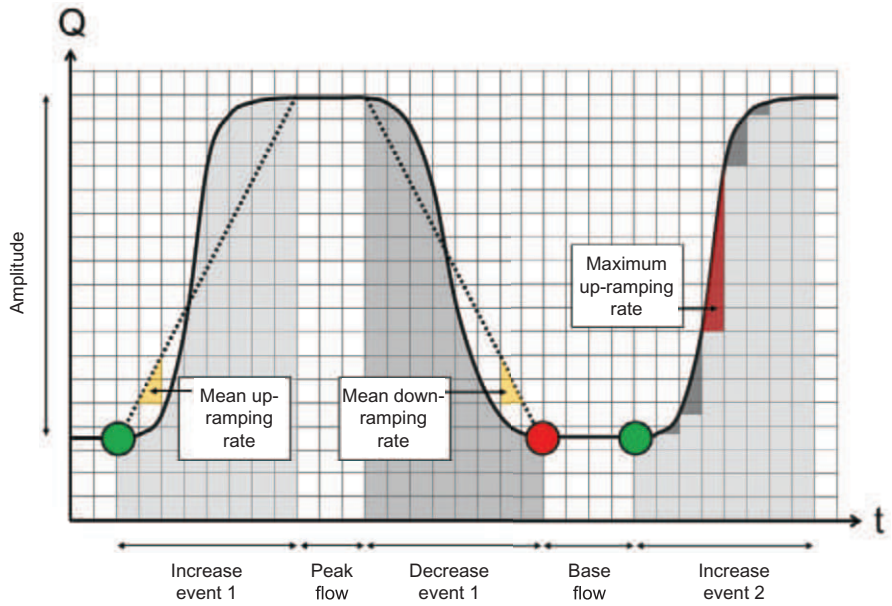

Fig. 3 A scheme of a hydropeaking hydrograph, linking operation start (green circle) and stop (red circle) to the flow regime components: peak amplitude, mean and maximum rate of change during up- and down-ramping, and peak flow or baseflow duration. The frequency and timing of hydropeaks (not illustrated here) describe how often and when (season, time of day) such flow events occur in a river. Modified after Greimel F, Zeiringer B, Höller N, Grün B, Godina R and Schmutz S (2016) A method to detect and characterize sub-daily flow fluctuations. *Hydrological Processes* **30**: 2063–2078. doi: 10.1002/hyp.10773.

fluctuations caused by intermittent renewable energy sources such as wind or solar. In essence, this current and future key function of the hydropower industry is linked to its capability of running hydropower turbines under peak-load conditions and shutting them off during phases of low electricity demand, possibly increasing hydropeaking events (Fig. 3). Indeed, such production schemes not only answer well to market demands but also constitute the backbone of the electricity production of mountainous countries such as Switzerland, Austria, Norway, and Sweden.

In addition to storage hydropower plants, also run-of-river hydropower plants may run a hydropeaking scheme, albeit at lower ranges between minimum and maximum production. A special sub-category of peak-operating hydropower plants are pumped-storage facilities that pump water to reservoirs at higher elevations during periods of low energy demand or costs. Once

the demand rises again, the pumped water is released and used to run the hydropower turbines (McManamay et al., 2016; Greimel et al., 2016). Moreover, other human activities can also cause hydropeaking-like conditions, e.g., manipulating gate structures, discharging effluents of wastewater treatment plants, or withdrawing river water for agricultural irrigation.

Hydropeaking hydrology principles

The hydrology of hydropeaked rivers differs from natural river hydrology in two distinct ways. Firstly, reservoirs store water (i.e., incoming river flow) to release it later when needed. Depending on their size, they can either cut off flood peaks (smaller reservoirs) or completely eliminate small and large floods (larger reservoirs). Such flow regulation results also in a homogenization or even total inversion of the seasonal flow regime downstream from the dam (Fig. 4A). Secondly, hydropeaking turbine operations, triggered by peaks in energy demand, result in rapid and often sudden flow changes which are not typical in natural river systems. Such operation schemes entail unnatural flood events in the downstream river section during peak-flow operation. During the shutdown, no or only little water remains in the river (Widén et al., 2021). In between these two flow scenarios, river levels rise (up-ramping) and drop (down-ramping) fast, thereby increasing the rate of change between flows of certain magnitudes (Figs. 3 and 4B–C).

These hydropeaks can be distinguished from natural flow fluctuation events by different intensity parameters such as the five flow regime components commonly used to describe river flows on various temporal scales (Poff et al., 1997). These flow regime components are flow amplitude or ratio, rate of change (also called ramping rate), peak frequency, event duration, and timing. For example, hydropeaking waves exhibit much faster ramping rates than flood waves occurring from rainfall or snow-glacier melt. Similarly, on a daily basis, hydropeaks also entail a higher baseflow: peak flow ratio, peak amplitude, and a shorter peak flow duration than natural flow fluctuation events. Moreover, the different stages of a hydropeaking wave—up-ramping, peak flow, down-ramping—are directly linked to the hydropower operational mode (Fig. 3).

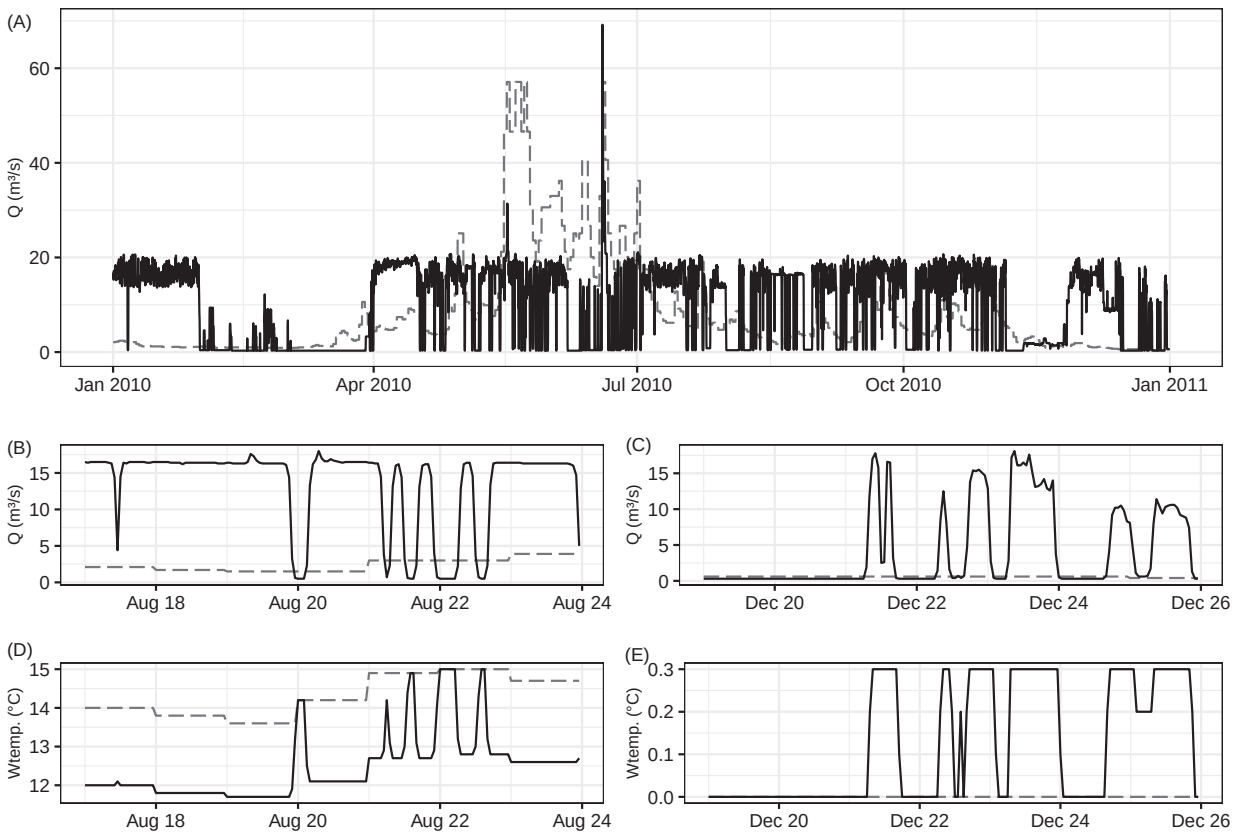

Fig. 4 Contrasting hydropeaking discharge (black solid line) in the Lundesokna River, Norway, with the modelled natural regime (grey dashed line). The panels show differences (A) in annual river flows, weekly river flows (B) in summer and (C) in winter, and weekly water temperatures (D) in summer and (E) in winter. Data resolution: 1 h. Data source: Casas-Mulet R, Saltveit SJ and Alfredsen KT (2016) Hydrological and thermal effects of hydropeaking on early life stages of salmonids: A modelling approach for implementing mitigation strategies. *Science of the Total Environment* **573**: 1660–1672. doi: 10.1016/J.SCITOTENV.2016.09.208.

Effects of hydropeaking

Hydrological regime alterations

Hydropeaking completely transforms the hydrological characteristics of a river on an annual, seasonal (Fig. 4A), daily and sub-daily time scale (Fig. 4B and C). In Europe's mountain rivers, for example, hydropeaking is most pronounced during winter when high peaks of energy demand—resulting in high-intensity hydropeaking—occur during the low flow period when runoff is held back in the form of snow and ice cover. Daily fluctuations of such magnitude only occur rarely and at specific times in free-flowing rivers, and with smoother ramping rates. Regarding peak frequency, glacier-influenced rivers can experience around 100 days per year with significant melt-events; but in hydropeaked rivers, peaks can occur even more frequently, for example, more than 300 days per year in Alpine rivers of Austria (Greimel et al., 2016), although this number can be quite variable—depending on the region, river, or season. In California rivers, for instance, more peaking generally occurs during the dry season than during the wet season. Also, drought years feature increased hydropeaking frequencies over non-drought years (Li and Pasternack, 2021).

Overall, such daily or sub-daily patterns of rapid flow fluctuations are typical of many storage hydropower plants and run-of-river facilities. In addition to characterizing hydropeaking stretches through analyses of single gauges, it shall be noted that flow parameters such as peak ratio, amplitude or ramping rates change along a river's course, underlining the necessity to also incorporate longitudinal viewpoints into more holistic assessments. Due to water retention effects, flow parameters such as peaking intensity usually reduce in the downstream direction. Often, the first few kilometers downstream from the turbine outlets feature the highest hydropeaking intensities. However, the peaks can often still be measured up to 40 km or further downstream of the tailrace (Moog, 1993).

Thermopeaking: Water temperature changes due to hydropeaking

Artificial reservoirs exhibit seasonally different temperatures and tend to form distinct thermal layers during warm and cold weather at the surface, through the water column, and at the bottom. Under such conditions, the release of hypolimnetic (i.e., bottom-layer) water from stratified reservoirs can lead to abrupt sub-daily changes in water temperature in the receiving water body. The pattern of these temperature changes, called 'thermopeaking', is closely linked to hydropeaking (Zolezzi et al., 2011). In temperate regions, these thermal waves lead to a sharp decrease in the stream temperature in summer—cold thermopeaking (Fig. 4D)—and to an increase in winter—warm thermopeaking (Fig. 4E). Similar to hydropeaking waves, the magnitude of temperature changes decreases with the distance from the turbine outlet (Vanzo et al., 2016a) and often there is a decoupling of hydrological and temperature waves (Toffolon et al., 2010; Zolezzi et al., 2011; Fig. 4B–E).

Geomorphological alterations

It is known that changes in sediment transport and deposition alter fundamental characteristics of the streambeds over long time scales and that those changes can alter flow hydraulic conditions, which in turn enable feedback processes that may be critical in hydropeaked rivers (e.g., regarding marked changes in turbidity). Hydraulic changes alter the sedimentary structure and processes acting on the river bed; these include mobility and transport (Vericat et al., 2020), particle entrainment (López et al., 2020), and fine sediment deposition, infiltration (clogging) or porosity (Casas-Mulet et al., 2018; Hauer et al., 2019). Streambed morphology can have a key role in buffering the ecological effects of hydropeaking. Also, considering that sediment transport is fundamental in shaping river habitat, preserving morpho-sedimentary dynamics may aid in reducing undesirable effects derived from peak-energy production (Batalla et al., 2021).

In hydropeaked rivers, changes over time become particularly evident at the river reach scale, and morphological conditions entail direct ecological consequences. For example, as sediment size and bed topography influence the movement of water through the river bed, any changes related therewith entail implications for the delivery of oxygen to fish eggs and embryos that develop within the subsurface zone (Batalla et al., 2021). Overall, braided reaches are considered rather resilient to hydropeaking as they offer the highest habitat diversity and very limited base-to-peak variation, thereby entailing only low drift rates of macroinvertebrates. Alternate bars, in contrast, are extremely sensitive environments to drift, but they do offer safer regions from stranding (see section "Ecological impacts linked to flow alterations" for more information). In turn, transitional morphologies between single-thread and multi-thread offer the best eco-hydraulic trade-offs, according to hydraulic modelling approaches (Casas-Mulet et al., 2015a; Vanzo et al., 2016b). Sedimentary structure at the patch scale is critical to sustain species micro-habitats and it is also affected by hydropeaking (Table 1). However, the exact mechanistic causes of all these bio-physical alterations and feedback mechanisms remain unclear; hence more research is still needed in this direction, also as a sound base to support rehabilitation programs.

Other abiotic changes due to hydropeaking

Hydropeaking can further entail changes in dissolved gases saturation ('saturopeaking'; Pulg et al., 2016) or underwater sounds ('soundpeaking'; Lumsdon et al., 2018). Saturopeaking refers to fluctuations of gas saturation that follows the pattern of hydropeaking waves, and soundpeaking describes temporal variations in the sound frequency composition; the reader is referred to

Table 1 Examples of abiotic river attributes affected by continuous hydropeaking.

Attributes	*Effect*	*Causal processes*	*Scale*
Water turbidity	Increase	River bed resuspension, bank erosion	River reach, i.e., 10^2 m
Bed armor	Increase	Selective particle entrainment, fine sediment depletion (winnowing)	Particle and patch, i.e., 10^{-3}–10^{-1} m
Bed roughness	Increase	Selective particle entrainment	Patch to reach, i.e., 10^{-1}–10^2 m
Bank stability	Decrease	Unsteady wave heights, pore pressure variation, peak flow duration, discharge amplitude	Reach, i.e., 10^2 m
Water surface width	Highly variable	Sudden and repeated flow increases and decreases	Patch to reach, i.e., 10^{-1}–10^2 m

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Moreira et al. (2019) for a concise overview on these topics. Recently, also 'carbopeaking' has been described as CO_2 leaks downstream of hydroelectric reservoirs (Calamita et al., 2021).

Ecological impacts

Hydropeaking is considered a key stressor in river ecosystems, altering habitat conditions, local food webs, and a suite of ecological processes. To illustrate flow-ecology relationships in hydropeaked rivers, the following section describes specific processes linked to separate flow parameters and phases of a hydropeak as described in section "Hydropeaking hydrology principles". Indeed, river biota shows distinct responses to those different flow alterations (Fig. 3; Table 2), which are also directly linked to morphological conditions and other physical changes (sections "Geomorphological alterations" and "Other abiotic changes due to hydropeaking").

The main biotic response variables used to quantify effects of hydropeaking are organism drift (involuntary downstream displacement) and stranding. Indirect effects include reduced food availability, decreased growth rates, as well as reduction in reproduction success and fitness. In time, these adverse effects lead to altered biotic community structures and changes in species composition in rivers subject to hydropeaking (Schmutz et al., 2015; Smokorowski, 2021).

Ecological impacts linked to flow alterations

Peak amplitude and base: peak flow ratio. Hydropeaked rivers experience fluctuating hydraulic forces. An increase in discharge leads to an increase in flow velocity and bottom shear stress. To cope with such quickly changing conditions, aquatic organisms such as macroinvertebrates and fish must invest significant amounts of energy to avoid detachment from the substrate or downstream displacement. Field and experimental studies have shown that this so-called involuntary or catastrophic drift of organisms is strongly linked to the amplitude and the flow maximum of hydropeaking events, which are key determinants of river hydraulics. The tolerance towards hydraulic stress differs between species and life cycle stages, which may exhibit varying sensitivity towards flow as well as different behavioral and physical adaptations to flowing water (Hayes et al., 2019; Smokorowski, 2021). Nevertheless, an increase in flow-related parameters, such as water depth and flow velocity, leads to increased physical stress acting on the animals and hampers vital processes, such as feeding. Further, the exceedance of hydraulic thresholds leads to detachment of organisms from substrates and downstream transport, which, if exceeding natural drift rates, depletes the populations (Schülting et al., 2016; Auer et al., 2017). Thus, tolerant species (which own morphological or behavioral adaptations like claws or the ability to quickly crawl into the interstices) often dominate over sensitive ones (e.g., surface-dwelling taxa that are exposed to flow changes) in hydropeaked rivers, which feature altered biotic community structures as well as reduced biomass (Moog, 1993; Hayes et al., 2021). Further, the flow amplitude is directly linked to the area of the dewatered shoreline, which in turn affects stranding of organisms. Flooding and drying of shore areas additionally lead to challenging conditions for riparian vegetation, since processes like germination and plant establishment are constantly disturbed. The water level and related parameters such as drag forces are directly linked to the flow amplitude and were found to be a key parameter determining plant survival. Under hydropeaking, species that own adaptations like adventitious roots are therefore favored (Bejarano et al., 2018, 2020).

Ramping rate. Another feature of hydropeaking waves are the fast rates of change in the flow increase and decrease (Figs. 3 and 4B–C). There is evidence that the up-ramping rate is significantly linked to stream organism responses: fast flow increases reduce the time response for seeking shelter, thus leading to increased drift rates of aquatic organisms when hydraulic conditions exceed tolerance thresholds (Schülting et al., 2019; Smokorowski, 2021). The decrease of discharge during a hydropeaking event plays a minor role regarding downstream drift. However, down-ramping strongly affects the risk that aquatic organisms strand on previously inundated areas that fall dry as water recedes back into the main channel. This phenomenon is especially relevant for fish (e.g., Young et al., 2011; Auer et al., 2017) but has also been documented for macroinvertebrates. As a general rule, the faster the down-ramping rate, the higher the stranding risk as animals fail to conduct timely lateral shifts with the receding water table. Fish larvae, in particular, are at greater risk of becoming stranded. On the one hand, larvae are still weaker swimmers; on the other hand, fish larvae inhabit river areas especially prone to drying out or being cut off from the river after a hydropeak (Greimel et al., 2018b;

Table 2 Summary overview that links hydropeaking flow alterations to abiotic properties, ecological processes and impacts, and describes associated mitigation options.

Flow parameter	*Abiotic effects/change in state*	*Ecological process*	*Ecological impact*	*Response: mitigation recommendation*	*Key references*
Peak amplitude, flow ratio, magnitude	Change in hydraulic forces Change in water level and wetted width Increased (sub-) daily maximum flow magnitude Substrate mobilization/ scouring Decreased (sub-) daily minimum flow magnitude Fine sediment deposition, clogging of gravel bars	Habitat shifts (to refugial habitats) Hydraulic stress Downstream displacement of fish and macroinvertebrates (catastrophic drift) Scouring of algae from the substrate Inhibition of germination and growth performance Fish (egg) damage and macroinvertebrate removal Soil moisture deficit and water stress for plants Desiccation or freezing of fish eggs or macroinvertebrates Restricted fish movements Reduction of suitable aquatic habitats and oxygen supply, habitat loss within interstices	Increased mortality Reduced reproduction success Food depletion Reduced population biomass Reduction in community richness Selection of tolerant species	Reduce peak flow amplitude and flow ratio, especially during critical seasons/times Decrease maximum peak flow magnitude Increase minimum flow magnitude between hydropeaks	Bretschko and Moog (1990), Moog (1993), Casas-Mulet et al. (2015a,b), Irvine et al. (2015), Bondar-Kunze et al. (2016), Bejarano et al. (2018) and Hayes et al. (2021)
Ramping rate	Up-ramping: unnaturally rapid flow increase, quick increase in hydraulic forces Down-ramping: unnaturally rapid flow decrease, quick drying of previously wetted areas	Downstream displacement of fish and macroinvertebrates (catastrophic drift) Hampered plant germination Stranding Hampered plant germination	Increased mortality Reduced population biomass Selection of flow tolerant species	Lower ramping rates below ecologically relevant rates of change	Young et al. (2011), Bruno et al. (2016), Hayes et al. (2019), Moreira et al. (2019), Schülting et al. (2019) and Bejarano et al. (2020)
Duration	Extended periods of minimum and maximum flows	Increased likelihood of macroinvertebrate and fish (egg) desiccation and death following stranding Aquatic plant stress when emerged too long Riparian plant stress when inundated too long	Increased mortality Reduced population biomass Changes in species composition	Smoothen (sub-) daily hydrograph curves	Perry and Perry (1986), Casas-Mulet et al. (2015a,b) and Bejarano et al. (2018)
Peak frequency	Increased number of flow reversals entail recurring fluctuations of water level and hydraulic forces	Habitat shifts (to refugial habitats) Involuntary drift Stranding Frequent inundation of riparian areas	Higher energy consumption and less feeding time Reduced population biomass Reduced growth and reproduction success Increased mortality Changes in species composition (selection of tolerant species)	Lower hydropeaking frequency, especially of large peaks and during critical seasons (e.g., reproduction or early life-cycle stages)	Bauersfeld (1978), Schmutz et al. (2015) and Hayes et al. (2019)
Timing	Seasonality Time of day Thermopeaking	Increased macroinvertebrate drift during warm period Increased fish stranding at larval stages and/or during cold period Increased macroinvertebrate and fish larval drift and fish stranding during night Thermal modification can lead to increase or decrease in above mentioned drift- and stranding patterns depending on direction and organism	Increase in above-mentioned impacts if hydropeaking occurs during sensitive times Changes in structural and functional community patterns Altered life cycle patterns Possible intensification or mitigation of some of the above-mentioned impacts	Adapt mitigation frameworks such as flow rules to ecologically-sensitive times, e.g., by implementing an 'emergence window' Reduce amplitude of temperature changes	Kennedy et al. (2016), Greimel et al. (2018b), Hayes et al. (2019) and Moreira et al. (2019) Bruno et al. (2013), Casas-Mulet et al. (2015a,b, 2016), Schülting et al. (2016), Vanzo et al. (2016a) and Bondar-Kunze et al. (2021)

Hayes et al., 2019). In this context, the local morphological characteristics play an important role: The risk of stranding is potentially higher if low sloped and heterogenous riverbanks with coarse sediment are present. However, such river banks also provide better habitat conditions for young fish, compared with steep and homogenous riparian structures (Larrieu et al., 2021). Finally, studies showed that both rapid flow in- and decreases reduce germination success of flood-intolerant species of riparian vegetation (Bejarano et al., 2020).

Frequency and duration. Drift of macroinvertebrates was found to decrease quickly during the extent of the peak flow phase; in contrast, stranding often increases with the duration of peaking due to higher colonization rates of the shore habitats (Perry and Perry, 1986). The duration of dewatering in the ramping zone is also key to determine the potential survival of stranded organisms in isolated pools (Young et al., 2011) as well as in the subsurface or hyporheic zone (Casas-Mulet et al., 2015b). The frequency of general hydrological disturbances is known to affect aquatic communities. In the case of hydropeaking, some species, such as juvenile grayling (*Thymallus thymallus*) may show (temporal) adaptation behavior to recurring peaking (Auer, unpubl. data). However the effects may also accumulate with increased peaking frequency (Bauersfeld, 1978; Bruno et al., 2016). Increasing frequency and duration of hydropeaking was found to intensify stress on riparian vegetation and affect germination as well as plant survival (Bejarano et al., 2018, 2020).

Timing. The effects of hydropeaking on aquatic organisms can largely vary between seasons and even between different times of the day. One major reason for seasonal variation is that the sensitivity towards hydraulic stress is strongly life stage-specific. For example, as mentioned above, stranding can be observed mostly for fish larvae as fish become less susceptible to stranding as they grow in size (Hayes et al., 2019). In addition, the seasonal changes in water temperature strongly affect organism responses to hydropeaking as lower water temperature during winter lowers the activity of most species and subsequently affects drift and stranding patterns. Studies have shown that the drift and stranding differ between day and night because of a combination of light intensity and organism activity (Smokorowski, 2021). For example, macroinvertebrate drift is commonly lower during the night because insects actively seek flow-exposed areas during the night for feeding, among other reasons.

Ecological impacts linked to thermal alterations

Water temperature is a key physical property of river flows and a primary driver for community patterns of riverine organisms and for ecological processes. Hence, thermal modifications caused by the operation of hydropower can significantly affect river biota. However, the effects of thermopeaking on aquatic communities have not been extensively studied, and it remains a challenge to disentangle the effects of hydro- and thermopeaking (Bruno et al., 2013). In any case, thermal modification may act as an additional stressor on periphyton, macroinvertebrates and fish, leading to changes in structural and functional community patterns as well as to altered life cycle patterns. A study on periphyton development under combined hydro- and thermopeaking showed that sudden fluctuations in flow and water temperature affect biomass and community structure: cold thermopeaking in summer enhanced algal biomass and diatom development, whereas warm thermopeaking in winter led to decreased algal biomass development and an increase in green algae (Bondar-Kunze et al., 2021). Through a modelling approach, Casas-Mulet et al. (2016) illustrated how warm thermopeaking events encourage early salmonid embryo hatching in winter, and increase stranding mortality in alevin stages during dewatering events, with egg stages being less susceptible to desiccation. Further experimental studies have shown that hydropeaking-induced macroinvertebrate drift and fish stranding patterns may change in combination with warm and cold thermopeaking (Carolli et al., 2012). The directions of response are, however, quite variable and more research is needed to identify general patterns (Smokorowski, 2021) (Table 2).

Socio-cultural impacts: Ecosystem services

Hydropower production schemes and hydropeaking affect not only the biotic river community, but they can also influence other ecosystem services that river systems provide. In principle, hydropeaking can impact each ecosystem service that depends on the biotic and abiotic parameters previously described as flow, morphology, and sediment transport. In contrast to river biota, hydropeaking shows positive and negative relations with ecosystem services. For example, in late summer to early fall, only hydropeaking events provide suitable conditions for recreational services such as rafting and kayaking in Alpine rivers: during baseflow conditions, water depth and water velocity—two parameters directly linked to river flow—may not be sufficient to enable boating (Carolli et al., 2017b). Higher river flows due to hydropower production have also been linked with enhanced user preferences and with a higher aesthetical value (Pflüger et al., 2010). In contrast, hydropeaking also shows negative effects on ecosystem services: by affecting fish habitat and species communities. Hence, hydropeaking can negatively influence recreational services such as angling (Carolli et al., 2017a).

Mitigation measures

The heavily altered state of many hydropeaked rivers calls for the timely implementation of effective measures to counteract many of the above-described environmental effects (Table 2). In this regard, hydropeaking mitigation measures can be grouped into two broad categories: (i) hydrological and (ii) morphological measures. While the first group of measures aim to modify the peak hydrograph directly, the second group seeks to mitigate adverse effects indirectly by improving hydraulic conditions in the affected river section (Greimel et al., 2018b; Table 3).

Table 3 Hydropeaking mitigation measures and emerging alternative storage systems—a non-exhaustive overview.

Measure group	*Measure type*	*Details*	*Related costs and concerns*
Hydrological mitigation: operational	Increase of residual flow magnitude	Higher environmental flow allocation to reduce drawdown range, esp. during critical periods	Decline in revenue Loss of flexibility
	Turbine flow limitation	Lower peak flow magnitude	Decline in revenue Loss of flexibility
	Anti-cyclical operation of different hydropower plants	Lower peak flow and increase baseflow for a more constant flow in the whole river system	Decline in earnings due to production during low demand Loss of flexibility Legal constraints (e.g., water table prescription in reservoir)
	Lower up- and down-ramping operations	Decrease flow ramping to avoid drift and stranding of organisms	Decline in revenue Loss of flexibility
Hydrological mitigation: constructional	Powerhouse outflow into a lake (or ocean or fjord)	Turbine outlet directly connected to a lake to avoid hydropeaking in the river	Lake too far away Construction costs Impact on lake ecosystem
	Powerhouse outflow into a side channel or tunnel	Parallel side channel or tunnel to evacuate the turbine water without impacting the river	Land availability Construction costs Groundwater impacts
	Compensation basin	Powerhouse outflow into a storage basin with a controlled outflow to the river	Land availability Construction costs Fluctuating water level (recreation) Volume depending on the turbine outflow
	Compensation cavern	Powerhouse outflow linked with an underground retention basin with a controlled outflow	High construction costs Volume depending on the turbine outflow
	Powerhouse outflow into a basin (of a run-of-river power plant)	Basin located on the river, controlling flow through turbines or weirs	Land availability Construction costs Fish migration, sediment transport
	Powerhouse outflow into lake and residual run-of-river flow release	Existing hydropower plant used in run-of-river mode for environmental flows release and new parallel system for peak flow production	Construction costs Decline in earnings due to run-of-river operations during low energy demand
Morphological mitigation: indirect measures	Channel widening	Widening of river cross-section to reduce peak amplitude and hydraulic forces	Land availability Construction costs
	Reconnection of tributaries and creation/ maintenance of side channels	Establish connectivity to instream flow refugia	Land availability Construction costs
	Channel restructuring: instream measures	Increase macro-roughness and enhance habitat structures	Legal and environmental constraints
Emerging alternative energy storage systems and complementary measures	Floating solar panels on reservoirs	Add additional energy generation source whilst lowering water evaporation losses	Construction costs Possible environmental constraints
	Inflatable balloons in reservoirs	Displacing water by balloons allows for a higher flexibility of energy production	Construction costs Operating costs Possible environmental constraints
	Compressing air into excavated caverns (air cushion underground caverns)	Underground caverns give additional water volume to the adjacent reservoir. In the caverns, air is used to displace water and subsequently to adjust water levels for hydropower production	Construction costs Operating costs
	Energy storage in batteries	Store energy in batteries and extract during phases of high demand	More research and development needed Construction costs
	Pumped-storage facilities	Turning storage hydropower into pumped-storage facilities guarantees production flexibility while not releasing all of the water into the river	Land availability Construction costs
Measure integration	Combination of measures	Combinations of different mitigation measures may lead to more cost-effective outcomes, for example, by combining a compensation basin and channel widening measures as depicted in Fig. 6.	

Modified from Person É (2013) *Impact of Hydropeaking on Fish and Their Habitat.*; Greimel F, Schülting L, Wolfram G, Bondar-Kunze E, Auer S, Zeiringer B et al. (2018b) Hydropeaking impacts and mitigation. In: Schmutz S and Sendzimir J (eds.), Riverine Ecosystem Management, pp. 91–110, Springer.

Hydrological mitigation measures

Hydrological improvements can be attained by either (a) operational or (b) constructional measures. The first adjusts the hydropower plant's mode of operation to reduce peak-intensity parameters such as lowering ramping rates, flow amplitude, or hydropeaking frequency. These hydrological changes may bring direct environmental improvements; for example, by reducing down-ramping to below critical thresholds fish stranding can be avoided (Fig. 5). Also, higher baseflows can be released to avoid critical river reaches falling dry between peaks (Hayes et al., 2019; Moreira et al., 2019). However, from the economic perspective, mitigation approaches that restrict turbine operation lead to lost profits due to loss of flexibility (Greimel et al., 2018a; Table 3).

The second sub-group, structural measures, includes add-on constructions to the existing hydropower facilities. If the river valley offers enough space, the construction of re-regulation or retention basins is an effective option to dampen hydropeaking intensity and increase minimum flows. The hydrological effects in the tailrace can be similar to those of operational measures mentioned earlier (Figs. 5 and 6). Depending on its size, retention basins usually do not require changes in the hydropower plant's operational mode as they catch and retain the peak flow in the basin, and ensure a smoother water release to the river. Except for reservoir construction investments, retention basins do not incur permanent losses of profits (Greimel et al., 2018a; Anindito et al., 2019). Another option to change hydropeaking hydrology is to build a hydropeak diversion power plant that pipes peak flows to a downstream facility. From an operator's perspective, this measure can increase economic revenue after investments are redeemed. From an ecological perspective, results may be far from optimum since the affected river reach turns into a residual flow stretch that requires specific environmental flow allocations. Hydro-numeric simulations for the Austrian GKI case study (see Table 4) show that peak-diversion can indeed lower fish stranding risk (Moreira et al., 2020). However, the hydropeaking stretch is only moved further downstream—albeit larger rivers can potentially cope better with (comparably smaller) peaks than smaller rivers. A further solution to avoid hydropeaking in rivers is to divert the peak into a lake or construct a retention basin at the turbine outflow of the diversion hydropower plant (Table 3).

Morphological measures: Indirect mitigation

The second mitigation block includes physical modifications in the channel of the hydropeaked river to improve habitat structures and/or to create refugial areas. Such morphological measures seek to mitigate adverse effects by indirectly improving hydraulic conditions in the river, but not affecting hydropower operation (Fig. 6). Channel widening or side channel maintenance can reduce flow amplitude and associated hydraulic forces, and tributary reconnection can aid recruitment of aquatic biota by providing spawning and rearing areas without hydropeaking. Placement of large blocks and deflectors may also enhance structural heterogeneity of the channel, helping to dissipate flow energy and offering refugia to fauna. A recent fish population study, however,

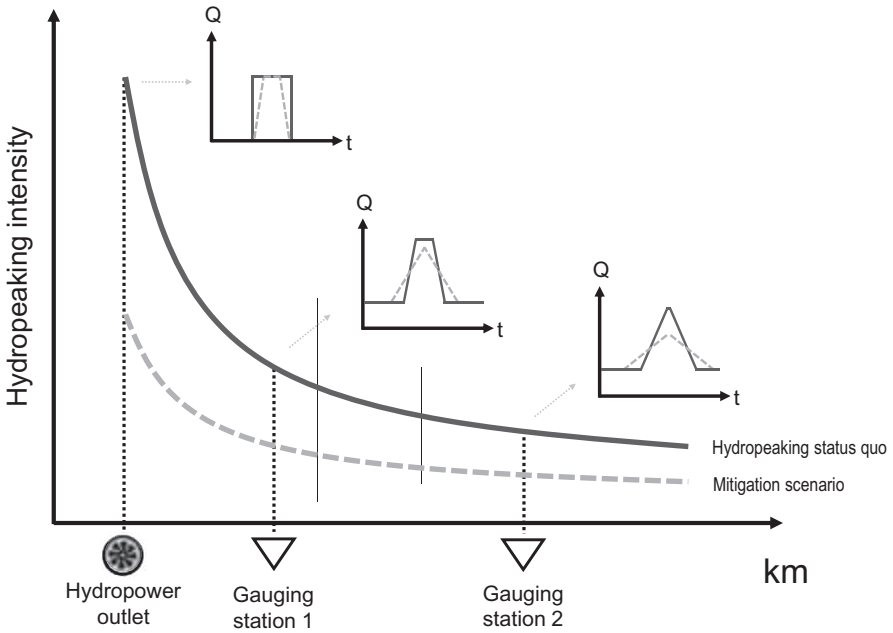

Fig. 5 Hydrological changes through operational and/or constructional measures can lower hydropeaking intensity in the affected river reach. Shown here is how hydropeaking intensity, such as down-ramping rate, changes in downstream direction (bottom graph) and how these hydropeaking waves are measured at the hydropower outlet and at two successive gauging stations (top three graphs). The dark grey solid line illustrates a hydropeaking status quo, the light grey dashed line a mitigation scenario based on hydrological improvements. Modified from Muhar S, Arnaud F, Aschwanden H, Binder W, Broggi M, Greimel F et al. (2019) Restoration. New life for the rivers of the Alps. In: Muhar S, Muhar A, Egger G, and Siegrist D (eds.), *Rivers of the Alps. Diversity in Nature and Culture*, pp. 320–343, Berne: Haupt.

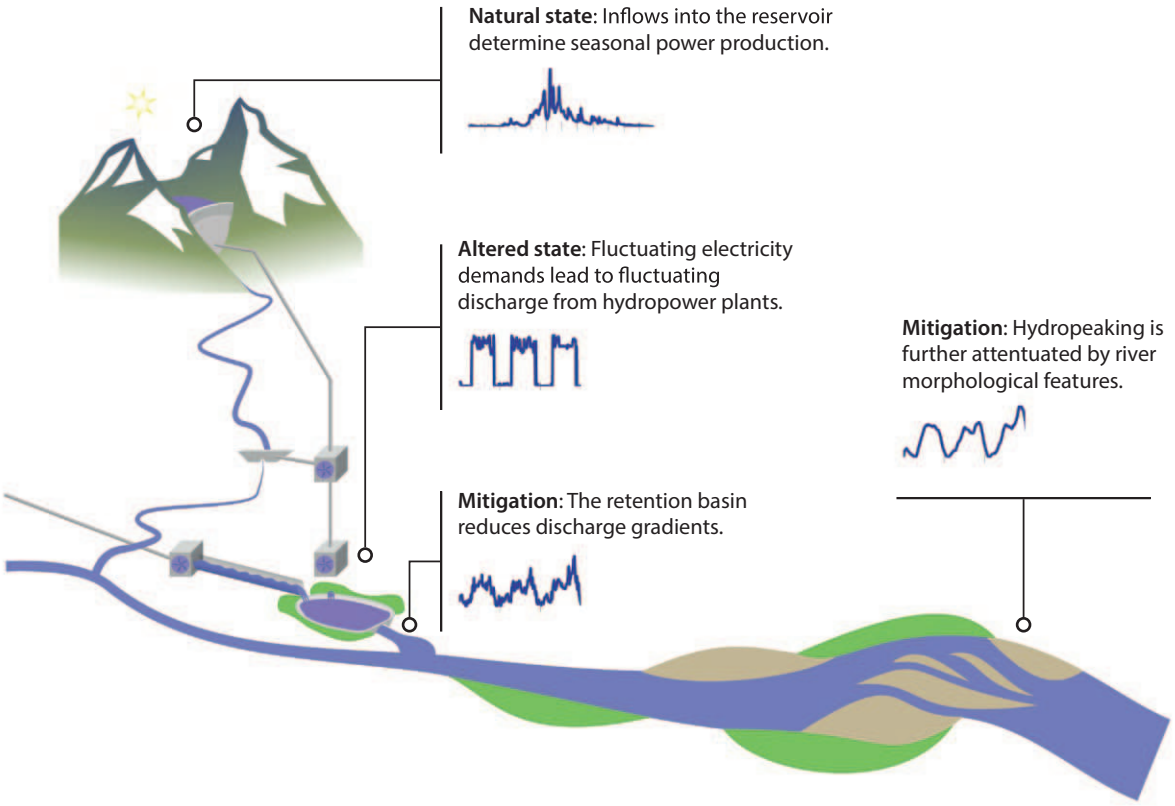

Fig. 6 A systems perspective on hydropeaking mitigation: how retention basins and morphological measures (e.g., channel widening, side channel creation) reduce peak intensity. Modified from Philipp Falke (MeteoSwiss).

indicated that 'the full benefits of river rehabilitation measures can only become visible if hydropeaking intensity is reduced at the same time' (Hayes et al., 2021). In this regard, it is not surprising that the combination of hydrological and morphological measures is projected to lead to greater ecological improvements at national scale (Greimel et al., 2018a).

Emerging alternative energy storage systems and complementary measures

Aside from the measures described above, which have hardly changed since the mid-1980s (Smokorowski, 2021), new (energy system-specific) methods or storage systems are arising. These solutions include, for example, the use of floating solar panels on reservoirs (Farfan and Breyer, 2018), inflatable balloons in reservoirs, or compressing air into excavated caverns to displace water (Storli and Lundström, 2019; Table 3). Also, electricity storage in electric vehicles to compensate for peak energy demands has been suggested (Román et al., 2019). A recent study suggests that by 2025 batteries will become economically viable to aid hydropeaking mitigation (Anindito et al., 2019). Indeed, affordable energy storage and solar systems are deemed sufficient to avoid severe hydropeaking in the renewable energy systems of the future (Haas et al., 2019).

Overall, such 'traditional' and new innovative measures or storage systems are needed to guarantee a *quasi*-green energy system and sustainable peaking production in the future, despite inevitable impacts (as discussed above). To date, however, hydropeaking is, at its heart, still a controversial issue. It is commonly recognized that hydropeaking cannot (yet) be entirely avoided. In this regard, its socio-economic benefits and balancing role must be weighed against its environmental effects.

Mitigation case studies

Despite the phenomenon of hydropeaking being globally widespread, there is still a lack of mitigation measures to be comprehensively implemented. Indeed, the literature contains only few such case studies. Most of them are from North America and Europe (Moreira et al., 2019). Some of these case studies are highlighted in Table 4 and include mitigation through a compensation basin, diversion hydropower plant, or operational restrictions.

For instance, the Upper Inn River, Austria, is affected by frequent hydropeaks with ramping rates exceeding ecological thresholds, heavily impacting fish populations. As a mitigation measure, a diversion power plant is currently being constructed. Once in

Table 4 Case studies illustrating hydropeaking and mitigation measures worldwide.

Name of site	*River, country*	*Coordinates*	*Current state and mitigation approach*	*Evaluation of mitigation measures*	*Key reference(s)*
Gemeinschaftskraftwerk Inn (GKI)	Inn River, Austria and Switzerland	47°4′4.78″N, 10°39′54.37″E	Newly constructed hydropower station diverting water from the Upper Inn River at the Swiss border 23 km downstream to the Austrian powerstation Prutz. Environmental flows and operational hydropeaking restrictions are implemented in the diversion stretch.	Construction still in progress.	Moreira et al. (2020) https://www.gemeinschaftskraftwerk-inn.com
Hydropower plant Alberschwende	Bregenzerach River, Austria	47°28′25″N, 9°50′ 59″E	In 1992, a new diversion hydropower plant was built together with a retention basin (volume: 150,000 m³) to buffer hydropeaking. Additionally, base flow is increased slowly 24 h prior to peaking operation to reduce total peak amplitude.	Reduction of peak flow ratio and ramping rate lead to macroinvertebrate biomass recovery, but regarding fish no improvement was documented.	Grasser et al. (1998) and Parasiewicz et al. (1998)
Hydropower plant Innertkirchen	Hasliaare River, Switzerland	46°42′30″N, 8°13′29″E	The following measures were realized from 2013–2016: construction of retention basins (total volume: 80,000 m³), morphological instream structures, increase of base flows.	A decrease of ramping rates led to an increase of macroinvertebrate biomass and fish productivity; however, fish stranding could not be significantly reduced.	Tonolla et al. (2017) and Schweizer et al. (2021)
Sokna kraftverk	Lundesokna River, Norway	63°08′59.5″N, 10°18′23.1″E	Constructed in 1964, the Sokna hydropower plant affects the Lundesokna River 5 km before it reaches the unregulated Gaula River. The upcoming relicensing process will consider either operational or constructional measures, given the legal requirements and the high conservation interest of the Gaula River.	Not yet implemented.	Casas-Mulet et al. (2016)
Steephill Falls hydropower plant	Magpie River, Canada	48°4′41.17″N, 84°44′18.23″W	From 2002–2007, an adaptive management experiment was run to test the notion that minimum flow allocations and ramping rate restrictions provide ecological benefits.	Macroinvertebrate abundance and diversity decreased after ramping restrictions were lifted, implying that restricted operations were protective of river biota.	Smokorowski (2010)
Gordon Power Station	River Gordon, Tasmania, Australia	42°44′25.79″S, 145°58′56.73″E	Adaptive management principles were applied to establish an optimal ramp-down rule to minimize seepage while allowing operational flexibility. Down-ramping is deemed necessary when bank saturation exceeds defined trigger values and power station discharge is above 150 $m^3 s^{-1}$.	The revised ramp-down rule was monitored and assessed since 2012 and was found to reduce seepage erosion.	https://www.hydro.com.au/environment/environmental-management/monitoring-the-gordon-river

operation, this facility will reduce ramping rates to levels considered adequate for protection of young-of-the-year fish, whilst enabling increased energy production in the region (Moreira et al., 2020). A diversion power plant and a compensation basin was constructed at the Austrian Bregenzerach River in the early 1990s, and evaluations of this measure showed a positive trend for macroinvertebrates but not for fish (Parasiewicz et al., 1998). The Swiss Hasliaare River is one of the best-known examples of compensation reservoirs. Recent evaluation revealed that particularly the combination of basins and instream measures led to achieving sought ecological targets (Schweizer et al., 2021; Table 4). The heavily hydropeaked Lundesokna River, Norway, is a major tributary of the Gaula River, one of the last unregulated rivers in Norway of high conservation value that entails special requirements for environmental protection. To date, no mitigation measures have been set in place. However, the upcoming relicensing process of the Sokna hydropower station pushes the conversation between the local council and the energy company to implement either operational constraints or structural measures to target key environmental needs in both rivers (Table 4). The Gordon Power Station is the largest power station in Tasmania, Australia. Hydropeaking at the Gordon was projected to increase following the commissioning of an undersea power cable to connect Tasmania with mainland Australia. A research and monitoring program was implemented from 2002 to 2020 to detect impacts on the ecology and fluvial geomorphology of the Gordon River caused by hydrologic changes resulting from joining the national electricity market. Under the program, a ramp-down rule to minimize seepage erosion due to hydropeaking was devised, implemented and refined through adaptive management (Table 4).

Synthesis

In this chapter, we illustrated links between peaking-power production and ecosystem integrity/function, as well as gave an overview of mitigation measures from a river-specific and energy-grid-specific perspective. In summary, hydropeaking remains a controversial topic. Storage hydropower offers to date the best way to store energy at the large scale, and the flexible energy generation capacity of start-stop production makes peaking power an indispensable part of the power fleet, in particular that of renewable energy systems with increased grid volatility due to solar and wind power generation. However, considering the manifold ecological impacts, it is necessary to establish and implement timely mitigation measures, despite their potential effects on energy market hydropeaking drivers. When considering mitigation strategies, both socio-economic and environmental values should be considered in trade-off analysis. However, it is necessary to acknowledge the existence of strong legislative frameworks than can be contradictive, for example, pertaining to the expansion of renewable energies and ecosystem conservation, making the decision-making process difficult. Future research should focus on evaluating and adjusting implemented mitigation measures based on complex realities, as well as acknowledge the diversity of bio-physical processes in rivers affected by hydropeaking worldwide.

Knowledge gaps

The following list presents a set of open core questions that, if answered, would aid the sustainable management of hydropeaked rivers.

1. To what extent does the impact of hydropeaking differ between scales and river types, for example, pertaining to different flow regimes (glacier-melt vs. non-glaciated regimes; temperate, tropical vs. semi-arid), river morphologies and sedimentary structures (straight vs. braided rivers; armoured vs. loose (mobile) bed rivers), groundwater influence (e.g., hyporheic vs. surface-dominant flows), or biocoenotic regions such as fish regions (headwaters vs. lowland rivers)?
2. How do prior river conditions influence ecosystem impacts of hydropeaking?
3. What are the direct consequences of organism drift and stranding on the individual organism and population level?
4. What are the effects of hydropeaking on the food-web structure in different river types and regarding the longitudinal gradient of a river?
5. Which biological metrics are most sensitive and could be included into a stressor-specific biological assessment method?
6. What are functional processes that govern hydropeaking impacts? Are results of impact analyses consistent through different spatio-temporal levels (e.g., from an event at the gravel bar to multi-year effects on wider regional hydroclimatic scales) so that generalized processes can be deducted?
7. How does the ecosystem stressor of hydropeaking interact with other pressures such as channelization, river-floodplain disconnection and tributary fragmentation, land-use change, water quality alteration, or (piscivorous) predators?
8. How can ecosystem impacts be assessed from the context of climate change and future socio-economic priorities?
9. What economic and social constraints hinder the spatial and temporal implementation of mitigation measures?
10. What kind of measures best mitigate the (ecological) consequences of hydropeaking, and how can their effectiveness be best quantified to serve as a decision-support for sustainable hydropeaking management?

Acknowledgments

Thanks to Stefan Schmutz and the section editors for feedback on an early version of this chapter. This research was funded in part by the Austrian Science Fund (FWF) [P 34061-B]. For the purpose of open access, the author has applied a CC BY public copyright license to any Author Accepted Manuscript version arising from this submission. The authors acknowledge the financial support of the MorphHab [PID2019-104979RBI00/AEI/10.13039/501100011033] and the MorphPeak [CGL2016-78874-R/AEI/10.13039/501100011033] research projects funded by the Research State Agency (AEI), the Spanish Ministry of Economy and Competiveness, Science and Innovation, and the European Regional Development Fund Scheme. Thanks also to the Economy and Knowledge Department of the Catalan Government through the Consolidated Research Group 'Fluvial Dynamics Research Group'—RIUS [2017SGR-0459] and the CERCA Program, as well as the support of the Alexander von Humboldt Stiftung through the fellowship awarded to RC-M.

See Also: Human pressures and management of Inland Waters: Agricultural Case Studies; Agricultural Pressures on Inland Waters; Biological Invasions: Case Studies; Biological Invasions: Impact and Management; Biological Invasions: Introduction, Establishment and Spread; Case Studies of Sediment Mining Activity; Case Studies of (Semi)Constructed Wetlands Treating Point and Non-point Pollutant Loads to Protect Downstream Natural Ecosystems; Citizen Science for Co-monitoring and Co-managing Impact on Ecosystems and Inland Waters; Constructed Wetlands for Urban Wastewater Treatment: An Overview; Effects of Hydrocarbon Extraction on Freshwaters; Effects of Mining on Surface Water; Effects of Mining on Surface Water—Case Studies; Emerging and Less Commonly Recognized Chemical Contaminants: Organic Micropollutants; Evolving Perspectives on Hydropower: Balancing Societal Benefits and Environmental Impacts; Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment; Hydromorphology: Case Studies; Hydromorphology: Overview and Assessment Methods; Hydromorphology—Interactions and Habitats; Hydropower: Case Studies in Sustainability; Hydropower in the Danube River Basin: Current Status and Emerging Challenges; Impacts of Large Dams on Harmful Algal Bloom Formation in the Tributaries of the Three Gorges Reservoir; Implications of Climate Change for Freshwater Fisheries; Inland Fisheries Management - Case Studies of Inland Fish; Inland Fisheries Management - Exploitation and Livelihoods; Measuring Impact, Overview and Reference Conditions; Microplastics in the Freshwater Environment; Moving Towards Water Sensitive Cities: A Planning Framework, Underlying Principles, and Technologies—Case Study Kunshan Sponge City; Physical Impacts of Sand Mining in Rivers and Floodplains; Sediment Mining: Development and Implementation of Policies; The Best Management Practices in Agriculture for Protection of Inland Water Ecosystems; The Role of Wetlands in Mitigating Impacts From Diffuse Agricultural Loads

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https://www.h2020hydroflex.eu/—HydroFlex project: Increasing the value of hydropower through increased flexibility.
https://sites.google.com/view/morphpeak/home—MorphPeak research project: Morpho-sedimentary dynamics in mountain rivers affected by hydropeaking.
https://ecopeak4fish.com/—EcoPeak4Fish research project: An integrated approach to support self-sustaining fish populations downstream hydropower plants.

Hydropower: Case Studies in Sustainability

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner

Glossary

Dam decommissioning Removal of hydroelectric generation facilities from a dam.
Dam removal Partial or full removal of a dam and appurtenant structures.
Environmental flows Dam releases dedicated to maintenance of environmental health.
Small hydropower Hydropower facilities with a small generating capacity, mostly less than 10 MW, often run-of-river.
Stoplogs Hydraulic control elements that are manually set to adjust water level or discharge in a river, canal, or reservoir.
Sustainable hydropower Hydropower facilities that minimize impacts on a river's flow regime and aquatic and riparian ecosystems.
Trash rack Structure that prevents water-borne floating debris from entering water intake.

Introduction

As a renewable, low carbon, and relatively low cost source of electricity, hydropower brings numerous benefits for economic development and a transition away from fossil fuels. However, hydropower facilities come with numerous social and environmental impacts, including altering aquatic and riparian ecosystems, displacing people, causing deforestation and species loss, impacting river-based subsistence and livelihoods, and altering coastal sediment fluxes. Globally, efforts to minimize the environmental impacts of hydropower dams are increasing. These efforts generally aim to:

- Minimize change in the river flow regime and flow velocities;
- Allow sediment to move upstream and downstream of the hydropower facility;
- Protect fish from mechanical injuring by rotating parts;
- Allow fish and other aquatic species a safe, easily detectable way upstream and downstream; and
- Minimize influence on habitats used for reproduction by fish and other aquatic life.

While these aspirations may not be achievable in all settings, new ways of building and operating hydropower facilities can lessen their environmental impacts. This chapter describes three increasingly-used advances in the design, operations, and management of hydropower facilities that aim to enable a more sustainable balance between energy production and social and environmental impacts. First, it discusses environmental flows, managing water releases to provide habitat and other ecosystem functions. Second, it explores small hydropower (plants that generate less than 10 MW) and the addition of energy generation facilities to existing dams and infrastructure. Finally, it discusses the decommissioning and removal of dams, an approach that is growing in prominence for dams that no longer meet their stated needs, or whose upgrades to address safety and/or environmental concerns would be prohibitively expensive. Each section begins with an overview of the approach and the challenges that it is trying to address, and then discusses how the approach works, best practices, and key challenges in implementation.

Environmental flows and hydropower

Hydropower facilities return water to rivers after it is used to generate electricity, but the magnitude and timing of the return flow may be significantly different than the natural flow regime in the river. Single-purpose hydropower facilities generally release water according to the schedule of electricity demand rather than the schedule of water needs by downstream ecosystems and other river users. Releases from multi-purpose dams may also adhere to schedules related to flood protection, reservoir recreational

services, or downstream water rights unrelated to ecosystem or other instream water needs. Because riverine ecosystems are adapted to natural flow levels, altered flow regimes can stress on riverine biota, alter geomorphic processes, and lead to fundamental changes in ecosystem condition over time (Poff and Zimmerman, 2010; Rolls and Bond, 2017). The temperature, dissolved oxygen, and sediment concentrations of water released from hydropower facilities may be significantly altered from natural levels, exerting further stress on downstream ecosystems (Olden and Naiman, 2010; Schmutz and Moog, 2018). Degraded downstream ecosystems provide fewer ecosystem services, reducing the benefits enjoyed by riverside communities and others using the river (Anderson et al., 2019).

Environmental flow releases are an operational measure intended to mitigate the impacts of altered flow regimes downstream of hydropower facilities or other water infrastructure. They are also applied more broadly in water allocation planning and management to mitigate the effects of excessive water withdrawals for agriculture and other consumptive use (Horne et al., 2017). Effective environmental flow releases mimic essential components of the natural flow regime and include a range of flow levels that create aquatic habitats, are synchronized with the life history patterns of aquatic organisms, maintain lateral and longitudinal connectivity, and discourage invasions of exotic species (Bunn and Arthington, 2002).

Awareness of and guidelines for environmental flow releases from hydropower facilities are becoming more prominent. For example, the International Hydropower Association includes environmental flows as one of the topics in its Hydropower Sustainability Assessment Protocol (International Hydropower Association, 2020). The International Finance Corporation (IFC) of the World Bank Group has issued guidance on environmental flows for hydropower projects that are aligned with its sustainability policies and standards (IFC, 2018). The European Commission has issued guidance on the requirements for hydropower in relation to EU Nature legislation, which includes environmental flows (European Commission, 2018). However, the implementation of environmental flows at hydropower facilities and in other water management settings remains limited, prompting calls for a global action agenda to accelerate their implementation for protection of rivers with hydropower plants (Arthington et al., 2018).

The potential for a hydropower facility to alter a river's flow regime depends on the volume of water stored in its reservoir relative to the flow of the river. A commonly used index for this potential is the *degree of regulation (DOR)*, which reflects the proportion of a river's annual flow that can be stored (Lehner et al., 2011). DOR values range from near zero for run-of-river facilities to greater than 100% for reservoirs large enough to store all water flowing in the river during an average year. Akosombo Dam on the Volta River and Kariba Dam on the Zambezi River represent extreme cases, as both have a DOR index greater than 300% (Lehner et al., 2011). Consideration must also be given to the cumulative effects of multiple hydropower facilities in a single river basin, which compound the impacts and limit the effectiveness of implementing environmental flow releases in any one facility.

The actual degree of flow alteration downstream of hydropower facilities depends on how the dam is operated, the schedule of hydropower production, and the design and configuration of the facility. Operating rules will change depending on the purpose of the dam and water levels in the reservoir throughout the year. Some hydropower facilities have the objective of contributing to the electrical base load and are operated to generate steady levels of electricity, while others vary electricity production hourly depending on demand and changing electricity prices. Hydropeaking associated with hourly variations in electricity generation produces some of the most severe flow alteration, with rates of change so large that biota are flushed downstream when flows ramp up, and fish and other organisms are stranded on river banks when flows are subsequently reduced (Moreira et al., 2019). Facilities that position the power plant some distance away from the dam will create a depleted (or de-watered) reach between the dam and the tailrace where water from the turbines is returned to the river. The length of depleted reaches can be tens of kilometers. When a power plant is located in a separate river basin, water losses from the dammed river may be permanent.

Advances in environmental flow science and practice provide solutions to address each of the flow alteration situations described above. Implementing environmental flows is enabled by policy and legislation prioritizing minimal environmental water objectives over other uses, knowledge of the flow requirements to meet downstream environmental objectives, and hydropower facilities operationally capable of releasing the required environmental flows (Owusu et al., 2021).

Environmental flows appear both explicitly and implicitly in major water policy and legislation around the world. In some cases such as South Africa and Peru, environmental flows are mentioned in national water laws and prioritized over other water uses (Ley No 29338-Ley de Recursos Hidricos, 2009; National Water Act 36 of 1998, 1998). In Ecuador, environmental flows even appear in the country's constitution (Constitución de la República del Ecuador, 2008). In federal republics like the United States, environmental flows are incorporated into state laws and statutes (Boyd, 2003). The European Union recognizes environmental flows as an element of river hydromorphic condition, which together with biological and chemical elements determine the ecological status of water bodies. The EU has set a goal of achieving *good* ecological status of all of its water bodies and issued guidance on how environmental flows factor into achieving this goal (European Commission, 2015). In the absence of legal treaties but in the spirit of cooperation, some countries like those comprising the Nile River Basin have agreed on a basin-wide strategy for assessing and implementing environmental flows. The strategy describes a common framework for incorporating environmental flows into water resources management in the basin countries, but the legal and regulatory details remain specific to each country (NBI, n.d.), and procedures for implementation are still under development.

While laws, regulations and international agreements provide the enabling conditions for environmental flows in hydropower facilities, critical points for their assessment and implementation are the initial design phase of a new project and the relicensing phase of existing projects. Each of these involve environmental assessments, which include the impact of downstream flow alteration. Specific guidance on environmental flows in hydropower environmental assessments has been published by the IFC and the World Bank (IFC, 2018; Krchnak et al., 2009), and the Inter-American Development Bank has issued a White Paper on the

topic (Anderson, 2013). Relicensing processes, such as those conducted by the Federal Energy Regulatory Commission (FERC) of the United States, require environmental assessments that consider environmental flow releases (Schramm et al., 2016).

An illustrative case for environmental flow implementation during the relicensing process is the 2016 revision of the Water Control Plan for John H. Kerr Dam and Reservoir in the United States (US Army Corps of Engineers, 2016). Kerr reservoir was completed in 1952 for purposes of flood control and hydropower production. Environmental flow requirements were not assessed and the natural variability of the downstream flooding regime was reduced significantly. This resulted in the degradation of floodplain forests and other riparian and in-stream biota and communities (Pearsall et al., 2005). During the FERC relicensing process, the operation of Kerr Reservoir was changed to release a flow approximately equal to the average unregulated inflow to the reservoir over the preceding week. This converted the facility to a quasi-run-of-river operation, intended to more closely mimic natural flow variability (US Army Corps of Engineers, 2016).

Frameworks and specific methodologies for the assessment of environmental flow requirements downstream of hydropower facilities are well established and adaptable to different spatial scales, level of detail, and local capacity. Decisions about the specific assessment methodology to be applied will depend on the known or potential impact of the hydropower facility on downstream river reaches (IFC, 2018). For example, low-resolution environmental flow assessment methodologies considering only hydrological data may be sufficient for run-of-river hydropower facilities resulting in small alterations in the downstream flow regime. Conversely, high-resolution methodologies should be applied for facilities resulting in major downstream flow alterations, especially in cases where downstream reaches are of high conservation, social, or economic value (Opperman et al., 2018). Determination of final environmental flow levels requires societal choices about the level of ecological condition to be maintained. These choices are often reflected in laws and regulations but case-based choices are also needed. Incorporating these social dimensions into environmental flow assessment requires effective stakeholder engagement (O'Keeffe et al., 2019).

In addition to releasing sufficient base flows, studies have emphasized the need to reintroduce more regular flood pulses downstream of hydropower facilities (Olden et al., 2014). Numerous facilities have changed their operation to release more effective environmental flows. Notable examples include Kerr Dam mentioned previously, Three Gorges Dam on the Yangtze River in China, and Katse Dam on the Malibamals'o River in Lesotho (Brown and King, 2012; Cheng et al., 2018).

Once quantified, a range of strategies have been devised to re-operate hydropower facilities in ways that also minimize losses in power production. These include the construction of re-regulation (or compensation) reservoirs downstream of hydropower facilities, use of pumped storage facilities, balancing re-operation measures among multiple facilities in a cascade, and optimizing power generation across multiple energy sources, including wind and solar (Richter and Thomas, 2007). Environmental flow releases into depleted reaches may also be used to generate electricity using smaller turbines. Measures to address water quality issues include sluice gates to increase downstream fluxes of sediment, intake points from various levels in the reservoir to better control water temperatures, and aeration techniques to reduce hypoxia in released waters. Re-operation of hydropower facilities and implementation of the measures mentioned may be limited by the engineering design of facilities (e.g. facilities physically incapable of releasing prescribed environmental flows) as well as contractual or licensing issues.

Small hydropower

Small hydropower (SHP) is often formally defined by the power plant capacity, defined in megawatts (MW). The specific capacity varies considerably around the world. Differences in a country's hydropower potential, hydropower development, and history result in small hydropower limits that vary from 1 MW (Burundi, Ghana, Nigeria, Zimbabwe) to 10 MW (European Union, United States) to 50 MW (China, Canada) (Liu et al., 2019).

While large hydropower often entails big dams and reservoirs that store a large quantity of water, small hydropower schemes are mainly run-of-river plants with little or no storage impoundments and only a small dam or weir that diverts a portion of the river's flow. The absence of a storage facility minimizes alteration of the river's flow, lessening impact on the hydrological regime. Water leaving the turbine has the same quality and quantity as upstream of the plant. SHP schemes can also assist in the maintenance of the river basin by recovering flowing waste from the river stream and providing a site to monitor hydrological conditions. As any floating waste accumulates on the inlet trash racks and must be collected and deposited out of the river, small hydropower helps in reduction of floating debris and especially plastics in the rivers. Additionally, most SHP plants have a hydrological monitoring station that provides data useful for power generation and river management more generally.

While small hydropower mostly has less environmental impact than larger hydropower facilities, attention to sustainable developments can minimize possible negative impacts. Sustainable small hydropower aims to minimize the facility's influence on the river flow regime, flow velocities, and river dynamics, influence on transport of sediment and seeds from plants along the river, and influence on fish mortality and migration. In recent years, small hydropower developments are concentrated on minimizing these negative effects and adjusting facilities to given site conditions and environmental needs. Small hydropower, therefore, is not just a copy and downsizing of the standard large hydropower; rather it comprises new environmental developments and improvements that make hydropower more sustainable.

New hydropower technologies are enabling more environmentally friendly small hydropower. One such advance is the shaft power plant concept (Sepp et al., 2016), which minimizes the negative environmental influences on the river. In a shaft power plant, the whole power plant, turbine, and generator unit are located completely underwater (Fig. 1). Water feed takes place via a horizontal inlet, situated on the original riverbed upstream of the existing weir structure. A drop-in inlet equipped with a horizontal

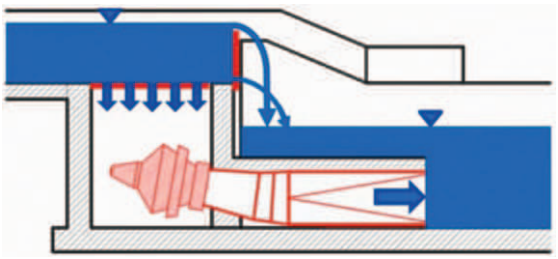

Fig. 1 Concept of the shaft turbine solution (Sepp et al., 2016).

trash rack suppresses entrance of debris and larger sediment in the shaft and subsequent damage to the equipment. Because of its simple rectangular form, the shaft can be constructed directly in the riverbed and avoids costly diversion infrastructure. The relatively simple and not hydraulically optimized structure increases hydraulic losses, but this disadvantage is compensated by the low velocities on the trash rack and within the shaft. As the weir determines water level and flow velocity in the upstream river course, the plant does not affect flow velocities, and the box-type hydropower plant has no additional negative effects on the flora and fauna of the river. Fish migrating downstream should not be sucked through the trash rack because of the low flow velocity. A specially developed gate with an opening in the weir downstream the screen enables fish migration downstream and flushing of the trash rack. Upstream migration is achieved by standard fish migration systems and fish ladders or ramps. The primary disadvantage of the outlined concept is accessibility in case of maintenance. Owing to the underwater setup, the hydro machinery and the generator access have to be achieved by setting mobile stop logs to prevent water access. The system has been tested on a laboratory version at Technical University Munich and at a plant built on a weir in Loisach, Bavaria. The power plant with two shafts and 420 kW power produces 2.4 GWh per year, enough energy for 800 households.

Fish mobility and fish mortality are common concerns at hydropower plants. Fishways, including fish ladders, lifts, ramps, or bypass channels, can help mitigate impacts to fish and are commonly included as part of sustainable hydropower design. While many fishways include various forms of pool passes, recent developments in fishway design include the well-known Denil passage (Seidl, 2021) and a specially developed Fishcon lock (www.fishcon.at) and double hydropower screw (Fig. 2). In the Fishcon solution, fish migrate in both directions through a specially regulated pipe system and a double rotating Hydroconnect screw (www.hydroconnect.at) provides a fish lift and acts as a turbine to generate electricity. The internal screw drives water and migratory fish upstream, while the external screw is used for energy production and downstream fish migration. The Fishcon system is designed to

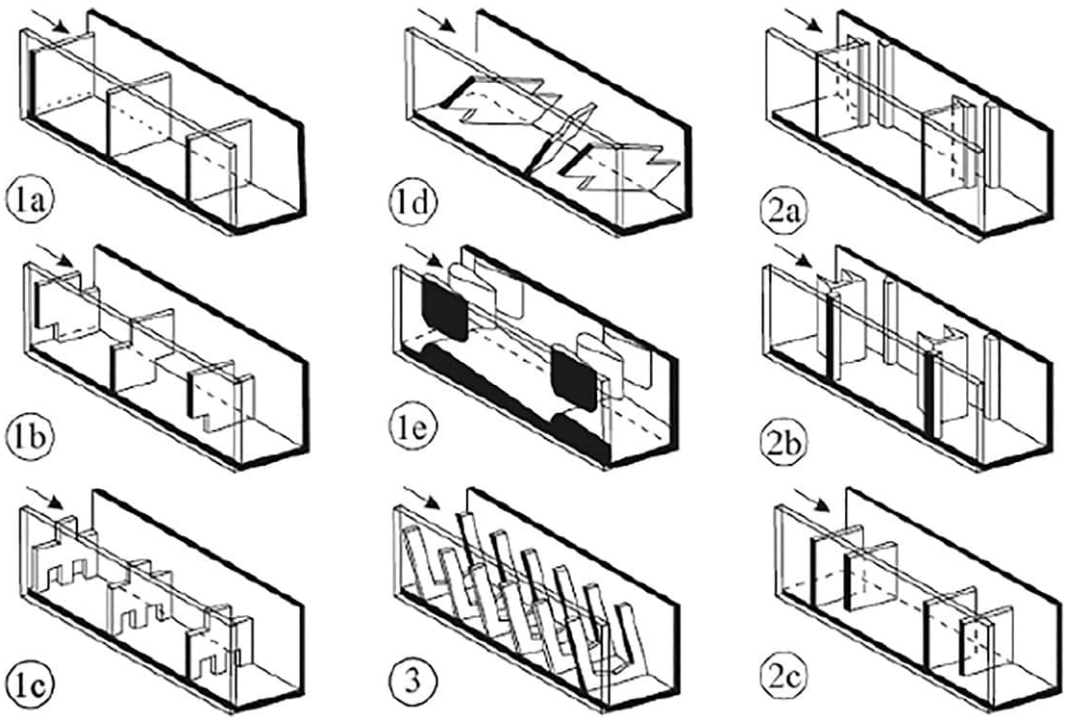

Fig. 2 Types of fishways: (1) pool passes, (1a) without and (1b-c) with orifices, (1d) rhomboid pass, (1e), ridge pass, (2a-c) slot and vertical slot passes, (3) Denil pass (Giesecke and Mosonyi, 1997).

satisfy the EU Water Framework Directive (European Parliament 2000/60/EC) requirements to minimize effects on fish movement. Specially formed blades, minimized gaps and low rotational speed reduce the possibility for fish to be harmed by the Hydroconnect screw, but similar philosophy is also used by other fish-friendly turbines, such as the Alden turbine (EPRI, 2011).

The development of alternative hydropower plants in existing hydro-technical structures represents an additional and profitable solution for energy generation with low environmental impact (Marence et al., 2016). Possible implementations are drinking water or sewage systems, irrigation dams and channels, old water mills, dams that are not used for hydropower, navigation locks, hydraulic industrial systems, cooling and heating water, or desalination systems. The addition of hydropower can also contribute to the partial completion of a circular energy cycle, allowing hydraulic infrastructures to reduce (or even revert in a long term) the anthropogenic impact of such systems. Hydropower incorporated into existing hydraulic infrastructures, where electricity generation was not a primary objective, can be an attractive solution for implementation in developed and developing energy systems for several reasons (Marence et al., 2018):

- the environmental and social impacts of the existing hydro-technical structures are known, defined and mostly accepted;
- installation of new hydropower in the existing system reduces construction costs, construction time, and GHGs emissions during the construction phase;
- lower construction costs with a shorter payback ratio make the solutions attractive for investment;
- uncertainty related to resource availability, especially obtainable water flow and energy head, is reduced;
- operational costs can be lessened by synergies in operation; and
- modifications to add hydropower create the possibility for additional social and environmental improvements to the facility.

An example of the implementation of such hidden hydropower is the hydropower plant integrated in the weir structure developed for water management on Dommel River in Sint Michielsgestel in the Netherlands (Marence et al., 2016). The weir, which has just 1.8 m head (vertical elevation difference), was constructed in 1970, but was not used for electricity generation until 2015 when a screw turbine with the maximal discharge of 10 m^3/s was installed. The plant delivered 120 kW in the local grid. The innovative project was financed with 75% crowdfunding, as almost 500 participants from the region bought certificates in the power cooperative. Participants receive a return in free power and dividends. The expected return for the crowdfunders is 4–8% annually.

Finally, small hydropower is a valuable energy source for rural electrification and support of local grids. Providing electricity to rural areas, especially in the developing world, often requires high investment costs owing to geographical barriers (distance and terrain). Extending the grid with renewable energy sources is a valuable alternative. Small hydropower, in contrast to solar and wind, can provide continuous day and night energy supply for a community, although it may vary with seasonal changes in river flows.

Dam decommissioning

Dam decommissioning refers to removal of hydroelectric generation facilities and often the entire dam. Decommissioning emerges as a solution when a dam poses a safety risk, no longer serves its intended purpose, or no longer meets current social, environmental, and/or economic values. In these instances, removing the dam can be less expensive than repairing or maintaining the dam, let alone upgrading the facility to meet new needs. Rates of decommissioning have increased, especially in Europe and North America; these continents have seen the most dam removals to date, with an estimated 1700 in the United States (USA) and 5000 to 6000 in Europe (American Rivers, 2019; Gough et al., 2018; Vahedifard et al., 2021). Available statistics do not distinguish hydropower dams from other types, but the motivations and responses for dam removal are relatively similar across project types.

Aging is a common factor underlying dam removal. In North America and Europe, many dams were built in the 20th century, making many of these dams past their 20- to 40-year designed lifespan. While age is not the only cause of dam failure, older construction materials are more prone to structural problems. If a dam poses a safety risk, removal often becomes a favored option. Even if the dam is still structurally sound, the original demand for hydroelectricity may have waned. For instance, the Sofieholm power plant in Sweden was built in 1909 to power a textile factory, but the factory has long since closed; combined with impacts on local fish populations, the lack of power demand led to the facility's removal (Sofieholm Hydroelectric Powerplant, River Nianån, Sweden, 2017).

A second common reason for removal is sediment accumulation in the reservoir. Sediment build up increases safety risks, reduces the usable capacity of the reservoir, and can damage turbines. Depending on current or historic upstream land uses, reservoir sediment can also be contaminated, with common contaminants including heavy metals, Dichlorodiphenyltrichloroethane (DDT), polychlorinated biphenyl (PCB), and radionuclides (Evans and Wilcox, 2013; Foley et al., 2017). Sediment build-up can be addressed without removing the dam (e.g., through dredging or pulsed flows through low-lying outlets). However, if the cost of sediment removal outweighs the benefits of power generation (or other water supply/flood control purposes), decommissioning the dam is economically favorable.

Sediment volumes that are large or contaminated can complicate the decommissioning process, requiring a slower and/or more expensive removal to allow for remediation. For instance, decommissioning and removal of the Glines Canyon and Elwha Dams on the Elwha River, United States–the largest hydropower dam removal to date, with 21 million m^3 of trapped sediment—required a phased removal, with staged drawdowns over multiple years (Magirl et al., 2015). Likewise, the Milltown Dam on the Clark Fork River, United States, contained mining-derived sediments with elevated concentrations of arsenic, copper, lead, and zinc; removing the dam without releasing large volumes of contaminants downstream required both a phased drawdown and dredging of the removed sediment (Evans and Wilcox, 2013).

A third common reason for removal is the hydropower facility's impacts on ecosystem function. As understanding of dams' impacts on aquatic and riparian ecosystems has expanded, social pressure for their removal has increased. Dams may be removed to provide upstream habitat for migratory fish, to restore natural (undammed) flow regimes, and/or to reconnect coastal sediment systems. All three motivations underlay the Elwha Dam removal. Ecologically-inspired dam removals often occur because of regulatory triggers, as updating the facility or its operations to meet new environmental requirements (e.g., for fish passage or water quality) may not be cost-effective. In the United States, the conversation about decommissioning hydropower dams often arises when the facility needs to renew its operating license from the Federal Energy Regulatory Commission (FERC) (Doyle et al., 2003). Likewise, in Japan, water rights renewals often trigger debates about dam removal in rivers with declining fish abundance (Noda et al., 2018) (Fig. 3).

The decision to decommission a dam is rarely straightforward. Many decommissionings for larger dams are subject to intense debate, with politicians, regulators, business interests, and members of the public variably raising concerns about impacts on energy supply, costs, flooding, and cultural preservation. This debate often delays removal. For instance, removal of two dams on the Sélune River, France was decided in 2009, but was followed by substantial criticism by local elected officials (Germaine and Lespez, 2017), and it took over a decade to actually remove the dams. Similarly, after local fishermen suggested removing the Arase Dam, Japan in 2003, a newly elected government reversed the decision; the dam was not removed until 2018 (Noda et al., 2018; Ohno, 2019).

Even in cases where the decision is met by widespread support, regulatory hurdles can also delay removal. The proposed removal of the Klamath Hydroelectric Project (a series of four dams in California and Oregon, United States) resulted in 2010 from a large-scale negotiation between the electrical utility, multiple American Indian tribes, irrigators, fisherman, and multiple federal and state agencies (Gosnell and Kelly, 2010). However, the removal timeline has been delayed numerous times because congressional and administrative leadership-both of which are required for formal approval–changes with each presidential administration.

Scientific studies on the environmental outcomes of dam removal is a growing area of research. For instance, only 10% of dam removals in the United States have been scientifically evaluated, with many of those studies focusing on relatively short-term timescales (Bellmore et al., 2017). Nevertheless, some general trends have been observed. First, impounded sediment moves relatively quickly, with the majority of sediment from the reservoir being transported downstream within several years (Foley et al., 2017). In some cases, erosion can occur very rapidly (in under a year). In the Condit dam removal in Washington State, United States, erosion extended upstream of the reservoir and occurred so rapidly that it blocked fish migration at the mouth of the river (Wilcox et al., 2014). However, phased removal–in which the dam is breached to allow some passage of water and sediment, but with a delay before removing the full dam-appears to slow down the sediment transport process (Foley et al., 2017).

Second, fish communities often respond quickly to removal of the barrier, with both fish species richness and life-history diversity increasing shortly after removal (Foley et al., 2017). Species recovery and distribution depends on species abundance and diversity pre-removal. For instance, decommissioning the Irving Power Plant in Arizona, United States, had no effect on native fish abundance except in stream reaches where exotic species had been removed (Marks et al., 2010).

Third, with few exceptions (like the Condit example), upstream environments and species are typically not altered by dam removal. The overall downstream response to removal varies substantially case by case. How and where sediment deposits depend on the volume of sediment, flow rates, the underlying geomorphology, and grain size distribution. This deposition is a critical factor shaping habitat post-removal. Downstream response also depends on whether there are other dams in the watershed. As for the former reservoir, ecosystems tend to be dominated by fast-growing riparian species, including some invasive species (Foley et al., 2017).

Fig. 3 Before and after removal of Elwha Dam. Left: September 2011. Right: May 2013. (Ben Cody, wikipedia).

Conclusion

As hydropower increasingly responds to demands to reduce negative social and environmental impacts, the provisioning of environmental flows and the development of small, run-of-river hydropower each provide promising ways to make hydropower more sustainable. In cases where sustainability cannot be improved or the dam is not operational, the decommissioning and removal of existing facilities can return the river to a more natural state. Each approach is growing in use, with new regulations and guidance to support its implementation. Likewise, the science behind these approaches is expanding, providing new knowledge that will help tailor their design and implementation for different sized dams, different hydrological systems, and different ecological needs.

However, there are still a number of key knowledge gaps. New technologies for more environmentally friendly small hydropower, such as fish-friendly turbines and permeable weirs, are in development but not yet widely deployed. Understanding how to optimize environmental flows (e.g., balancing instream flow requirements with flood pulses) for different hydrological and species contexts will enable more targeted implementation of environmental flows. In many jurisdictions, widespread deployment of environmental flows will also depend on enhanced legal provisions. And most dam removals to date have been relatively small systems; as more large dams are removed, the science will enable better guidance on how to phase breaching and removal.

Finally, across all three domains, a key challenge and opportunity is in making decisions at the scale of the watershed rather than the individual facility. Dams are often regulated as individual entities, but thinking at the basin scale can create opportunities for creative balancing between power generation and ecosystem needs (Opperman et al., 2011). Achieving basin-scale management may require new regulatory frameworks that coordinate multi-dam operation, collaboration across multiple government and civil society organizations, and—in transboundary rivers—multinational coordination (Zeitoun et al., 2013). However, designing and operating basin-scale hydropower systems can expand opportunities to promote sustainable hydropower generation.

Knowledge gaps

- Release of ecologically sufficient environmental flows at hydropower facilities. Too many hydropower facilities today fail to release adequate environmental flows to meet the needs of downstream aquatic ecosystems. Meeting ecosystem water requirements will require strengthening environmental performance standards and developing new hydropower technologies (e.g., low head hydropower turbines).
- Developing low head hydropower solutions. Existing turbine types are not suitable for generating in low head difference (few meters head) conditions. Developing new turbine types that could be used in such conditions can expand use of small hydropower solutions to locations without a large weir or dam.
- Building fish friendly turbines. Fish passing hydropower turbines can be injured mechanically, by pressure difference, and by cavitation. Development of turbines that reduce such injuries can make hydropower less harmful to aquatic species.
- Integrating hydropower into existing hydraulic structures. Many hydraulic structures are operated without associated hydropower. Installing hydropower facilities in these hydraulic structures can increase renewable energy production without requiring new dams to be built.
- Development of modular, environmentally friendly solutions. Using modular and predefined solutions for the new hydropower plants can reduce the construction costs and improve the project acceptance.
- Basin-wide optimization of dam decommissioning. Within a watershed, removing some dams and expanding power generation capacity at others can balance power generation and environmental benefits. Doing so will require new regulatory frameworks and multi-criteria optimization approaches.

See Also: Human pressures and management of Inland Waters: Hydropeaking: Processes, Effects, and Mitigation

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http://www.icshp.org/inshp/member.asp—International Center on Small Hydropower.
https://www.youtube.com/watch?v=WwcCqe39dW4&t=4s—The Global Dam Reoptimization Initiative.
https://www.youtube.com/watch?v=oOxjDmb6WF4—Environmental Flows (EFlows): Concepts and Methods.

Impacts of Large Dams on Harmful Algal Bloom Formation in the Tributaries of the Three Gorges Reservoir

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Algal blooms Proliferation of large populations of algae across the aquatic system (freshwaters/coastal margins) as a result of nutrient over-enrichment and associated factors.
Anthropogenic actions These are all human activities directly or indirectly affecting the environment, including the growth of harmful algae in aquatic systems.
Cyanobacteria The most problematic and widely studied phytoplankton taxon characterized by food web-disrupting, hypoxia-generating, toxin-producing, and large surface scum-producing blooms, especially during the summer.
Dam A barrier that stops or restricts the flow of surface water or underground streams. Reservoirs created by dams not only suppress floods but also provide water for activities such as irrigation, human consumption, industrial use, aquaculture, and navigability. Hydropower is often used in conjunction with dams to generate electricity. A dam can also be used to collect or store water which can be evenly distributed between locations.
Dissolved nutrients The fractions of the nutrients, composed of the organic and inorganic intermediates, which are highly soluble and readily utilized by a wide range of microorganisms in the water.
Epilimnion This is a term used to describe the upper layer of water, particularly in a stratified aquatic ecosystem due to high temperature and low mixing regimes.
Eutrophication Over-enrichment of the aquatic ecosystem with nutrients induced either naturally or artificially (anthropogenic).
Stratification Formation of vertical layers from the top (epilimnion) to the bottom (hypolimnion) waters of a lake or reservoir mediated by temperature differences and water density.
Surface density layers (SDLs) a very thin layer at the surface (<2 m deep) where the temperature changes rapidly with depth, leading to the development of strong density layering.
Three Gorges Reservoir (TGR) A large artificial reservoir formed by the direct hydraulic operations of the world's largest hydroelectric project, the Three Gorges Dam (TGD) in the Yangtze River Basin, China.
$\mathbf{Z_{mix}}$ Also referred to as the mixed layer depth, represents the top part of the water column where temperature and solute concentrations are vertically homogeneous due to wind-driven turbulence (mixing regimes).

General overview

Eutrophication, from human-induced, nutrient-over enrichment in freshwaters and coastal margins, has intensified globally. The anthropogenic form of eutrophication, referred to as cultural eutrophication (Domingues et al., 2011), is largely linked to the direct

consequences of human activities and has become a serious problem for many inland waters. This far exceeds the impacts from any natural increase of nutrients arising from weathering and natural buildup of nutrients (natural eutrophication) in the catchment. Aquatic ecosystems are vulnerable to multiple anthropogenic stressors, which are still increasing despite decades of awareness of the problems. One interacting pressure is the change of ecosystem and function of reservoirs created by damming or rivers, which are increasing globally to meet energy demands (Zarfl et al., 2015). There are many examples of freshwater ecosystems disturbed by the heavy proliferation of cyanobacterial blooms. Indicative examples are the Guadiana estuary bearing the Alqueva Dam, Portugal (Domingues et al., 2012) and the Yangtze River hosting the Three Gorges Dam, China (Ji et al., 2017). However, considering the pattern and economic incentive for urbanization and industrialization from damming, meeting the challenges of reducing eutrophication and harmful algal blooms (HABs) is extremely difficult. River damming is essentially driven by economic needs, representing a cardinal indicator for both social and economic developments across the world (Domingues et al., 2014). The Three Gorges Dam (TGD), is the world's largest hydroelectric project (Wang et al., 2013), with a total capacity of 22.5 million kW and a net annual power generation of 100 billion kWh, designed to meet the electricity demands in the middle and eastern China. The TGD constantly provides electricity to central, eastern, and southern China within an economic transmission distance of 400–1000 km, including the provincial regions of Henan, Hubei, Hunan, Jiangxi, Chongqing, Shanghai, Jiangsu, Zhejiang, Anhui, and Guangdong. The Aswan Dam (AD) is another example, constructed to regulate the flow of the River Nile, which serves as an electric provider to almost all of Egypt. The Aswan Dam contributes more than half of the total power supply in Egypt (Harold et al., 1996). Similarly, the large Alqueva Dam, built in 2002 in the Guadiana River (southern Portugal) and which provides electricity the whole Alentejo region, has highly controlled the freshwater flowing into the Guadiana estuary (Domingues et al., 2014). Other benefits of damming include providing water for drinking, irrigated agriculture, flood control, tourism, and navigation (Lehner et al., 2011; Ji et al., 2017). Freshwaters around the world are heavily regulated with $\geq$45,000 large dams built since the 1930s (World Commission on Dams, 2000; Mei et al., 2015).

There is a constant search for eutrophication and algal bloom abatement strategies that could guarantee a relatively eutrophication and algal bloom-free society without using global developmental indices, such as dams, as the opportunity costs. In this regard, different mitigation measures (physical, chemical, and biological) have been proposed and tested in both field- and laboratory-scale studies over the years, with some successes documented in a few applications (Nwankwegu et al., 2019; Paerl et al., 2016). Although, with the recent surge, succession, and evolution of more problematic algal bloom species in response to the exponential increase in anthropogenic activities, it appears that these abatement steps have not reversed the situation on a global scale (Nwankwegu et al., 2019). Damming has been shown to affect adversely downstream rivers, causing notable changes including alteration of ecology, change of channel morphology, modification of water level, disruption of downstream sediment transport, change in net water balance and regulation of flow regimes (Mei et al., 2015). This chapter, therefore, captures the impacts of dams, especially in promoting the global expansion of algal blooms with special reference to the two tributaries in the Three Gorges Reservoir (TGR), which are severely impacted by blooms due to accumulated dam operations over the years. Furthermore, it identifies anthropogenic actions, largely dominated by damming and urban discharge as the primary stressors for ecosystem vulnerabilities and algal blooms worldwide.

The Three Gorges Reservoir

There are 16.7 million reservoirs larger than 0.01 ha (surface area) on Earth (Lehner et al., 2011), and another 3700 major dams are either planned or under construction (Zarfl et al., 2015). Water flow control programs have fragmented over half of the large rivers on Earth (Wu et al., 2019). Reduced connectivity of rivers resulting from dam construction changes both physicochemical conditions and habitat utilization. Although there are substantive benefits for flood regulation and hydropower, dams modify the natural landscape of ecological functions across whole river basins (Simon, 2002; Maavara et al., 2020). Altered tributaries in the catchment change from lotic to lentic ecosystems (Resh et al., 1988), which, when combined with nutrient loading, provide favorable conditions for HABs composed of species such as *Microcystis*, *Dolichospermum*, *Anabaena* and *Aphanizomenon* (Cirés et al., 2013; Zhang et al., 2018; Xin, 2021).

The Three Gorges Reservoir (TGR) is the largest hydroelectric and flood control reservoir in the world. Its annual electricity production allows for a reduction of 50 million metric tons of coal consumption, preventing 120 million metric tons of CO_2 and 10,000 metric tons of CO emissions per year (Zhang et al., 2015). Completed in 2009, the impoundment of the reservoir resulted in a 100-m water-level rise, reaching 175 m above sea level. This project transformed a 660-km reach of the Yangtze River into a highly regulated reservoir. At high water levels, the serpentine reservoir contains 40 billion m^3 of water with an increased water surface area of 645–1200 km^2 (Fu et al., 2010). There are over 40 major tributaries (watershed areas $>$100 km^2) flowing directly into the TGR (Ji et al., 2017). These characteristics of the TGR provide a unique opportunity to study how dam construction and water flow management can result in novel threats to human and environmental health.

Before the construction of the dam, algal blooms were not common in the TGR basin (Zeng et al., 2007) but, following construction, the frequency and magnitude of HABs have intensified and become a serious concern (Zeng et al., 2007; Li et al., 2011; Zhang et al., 2015). Many studies have attributed these blooms to excessive nutrient inputs to the TGR (Zeng et al., 2006; Ye et al., 2007; Zhang et al., 2010; Gao et al., 2016). The elevated concentrations of nutrients, such as total nitrogen (TN), total phosphorus (TP), and silica (Si), are two- threefold higher than the reported threshold for eutrophication (Thomann and Muller, 1987). Drivers of these changes are high population densities and intensive agriculture in the TGR basin.

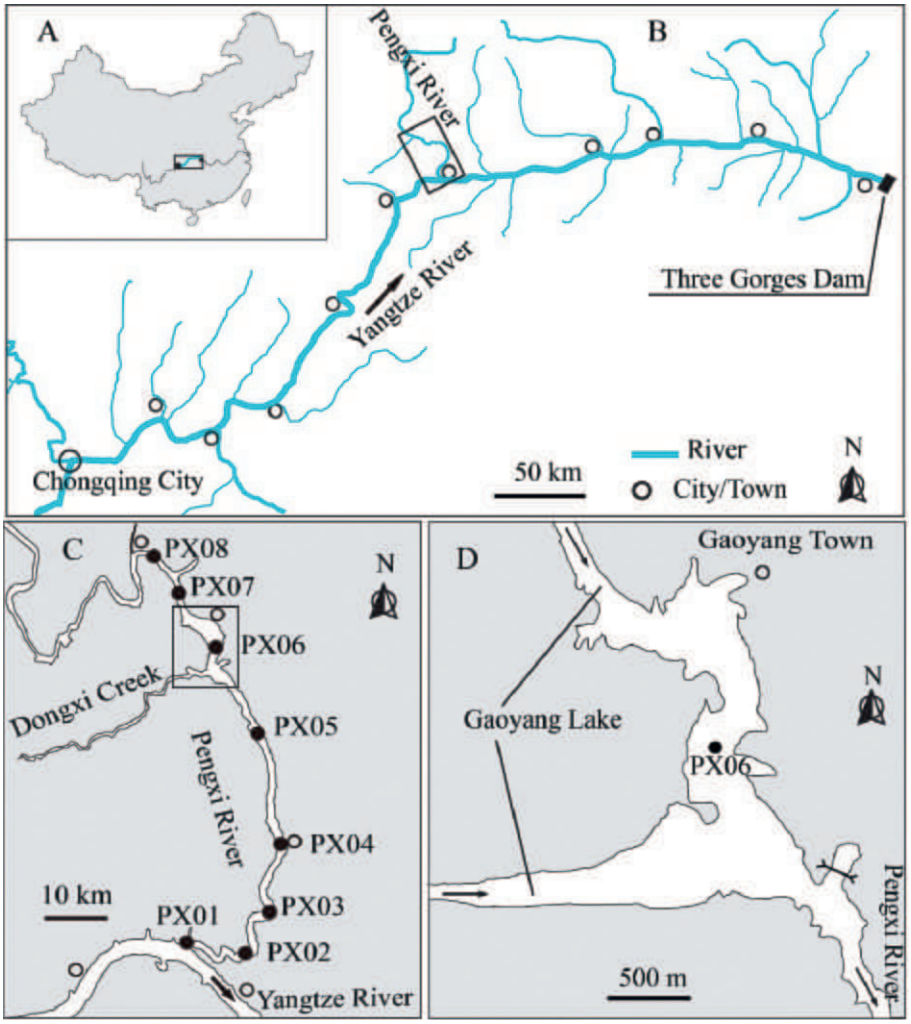

Fig. 1 Pengxi River and its Gaoyang Lake in the Three Gorges Reservoir area. (A) The location of the Three Gorges Reservoir in the Yangtze River Basin, China; (B) The location of Pengxi River in the Three Gorges Reservoir area; (C) The distribution of sampling points in the mainstream of Pengxi River; (D) The locations of the sampling point in Gaoyang Lake.

Decreased water velocities in tributaries have also been linked to the formation of HABs (Wang et al., 2013) as has the development of stable water columns (Davis and Koop, 2006; Yang et al., 2015; Liu et al., 2012; Conroy et al., 2014; McKay et al., 2018). As a result of flow control, water velocities in the tributaries of the TGR have declined from 0.5–1 m s^{-1} to 0.05 m s^{-1}. The main channel, however, has maintained a constant flow of 1.0 m s^{-1} (Wang et al., 2013).

The TGR is located in the middle stem of the Yangtze River, between Chongqing and Yichang City, receiving 40 1st order tributaries (watershed areas >100 km^2) (Fig. 1B) (Ji et al., 2017). Following impoundment of TGD, 50% of these major tributaries have had spring algal blooms (Yang et al., 2017; Zhang et al., 2020; Xiang et al., 2021) in most years, and a few of them have suffered from summer algal blooms (Nwankwegu et al., 2019). This shows the diversity of the mechanisms of algal blooms in different 1st order major tributaries in the same TGR catchment. Two major tributaries, Pengxi River in the middle reach of TGR catchment, and the largest 1st order tributary in catchment's northern bank and Xiangxi Bay, the second last 1st order tributary from the TGD, have been chosen to illustrate the diversity.

The eutrophication in Pengxi River, middle of the TGR

Brief description and geographical location

At the highest water level in winter, 175 m above sea level, TGR surface is 1080 km^2 with a storage of 39.3 billion m^3 (Zeng et al., 2019). The annual average water velocity in the main stem is 0.4 m s^{-1}, contrasting with the much slower flow, 0.01–0.21 m s^{-1}, in its tributaries (Lu et al., 2020; Zhang et al., 2020). The water level is maintained at 175 m above the sea level in winter to generate electricity, and 145 m in summer to create capacity for flood control. Nutrients in the main stem of the Yangtze River are considerably higher than in its tributaries, and water from the main stem flows back into the tributaries when the water level increases (Luo et al., 2007).

The Pengxi River(30°49′ ~ 31°42′ N, 107°56′ ~ 108°54′ E), also known as Xiaojiang, is the largest tributary on the northern bank of the TGR catchment (Zhang et al., 2020) with the main river channel of 182.4 km, with an annual average runoff of 3.41 billion m^3 and basin area of 5173 km^2 (Fig. 1). It is within a subtropical moist monsoon area, where the climate is temperate and sub-humid, with an annual average temperature of 18.6 °C, and annual average precipitation of 1100–1500 mm (Li et al., 2015). The Pengxi River is one of the TGR tributaries that are most prone to algal blooms, which tend to happen in April and May (Guo et al., 2011; Zhou et al., 2016; Zhang et al., 2020).

Gaoyang Lake (31°05′27.4″N′108°40′41.6″E) was formed in 2003 as a result of the water level increase associated with the TGD, and is in the middle reach of the Pengxi River. It has a surface area of 4–5 km^2 and a maximum width of 1 km (Fig. 1D) when the water table is at 145 m above sea level. The lake is affected by water level regulation in the TGR, and alternates between shallow (max depth: 10 m) in summer and deep (max depth: 40 m) during the rest of the year (Zhang et al., 2020). Since 2007, Gaoyang Lake has had the most severe algal blooms in the Pengxi River (Guo et al., 2011; Zhang et al., 2015, 2020).

Surface density layers (SDLs) with algal blooms in Pengxi River

Existence of SDLs in Pengxi River

Algal blooms in the tributaries in the TGR area are generally concentrated in the spring of each year, from March to May (Fig. 2) (Xiang et al., 2021). When blooms occur, the concentration of chlorophyll *a* (Chl-*a*) in the water body can exceed 400 μg L^{-1} (Zhang Xin, 2021). This does not conform to algal blooms typically observed in temperate lakes, where the increased algal biomass is frequently associated with periods of maximum heat content in late summer (Paerl and Huisman, 2008).

Thermal stratification is often critical to forming an algal bloom (Davis and Koop, 2006). Stable stratified systems ensure algae stay in the euphotic zone for photosynthesis, hence leading to algal blooms. In spring, in subtropical and temperate lake systems, the long fetches caused by wind on wide lake surfaces lead to unstable stratification and low water temperatures, hence preventing blooms from developing. In late summer, on the other hand, short-term (a few days) high temperatures enable stratification which creates an epilimnion (Fig. 3A) where the algal blooms occur (Paerl and Huisman, 2008).

Stratification in the tributaries in TGR including Gaoyang Lake does not create epilimnetic layers. The reason is related to the special topography of the TGR area. Over 95% of the TGR region is mountainous (Peng et al., 2006) with large elevation differences (~2000 m) between the water surface and mountain peaks (Li et al., 2001), resulting in very low wind speeds over the surface of the reservoir (e.g., 0.9–2.1 m s^{-1}, Yang et al., 2017). These characteristics, coupled with the limited fetch at the water surface width (<1 km), can prevent the development of breaking waves and the formation of an epilimnion. Instead, tributaries in the TGR form a unique stratification characterized by surface density layers (SDLs), a very thin layer from the surface (<2 m deep) where the temperature changes rapidly with depth. This leads to the development of strong density layering within the SDLs (Fig. 3B) with the minimal influx of nutrients from the lower water column (Zhang et al., 2020). For example, the change in water density from 30 °C to 33 °C is approximately 0.95 kg m^{-3}, whereas water density changes from 4 °C to 8 °C, commonly observed in lakes, is 0.12 kg m^{-3} (Tanaka et al., 2001).

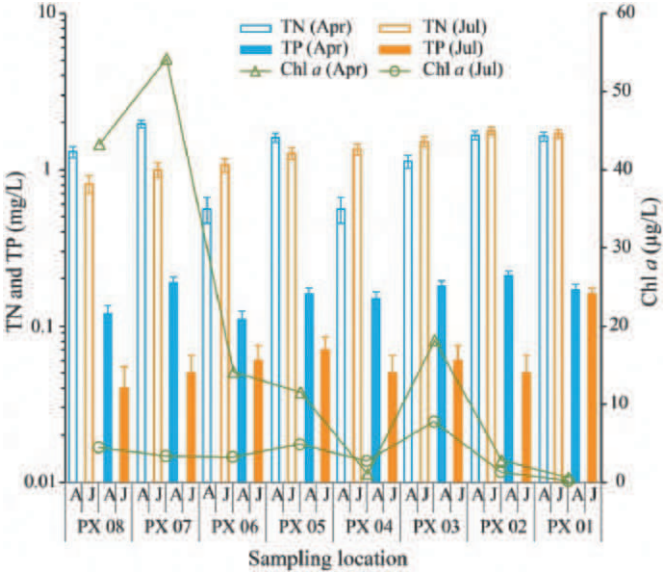

Fig. 2 Chlorophyll a (Chl a, μg L^{-1}), TN (mg L^{-1})and TP (mg L^{-1}) in Pengxi River, Three Gorges Reservoir in spring (A for April) and summer (J for July). PX01-PX08 are the sampling sites as shown in Fig 1C.

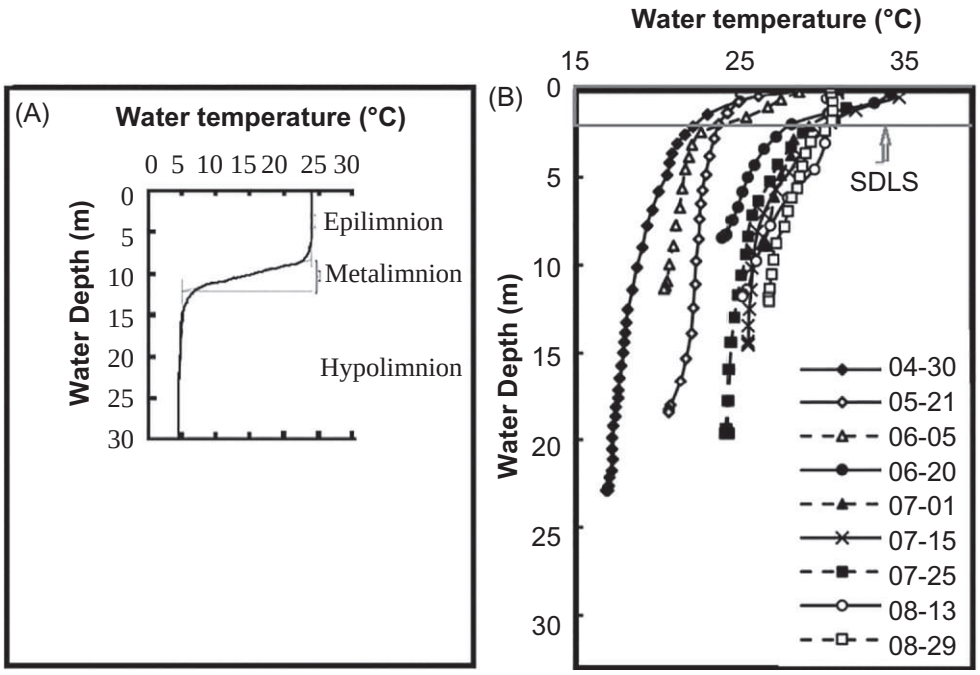

Fig. 3 The water stratification in general lakes and Pengxi River, a tributary of the Three Gorges Reservoir. (A) General model of stratification in temperate lakes. Note the depth of the surface mixing layer (epilimnion). (B) Water stratification of Gaoyang Lake, Pengxi River from spring to summer in 2013. 04–30 represents month and date, and so on. Note that there is almost no surface mixing layer.

SDLs is related to the algal blooms in the Pengxi River

Algal blooms in Gaoyang Lake are repeated events that develop with the onset of SDLs and disappear with the stabilization of SDLs. The algal blooms in Gaoyang Lake in 2019 are examples. During the 33-day continuous sampling process from April 15 to May 17, 2019, Chl-*a* in the surface water fluctuated daily (Fig. 4A). These fluctuations corresponded to the stratification at the same time (Fig. 4A and B). Stratification began from April 19 (4/19 in the figures) and dynamically changed afterwards (Fig. 4B). During April 21–23, April 28 to May 1, May 4–6, May 7–10, May 13–16, the mixing depth (Z_{mix}) of surface water bodies increased significantly because of wind disturbance, which resulted in several peaks of different magnitude of Chl-*a* concentrations. Especially on May 7–10, a wind speed of only 5.4 m s^{-1} (in the spring of Pengxi River, this is considered a strong wind) brought soluble phosphorus from the lower water column to the SDL (Fig. 4C), resulting in a severe bloom with Chl-*a* as high as 413 μg L^{-1} at the surface.

Why did the above-mentioned blooms die out? We found interestingly that during April 18–19, 24–27, May 2–3, and May 11, Z_{mix} of the water body was almost zero, i.e., as the temperature rose and stratification developed, the SDLs appeared, leading to minimal influx of nutrients from the lower water column, preventing further growth of algae. For example, from April 28 to May 2, the water changed from normal stratification to the formation of SDLs and Chl-*a* only increased slightly, because the dissolved total phosphorus (DTP) of the surface layer decreased to 0.003 mg L^{-1}. Similarly, the algal bloom with Chl-*a* as high as 250 μg L^{-1} from May 3–6 once again was brought to an end due to SDL formation, which reduced DTP in the surface water. This process illustrates an interesting phenomenon where even in a hyper-eutrophic system, the growth of algae sometimes faces the dilemma of nutrient deficiency due to nutrient limitation resulting from the formation of SDLs.

Implications of SDLs theory

SDLs theory can also explain why the tributaries in the TGR area rarely have blooms in the summer. The high temperature and low wind in the summer maintain the SDLs in summer leading to water surface temperature as high as 30 °C (Zhang et al., 2020). Nutrition and high-temperature stress might prevent the occurrence of algal blooms. Some studies have also attributed the lack of algal blooms in the summer to discharge of water from the TGD, which could make the flow faster than in spring, hence not suitable for algae to multiply. In fact, the average flow velocity of the Pengxi River in Gaoyang Lake from May to August is only 0.32 m s^{-1} (Zhang et al., 2020), which would not be high enough to prevent the occurrence of blooms (Wang et al., 2019; Li et al., 2021).

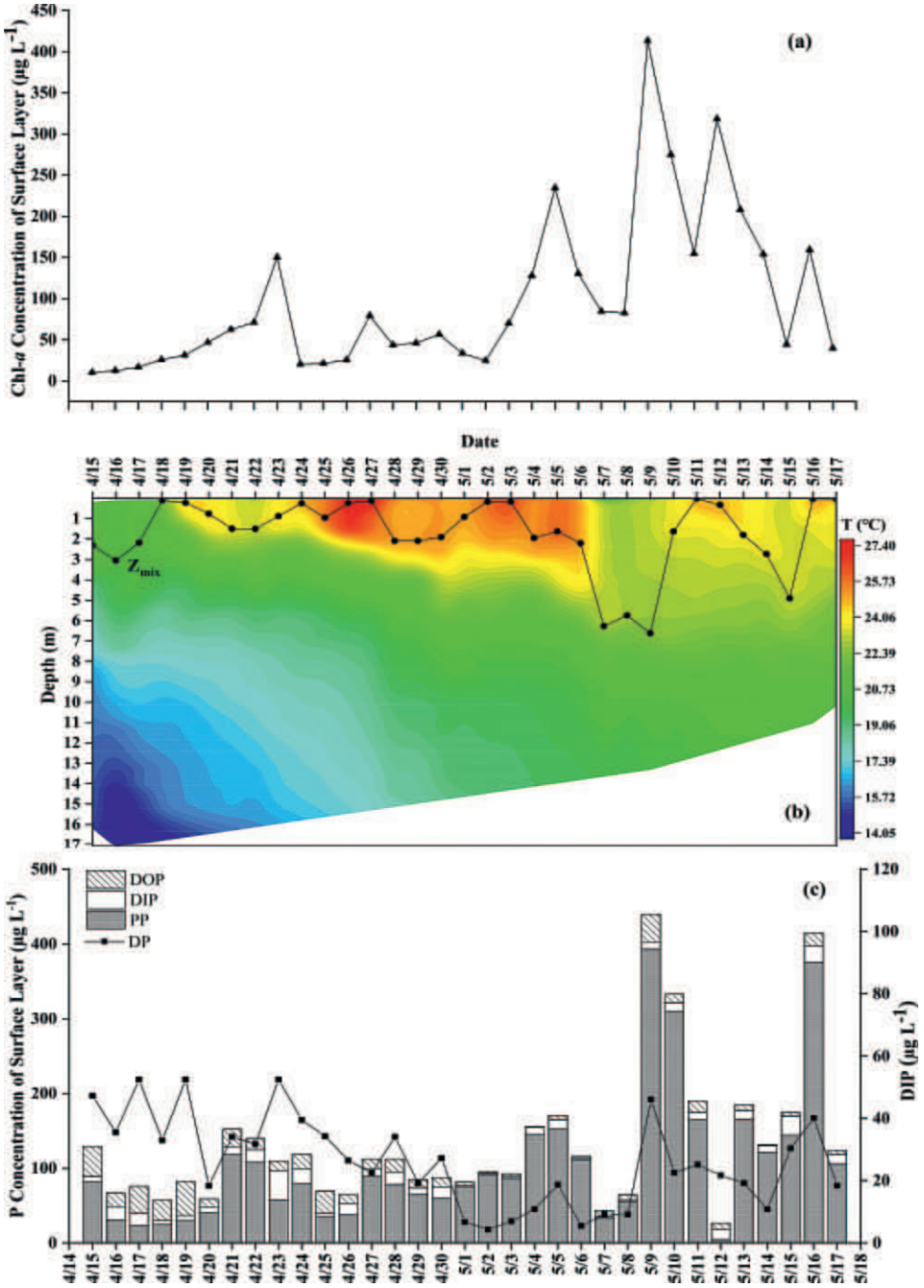

Fig. 4 The daily changes of chlorophyll a, stratification and surface phosphorus concentrations in Gaoyang Lake, Pengxi River, Three Gorges Reservoir from April 15 to May 17, 2019. (A) Daily change of surface chlorophyll-a; (B) Daily change of temperature and depth of surface mixed layer; (C) Daily change of phosphorus concentrations in the surface. PP, particulate phosphorus; DIP, dissolved inorganic phosphorus; DOP, dissolved organic phosphorus. TP (total phosphorus) = PP + DIP + DOP.

Eutrophication in Xiangxi Bay (XXB)

Xiangxi River

The Xiangxi River is the largest tributary in the lower reach of TGR in the Yangtze River. It has a length of 94 km, an average annual flow of 47.4 $m^3 s^{-1}$, watershed area of 3099 km^2 and is located within the latitude 31°04′–31°34 N′ and longitude 110°25′–111°06E′. It originates from Shennongjia National Park, Northwestern Yichang City, Hubei province, China. The Xiangxi River flows through Xingshan and Zigui Counties, north to south and empties into the mainstream of TGR in Xiangxi Town (Yang et al., 2015). Only 32 km away from the Three Gorges Dam, it is the second first-order tributary from the dam (Fig. 5).

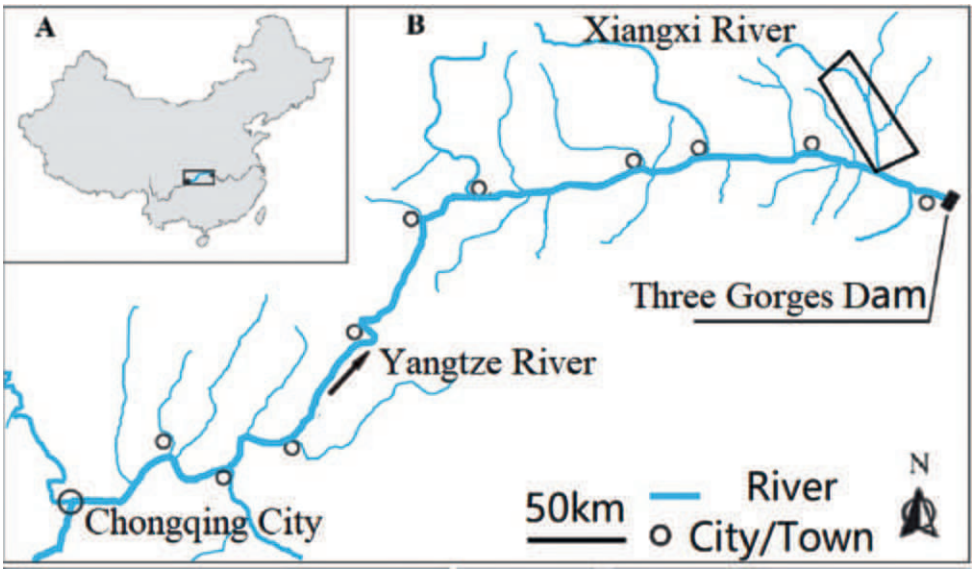

Fig. 5 Xiangxi River in the Three Gorges Reservoir. (A) The map of China; (B) The Three Gorges Reservoir.

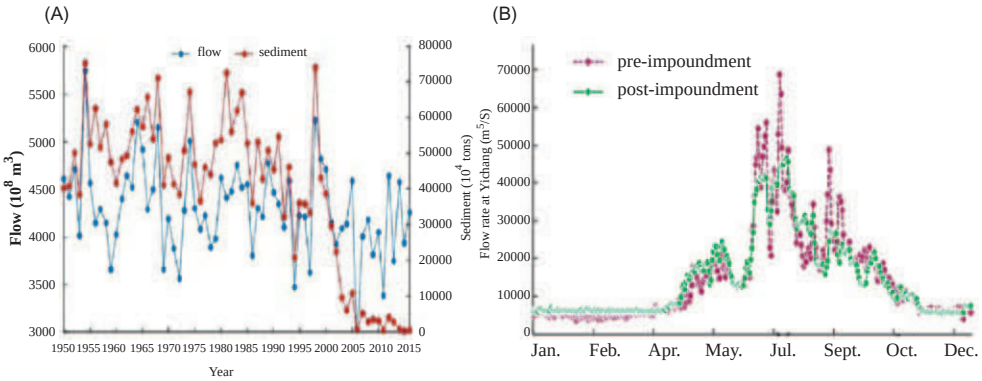

Fig. 6 (A) Variations in annual discharge (10^8 m^3), sediment discharge (10^4 metric tons), and (B) monthly flow rate (m^3 s^{-1}) in Yichang from upstream Yangtze River before (2002) and after (2012) the TGD impoundment.

The hydrodynamic conditions of Xiangxi River including annual flow volume, sediment discharge, and flow rate (Fig. 5) changed remarkably between the pre (1950–2002) and post (2003–2015) TGR impoundment eras. The backup effect of the mainstem of the Yangtze River caused the Xiangxi River to transform from fluvial (lotic) to a static state (Fig. 6), which is manifested by its long water retention time (179 days) and high suspended solids concentration. The first impoundment of the Three Gorges Reservoir in 2003 turned Xiangxi River into a deep bay (39.6 ± 22 m). Therefore, all the studies on the Xiangxi River after impoundment directly refer to the river as Xiangxi Bay (XXB).

The hydraulic operations of TGR have created four distinct phases of hydrodynamic cycles in XXB on a yearly basis: (i) phase of water supply between April to May (ii) phase of the flood around August, (iii) phase of impoundment (September) and (iv) phase of high-water level (December) (Li et al., 2020; Yang et al., 2015; Xu et al., 2011). In 2010 when the TGR finally reached its maximum water level of 175 m, the hydrodynamic backwater from the main stem of the Yangtze River extended to 40 km upstream in XXB (Ji et al., 2017; Jiang et al., 2018; Zhu et al., 2013).

The XXB receives nutrients from several anthropogenic sources including the chemical mining industries localized within Xiakou Town, most of which are close to the bank of the bay. XXB also has numerous drainage inlets through which highly concentrated domestic sewage from surrounding counties, is directly discharged into the bay (Zhou et al., 2012). Furthermore, there is a huge increase in dissolved N resulting from the influence of non-point sources into the tributary due to fertilizer from the extensive crop and animal agriculture in surrounding counties: Xingshan and Zigui both of which are located in Xiakou town. The increasing sewage discharge and constant point-source P loading from mining activities, also raise high P inputs. Consequently, the dramatic change in XXB hydrodynamics and nutrient budget has led to massive cyanobacterial blooms characterized by protracted water quality deterioration throughout the year, particularly in summer and spring. The blooms threaten public health and need urgent remedial attention.

Interactions between hydrodynamics and nutrient supply in XXB

Nutrient cycling in XXB shows strong sensitivity to the hydrodynamic factors, such as the stratified density current and water level fluctuations, intensified by the operations of the TGR. These hydrodynamic influences accentuate the anthropogenic nutrient loading and the development of cultural eutrophication. Yang et al. (2018) gave three potential classifications of the XXB density currents notably: the bottom layer intrusive current, dominant in winter; middle layer intrusive current, prevalent in both spring and summer; and the surface layer intrusive current, which is dominant during autumn. These density currents are reported to drive the mechanisms that supply a large amount of nutrients into the XXB exacerbating eutrophication in the bay. The middle layer intrusive current was identified to be responsible for the thermally stratified condition in those seasons (spring and summer). The critical depth hypothesis suggests that as long as the middle layer intrusive current continues to occur, unabated algal blooms outbreaks in XXB have a high probability to persist (Fig. 7).

Regulation of daily water-level fluctuations has been used by the reservoir managers to reduce the relative water column stability in order to mitigate HABs in some tributaries (e.g., Xiangxi River) but with limited success (Yang et al., 2013; Sha et al., 2015; Ji et al., 2017). Similar approaches to modifying water column stability have proven effective in controlling HABs in a relatively small reservoir in Spain (Rigosi and Rueda, 2012). However, the size of the TGR (660 km long and an average of 1 km wide) limits the use of water flow to manage water column stability for HAB control. Water-level fluctuations in tributaries far from the dam are relatively minor.

Previous studies (Ji et al., 2017; Yang et al., 2018) demonstrated that the operations of the TGD have a significant impact on water level regulations following the so-called eco-environmental friendly operation (EEFO), which involves closing for water retention and opening for discharge during the low flow and the high peak seasons, respectively (Ding et al., 2019). The TGD storage and discharge have potentially stimulated the massive phytoplankton growth in XXB. Specifically, the dam storage for water retention in low flow seasons (max. Water level = 175 m) allows water with high TN/TP to flow from the mainstream into the XXB while dam discharge during high peak seasons (min. Water level = 145 m) allows water with low TN/TP to flow into the mainstream (Chuo et al., 2019). The periodic water exchanges and nutrient fluxes, therefore, promote bloom development. This supports the concept that hydrodynamic factors, are important characteristics that control the mechanism of nutrient supply into the XXB, together with the anthropogenic nutrient inputs from agricultural runoff and urban discharge (N input), industrial wastewater, and domestic sewage (P input). These hydrodynamic characteristics essentially make the XXB different from the Taihu Lake, China and other freshwaters and reservoirs across the world. Lang et al. (2019) recently suggested that the primary cause of algal blooms, especially the spring bloom in the XXB, lies in the prevention of the upstream inflow from entering TGR, with nutrients enriching the upper and middle reach of XXB from winter to early spring. Furthermore, they proposed that bloom mitigation measures, such as improving the upstream hydrodynamic conditions and forcing the nutrients to flow into the TGR in the winter, should be prioritized to avert risks of HABs rather than the artificial tide operation of TGR (transitory water level regulations) frequently recommended in several studies (e.g., Liu et al., 2012).

It is important to note, however, that the development of algal blooms in the XXB could partly be attributed to point and non-point source pollution. Blooms were not reported in that area before the TGD impoundment, thereby implicating anthropogenic stressors as the principal triggers of blooms in the XXB, assisted by the hydrodynamic conditions and the nutrient cycling pattern.

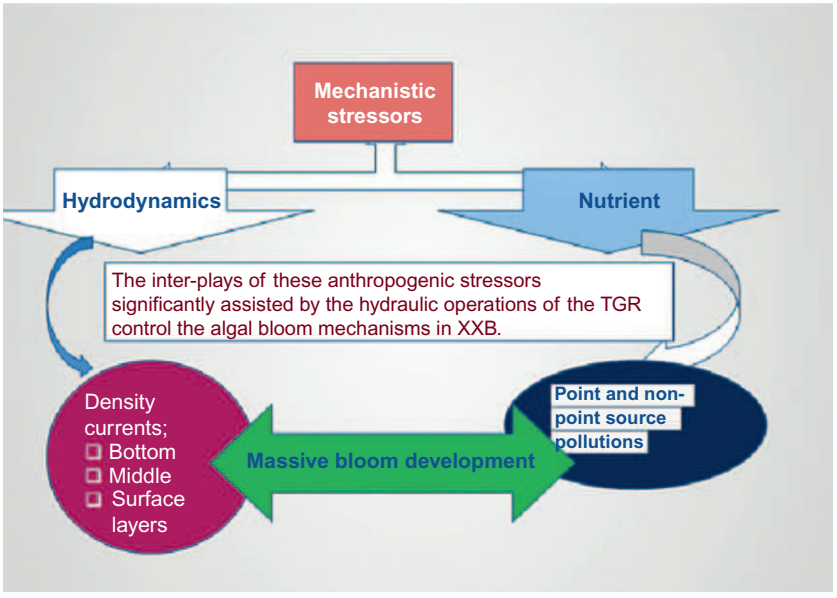

Fig. 7 Summary of the mechanisms underlying the proliferation of harmful algal bloom in the Xiangxi tributary in the Three Gorges Reservoir.

Management implications

Dammed tributaries with different morphologies and land-use activities can experience different intensities of algal blooms. Management of algal blooms in the TGR will need to account for differences among the tributaries with respect to how sensitive they are to dam operation and their varying morphologies and land-use patterns. For example, in order to disrupt the formation of stratification, regulation of daily water-level fluctuations is effective in the tributaries close to the dam including Xiangxi Bay. By contrast, local artificial mixing of the water column, including aeration, would not be effective to control algal blooms in the tributaries in the middle and upper reach of the TGR due to nutrient resupplies from the lower water column to the algae at the surface, associated with SDLs. Therefore, we suggest that tributary-specific management plans will be more effective than an overall reservoir management strategy in the TGR.

The construction of dams results in reservoirs that vary in their susceptibility to HABs. Our study demonstrated that the upper reaches of tributaries, are more vulnerable to algal blooms because of dam operations and formation of SDLs. The formation of SDLs, are a phenomenon that might be unique to reservoirs that are confined within deep canyons that prevent surface wind mixing. A long-term nutrient reduction policy is proposed as it is unlikely that nutrient management within the TGR will immediately address the control of algal blooms. Therefore, future research should address the interaction of hydrological phenomena, such as the formation of SDLs and nutrient bioavailability. Furthermore, our studies have demonstrated that during the algal bloom seasons in either Pengxi River or XXB, the nutrient cycling between the upper and lower water column and the sediment is key to initiating algal blooms. Reducing diffuse nutrients inputs takes decades (Müller et al., 2014; Fastner et al., 2016), but using floating macrophyte mats to absorb N & P in the upper water layers during the bloom season could be effective for mitigating the blooms and speeding up the removal of nutrients, especially P (Wang et al., 2020; Colares et al., 2020).

Conclusions and knowledge gaps

This chapter evaluates the impact of human pressures on the environment, especially in promoting harmful algal blooms in freshwaters. It uses as a reference, the two rivers (Pengxi and Xiangxi) in the Three Gorges Reservoir to explore the effect of these anthropogenic actions on the aquatic ecosystems. In summary, the studies on eutrophication in the two TGR 1st order tributaries, Pengxi River in the middle reach, and Xiangxi River near the TGD, demonstrate that the mechanism of algal blooms is case-based. The continuous blooms of Pengxi River and Xiangxi River cannot be simply attributed to the excess of nutrients although these systems are hyper-eutrophic. The important findings/knowledge gaps, therefore, include:

- The TGR is exposed to multiple anthropogenic pressures, dominated by dams and nutrient enrichments from point and non-point sources;
- Dam closure in the TGR has resulted in the creation of numerous artificial and vulnerable tributaries, which are severely impacted by HABs;
- The mountainous topography of the TGR catchment leads to the formation of unique surface density layers where nutrient deficiency could happen during algal bloom season among the hyper-eutrophic waters;
- Strong nutrient regulations (multiple reduction strategy) would greatly assist in HABs abatement in the TGR;
- Although both Pengxi and Xiangxi Rivers are freshwater systems in the TGR, they show different severities in their bloom seasons, while maximum HAB events occur during summer in the Xinagxi River, the most severe HAB event is reported during spring in the Pengxi River.

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Effects of Mining on Surface Water

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner

In memoriam Li Wenliang (李文亮)—and the million others.

Glossary

To date, a comprehensive English language mine water glossary does not exist. In most cases, the glossary in the GARD Guide (www.gardguide.com) or in McLemore (2008) might be a first stop.

Acid/Acidity Acid/Acidity are two different concepts. "Acid" refers to the proton acidity and is measured with a pH-meter. Acidity is the sum of the proton acidity, metal acidity and other naturally occurring acids. It is determined by titration.

Adit Adit is a horizontal or close to horizontal tunnel or gallery that connects the surface with an underground mine.

Barite Barite is a sulfate mineral with the formula $BaSO_4$.

Calcite Calcite is a carbonate mineral with the formula $CaCO_3$.

Dolomite Dolomite is another carbonate mineral with the formula $CaMg[CO_3]_2$.

Electrical conductivity Electrical conductivity is a measure for the potential of a liquid to conduct electricity. In general, the more ions are dissolved in a liquid, the higher this value will be, which is usually measured in mS cm^{-1} or µS cm^{-1}. It is compensated to either 25 °C or, more seldom, to 20 °C. Because of this characteristic, the electrical conductivity can be used for a quick indication of a mine water's contamination status.

 https://doi.org/10.1016/B978-0-12-819166-8.00036-0

Feldspar Feldspar is a collective name for a large group of silicate minerals with the formulae $KAlSi_3O_8$, $NaAlSi_3O_8$, and $CaAl_2Si_2O_8$.
Heavy metal Heavy metal is a music style. According to the International Union of Pure and Applied Chemistry (IUPAC), no other usage is recommended (Duffus, 2002), as there are more than 40 definitions, thus rendering the meaning vague.
Marcasite Marcasite is a sulfide mineral with the formula FeS_2. Though chemically identical to pyrite, it has another crystal structure.
Mine water Mine water or mining influenced water (not: mine wastewater, mining impacted water, mining affected water) is all the water in a surface or underground mine or seeping through waste rock. Strictly speaking, the water from the processing plant and the tailings is process water, as it contains human-induced process chemicals.
Ochre Ochre is a collective term for yellow to dark orange iron oxides with a clayey to sandy composition.
Orphaned Orphaned mines are abandoned mines that are ownerless.
pH pH is a parameter that expresses the activity of protons (positively charged hydrogen ions) in liquids. There is nothing such as a "pH-scale" and it has no units as it results from the calculation of a logarithm. The lowest, that means most acid, ever measured pH in nature is −3.6 and the highest alkaline one 13. It is measured with a pH-probe.
Pyrite Pyrite is a sulfide mineral with the formula FeS_2. Though chemically identical to marcasite, it has another crystal structure. When pyrite or marcasite come into contact with water and oxygen, acid mine drainage or acid rock drainage forms.
Pyrrhotite Pyrrhotite is a sulfide mineral with the formula $Fe_{(1-x)}S$; $x = 0–0.2$. In contact with water and oxygen, this mineral also forms acid mine or rock drainage.
Redox potential This parameter indicates the sum of all oxidation and reduction reactions in a liquid and is an expression for the "free" electrons in a solution. It provides a measure of the oxidizing or reducing tendency of this solution. A redox potential below zero millivolt (mV) indicates reducing and a redox potential above zero millivolt an oxidizing environment. It is measured with a redox probe and must be corrected to the standard hydrogen electrode (www.Wolkersdorfer.info/orp).
Semi-metals Semi-metals (metalloids) are elements that show characteristics of both metals and non-metals or either of them. Commonly recognized semi-metals are arsenic, boron, germanium, antimony, silicon, and tellurium.
Suspended Solids (SS) Suspended Solids are all the smaller particles in a liquid that stay suspended. They may settle once the liquid's velocity slows down or when time passes.
Tailings Tailings are the fine-grained residues of mineral processing and contain currently uneconomic crushed and milled rock and chemicals from the processing plant. Tailings are stored in sludge ponds, called tailings dams or are dry stacked in tailings disposal sites.
TDS (total dissolved solids) TDS are indicative for the sum of all inorganic and organic ions dissolved in a liquid. The higher the TDS concentration, the more ions are dissolved, which means the water is more mineralized. In mining influenced water, it must be measured by gravimetry and not approximated by a simple calculation from the electrical conductivity (Hubert and Wolkersdorfer, 2015).
Trans-drainage basin diversion Trans-drainage basin diversion means that water from one river drainage basin is transferred into another drainage basin by way of pipes or channels.

Introduction

Mining includes modern, small-scale, and artisanal surface mining, strip mining, placer mining, underground mining, solution mining, *in situ* mining, quarrying, or the extraction of groundwater. Approximately 240,000 km^2 of the Earth's surface are covered by abandoned, closed, or orphaned mines (Wolkersdorfer, 2008). There, pollution pathways include surface, groundwater as well as aerial deposition (Fig. 1), and potentially contaminated sediments might collect in the stream beds and lakes. Mining influenced water can develop acid (below pH 5.6), circumneutral (between pH 5.6 and 8), or basic pH values (above pH 8), and in terms of dissolved matter, it can be dilute, mineralized, or saline (Nordstrom et al., 2015). Once inland waters are contaminated by mine water, their remediation can take long and may involve large financial burdens (ERMITE Consortium et al., 2004).

Protecting the environment from pollution, both from tailings and from the mine workings is a complex problem (ERMITE Consortium et al., 2004), and its solution takes the combined efforts of many partners. Unquestionably, the best protection of the ecosphere would be to prevent mining entirely or, alternatively, recycle all used metals, rocks or aggregates (European Innovation Partnership on Raw Materials, 2016). Yet, both options are currently not feasible in face of the demand of a growing world population for raw materials. Therefore, responsible and sustainable mining uses a life cycle assessment including the "mining for closure" principle and the "cradle-to-grave" approach (Idowu et al., 2013; Northey et al., 2018; Peck et al., 2005; Wörlen et al., 2005).

Examples in this article are not chosen to single out individual mine sites or mining houses, but as relevant examples describing a particular mechanism or case. Many of the well documented mine sites are operated by responsible companies that openly discuss their problems, while many heavily polluting mine sites (Earthworks and Oxfam America, 2004) are inadequately documented,

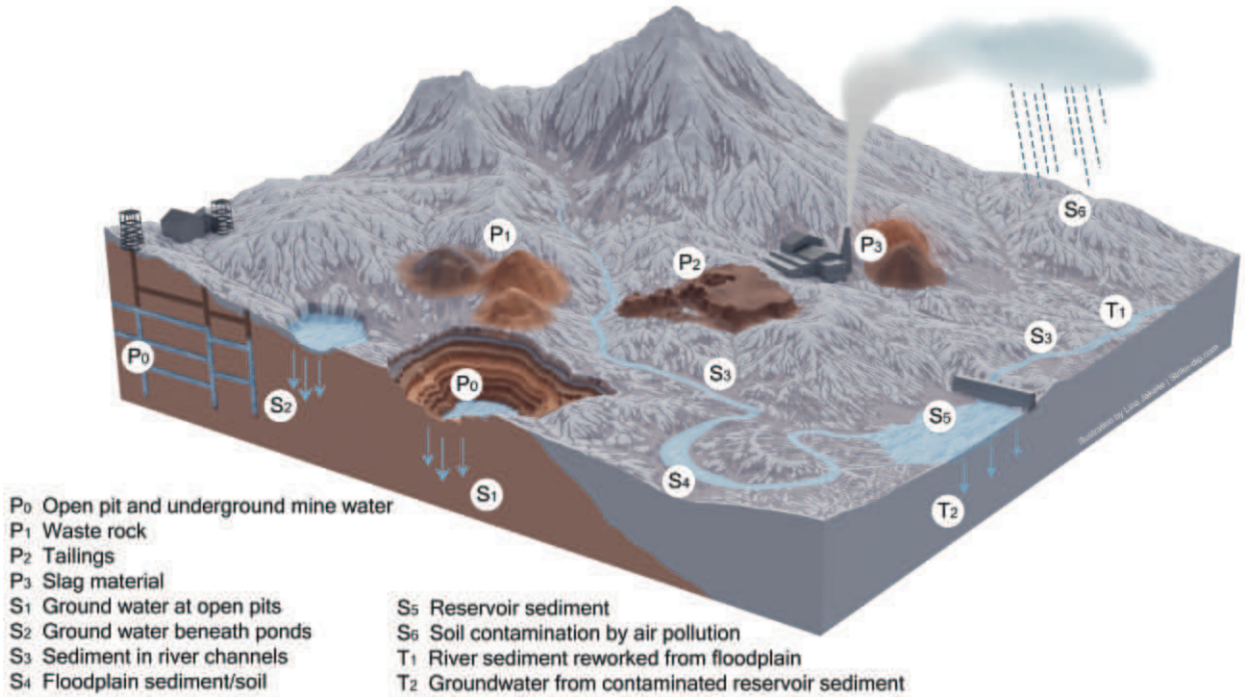

Fig. 1 Pollution pathways in the mining environment. P: primary contamination, S: secondary contamination, T: tertiary contamination. Modified after Moore JN and Luoma SN (1990) Hazardous wastes from large-scale metal extraction—A case study. *Environmental Science & Technology* 24(9): 1278–1285, https://doi.org/10.1021/es00079a001.

because the owners restrict publication of unwanted results or access to these sites. In addition, it is noteworthy to state that responsible mining tries to avoid lasting environmental damages. Responsible mining ensures that the mining operation has its social license to operate and mining remnants are mitigated as well as remediated to near pre-mining conditions as best as possible (International Council on Mining and Metals, 2008).

What is mining influenced water

Evolution of mining influenced water

Mining interferes with the natural geological conditions and transforms an often reducing environment, in which the minerals were thermodynamically stable, into an oxidizing one. These changes to the environment bring the minerals in contact with water, oxygen and an abundance of microbes that immediately take advantage of the new thermodynamic conditions and possibilities (McLemore, 2008; Wildeman and Schmiermund, 2004).

Sulfate enriched mine water predominantly results from the microbially catalyzed oxidation of the iron-sulfides pyrite, marcasite and pyrrhotite to sulfate and acid (Fig. 2), whereby pyrite and marcasite are the most common of these minerals in coal, base metal and gold deposits (Blowes et al., 2014; Nordstrom, 2011). In total, the process involves four steps, which shall be described for pyrite (Stumm and Morgan, 1996). Firstly, pyrite reacts abiotically with water and oxygen (I) or is used biotically by microorganisms for their metabolism. This results in high concentrations of dissolved sulfate, ferrous iron (Fe^{2+}) and protons. In the next step (II), the ferrous iron is oxidized to dissolved ferric iron (Fe^{3+}) which either oxidizes the pyrite to form more ferrous iron (III) or it reacts with the water and oxygen to form iron-oxihydrate precipitates (IV). Microorganisms, such as *Acidithiobacillus thiooxidans*, accelerate these relatively slow abiotic reactions 1 million times (Wolkersdorfer et al., 2020).

When carbonate or silicate minerals are present, they partly counteract the above reactions, as they buffer the produced protons. This means that the protons react with minerals such as calcite, dolomite, or feldspars, resulting in their dissolution and releasing their elements into the water. As the pH of the receiving inland waters will buffer pH from these reactions, many metals or metalloids will precipitate (Fig. 3) or co-precipitate, subsequently improving the water quality (Stumm and Morgan, 1996).

In the case of saline mine waters, the evolution is completely different. It is normally a physical process, by which solid salts are dissolved until they reach a (semi)stable equilibrium with the mine water. In mines with soluble salts, the physical and chemical reactions involved can be complicated, as the various solubilities of salts substantially change with temperature, saturation of the salts and the brine's composition (Herbert and Sander, 1987).

When pyrite oxidation as well as saline waters combine, the results are saline mine waters with elevated (semi-)metal and sulfate concentrations. This is often seen in coal mine discharges regardless of where on Earth they occur.

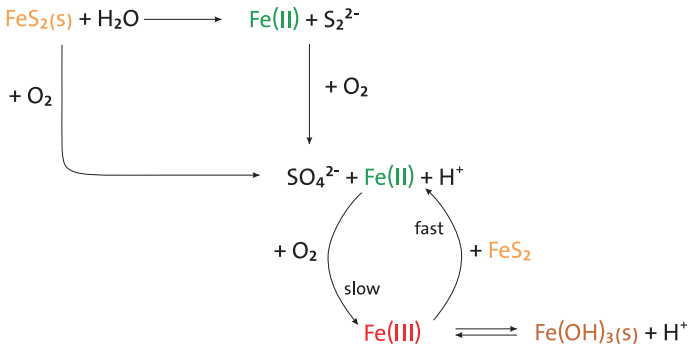

Fig. 2 Diagrammatic representation of the pathways during abiotic pyrite/marcasite oxidation. Based on information in Kester DR, Byrne RH and Liang Y-J (1975) Redox reactions and solution complexes of iron in marine systems. *ACS Symposium Series* 18: 56–79, https://doi.org/10.1021/bk-1975-0018.ch003; Singer PC and Stumm W (1970) Acidic mine drainage—The rate-determining step. *Science* 167(3921): 1121–1123, https://doi.org/10.1126/science.167.3921.1121; Stumm W and Morgan JJ (1996) *Aquatic Chemistry—Chemical Equilibria and Rates in Natural Waters*. 3rd edn., New York: Wiley & Sons.

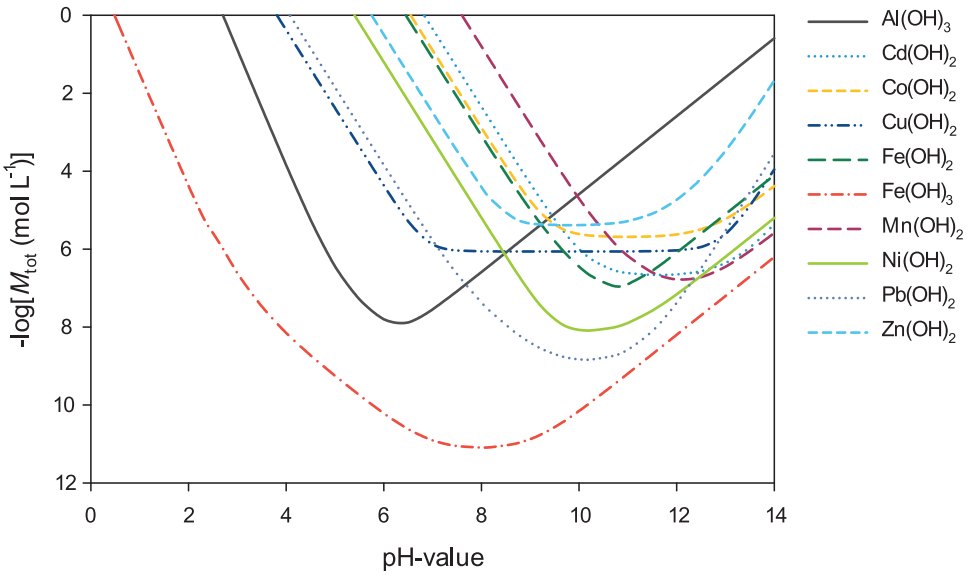

Fig. 3 Solubility of environmentally relevant metal hydroxides as a function of the pH value. Modified and supplemented according to Cravotta CA, III (2008) Dissolved metals and associated constituents in abandoned coal-mine discharges, Pennsylvania, USA. Part 2: Geochemical controls on constituent concentrations. *Applied Geochemistry* 23(2): 203–226, https://doi.org/10.1016/j.apgeochem.2007.10.003, original data obtained from Charles A. Cravotta III, pers. comm. 2013.

Mine water—Surface water linkages

To keep a mine operating, it needs a sustainable water management plan in place that accounts for pumping the water from the mine workings, supply of water for ore processing, dust suppression and human use. All these water streams in and around the mine need to be known to manage the water balance reliably (Punkkinen et al., 2016). Predominantly, the mine dewatering affects the groundwater, but in several cases also ecological affects might occur as surface water is diverted around a mine site, especially when trans-drainage basin diversion occurs (Marcus, 1997).

As long as a mine is operating, pumped water, as well as tailings dam and waste rock dump seepage water will come into contact with surface water, mostly following treatment—unless a mine operates in dry areas with a lack of groundwater. Once mining commences, the open voids will start to be filled with groundwater and the mine starts to flood, a process that usually takes years to decades. When the water level in the mine reaches the lowest discharge point, the mine water will start to discharge into the receiving water courses (Wolkersdorfer, 2008) or terminal pit lake sinks (McCullough et al., 2013). Those linkages between mine water and surface water can take many different forms: seepage from shallow underground workings, discharges from pit lakes, bore holes, adits, inclines, or shafts. Seepage can also occur through overburden and especially from collapsed hanging wall areas and may contribute notably to surface water contamination. For protecting the environment, shaft or adit discharge is preferable, as the water can be directed towards an active or passive mine water treatment plant.

Tailings are nearly always connected to inland waters, except when located in arid areas or they undergo submarine disposal (Dold, 2014). Tailings dam water sees various forms of linkage to surface water such as overflow, seepage water into surrounding water courses or indirectly though seepage into the groundwater, which might then emanate to the surface downstream of the tailings dam (Fortuna et al., 2021).

Waste rock usually contains residues of the mining operation that are deemed currently economically unviable. If this material is chemically inert, the seepage water should pose no detrimental effects on the surface water other than modest increases of electrical conductivity or suspended solids content. Should the waste rock contain minerals (e.g., disulfides or efflorescent minerals) that produce acidity or elevated contaminant concentrations during weathering, the discharged seepage water may cause detrimental effects to the receiving water bodies.

Physico-chemical characterization

Mining influenced water can be characterized by its physico-chemical parameters such as temperature, electrical conductivity, pH, redox potential, turbidity, color, and oxygen saturation. These are mainly interdependent from each other and normally there is no correlation between them, though temperature affects the solubility of oxygen, or pH the solubility of many metals. In addition, all these variables and parameters show high variability, ranging, for temperature, pH, and redox potential for example, from −2 °C to 58 °C, −3.6 to 13 and −500 to 900 mV, respectively.

High suspended solid loads and turbidity are common for many mining influenced waters. Turbulence keeps colloid-sized particles or flocculated oxyhydroxides in suspension and results in high concentrations of iron and aluminum in the water. Metal attenuation reactions can sometimes be recognized in the water by turbidity in certain places (Schmiermund and Drozd, 1997).

Mine water can discharge at elevated temperatures of up to 58 °C, resulting from either exothermic reactions or the geothermal gradient. For surface waters, the discharge of warm water can then provide habitats for non-native species, with sightings of released aquarium fish at mine water discharge points in Germany (personal observations), and a reduction of less heat tolerant species.

Very often, mining influenced water is colored, whereby the color depends on the water's constituents and colors the receiving inland waters. Iron rich water has usually colors that range between orange, brown and red, whilst copper rich effluents are greenish to blueish and nickel rich mine water has light blue to green colors. Aluminum and elevated alkalinity results in white colors. This coloring can either be due to dissolved metals (e.g., iron, copper, nickel) or to suspended precipitates, for example gibbsite.

Chemical composition

The chemical composition of mine water shows a high degree of variability (Table 1). This is due to the large spectrum of geological settings (Smith and Huyck, 1999) and the biological, chemical and physical processes involved (Plumlee et al., 1999). In addition, the solubility of the metal hydroxides controls their concentrations in the mining influenced waters and the receiving water courses (Fig. 3).

Some of these elements in mining influenced water will appear in cationic species, such as calcium, others in anionic species like chloride—writing about an element as a constituent of mine water, therefore always implies it is in its ionic form. Extremely rarely, mine water will contain elements in their elemental form; exceptions might be the non-reactive and non-toxic noble gasses. Some of these elements are found more often in mine water, such as protons, iron, copper, aluminum, arsenic, chloride or manganese, others are less abundant, such as molybdenum, selenium, mercury, vanadium, or chromium. Yet, mine water contains water, H_2O, at a concentration of 55.5 mol L^{-1}. The next group of mine water constituents comprise the main ions of water: calcium, sodium, potassium, magnesium, hydrogen carbonate, sulfate, chloride, nitrate at an average concentration of around 0.5 mol L^{-1} and the trace ions at an average concentration of 0.005 mol L^{-1}, which accounts to just 0.01% of the molar composition of water. These are average numbers, as in the case of the Iberian Pyrite Belt, the sulfate concentrations in the mine water account for approximately 2.9% of the water's ionic composition.

Not only does mining influenced water have a different chemical composition depending on the type of ore deposit, host and country rock, and the chemistry of the receiving water itself, but it also changes over time. When water discharges from underground mines, the first flush effect results in elevated concentrations of the most relevant components (Younger, 1997) for a longer time span. These elevated concentrations and the low pH values will impair and color inland waters for years to decades and will have negative effects on the ecological balance compared to pre-mining conditions. One of the reasons is that many elements usually show a higher solubility and often bioavailability at low pH values (Neil et al., 2009; Smith and Huyck, 1999).

Mine types and characteristic effluents

Introduction

Every ore body or mine type develops its characteristic effluent chemistry (Table 1). Reasons for this are the geochemical and hydrogeochemical reactions occurring during water–rock interaction. By knowing the geological, mineralogical, and climatic background of a mine site as well as the mining method applied, first estimates about the mine water chemistry and potential effects on surface water can be made (Plumlee et al., 1999). As described in the previous chapter, the final composition of the mine water is an interplay of various chemical and microbiological reactions and usually shows a high temporal and spatial variability. Their principles are identical at all mine sites around the world. Yet, the particulars are controlled by the site-specific conditions (Table 2).

Table 1 Composition of different mine waters with the most predominant mine water constituents.

Locality	*pH*	SO_4^{2-}	Fe_{tot}	*Al*	*Mn*	*Zn*	*Cu*
Iron Mountain California, USA (Cu)[N99]	0.5	118,000	20,300	2210	17	2010	290
Iberian Pyrite Belt, Portugal[a]	1.4	157,229	52,767	7072	155	1885	2243
Cae Coch, Wales (pyrite)[B97]	2.5	5110	1460	84	3	1	0.2
Río Tinto, Spain (Cu, Au)[O20,b]	2.7	1123	145	65	5.3	16	15
Lappwald Lake, Lusatia, Germany (lignite)[L20]	2.9	1700	6.4				
Kizel Coal Basin, Russia (coal)[M18]	3.0	3992	1608	79	13	0.4	–
Western Basin (8 shaft), S. Africa (Au)[c]	3.0	2410	54	<0.1	15	0.06	<0.01
Fanie Nel Discharge, S. Africa (coal)[c]	3.2	1217	265	31	20	2.3	0.072
R. Hipper Discharge, UK (coal)[B97]	3.6	1044	101	17	4	0.2	0.007
Ynysarwed, Wales (coal)[B96]	4.2	1554	180	<0.5	6	0.06	–
Oatlands waste rock dump, UK (coal)[B96]	5.5	146	287	1	5	0.05	<0.007
Gernrode Harz Mts., Germany (fluorite)[H04]	5.7	86	16	–	–	0.36	0.05
Straßberg Harz Mts., Germany (fluorite)[R00]	6.3	359	31	–	6	0.9	0.08
Dunston Chesterfield, UK (coal)[B96]	6.3	210	11	<0.05	1.3	<0.007	
Duke's level Buxton, UK (coal)[B96]	6.3	83	5	0.08	0.4	0.05	0.005
Allen Hill Spaw, UK (metal)[B96]	6.5	124	15	0.1	2	0.003	–
Niederschlema, Germany (U)[W96]	7.1	1138	3	0.4	3	0.1	0.03
1B Mine Pool (B-185), Canada (coal)[c]	7.1	1100	3.6	0.003	7.8	0.01	0.001
Cosbuden lake, Lusatia, Germany (lignite)[L20]	7.2	800	0.01				
Frazer's Grove Yorkshire, UK (fluorite)[J02]	7.6	76	0.4		0.8	0.2	–
Mine № 3, Svalbard (coal)[B04]	8.2	7	<0.01	<0.02	0.004	0.055	<0.005
Schwaz, Austria (dolomite, fahlore)[c]	8.4	13	< 0.01	–	0.002	0.022	0.04

Bold lines refer to the five case studies and superscript indices to the references.
[a]T. Valente.
[b]Median values 2017/2018; concentrations in mg L^{-1}. The Iberian Pyrite Belt stretches from Portugal to Spain, and the Río Tinto is one of the prominent rivers in the district.
[c]Unpublished data from Ch. Wolkersdorfer.

Sources: B96: Banks D (1996) The hydrochemistry of selected coal mine drainage and spoil-tip run-off water, Longyearbyen, Svalbard. *NGU-rapport* 96(141): 1–22; B04: Banks D (2004) Geochemical processes controlling minewater pollution. In: Prokop, G. et al. (eds.) *Conference Papers*, pp. 17–44. Wien: Umweltbundesamt; B97: Banks D, Younger PL, Arnesen RT, Iversen ER and Banks SB (1997) Mine-water chemistry: The good, the bad and the ugly. *Environmental Geology* 32(3): 157–174, https://doi.org/10.1007/s002540050204; H04: Hasche A and Wolkersdorfer C (2004) Mine water treatment with a pilot scale RAPS-system. *Wissenschaftliche Mitteilungen* 25: 93–99; J02: Johnson KL and Younger PL (2002) Hydrogeological and geochemical consequences of the abandonment of Frazer's grove carbonate hosted Pb/Zn fluorspar mine, North Pennines, UK. Special Publication. *Geological Society of London* 198: 347–363, https://doi.org/10.1144/GSL.SP.2002.198.01.24; L20: Lausitzer und Mitteldeutsche Bergbau-Verwaltungsgesellschaft mbH (2020) *Wasserwirtschaftlicher Jahresbericht der LMBV mbH—Zeitraum 01. January—31. Dezember 2019 [Water Management Annual Report of LMBV mbH—Period of 01 January—31 December 2019] (Report)*. Senftenberg: Lausitzer und Mitteldeutsche Bergbau-Verwaltungsgesellschaft mbH. Available: https://www.LMBV.de/files/LMBV/Dokumente/Wassermanagement/Wasserjahresberichte/20200421%20Wawi_JB_2019_mit_Anlagen.pdf; M18: Maksimovich NG and Pyankov SV (2018) Кизеловский угольный бассейн—экологические проблемы и пути решения *[The Kizel Coal Basin—Ecological Problems and Solutions]. Perm, Raritet-Perm Publishing House; N99*: Nordstrom DK and Alpers CN (1999b) Negative pH, efflorescent mineralogy, and consequences for environmental restoration at the Iron Mountain Superfund site, California. *Proceedings. National Academy of Sciences. United States of America* 96(7): 3455–3462, https://doi.org/10.1073/pnas.96.7.3455; O20: Olías M, Cánovas CR, Macías F, Basallote MD and Nieto JM (2020) The evolution of pollutant concentrations in a river severely affected by acid mine drainage: Río Tinto (SW Spain). *Minerals* 10(7): 598, https://doi.org/10.3390/min10070598; R00: Rüterkamp P and Meßer J (2000) *Untersuchungen zur hydraulischen und hydrochemischen Situation in den drei Teilrevieren der gefluteten Flussspatgrube Straßberg [Investigations on the hydraulic and hydrochemical situation in the three sub-areas of the flooded Straßberg fluorspar pit] (Report № 1710–99-285)*. Essen: Deutsche Montan Technologie GmbH; W96: Wolkersdorfer C (1996) *Hydrogeochemische Verhältnisse im Flutungswasser eines Uranbergwerks—Die Lagerstätte Niederschlema/Alberoda [Hydrogeochemical conditions in the mine water of a uranium mine—The Niederschlema/Alberoda deposit]*. Clausthaler Geowiss. Diss., vol. 50, 1–216.

Table 2 Commodities and typical parameters impairing inland waters. EC: electrical conductivity; SS: suspended solids.

Commodity	*pH*	*EC*	SO_4^{2-}	*Fe*	*Al*	*Cu*	*Zn*	*U*	*Ra*	*Cl*	*Hg*	*As*	*N*	*SS*
Coal and Lignite	◆	◆	◆	◆	◆					◆				
Gold	◆	◆	◆	◆				◆			◆	◆		◆
Salt		◆								◆				
Iron	◆		◆	◆										
Copper	◆	◆	◆		◆	◆								
Lead/Zinc	◆	◆	◆				◆							
Uranium	◆	◆	◆					◆	◆			◆		
Diamonds		◆											◆	◆
Aggregates, Building Stones, Quarries													◆	◆
Others	◆	◆	◆	◆									◆	◆

In the absence of disulfides or pyrrhotite in the host rock, (di-)sulfide weathering will not occur, and the mine water will not be acid. Yet, this does not guarantee that the mine water will be of good quality, as some elements are mobile under circumneutral or alkaline conditions. Such examples are elevated antimony concentrations in carbonate rocks (Wolkersdorfer and Wackwitz, 2004) or zinc-enriched mine waters in carbonate-hosted lead/zinc deposits (Johnson and Younger, 2002). When neither disulfides nor (semi-)metals that are mobile under elevated pH values nor water-soluble salts exist, the mine water quality will be within regulatory limits. In these cases, the mine water might even be used as drinking water without treatment (Wolkersdorfer, 2008).

Because the number of working and abandoned mines is large, mining influenced water can become a burden to humans and the environment when this water is polluted. Plumlee et al. (1999) compiled which type of ore body will very likely develop what type of mine drainage. Though their compendium is quite U.S.-based, it is of uniform relevance, as the geological, physical, biological, and chemical processes of mine water geochemistry are identical all around the world.

Coal and lignite

Coal and lignite often contain varying proportions of disulfides because the depositional conditions favored the precipitation of these minerals (Pohl, 2020). Occasionally, the sulfur content of coal can reach up to 6%, which can produce substantial amounts of acid when not buffered by carbonate rocks. A general rule is that the higher the sulfur content, the higher the concentrations of the potential pollutants sulfate and iron (Younger, 2002). Common potential pollutants of concern from coal or lignite mines are acid, iron, sulfate, sodium and chloride.

Nearly all coal or lignite mining operations develop acid mine drainage if no precautions are taken, such as mixing the overburden with lime or co-depositing disulfide-rich material with buffering material. Mining methods substantially influence the final mine water quality after mining stops (Mentz et al., 1975). When the coal mine can be flooded, the water quality may gradually improve due to the first flush effects. Many long abandoned coal mines discharge water of good quality (Wolkersdorfer and Bantele, 2013). Yet, when large portions of the mines are open to the atmosphere, pyrite oxidation will continue in perpetuity and the discharge water quality may not substantially improve over time. pH values can be below pH 4 and sulfate as well as iron concentrations can be in the upper milligram to lower gram per liter range (McCullough et al., 2008; Prediction Workgroup of the Acid Drainage Technology Initiative, 2000). A contaminant that only received attention in recent years are PCBs (polychlorinated biphenyl) from hydraulic fluids discharged from German hard coal mines. Although most of the PCBs are below the detection limit in the water phase, they can be detected at some selected sites and concentrate in the sediments (Landesamt für Natur Umwelt und Verbraucherschutz NRW et al., 2018). Underground coal mines often have mine water with an elevated mineralization resulting from brines with high chloride and sodium concentrations. In some coal mine waters, barium concentrations cause barite precipitation when this mine water comes into contact with sulfate rich waters (Gombert et al., 2019).

Gold

One of the largest environmental impact areas of a historic mining operation is the Spanish Unesco World heritage site Las Médulas. Using a special type of hydraulic mining, called *ruina montium*, the Romans removed substantial amounts of overburden to access alluvial gold, making the site their largest gold operation (Revuelta, 2018). During the operation, about $84 \cdot 10^6$ m^3 of gravel, sand and silt were moved (Sanchez-Palencia et al., 2000) and sedimented into the receiving water courses and lakes. Similar situations can still be found in other parts of the world, where gold is mined by hydraulic mining. Yet, the most common mining method for gold in modern times is surface and underground mining combined with cyanide leaching. As gold co-occurs with disulfides, and sometimes uranium, gold mining usually results in highly acidic water with low pH values and elevated sulfate and iron concentrations. Because gold is not only mined in large scale operations, but in small-scale as well as illegal operations, often referred to as artisanal mining, environmental pollution from gold mining sees various forms (Riaz et al., 2019). They include mercury and suspended solids pollution and river course modifications from small or illegal mining operations as well as acid mine drainage and sulfate pollution from abandoned large scale operations. During large-scale active operations, mine and runoff water treatment ensures compliance to regulatory requirements, but cyanide or sulfate pollution is a common problem in these operations when not handled properly (Acheampong et al., 2010). Large areas in the Colorado's Rocky Mountains are polluted by acid mine drainage from abandoned gold mines. Waste rock piles, tailings and unremediated mine galleries discharge large amounts of metals into the receiving water courses, such as the Animas River Watershed (U. S. Department of the Interior—Bureau of Reclamation, 2015). Common parameters of concern from gold mines are acid, iron, sulfate, mercury, cyanide, suspended solids and arsenic.

Salt

Common salt and potash mining for NaCl, KCl and some Mg-salts, results in large residues of unwanted salt bearing material that is open to the atmosphere and is prone to weathering (Fig. 4). This causes elevated total dissolved solids concentrations as well as chloride, sodium and potassium-concentrations in the receiving water courses. An additional source of contamination is water pumped from the underground workings or the accidentally collapsed salt domes (Kolesnikov and Laskina, 2019). In France, for example, salt is mined by dissolving large salt domes until they purposely collapse and form surface depressions that will fill with water. This mining technology will alter surface water courses in addition to the groundwater regime. Parameters of concern are

Fig. 4 Salt waste rock piles of the Unterbreizbach and Hattorf mines in Germany. In the foreground the receiving water course Werra. Photograph: Christian Wolkersdorfer.

elevated electrical conductivity and the before mentioned ions. These types of lakes can develop pH values of up to 9 and electrical conductivities of 134 mS cm^{-1} (Żurek et al., 2018). Some of these collapse lakes are used for balneological applications in Romania (Mara et al., 2008), and the Wieliczka salt mine in Poland is a UNESCO world heritage site. During the course of time, salt mines will commonly stratify with a less mineralized water body overlaying highly mineralized mine water (Wolkersdorfer, 2008). Common parameters of concern are elevated electrical conductivity, sodium-, chloride- and potassium-concentrations.

Iron

From a pollution point of view, iron or pyrite mines can be classified into two types: carbonate/oxide (hematite)- and sulfide-based ores. While iron oxides, such as these in Australia's Pilbara or Brasilia's Iron Triangle seldom pose a chemical threat to water courses, the opposite is true for iron disulfide mines such as California's Iron Mountain or Finland's Pyhäsalmi mines. Most of the banded iron formation mines in Brazil discharge mine water with electrical conductivities between 100 and 300 µS cm^{-1}, as low as rainwater (Quadros Amorím et al., 1999). If pollution into water courses occurs, it is mainly related to processing plants or to adjacent gold mining operations. Similar situations occur for iron carbonate mines, such as those in the German Siegerland area, where the pH values are circumneutral and metal concentrations are low (Heyl, 1954). Yet, the weathering products of iron (di-) sulfide minerals such as pyrite, marcasite and pyrrhotite pose a substantial threat to surface water courses. While pyrite and marcasite in mining wastes tend to oxidize to sulfuric acid, pyrrhotite oxidation seems to produce elemental sulfur with a lower acidity in the resulting mine drainage (Schumann et al., 2015). In the vicinity of sulfidic iron mines, pH values of 2–3, iron concentrations of several grams and high sulfate concentrations in the several hundred grams concentration range are common (Adams et al., 2007). The lowest natural pH value ever measured is from the Californian Iron Mountain pyrite mine and was as low as −3.6 (Nordstrom et al., 2000). Common parameters of concern are low pH values, high iron and sulfate concentrations.

Copper

In nearly all copper mines in the world (di-)sulfide minerals are present (Pohl, 2020) and therefore, there is a high likelihood that the mines will discharge acid mine drainage or highly mineralized mine water. Besides copper and iron, these deposits contain a large set of other potentially toxic, chalcophile metals (Arndt et al., 2015), which comes as no surprise as the term chalcophile derives from the Greek word *χαλκός* for copper. Copper is mined in surface, underground and solution mines, and there is no substantial difference in the list of elements that can be found in the effluent. One exception is the effluent of solution or heap mining, which is usually extremely acid, but normally not discharged without treatment (but might leak into the subsurface). Main contaminants or parameters of concern from copper mines, independent of type, are low pH values, elevated electrical conductivities, and sulfate as well as iron concentrations that are the higher the lower the pH value is (Šerbula et al., 2016). At Parys Mountain in Wales, pH values of 2.5–3.7 and sulfate concentrations of 0.4–3 g L^{-1} were reported with Fe showing 67–708 mg L^{-1} and Cu 7–44 mg L^{-1} (Rees, 2005). Similar conditions occur at other copper mines in the area (Mullinger, 2004), but the Welsh Parys

mountain site has the fate of the highest pollution rank. Very similar conditions occurred at the Mount Lyell copper-gold mine in Tasmania, Australia, with pH values around 3, concentrations of sulfate 0.2–14, Fe 53–2200, and Cu 9–180 mg L^{-1} (John and Partners Pty. Ltd., 1996).

Lead/Zinc/Silver

Potential effects of lead and zinc mining on water courses highly depend on the geological setting of the deposit. Some European lead/zinc mines pose only small or negligible effects, while geologically similar lead/zinc mines in the U.S. cause detrimental environmental effects from secondary minerals and efflorescent salts (Alpers et al., 2000) around mine waste piles and processing plants (Besser et al., 2009). In these carbonate-hosted deposits, as long as the buffer capacity of the carbonates is not consumed, the pH values will be in the upper circumneutral range. Lead and to a lesser extent zinc are less mobile at these pH values (Fig. 3), and therefore the effects on the water courses are normally small, with exceptions such as the Swedish Lovisagruvan mine (Fahlqvist et al., 2012), where lead and zinc concentrations are ecologically relevant and pose a threat to the aquatic environment.

There might be some immediate increases of electrical conductivity after a mine is flooded, which results from the dissolution of secondary minerals in the open mine voids. Contamination also occurs when the pyrite- and marcasite-rich zones of these deposits are exposed to oxygen and humidity for a longer time. In these cases, the buffer capacity of the carbonate host rocks might become exhausted and acid or metal enriched mining influenced water develops, such as in the case of the Polish Chrzanów or the Picher, Oklahoma Mining Districts (Czop et al., 2007; DeHay et al., 2004). When conditions such as in the Alaskan Red Dog mine (Knapp, 2004) or the Picher Mining District (Tar Creek Superfund) occur, which can be considered one of the most polluted mining areas in the world, then the effects on the water courses will be detrimental. Reason for this pollution is the co-occurrence of lead and zinc with large deposits of disulfides. At the Red Dog mine, pH values of 3–5 with Zn concentrations between 0.3 and 3.3 g L^{-1} and TDS of up to 15.4 g L^{-1} have been reported. In Germany's long-abandoned central Harz Mountains silver/lead/zinc mining area, pH values are relatively high and elevated metal or semimetal concentrations can only be found in selected hot spots (Bozau et al., 2017). Common parameters of concern are lead, zinc, electrical conductivity, and a low pH value.

Uranium

Uranium mining operations can be underground or in open pit mines. The mining technologies involved are either conventional mining or solution mining (Woods, 2018). Due to the high mobility of uranium in oxidizing environments and the co-occurrence with (di-)sulfides, uranium mining sites can often be considered problematic for the aquatic environment. Besides suspended solids from tailings sites and waste rock repositories, sulfate, uranium, radium, and low pH values are commonly found around working or abandoned uranium mine sites (Metschies et al., 2016; Vaupotič and Kobal, 1999; Woods, 2018). Immediately around the mine, tailings or waste rock sites, macrozoobenthos can be impaired when the metal concentrations in the receiving water courses exceed toxic concentrations (Humphrey et al., 2012; Trontelj and Ponikvar-Zorko, 1998). These effects of surface water contamination can last for a substantially long time when the groundwater is infiltrating surface water (Baacke et al., 2015). As iron is also mobile in low pH-environments, elevated iron concentrations are common in uranium mining areas. When the pH values increase over the course of the stream, ironoxides and the sorbed (semi-)metals can precipitate or co-precipitate. This can cause elevated (semi-)metal concentrations in the stream sediments (Neiva et al., 2014). Common potential pollutants are uranium, radium, arsenic, sulfate and low pH-values.

Diamonds

Reports about environmental pollution of river courses resulting from diamond mining are comparably rare—contrary to the connected social issues known under the term "blood diamonds" (Bieri, 2010). Yet, the large tailings dams and open pits as well as placer mines impair the local water courses with suspended solids and minor chemicals from the extraction process (Yelpaala and Ali, 2005). The reason for the relatively low effects on water courses is the host rock (kimberlite, lamproite, or lamprophyre), which is not prone to acid production (Ochieng et al., 2009). Some of the largest diamond mines in the western world are in areas that need to be protected because of their pristine character and the interests of indigenous peoples (van Luijk et al., 2020) and therefore discharges from these mines are strictly regulated. Yet, some diamond mines might develop an elevated mineralization and metal toxicity (McCullough and Sturgess, 2020).

In northern Canada, diamond mine water might have elevated electrical conductivities due to an increasing mineralization trend with depth (Herrell et al., 2018), and in some cases elevated nitrate or ammonia concentrations evolved as a result of explosives being abundant in the tailings and waste rocks (Bailey et al., 2013). In addition to that, high phosphate and chloride-concentrations exist.

A rare source of pollution to surface waters in the Russian Yakutia (Sakha, Якутия) diamond mining district is worth mentioning: radioactive nuclides from 12 "peaceful" underground nuclear explosions. Nuclides from the "backfired" nuclear explosions polluted the nearby environment. In addition, surface waters are contaminated with potentially toxic elements which also impair the people's health (Yakovleva et al., 2000). Common pollutants of concern are mineralization, nitrate, ammonia.

Aggregate mining, building stones, quarries

Gravel and building stones comprise the world's largest amount of mined raw materials (Langer and Arbogast, 1998). Chemically, these types of mines seldom pose a risk for inland waters, but the suspended solids can cause a substantial change to water courses and aquatic life (Fig. 5). When aggregates are mined in alluvial deposits and the number of mines along a stream is large, they disturb fish and other wildlife (Marcus, 1997). Because of the high transport costs of aggregates and building stones, quarries are usually built in the vicinity of built-up areas (Langer and Arbogast, 1998). There, they often pose a visual threat in the landscape, and locals might complain about noise, vibration, or dust pollution (Schneider and Wolkersdorfer, 2021; Vandana et al., 2020), even though they can be advantageous as they provide recreational areas and new habitats for aquatic ecosystems.

A case of acid mine drainage formation was the greywacke quarries Großthiemig and Brößnitz, Germany, where pH values of 2.9 and iron concentrations of up to 80 mg L^{-1} were measured (Gerstenberg, 2005) and a pilot passive treatment system was installed (Hubrig et al., 2014). Highly alkaline conditions developed in the Górka limestone quarry, Poland, with average pH values between 12 and 13, resulting from industrial waste deposited into the quarry during its operation (Czop et al., 2008). Pollutants that can be seen more often in water courses around quarries are nitrogen compounds, originating from unused explosives (Karlsson and Kauppila, 2015).

Some of the negative effects of aggregate mining or quarries is the modification of water sheds as the rocks or sediments are removed. This can result in changes of water courses as the water is flowing into different directions compared to pre-mining conditions (Langer and Arbogast, 1998). In addition, instead of diffuse flow of water into receiving steams, point sources with sometimes elevated flow might develop. Because groundwater levels might fall during mining, water courses could also fall dry during the duration of the quarrying. Even after quarrying ceases, and when the quarry is large, a cone of depression might persist and impair surface water courses. Common parameters of concern are elevated concentrations of suspended solids and modification of water courses and arsenic in limestone quarries.

Others

Platinum mining usually results in contaminated effluents from the tailings areas, but seldom from the mine drainage *per se*. These effluents contain elevated concentrations of nitrogen oxide and TDS (Skinner, 2018). Around vanadium processing plants, ground and surface water has been reported to contain elevated vanadium concentrations (Kamika and Momba, 2014). Apatite and Iron-Apatite mines sometimes develop elevated phosphate concentrations in mine and tailings waters (Makarov et al., 2019; Reta et al., 2019). In recent years, selenium has been a matter of environmental concern in a range of mines, with Sudbury/Canada possibly leading this list (Warren, 2013). Elevated concentrations of the semi-metal Sb regularly occur in carbonate-hosted mines (Ilavský and Barloková, 2019; Wolkersdorfer and Wackwitz, 2004).

Potential contaminants that are seldom discussed within the mining context are organic compounds. They might be PAH, PCB, or oil from the mine workings itself or organic chemicals used in mineral processing.

Listing common pollution indicators for "other" mines is not useful, as they are highly variable and depend on the deposit type and the respective mine site. Yet, experience suggests, these are low pH, high sulfate, and TDS as well as suspended solids.

Fig. 5 Aggregate mining in the Nakkhu Khola River valley (नखखु खोला), Katmandu, Nepal. Photograph: Christian Wolkersdorfer.

Chemical and physical effects on surface waters

Lakes

Acidity, mineralization, metal toxicity, and suspended solids are the main pollutants influencing lakes by mining influenced water. In most cases, these have negative effects on the ecosystems and to variable extent individual species (Tuovinen et al., 2012), especially where the mining influenced water directly enters the lake (Hartwig et al., 2005). Acid mine drainage increases the acidity in lakes, and as a result of the low pH values the metal concentrations increase (Castendyk and Eary, 2009; Gray, 1997). Pit lakes strongly differ from natural lakes and their shape and size influence their chemical and physical parameters, as their relative depths are markedly higher (Geller et al., 2013). Lake stratification is a function of the lake's wind fetch and solar irradiation as well as forces such as surface and groundwater density and heat (Hipsey et al., 2019). Due to their great depth, pit lake stratification occurs with an increase of total dissolved solids and electrical conductivity with depth (Castro and Moore, 2000). Influenced by high concentrations of dissolved substances, the color in mine lakes can vary between red (due to ferric iron with pH below 3) and blue/turquoise (aluminum buffer reactions at pH around 5). Besides the chemical changes of the natural lake's composition (Borvinskaya et al., 2017), suspended solids impair the lakes' ecosystem and physical conditions, though the low energy environment of lakes supports a fast settling. These sediments can even be used as geochemical markers and allow to reconstruct the mining history (Callender, 2000). Because lake sediments are large repositories of potentially toxic elements, changes in the pH or redox conditions can remobilize these elements (Azcue and Nriagu, 1993).

Streams

In flowing waters there is a constant exchange of water with various physico-chemical parameters, and, consequently, the effects of mine water on the streams are characterized by dilution and buffering. Well-buffered streams are less affected by acidification compared to sedimentation or elevated metal concentrations (Bell and Donnelly, 2006; ERMITE Consortium et al., 2004). Once the buffer capacity is consumed, and depending on the pH, mineralization, hardness and dissolved organic matter, streams can develop eco-toxic concentrations of metals and metalloids and the ecosystem will be under pressure (van Dam et al., 2019) as described in the section "Biological and ecosystem effects".

Depending on the chemical composition of the discharged water, adsorption of metals onto sedimentary particles and plants can occur. If oxidizing conditions and neutral pH values dominate, metals can adsorb on clays, organic matter as well as on Mn-, Al- and Iron-oxides (Dong et al., 2007; Miller et al., 1996). Dissolved iron, which occurs most commonly in mine water influenced streams typically precipitates as oxides and hydroxides in the streambed close to the discharge point and is often visible (Mestre, 2009). These suspended iron oxyhydrate solids and the reddish color of dissolved iron in low pH-conditions cause many mining influenced streams and rivers to appear in reddish to orange colors (Fig. 6). In addition, the mining influenced water sometimes reduces the surface tension in the stream, which results in the formation of foam (Lottermoser, 2010).

When streams or rivers are used as raw water for drinking water production, discharges of mining influenced water can substantially impair the fresh water supply chain (McCarthy and Humphries, 2013). Remediating these surface water courses, especially in rural areas, can be challenging as well as time and cost consuming (ERMITE Consortium et al., 2004; Sumi and Gestring, 2013).

Fig. 6 Mine Water discharge of the Heinrich colliery, Germany, into the river Ruhr. Suspended iron oxyhydrates flocculate as they get oxidized. On the left of the discharge, the precipitates stain the riverbanks, and, on the right, the fresh water of the Ruhr can be seen. Photograph: Marlene Julia Fromm.

Precipitates in surface waters

Changing environmental conditions, such as aerating mixing processes when mining influenced water discharges into surface waters (Máša et al., 2012), initializes various physical and chemical processes which might result in precipitation. These processes are evaporation, oxidation of reduced species, changes in pH value and redox potential, flocculation, or coagulation. In mining influenced water, the most common precipitate is ochre ("yellow boy") which is a mixture of iron oxyhydrates and sulfate minerals, although the formation of ferrihydrite ($Fe_5HO_8{\cdot}4H_2O$), goethite (α-FeOOH) or schwertmannite [$Fe_8O_8(OH)_6SO_4$] differs based on the local conditions (Kairies et al., 2005; Schwertmann et al., 1995). Additionally, the visual appearance of ochre is quite different, ranging from gelatinous flocculants, suspended colloids, medium soft mud, foam on the water surface, coating on rocks to hard and thick encrustations. Most precipitates sorb or co-precipitate with trace elements like arsenic, cobalt, nickel, and zinc, as the ochre has a high specific surface area and is therefore responsible for mobility, fate and transport of trace elements in mining influenced waters (Kairies et al., 2005; Schemel et al., 2000). Other precipitates are aluminum oxyhydrates, which also sorb potentially toxic elements and contribute to the improvement of the waters conditions (Rothenhöfer et al., 2000). These characteristics of accumulating (semi-)metals are widely used as a means of geochemical exploration in natural waters (Förstner, 1981).

Biological and ecosystem effects

Biological effects of mine drainage on the aquatic ecosystem range from severe effects that kill most macroinvertebrates and fish to improvements of the water quality when unpolluted mining influenced water drains into a polluted water course. These effects can result from large mining operations, mining accidents or by artisanal mining (Dabrowski et al., 2013; Hernandez et al., 1999; Macdonald et al., 2014, 2015). Effects on fish can vary depending on the animal's age: whilst juvenile fish might avoid mine water influenced streams, adults might be able to survive in the elevated pollutant concentrations. Ecosystem management programs need to be site specific, taking into consideration the high variability of geological and climatic conditions. When all the relevant factors are considered, potential negative effects of such a program can be avoided (Kruse Daniels et al., 2013).

A common pollutant is particulate matter like clay, silt, or sand from tailings dams, waste rock piles, or aggregate mining (Greig et al., 2005). Examples for this are the Ok Tedi mine in Papua New Guinea (Low and Gleeson, 1998) or the abandoned Mount Lyell Copper deposit in Australia (McPhail et al., 2001). Increased turbidity due to suspended solids also decreases light penetration into the water and therefore reduces photosynthesis (Wood and Armitage, 1997). Additionally, fish gills can become clogged, or fish eggs can suffocate due to settled suspended matter (Bilotta and Brazier, 2008; Butler and Ford, 2018). This inhibits the growth of algae or microorganisms and therefore prevents macroinvertebrates or fish from getting enough food, as the functioning of the food web for the biological survival of surface waters is interrupted. Additionally, biofilms might accumulate potentially toxic elements that concentrate in the higher organisms (Hobbs et al., 2019). Consequently, they move away or die, and the surface water becomes biologically dead. Yet, this does not necessarily imply that the water is *a priori* toxic. Another negative effect on livestock is the reduction of oxygen by processes that oxidize reduced constituents or organic matter (Weiner, 2010).

A positive biological effect on mine water quality is the filtering effect of sediments and the biota in natural wetlands. In many cases, it has been observed that the quality of mining influenced water substantially improves downstream of natural wetlands (Fyffe et al., 2015; Haarstad et al., 2012). This known effect has been used to construct the first artificial wetland for mine water treatment (Kleinmann et al., 1985). Yet, as the contaminants accumulate in the natural wetlands, unexpected incidents like flood events, droughts, or earthquakes might impair the pollutant deposits and could release them to downstream receptors.

Management and mitigation of mining influenced water

Principles of mine water management

Mitigation of the effects caused by mining influenced water is performed in one of five ways: avoidance, natural attenuation, active treatment, passive treatment, and *in situ* treatment. During a mining operation, negative effects on the environment cannot be completely avoided. However, because society relies on an input of raw materials, managing the risks from potential contaminants in mining influenced water to acceptable levels is a trade off against benefits acquired from operation. Ultimately, pollution arising from mining operations must be reduced by modifying the mining methods or averted by technical means (Skousen et al., 2019; Wolkersdorfer, 2021).

One of the key requirements to understand and optimize management and mitigation of mining influenced water and its effect on the surrounding inland water systems is monitoring (McLemore et al., 2014). This could also include participatory water quality monitoring (International Council on Mining and Metals, 2015), which assists in engaging local communities in developing remediation options.

Avoidance

In principle, the best avoidance strategy would be to separate disulfides from water and oxygen to inhibit oxidation. In the context discussed herein avoidance includes all measures that prevent and slow down the evolution of mining influenced water or keep

water away from the mines. The latter is achieved by installing cut-off walls, or surface water can be diverted around open pit mines (Steffen Robertson and Kirsten (B.C.) Inc and Norecol Environmental Consultants and Gormely Process Engineering, 1990). By reduction or segregation of acid-producing materials, the weathering processes are minimized, and (di-)sulfide oxidation is reduced. This requires sophisticated prediction and mine planning methods that allow a controlled flow of inert, acidic, and neutralizing rock material. In modern mining operations, exploration data, real time data, block models and artificial intelligence are used to direct the waste material to an appropriate location (More et al., 2020). In open pit mines, thorough mine planning including mixing of alkaline with acid producing material is recommended (Drebenstedt and Struzina, 2008; Wisotzky, 2004). Dams in underground mines separating disulfide rich areas from water and oxygen can prevent the formation of acid water or its discharge. Dry seals at mine entrances reduce oxygen contact with disulfide rich strata, while wet seals prevent oxygen contact and water discharge (Foreman, 1971). Tailings and waste rock can be managed with dry or wet covers, which can substantially reduce oxygen diffusion and slows down pyrite oxidation. Dry covers are layers of soil and gravel above mining waste repositories while wet covers could be ponded water on top of tailings (European Commission, 2009; Moncur et al., 2015).

Natural attenuation

Natural or intrinsic attenuation is a process by which nature without human interaction mitigates the negative effects of mine effluents on receiving water courses, and this process has occurred since humans first mined. In general, attenuation is a slow process but an effective one, and in many cases, several decades of attenuation processes results in acceptable environmental conditions. Natural attenuation uses energy, such as solar energy and potential energy, and is assisted by microbes which oxidize or chemically reduce various contaminants in the mining influenced water. Very often, (semi-)metals are sorbed to suspended solids and by their removal in natural wetlands or when iron flocculants settle, the water quality continuously improves. Other mechanisms are simple settling of suspended solids while the water's velocity decreases, e.g., during flow into lakes. Natural attenuation also depends on dilution effects during rain events and on time, as several natural processes are a function of time. A commonly observed effect in flooded mines is the first flush, which lasts 3–5 times as long as it took the underground mine to be flooded (Younger et al., 2002). While the mine workings are flushed by relatively clean ground or rainwater, effluent salts and secondary minerals are washed out into the receiving water courses (Wolkersdorfer, 2021; Younger et al., 2002).

Active treatment

Active treatment implies the use of chemical reactants, the supply of energy, and a continuous monitoring of the plant (Skousen et al., 1998; U. S. Environmental Protection Agency, 2014). This active process removes unwanted substances and ensures discharge criteria are met. Criteria for the selection of the various active treatment methods are the concentration, load, and chemical composition of the mining influenced water. Among the most common active processes are neutralization (especially Low Density Sludge and High Density Sludge treatment), and membrane processes (e.g., reverse osmosis). Although there are more than a dozen different active processes on the market, most of them are of marginal importance in the mining industry as they are unsuitable for high volumes of water or the cost of operation are high.

Passive treatment

Passive mine water treatment is the improvement of water quality using only naturally available energy sources in gravity-flow treatment systems (such as wetlands or subsurface-flow bioreactors) which are designed to require only infrequent (albeit regular) maintenance to operate successfully over their design lives (literally from PIRAMID Consortium, 2003). Treatment is achieved entirely through potential (differences in altitude), solar or biological (bacteria) energy, and systems like that are operating from cold to warm climate zones. Passive systems include oxic or anoxic limestone drains, constructed aerobic or anaerobic wetlands, reducing alkalinity systems (RAPS, also called SAPS), settlement ponds, permeable reactive walls or vertical flow reactors (Brown et al., 2002; Wolkersdorfer, 2021). Passive systems, compared with active systems, usually cannot handle large volumes of mining influenced water or elevated pollutant concentrations.

In situ-treatment

In situ-treatment is of particular importance for surface waters. One of the most common processes is in-lake treatment such as adding lime to pit lakes by boats or pipes (Benthaus et al., 2020). Water courses are sometimes treated by applying alkaline material directly into the flowing wave (Gusek and Figueroa, 2009; Uhlig et al., 2016). Especially for diffuse inflow of mining influenced waters, the construction of reactive walls (Bowden et al., 2005) can be used as an *in situ* option. Another avoidance or *in situ* method is stratification in flooded mines, which reduces the discharge of mine water with poor quality, as higher mineralized, thus more polluted mine water, remains in the deeper parts of the mine (Wolkersdorfer, 1996). A general recommendation which method to apply cannot be made before a detailed site investigation is first undertaken.

Synthesis

Mining influenced water commonly evolves around underground and open pit mining operations through microbially catalyzed pyrite oxidation. For pH, these waters can be acid, circumneutral or basic, and from a mineralization point of view, dilute, mineralized or saline. Depending on the type of raw material, the pollution load of the mining influenced water and the pollutants of concern can vary substantially. This, consequently, has different effects on inland waters, which can be minimal in the best case and detrimental in the worst one. Potential effects are suspended solids, diversion of water courses, highly variable flows and a toxicity that impairs the ecosystems of the lakes, streams, and rivers. Many mining influenced waters have no effect on the receiving inland waters at all, some are even used as drinking water, because the first flush already passed. Yet, the most prominent effect on inland waters are red to orange stains from precipitates, a reddish to orangish color of the water, and a change of the aquatic ecosystem composition. Various mitigation options are available, ranging from doing nothing, commonly referred to as natural attenuation, to passive treatment and to active mine water treatment. *In situ*-treatment options are rarely used, but future developments will see these options more often.

To increase the public acceptance of mining operations, there is a need for improving communication and the availability of information. This ensures that the reasons for mining influenced water are understood and the measures of the mining houses to mitigate these effects are better known. Yet, the best solution would be if future developments and innovations would reduce the pollution emanating from mining operations such, that there are no effects on inland waters at all.

Knowledge gaps

In relation to mining influenced inland waters, there are no knowledge gaps *per se*. Yet, there are many questions that need to be answered to increase the acceptance of mining in the public and to protect aquatic ecosystems. To a large degree, most of the solutions already exist, but economic pressures or irresponsible behavior often restrict their utilization. One of these solutions would be the valorization of mining residues, such as waste rock piles, tailings, or polluted mine water. Yet, much research will be needed to find applications for all the relevant water pollutants and mining residues. In addition, many treatment options for mine water are cost intensive, i.e., expensive, and financial restrictions or the competition on the market restrict their implementation. Therefore, there is a need for cheap and reliable treatment solutions, or, at least, treatment solutions which leave water, valuables and not much more than a footprint. Especially research on *in situ* remediation including the understanding of the mines' hydrodynamic conditions is needed. A knowledge gap is also the exact interplay between mining influenced water and the groundwater, the resilience of ecology to mining pollutants and how, precisely, contaminants affect humans and livestock too.

One gap is the site specific and temporal prediction of the water quality of working and abandoned mines and where diffuse mine water discharges will occur after mining ceases. Therefore, a world equation for mine water would be needed. This means, modeling and simulations should be able to predict exactly what mine water quality might be expected in each single stage of the mining operation, including the prediction of the mine water's potential toxicity on various aquatic species. Though first approaches for the chemical composition exist (Chetty et al., 2020; Van der Sloot and Van Zomeren, 2012), the mining community is still a large step away from a unifying solution.

On the monitoring and information side there is a need for new sensors where scaling would be inhibited, and no wipers or shutters are necessary to remove the fouling on the electrodes. As larger data sets are continuously collected during mining operations, big data operations and artificial intelligence are needed to optimize mining operations and reduce pollution. Additionally, an improved information policy and true information to the public is a key requirement to increase the acceptance of mining on one side and to reduce pollution by artisanal miners on the other side.

Modern civilization will need raw materials forever. Because a circular economy will not be able to supply a growing world demand while the population increases, mining operations will also be needed in the future. Therefore, it is essential that future mining operations and the mining houses will do everything that is needed to protect inland waters and groundwaters alike.

Acknowledgments

We acknowledge our colleagues Altus Huisamen, Stephanie Lohmeier, Nikolai Georgievich Maksimovich, Cherie McCullough, Jesús Montero, Maria Almudena Ordoñez Alonso, Carlos Ruiz Cánovas, Oliver Totsche, and Anne Weber for commenting on early versions of this section. Thanks also to the handling editor Stuart Warner for his valuable input.

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mineclosure.gtk.fi—Geological Survey of Finland.
www.mend-nedem.org—MEND (Mine Environment Neutral Drainage) Canada.

Effects of Hydrocarbon Extraction on Freshwaters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Biotic homogenization Biotic homogenization is defined as the increase in similarity (or decrease in beta-diversity) among ecological communities over time, at the genetic, taxonomic or functional levels.

Coal seam gas Coalbed methane is known as coal seam gas in Australia.

Coalbed methane Natural gas contained in coal beds. Although extraction of coalbed methane was initially undertaken to make mines safer, it is now typically produced from unmineable coal seams.

Command-and-control regulations: Command-and-control regulations are by far the most commonly used to minimize damage caused by unconventional oil and gas extraction. They are most often used by countries where regulators are under-capacitated to police self-regulation, such as developing countries.

Conventional oil and gas Conventional oil and gas resources are produced from conventional reservoirs. Conventional oil is trapped underneath seals in deep porous geological formations. Gas that occurs in association with this oil, is called associated gas. This oil and gas migrated from unconventional reservoirs like shale. Gas that occurs in a porous formation underneath a seal and that is not associated with oil, is called non-associated gas.

Conventional reservoir For oil gas reserves, conventional hydrocarbons refer to hydrocarbons that are produced from reservoirs that do not require stimulation to produce the gas. These reservoirs typically have permeabilities larger than 1 milliDarcy. The oil in these reservoirs migrated from source rocks and accumulated in the reservoirs (commonly porous sandstone or carbonate). Conventional reservoirs are capped by impenetrable material (often shale or salt) that keeps the conventional oil in place.

Darcy A unit of permeability. A medium with a permeability of 1 Darcy permits a flow of 1 cm^3/s of a fluid with viscosity 1 cP (1 mPa•s) under a pressure gradient of 1 atm/cm acting across an area of 1 cm^2.

Depressurization Depressurization is the act of lowering the reservoir pressure below the saturation point (i.e., the critical desorption pressure), which causes gas to desorb from the microporous structure and flow toward the wellbore, where the gas can be produced, processed, and delivered to market. Depressurization can be accomplished by allowing free gas within the naturally occurring or induced fractures in the coal to flow to the surface, or by pumping out any natural fluids occupying the connected cracks and fractures. This fluid can be a combination of formation water and free gas.

Ecosystem engineers Keystone species that create, modify, maintain or destroy a habitat. Their behavior strongly affects other organisms (e.g., impact on species richness) and landscape heterogeneity.

Ecosystem services The benefits provided by the natural environment and from healthy ecosystems to humans.

Enhanced oil recovery (conventional oil and gas): Enhanced recovery can follow primary recovery during conventional oil and gas extraction to maintain pressure and keep up the oil production rate. Enhanced recovery is divided into secondary and tertiary recovery and may use large volumes of water.

Environmental crime Any violation of an environmental regulation for which criminal liability may be imposed. Regulations must contain provisions that establish criminal liability for violations. Criminal enforcement of environmental regulations is often used in only the most egregious cases, where the actual or potential damages are excessive or where the violator is a repeat offender. Although criminal enforcement actions are mainly taken to deter future misconduct by the individuals charged, their greater impact may be to deter those who are contemplating similar offenses.

Environmental justice/injustice Environmental justice implies that everyone in society, regardless of their social class, status, background, race, ethnicity or gender must share equally in the benefits, risks and negative impacts of developments. Environmental injustice occurs when some people or groups, as a result of their social class, status, background, race, ethnicity or gender, experience most of the harm and risk associated with development, while not receiving a fair share of the benefits.

Flowback (unconventional oil and gas) Fluid that is returned to the surface after hydraulic fracturing has occurred, but before the well is placed into production. It typically consists of returned fracturing fluids in the first few days following hydraulic fracturing which are progressively replaced by produced water.

Groundwater Water that occurs below the surface of the Earth, where it occupies all or part of the void spaces in soils or geologic strata.

Hydraulic fracturing fluid Fluid used to perform hydraulic fracturing; includes the primary carrier fluid, proppant material, and all applicable additives.

Hydraulic fracturing The act of pumping hydraulic fracturing fluid into a formation to increase its permeability. Hydraulic fracturing has been used in the industry in various forms, for either stimulation of water wells to produce water, or for stimulation of oil and gas wells to produce oil and/or gas. Various technologies can be combined or used separately during hydraulic fracturing. It may involve the use of only water (for water well stimulation) or a combination of any or all of four separate technologies, viz. directional drilling, the use of high volumes of fracturing fluids, the use of chemical slickwater additives, and the use of multi-well drilling pads. When all four technologies are combined it is more specifically called 'high-volume slickwater long-lateral' (HVSLL) stimulation. Hydraulic fracturing as used in the oil and gas industry commonly includes the usage of 0.5–2% slickwater additives, large volumes of proppant as well as large volumes of fluid. Base fluids that may be used may include water, liquid petroleum gas, or other gases such as nitrogen or carbon dioxide. Synonyms for hydraulic fracturing as used in the oil and gas industry include 'slickwater fracking' (slickwater in short), "high volume hydraulic fracturing,", or just "fracking."

Hydrocarbon A naturally occurring organic compound comprising hydrogen and carbon. Hydrocarbons can be as simple as methane [CH_4], but many are highly complex molecules, and can occur as gases, liquids or solids. The molecules can have the shape of chains, branching chains, rings or other structures. Petroleum is a complex mixture of hydrocarbons. The most common hydrocarbons are natural gas, oil and coal.

Injection well An injection well is used to place fluid underground into porous geologic formations. These underground formations may range from deep sandstone or limestone, to a shallow soil layer. Injected fluids may include water, wastewater, brine (salt water), or water mixed with chemicals.

Market-based regulations Market-based regulations encourage behavior through market signals rather than through explicit directives regarding pollution control levels or methods and allow companies to determine the best way to control or minimize pollution (Zhang, 2013).

Peak oil The hypothetical point in time when the global production of oil reaches its maximum rate, after which production will gradually decline.

Primary recovery (conventional oil and gas) Primary recovery is used in the first stage when natural pressures in the oil reservoir are sufficient to bring oil to the surface. No additional water is needed during this stage of conventional oil extraction.

Produced water Natural fluids that are displaced from the geological formation that holds the hydrocarbons, which can contain substances that are found in the formation, and may include dissolved solids (e.g., salt), gases (e.g., methane, ethane), trace metals, naturally occurring radioactive elements (e.g., radium, uranium), and organic compounds. It includes water moving in from adjacent aquifers or formations. In conventional oil formations it also includes water injected in the formation during water and steam flooding.

Regulations Environmental regulations are rules to protect public health and the environment from adverse effects by the oil and gas industry. There are three types of regulations: command-and-control, market-based and voluntary.

Reserves (proved) The quantity of energy sources estimated with reasonable certainty, from the analysis of geologic and engineering data, to be recoverable from well-established or known reservoirs with the existing equipment and under the existing operating conditions.

Reservoir (oil or gas) A subsurface, porous, permeable or naturally fractured rock body in which oil or gas has accumulated. A gas reservoir consists only of gas plus fresh water that condenses from the flow stream reservoir. In a gas condensate reservoir, the hydrocarbons may exist as a gas, but, when brought to the surface, some of the heavier hydrocarbons condense and become a liquid.

Resource curse The resource curse (or the paradox of plenty) refers to the failure of many resource-rich countries to benefit fully from their natural resource wealth (such as oil and gas, land and water), and for governments in these countries to respond effectively to public welfare needs. Sharing resources such as land, water, and minerals can create conflict between the extraction companies and the communities. While one might expect to see better development outcomes after countries discover natural resources, resource-rich countries tend to have higher rates of conflict and authoritarianism, and lower rates of economic stability and economic growth, compared to their non-resource-rich neighbors.
Secondary recovery (conventional oil and gas) Secondary recovery employs water in the form of waterflooding, or gas injection, to displace the oil and drive it to the surface.
Shale gas Natural gas that remains tightly trapped in shale and consists chiefly of methane, but with ethane, propane, butane and other organic compounds mixed in. It forms when black shale has been subjected to heat and pressure over millions of years, usually at depths of 1500–4500 m below ground level.
Shale A fine-grained sedimentary rock composed mostly of consolidated clay, silt or mud. Shale is formed from deposits of mud, silt, clay, and organic matter, usually laid down in calm seas or lakes.
Subsistence lands Land areas where indigenous/local communities hunt, fish, and gather wild-growing fruit and vegetables.
Surface water Any body of water above ground, including streams, rivers, lakes, wetlands, reservoirs, and creeks.
Tertiary recovery (conventional oil and gas) Tertiary recovery employs steam or gas to change the makeup of the oil reservoir to enhance the recovery of oil in the reservoir.
Tight sands A geological formation consisting of a matrix of typically impermeable, non-porous tight sands.
Unconventional oil and gas Unconventional oil and gas resources are produced from unconventional reservoirs. Unconventional oil and gas include oil sands, oil shale, shale gas, and coalbed methane.
Unconventional reservoir Reservoirs, which require hydraulic fracturing for the extraction of hydrocarbons occurring in these reservoirs, where the permeability is less than 1 milliDarcy.
Voluntary regulations Voluntary regulations are usually innovative voluntary actions that oil and gas companies take to improve environmental quality, natural resource utilization or their environmental performance.
Waterflooding A form of enhanced oil recovery where the energy required to move the oil from the reservoir rock into a producing well is supplied from the surface by means of water injection and the induced pressure from the presence of additional water.

Hydrocarbon extraction overview

This chapter explains hydrocarbon extraction processes and discusses its effects on inland water resources. Oil and gas are important energy sources for human society, with the oil industry being the largest international industry in the world. The transportation of goods, manufacturing of plastics and fertilizers, and electricity generation all depend to a large degree on oil and gas (Robbins et al., 2014). Societies have, therefore, invested heavily in oil and gas infrastructure and equipment, such as vehicles and roads (Van Vactor, 2010). However, this industry also uses substantial amounts of freshwater (Spang et al., 2014) and influences water resource quality, and as such, has a considerable impact on the world's freshwater resources (see section "Risk and impacts on water resources").

Although oil has been extracted since the early 1900s, it became the dominant form of energy with the discovery of many of the largest conventional oil reserves in the Middle East just before and after World War Two. Before then, coal was far more important. Since the end of World War Two, the use of oil for energy generation has been a critical factor in increased global prosperity (Van Vactor, 2010). To ensure ongoing economic development, countries tried to procure sufficient and stable supplies of oil and gas from countries with such resources or, where possible, by producing their own. This has contributed to energy crises, such as the 1973 oil embargo by oil-producing nations that triggered worldwide oil shortages (Harper and Snowden, 2017).

Oil and gas derive from compressed and cooked organic matter that was buried to significant depths over millions of years and occurs in conventional and unconventional deposits (Fig. 1). From the 1970s to the 1990s conventional oil was produced in surplus, after which conventional oil supplies started to decline. Since the early 2000s, alternative hydrocarbon sources in the form of unconventional oil and gas were targeted, enabled by hydraulic fracturing and horizontal drilling (Van Vactor, 2010; Bilgili et al., 2020). The United States lead in the extraction of unconventional resources, where it accounted for 44% of gas production in 2014 (Bilgili et al., 2020). Natural gas production in the United States may more than double over the coming 30 years (Bilgili et al., 2020). Because unconventional resources step in where conventional resources are declining, there is no foreseen imminent peak in oil production (peak oil).

Risk and impacts on water resources

Hydrocarbon reserves are increasingly being targeted in some of the most remote and pristine areas on our planet (Morley, 2017), including the East African Great lakes area (Verheyen et al., 2016) and Amazonia (Fig. 1 and Box 2: Oilfields in Amazonia). Oil production in developing countries increased over threefold from 1973 to 2008, often involving the use of controversial

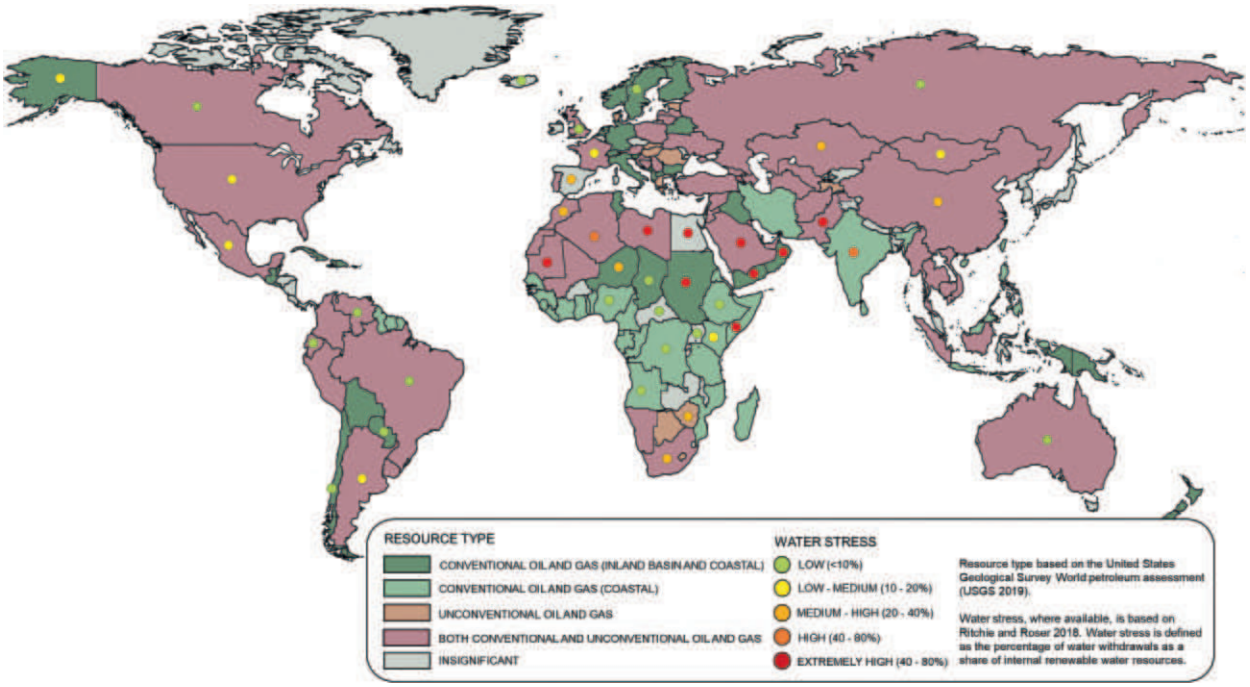

Fig. 1 Global distribution of conventional and unconventional oil and gas resources and associated water stress per region. Image source: S Esterhuyse.

technologies such as hydraulic fracturing. The oil industry uses approximately 40% of the annual 52 billion m^3 of freshwater that is consumed to meet the global requirement for energy and fuel (Spang et al., 2014). With the emergence of unconventional oil and gas extraction techniques, this share is expected to rise, with dire effects on water-scarce countries (Fig. 1).

It is estimated that most future oil and gas projects will be situated in developing countries, to allow for export and to address increased energy needs as their economies grow. Although technological advances make the extraction easier and less risky, poor management and lack of oversight often lead to environmental degradation and water resource pollution. Impacts on water resources occur at the exploration, extraction, and post-extraction stages of hydrocarbons. Fig. 2 illustrates the main impacts for conventional and unconventional oil and gas extraction, while Tables 1 and 2 provide detailed information on the possible impacts.

The negative impacts of hydrocarbon extraction on water resources are viewed as one of the most significant biophysical impacts (Rosa et al., 2018), both in terms of the effects on water quantity and water quality, while water-related negative socio-economic and biophysical impacts are also far-reaching. These impacts are discussed in detail below. As oil and gas are increasingly being extracted in biologically rich regions of the world, it will likely pose a greater threat to biodiversity, especially in areas with high aquatic biodiversity such as in South America, see Boxes 1 and 2 (Harfoot et al., 2018) and Africa (Verheyen et al., 2016, Box 3).

Conventional oil and gas extraction impacts

The effects of conventional oil and gas extraction on water resources are less than for unconventional extraction, although impacts can still be significant. Water use during conventional oil extraction is typically less than for unconventional resources (Scanlon et al., 2014), but largely depends on the geological characteristics of the reservoir. Primary recovery is used during the first stage of oil recovery when natural pressures in the oil reservoir are sufficient to bring oil to the surface. However, as reservoir pressure declines, enhanced oil recovery methods may be employed to increase oil production. Primary recovery may be followed by secondary recovery that includes waterflooding and even tertiary recovery that includes steam injection, to drive residual oil to the production wells (Parra et al., 2020). Water use during primary production is minimal, but can be significant during the secondary production phase (Scanlon et al., 2014). The additional water demand of conventional oil and gas extraction on local water resources can lead to conflicts between water users in water-stressed areas or in times of drought (Sohns et al., 2016).

In terms of water quality impacts, conventional oil and gas extraction generates wastewater in the form of produced water and spent drilling fluids. Produced water is the largest wastewater source by volume. It can contain metals, sediments, and chemicals that may be radioactive and toxic (Parra et al., 2020). Produced water disposal is a concern—if it is injected into wells for disposal or enhanced oil recovery, it may induce seismicity. The alternative is the disposal of this wastewater at hazardous waste sites or treatment at wastewater treatment plants equipped for these types of waste, which many countries are not equipped to handle.

Unconventional oil and gas extraction impacts

Of the negative environmental effects of unconventional oil and gas extraction (Esterhuyse et al., 2016a,b), the most immediate effects are those on water resources. Because a stimulation method such as hydraulic fracturing is typically required to extract

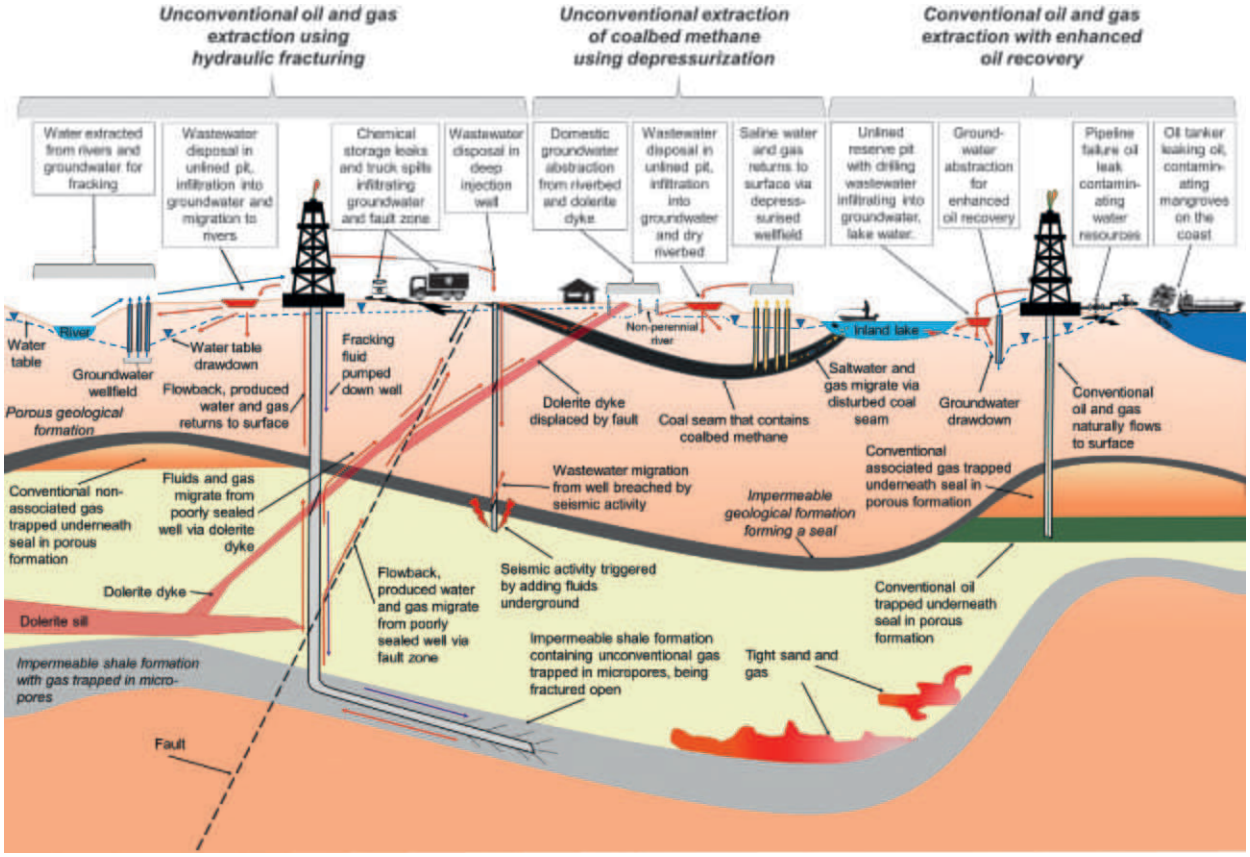

Fig. 2 Conventional and unconventional oil and gas extraction processes and their impacts. Image source: S Esterhuyse.

unconventional resources, it is often more water-intensive than conventional oil extraction (Kondash et al., 2018). Where one drilling well operation could consume approximately 500 m^3 of water without fracking, a fracking well consumes 20 times that amount (Goodwin et al., 2012). Water for fracking is often sourced in the vicinity of the fracking well, making local groundwater reserves a common target. In 2015 in the Eagle Ford shale, US, fracking operations consumed approximately 30% of the area's total groundwater (Steadman et al., 2015). Compared with conventional oil and gas extraction, fracking will lead to even higher localized competition between water users in water-scarce and drought-prone areas (Fig. 2, Tables 1 and 2).

Next to produced water, an additional wastewater stream in the form of flowback is generated during unconventional oil and gas extraction. The chemistry of the flowback depends on the chemical makeup of the hydraulic fracturing fluid and may contain various toxic and carcinogenic organic contaminants (McIntosh et al., 2018). The water quality impacts of unconventional oil and gas extraction are therefore typically larger than for conventional oil and gas extraction. Produced water and flowback can contaminate freshwater aquifers due to poor oil and gas well integrity, or due to migration of these fluids via fracture zones. Fracking fluid and wastewater can contaminate surface waters via leaks and spills. Wastewater disposal in underground injection wells can also cause seismicity and has significantly increased induced seismicity in Canada, the United States, the United Kingdom, and China, in some cases causing earthquakes as large as magnitude 5.7 (Schultz et al., 2020). The density of oil and gas wells, which are higher than for conventional oil and gas production, can also have cumulative negative effects on aquatic ecosystems (Entrekin et al., 2011a,b; Dauwalter, 2013).

Acute impacts from spills and leaks

Marine oil spills in coastal areas often have dire effects on mangroves (see Box 1). Mangroves form a relatively small, but distinctive biome that delivers unique ecosystem services to coastal communities, and that serves as a nursery for many marine species.

Even though marine oil spills are more publicized, inland oil spills occur more frequently, often affect sensitive freshwater environments and have larger impacts on public health (Yoshioka and Carpenter, 2002; Kingston, 2002; Azevedo-Santos et al., 2021). The acute impacts from oil spills are more severe than the chronic impacts of extraction and processing (Etkin, 2011). Spills can occur in any phase of the process, including the extraction of crude oil and the transportation of refined fuels. During the extraction phase, oil spills tend to cause acute impacts, whereas small chronic spillages occur most frequently in the transportation

Table 1 Biophysical impacts of conventional and unconventional oil and gas extraction present in the landscape.

Activity	*Phase*	*Aspect*	*Possible positive impacts*	*Possible negative impacts*
Conventional oil and gas	Exploration phase	Surface water and vegetation	• Possible new species identified	*Seismic exploration:* • Increased sediment load in rivers due to increased erosion from seismic exploration (A) • Seismic vibration affects freshwater invertebrates and vertebrates (e.g., fish) (A) *Drilling fluid and produced water discharge, leakage or spill:* • Drilling fluids leaching into surface water via groundwater or via overland flow from surface spillages contaminate rivers, pans, lakes (A) • Diesel pollution reduces abundance and diversity of freshwater organisms (e.g., invertebrates and fish) (A) *Infrastructure development (seismic lines, road development, river crossings, limited wellpad development):* • Increased sediment delivery to river may impact critical habitats (e.g., fish spawning habitat), cause turbidity and reduce visibility for predators (A) • Native species richness and abundance tend to decrease, and the introduction, establishment and spread of nonnative species are favored (A/C) • Disruption of fish migration due to increased sedimentation, pollutants, turbidity and fragmentation (from road crossings in rivers) (A) • Road construction to remote areas allows entry of deforesters and consequent vegetation loss • Declined plant biodiversity, habitat loss and fragmentation (for drill site and road construction) (A) • Favors the introduction, establishment and spread of nonnative species (A/C) • Surface spills of hazardous material (drilling fluid and produced water) impacting on vegetation (A) *Water sourcing from rivers for drilling:* • Reduced streamflow in perennial rivers (A) • Loss of critical habitats (e.g., refuge and spawning) in rivers and lakes (A) • Loss of river migratory passages lead to loss of mobility, reduced food availability, fragmentation and isolation of fish assemblages (A) • Water quality changes, heat death of fishes in isolated pools and lakes, higher contaminant impact on fish during low stream discharge or isolation periods (A) • Reduced fish fitness and health due to increased predation, intra- and interspecific competition and crowdedness in isolated pools (A)
		Groundwater	• Develop a better understanding of the deeper geology and geohydrology	*Unknowns:* • Difficult to identify aquifers at risk for contamination since deeper geology and structures are unknown (C) • Artesian basin conditions may cause upward migration of formation water (C) *Saline water produced during drilling:* • May contaminate aquifers via well or via reserve pit leak (A/C) *Drilling fluid and produced water discharge, leakage or spill:* • Drilling fluids (e.g., diesel) leaching into groundwater or via overland flow from surface spillages contaminate rivers, pans, lakes (A/C) *Water sourcing from groundwater for drilling:* • Reduced groundwater levels and quality (A/C)
		Seismicity	• Not known	*Increased seismicity during drilling:* • Level of seismicity may increase, but extent of increase is uncertain (A/C) • Possibility to observe or induce and/or trigger a strong seismic event (A/C)

Table 1 (Continued)

Activity	*Phase*	*Aspect*	*Possible positive impacts*	*Possible negative impacts*
Conventional oil and gas	Extraction phase	Surface water and vegetation	• Possible new species identified	*Wastewater and oil discharge to water bodies* via *leaks and spills*: • Flowback and produced water contaminate rivers/lakes (A/C) • Water quality changes in isolated pools and lakes, heat death of fishes in isolated pools, higher impact of contaminants on fish during periods of low stream discharge or isolation (A) • Reduced fish fitness and health due to increased predation, intra- and interspecific competition and crowdedness in isolated pools (A) • Reserve pit leaks may lead to contamination and/or mortality of fish and waterbirds (A) • Changed community structure and/or high mortality of organisms (e.g., zooplankton, macroinvertebrates, fish, water snakes, waterbirds) via oil spills from tanker trucks and pipelines (A/C) • Spills from pipelines and boats cause direct impacts on mangroves forests (e.g., loss of native mangrove growth and favoring nonnative plants), and indirect impacts on other organisms that inhabit these ecosystems (e.g., crustaceans and fish) (A) *Infrastructure development (roads, river crossings, extensive wellpad development, wastewater treatment)*: • Fragmentation of habitat and reduced colonization and fish diversity (C) • Truck traffic accelerates erosion, leading to changes in sediment delivery to river, reduced habitat and visibility, lower fish productivity and fitness, lower levels of recruitment and possible effects on the food web (A/C) • Changes in macroinvertebrates diversity and density, and in fish assemblage structure (A) • The introduction, establishment and spread of nonnative species (A/C) • Impacts on vegetation same as for the exploration phase but on a larger scale, and: • Decreased habitat complexity and loss of ecosystem services (A/C) *Land-use changes*: • Increased sediment delivery to river may impact critical habitats (e.g., fish spawning habitat), cause turbidity and reduce visibility for predators (A) • Increased sediment in stream/river can contribute to eutrophication (A) • Loss of fish, amphibians and invertebrates diversity, and disruption of fish migration due to increased sedimentation, pollutants, turbidity and fragmentation (from road crossings in rivers) (A) • Land use change could isolate rivers, pans and lakes, resulting in genetic isolation and reduction in number of refugia (C) • Displacement and decrease in richness/abundance of native species (A) • Favors the introduction, establishment and spread of nonnative species (A/C) *Water sourcing from rivers for drilling:* • Removal of water from rivers may affect hydrology of water resources, change the interactions of freshwater communities and ecosystem functions (A) • Reduced streamflow in perennial rivers (A) • Loss of critical habitats (e.g., refuge and spawning) in rivers and lakes (A) • Loss of river migratory passages lead to loss of mobility, reduced food availability, fragmentation and isolation of fish assemblages (A) • Decrease in resource connectivity, reduction in abundance and diversity of invertebrates and fish, increase in tolerant species (A) • Groundwater abstraction leads to loss of baseflow to springs, loss of hyporheic flow, loss of refuge habitat, water quality and volume changes (C)
		Groundwater	• Same as for exploration phase	• Same as for exploration phase and: • Larger scale sourcing of water from local aquifers may induce aquifer connectivity, change groundwater levels, cause contamination and seismic activity. • Large scale surface activities contaminate aquifers via surface water-groundwater interaction. • Large scale wastewater poses serious challenges if not managed properly. • Poor well integrity may cause leakage of gas or fluids and groundwater contamination.
		Seismicity	• Not known	• Same as for exploration phase but on a larger scale

(*Continued*)

Table 1 (Continued)

Activity	*Phase*	*Aspect*	*Possible positive impacts*	*Possible negative impacts*
Conventional oil and gas	Post-extraction phase	Surface water and vegetation	• Risk of surface water contamination lowers	*Wastewater and oil discharge from leaks and spills:* • Long-term impacts of contamination on rivers, pans, lakes (C) • Unknown impact of specific chemicals on individual species or on freshwater communities (A) • Reduced habitat quality, reduced fish fitness and health and increased freshwater mortality due to exposure to toxic substances (A/C) • Reduced availability of food sources (e.g., invertebrates) (A) • Bioaccumulation of toxic substances in the food web (A) *Poor oil well integrity and well leaks:* • Possible contamination over long-term via surface water/groundwater connectivity if oil wells leak over long-term (A/C/L) *Disturbed area:* • Continued stream/river degradation (C) • Susceptibility to nonnative species invasion may continue for years (C) • Resuspension of pollutants after clean-up (C) • Migration of polluted ground- and/or surface water pollution to the rooting zone—vegetation die-back (A/C) • Success of vegetation rehabilitation uncertain (C/L) • Continued habitat fragmentation, due to poor upkeep of existing infrastructure, roads or nonnative invasive species control (C) • Continued loss of plant biodiversity and ecosystem services (A) • Possible establishment and spread of nonnative plants (A/C) • Illegal trade of endangered plants due to access roads (A)
		Ground-water	• Pollution risk in the area where fracking is ceased, lowers	• Aquifer pollution from oil production may only surface years after a pollution incident (A/C/L) • The extent of possible long-term contamination in freshwater aquifers could not be predicted (A/C/L) • Inability to rehabilitate contaminated aquifers in complex geology (physically and economically) (A/C/L) • Well abandonment and long-term monitoring may be problematic (A/C/L) • Oil and gas well casing failure and leakage may pose long term legacy issues and lead to inevitable groundwater contamination (A/C/L)
		Seismicity	• Not known	• Possible post-extraction seismicity
Unconventional oil and gas	Exploration phase	Surface water and vegetation	• Possible new species identified	*Seismic exploration*: • Same as for conventional oil and gas exploration *Drilling fluid, fracking fluid and wastewater (produced water and flowback) discharge during fracking pilot well testing*: • Drilling fluids, fracking fluids, wastewater leaching into surface water via groundwater or via overland flow from surface spillages contaminate rivers, pans, lakes (A/C/L) • Pollution reduces abundance and diversity of freshwater organisms (e.g., invertebrates and fish) (A/C) *Infrastructure development (road development, river crossings, limited wellpad development, seismic lines)*: • Impacts on surface water and vegetation same as for conventional oil and gas exploration, and: • Surface spills of hazardous fluids (drilling fluid, fracking fluid and wastewater [produced water and flowback]) during fracking pilot well testing can cause impact on vegetation (A) *Water sourcing from rivers for UOG extraction:* • Same as for conventional oil and gas exploration, but on larger scale, since fracking uses much larger volumes of water *River sand mining to obtain proppant for fracking:* • Increased surface water turbidity (A) • Removal of sand may impact on freshwater organisms in alluvial aquifer/hyporheic zone (A) • Increased sediment deposition in rivers could increase turbidity and limit habitat and food available to invertebrates and fish (A)

Table 1 (Continued)

Activity	*Phase*	*Aspect*	*Possible positive impacts*	*Possible negative impacts*
		Groundwater	• Develop a better understanding of the deeper geology and geohydrology	*Unknowns:* • Same as for conventional oil and gas exploration *Drilling in shale:* • Possible shale instability with associated borehole problems such as hole collapse, stuck equipment, plastic flow, fracturing, circulation loss and poor well control may cause contamination (C) *Saline produced water during CBM extraction* • Large quantities of saline water produced by CBM contaminate aquifers if aquifers and coalbed formations co-occur (A/C/L) *Hydraulic fracturing pilot testing* • Groundwater contamination if hydraulic fracturing is allowed during the exploration phase, both for coalbed methane and shale gas formations (A/C/L)
		Seismicity	• Not known	*Increased seismicity:* • Same as for conventional oil and gas exploration but on a larger scale
	Extraction phase	Surface water and vegetation	• Possible new species identified	*River sand mining to obtain proppant for fracking:* • Same as during exploration phase but on larger scale *Drilling fluid, fracking fluid and wastewater (produced water and flowback) discharge during fracking:* • Various sources of pollutants may impact rivers on a much larger scale than exploration (A) • Increase of sediment and contaminants may impact freshwater organisms physiology or behavior and alter ecological community interactions (A/C) *Infrastructure (Extensive road development, river crossings, extensive wellpad development, wastewater treatment plants)*: • Impacts on surface water and vegetation same as during conventional oil and gas extraction, but on larger scale *Water sourcing from rivers for UOG extraction:* • Same as during exploration phase but on larger scale
Unconventional oil and gas		Groundwater	• Using safer chemicals (e.g., gasses or plant-based oils) • Using green in fracking	• Same as for exploration phase and: • Large scale sourcing of water from local aquifers may induce aquifer connectivity, change groundwater levels, cause contamination and seismic activity (A/C/L) • Shale drilling over large regional areas may cause diffuse contamination (A/C/L) • Surface activities over large regional area contaminate aquifers via surface water-groundwater interaction (A/C/L) • Wastewater produced in large quantities during extraction poses serious challenges if not managed properly (A/C/L) • Poor well integrity may cause leakage of gas or fluids and groundwater contamination, also for CBM (A/C/L) • Large scale extraction of water from CBM causes geology and aquifer deformation, subsidence, decreased baseflow and reduced springflow (A/C/L)
		Seismicity	• Not known	*Increased seismicity:* • Same as during conventional oil and gas extraction but on larger scale
	Post-extraction phase	Surface water (quality) and vegetation	• Risk of surface water contamination lowers	*Drilling fluid, fracking fluid and wastewater (produced water and flowback) discharge during fracking:* • Same as for conventional oil and gas post-extraction phase and: • Not all chemicals used in fracturing fluids are known, therefore unknown chemical impacts are uncertain(A/C/L) • Pollutants may impact rivers (A/C/L) • Possible contamination via groundwater pathway due to interconnected resources (A/C) *Disturbed area:* • Surface water and vegetation impacts same as for conventional oil and gas post-extraction
		Ground-water	• Pollution risk in the area where fracking is ceased, lowers	• Aquifer pollution from deep shale layers may only surface years after a pollution incident (A/CL) • The extent of possible long-term contamination in freshwater aquifers could not be predicted at this stage (A/C/L) • Country/territory not able to rehabilitate contaminated aquifers in complex geology (physically and economically) (A/C/L) • Well abandonment and long-term monitoring may be problematic (A/C/L) • Oil and gas well casing failure and leakage may pose long term legacy issues and lead to inevitable groundwater contamination (A/C/L)
		Seismicity	• Not known	• Same as for conventional oil and gas post-extraction but on larger scale

Azevedo-Santos et al., 2021; Couceiro et al., 2010; Dauwalter, 2013; Duke, 2016; Entrekin et al., 2011a,b; Esterhuyse et al., 2016a,b; Etkin, 2011; Fefilova, 2011; Harfoot et al., 2018; Jones and Pejchar, 2013; Jones et al., 2015; Laurance et al., 2009; Masnik et al., 1976, McCleneghan et al., 2002; O'Rourke and Connolly, 2003; Osborn et al., 2011; Pring and Polunin, 2010; Ramirez, 2010; Song et al., 2008; Trail, 2006.

A, Acute impact; C, Chronic impact; L, Legacy impact.

Table 2 Water-related socio-economic impacts of conventional and unconventional oil and gas extraction.

Socio-economic impacts for oil and gas extraction during exploration, extraction and post-extraction

Activity	*Phase*	*Possible positive impacts*	*Possible negative impacts*
Exploration and extraction phases	Population	• No water-related impacts indicated in literature	• Short- and medium-term population influx place pressure on natural and social environment (e.g., water resources and water & sanitation infrastructure) (A)
	Economic	• Infrastructure development (e.g., roads, water, sanitation)	• "Boom-town" effect": pressure on existing infrastructure and social services (e.g., water and sanitation); pressure on municipal services (i.e., wastewater management) (A) • Decline in tourism potential stemming from land-use changes, degradation of pristine environments, biodiversity loss, and reduced water quality (A/C)
	Agriculture and food security	• No water-related impacts indicated in literature	• Diverting scarce water resources from agriculture to oil and gas interests (A) • Long-term impacts from dust pollution, water shortages and quality on crop production are uncertain (C) • Land-use changes affect availability and productivity of agricultural land (C/L) • Chemicals used in extraction may impact reproductive health of animals (C/L) • Rural livelihoods affected by reduced access to, and availability of, wild food sources (e.g., fish) (A/C) • Damage to agricultural land from oil spills (A/C)
	Health and social well-being	• No water-related impacts indicated in literature	• Naturally occurring radioactive materials from produced water can have health implications (A/C) • Water quality issues may contribute to increased risk of chronic diseases (e.g., cancer and asthma), especially in vulnerable groups (children and elderly) (C/L) • Risk of reproductive health issues uncertain (C/L) • Psychological impacts: perceived health risks, frustration, and anxiety over nuisances such as increased traffic and noise (A/C) • Social conflict: between community members; community and local/national government; community and oil and gas companies (A/C) • Loss of access to cultural sites and rituals (i.e., baptisms in rivers) (A/L) • Increased risk of injury and death (i.e., from accidents and oil spills) (A/C)
Post-extraction phase	Population	• Population decline reduces pressure on fragile natural environments and scarce resources	• No water-related impacts indicated in literature
	Economic	• No water-related impacts indicated in literature	• No water-related impacts indicated in literature
	Agriculture and food security	• No water-related impacts indicated in literature	• Land unsuitable for farming after oil and gas resources are depleted due lingering impacts on soil, and water quality and quantity (L) • Declining food security (A)
	Health and social well-being	• No water-related impacts indicated in literature	• Lingering health issues (e.g., cancer) (L) • Birth defects as a result of exposure to mutagenic chemicals (L)

Anderson and Theodori, 2009; Anderson, 2018; Canfield et al., 2020; Faber, 2020; Jacquet, 2014; Esterhuyse et al., 2016a,b; Redelinghuys, 2016; Schneller et al., 2020.
A, Acute impact; C, Chronic impact; L, Legacy impact.

Box 1 Oil in mangroves.

While not inland waters, mangroves are critical transition zones that link land, freshwater habitats, and the sea. They form a relatively small, but distinctive biome that delivers unique ecosystem services to coastal communities, and that serves as a nursery for many marine species. Oil contamination from ship transportation spillages and accidents during exploitation and pipeline transport, has severely affected these ecosystems (Duke, 2016). Mangroves often occur within large bay areas in tidal areas and river mouths in the tropics and subtropics, where important ports have been and are being constructed. The intense movement of large ships increases the chances of both acute accidental oil spills and smaller oil leaks. Additionally, mangroves are found within several of the world's main hydrocarbon extraction sites, such as the Persian Gulf, the Gulf of Guinea (including the Niger delta), the Caribbean Sea, and the Gulf of Mexico. Mangrove ecosystems are extremely vulnerable to oil contamination, particularly to large acute oil spills, but also to chronic oil contamination incidents. Understanding and distinguishing synergistic acute and chronic responses, as well as the singular effects of contamination, and negative impacts that stifle mangroves, are all essential to predict the ecological consequences of spillages more accurately, and for modeling subsequent impact and recovery.

Over the last few decades, large oil spills in and around the Port of Paranaguá in southern Brazil severely impacted mangroves. In 2001, the oil tanker Norma leaked 392,000 L of naphtha, contaminating 3000 m^2 of the Paranaguá bay, while a leaking Petrobras pipeline released 4000 L of diesel oil into the Caninana stream. The pipeline leak damaged the local fauna and flora (including mangroves) and led to the prohibition of fishing. In 2004, the Vicuña vessel exploded in the port and released millions of liters of oil and methanol into the bay. This contamination severely damaged the environment, while locals whose income depended on fishing, were compromised during fishing prohibitions. In the same year, a train derailing released 4000 L of fuel into the Caninana stream, while a Petrobras truck collision released 30,000 L of oil into the Padre and Pinto rivers, with all these pollutants ultimately reaching the mangroves. All these acute oil spills occurred within only 5 years and affected the same mangrove areas in the Paranaguá, Antonina, and Guaraqueçaba bays of the Paranaguá Estuarine Complex.

Nowhere on earth are the effects of careless oil exploitation in mangrove areas more visible than in the Niger Delta (Nigeria). This ecologically sensitive delta contains the largest section of mangroves in Africa, but is also rich in oil and gas resources (Ayanlade and Howard, 2016). Oil and gas production in this region causes some 300 oil spills a year, with leaking pipes, and toxic waste leaching into groundwater from unlined pits, killing fish and wildlife and making it hard to grow crops (Faber, 2020). The Nigerian government has committed many human rights abuses against people protesting the destruction of the delta by the oil and gas industry (Wong, 2020).

Over the last six decades, over 200 prominent oil contamination incidents were reported to have negatively affected mangroves across the world. Together, these account for at least 5 million tons of oil that have been released upon up to 2 million ha of mangrove, killing or altering over 126,000 ha of mangrove flora (Duke, 2016). With less than 15 million ha of mangrove cover left as of 2020, this renders mangroves as one of the biomes most affected by the oil and gas industry. However, given the lack of reporting, these are probably grave underestimates. Oil spills' effects on mangroves can be measured by calculating the total and relative areas of dead vegetation post oiling. Such data have however only been reported on a relatively small number of incidents. This is mostly due to incomplete or unavailable data on oil spill impacts and a global disparate bias in terms of large regions and countries. The biggest data gap on indirect long-term contamination, is chronic and diluted leaks in or near large ports and extraction platforms and their sublethal effects in terms of complex animal and plant ecological interactions. Abnormal changes in the condition of either plants or animals will affect other organisms and abiotic parameters and conditions. Small and large crustaceans, such as crabs, modulate the availability of resources to other species by changing ecosystem components (Jones et al., 1994), and thus provide many ecosystem services, including burrowing that improves sediment aeration and nutrient turnover and enhances water exchange, among others (Duke, 2001). To redress ineffective oil spill reporting in mangrove ecosystems, Duke (2016) recommends updating operational planning and action standards, highlighting that selective trials during a spill are an opportunity to rehabilitate contaminated mangroves that can guide future clean up responses. Such data must be publicly available.

(*Continued*)

Box 1 (Continued)

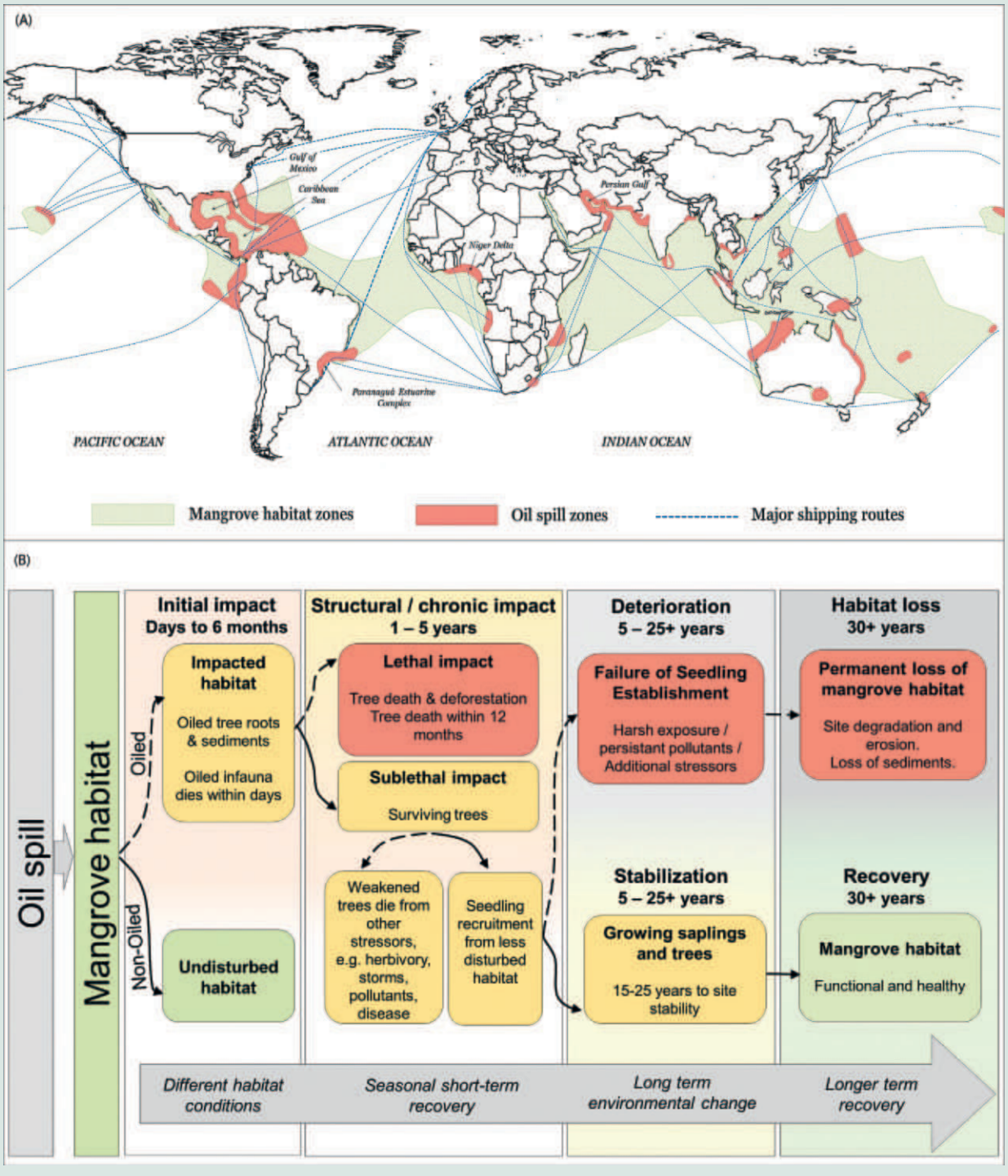

Fig. 1.1 (A) Mangrove habitat zones, major shipping risk routes and oil spill zones (adapted from Duke, 2016) and (B) Schematic diagram showing the effects of large oil spills on mangrove habitat (adapted from Duke, 2016) (Image source: S Esterhuyse).

Box 2 Oilfields in Amazonia.

Oil extraction has been particularly harmful to tropical forests and aquatic ecosystems of the Amazon Basin (Martínez et al., 2007; Yusta-García et al., 2017). In the upper reaches of the Amazon, in Ecuador and Peru, 12.1 million liters of produced water per day, 60 thousand liters of suspended oil per day, and large volumes of toxic mud have been released since 1990 (Martínez et al., 2007; Yusta-García et al., 2017). Instead of pumping the produced water, which contains salts, heavy metals, and other toxins, back into the wells, it was released into the rivers (Kimerling, 2006). The Trans-Ecuadorian pipeline, which connects the main production site of Lago Agrio (Ecuador) with the Pacific Ocean, also leaked approximately 73 billion liters of oil between 1964 and 1993. This represents 1.8 times the volume of the better-known 41-billion liter Exxon Valdez oil spill (Kimerling, 2006; Sebastián and Hurtig, 2004). In 1989, feeder pipelines were leaking 5400 L per day (Sebastián and Hurtig, 2004).

Major oil spills however still occur in this region, such as in the Coca River in 2009, 2013, and especially in 2020, when a 2.5 billion liter spill impacted the Kichwa Indigenous people (Koenig, 2021; Ricci, 2021). These operations also seriously degraded the fisheries in Ecuador's Napo and Coca Rivers, and what locals described as a "splendid" variety of fish in these two major river basins, was essentially destroyed (Kimerling, 2006). Amazonian fish are particularly sensitive to oil spills because many species have evolved adaptations to oxygen-poor water, leading them to come to the surface where they would encounter floating oil (Almeida-Val et al., 1999). These fish include the pirarucu or paiche (*Arapaima* spp.) air-breathing species and specially-adapted gilled species that exploit the oxygen-rich film at the water surface (Val and Almeida-Val, 1999). Salts from produced water also significantly alter regional saline concentrations (Moquet et al., 2014), and act as invisible barriers blocking fish migrations (Kimerling, 2006). The oil is not only toxic to fish (Sadauskas-Henrique et al., 2016) but also reduces the abundance and diversity of aquatic invertebrates, as shown by studies of spills near Manaus, Brazil (Couceiro et al., 2006, 2007). This undermines the base of food chains that support fish populations.

Even though Brazil already suffered significant oil and gas extraction environmental impacts, including from the upstream Ecuadorian and Peruvian operations, it still plans large-scale oil and gas extraction in the "Solimões" region (Brazilian for the Upper Amazon River, upstream of the confluence with the Rio Negro at Manaus) (Consórcio PIATAM/COPPETEC and EPE, 2020). A relatively small extraction site has operated since 1988 in this area at Urucu (purple areas in Fig. 1.1). Expanding these operations within the Solimões region would however affect an area of 740,946 km^2, which is larger than the United States state of California (Fig. 2.1).

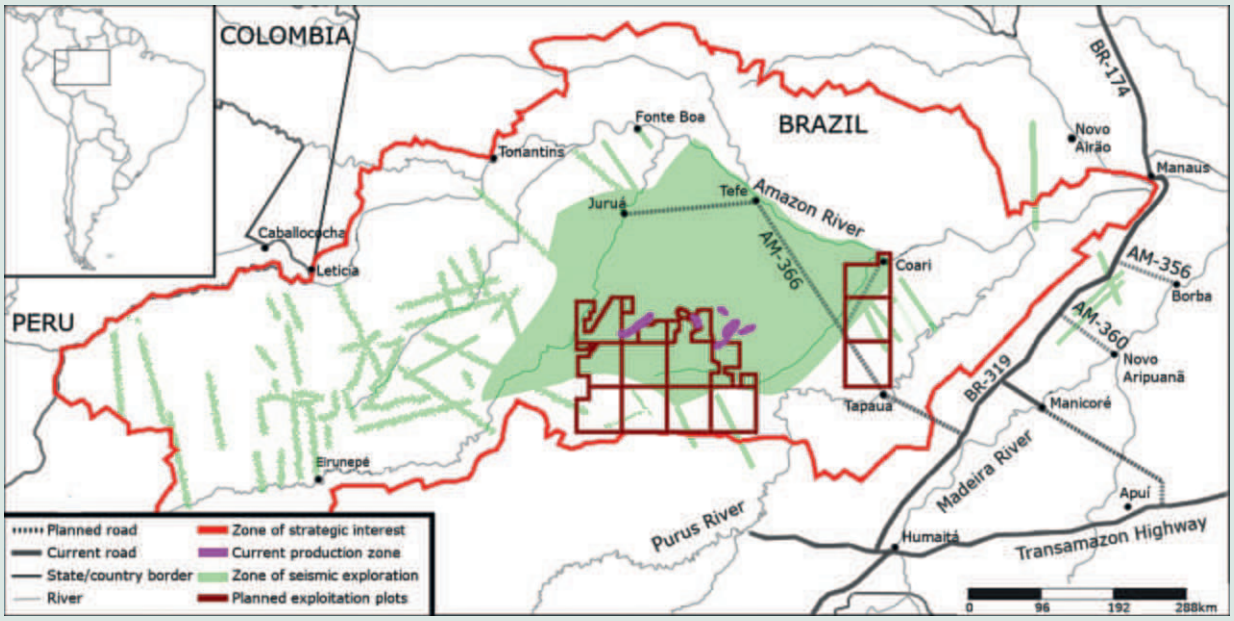

Fig. 2.1 Map of oil and gas drilling blocks in the state of Amazonia, showing the current production zone and the region where seismic surveys have already taken place. In this the 'zone of seismic exploration', around 185,000 km of seismic surveys were performed before 2019 (See Consórcio PIATAM/COPPETEC and EPE, 2020 for detailed map of survey transects). The project's 'zone of strategic interest' is larger than the United States state of California. The controversial BR-319 and the planned AM-366 highways would provide deforesters access to the vast area of intact rainforest west of the Purus River (Fearnside and Graça, 2006). Oil block connections to this road would likely spread deforestation throughout the Trans-Purus region (Fearnside, 2020a). (Image source: M Van Steenberge).

Currently, extraction sites at Urucu have no road access and are treated like oil platforms at sea (the "platform" model). The lack of roads has prevented settlement, land grabbing, and deforestation. With possibly thousands of wells to be drilled in the Solimões expansion project, road access would however be much cheaper. Oil companies will likely pressure the government to connect project areas to major roads, despite this not being part of the official project plan. A connection to the AM-366 highway that will connect the BR-319 (Manaus-Porto Velho) highway to Tefé, Coarí, and Juruá (Fig. 1.1), is most likely.

The first oil extraction rights, located on the planned AM-366 route, have already been sold to Rosneft (Departamento Nacional de Infraestrutura de Transportes (DNIT), 2020), the Russian oil company accused of causing over 10,000 annual oil spills worldwide (The Guardian, 2015). Oil spills and leaks from pipelines connecting wells to central hubs and from there to Coarí via larger pipelines, are an inherent risk. The Solimões project itself could, however, incentivize the AM-366 road construction, where an illegal 'branch' road already exists along the first stretch of the planned route (Fearnside et al., 2020). Such road access would initiate uncontrolled deforestation (Fearnside, 2017) and land grabbing (Ferrante et al., 2021). At risk is Brazil's last major block of intact Amazon forest: the Trans-Purus region between the Purus River and Brazil's border with Peru (Fearnside, 2020a,b). The environmental services of the Trans-Purus forest not only curb global warming and maintain biodiversity, but also maintain water-cycling that supplies rainfall to São Paulo and other major Brazilian population centers and neighboring countries (Fearnside et al., 2020).

Box 3 Different approaches to water resource protection during oil and gas extraction in water-scarce areas of Southern Africa.

There are many similarities between the Namibian Okavango and South African Karoo oil and gas extraction areas—both are water-scarce and in both cases, locals depend extensively on groundwater resources. The Namibian Kavango basin also has the same geology and depositional environment as the South African Karoo basin and is an extension of the South African Karoo Supergroup (Catuneanu et al., 2005; Werner, 2006). The approaches toward managing and protecting the scarce water resources of these two areas, however, differ widely and are discussed below.

Case study 1: Okavango

Reconnaissance Energy Africa (ReconAfrica), a Canadian oil and gas company, holds a license to explore both conventional and unconventional oil and gas over an area of approximately 35,000 km^2 in the northern parts of Namibia and Botswana (Tan, 2021), Fig. 3.1. These areas include the Namibian headwaters of the Okavango delta and the Kavango-Zambezi transfrontier conservation area (KAZA). The KAZA has one of the most diverse ecosystems on the planet, borders three national parks, and covers 11 community conservancy concessions. A world heritage site that lies within ReconAfrica's PEL001 exploration area, Tsodilo Hills, was excluded from their license area in 2021 after intervention by United Nations Educational, Scientific and Cultural Organization (UNESCO) (2021).

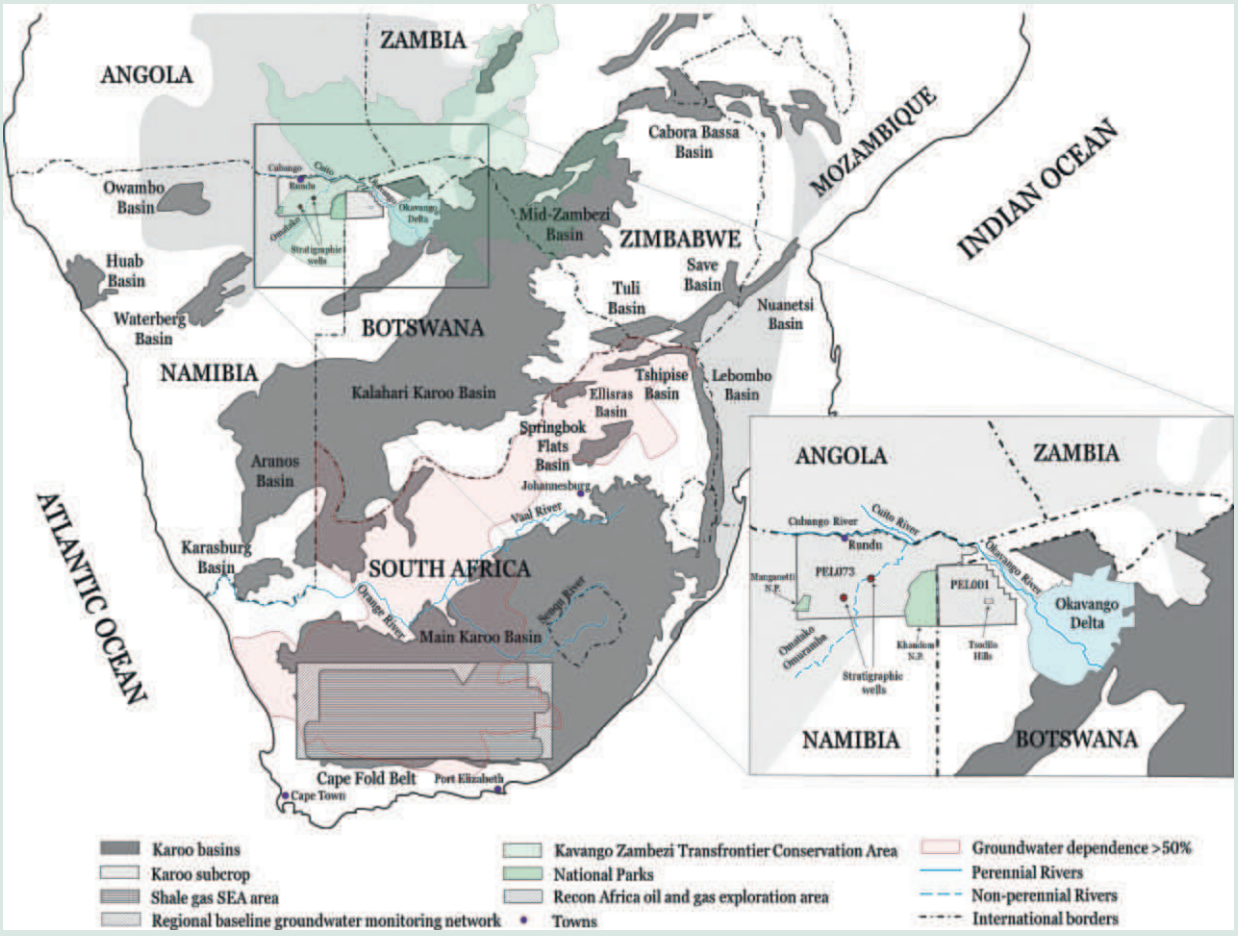

Fig. 3.1 Map of Southern Africa with the South African Karoo and Okavango delta case studies, showing relevant rivers and geological basins (Image source: S Esterhuyse).

Groundwater is especially important in the arid PEL073 ReconAfrica license area in Namibia. Because the Omatako River within PEL073 is ephemeral, rural people rely predominantly on shallow groundwater, especially close to the river (Jones, 2010). Groundwater is used for domestic and livestock supplies to villages, rural communities, and farms (Christelis and Struckmeier, 2011). The boreholes and dug wells that supply water are concentrated, as are the people, along the Omatako river valley.

ReconAfrica has started to drill their first exploratory well within the Omatako river valley in January 2021 (Barbee and Neme, 2021) and reports surfaced that the reserve pit where returned drilling fluids and wastewater is being stored, is not lined (Barbee, 2021). This poses a serious contamination risk to the groundwater resources in the Omatako valley. With a shallow groundwater level of less than 30 m, and with sandy unconfined aquifers into which contaminants can easily migrate, the groundwater in the Omatako valley is especially vulnerable (Christelis and Struckmeier, 2011). Recharge of the groundwater system occurs mainly via the river systems (Jones, 2010). Once aquifers in arid areas are contaminated, it is nearly impossible to clean up, and this contamination, therefore, poses a legacy contamination risk.

Future exploration that may include drilling in the PEL001 license area near the Okavango delta in Botswana, also poses a legacy contamination risk to the delta. The Okavango delta does not have an outlet to the sea, and any contamination that enters the delta will therefore accumulate, as confirmed by a continued increase in the salinity of the water in the delta over time (Oromeng et al., 2020).

Box 3 (Continued)

Both Namibia and Botswana require environmental impact assessments for oil and gas extraction, and public participation as part of the EIAs. There were, however, numerous reports of poor public participation (Esterhuyse, 2020) when ReconAfrica applied for its licenses. ReconAfrica is dismissive of any water impact that may emanate from its activities (Barbee, 2021). The poor management and lax regulation of oil and gas exploration in the Okavango threatens its water resources and should be handled with much more care.

The exploration areas cover a large region of extremely sensitive areas and span across international borders. A strategic environmental assessment should therefore have been performed in addition to the EIAs. A baseline of water resources in the license areas has not been done, nor do proper regulations exist to protect its water resources. The apparent lack of transparency of ReconAfrica in sharing information about its activities (Barbee and Neme, 2021) is also worrying. Without transparency, Botswana and Namibia may not be able to avoid a resource curse, and would not be able to properly manage or monitor the transboundary effects of exploration and extraction activities on the shared water resources.

Case study 2: Fracking in South Africa

Unconventional gas extraction using hydraulic fracturing is seen as a way for South Africa to achieve energy security and can assist the country in meeting its socio-economic development agenda (Ndlovu and Inglesi-Lotz, 2019). In 2011, Shell applied for a shale gas extraction license, covering approximately 180,000 km^2, in the central part of the country in an area known as the Karoo (Fig. 3.1). The mean annual precipitation in the Karoo ranges from 500 mm in the east to less than 100 mm in the west. The arid Karoo is ecologically sensitive and most of its rivers are ephemeral (Esterhuyse et al., 2016a,b). Groundwater is therefore its most important water source, with most agriculture and towns in the central and western Karoo depending on it (Fig. 3.1).

The limited water resources and sensitive landscape limits economic and agricultural activities (Walker et al., 2018). Agricultural activity, supporting around 100,000 people in the area (Oettle et al., 2016; Murcott and Webster, 2020), mostly focuses on livestock farming, including dairy farming and wool and meat production, but also includes other activities such as seed crop production. The Karoo people have low employment levels and are poverty-stricken, with a high dependency on social grants (Redelinghuys, 2016). They cannot mitigate the impacts of water pollution and water scarcity. Karoo towns also experience ongoing issues with service delivery that fuel social and political unrest. Service delivery protests are strongly linked to water access, which is exacerbated by the limited institutional capacity of the poorly functioning municipalities (Atkinson et al., 2016).

Fracking can potentially disrupt the Karoo's natural ecosystem through the use and pollution of scarce water resources, negatively impacting the health and wellbeing of the people and the natural environment. Because of this, a strategic environmental assessment (SEA) for shale gas development has been done in the Shell permit area (Scholes et al., 2016), Fig. 3.1. This SEA highlighted the risk of shale gas development for polluting Karoo groundwater resources, and crucially stated that no additional inland water is available for fracking. Because of this, the Petroleum Agency of South Africa commissioned the development of a regional baseline groundwater monitoring network (Groundwater Division of the Geological Society of South Africa (GWD GSSA), 2021) to assess the baseline groundwater quality and quantity. South Africa is also developing regulations to protect water resources during fracking (Republic of South Africa (RSA), 2021). These management tools will assist in protecting the scarce Karoo water resources, and no UOG extraction licenses are being granted until these management tools are in place.

phase. Given the uneven distribution in oil and gas production and consumption, oil and gas are transported over large distances using tanker trucks, rail, and, most importantly, pipelines (Michel and Fingas, 2016). As many streams and rivers are crossed by roads, freshwater environments are highly susceptible to the impacts of spills from tanker trucks (Laurance et al., 2009). These aquatic ecosystem impacts can extend over long distances from the source and affect fish, crustaceans, reptiles, birds, and mammals. Although pipelines can economically transport enormous volumes of oil over large distances, they come with an inherent risk of oil spills, often resulting in the contamination of surface waters. A review of Canadian oil leaks from pipelines revealed that spills were frequent, variable in scale, and posed a wide range of potential adverse environmental effects. Additionally, pipeline oil spills were difficult to predict, posing challenges to management and policy (Kheraj, 2020). To detect spillages, companies rely on high-tech (automatic monitoring) and low-tech techniques (pipeline walkers, helicopter patrols). In developing nations, however, and in regions with weak governments, relaxed environmental regulation increases the risk of undetected leakage. Pipelines are often targeted during armed conflicts, especially in areas with a rich oil wealth (Le Billon, 2013), and also face significant threats from vandalization and cyber-attacks (Oluwatuyi and Ileri, 2013; Dancy and Dancy, 2017), which increases leakage risks. Because of these risks, the construction of new pipelines, especially through culturally or ecologically sensitive land, is increasingly opposed.

Ecological impact on aquatic communities

The direct impacts of oil and gas extraction on biodiversity and ecosystem services include habitat loss and fragmentation, pollution, changes in water resources and flow regimes, alterations in the structure of freshwater communities (Entrekin et al., 2011a,b; Jones et al., 2015), and changes in wildlife habitat use (O'Rourke and Connolly, 2003) (Table 1, Fig. 2). Although the composition of petroleum varies greatly, crude oil is a mixture of (cyclo)alkanes and (poly) aromatic hydrocarbons (PAHs), with, to a lesser degree, sulfur- and nitrogen-containing hydrocarbons and trace metals. Several PAHs are carcinogenic and/or acutely toxic to aquatic organisms (Echols et al., 2009).

In freshwater environments, oil droplets can attach to suspended matter to form oil-particle aggregates. Even after complete clean-up of an oil spill, these can resuspend in the water column (Zhu et al., 2018). Toxic resuspended oil from oil spills, as well as flowback, produced water, and wastewater can result in wildlife mortality (Etkin, 2011). This toxicity can impact all levels of biological organization (from organism to ecosystem or landscape), reach different spatial scales (from localized to expanded regional impacts), and may continue for years (Azevedo-Santos et al., 2021). At the individual level, potential oil spill impacts include changes in the behavior, morphology, or life history of native species, while at the population level, impacts include changes in the abundance and distribution of native or non-native species. At the community level, oil and gas extraction impacts can cause

extirpations and species extinctions, but more commonly causes changes in species composition and diversity or abundances and interactions. These alterations can cause biotic homogenization and changes in the size and structure of food webs. At the ecosystem level, oil spills can affect and even alter entire river ecosystems. It can directly affect certain ecosystem engineers, e.g. bivalves, due to their high filtration rates, and can change primary productivity from food webs based on macrophytes to food webs based on benthic algae. Furthermore, impacts at the lower levels of biological organization may affect the higher levels, which can lead to a decrease in biodiversity and deterioration of genetic heritage (Gomes et al., 2000).

In addition to the direct impacts, indirect threats of oil and gas exploration can exacerbate the negative impacts on ecosystem functioning and biodiversity loss. Exploratory drilling can open up new areas, leading to the expansion of logging, hunting, and human settlements, as well as the introduction of non-native species (Laurance et al., 2009). These indirect threats pose challenges in tropical forests, as they lead to deforestation, with oilfield access roads providing access to settlers and other actors who invade and clear the forest. In Ecuador, 500 km of roads were built for oil extraction by 1989, leading to 10,000 km^2 of land being claimed by settlers, in addition to the entry of agribusiness, ranching, and logging (Kimerling, 2006). This is a harbinger of one of the dangers of Brazil's massive plans for oil and gas extraction in the western portion of its Amazon region (see Box 2).

Socio-economic impacts

Oil and gas development has profound and often long-lasting impacts on surrounding communities (Table 2). While some socio-economic benefits include increased job opportunities and improvements in infrastructure such as roads, these benefits are often gained at the expense of community cohesion, human health, and wellbeing, and local livelihoods (Appel et al., 2015; Jenkins et al., 2016; Scanlan, 2017). Existing social, political, and economic inequalities further result in an unfair distribution of benefits, risks, and harm associated with these developments. This is referred to as environmental injustice. Negative impacts disproportionately affect vulnerable and marginalized groups and communities that are least able to protect themselves (Inkpen and Moffett, 2011), such as ethnic minorities, indigenous communities, rural communities, the poor, and women. These vulnerabilities are often intersecting (Canfield et al., 2020; Long et al., 2020).

Areas surrounding oil and gas developments experience an influx of people, drawn by the possibilities of employment and economic development. Rapid population increases lead to increased pressure on natural resources such as water and land (Ayanlade and Howard, 2016). Oil and gas extraction furthermore contribute to pollution of air, water, and land, and this pollution has implications for human health and wellbeing. Chemicals used in unconventional oil and gas extraction processes that are released into the environment may gradually contaminate water resources, with the impacts on human health only becoming apparent with time. These chemicals have been linked to the development of cancers, birth defects, miscarriages, and other diseases and much uncertainty remains to what extent unconventional oil and gas extraction contributes to the development of these diseases (Finkel, 2016; Gorski and Schwartz, 2019). In the case of oil spills, surface and groundwater sources are contaminated, killing wildlife and fish and ruining the resource base on which local people depend for subsistence (Faber, 2020).

Poor or indigenous communities often rely on freely available ecosystem services for subsistence. Some 25% of poor rural households' livelihood resources such as firewood, medicinal plants, and food are obtained directly from the environment (UNEP, 2016; FAO, 2018). Additionally, small-scale fisheries are a major source of protein and income for the rural poor (Béné et al., 2009). When local communities lose access to wild food source areas, and when environmental pollution from oil and gas extraction and transportation exacerbate resource scarcity, it affects their food security and income generation. Particularly in water-scarce areas, access to and availability of clean water are critical community concerns. Communities downstream from such developments may experience dropping water levels in rivers, lakes, and wetlands. Falling water levels can disconnect indigenous populations from accessing subsistence lands as they are unable to reach these lands by boat (Scanlan, 2017; Westman and Joly, 2019).

Legacy impacts

Legacy impacts are long-term impacts that span over multiple generations and that are not easy to fix. Oil and gas extraction can have legacy impacts on both surface water and groundwater. On a local scale, leaking oil and gas wells can contaminate groundwater resources, which often cannot be cleaned up easily, if at all (National Research Council (NRC), 2013). This can lead to a permanent loss of the groundwater resource, meaning that communities must rely on other water sources or imported water over the medium-term. Over the long-term, communities may even be displaced because of a loss in livelihoods due to the groundwater supply loss.

On a regional scale, the abandonment of oil and gas wells, or the poor sealing of wells after well decommissioning, may lead to long-term groundwater contamination legacy issues (Australian National University (ANU), 2012). Davies et al. (2014) report that between 1.9% and 75% of wells from different oil and gas extraction areas worldwide, failed, but estimates are that almost all wells would eventually leak and potentially contaminate groundwater due to the mechanical failure of well casings (Bishop, 2011). Apart from contaminating groundwater resources, abandoned oil and gas wells also release methane into groundwater and the atmosphere. In the US alone, the oil and gas industry has abandoned about 3.4 million wells that were used over the past 100 plus years of drilling. These wells emitted an estimated 290 kt of methane into the atmosphere in 2018 alone (Environmental Protection Agency (EPA), 2021). The large number of wells that are drilled to access oil and gas resources, makes the regional legacy impact of leaking wells considerable.

Oil and gas extraction can also have vast impacts on surface water resources. If planned oil and gas drilling in the Okavango catchment contaminates the Okavango delta, it will lead to legacy contamination impacts (see Box 3: Okavango case study).

Similarly, legacy impacts can also be expected if current initiatives for oil exploration will lead to exploitation in the East African Great Lakes. Oil exploration is advanced in Africa's largest freshwater reservoirs, including the rift valley lakes Tanganyika, Malawi, and, lately, Albert, threatening their unique ecosystems and biota (Verheyen et al., 2016). As these are crucial in terms of water, food, and livelihoods for millions of people, an oil spill would markedly affect the health, water supply, and food security of local communities. The remote location of these lakes impedes quick and effective reactions to oil spills and as appropriate infrastructure is currently unavailable, bringing in heavy equipment at the time of a spill would be cumbersome, logistically impossible, or prohibitively expensive. Additionally, several of these lakes have very long flushing times, which means that recovery from an oil spill could take millennia. For Lake Tanganyika, which contains about one-fifth of the world's surface freshwater, the flushing time is approximately 7000 years (Verheyen et al., 2016). Finally, these lakes form the headwaters of some of the continent's largest rivers, including the Congo, the Nile, and the Zambezi. An oil spill in these lakes, which are home to thousands of endemic species, would therefore be a global biodiversity catastrophe. An accident might deal a devastating blow to these ecosystems, which have already been rendered fragile by anthropogenic stressors such as overfishing, deforestation, and global warming.

Long-term legacy impacts are possibly the least studied and understood, because impact monitoring usually ceases soon after oil and gas extraction stopped. This stresses the importance for governments to consider long-term financial planning to address legacy issues while hydrocarbons are still being extracted (National Academies Press (NAP), 2018), by investing some of the funds derived from current production to address potential future environmental issues.

Management of oil and gas extraction

Preventing impacts of oil and gas extraction on water resources is a very important but often neglected aspect of management. The precautionary principle, an international environmental law approach, is important to prevent negative impacts from high-risk activities, especially when considering climate change and increasing future water scarcity. The most salient example of the application of the precautionary principle is the placing of moratoria on fracking, or its outright banning in many countries (Esterhuyse et al., 2019). This principle is also especially important for groundwater resource protection because polluted groundwater resources often cannot be remediated. The precautionary principle should be used in conjunction with risk management tools, such as Environmental Impact Assessments (EIAs), Strategic Environmental Assessments (SEAs), water resource baselines, and the regulation of the oil and gas industry, to minimize negative impacts (see Box 3: South Africa case study).

Whereas EIAs assess the impacts of oil and gas development on a project level, SEAs assess broader potential impacts of plans, policies and programs, including cumulative impacts in a regional context (Esterhuyse, 2018). EIAs and SEAs must be independent to ensure evidence-based decision making that considers and addresses any environmental and societal damage that may ensue from extraction, including national or ethnic conflicts.

Baseline studies provide information on water resources before oil and gas extraction starts. Baseline data on existing water use can ensure that water uses are considered and protected before allocating water resources for extraction, while baseline water quality information alert regulators to contamination events, which can also be used to determine rehabilitation targets (Esterhuyse et al., 2019). Baselines are indispensable for establishing a legal basis for proving contamination, identifying the party responsible for the contamination, or for a company to refute a contamination claim (Esterhuyse et al., 2019).

A very important government tool to minimize impacts on water resources is regulation (Esterhuyse et al., 2019). The most effective regulatory framework includes both 'hard' command-and-control regulations and 'soft' market-based and voluntary regulations that are effectively enforced. Enforceable regulations contain provisions that establish criminal liability for cases where regulations are violated, commonly known as environmental crime. Where regulations are contravened, fines or sanctions can be imposed, for example, in 2021 Shell was ordered to pay over $111 million for water contamination in the Niger Delta (British Broadcasting Corporation (BBC), 2021). Regulations should also require public disclosure of the oil and gas operations. Disclosed data should be stored in publicly accessible databases to allow for independent scientific review of data by government, academia, and the private sector, which will allow for timely and appropriate adaptive management and the amendment of regulations as necessary.

Once contamination has occurred, clean-up and mitigation are required to minimize the negative effects on water resources. Here, the 'polluter pays' (see above example) and 'cradle-to-grave' principles are useful for holding the polluting companies liable, assuming that the polluter can be identified. However, even if companies pay for remediating water resources, the remediation of groundwater pollution (which mostly includes pump-and-treat and in situ bioremediation methods) is often unsuccessful (National Research Council (NRC), 2013), which is why groundwater pollution should be prevented at all costs. Ogoniland in the Niger Delta, home to the third-largest mangrove ecosystem in the world (see Box 1), is one of the most striking examples of groundwater pollution by oil and its lack of remediation success. Here, the groundwater of 69 sites covering around 1000 km^2 was severely contaminated with oil, mostly from leaking pipelines. Several years after these sites were contaminated, and after various clean up attempts, they are nowhere near remediated (UNEP, 2011; Gundlach et al., 2021). Remediation of surface water, which is also not always successful, includes biological, chemical, physical and chemical, thermal and heat, electric and electromagnetic, acoustic, and ultrasonic treatment methods (Ossai et al., 2020).

Establishing protected areas also protects regional sensitive aquatic environments. However, the difficulty in protecting aquatic environments from hydrocarbon extraction and its often significant impact on the livelihoods of riparian residents is globally evident. Numerous incidents worldwide, such as spills from drilling sites, lead to local claims of water pollution and health effects on human communities and their livestock.

Rather than opting for sustainable development strategies, governments often circumvent legal barriers by issuing hydrocarbon exploration and extraction permits in sensitive and even protected areas (see Box 1: Niger Delta and Box 3: Okavango case study). This negatively affects freshwater habitats that are the source of livelihoods for riparian populations and that contribute to sustainable economic development. The problem is most pronounced where governments want to quickly build up their state revenues, while a lack of resources to manage protected areas further compounds the issue. It is also important to note that these protected areas represent only a fraction of the scientifically identified priority biodiversity areas.

To avoid the prioritization of short-term gains over the long-term sustainable livelihoods of people living in oil and gas target areas (La Vina et al., 2010), governments should develop economically and ecologically viable extraction strategies in collaboration with regional stakeholders and scientists throughout the decision-making process. Norway is an example of where civil society influences petroleum governance to ensure sustainable development (Overland, 2018) Community initiatives to conserve natural habitats during hydrocarbon extraction can complement central government initiatives. Decentralized management of sensitive and protected areas is an obvious, if not a more viable solution, given the difficulties that the respective responsible central agencies sometimes face.

Sound environmental principles, such as the development of specific guidelines for public participation, should be incorporated during protected area management planning. Implementation of these principles requires unfettered access to information, including maps, relevant rules and regulations; and results on energy resources within protected areas. Only with these kinds of tools can local communities curb their governmental aspirations of sudden wealth, and prevent discrimination, dispossession, and long-term health problems.

The future of oil and gas extraction

The energy sector is the source of around three-quarters of greenhouse gas emissions (IEA, 2021) and holds the key to averting the worst effects of climate change, which is perhaps the greatest challenge humankind has faced. Climate change and its effects are inextricably linked to water resources (Stephens et al., 2020), leading to sea-level rise, climate extremes with more severe droughts and floods, irreversible effects on aquatic ecology, more water scarcity, and massive economic loss (Betts et al., 2018). Sea-level rise could in turn further endanger mangroves and also lead to coastal freshwater aquifers being intruded by saltwater, further limiting freshwater supplies. To limit such negative effects, the long-term increase in average global temperatures must be limited to 1.5 °C, as required under the international Paris Agreement, by achieving net-zero carbon emissions by 2050 (IEA, 2021).

The path to net-zero emissions by 2050 requires an immediate and massive deployment of all available clean and efficient energy technologies. Reaching net-zero emissions by 2050, with a world economy in 2030 being some 40% larger than today, requires a worldwide increase in energy efficiency, emissions reductions from the energy sector in CO_2, and a drop of 75% in methane emissions from fossil fuel production (IEA, 2021).

Future energy requirements predict that energy demand reaches a plateau from around 2030 onwards and that gas will become increasingly prominent over the coming years (McKinsey, 2021). It is predicted that gas will fuel the energy transition and overtake oil to become one of the world's largest primary energy sources by 2025 (International Energy Administration (IEA), 2019). The European Union sees gas as a critical transition to renewable energy and is of the view that substituting coal and oil with gas could help to reduce carbon emissions (European Commission (EC), 2012, International Renewable Energy Agency (IRENA), 2018). Although large-scale investment in natural gas may help in transitioning from coal and oil to renewables, gas can only temporarily fulfil this role because it still emits CO_2 and CH_4. Over the long-term, natural gas extraction can therefore work against reaching the climate goals (Gürsan and de Gooyert, 2020).

Oil majors are already significantly increasing the share of gas in their portfolios, and despite fossil fuel extraction having to end to avoid catastrophic climate change (IEA, 2021), continued investment in new gas developments is still expected. It is however of the utmost importance that any new oil and gas developments limit negative water resource impacts. Considering climate change (International Panel on Climate Change (IPCC), 2021) and biodiversity loss (Dasgupta, 2021), governments must in the long run limit CO_2 and CH_4 emissions by moving away from fossil fuel extraction, and pursue sustainable engagements with Nature that enhances our wellbeing and that of our descendants.

See Also: Human pressures and management of Inland Waters: Biological Invasions: Introduction, Establishment and Spread

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Relevant websites

https://certmapper.cr.usgs.gov/data/apps/world-energy/—World Petroleum Assessment.
https://ourworldindata.org/water-use-stress—World Water Stress.
https://oilspillmonitor.ng/—Nigerian Oil Spill Monitor.

Effects of Mining on Surface Water—Case Studies

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

In memoriam Li Wenliang (李文亮)—and the million others.

Glossary

Acid mine drainage Acid mine drainage is mining influenced water with a pH below 5.6, characterized by high proton, (semi-) metal and sulfate concentrations and an elevated mineralization.

Acid rock drainage Acid rock drainage is a low pH water resulting from pyrite oxidation in natural rocks.

Acidithiobacillus thiooxidans *Acidithiobacillus thiooxidans* is a microorganism catalyzing pyrite oxidation by a factor of up to one million. It gains its energy from the oxidation of sulfur.

Atlantic Forest Atlantic Forest is a South American biome, characterized by high biodiversity and endemism.

Barite Barite is a sulfate mineral with the formula $BaSO_4$.

Bootleg workings Bootleg workings are a historic or traditional mining method which extracts the raw material down to shallow depths leaving a bootleg type opening underground.

Category of accident risk Category of accident risk of a dam refers to the aspects of the dam itself that may influence the probability of an accident: project aspects, structure integrity, conservation, operation and maintenance status, and compliance with its Safety Plan.

Cone of depression Cone of depression is the subsoil area that becomes dewatered when mines are pumped.

Decommissioning Decommissioning is the final termination of a mining or processing operation, removing plant and equipment, and disposing wastes.

Digital twins Digital twins are computer simulations of water treatment plants to understand and visualize all relevant processes that would occur in the real plant.

Dry stacking Dry stacking is a process by which dewatering of tailings can be done with the help of vacuum or pressure filters, with the aim of stacking the tailings afterwards.

Efflorescent salts Efflorescent salts are minerals that are formed when mineralized mine water evaporates and leaves back easily water-soluble minerals.

Electrical conductivity Electrical conductivity (EC) is a measure for the potential of a liquid to conduct electricity. In general, the more ions are dissolved in a liquid, the higher this value will be, which is usually measured in mS cm^{-1} or µS cm^{-1}. It is compensated to either 25 ∘C or, more seldom, to 20 ∘C. Because of this characteristic, the electrical conductivity can be used for a quick indication of a mine water's contamination status.

First flush First flush is the fast increase of water constituents after an underground mine is flooded and the subsequent decrease of these constituents' concentrations over time, while fresh water kärchers the mine workings.

Geochemical barrier Geochemical barrier is a subsoil remediation method that uses reactive material in a permeable, vertical layer of various length, depths, and thickness to react with pollutants in flowing groundwater.

 https://doi.org/10.1016/B978-0-12-819166-8.00085-2

Iberian Pyrite Belt Iberian Pyrite Belt is the world's largest single ore district for copper and iron ore stretching from Spain to Portugal.
In-lake-neutralization In-lake-neutralization is an open pit mine water remediation method using various chemicals and gasses applied to the mining influenced water to increase the pH of acidified open pit lakes.
Inundation Inundation is an accidental inflow of water into mine workings, predominantly underground mines, eventually causing the mine to flood.
Karstified Karstified rocks are mainly composed of carbonate minerals that are dissolved by acidic ground water, leaving back caves or sinkholes.
Leptospirillum ferrooxidans *Leptospirillum ferrooxidans* is a microorganism that catalyzes pyrite oxidation by a factor of up to one million. It gains its energy from the oxidation of iron.
Micro-/macrocosm Micro-/macrocosm is a lake remediation method using enclosures of various size installed in open pit lakes and filled with various reactive substrates to inhibit microbial growth and subsequently sulfate reduction and metal precipitation.
Mine pool Mine pool is not a public swimming location underground, but the sum of all the polluted or unpolluted water collected in an underground mine.
Mine water Mine water or mining influenced water (not: mine wastewater, mining impacted water, mining affected water) is all the water in a surface or underground mine or seeping through waste rock. Strictly speaking, the water from the processing plant and the tailings is process water, as it contains human-induced process chemicals.
Mudflow Mudflow is a mass movement that involves an extremely rapid to fast, sometimes surge-like flow of debris, sediments, and sludge. In the presence of substantial amounts of water, the material may become partially or completely liquid.
Ochre Ochre is a collective term for yellow to dark orange iron oxides with a clayey to sandy composition.
Passive treatment Passive treatment is a remediation method for polluted mine water or soil which uses only natural or potential energy, plants, and microorganisms for improving mine water quality.
Process intensification Process intensification is a method to optimize an existing process, instrument, or device such that its use is optimized. The addition of a centrifugal governor to old style steam engines by James Watt is considered a process intensification bringing steam engines to save and reliable use.
Pyrite Pyrite is a sulfide mineral with the formula FeS_2. Though chemically identical to marcasite, it has another crystal structure. When pyrite or marcasite come into contact with water and oxygen, acid mine drainage or acid rock drainage forms.
Reactive wall Reactive wall see geochemical barrier.
Siltation Siltation is often a result of soil erosion or sediment pollution whose particle size is mainly in the silt or clay range. It may result in the pollution of water courses.
SPOT-6/LANDSAT-8 SPOT-6/LANDSAT-8 are satellite systems that are capturing the earth's surface by means of scanners or cameras with various wavelengths.
Tailings Tailings are the fine-grained residues of mineral processing and contain currently uneconomic crushed and milled rock and chemicals from the processing plant. Tailings are stored in sludge ponds, called tailings dams, or are dry stacked in tailings disposal sites.
Tailings dams Tailings dams contain the residues of raw material processing, and the dams are typically built of loose material.
Trophic levels Trophic levels are the different hierarchical levels from primary producers to primary and secondary consumers in a food chain.

Introduction

Selecting suitable case studies for mining influenced surface waters is an easy task because there are so many well-described studies from around the world. However, this does not imply that all mining operations cause pollution in the receiving water bodies or are prone to tailings dam failures—it just means that those that occur are often well studied. The intention behind selecting the following sites as case studies was: to describe and illustrate some important mining influenced rivers/streams; to describe the pollution sources and potential remediation options in these rivers/streams; and, to indicate that irresponsible conduct could cause severe regional, social and environmental effects (Table. 1). In addition, these sites are all located in mining areas of outstanding importance to human's mining history—which will be left to historians and archeologists to document. Besides the case studies presented, here could also be a case study about the Loisach rivulet near Biberwier in Tirol, which once was affected by lead, zinc, and silver mining, but now is a beautiful mountain stream. Or the Sabie River in South Africa could be shown, which is partly fed by abandoned gold mine discharges, and now used as drinking water and for recreational purposes for the town and tourists of Sabie. Moreover, this section could include the Metsämonttu mine in Finland, where natural attenuation and a small constructed aerobic wetland decrease the iron concentrations below the detection limit before the mine water enters a Natura 2000 protected river system. However, images of clean water are less impressive in this context than images of red or orange water—though the Cape Breton Island section shows a clean-water image for Cadegan's Brook, which is an excellent example of successful remediation measures. This section's intention is also to present case studies from which we can learn how to tackle the problems associated with polluted mine water and with the storage of mining residues, such as tailings.

Table 1 Details of the presented case studies and reasons for their inclusion. Geographical co-ordinates in WGS84 of the area's center.

Country	*Canada*	*Spain*	*Germany*	*South Africa*	*Russia*	*Brazil*	*Brazil*
Region	Cape Breton Island	Iberian Pyrite Belt	Lusatia lignite mining	Western Basin Witwatersrand	Kizel Coal Basin	Germano Mine Complex	Córrego do Feijão Iron Mine
Affected Watercourses	Cadegan's Brook	Río Tinto, Río Odiel	River Spree, open pit lakes	Tweelopiespruit	Poludennyi Kizel, Yaiva	Doce River	Paraopeba River
Raw Material	Coal	Copper, Gold	Lignite	Gold	Coal	Iron	Iron
Reason for Inclusion	Passive treatment system	Never ending natural and anthropogenic pollution	Process intensification resulted in new solutions	Active treatment and natural wetland	Economy politically more important than environment	Mining environmental accident	Industrial, humanitarian, and environmental accident
Co-ordinates	46°11′51″N 60°00′13″W	37°29′35″N 6°34′43″W	51°35′36″N 14°22′50″E	26°6′22″S 27°47′44″E	58°51′39″N 57°44′35″E	20°13′53″S 43°26′33″W	20°07′11″S 44°07′17″W
Authors	CW, EM	CW, EM	CW, EM	CW, EM	CW, EM	VSD, PC, JRSV	VSD, PC, JRSV

From a large range of possible case studies that can illustrate environmental management of mining, seven have been chosen because of their importance in this context. Yet, all case studies are representative for the many thousands of mining influenced streams, rivers, and lakes around the world.

Cape Breton Island, Canada

Mining influenced water from Cape Breton Island's 1B mine pool is treated by a passive aerobic constructed wetland system. This system substantially improves the water quality in the receiving water course, Cadegan's Brook, and the Atlantic Ocean as the final recipient.

The subsequent discussion about mine water in the 1B mine pool on Cape Breton Island, Nova Scotia (NS), Canada, is based on publications of Amirault et al. (1993), Calder et al. (1993), Forgeron (2007), Frost (1964), Government of Canada (2016), MGI Limited et al. (2003), Moreland (2013), Shea (2008, 2009), and Wolkersdorfer (2011).

Coal mining on Cape Breton Island (Fig. 1) is the oldest of its kind in Northern America and dates to 1685, when French soldiers worked coal seam outcrops in the Sydney/NS area. First commercial coal mining began in 1720, when a coal mine was opened in Cow Bay (Port Morien). In 1999, triggered by a flooding accident, mining ceased for economic reasons. Until then, 45 major underground and undersea coal mines were in operation on Northern industrial Cape Breton Island. They stretched from Big Bras D'Or in the northwest to Port Morien in the southeast.

One of the largest of these underground coal mining operations was around Sydney/NS, with the 1B mine pool holding most of the polluted mine water in 10 individual, interconnected mines. They stretched several kilometers into the Atlantic Ocean, and the mine pool has an estimated volume of 76.8 million m^3. With the № 26 colliery, mine water rebound started in 1985, when the first pump in 1B shaft was shut down. In 1999, the last of these 10 mines, the Phalen Colliery, closed after a controlled flooding, which ended in 2002. Since then, the mine water level is kept below sea level and under the discharge point to the Atlantic Ocean by a sophisticated pumping scheme. Since 2009, the discharged mine water from the Neville Street pumping scheme is treated in a passive mine water treatment system which was expanded in 2016 to treat a larger volume of mine water. Aim of the pumping and treatment scheme is to protect Cadegan's Brook from deteriorating and the Atlantic Ocean from receiving elevated concentrations of potentially toxic metals and sulfate through the 1A outfall. If polluted mine water would enter the Atlantic Ocean, the local lobster fishing would be impaired and an important source of income for Cape Bretoners would cease.

At the time of the flooding accident, two mines were still in operation, and to ensure safe operation, pumping in the 1B shaft was restarted in 1992 to prevent the Phalen Colliery from flooding. Though the water quality was good at initial sampling ([Fe] 0.004 g L^{-1}, pH 7.2, EC 9.1 mS cm^{-1}), it soon deteriorated to unacceptable iron concentrations and electrical conductivities ([Fe] 2.1 g L^{-1}, pH 3.9, EC 48.4 mS cm^{-1}) staining the Atlantic Ocean orange to yellow for a length of several kilometers.

All the mine water that was and is pumped from the Neville Street pumping scheme is discharged into a small stream, Cadegan's Brook, and from there, after a 3 km long course, it drains into Indian Bay (Atlantic Ocean) near Bridgeport. In addition, the main infiltration into the 1B mine pool seems to be connected with this brook, flowing from South to North in the communities of Reserve Mines, Glace Bay, and Dominion. Before the passive mine water treatment system went into operation, all the pumped mine water reached the brook, and consequently the sea. Flow in the brook varies substantially (80–260 L s^{-1}), depending on the precipitation, and in winter it is frozen. Upstream the mine water discharge location, the brook flows through a wetland area which formed above bootleg workings and sinkholes at MacKay's Corner. These bootleg workings are located above the № 5 colliery workings and surface water infiltrates into these mine workings to a degree not known precisely. Infiltration into the abandoned mine workings also appears downstream the mine water treatment plant's discharge, which accounts to approximately 3% of the total flow of Cadegan's Brook.

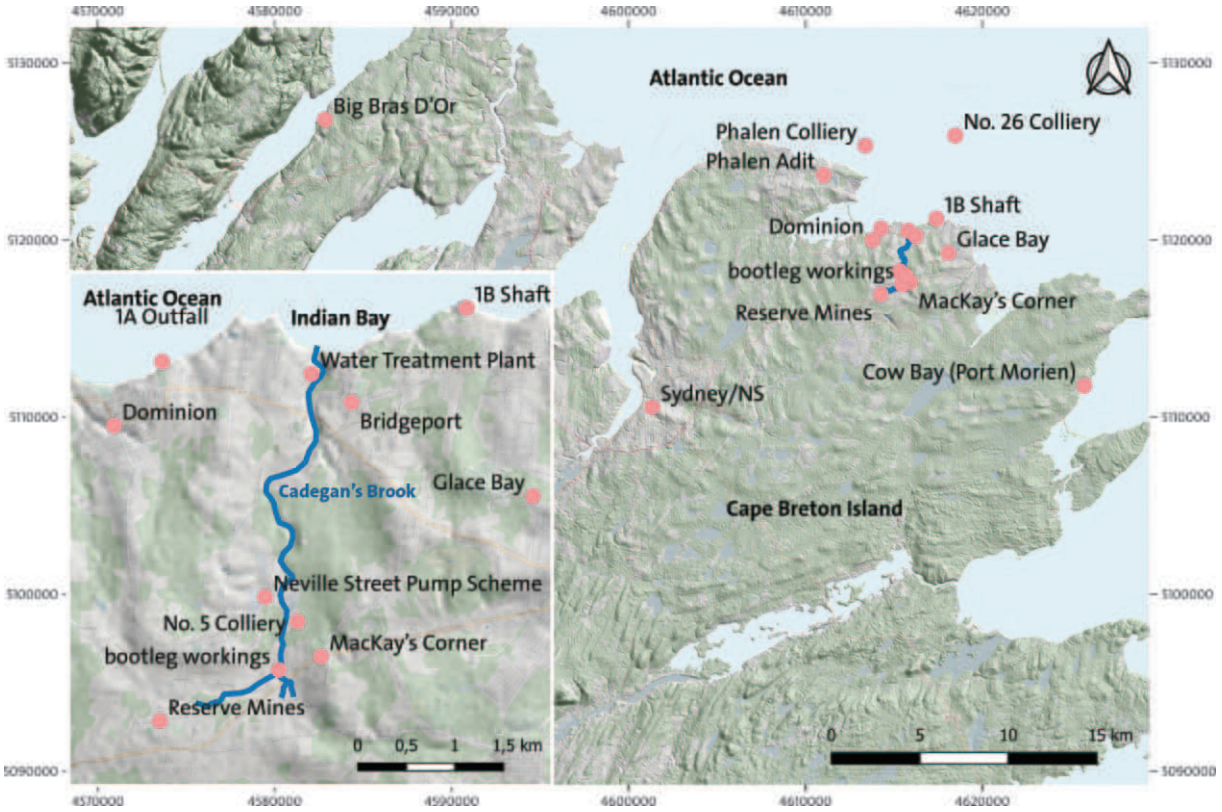

Fig. 1 Details of the Sydney/NS coal mining region. Sources: Open Street Maps community, Nova Scotia (NS) Department of Natural Resources.

In 2003, before the passive water treatment system went into operation, total dissolved solids upstream the discharge locations ranged between 72 and 364 mg L^{-1}, and downstream between 160 and 1400 mg L^{-1} (controlled by the sulfate concentration), while upstream iron concentrations were 0.1–2.5 mg L^{-1}, and downstream concentrations up to 1.7 mg L^{-1}. After the treatment system went into operation, upstream electrical conductivity was about 385 µS cm^{-1} and downstream about 1124 µS cm^{-1} but improved along the course of the brook to 100–200 µS cm^{-1} (2009 and 2011 data). Iron concentrations downstream of the discharge location were in the range of 0.4–0.8 mg L^{-1}. This shows that the brook's chemical water quality improved after the mine water treatment system became operational.

Before the passive treatment system came into operation in 2009, Cadegan's Brook was heavily stained with iron precipitates up to its mouth at Indian Bay. Even after the water quality improved, these precipitates still existed and made the stream bed muddy nearly everywhere. In 2013, four years after the passive mine water treatment system's construction, a benthic macroinvertebrates study was conducted. This study showed that the brook's water quality improved (Fig. 2) and reached acceptable water quality standards, indicating that the mine water remediation scheme was successful.

Río Tinto, Spain

This case study about the Río Tinto River exemplifies how thousands of years of mining results in a unique ecosystem with highly acid water. It also shows that some mining influenced inland waters became so highly polluted that they will very likely never be remediated.

The following discussion for the Spanish and Portuguese Río Tinto River is based on publications by Ariza (1998), Chacon-Baca et al. (2021), Grande et al. (2014), Leblanc et al. (2000), Nieto et al. (2007), Olías et al. (2020), Olías and Nieto (2015), Olías et al. (2004), Ruiz Cánovas et al. (2019), Sainz and Loredo (2005), Salkield (1987), and Torre et al. (2014).

Without question, the 4000 km^2 river basins of the Spanish Río Tinto and Río Odiel in the Iberian Pyrite Belt are the blueprints for mining affected streams *per se* (Fig. 3), but the microbiological inventory of the rivers indicate that already the earliest mines might have found a stream colored in red. Mining in the area dates back 4500 years to the Copper Age and left around 100 km of the Río Tinto polluted with acid mine drainage. In summary, the mass of the pyrite ore in the Iberian Pyrite Belt is estimated to be more than 10 Gt. Most of the ore deposits were mined for zinc, copper, lead, gold, silver and for sulfuric acid production. As the ores were mined in near surface ore bodies, vast quantities of pyritic mining residues exist in the area. This resulted in acid mine drainage with average pH values between 2.2 and 2.5, which directly discharges into the receiving water courses of the Tinto and Odiel rivers. First

Fig. 2 Optically clean Cadegan's Brook water downstream the Dominion water treatment plant. Algae growing on the rocks are indicative of elevated nutrients' concentrations. No visual indication of mining influenced water can be seen. Photograph: Christian Wolkersdorfer.

Fig. 3 Río Tinto at Zalamea la Real (Huelva, Andalucía, España). Source: LBM1948 (Luis Bartolomé Marcos), CC BY-SA 4.0, via Wikimedia Commons.

accounts on the river's pollution date to the year 1556, when priest Diego Delgado noticed that there are neither animals in the water nor do the locals use the water for consumption. Yet, he reports that the water will heal eye diseases when applied for external use. Because of the large amounts of highly acidic and metal enriched water, the rivers comprise dozens of kilometers of red to yellow colored water resulting mainly from the high iron concentration. Thus, the name Río Tinto: the red river. This is also the region where the initially British-German mining house Rio Tinto coined its name, as their mining activities started in the headwaters of the Río Tinto in 1873.

Metal and sulfate concentrations in the Río Tinto decrease along the course of the river and show seasonal fluctuations, which also occur in the Río Odiel. As in other mining affected streams, the metal concentrations and the electrical conductivity increase with decreasing pH values of the water. At the river's mouth, sulfate concentrations are still around 1 g L^{-1} and Fe concentrations around 14 mg L^{-1}, while upstream, sulfate concentrations are in the range of 111–1460 mg L^{-1} and Fe concentrations in the range of 4–316 mg L^{-1}. During rain events, the pollutant load increases, which is an indication of efflorescent salt deposits along the riverbanks and the mining residues being dissolved and flushed into the stream. Depending on the element, 30–98% of the load results from these periods of rain. Geochemical signatures indicate a common source area of the two rivers. Though the headwaters of the streams emanate within the pyrite rich host rocks, the rivers' current conditions are mainly the result of the historic mining activities. Natural acid rock drainage is a very minor contribution to the rivers' acidic conditions.

Though the rivers, as commonly assumed, look inhabited, they host an abundance of extremophile organisms, including algae, fungi, and bacteria. At least 1300 species have been identified and give evidence that the earliest Bronze Age miners might already have found a stream colored in red because of pyrite oxidation by *Acidithiobacillus ferrooxidans* and *Leptospirillum ferrooxidans*.

Unfortunately, all efforts to fully remediate the Río Tinto and Odiel areas—though it would be technically feasible and is studied for the Río Odiel—will be without success, as the mass of pyrite is so large that measures to mitigate the abandoned mines or the river will be only short lived. However, for reopening a mine in the Odiel watershed, the regional government, in view of past environmental liabilities, required the mining company to progressively reduce discharge loads to the Río Odiel. A reduction of 30% must be achieved before the third year after exploitation starts, 50% before the sixth year and 100% before the tenth year. Treatment facilities in these two watersheds, be they active or passive, might possibly work *ad infinitum* and will only result in local improvements. When the Spanish government announced that the mouth of the Tinto and Odiel rivers shall be rehabilitated, a group of biologists remarked that the microbial community in the rivers is unique and needs to be protected. This resulted in the whole Río Tinto being announced a protected area by the Andalucían government. A mixture of mining heritage, geo heritage and natural conservation in combination with selected rehabilitation areas might be assumed the best solution for these mining influenced streams.

Lusatia, Germany

After the German Reunification in 1990, it became obvious that the abandoned lignite mines in Lusatia could not be remediated with standard technologies. In a combined effort of the state, universities and consulting companies, process intensification resulted in new technologies to start the remediation of the area. In addition, the post-mining landscape will be converted to a tourist region in future.

The subsequent discussion about open pit lignite mining in Lusatia, Germany, are based on the following publications by Benthaus et al. (2020), Geller et al. (2013), Janneck et al. (2018), Kaden (1997), Luckner and Totsche (2017), Märten (2006), Merkel et al. (2005), Strzodka et al. (2013), Weber et al. (2019), and Wolkersdorfer (2021).

Lignite mined in Lusatia (Lausitz), southeast of Berlin, was the principal energy source of the former German Democratic Republic, with 200 Mt. mined in 1990 and a maximum of 1.2 km^3 of mine water pumped in 1985. A centralized, socialist planning regime prioritized lignite and energy production over environmental protection and left an area of 200,000 km^2 affected by mining, with a groundwater table lowered by up to 100 m and a cone of depression up to 13 km^3. After reunification, priorities changed in the 1990s, and the partly uneconomic opencast lignite mines slowly ceased, leaving only economically feasible mining in operation. Mine closure and a subsequent increase of the groundwater level filled the open pits. Today, remediation in the Lusatia area can be considered one of the world's largest lignite mining remediation projects with nearly 100 pit lakes being managed.

Most of the lignite is found under 20–80 m Quaternary sandy to clayey overburden which had to be dumped, mainly inside the open voids of the pits. As the coal and overburden contains pyrite, the ground and mine water quality substantially deteriorated with lower pH values around 2.5, sulfate concentrations up to 3 g L^{-1}, Fe up to 360 mg L^{-1} and Al up to 40 mg L^{-1}. While the groundwater level rose, the open pit mines (which can be considered windows to the groundwater) flooded, and some water courses suffered from ferrous, acid mine drainage. This, together with elevated sulfate concentrations, affected predominantly the river Spree, which feeds the Unesco Biosphere Reserve Spreewald (designation date 1991) and flows through the German capital Berlin, where it is, among others, used as infiltration water for drinking water production.

To remediate the negative effects of the acidic and mineralized mine water in the open pit lakes, numerous techniques were tested, but standard technologies were not able to tackle the problem reliably. Even using sludges from mine water treatment plants was tested for by-product recovery. Most of the preliminary treatment methods failed because of the very specific conditions in Lusatia. Obstacles for passive technologies incur high costs for the large areas needed, a reduced process control compared with active methods, and the vast volumes of mine water in Lusatia that would have to be treated passively. Nonetheless, less than a dozen passive systems were tested in the Lusatia area. Microcosms ($\approx$20 m^3) and macrocosms ($\approx$4500 m^3) in the lakes were successful only in or near the enclosures itself but could not cope with the whole lake volumes. Active treatment of all the mining influenced water was also not feasible because of the large water volumes. In addition, the mine water does not occur as point sources, but as diffuse flow through the overburden and waste materials to the lakes, streams and groundwater.

Finally, a twofold approach was initiated: (1) developing a lake landscape (Lausitzer Seenland: Lusatian Lake Land) such that it can be managed for touristic and environmental purposes; and (2) improving standard technologies that were not successfully mitigating the negative effects of the acid mine drainage, by optimizing a technology that was adapted from experiences in acid rain mitigation in Scandinavia in the 1970s: in-lake-neutralization. After initial issues with the lime, caustic soda, and limestone distribution in the lakes and finding the appropriate application technology, the remediation company developed a land and vessel-based application of neutralizing agents. During the early phases, it became obvious that in all cases of in-lake-neutralization, monitoring is important. Successful application and calculation of lime or limestone masses is only possible with a full understanding of the geochemical mechanisms in the water columns of the lakes.

So far, in 13 Lusatian lakes, with 4–6 to follow, in-lake-neutralization has been successful (Fig. 4). In all cases, the lakes' acidity substantially decreased while the alkalinity rose. pH values increased to around 7 and Al concentrations decreased to below the detection limit, as in the case of Lake Partwitz. Yet, in-lake-neutralization is not a clear or short-term solution, as it requires regular repetition as long as the pyrite oxidation in the overburden and waste rock persists and the acidic groundwater flows through the lakes.

Fig. 4 In-lake-neutralization in a Lusatian mining lake by means of the "Barbara" vessel. Inset: input system between the vessel's hulls. Source: LUG/LMBV.

Western Basin, South Africa

In the Western Basin of the South African Witwatersrand, active mine water treatment and a natural wetland are improving the mine water quality. It is also an example of lengthy discussions by various interest groups with highly variable scientific backgrounds.

The subsequent discussion about mining influenced water in the Western Basin of South Africa's Witwatersrand gold fields are based on publications by Coetzee et al. (2003), Digby Wells and Associates (Pty) Ltd. Co (2012), Frimmel (2019), Hobbs and Cobbing (2007), Liefferink and van Eeden (2010), Robb and Robb (1998), Shapi et al. (2020), Turton (2013), Wolkersdorfer and von Hünefeld-Mugova (2018), and Yibas (2020).

South Africa hosts the largest gold deposit in the world: the Witwatersrand basin, comprising nine gold fields of economic importance and covering an area of 400 km^2. Mining started in 1884 and is still ongoing. Though the production is in a decline since its peak in the 1960s, it is still the location where most gold was mined worldwide. In 2020 this was 53 kt, accounting for 30% of the world's gold production to date. In addition, the gold "reefs" are enriched in uranium, which was produced concurrently to gold in some of the mines, amounting to 75 kt. As most mines did not focus on uranium extraction, a large accumulation of uranium in the remaining and abandoned tailings dams along the current and former gold extraction locations remains. Currently, 270 mining residues such as tailings dams and waste rock piles are known, which—to a smaller or larger degree—contribute to the contamination of surface waters within the whole Witwatersrand basin. Due to the lack of buffering minerals in the tailings material, tailings release substantial amounts of acid, sulfate, (semi-)metals and suspended solids. Since mining in the three largest basins has largely ceased, groundwater is filling the open voids and gradually floods the abandoned mine workings. In June 2002, the first of these basins was fully flooded, and the Western mine pool started to overflow through borehole BH1 and the Black Reef Incline shaft into the receiving water course, the 10 km long Tweelopiespruit rivulet in the Mogale (Krugersdorp) Municipality, which originates at Robinson Lake west of Johannesburg. Though this discharge did not happen unexpectedly, as several experts where aware that this would happen since around 1996, authorities and decision makers reacted with astonishment, and a series of reports, political discussions, scientific papers and decisions began to tackle the negative environmental effects of this acid mine drainage discharge. This discharge of the West Wits Mine was especially problematic in two ways: (i) the Tweelopiespruit flows through the Krugersdorp Game reserve, leading to the Bloubankspruit; and (ii) then flows though the Unesco World heritage area "Fossil Hominid Sites of South Africa" (*vulgo* "Cradle of Humankind"). As the caves are within the dolomites of the Malmani Subgroup, there was concern that the acid mine drainage might dissolve the dolomite and therefore negatively affect the cave's integrity.

Initial monitoring of the 6–9 $m^3\ min^{-1}$ mine water discharge showed the water quality to be extremely poor, as would have been expected shortly after the initial stage of the first flush. Electrical conductivity was around 3.6 mS cm^{-1}, pH 3.4, sulfate 2.5 g L^{-1} and Fe as well as uranium concentrations reached 235 and 0.9 mg L^{-1}, respectively. Unaffected springs in this area would have electrical conductivities around 1 mS cm^{-1}, a pH of 6, sulfate 0.5 g L^{-1} and Fe of 0.1 mg L^{-1}.

On contact with the atmosphere, the mine water quickly oxidizes and hydrolyzes, resulting in a pH decrease downstream of the discharge locations. These processes stained the Tweelopiespruit with thick deposits of ochre and barite, substantially affecting aquatic life and the stream's appearance downstream of the discharge locations. As an operational mine (at that time Harmony

Gold) with a working water treatment facility was close to the discharge points, collection ponds and a pumping scheme to the mine water treatment plant were constructed. There, the acid mine drainage was treated in a neutralization process, which in a modified form is still ongoing today.

Based on numerous expert reports and pressure from the public, NGOS and politicians (sometimes with risk of supporting particular interests), it was decided to keep the water level at an "environmentally critical level" (ECL) of 167 m below surface. This is accomplished by means of a pumping scheme in the № 8 and 9 shafts and upgrading the existing mine water treatment plant to handle a volume stream of 18–22 $m^3\ min^{-1}$. Currently, this scheme, financed by the South African government's tax revenues, is maintained by Sibanye Gold.

Mine water treatment in this plant is a standard neutralization method with aeration, settling, liming and coagulation. From the mine water treatment plant, the mine water is pumped into a large, unlined sludge settling pond, and from there, by gravitational flow, discharged into the Tweelopiespruit. Further, it flows through 1.7 km of natural wetlands before it enters the Krugersdorp Game Reserve (Fig. 5). Though the mine water, after treatment, is still highly mineralized, with electrical conductivities between 3.0 and 3.6 mS cm^{-1}, the pH values in the stream substantially increased to circumneutral conditions. However, maintaining the treatment has been challenged by vandalism to the electricity system, and low maintenance of the plant. Most of the red stain in the Tweelopiespruit has meanwhile been flushed or is covered with gypsum precipitates that build up as long as the treated mine water is oversaturated in regards to gypsum. Additionally, the soils along the Tweelopiespruit still contain elevated concentrations of potentially harmful elements originating from pre- and post-flooding times. Flow in the Tweelopiespruit is highly variable between 3 and 50 $m^3\ min^{-1}$, being a function of pumped mine water and rain events. As the pumping rate in the № 8/9 shafts is not at a constant rate, the mine water table is substantially fluctuating. This causes a large beach in the mine water pool, which constantly causes pyrite oxidation and represents the main source of contaminants for the mine water. In addition, the mine water body is stratified, with a better water quality on top of mine water with a worse quality. Pumping at excessive rates, therefore, decreases the water quality as bad quality water reaches the pumps.

In consequence, though the water quality in the Tweelopiespruit has improved since 2002, water treatment must continue for a long time until the first flush phase is over, and the water table can be kept at a more constant level. Eventually, keeping the mine water level at the ECL in № 8/9 shafts can cease as there might be no immediate danger to the dolomite caves, and mine water with a better quality can be treated and discharged into the Tweelopiespruit. This will result in near natural pH values and a low mineralization, resulting in a recovery of the natural ecosystem.

Kizel Coal Basin, Russia

Russia's Kizel Coal Basin is an example of environmental pollution resulting from a policy that considered economics being more important than environmental protection. It is also an example of some individuals trying to improve the situation, and of a policy change that now tries to remediate the environmental impacts of the past.

For the following discussion about the Russian Kizel Coal Basin in the Ural Mountains, the following English and Russian publications have been used: Berezina et al. (2018), Blinov and Krasilnikova (2019), Imaykin (2014), Khayrulina et al. (2016), Maksimovich et al. (2019), Maksimovich and Pyankov (2018), Maximovich (2008), Maximovich et al. (1995), and Pyankov et al. (2021).

One of the largest areas in the Ural Mountains polluted by acid mine drainage is the Kizel Coal Basin. This coal basin is part of three river basins: the Yayva (with the North Vil'va and the Bol'shoi Kizel tributary), the Kos'va, and the Chusovaya (with the Us'va and the South Vil'va tributaries) basins. All these rivers are tributaries of the Kama river basin, and the area has an average annual rainfall of 800–900 mm. Various coal mines were worked from 1796 until mining terminated in the early 2000s and covered an area of 2000 km^2 with a north–south extension of 100 km and a width of 15–20 km. After mining ceased, the groundwater table in the more than 1000 m deep underground mines rose gradually until the mine water discharged to the surface and into the receiving water courses. These discharge locations have pH values between 2.3 and 4.5 with an average discharge of 15–25 million m^3 and a maximum of 75 million m^3 annually. More than 100 waste rock piles and tailings ponds (50 million m^3 of material) contribute to the pollution with a drainage mine water volume of 32 $m^3\ h^{-1}$. Approximately 90% of this water draining the waste rock and the abandoned mines discharges into the receiving water courses, and in some cases the mineralization is up to 35 g L^{-1}. Currently, there are still 19 mine water discharges and more than 100 waste rock and tailings piles contributing to the pollution load.

Geologically, the Kizel Coal Basin is highly karstified, which resulted in large ingress volumes during the active mining period. It is assumed that annually $\approx$100 million m^3 of acid mine water was discharged into the local streams without any treatment, causing substantial damage to the ecosystems.

Source for the acid mine drainage is the pyrite in the coal seams which reached up to 9%. Its oxidation resulted in highly acidic mine waters with low pH values, and of the 26 ions and elements found with elevated concentrations, 12 show 10–1000 times higher concentrations than the local background. On average, the Bol'shoi River receives annual sulfate loads of 15,300 t, an Fe load of 6000 t, Al of 400 t and Mn 57 t. These mine waters change the type of the natural rivers from HCO_3-Ca to SO_4-HCO_3-Ca when the mineralization is 700–760 mg L^{-1} and SO_4-Fe-Al-Na-Ca in cases where the mineralization goes up to 3–35 g L^{-1}. Many of the receiving water courses are covered by thick layers of precipitates (ochre) and, therefore, cause substantial smothering of stream beds and local biota (Fig. 6). In many locations, acid-tolerant green algae give indication of the low pH values and the high metal and acidity concentrations. In some of these locations, the soil's pH is around 3 and prevents most plants from growing.

Fig. 5 Abandoned flow gaging station at the end of the natural wetland area of the Tweelopiespruit. Corrosion from the initial acid mine drainage and gypsum precipitates from the treated mine water can be seen at the flow gages' outflow. Photograph: Christian Wolkersdorfer.

Fig. 6 Thick ochre precipitates from acid mine water discharging from an abandoned mine in the Kizel Coal Basin. Photograph: Christian Wolkersdorfer.

After the breakdown of the USSR and the closure of many of the mines, it was found relevant to remediate these heavily polluted areas. Using SPOT-6 and LANDSAT-8 satellite data as well as sampling around 200 sites, provided identification of biologically inactive stream sections. Geochemical and GIS (geographical information system) modeling identified the priority locations for environmental protection activities, which will help to decrease the negative effects of the acid mine drainage by about 40%. It is anticipated that the mine water will be treated by means of active and passive mine water treatment systems. First on-site tests showed that some of the acidic soils can be reclaimed with limestone, selected plants, and grass mixtures. By doing so, acidic soils as

well as acid mine water discharges could be successfully remediated. Other remediation methods planned are geochemical barriers (better known as reactive walls), which modify the groundwater's composition before it reaches the rivers. Yet, it will take decades until the severe pollution and damage to the rivers in the Kizel Coal Basin will be remediated and a close to natural condition will be restored.

Mariana and Brumadinho Dams, Brazil

Both the Mariana and Brumadinho tailings dam failures exemplify the importance of reliable measures to contain ore processing residues. They show how ignoring geotechnical principles and state of the art technologies can result in accidents with severe ecological and social negative effects on the surrounding areas and downstream water courses.

Introduction

Brazil holds more than 800 mine tailings dams, of which about 400 are classified into some category of accident risk (Agência Nacional de Mineração (ANM), 2021). Most of these tailings dams are located in Minas Gerais State, which is a metal-rich region and has a long history of land use focused on extensive mining activities (Jacobi et al., 2011; Hatje et al., 2017). This State also holds the largest number of mine tailings dams in Brazil rated as high accident risk (Agência Nacional de Mineração (ANM), 2021), posing a severe potential threat of both social and environmental disaster (Nazareno and Vitule, 2016; Kamino et al., 2020; Azevedo-Santos et al., 2021).

Fundão Dam, Mariana

In November 2015, the Fundão tailings dam broke in the Bento Rodrigues District, Mariana City, Minas Gerais State. About 43 million m^3 of iron mine wastes were released into the Doce River basin. This spill is considered one of the world's largest mining environmental disasters. Individual mud waves reached a height of 10 m, and the tailings deposit layers were between 50 cm and 3 m thick. During the spill, the Bento Rodrigues District was partly buried by the mudflow, and its entire population of approximately 600 people displaced. The mudflow traveled 668 km along the Doce River, before reaching the Atlantic Ocean approximately 15 days after the dam ruptured (Escobar, 2015; Carmo et al., 2017; Fig. 7). This toxic mudflow polluted drinking water and decimated the aquatic fauna of the Doce River, also affecting the soil and flora of floodplain areas (Lambertz and Dergam, 2015; Garcia et al., 2017).

The most striking short-term negative effects caused by the tailings were siltation of entire rivers, changes to channels and river dynamics (i.e., the interactions among flow, sediment transport, and morphology), spread of chemical compounds, and the destruction of terrestrial and aquatic ecosystems (Fernandes et al., 2016; Garcia et al., 2017). This disaster resulted in water contamination and caused the death of entire fish, amphibians, mammals, turtles, birds, and invertebrates populations (Lopes, 2016; Carmo et al., 2017). Long-term effects include increased metal concentrations in the sediment, toxic effects at different trophic levels, metal accumulation in fish muscle tissue along with cytotoxic, genotoxic and mutagenic effects, and in water and sediment (Vergilio et al., 2021). In addition, the tailings led to vegetation loss and damaged several protected areas (Lopes, 2016; Carmo et al., 2017). This severe accident killed 19 people, affected several down-stream municipalities and hundreds of thousands of people (including Krenak and Guarani indigenous tribes), caused the loss of natural and cultural heritage, increased the exposure to toxic elements (mainly arsenic, mercury and lead) and impaired the local economy (Fernandes et al., 2016; Carmo et al., 2017; Valle, 2020; Koppe, 2021).

Fig. 7 The toxic mudflow in the mouth of the Doce River reaching the Atlantic Ocean in Regência, Espírito Santo State. Photograph: Hauley Valim.

This mining disaster is still causing negative ecological and socio-economic effects because adequate tailings removal was either inefficient or not carried out at all. One year after the dam rupture, about 0.17 million m^3 of tailings were cleaned from affected areas, and after 3 years, about 48% were removed (Carmo et al., 2017; Cionek et al., 2019). Yet, the long-term effects of the spillage must be accounted for, and the environmental recovery of areas affected by tailings will take a long time.

This tailings dam failure could have been avoided if proper maintenance of the dam and surrounding areas had been performed. Mine residue dams require constant maintenance, aiming to reduce the likelihood of leaks or dam failures, and minimizing ecological and social damage (Sergeant and Olden, 2020). In addition, multidisciplinary efforts and investments should be periodically dedicated to rigorous inspection, monitoring, and environmental licensing (Cionek et al., 2019). A potential solution to the waste in mine dams could be dry stacking, which causes less environmental impacts compared with current tailings storage (Gomes et al., 2016). Another important strategy in tropical environments should be the construction of tailings ponds and infrastructure resisting large influxes of water (i.e., tropical storms rainfall; Edwards and Laurance, 2015).

Córrego do Feijão Dam, Brumadinho

In January 2019, the B1 Dam at the Córrego do Feijão Mine ruptured in Brumadinho City, Minas Gerais State. This disaster spilled 12 million m^3 of iron mining waste, with 10 m high mud waves, spreading for 10 km and reaching the Paraopeba River, a major tributary of the São Francisco River (Fig. 8).

Shortly after the dam ruptured, the mudflow hit the mining company buildings, as well as hotels and farms in the region, killing more than 270 people (Olden et al., 2019). Severe negative short-term effects on water quality and sediments of the Paraopeba River resulted from this toxic mudflow, including an increase in water turbidity, high metal and nutrient concentrations, increase in iron tolerant bacteria, toxic effects at different trophic levels, and metal accumulation in fish muscle tissue, requiring future studies to monitor the long-term consequences in this river (Thompson et al., 2020; Vergilio et al., 2020). This disaster jeopardized the water supply of cities in the surrounding area and affected fish and bird species (Pereira et al., 2019; Salvador et al., 2020). The spill of the tailings caused a major change in land cover, severe loss of Atlantic Forest vegetation, and impaired agricultural areas (Pereira et al., 2019; Rotta et al., 2020).

Post-disaster actions following the Brumadinho dam rupture were conflicting. A study reported that the mudflow reached the Retiro Baixo Hydroelectric Dam (302 km downstream from the collapsed dam, in the Paraopeba River), while another study reported that the mudflow reached the Três Marias Dam's reservoir (around 330 km from Brumadinho, in São Francisco River; Salvador et al., 2020). In addition, a controversial action was proposed by the Brazilian National Water Agency (Agência Nacional de Águas e Saneamento Básico, ANA), which planned to use the Retiro Baixo Hydroelectric Dam to prevent the spread of mine tailings; however this strategy has been considered ineffective in restricting the environmental and social damage along the tailings' travel path (Hatje et al., 2017; Cionek et al., 2019).

Upstream tailings dams like that in the Córrego do Feijão Mine are cheaper, occupy smaller areas, and require less material for construction than other tailings dams, since new tailings are accumulated on top of previous deposits (Kossoff et al., 2014; Rotta et al., 2020). However, this tailings dam model is considered highly risky, mainly due to the potential of static liquefaction, a process in which solid materials behave like liquids, which can trigger the dam's collapse (Kossoff et al., 2014). Brazil's National

Fig. 8 Mudflow from the collapse of the B1 Dam at Córrego do Feijão Mine, Brumadinho City region, Minas Gerais State, a tailings dam failure that caused severe social and environmental impacts. Photograph: Isis Medeiros.

Mining Agency (Agência Nacional de Mineração, ANM) planned to ban upstream tailings dams after the Córrego do Feijão Dam collapse in Brumadinho (Spring, 2019). The collapse of the Brumadinho Dam was a major global warning of the risks posed by unsafe, rudimentary, and antiquated mining dams (Koppe, 2021). Every mine is unique in terms of its geography, physical setting, or environmental context. Nevertheless, only with science-based safety guidelines and stricter enforcement, can the chances of repeating a disaster like this be minimized (Olden et al., 2019).

Technological improvements, and the future of mine tailings dams

Emerging technologies, while expensive, have some promising alternative solutions, that include approaches such as paste and thickened tailings, tailings reuse, recycling and reprocessing in combination with proactive management in a way to combine the separation of sulfide by flotation and the use of cemented paste backfill as soil support. For instance, novel mine tailings are usually stored above ground or in impermeable plastic casings below the surface, which make them less likely to seep into the ground and contaminate groundwater and adjacent watercourses (Edraki et al., 2014). Alternatively, wetland integrated systems are easy, affordable to build and relatively low maintenance alternatives since they are efficient in regions that do not have too cold winter months.

After these two mine tailing dam disasters, the Brazilian Government has decided to decommission all mines with upstream characteristics similar to the Fundão and Córrego do Feijão Dams. This decommissioning would involve removal of the wastes deposited in the tailings dams, construction of new dams or transportation to preexisting dams to accommodate them, and finally their inactivation. Nevertheless, this change represents a challenge in terms of time, investments and efforts required to do so. Undoubtedly, the environmental impacts and human toll were high for Minas Gerais State, for companies and the regions involved as a whole.

Conclusions

Mining activities and residues such as tailings or mine water can cause substantial negative effects to inland waters. One of the most noticeable and destructive, but fortunately rare accidents, are tailings dam failures which often impair socio-economic balances, along with regional pollution that damages both aquatic and terrestrial ecosystems. Less obvious is the pollution caused by mining influenced water, although iron rich mine water often visually impairs water courses. Solutions to these effects on inland waters and the ecosystem would be mining bans in sensitive regions or more stringent control measures.

All case studies show negative effects on the surrounding environment, sometimes hundreds of kilometers from the mine site. Though some of them can be corrected, some of them will last for a very long or indefinite time. It can be concluded that reliable and sustainable treatment options, state of the art mine residue storage or encapsulation and stringent monitoring, as well as legislative measures and enforcement are necessary for environmentally safe operations.

Knowledge gaps

One of the main knowledge gaps in the mining context is how to prevent environmental pollution or loss of life under all circumstances. Yet, as long as humans are involved in the processes, mistakes, misinterpretation or negligent behavior cannot be fully avoided. Though substantial research has been done after the Aznalcóllar and Baia Mare tailings dam failures (e.g., Hernandez et al., 1999; Macklin et al., 2003), how nature recovers from these types of events still remains unclear and requires further research. It is also not well-known which methods can be most effective to assist the recovery of the freshwater and terrestrial ecosystems that are affected.

More research is needed in sustainable mine water remediation techniques. This is especially relevant when considering the economic cost/benefit of recovery of valuable material from the mine water including the circular economy aspects of mining and the interplay with mine water issues. Treatment options that selectively recover metals or semi-metals would be able to partly assist in the remuneration of the costs incurred. Moreover, digital twins of active and passive mine water treatment systems are not available so far. Finally, artificial intelligence or machine learning is required to optimize mine water management and help in adjusting to future scenarios. Detailed studies into the micro- or small-scale effects of mining influenced water or tailings dam failures on the local or regional economy as well as the social structure are only rarely conducted.

Acknowledgments

CW & EM acknowledge our colleagues Altus Huisamen, Stephanie Lohmeier, Nikolai Georgievich Maksimovich, Cherie McCullough, Jesús Montero, Maria Almudena Ordoñez Alonso, Carlos Ruiz Cánovas, Oliver Totsche, and Anne Weber for commenting on early versions of this section. VSD, PC & JRSV thank Fabrício de A. Frehse for assistance in finding suitable photographs, Hauley Valim for letting us use his photograph for Fig. 7 and Isis Medeiros for providing her photograph for Fig. 8.

See Also: Human pressures and management of Inland Waters: Effects of Mining on Surface Water; Constructed Wetlands for Urban Wastewater Treatment: An Overview

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Physical Impacts of Sand Mining in Rivers and Floodplains

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Alluvial deposit Material deposited by rivers. It consists of silt, sand and gravel, as well as much organic matter.
Bar skimming Mining method which consists in removing all the material in a sand bar above a reference line.
Braided river River which consists of a network of river channels separated by small, often temporary, islands called braid bars.
Delta Landform created by deposition of sediment that is conveyed by a river as the flow leaves its mouth and enters an ocean, sea, lake or reservoir.
Floodplain Area adjacent to a river, formed mainly of river sediments and subject to flooding.
Mining pit Excavation or cut made at the surface of the ground for the purpose of extracting mineral (e.g., sand).
Mud blanketing River process by which high concentrations of silt and clay may end up covering river landforms.
Nick point Part of a river or channel where there is a sharp change in channel slope.
Pool Deep areas of a river where water runs slow.
Riffle Shallow area of a river where water runs fast and is agitated by rocks, gravel or coarse substrate.
Sand Fragments of rock and soil with a specific grain size in between 1/16 mm and 2 mm. It is thus finer than gravel and coarser than silt.
Sediment regime Term used to refer to the sediment budget (amount, type and timing of sediment inputs, transport, storage and outputs) of the river system as well as the way water and sediment interact to drive river conditions.
Sediment transport capacity Term used to define the maximum load of sediment that a given flow rate can carry. It is referred to as net erosion or deposition, respectively, when the actual sediment load is below or above the transport capacity.
Sediment General term used to refer to mineral particles, which have been created by the weathering of rocks and soils and transported by natural processes, such as water and wind. Sediments include, in order of decreasing size, boulders, gravel, sand and silt. *Particulate matter* is sometimes used as a synonym of *sediment*. However, this is often not considered in the topic of sand mining.

Introduction

Sand is used massively in construction, as well as for other applications such as glass production and electronics manufacturing. As a result, sand mining has become an expanding business due to the rapid population growth. Globally, humans consume up to 25 billion metric tons of sand every year, equivalent to 9 kg per person per day (Koehnken and Rintoul, 2018).

Sand is primarily removed from alluvial deposits (see Fig. 1). This extraction is carried out either from instream mining or from excavation pits in river floodplains. Instream sand mining consists of extracting sand directly from river bed. Removal of bed sediment is normally carried out by two common methods: pit excavation and bar skimming (see Section "River channel" for further details). Excavation pits in river floodplains are in turn defined as dry or wet pits, depending on whether the depth of the excavation crosses the groundwater table (wet pit) or not (dry pit).

Fig. 1 Sand mining activities at Borkena River, Ethiopia (left, center) and a truck of sand extracted from wetlands of Lake Victoria (Uganda) for construction in Kampala. Credit to K. Irvine.

Sediment deposited in alluvial deposits is composed of gravel (diameter from 2 mm to 256 mm), sand (diameter from 1/16 mm to 2 mm) and silt (diameter less than 1/16 mm). Alluvial sediment is particularly desirable in construction because weak materials are eliminated by abrasion and resulting particles are durable, clean of impurities (washed by fresh water) and with irregular shapes that bind well with cement. Gravel is also mined since it is a key mineral used in the construction industry, but not to the same degree as sand. Uses of sand go beyond construction and span multiple manufacturing processes.

Despite the well-known impacts of sand mining on river morphology and sediment transport, this significant environmental problem is mostly ignored by policy makers and, to a large extent, unknown by the general public (Koehnken and Rintoul, 2018). In the following section, we outline the main impacts derived from sand mining.

Role and importance of sediment in fluvial systems

The sediment particles (gravel, sand and silt) are important for ecology, safety, economic and societal functions of rivers. They are drivers of landscape change and ensure a coherent continuum of mineral, chemical and biological components along river valleys. This continuum constitutes the sediment regime or budget in terms of amount, type and timing of sediment inputs, transport, storage and outputs, as well as the way water and sediment interact to determine river conditions (Wohl et al., 2015). Any disturbance of sediment regime is of potential concern as it affects a broad range of river functions and management, primarily: (i) flood control: varying grain size distribution of the river bed results in a change in roughness, which can have notable impacts on measured and estimated water levels; (ii) lotic system: changes in the fluvial sediment supply result in a change in river bed variability and composition which can have positive or negative impacts on the species populating river reaches; (iii) river restoration/rehabilitation activities: the understanding of the sediment transport dynamics of the restoration reach is a crucial factor for successful design of restorative measures; and (iv) hydropower production: changes related to the sediment regime have an impact on the management actions of reservoirs (e.g., reservoir siltation).

River channel

River forms and river processes are deeply affected by changes in sediment regime. Extensive instream mining cause a major disturbance of the sediment regime. As a result of the sediment removal, the natural sediment continuum of the river, along with channel morphology and instream bed forms are altered (Kondolf, 1997).

Instream removal from the channel bed disrupts the river reach sediment balance at the local scale, but the impact can also extend both up and downstream from the point of extraction. Removal of bed sediment is normally carried out by two common methods: pit excavation and bar skimming. The choice of which type of sediment removal that occurs is dependent on the nature of the river channel and the opportunity, or ease, of extraction. In both cases, an imbalance is created between sediment supply and transport capacity due to mining activity that is propagated downstream, upstream or in both directions.

Excavation pits generate local incisions with steep slopes (see Fig. 2). At the upstream edge of such pits, the slope accelerates flow, leading to an increase of shear stress and sediment transport capacity. This area is called the nick point. Each nick point evolves moving upstream due to river erosion to adjust to the base level (Knighton, 1984; Kondolf, 1998). Thus, with a steady flow, a series of nick points can be generated that migrate upstream from the initial bed incision. Excavation pits act as sediment traps for much of the incoming sand supply. Thereby downstream of these pits, there is insufficient sediment load, and the river sediment transport capacity can only be satisfied with the sediments eroded from the bed. River erosion and resulting bed degradation, therefore, occurs upstream and downstream of the pits.

Bar skimming (or scalping) mining consists of removing all the material in a sand bar above a reference line. This widens the river channel and consequently, slows the flow velocity causing upstream sediment supply to be deposited locally in the mining area. Downstream, the flow arrives with a sediment load deficit and compensates by eroding material from the river bed. Ultimately,

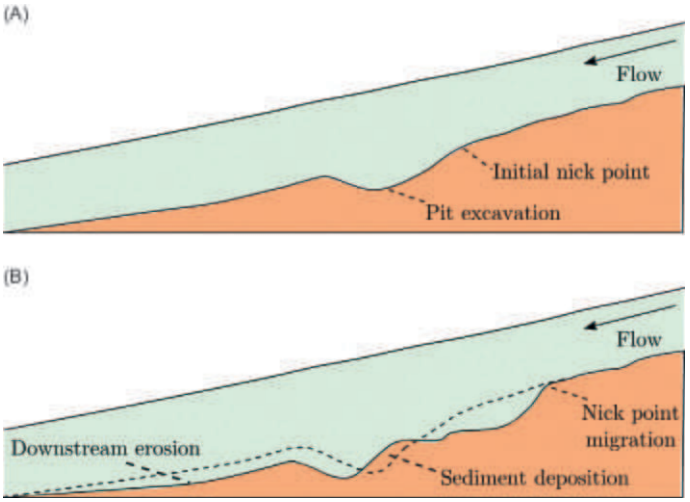

Fig. 2 River bed erosion due to pit excavation for sand mining. (A) Pit excavation causes the formation of a nick point. (B) The continuous shear and sediment transport capacity of the river flow forces the nick point to migrate upstream. The pit is partially filled with incoming sediments. A sediment supply deficit occurs in the downstream part and sediment transport capacity is satisfied with the material eroded from the river bed.

this leads to severe bed incision. In addition, bar skimming causes other problems such as lateral channel instability, bank erosion and bank retreat, abrupt modification of the floodplains, and higher mobility of loosened sediments (Kondolf, 1998).

In braided river systems, the combination of the two river processes derived from sand mining, bed incision and lateral widening, may lead to the formation of a unique deep channel. Former lateral active channels and gravel bars may quickly be colonized by thick vegetation, leading to the formation of stable islands in the former braided area and thereby, supporting the stability of the new river channel layout (Padmalal and Maya, 2014).

River sediment granulometry

Sand mining activities selectively remove medium to very fine sands, which are the ones used in the construction, glass and electronics industries. Over time, the river reach experiences changes in the granulometry characteristics of the sediment material. The river bed at the mining site suffers coarsening as a result of the selective removal of fine particles (Knighton, 1984; Kondolf, 1998; Padmalal and Maya, 2014). This reduces habitat complexity and riffle-pool structures, directly affecting ecosystem structure and function. This can alter ecosystem processes and the prevalence and distribution of vegetation, fish and benthic communities.

The granulometry of the river bars is also affected by sand mining since the natural sediment sorting is abruptly altered and only the larger (cobbles and pebbles) and the finer sediment particles (silt and clay) remain. High concentrations of silt and clay transported downstream may end up covering sand bars (*mud blanketing*), leading to the permanent stabilization of these river forms by fostering vegetative growth.

The process of size-selective mining facilitates the formation of sediment laden plumes of fine material, that travel and deposit downstream, potentially clogging the river bed (and thus, making it unsuitable as habitat for many organisms, see, e.g., Owens et al., 2005) or reducing the channel conveyance (and thus, increasing the risk of flooding, see, e.g., Kemp et al., 2011). Sediment plumes reduce the depth of light penetration in rivers, which in turn reduce algae and aquatic vegetation growth in slower flowing rivers, typically in the downstream reaches.

Floodplains

Excavation of instream pits near floodplains causes the alteration of the natural course of rivers. The continuous removal of sand, systematically enlarges the size of the pits, ultimately reaching the river bank causing collapse. As a result of this, river banks recede and the river channel is widened, modifying the local hydraulic and morphological conditions of the river reach (Juez et al., 2019). The receding of river banks and the widening of river channel causes the lowering of the water level, and eventually the lowering of the groundwater table. This has implications for local human communities who rely on these water resources. A lower groundwater table also has negative implications for the vegetation covering the floodplains, where meadows and trees may dry out, and thereby deprive biota of cover, shade, nursery areas or supply of food. This can have an important effect on the whole floodplain ecology, modulating the production for fish and other animals that use the floodplain as part of their production cycle.

Dry sand mining on floodplains can also impact the natural course of rivers. This mining method consists of excavating deep pits near river channels. The pits may be flooded during high river flows, causing them to be completely eroded, and thereby creating a

permanent alternative river channel. Sometimes, the flooded pit is partially eroded and remains disconnected from the main channel, creating a stagnant water body. Dry sand mining on floodplains may also have an impact on the groundwater table. Pits are pumped dry to guarantee access to the sand resource. Thereby, if the pit is deep enough to intercept the groundwater table, the steady pumping may alter aquifer dynamics (Padmalal and Maya, 2014).

Built infrastructure

As highlighted above, sand mining activities can cause channel degradation up or downstream from the mining activities, resulting in damage to infrastructure. This may include bridge piers being undermined, or buried pipelines, intake structures for dams or irrigation channels becoming exposed. In some parts of South East Asia, numerous irrigation structures and wells used for extracting water for human and animal consumption have been abandoned because of the lowering of the river bed and consequently, of the river water intake level (Padmalal and Maya, 2014). In addition, sand removal at sites close to the sea, facilitates the saline intrusion into freshwater channels, leading to problems of corrosion in the existing infrastructure, and changes to biotic communities.

Water quality

Continuous resuspension of sediments due to removal of instream sand have an impact on river water quality at the mining site and downstream. These sand mining activities lead to an increase of turbidity in the main channel, which can hinder fish visibility, thus impairing visual feeding behavior, and fish spawning by clogging the downstream river reaches, causing zoobenthos scouring (Sternecker et al., 2013; Blettler et al., 2015). Human populations living downstream of the mining site may have to address increasing water treatment costs due to the high concentration of suspended sediment.

Nutrients and other pollutants are often attached to the sediments. Due to the high concentration of sediment in suspension, and consequently, the high concentration of nutrient content, the ecosystem of river reaches located downstream mining sites may be altered by the proliferation of vegetation and other living organisms. For instance, sand excavation process may release large quantities of nutrients from the sediment and promote eutrophication, giving rise to increasing growth of benthic macrophytes and algae, and associated biofilms. When nutrient enrichment from sediment mining affects downstream lakes this can manifest as algal blooms (Zou et al., 2019). Furthermore, alterations in the incoming rate of nutrients attached to the sediments may cause the arrival of invasive species, as new conditions can be more suitable for exotic plants than for native plants (Zou et al., 2019).

Sediments can fix pollutants, reducing their bioavailability, i.e., they become contaminated sediments (SedNet, 2004). During sand mining activities, oil spills and oil leaks from excavation heavy machinery and transportation vehicles, can occur. As a result, these pollutants can be adsorbed by sediments and conveyed downstream by the river (this is especially relevant for hydrophobic pesticides, such as endosulfan, see, e.g., Weber et al., 2010). Contaminated sediments can be transported by the river flow, acting as a potential source of pollution to surface water and groundwater, and need to be handled with special techniques (SedNet, 2004).

Riparian environment

Extensive areas of farmland, timber reserves and natural habitats are lost from riparian-areas due to the excavation of pits for sand mining (Koehnken and Rintoul, 2018). Degraded habitats near rivers result in the drop of number and type of fish, loss of biodiversity and loss of leisure potential. The destruction of the soil profile, leads to heavy impact above of surface water levels, and below the river bed on the groundwater table, resulting in the reduction in biodiversity of both aquatic fauna and flora. The disappearance of natural vegetation and trees near the river banks can increase water temperature (lack of shadows, see, e.g., Ptak et al., 2019) as well as limit the woody debris-supply to the water body, important for instream habitats (Wyżga et al., 2009; Nagayama and Nakamura, 2010). Finally, sand mining requires heavy excavation machinery, transportation vehicles and the construction of routes to the site. These activities generate a lot of noise and other disturbance, expelling away local birds and terrestrial animals (Padmalal and Maya, 2014).

Deltas

Rivers convey sediments from the hill slopes to the low hills and further downstream to lakes, and ultimately to deltas, seas and oceans. From the vast quantity of river sediments supplied to the coast, only a fraction of this material settles in the estuarine environment. Most of the finer material, clay and silt, travels offshore where it eventually deposits. In contrast, most of the sand fraction remains in the coastal areas and is moved by currents and waves, thus delivering material to the deltas and beaches. Sand mining activities may reduce the volume of sediment conveyed by the river and supplied to the river delta and coastal zone (Jordan et al., 2019). Due to this deficit in the sediment supply, deltas can erode and degrade, reducing their capacity as highly productive agricultural areas. Furthermore, deltas and coastal areas play an important role as a natural defensive system against storms and extreme weather events. Degradation of delta areas can lead to an accelerated erosion of dune systems, thereby increasing the risk of devastating flooding events for local communities (Sumi and Hirose, 2009).

Management and mitigation strategies

Important environmental and socio-economic impacts are caused by sand mining activities. Therefore, it is important to protect rivers courses and water resources by following guidelines that regulate and control sand mining activities. To this end, several management and mitigation strategies can minimize the related impacts identified above. In the following we briefly outline these:

- Reinforce national Water Resources Policy to protect the river environment, control illegal sand mining activities and instigate sand auditing initiatives.
- Develop and implement public awareness programs about the potential environmental impacts from increasing demand for sand.
- Introduce a sustainable extraction of river sand policy. Field campaings should be carried out to monitor and assess site specific flow and sediment regimes. It could be possible to determine the volume of sediment that could be sustainably removed within the variability of the sediment load of the river and without jeopardizing the integrity of the river reach (Rempel and Church, 2009).
- To carry out pre-sand and post-sand mining baseline survey at both the local and river basin scale to audit the exact volume of sand removed from the river bed.
- To prohibit sand mining activities during periods of high biotic activity, such as fish migration or fish spawning period.
- To introduce a recycled concrete policy in construction. This strategy could serve to reduce the global demand of sand.
- To replace the sand with other materials for the construction industry. There are currently a number of initiatives which pursue to re-use organic (e.g., walnut shell) and non-organic wastes (e.g., rubber tyres, ashes or plastic waste) as aggregates in concrete production.

Knowledge gaps

Major knowledge gaps relating to impact from, and management of sand mining are:

- Research in rivers where in-stream sand mining is active is required to enhance understanding and quantification of impacts.
- Further exploration of new management and remediation strategies for rivers.
- Research into economic factors that can help local communities to carry out sustainable sand mining activities.
- Technical opportunities to replace the sand with other materials for the construction industry, better recycling for a more circular economy of construction materials, and their economic feasibility under consideration of internalized environmental impacts.

See Also: Human pressures and management of Inland Waters: Emerging and Less Commonly Recognized Chemical Contaminants: Organic Micropollutants

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Further reading

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Relevant website

https://spatialagent.org/Sedimentation/—World Bank On line Guidance Tool to Sediment management.

Sediment Mining: Development and Implementation of Policies

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Aggradation Sediment deposition that raises the level of the stream channel or land surface.
Aggregates Granular materials for construction, mostly extracted from marine, river and lake water bodies.
Balanced sediment regime A balance between sediment supply and transport capacity that maintains specific physical processes and forms within the river corridor.
Sustainability The ability of ecosystems to remain diverse and productive; in a physical context, may refer to the ability of a system to continue functioning or providing natural resources.
Terrace (river) A former channel or floodplain surface now elevated above contemporary flood levels as a result of continued deposition on the floodplain or incision by the active channel.
Thalweg The line of lowest elevation within a river; the line of the fastest flow along a river channel.

Introduction

This chapter introduces sediment mining in rivers as a significant environmental issue and highlights pathways to sustainability through integrated river basin management. The chapter presents biophysical impacts of sand mining on rivers in terms of biophysical, ecologic and socio-economic impacts, discusses current management approaches, and highlights the critical aspects that need to be addressed for sustainable sediment extraction. To this aim, an approach adopted within the European Union (EU) is presented, and its transferability to very different contexts discussed.

Sand mining: A global problem

Sand and gravel are an essential resource for ecosystems, and for socio-economic growth. Freshwater aggregates, i.e., granular materials derived from rivers and lakes, are the preferred material, particularly for mixing concrete. Compared with aggregates sourced from the ocean or terrestrial sources, freshwater aggregates are clean, of desirable physical properties, and have low costs of processing and transport. Marine sand has to be processed to remove corrosive sodium salts that can undermine structure stability, although it is commonly used for reclamation. Rounded desert sand has undesirable mechanic properties in a concrete mixture. In all cases, the environmental costs of aggregate mining are rarely internalized and accounted for in relevant decisions on alternative locations or materials. Therefore, such activity is still profitable and widely practiced, especially in growing economies (e.g., Bravard et al., 2013; Hübler and Pothen, 2021; Beiser, 2018), whereas its sustainability is not yet ensured by current regulations (e.g., Bendixen et al., 2021; Torres et al., 2021; Hackney et al., 2021).

The dimensions of the phenomenon and its effects are immense: sand and gravel constitute the highest volume of material extracted worldwide (e.g., UNEP, 2019; Cooper et al., 2018; UN Comtrade, 2020), at a rate by far exceeding the renewal rate (e.g., UNEP, 2014). Extraction of sand is projected to double by 2060 due to the increasing demand (OECD, 2019), with likely severe impacts on ecosystems, and serious implications for sand supply for human activity that pose risks for economic activity and social conflicts (e.g., Hübler and Pothen, 2021; Beiser, 2017).

The problem is complex and needs to be addressed at several levels (UNEP, 2014): (a) reducing consumption and providing incentives for alternatives; (b) reducing the impacts of mining through scientifically based planning; and (c) regulating aggregate extraction from national and international water bodies. For the purposes of this chapter, the last two aspects, related to freshwater sediment mining, are addressed.

Sand mining in rivers

Aggregate mining (commonly referred to as "sand mining") in rivers is the activity by which sediments (gravel and sand deposits) are extracted from river channels, floodplains or terraces (Sear and Archer, 1998; Kondolf, 1994a). Aggregates can also be a side product of mining for precious metals in river sediments (placer mining).

River sediment mining activities can be classified according to locations (river channel, floodplain or terrace) and technique of extraction. Three main mining techniques for (river) in-channel mining and their relation with water table can be identified (e.g., Kondolf, 1994b; Kondolf et al., 2001): (a) dry-pit mining, in ephemeral streams, by e.g., bulldozers; (b) underwater wet-pit mining, by e.g., dredges; (c) bar skimming, by scraping off the top layer from a gravel bar, above water level (Fig. 1). Alluvial sediments are also extracted from adjacent floodplains and older terrace deposits (and from tributary lakes). The extraction of sediments can occur at an industrial scale, with heavy machinery, or as artisanal informal mining, using hand tools. The impacts of both approaches can be comparable, as artisanal mining can involve up to a thousand people working on the same river site concurrently (Cordy et al., 2010).

Often, sediment budgets of rivers are already heavily impacted by human interventions, for example, the trapping of sediment in dams already leads to a downstream reduction in sediment transport. Sediment mining compounds those effects. In natural conditions, rivers often have aggrading reaches, where sediment accumulates temporarily as it moves through a river system (Schmitt et al., 2017). Aggradation can be emphasized by certain management actions, e.g., flow diversions which reduce discharges in rivers or increased sediment supply from land use change and mining. Such anthropic aggradation can create problems for flood protection, navigation, and water infrastructure and sediment removal and subsequent use can be used for temporary mitigation. Similarly, excess sediment accumulated in reservoirs might be suitable for human uses. Lastly, rivers are often incised because of upstream sediment trapping in dams, thus disconnecting the river from its original floodplains. In some cases, artificial lowering of the floodplains (e.g., Dufour and Piégay, 2005) has been used to restore lateral connectivity, while selling the removed material to set-off parts of the costs.

Effects of sediment mining and implications for regulatory frameworks

Historically, sediments have been regarded as an infinite resource to be exploited in order to sustain human activities. As such, they have been reflected inside relevant policies, but only in the last decades have environmental considerations been considered or integrated into regulations. Extraction of sediments has been addressed independently from the different "nature" of the sites of extraction, equating mines and quarries to rivers and considering the effects of mining as localized, leading to the illusion of restoring sites of sand mines in rivers after exploitation (e.g., Kondolf, 1993; 1994b) and, consequently, irreversible damage to river systems. The wide-ranging effects of sediment mining in river channels and in adjacent floodplains are now well acknowledged (e.g., Collins and Dunne, 1990; Kondolf, 1994b, 1997; Rinaldi and Simon, 1998; Ladson and Judd, 2014; Comiti et al., 2011; Comiti and Scorpio, 2020; Wohl et al., 2015; Koehnken et al., 2020).

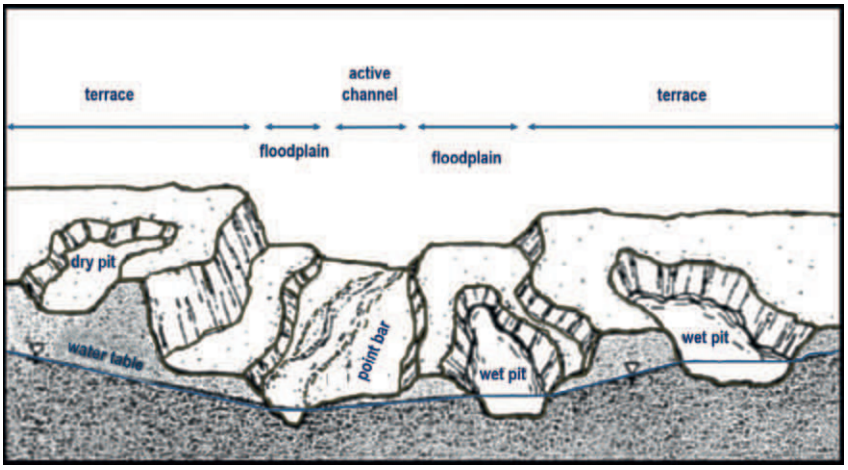

Fig. 1 Diagram of active river channel, floodplain and terraces, and relation between pit elevations and water table. Modified from Kondolf GM (1994a) Environmental planning in regulation and management of instream gravel mining in California. *Landscape and Urban Planning* 29: 185–199.

River mining triggers erosion, incision, and channel instability upstream and downstream of instream mining pits. River mining thus undermines structures, disrupts habitats, and alters hydraulic connections between channels and groundwater and floodplains far beyond the site of the actual mine. These processes also impact other economic sectors, such as tourism, agriculture, water supply and public and private infrastructure (Kondolf, 1997; Cooper et al., 2013). In large rivers, sediment mining can be sufficient to imbalance sediment budgets and eventually affect downstream coasts and river deltas (Schmitt et al., 2017, 2021; Hackney et al., 2020). The effects of sand mining can thus extend to dramatically wider temporal and spatial scales than the mining site, and are amplified if sediment mining occurs in degrading reaches and concurs with other pressures. Indeed, in terms of effects, sand mining can considerably exceed other pressures (e.g., Campana et al., 2014; Comiti et al., 2021—Figs. 2 and 3). Recovery from such effects is based on the capacity to restore a balanced sediment budget (e.g., Kondolf, 1997).

With such severe implications, sediment mining in rivers and lakes should only be allowed if better environmental options are not available or not sufficient to satisfy the demand. If alternatives are unavailable, it should be determined that aggregate mining

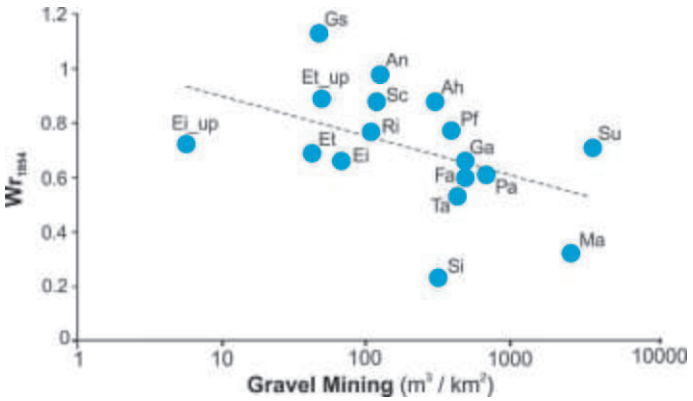

Fig. 2 Channel narrowing since 1954 (Wr_{1954}) in streams (represented as blue points) subject to intensive sediment mining since the 1950s compared with relative gravel mining intensity for some alpine rivers, represented in blue dots. Gravel mining shows clearly a significant negative relationship with the channel width trend. From Comiti F, Scorpio V, Andreoli A and Coviello V (2021) Management of coarse sediment fluxes and morphological dynamics of Alpine rivers: Lessons learned from South Tyrol (Eastern Italian Alps). *Proceedings of the International Symposium on Bedload Management. Interlaken, Switzerland*, 8-10.11.2021 (in publication).

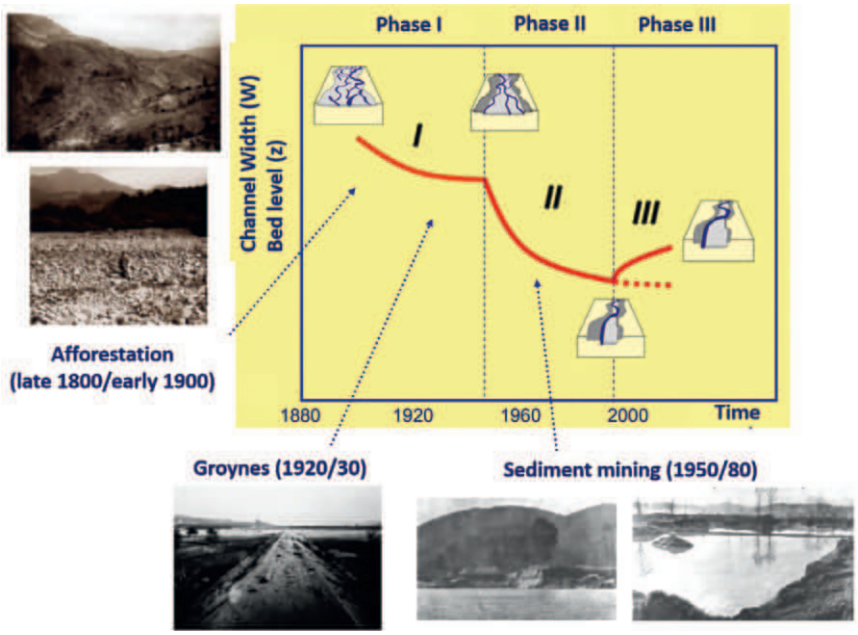

Fig. 3 Evolution of Magra River channel (Italy) in response to the different pressures in the catchment. In Phase II, the effect of sediment mining prevails, exacerbating incision and narrowing. The effect of environmental legislation enforced since the late 1980s is evident at the end of the 1990s, with an inversion of trend characterizing the current period (Phase III). Modified from Rinaldi M, Nardi L and Scozzafava R (2012) Studio del F. Magra e degli affluenti principali dal punto di vista geomorfologico a seguito dell'evento alluvionale del 25/10/2011 e definizione delle azioni e degli interventi di messa in sicurezza. https://www.regione.toscana.it/documents/16409/11270781/Univ_Firenze_Rinaldi_Effetti_Morfol_F_Magra.pdf/1fc79fdc-0923-448f-87ff-8a072fb3a950.

will not cause significant effects on ecosystems and society, such as increasing flood risk. Impairing water supply; or, undermining the stability of infrastructures and navigation. However, verifying such conditions requires: (1) a detailed knowledge of sediment dynamics in the catchment (e.g., Rinaldi et al., 2009, 2015), based on monitored and modeled information, including historic (Box 1); (2) a consistent map of current and future sediment demand per sector (e.g., cement, road bases, land reclamation and coastal protection etc.) and supply sources to meet such demand; and (3) expertise in implementing scientific assessment by relevant public bodies.

Box 1 Aspects recommended to underpin regulations on sediment mining (modified from Rinaldi et al., 2005).

1. Accurate analysis at the catchment and reach scale to understand if a river is aggrading, i.e., if there is a natural surplus of sediment.
2. If aggrading reaches exist: (i) identification of aggrading reaches, based on evolutionary trend of river channel and of the possible points of extraction; (ii) setting extraction rates to be lower than the replenishment rate from upstream (and ideally related to the excess volume that would cause aggradation); (iii) estimation of effects (environmental, socio-economic) of different extraction scenarios based on the demand.
3. Monitoring programs to control the extracted volumes, the modifications to channel sections and the ecological and morphological consequences.
4. Adaptive management, to review the permits based on the monitoring results.

Adopting basin scale approaches to manage aggregate mining

The spatial scale of river processes (catchment to site) and the cumulative impacts of the different socio-economic activities on them, require that sediment mining is addressed in the frame of integrated river basin planning. The benefits of resource extraction from freshwater bodies can then be assessed against the environmental costs of their present and future impacts.

Some regulations on aggregate mining require evaluating cumulative impacts of mining, although not indicating up to which extent (river reach compared with catchment). Other regulations address river mining within the wider context of an integrated catchment management framework, and do thus explicitly require a cumulative impact assessment. The latter is the case of the European Water Framework Directive (WFD; European Parliament and Council, 2000), which is legally binding for all member states of the European Union. The WFD aims to protect European water bodies and promote their sustainable use through successive river basin management planning on six-year cycles for all European basins, and implementation of measures to achieve the "good status" or "good ecological potential" of water bodies as defined in the WFD, except in some well-defined and motivated circumstances (EC, 2009).

The WFD recognizes the fundamental role of sediments and related morphodynamic processes in sustaining habitats and aquatic ecosystems, as well as the socio-economic needs related to sediments (e.g., aggregate supply, flood risk management, navigation) and promotes a risk-based approach to manage them sustainably at the catchment level. According to WFD, human activities potentially downgrading water body's conditions (e.g., water abstraction, river engineering, sediment mining) cannot be allowed unless specific conditions are verified. Sediment mining is not specifically mentioned in the WFD, but it is considered as a significant pressure on water bodies and, as such, it must undergo well-defined assessment procedures (e.g., EC, 2020). Sediment mining has to be managed at the catchment scale and allowed only if it does not undermine the achievement of good status of water bodies or the deterioration of some components. If so, it has to be reliably demonstrated that there is an "overriding public interest" in developing sediment mines (e.g., according to national strategies on aggregate supply) and that better environmental options (e.g., using alternative aggregates from quarries or floodplains) are technically impossible, prohibitively expensive, or having a worse overall environmental consequence (European Commission, 2009, 2018).

The WFD encourages two level assessments, a strategic system-scale assessment and an assessment at project-scales (e.g., European Commission, 2018, 2020). At systems scales (e.g., for international river basins or nationally) other means than mining for achieving the scope (e.g., importing aggregates, using alternative materials) have to be screened and evaluated, internalizing environmental costs of each alternative (e.g., other building materials, imported aggregates). The analysis at the strategic level will identify the national quota for aggregate mining based on the national demand for aggregate (considering for different uses, e.g., cement production, road subbase, industrial products) and screen potential riverine sources for aggregates based on productivity and ecological value. At the project level, alternative projects in the potential river stretches have to be assessed against the criteria whether other means (e.g., mining river terraces, sediment deposits in human-made reservoirs deltas, and quarries) can serve the same purpose with less environmental impacts. This includes also different project designs (e.g., different extraction techniques) which are technically feasible and not disproportionately costly. Once the project is selected, a monitoring program for river conditions has to be implemented and extraction regimes need to be adapted if that is the case. WFD has greatly contributed to prevent or limit in-stream mining in Europe, or corroborated the implementation of preceding environmental legislation addressing sediment mining.

Regulations on sediment mining and sustainable sediment management

No binding international convention regulates river sand mining and related trade, or commits countries to develop and implement sustainable management policies, although indirectly (i.e., conventions on environmental impact assessment in transboundary catchments or on the protection of nature and biodiversity) some protection could be considered to be in place. Outside of the

Europe and North America, or partly Australia, regulatory policies on sediment mining that are effectively implemented are still few, especially in developing countries, where demand for aggregates is very high and mining provides much employment.

Regulatory frameworks that recognize the environmental impacts of sediment mining in rivers and the necessity of a sustainable approach focus on the concept of a balanced sediment budget. The ways this concept is transposed into mining limits can be mainly summarized as follows:

1. *Definition of a "Red line"*, in terms of minimum elevation of the thalweg. Mining is permitted only if the river bed does not incise below this line that is annually re-evaluated on the basis of topographic surveys. Such a criterion is used in several countries but usually expressed as depth below the riverbed, and not as absolute elevation above a datum (e.g., Ministry of Environment and Water of Malaysia, 2009) and thus incision cannot be prevented;
2. *Definition of an annual replenishment rate* (sediment supply from upstream). Mining is permitted if the extraction rate is equal to or less than the replenishment rate. In many countries, extractions are permitted at the replenishment rate, and mostly calculated as a long-term average of annual sediment supply. This criterion is effective in preventing incision only if the actual replenishment rate is calculated based on that year's data (given the high interannual variability) and if the extraction rate allows for supplying the downstream reach (e.g., SEPA, 2012; Malaysia, 2009). River-wide estimation of annual replenishment is often imprecise, due to the assumptions in sediment modeling and measurement (e.g., Kondolf et al., 2001). Site-specific evaluation of the annual deposited sediment, carried out by specific surveys, is far more reliable, especially to define sound extraction rates; and.
3. *Definition of management rules based on empirical studies*. Recognizing the complexity of river systems and the geomorphic processes that shape them, science has developed solid methods to monitor and analyze sediment transport, and approaches to estimate sediment budgets and the effects of mining on sediment transport and, in general, on river systems. Scientifically based monitoring is indispensable to set reliable estimations of sediment yields, rates and effects, and is essential to calibrate models. In facts, numerical models alone cannot provide specific and secure predictions of the effects of certain extraction rates on channel changes and transport rates, as they are limited by the simplifying assumptions on geomorphic processes and the lack of relevant data to feed and calibrate them (e.g., Kondolf et al., 2001). Regulations that are underpinned by such scientific outcomes are still few.

Regulatory frameworks differ in the way how these aspects are translated into binding regulations, and in the capacity to provide effective technical indications, related to the availability of specific research in the relevant areas. Where comprehensive research has been carried out on the effect of river mining in specific catchments (e.g., Europe, North America), strict rules have followed (Koehnken et al., 2020) and in-river mining is prohibited or limited to some specific uses (e.g., flood risk mitigation, river restoration), subject to sustainability criteria (e.g., WFD). An example is provided in Box 2, related to the Scottish regulation on sediment management, which implements and specifies the WFD dictate in terms of guidance and criteria for sediment mining (Scottish Environment Protection Agency, 2010, 2012).

Box 2 General criteria for authorizing extraction of sediments related to some uses. Source: Scottish Environment Protection Agency (2012).

Aggregate extraction for commercial use. Consideration should be given to using aggregate that is not sourced directly from the aquatic environment. May be justified where resource is abundant compared to usage; local habitats are insensitive to such removal; assessment of sediment budget has been made and extraction practices are good. The operator should demonstrate that these conditions have been met and that a sustainable balance can be achieved. Where these conditions are not met, the activity is unlikely to be justified.

Flood management. May be justified in cases where it is demonstrated that sediment accumulation is increasing flood risk and the benefits of removing sediment can be quantified (e.g., using hydraulic and/or sediment transport modeling or other agreed method) and there are no other significantly better environmental options. However, it is likely that sediment will continue to accumulate in problem areas; therefore consideration should be given to longer-term alternatives for flood protection. It is more likely to be justified if part of a catchment flood management strategy. May be difficult to justify if the problem could be resolved by addressing an identifiable root cause of increased flood risk.

In countries where in-stream mining is still a widespread practice, guidelines to achieve sustainable mining may exist, although often poorly implemented. Technically solid national guidelines incorporating geomorphic-based approaches to sustainable mining have been issued, with procedures in place to identify the steps to identify sites, extraction methods, extraction rates and a comprehensive monitoring programme (e.g., Department Irrigation and Drainage, Malaysia, 2009). They are extremely valuable, but unfortunately not compulsory. Federal Guidelines to regulate the entire sediment value chain (from State demand to extraction rates, to trade) have been developed in India (Ministry of Mines, India, 2018). Nevertheless, they are not binding unless States enact them. Moreover, as sand mining controls are devolved to a large number of Districts, sustainable sediment management at the catchment-scale is not possible, as there is no coordination in defining coherent criteria across upstream and downstream districts. In the Mekong, where sand mining rates exceed replenishment rates by far and where natural sediment supply is heavily reduced by upstream dams, countries like Cambodia have banned export of sand, which was mostly exported to countries like Singapore for land reclamation (Kondolf et al., 2018; Bravard et al., 2013). However, enforcement seems patchy, as there is still a major sand trade

between Cambodia and whose sources are poorly traceable. Also, local sand demand is still exceeding supply rates, creating significant impacts on local river channels and the Mekong Delta (Schmitt et al., 2021). In some African countries, regulations have been issued, but the phenomenon is far from being governed. Where governance is lacking, mining is ongoing, as is illegal sand trade.

Promoting sustainable sediment management

Sediments, like water, require river basin governance. This implies agreements and a shared vision among different administrative entities, e.g., countries, in the case of international river basins, or sub-national entities (e.g. Hettiarachchi, 2019; Leal Filho et al., 2021). Yet, basin scale information on sediment dynamics and the effects of sediment mining is often scarce, but it is essential to underpin evaluations through scientific approaches. While numerical models can help to understand the basin scale sediment transport and pinpoint sediment supply rates, source areas, and aggrading reaches (Rinaldi et al., 2009, Schmitt et al., 2016, 2018), reliable evaluations need reliable monitored data as input, especially in complex systems. Given the complexity of sediment dynamics and related uncertainty, precautionary principles have to be applied proportionally to the lack of monitored data, and applications for sediment mining should only be taken into consideration if supported by sufficient monitored data.

Sediment transport and hydraulics are not intuitive matters. The devastating large-scale effects of apparently localized extractions are not commonly understood, and sometimes denied by non-experts and underrated among technicians. Education to increase awareness on such issues both among a wider public and practitioners is indispensable to promote an effective shift to sustainability. Comprehensive cost-benefit analysis and internalization of environmental costs are needed to provide incentives for research on alternative sources of sand and other aggregates.

Water and sediments are basic components of ecosystems and economies. While sediment dynamics and human uses should be analyzed, evaluated and managed at the catchment scale (e.g., Wohl et al., 2015), this is scarcely recognized in national policies and in terms of regional or global conventions. However, there is hope as new initiatives promote sustainable sediment management in international river basins, providing recommendations, technical guidelines for monitoring and management, and education (see. Box 3).

Box 3 Recommendations for sustainable sediment management in international river basins (UNESCO, 2011).

Recommendation 1: Sediment management (quantity and quality) should become a part of all river basin management plans.
Recommendation 2: Encourage soil conservation initiatives, in particular on steep agricultural land.
Recommendation 3: There is a need to work with international agencies such as the ISI in developing a commonly accepted international protocol for measuring erosion, sediment transport and sedimentation in river systems.
Recommendation 4: It is important that efforts should be made to involve the community in sediment control and management and to provide sufficient information on how they can improve river health and contribute to sediment management.
Recommendation 5: Sediment management must be based on a sound understanding of the sediment dynamics of the river basin involved. There is a need to clearly define the sediment budget or balance of a river system and collate available data to identify knowledge gaps and further enhance understanding of sediment issues on a global scale.
Recommendation 6: Sediment management plans should be periodically reviewed to ensure that they are in line with international best-practice.
Recommendation 7: The potential downstream impacts of any river structures and sediment management strategies must be considered.
Recommendation 8: There is a need for investment in capacity building to ensure that water management personnel understand and engage with sediment issues effectively.
Recommendation 9: Further investment in sediment research must be encouraged, particularly in developing countries.
Recommendation 10: There is a need to increase institutional cooperation and collaborate with international partners to share research and experiences.
Recommendation 11: The ISI network should include representatives from all regions of the world (with perhaps one representative who is a key expert in sediment from each of the major sediment-laden river systems of the world).
Recommendation 12: The precautionary principle should be applied in sediment management. The complexity of sediment transport processes and associated uncertainties makes the application of the precautionary principle important to management.

Conclusion/Synthesis (respond to aim)

Aggregates underpin natural systems as well as human-built infrastructure and are the second most extracted global resource after water. Impacts, benefits and alternatives to sediment mining from rivers need to be addressed, managed and governed at the river basin scale and underpinned by a solid knowledge of sediment flows in the catchment.

Most regulatory frameworks are insufficient to sustainably manage sediments (e.g., Kondolf, 1997; Rinaldi et al., 2005; UNEP, 2019). This is also due to the lack of adequate information (Sreebha and Padmalal, 2011) and of any specific international convention regulating sediment mining and trade, particularly in developing economies.

Given the severe implications of sand and aggregates extraction, sediment mining in rivers and lakes should only limited to cases where no less impactful option is available to satisfy a particular demand for sediments (e.g., alternative aggregates/materials for constructions from recycling or lower-impact natural sources, natural flood mitigation strategies), and, if so, where it is not causing significant effects on ecosystems and society.

Evaluation of both conditions require: (i) a detailed knowledge of sediment dynamics and potential supplies in an entire river catchment, based on monitored and modeled information; (ii) consistent information on future sectorial sediment demands (e.g., cement, road bases) and potential alternative sources to meet such demand; and (iii) expertise in implementing scientific assessment approaches for adaptive management of sediment extraction and its impacts and suitable regulatory frameworks—especially in transboundary river basins.

Knowledge gaps

(a) Understand rates of extraction, demands, and their future trajectories.
(b) Quantify impacts of mining on river processes, ecosystems, and livelihoods through modeling and field-based assessments to better quantify and internalize socio-environmental impacts of mining.
(c) Process based quantification of sustainable mining rates through understanding how sediment is generated and moved through a catchment (using local assessments, numerical models, and potentially remotely sensed data) in a modular manner (from basin-scale screening to more local assessments).
(d) Technical opportunities to replace sand in construction with other materials, better recycling for a more circular economy of construction materials, and their economic feasibility under consideration of internalized environmental impacts.

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https://spatialagent.org/Sedimentation/—World Bank On line Guidance Tool to Sediment management.
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Case Studies of Sediment Mining Activity

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Introduction

Sand and gravel are the most mined resources in the world. They are used mainly for construction, either to make concrete and asphalt or to build reclamation areas (The Economist, 2017). Mining for construction is mainly made in rivers, which puts these at great pressure. The rates of mining are at this moment higher those of natural supply of sediment, and it is estimated that by mid-century the demand will be higher than the supply with serious consequences for price (Bendixen et al., 2019; Sverdrup et al., 2017). Several authors designate sand as new gold (Jappe, 2020). It is thus no surprise that the main regions of the world where sediment mining is observed at the moment are the ones where a boom of urbanization is happening, East Asia, India, and Africa.

Sand and gravel mining for construction can be far away from where it is used, increasing the global footprint of the construction industry. Dubai city is in the proximity of sand-supplied landscapes; however, this sand does not offer the right characteristics for construction forcing Dubai to export sediment from Australia for reclamation works such as the building of artificial islands. Singapore, the world largest importer of sand to support its expansion, buys sediment from neighboring countries but also from Malaysia, Vietnam, and Indonesia (Hall, 2020).

Regulations and restrictions have been put in place by several nations after serious consequences were observed such as islands and beaches disappearances and infrastructures (bridges and building abutments) collapses due to foundation erosion. Many countries in the world regulated or completely blocked the export of mined sediment, which however did not stop the world sand extraction which is now in the hands of criminal gangs and black markets (Jappe, 2020). Sand and gravel extraction can be done, both in daylight and during the night, by a huge variety of methods: through the use of heavy machinery such as dredging boats and suction pumping, to more informal methods such as digging with shovels and bare hands (Bendixen et al., 2019).

Here we provide three examples of sand mining activities in which unregulated or poorly regulated sand mining activities happen or have happened in the past. In the three, mining rates were higher that sediment supply from upstream, causing a sand deficit situation in the rivers, and in the three important consequences are observed in terms of environmental impact, socioeconomic changes and safety. The case studies here presented are: (i) in Indonesia, excessive and unregulated sand mining in the slopes of the Mount Merapi volcano (province of Yogyakarta) are changing the landscape, endangering downstream infrastructures due to erosion and scouring, and changing the local socioeconomic structure; (ii) in Portugal, poorly monitored sand mining activities occurring for a century in river Douro enabled the dramatic collapse of the Hintze Ribeiro bridge which happened in March 2001 and took the lives of 59 persons; and (iii) the excessive sand mining in the heavily human-modified Mekong delta which is one of the main responsible activity for the previewed disappearance of the delta by the end of the century. In each case study, a general description of the sedimentary systems and the mining activities is given, and how the sediment mining activities relate with the observed or anticipated consequences.

The slopes of the Mount Merapi volcano in Indonesia

Climate change and intensive pressure on land use caused an increase on sediment-related disasters in Indonesia in the last years (Surtiari et al., 2017). This is the case of Mount Merapi slopes (province of Yogyakarta), which drains to Progo river which flows into the Indian Ocean. Mount Merapi erupts frequently (Anwar et al., 2017; Gertisser et al., 2012), and a considerable amount of sediments are directly produced by eruptions feeding the volcano slopes. These sediments are responsible for a complex morphological system located between the Mount Merapi volcano and the Indian Ocean, where the river Progo is one of the main features. Downstream, in the coast of the special region of Yogyakarta, these sediments are essential to maintain the barchan dunes, a rare geophysical feature found here.

The activation of the sediments produced by the Mount Merapi volcano by rainfall originate lahar flows, a rapid downhill flow of water and volcanic rock (Lavigne et al., 2000). These have devastating impacts on downstream valleys (Jenkins et al., 2015),

representing the main cause of local secondary hazard (Lavigne et al., 2000; Solikhin et al., 2015). In recent years, safety works including the construction of Sabo dams (Lavigne et al., 2000) decreased considerably the risks against debris flow by retaining the sediments upstream of the valley, and prompting economic development in the region.

The sediment produced by Mount Merapi volcano is an important economic asset, and mining of sand and gravel (Fig. 1), trapped by such protection works as the Sabo dams, became an engine of socioeconomic progress. The sediments are of high quality for construction, making this activity highly lucrative and creating important job opportunities and local incomes (Ikhsan and Fujita, 2012). Infrastructure development was a driver for sand mining activities already in the 1970s. In the 2000s the mining activities intensified after the building of many Sabo dams which trapped the sedimentary material from the Mt. Merapi eruptions that occurred in 1994, 1998, 2006 and 2010. So far, more than 250 Sabo dams of various types have been built around Mt. Merapi.

However, in recent years, the excessive retention of sediment by the protection works and its over-extraction has led to a lack of sediment supply downstream (Gob et al., 2016). Recent records show annual volumes of sediment abstraction from the Mount Merapi slopes of about 4 Mm^3 is similar to the annual production of sediment by the volcano, estimated as 3.9 Mm^3. Legono (2005) refers that the amount of sediment extracted from the Krasak Sabo dam (one of the tributaries of river Progo) in the slopes of Mount Merapi is higher than the upstream supply from recent eruptions. The degradation of the Lower Progo is already happening because of sand mining, estimated as more than 0.10 m/year (Ikhsan et al., 2010).

While the retained sediments are not conveyed downstream to the valleys anymore as they are exploited by mining activities, traditional agriculture practices are now being abandoned in favor of this new economic activity (Ikhsan et al., 2010). Sand mining has an effect on the community's economy, increasing employment opportunities as miners, heavy equipment operators, truck drivers, collectors and sellers of sand. This shift contributes to a sudden change of the local socio-economy which previously was based mainly on local small-scale food production.

Morphological degradation of downstream valleys (with ecological and security consequences) and lack of sediment feeding to coastal areas (essential to maintain barchan dunes, a popular local attraction), result from the lack of natural supply. Excessive river bed degradation, scouring of bridge piers and bank erosion are already observed in the Progo River. The proliferation of sediment mining in the Mount Merapi slopes induces abandonment of agriculture fields which is the basis of local subsistence. Sediments convey nutrients essential for ecology and food production, and reduction of its supply changes downstream habitats and fluvial connectivity.

The slopes of the Mount Merapi are a perfect living lab where a complex nexus between sediment, socio-economy, environment and safety exists. Ikhsan & Fujita (2012) and Legono (2005) illustrate very well the complexity and fragility of this geographic system and how linked geophysical aspects are to local socio-economy, governance, environment and safety. Legono (2005) discusses clearly the need for national and regional policy to regulate the sediment management whilst taking into account all these interdependent aspects.

The Mount Merapi geomorphology system is an intriguing and truly multidisciplinary problem. The sediment management in the Merapi slopes requires an integrated approach which considers the over-retention and exploration of sediments, aspects related to fluvial connectivity and morphology, coastal protection, and to socioeconomic security. Underlying geophysical substratum and the socio-economy of a basin have feedback mechanisms yet to be fully understood.

Fig. 1 Sand mining activities in the downstream reach of Progo river, Indonesia. Source: A. Kurniawan.

The bridge Hintze Ribeiro in Portugal

On the night of 4th March 2001, the bridge Hintze Ribeiro in the north of Portugal, constructed in the end of the 19th century, collapsed causing the fall of one bus and three cars and the instant death to its 59 passengers. The accident provoked a political crisis with intensive coverage by national media of death and suffering (Araújo, 2016), and raised skepticism in the capacity the national technical and engineering community.

The bridge, also known as bridge Entre-os-Rios, was located roughly 500 m downstream of the confluence of the river Tâmega with a bend in the River Douro. It was located in the heavily modified valley of the Douro river, about 15 km upstream of the Crestuma-Lever dam in the boundary of its reservoir. Upstream, several major dams impounded the main rivers: Torrão in river Tâmega and Carrapatelo in River Douro are the first dams upstream of the bridge section (Antunes do Carmo, 2014). In Douro, upstream of Carrapatelo, 12 other dams exist in Portuguese and Spanish territory.

The collapse of the bridge Hintze Ribeiro happened with the passage of the fifth consecutive flood wave in the River Douro in a sequence which started on 6th December 2000 (Antunes do Carmo, 2017). All the peak discharges of these five floods were above 8000 m^3/s, and the discharge was kept always above the value of 2000 m^3/s during these 3 months. The permanence of high values of discharge favored sediment movement, not allowing time for the reposition of sediment deposits; furthermore, values of discharge higher than between 2200 and 2600 m^3/s were estimated to be critical for the occurrence of riverbed erosion in this river section (Rocha et al., 2008). As far as it was possible to know, the flood of the Douro river between December 2000 and March 2001 was associated with a return period of more than 100 years (Silva, 2008).

The collapse of the bridge included one pier (the pier P4), two of the adjacent deck slabs and a third contiguous slab (Fig. 2). Pier P4 was in the inner edge of a bend in the river Douro, which is a natural area for sediment deposition; consequently, after the construction of the bridge pier P4 was enveloped by a sand bank, which conferred extra support to its foundation. This sand bank was 4–5 m higher than the normal water surface in the river (Silva, 2008).

After the accident, the position of the collapsed pier, tilted towards upstream, indicating that the collapse happened due to infra-excavation of its foundation (Antunes do Carmo, 2017). In contrast with the other two piers of the bridge which were located in the outer edge of the river bend, P2 and P3, pier P4 were not protected against local scour (Rocha et al., 2008). Several reports prior to the accident say that, although a century-old bridge with some conservation problems, structurally the bridge was generally in good state (Silva, 2008).

Through numerical modeling, the direct influence of hydrodynamics in the collapse of pier P4 was discarded (Rocha et al., 2008). Hence, four mechanisms related to river morphology were identified as possible causes of the accident, alone or combined: temporary riverbed incision due to the floods passage (short-term); local scour of the pier P4 foundation (mid-term, happening regularly in the winter season); morphology alteration due to sand mining activities (long-term); and, channel incision due to sediment supply depletion (long-term).

Extreme floods are not exceptional in the Douro valley, and similar intense floods occurred in February 1979, December 1989 and January 1996. These must have had a similar temporary effect in terms of channel incision, however the state of the riverbed previous to these floods must have been different.

The sand bank which enveloped the pier P4 in the beginning of the 20th century, disappeared completely by local mining activities of the bank itself, and never replenished because of the lack of upstream supply. After having exhausted this sand bar, miners continued the sand extraction along the river and in the reservoir of Crestuma-Lever, upstream and downstream of the bridge location. These mining activities provoked a general incision of the riverbed in the surroundings of the bridge at rates as high as 0.20 m/year (Sousa and Bastos, 2013). From 1913 to 1982 a total incision of the riverbed of 11.5 m was observed in the surroundings of the pier P4 (a rate of 0.17 m/year). Between 1982 and 1989 this incision accelerated and, during this 7 years period, it increased 1.5 m (Rocha et al., 2008). The rate of sand mining exceeded the rate of replenishment due to the natural flux of sediment.

Regarding long-term channel incision, the possibility of lack of sediment supply due to retention in the upstream reservoirs was excluded according to an official report from 2002 by the governmental agency IPTM—Instituto Portuário e dos Transportes Marítimos do Norte (Rocha et al., 2008). However, the section where the bridge of Hintze Ribeiro was located, lack of supply was verified to be caused by upstream sediment extraction.

The main conclusions regarding the causes of the collapse of the bridge Hintze Ribeiro indicate that this was due to a combination of extreme local erosion and riverbed incision provoked by five consecutive flood waves (short-term), acting upon an already incised and altered morphology due to sand mining (long-term). As shown, when the extreme floods in the Douro river occurred between December 2000 and March 2001, the stability of the foundation of pier P4 was already weakened by riverbed incision. The wave of floods provoked an extra debasement of the foundation of about 4 m, which lead to a critical infra-excavation and the consequent collapse of the pier P4 (Antunes do Carmo, 2017; Rocha et al., 2008). This example showed the need for continuous and accurate monitoring of infrastructure which are founded in susceptible riverine environments, and the need to create and enforce regulated sediment mining activities in rivers.

Fig. 2 Bridge Hintze Ribeiro after the collapse on 4th March 2001. From: https://www.publico.pt/2019/03/04/fotogaleria/entreosrios-393355 and https://observador.pt/2021/03/04/20-anos-desde-a-queda-da-ponte-hintze-ribeiro-presidente-da-republica-evoca-a-memoria-das-59-vitimas-mortais/.

The Mekong delta: Stories of subsidence and coastal erosion

Mekong delta is an important agricultural area for Vietnam, where more than 50% of the national yearly paddy rice harvest is produced (Thuy and Anh, 2015). Nevertheless, its genesis is rather young, as it developed due to a mixture of tectonic processes with an important accumulation of sediment transported by the river Mekong during the last 10,000 years (Tanabe et al., 2003), and an extensive human interference in the last two centuries. The Mekong delta, with an area of about 40,000 km^2, has been heavily modified by human influence from a system of two channels to an intricated system of channels, dykes and floodplains. The actual network of multiple connected channels measures more than 50,000 km (Hung et al., 2012).

Within the last decades, upstream dams in such countries as China, Cambodia and Laos, besides storing water and deviating it from the river for use in local agriculture and water supply, also retain and accumulate sediment in their reservoirs (Räsänen et al., 2017). As direct consequences, the sediment discharge of the Mekong decreases (Räsänen et al., 2017), and the supply available to be transported along the Mekong river substantially decreased (Li et al., 2017). This serious deficit of sediment supply due to upstream retention is exacerbated by sand mining (Fig. 3) which occurs directly in the Mekong river and its tributaries (Brunier et al., 2014; Dastgheib et al., 2016).

The average elevation of the whole delta is roughly 0.8 m above sea level (Minderhoud et al., 2019). The lack of upstream sediment, which is retained or extracted from the river, has serious consequences in the stability and maintenance of the Mekong delta sedimentary system. The lack of upstream supply of sediment disturbs the natural sediment balance in the Mekong channels creating the so-called hungry waters (Kondolf, 1997) which will contribute to channel incision, bank erosion and scouring of bridge piers and endangering of other infrastructures founded in the riverbed.

In addition to the sedimentary factors, other endangerment to the stability of the delta include the loss of the protective mangrove coastal belt (Besset et al., 2019), and progressing coastal erosion (Li et al., 2017). All these factors, which are magnified by climate change induced sea level rise and accelerating subsidence due to groundwater over abstraction, exert a heavy pressure on the delta which is predicted to disappear almost completely by the end of the century (Kondolf et al., 2018).

The long-term sediment yield in the Mekong river was formerly estimated to be between 145 Mt./year (Liu et al., 2013) and 160 Mt./year (Walling, 2009). However, more recent research indicates that the suspended sediment transport is 75% less than assumed previously (Vinh et al., 2016). This may be attributed to more accurate calculation methods but could also be a consequence of sediment trapping by the reservoirs. Mining activities aim at the coarser sediments in the riverine systems; hence, mining activities have an impact mainly in the sediment transported in the form of bedload (near the river bed) rather than the sediments transported in suspension.

In comparison with the sediment transported in suspension, the annual bedload yield was estimated to be less than 1% of the total suspended sediment transported for the period from 1981 to 2014 for the Vietnamese Mekong. Based on these numbers, the total sediment flux (traveling under suspension and as bedload) entering the Lower Mekong Delta can be estimated to be 6.16 ± 2.07 Mt./year which is far less than the sediment extracted by mining activities which was estimated to be between 37 and 62 Mt./year over the similar period. This indicates, therefore, a huge deficit between sediment supply and extraction by mining (Hackney et al., 2020). These amounts of mined sediment agree with the previously published numbers which estimated the instream mining for the Lower Mekong River to be around 55 Mt./year (Bravard et al., 2013). An overview on the sand mining volumes and their respective extraction location is given in Fig. 3.

For 2018, the sand extraction rates by mining were estimated to be 4.64 ± 0.31 Mm^3/year for a 20 km river section along the Tien river (the main northern branch of the Mekong delta in Vietnam). These calculations were based on indirect methods such as bathymetric maps and simulation of local refilling processes. As mining is interrupted during the flooding periods of the wet season, local mining pits were refilled after a few months by the transported sediment and also by the sediment from the collapsing of the pit shoulders; these calculations assumed the possibility of a complete refilling within a period of 6–12 months.

Fig. 3 Sand deposition along the river bank (Tan Hue) of the Mekong. Source: F. Nestmann.

The cumulative amount of sand mining was reported to be 17.77 Mm^3/year for the whole area of the Vietnamese Mekong Delta based on governmental data. However, the authors consider their calculations for the total extracted sand amount as rather conservative, as their observed extraction amount for the Tien Giang province was 0.51 mi m^3 for 2018 while dredging was prohibited for the whole province during that period (Jordan et al., 2019). Those numbers show a considerable disparity, indicating the difficulty of consistent data collection and interpretation. Nevertheless, they all show concerning trends of substantial annual sediment deficits.

The negative impacts of the extensive sand mining in the Mekong delta to the riparian ecology is well documented by several studies focusing on the sediment balance, channel incision, salinity intrusion and river bank destabilization. Research in morphology changes of the two main channels of the delta network, the Mekong and Bassac, showed a mean incision of the channel with around 1.3 m between 1998 and 2008. In parallel, and over the same period, the loss of bedload supply was estimated to be about 90 mi m^3 for the Mekong channel and to be about 110 mi m^3 for the Bassac channel. As both effects showed a weak correlation to hydraulic parameters, they could not be related to the dam induced decreasing discharge of the Mekong (Brunier et al., 2014), but rather to upstream retention and extraction of sediment from the system.

The progressing incision of the river channel due to sand mining increases the relative riverbank height. It was found that this induces seasonal bank instability (Fig. 4) which is a threat to key infrastructure (e.g., bridges) and communities located along the river (Hackney et al., 2020). As sand mining reveals negative effects to the environment, predicting the impacts from sand mining to the river morphology becomes of utmost importance. Recent studies of the Mekong segment in the An Giang province, by means of numerical modeling and bathymetry measurements, show clearly the impact of the mining in altering river morphology (Kim et al., 2020).

The seasonal flooding of the Mekong is essential to the local agriculture, as it conserves floodplain biodiversity and supplies fertile sediments to the agricultural areas in the delta (Vinh et al., 2016). Within the last 20 years (1995 to 2015), a significant decrease of flood frequency and duration could be observed. This may be directly related to the lowering of water levels as effect of intense riverbed mining while the river discharge remained constant over the same period (Park et al., 2020). The river impoundment by dams may be responsible to changes in the hydrological regime as well.

The incision of the river bed has an impact on the intrusion of tidal waves as well, allowing the seawater to move further inland during high tide. This is documented by an increase of salinity in the delta channels (0.2–0.5 PSU/year, Fig. 5) and an increase of the tidal amplitude within the delta (a rate of reduction of 2 cm/year). At the same time, the offshore tidal amplitude increased 1.2–2 mm/year due to climate change induced sea level raise. Both effects could be directly related to bed level incisions (2–3 cm) in response to sediment starvation due to the combined effect of sand mining sediments trapping by the upstream dams (Eslami et al., 2019).

On a concluding note, sand mining along the Vietnamese Mekong river delta already shows its negative impacts in terms of ecology and human life. Extraction rates, allied to retention upstream of dams, are likely to be higher than the natural supply at this moment already. As shown, diversity in the numbers which support these conclusions, means that extra efforts are needed on reliable data collection and further investigation of the sediment balance of the system. However, the actual numbers may even underestimate the situation due to additional unregistered extraction which is not considered in the abovementioned studies. Furthermore, as more dams are already planned in Cambodia and China, the impact of this in the sediment balance is expected to disturb further the sedimentary system by decreasing the sediment supply. Due to its agricultural importance, prompt solutions are needed on the national (restriction of sand mining) as well as on the international (transboundary river management) level to maintain the Mekong Delta for future generations.

Fig. 4 Eroding river bank close to Long Chau. Source: F. Nestmann.

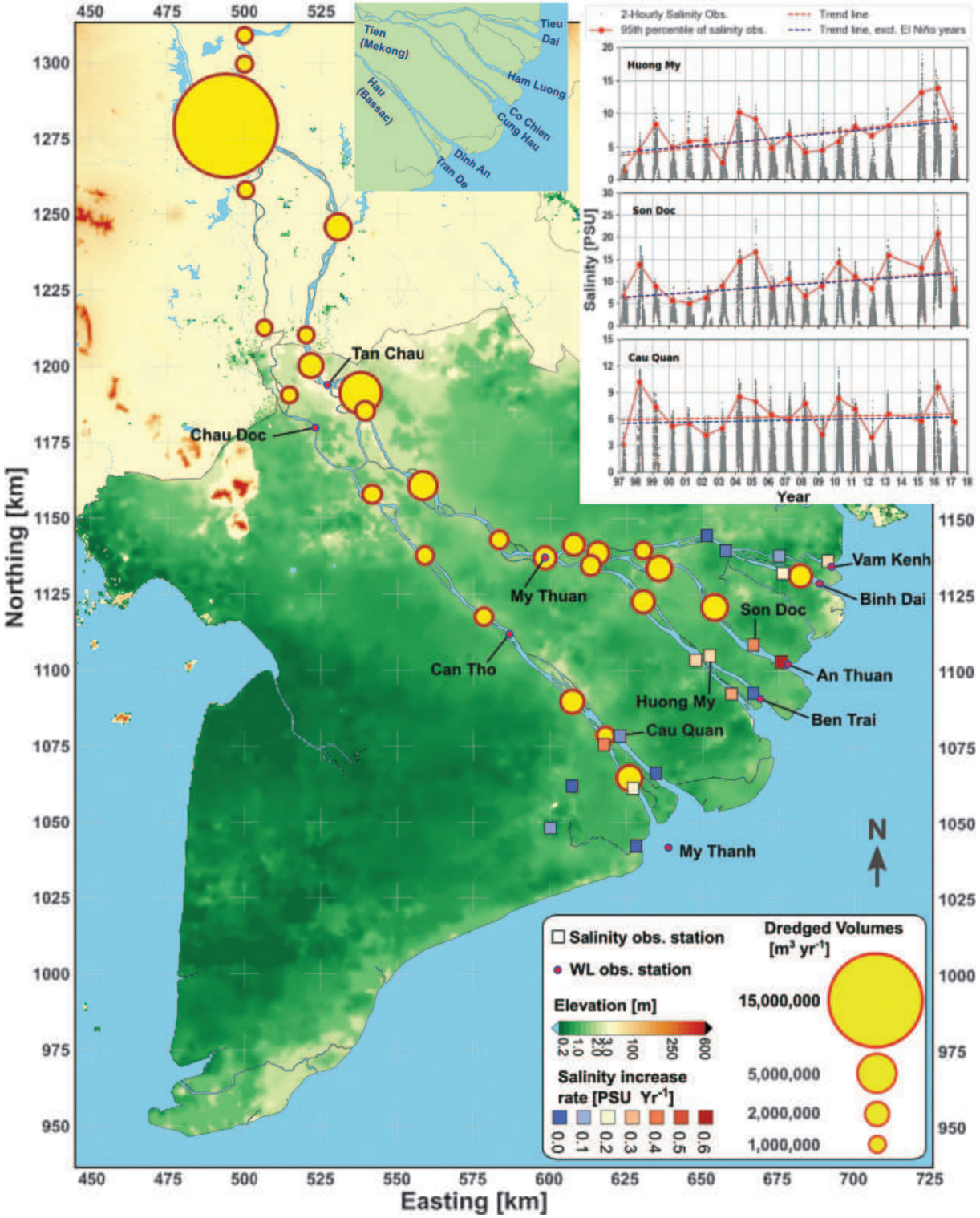

Fig. 5 Estimated sand mining volumes and salinity increase. From Eslami S, Hoekstra P, Nguyen Trung N, Ahmed Kantoush S, van Binh D, Duc Dung D, Tran Quang T, and van der Vegt M (2019) Tidal amplification and salt intrusion in the Mekong Delta driven by anthropogenic sediment starvation. *Scientific Reports* 9(1): 1–10. https://doi.org/10.1038/s41598-019-55018-9.

Conclusions

The case studies illustrate current and likely future problems with sand mining for river morphology, with important consequences for human safety and river ecology. The three case studies presented have in common a poor or no regulation and monitoring of the mining activity, and highlighted by fact that rates of sediment extraction are higher than the rate of upstream sediment supply. In some cases, the excess sand mining is happening at this moment, with negative consequences which are already observed or are expected to happen in the near future. In another case, the consequences were felt after years of excessive extraction, showing that the recovery of these natural sedimentary systems is long-term. The scale of the problem of excessive sediment extraction is global and often increasing. At the moment this is happening mainly in economically developing societies, where construction and land reclamation is occurring at unprecedent levels. Following the current rhythm of sediment exploitation, by mid-century the demand for sediment for construction will be higher than the supply, which will have negative, and unprecedent, consequences for the morphology of the world's sedimentary systems, as well as for the costs of construction.

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Emerging and Less Commonly Recognized Chemical Contaminants: Organic Micropollutants

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Bioaccumulation The increase of concentration of a pollutant in organisms exposed to the substance in the environment. Bioaccumulation effects occur at one trophic level and are governed by the rate of metabolism of the pollutant by the exposed organism. If the metabolic rate is low or negligible the pollutant is poorly broken down and can be adsorbed in the organism's tissue. When the rate of adsorption and storage exceeds the rate of excretion the pollutant accumulates in the organism's tissue. Further, bioaccumulation can be exacerbated if the pollutant has lipophilic (tendency to dissolve in lipids) characteristics.

Biocide A substance designed to eliminate an undesired organism. Biocides include herbicides, fungicides and insecticides. A biocide contains one or more active ingredients, being a chemical, plant extract, pheromone or microorganism that has action against pests or on plants, parts of plants or plant products.

Biomagnification The amplification of concentration of a pollutant in the environment along the food chain. Biomagnification effects occur at successive trophic levels, culminating in elevated concentrations in top predators.

Endocrine disruptor (ED) Exogenous (of external origin) substance with potential to cause adverse health effects of an organism by altering the function of its endocrine system. Adverse effects range from reproductive impairment, immune system decline and developmental and cognitive deficits. Moreover, endocrine disruptors can cause mutagenicity, carcinogenicity and teratogenicity, thus affecting progeny and sub-populations.

Negative removal efficiency The increase in concentration of a chemical substance through wastewater treatment processes. The effect is caused by the breakdown of precursor molecules (e.g., polymers, metabolites or conjugates) into the chemical under investigation, causing an increment between influent concentration and effluent concentration of the substance.

Organic micropollutants Organic (carbon based, either aliphatic or aromatic) chemicals of anthropogenic origins occurring in the environment at trace level concentrations of ppb to ppt, or $\mu g\ L^{-1}$ to $ng\ L^{-1}$, with potential to cause adverse environmental effects and hazard to human health.

Perfluoroalkyl substances Organic (aliphatic, non-cyclical) compounds on which fluorine atoms replace all the hydrogen substituents in the moiety.

Persistent organic pollutant (POP) Organic (carbon based, either aliphatic or aromatic) compound, including its transformation products, with determined characteristics of persistence in the environment, bioaccumulation, potential for long-range environmental dispersion and known adverse effects or toxicity to human health or to the environment.

Personal care product (PCP) Beautification or personal hygiene substance for topical (superficial) application. Cosmetics, perfumes, deodorants, creams and lotions, dental care products, soaps and shampoos are examples of personal care products. Emissions of parabens, a family of preservatives, and the antimicrobial disinfectant triclosan are primarily linked to personal care products.
Pharmaceutical substance A substance containing a pharmaceutically active ingredient providing pharmacological activity or direct effects on disease prevention, treatment or palliation or direct effect in adjusting, restoring or altering physiological functions.
Pseudo-persistence Effect caused by continuous emission, or flux. Numerous organic micropollutants susceptible to degradation in the environment are candidates for pseudo-persistence characteristics. The characteristic is simulated by the ubiquitous presence of a substance in the flux of effluent to the aquatic environment.
Surfactant A substance lessening the surface tension of a liquid, thus enhancing its dispersion by increasing wetting, spreading and penetrating properties. Surfactants are used in detergents, both for household and industrial applications, polymers, paper industry processes and textiles. The principal organic micropollutant deriving from surfactants is nonylphenol.

Introduction

Chemical contaminants are consistently associated with anthropogenic progress. Whether medicinal drugs improving public health, veterinary drugs and agrochemicals fortifying food security or flame retardants minimizing fire hazards, the benefits provided by these chemicals are considerable and phasing out or elimination of some classes of these substances can spark contentious socio-economic arguments.

Concern about the occurrence of micropollutants in water is not recent; in fact, the Commission of the European Communities (1981) began hosting symposia on the theme in the late 1970s. However, with novel chemicals discoveries and advancements in analytics, the defining scope of organic micropollutants has changed considerably. Today, substances characterized as organic micropollutants include perfluorinated compounds (PFCs), biocides, human and veterinary pharmaceuticals, steroid hormones, Personal Care Products (PCPs) and surfactants (Stasinakis and Gatidou, 2019). Organic micropollutants occur in the water column at trace level concentrations of ppb to ppt, or $\mu g\ L^{-1}$ to $ng\ L^{-1}$ range, have the potential to cause adverse environmental effects and can pose a risk to human health. Hazard assessment of organic micropollutants is conventionally characterized by Persistence, Bioaccumulation and Toxicity (PBT) and Endocrine Disrupting (ED) properties (European Chemical Bureau, 2003).

Due to the scale of classes of organic micropollutants and the enormous variety of their applications, this article is merely a digest of the topic. The complexity of this anthropogenic pressure on water resources is perhaps better conveyed by presenting the most common sources of organic micropollutants and their pathways to the aquatic environments. Fig. 1 broadly depicts the main applications of organic micropollutants; it is immediately clear that these substances have extensive socio-economic merits. Nevertheless, their emission to the aquatic environment has ramifications. In addition to the impact of single organic chemicals, the interactions and synergies of mixtures of substances, particularly mixtures of different classes of organic micropollutants, is an ever-increasing concern recurrently addressed in this article. Further, contemporary policy response, invariably grounded on hazard potential, forms another reoccurring theme of the article.

Owning to high chemical stability, lipophilic characteristics and consequent likelihood for biomagnification, PFCs are particularly hazardous chemicals. Recently, the PFC class of per- and polyfluoroalkyl substances (PFAS) has been under significant scrutiny and policy action at European level is imminent (Council of the European Union, 2019). In fact, emphasis on monitoring programs in aquatic environments focusing on one specific class of PFAS, the perfluorooctane sulfonic acid and its salts (PFOS), is intended to inform on the occurrence and persistence at global level (UNEP, 2017). Furthermore, recent EU policy for drinking water, stipulating routine monitoring for PFAS Total and Sum of PFAS (from a list of 20 PFCs) to commence by 12 January 2026, demonstrates the concern with risk to human health posed by this class of organic micropollutants (European Union, 2020).

Pesticides, herbicides and other parasite control substances are another class of organic micropollutants rigorously addressed in world-wide policy. Biocides, for instance the antifouling tributyltin, were among the initial micropollutants addressed by the Commission of the European Communities (1991). Nonetheless, biocides continue to raise concern for both the health of the aquatic environment and human health; in fact, regulatory instruments are periodically reviewed and updated to incorporate findings of systematic investigation programs (Secretariat of the Stockholm Convention, 2018; European Commission, 2020a; Gomez Cortes et al., 2020).

Awareness of the occurrence of pharmaceutical products in aquatic environment, raised by decades of academic research (Daughton, 2016), has finally kindled a response from global institutions for methodical evaluations and assessment to inform future policy responses (Kümmerer, 2019; OECD, 2019). Once again, recent EU policy for drinking water provided for investigations to be concluded and findings disseminated by 12 January 2029 on the potential threat posed by pharmaceuticals in source water (European Union, 2020). Of particular concern are the endocrine disrupting effects of synthetic steroid hormones 17β-estradiol (E2) and 17α-ethinylestradiol (EE2). Both drugs, administered primarily as sex hormones, were two of the only three pharmaceuticals first added to the Priority Substances Directive watch list (European Union, 2013).

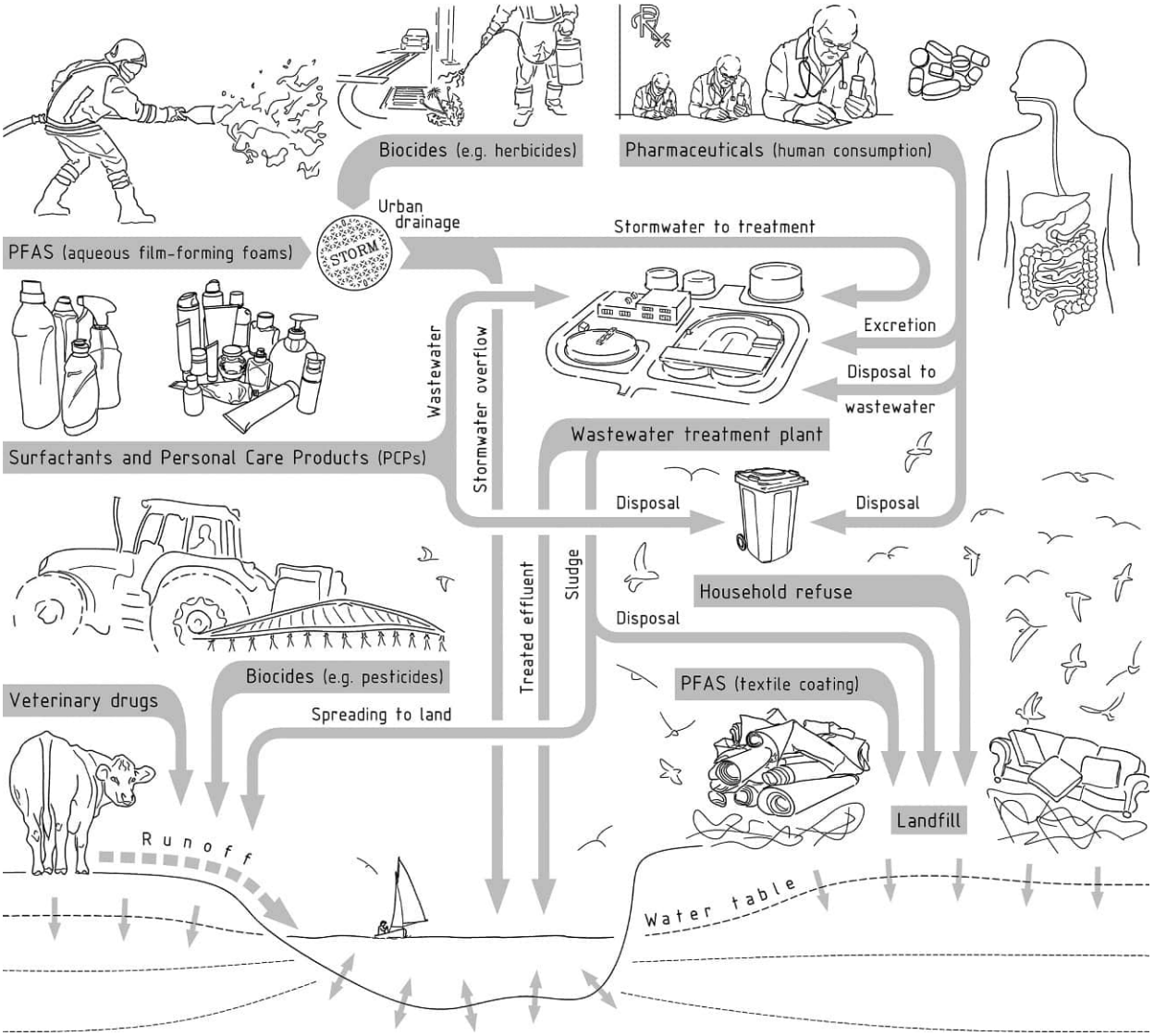

Fig. 1 General pathways of organic micropollutants to the aquatic environment.

Lastly, although surfactants and personal care products remain largely unregulated substances, these are noteworthy organic micropollutants because of their widely reported ED and ubiquity in the aquatic environment.

Biocidal substances

Biocidal substances (e.g., herbicides, fungicides and insecticides) are products designed to eliminate an undesired organism. Among other ingredients, biocides contain at least one active substance. An active substance can be either a chemical, plant extract, pheromone, or microorganism that has action against pests or on plants, parts of plants or plant products (European Commission, 2009). From a chemical point of view, biocides classify as inorganic (e.g., salts and oxides containing copper, lead) and organic (carbon compounds), the latter being more commonly used worldwide. Depending upon the presence of different elements such as chlorine, phosphorus, or nitrogen, and functional groups, organic biocides fall into four families: organophosphates, carbamates, triazines, and phenoxys. Within a given chemical family, biocides show close chemical structures and share similar behaviors when discharged into the environment. Aquatic biocidal pollution mainly results from agricultural and urban applications and its occurrence highly depends on land use, season, and rainfall-runoff events. A brief description of representative biocides of timely importance is provided below.

Glyphosate

Glyphosate or *N*-(phosphonomethyl)glycine is an active substance in commercial formulations for control of broadleaf weeds and grasses worldwide. Glyphosate disrupts the regulation of the synthesis of aromatic amino acids and secondary compounds in plants, fungi and bacteria (Funke et al., 2006). Glyphosate and aminomethyl phosphonic acid (AMPA), its primary transformation product, persist in the environment because of the inert nature of the carbon-phosphorus bond, which causes strong enzyme inhibition and thus hinders further degradation. Glyphosate and AMPA adsorb to clay or organic matter; consequently, both tend to accumulate in soils. Erosion, irrigation and rain events mobilize glyphosate and AMPA, explaining their presence in surface and groundwaters as well as sediments (Van Bruggen et al., 2018). In combination with surfactants (e.g., polyethoxylated tallowamine), glyphosate impacts aquatic fauna at different trophic levels (microalgae, protozoa, mussels, crustaceans, frogs, and fish). Conversely, it poses a low acute toxicity to amphibians, reptile, and mammals. Studies on the chronic exposure of humans to glyphosate provided inconclusive results and more research is needed to determine its safety (Agostini et al., 2020).

MCPA and 2,4-D

Both 4-dichlorophenoxy acetic acid (2,4-D) and 2-methyl-4-chlorophenoxyacetic acid (MCPA) are the most common phenoxy acids applied for post-emergent control of terrestrial and aquatic broadleaf weeds. These acids mimic indoleacetic acid, a growth phytohormone. When sprayed on broadleaf weeds at high concentrations, 2,4-D and MCPA stimulate a rapid, uncontrolled growth leading to tissue death. Because of their high solubility, 2,4-D and MCPA stay in water rather than partitioning to solids, which implies a high environmental mobility and explains the frequent detection of these acids in surface waters and aquifers worldwide (Muszyński et al., 2020). Biodegradation is the main removal mechanism for phenoxy acids in aquatic systems. Nevertheless, lack of microbial acclimatation or oxygen limitations can lead to their persistence, particularly in groundwater. Both 2,4-D and MCPA exert low toxicity toward aquatic fauna (Britt et al., 2003) and no sufficient relationship, at environmentally relevant concentrations, has been found between 2,4-D and MCPA and carcinogenic effects on humans.

Amitrole

Amitrole (3-amino-1,2,4-triazole) is used to control grass and broadleaf weeds. Amitrole accumulates in soils and, because of its high solubility, may leach to surface water and groundwaters as a result of runoff. Microbes in soil, sediments and wastewater processes degrade amitrole under aerobic conditions (European Food Safety Authority, 2014). Owing to its solubility and hydrophilicity, no significant bioaccumulation of amitrole has been reported in animals and humans.

Endosulfan

Endosulfan (6,7,8,9,10,10-hexachloro-1,5,5a,6,9,9a-hexahydro-6,9-methano-2,4,3-benzodioxathiepine-3-oxide) is an organochlorine biocide used for controlling pests and mites by generating neurotoxic effects (i.e., hyperstimulation) (Berntssen et al., 2017). Upon application, receiving soils act as a primary reservoir of endosulfan in the environment; because of its hydrophobic properties, endosulfan has shown high mobility across environmental compartments. Classified as a semi-volatile compound, endosulfan is prone to evaporation; subsequent atmospheric transportation may occur, resulting in wide dispersion and remote deposition from application sites. Endosulfan transfers to water bodies through runoff and favors accumulation onto sediments once in the water column (Weber et al., 2010). Both microbial and abiotic processes transform endosulfan in the environment: bacteria oxidize endosulfan to the respective sulfate, whereas endosulfan diol forms after alkaline hydrolysis. These intermediates exert similar toxic effects on biota and humans. Chronic exposure to endosulfan leads to bioaccumulation in fish; acute exposure results in neurotoxicity (hyperactivity and convulsions) in animals and humans; severe poisoning can lead to organ failure and death.

Per and poly-fluorinated chemicals

Per- and polyfluoroalkyl substances (PFAS) are organic (aliphatic) compounds on which fluorine atoms replace all the hydrogen substituents in the moiety (Fig. 2). The covalent bond between carbon and fluorine provides to the perfluoroalkyl molecules both strong chemical and thermal resistance as well as oil- and water-repellent properties.

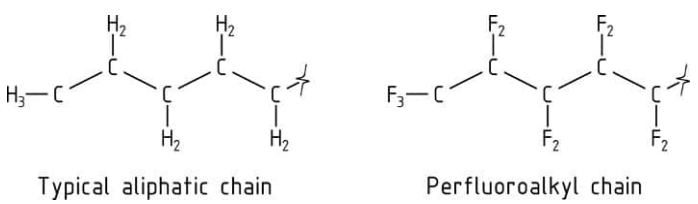

Fig. 2 General difference from aliphatic to perfluoroalkyl chains.

Because of these distinctive features, PFAS have resulted in varying commercial applications such as stain-resistant coatings, water-resistant fabrics, metal plating paints, pesticides, fluoropolymers, greaseproof paper, and aqueous film-forming foams used in firefighting (Alexander et al., 2008). PFAS enter aquatic environments either through direct emissions caused by manufacture, usage, and disposal of commercial products (Fig. 1), or indirect emissions from the breakdown of precursor substances, mainly larger derivatives and polymers both of which include perfluoroalkyl moieties (Prevedouros et al., 2006). While PFAS represent a wide chemical family comprising 268 individual compounds, special attention is paid to long-chain perfluoroalkyl carboxylic or sulfonic acids for regulatory purpose (Buck et al., 2011). Present in the ng L^{-1} level, perfluorooctanoic acid (PFOA) and perfluorooctanesulfonate (PFOS) are the most frequently detected fluorinated substances in ambient water (Arvaniti and Stasinakis, 2015).

Most of the PFAS withstand conventional wastewater treatment processes and effluents can contain PFAS originating from domestic and industrial sources. Furthermore, PFAS can be subject to negative removal efficiency. When comparing influent with final effluent concentrations, several studies have reported increasing concentrations of perfluoroalkyl acids (PFAAs) such as perfluorocarboxylic acids (PFCA) and perfluorosulfonic acids (PFSA) (Arvaniti et al., 2014; Filipovic and Berger, 2015). These concentration increments could be attributed to breakdown of polymers (e.g., such as polyfluoroalkyl phosphoric acid esters, fluorotelomer sulfonic acids, fluorotelomer sulfonates, and fluorotelomer alcohols) which act as PFAS precursors. Coggan et al. (2019) conducted an extensive PFAS sampling campaign across 19 Australian wastewater works. The total concentration of 21 targeted PFAS rose in both aqueous and solid phases through the treatment processes from influent to primary effluent, secondary effluent, final effluent, and recycled water. These concentration increments in treated effluents represents a continuous discharge of short-chain PFAS into receiving waters.

Environmental impact and potential risk to human health

Because of their profuse use, PFAS accumulate in aquatic environments and have consistently been detected in biota and humans. The accumulation of PFAS in both surface water and groundwater can be attributed to the limited removal efficiencies of conventional treatment processes (Kucharzyk et al., 2017). Of particular concern is the PFAS presence in water bodies where abstraction for drinking purposes takes place. Cousins et al. (2016) concluded that PFAS present in groundwater will result in contamination difficult to treat.

In terms of human exposure, the European Food Safety Authority Panel on Contaminants in the Food Chain defined tolerable weekly intakes of 6 and 13 ng kg^{-1} bodyweight for PFOA and PFOS, respectively (Knutsen et al., 2018). For both compounds, the Panel reported higher doses than the recommended intakes across a significant fraction of the population. Rising serum total cholesterol levels (PFOA and PFOS) and attenuation of immune response in children's vaccinations (PFOS) are the critical effects observed in humans.

Pharmaceuticals

Contrasting with other organic micropollutants, pharmaceuticals, at least those used for human therapy, have a number of distinctions preventing stringent regulation of their emission to the environment.

Drug discoveries from the 1950s onward contributed immensely to the well-being of society and significantly increased life expectancy (Rowland et al., 2012). Furthermore, medical progress yielded earlier diagnoses, leading to extended drug therapy regimes aimed at postponing disease onset or prolonging the morbidity period (Fries, 2005). Generally referred as pharmaceuticalisation of society (Conrad, 2005), the gained health improvements came at the cost of global dependence on this class of chemicals along with the interrelated environmental ramifications. Essentially, the human health benefits redeemed by society make the regulation of emission of pharmaceuticals products a highly ethical issue. The solution will require a multifaceted response from source control to end of pipe abatement (Kümmerer, 2019; OECD, 2019; European Commission, 2020b).

Other environmentally relevant aspects unique to pharmaceuticals are the sheer number of Active Pharmaceutical Ingredients (APIs) available from a global list of over 3000 APIs, their intended biological actions and their interactions when administered concurrently. By definition, therapeutic drugs are designed to have a specific biological effect, potentially replicated on organisms populating aquatic environments receiving discharge of pharmaceutical residue.

Lastly, numerous monographs on drug interaction on human patients are routinely consulted to prevent hazardous side effects caused by administration of multiple APIs; yet, knowledge on the consequences of discharging cocktails of drugs to aquatic environments is currently limited. Concerningly, the Joint Research Centre of the European Commission rates the risk of mixtures three orders of magnitude higher than exposure to individual pharmaceuticals, clearly stressing the need for extensive environmental impact research.

Regulation and management

Agencies such as the European Medicine Agency (EMA) and the Food and Drugs Administration (FDA) are responsible for the Environmental Risk Assessment of new drugs for which marketing authorization is sought. However, determinations of these assessments are merely informative and neither agencies can take into consideration adverse environmental ramifications in their decision to approve novel human pharmaceuticals (OECD, 2019). Furthermore, the mandatory submission of environmental risk

Table 1 Timeline of inclusion of pharmaceuticals to the watch list of Priority Substances Directive 2013/39/EC.

Drug class	*Year of inclusion to watch list*			
	2013[a]	*2015*[b]	*2018*[c]	*2020*[d]
NSAID	Diclofenac	Diclofenac		
Estrogens	17α-ethinylestradiol (EE2)	17α-ethinylestradiol (EE2)	17α-ethinylestradiol (EE2)	
	17β-estradiol (E2)	17β-estradiol (E2)	17β-estradiol (E2))	
Macrolide antibacterials		Erythromycin	Erythromycin	
		Clarithromycin	Clarithromycin	
		Azithromycin	Azithromycin	
			Amoxicillin	Amoxicillin
			Ciprofloxacin	Ciprofloxacin
Sulfonamides and trimethoprims				Sulfamethoxazole
				Trimethoprim
Psychoanaleptic antidepressants				Venlafaxine and *O*-desmethylvenlafaxine
Antifungal azole compounds				Clotrimazole
				Fluconazole
				Miconazole

[a]Source: European Union (2013) Council Directive 2013/39/EC of the European Parliament and of the Council of 12 August 2013, Amending Directive 2000/60/EC and 2008/105/EC as regards priority substances in the field of water policy. *Official Journal of the European Union* L226: 1–17.

[b]Source: European Commission (2015) Implementing Decision (EU) 2015/495 of 20 March 2015 establishing a watch list of substances for Union-wide monitoring in the field of water policy pursuant to Directive 2008/105/EC of the European Parliament and of the Council. *Official Journal of the European Union*, L78: 40–42.

[c]Source: European Commission (2018) Implementing Decision (EU) 2018/840 of 5 June 2018 establishing a watch list of substances for Union-wide monitoring in the field of water policy pursuant to Directive 2008/105/EC of the European Parliament and of the Council and repealing Commission Implementing Decision (EU) 2015/495. *Official Journal of the European Union* L141: 9–12.

[d]Source: European Commission (2020a) Implementing decision (EU) 2020/1161 of 4 August 2020 establishing a watch list of substances for Union-wide monitoring in the field of water policy pursuant to Directive 2008/105/EC of the European Parliament and of the Council. *Official Journal of the European Union* L257: 32–35.

assessments as part of the dossier for marketing authorization applications has only been recently introduced; consequently, for the majority of legacy pharmaceuticals on the market, their potential ecotoxicological impact on receiving environments remains unknown (Kümmerer, 2019). Essentially, emission of human pharmaceuticals to the environment arising from utilization remains unregulated. Nonetheless, recent actions taken by the European Commission clearly demonstrate that future policy will be guided by determinations of monitoring programs. In fact, periodic revisions to the watch list stipulated by the Priority Substance Directive (European Union, 2013; European Commission, 2015, 2018) have seen the addition of numerous pharmaceutical products, particularly antibacterial drugs (Table 1), intended to inform the decision making process.

Market authorization for veterinary drugs constitute another equally important source of emission, albeit access to market for veterinary drugs is more stringent and environmental impacts are taken into consideration in the decision to grant marketing authorizations.

Sources of environmental loading and fate in ambient water

Municipal wastewater treatment plants constitute the primary source of discharge of human pharmaceuticals to aquatic environments (Fig. 1). Administered pharmaceuticals are excreted by patients in various percentages of the original dose either as unchanged parent compounds, metabolites or conjugates (Petrie et al., 2015). Yet another form of emission is the disposal of unused or expired pharmaceuticals into sewers or in household waste (Ruhoy and Daughton, 2008); fortunately, numerous national take-back schemes have been implemented to address the latter form of emission (OECD, 2019). Although healthcare facilities represent another important source of discharge to wastewater, their share of emission constitutes a small fraction of the total environmental loading (OECD, 2019). Veterinary applications are yet another significant, albeit markedly more diffuse, source of pharmaceutical emission (Kümmerer, 2019). The Non-Steroidal Anti-Inflammatory Drug (NSAID) diclofenac, for example, is commonly administered to livestock.

Wastewater treatment efficacy varies considerably among pharmaceuticals, ranging from complete removal to negative removal rates. The latter consist of an increase in concentration of some compounds caused by the action of organisms in biological wastewater treatment. Metabolites and conjugates present in influent streams can undergo deconjugation, converting back to the original parent compound, thus incrementing the concentration between influent and effluent (Evgenidou et al., 2015; Daughton, 2016). Diclofenac is one of the chemicals known to undergo deconjugation in biological wastewater treatment processes (Peake et al., 2015).

Numerous tertiary treatment technologies designed for pharmaceutical removal exist. Processes revolve around filtration, adsorption and oxidation, often used in various combinations. Activated carbon in granular or powdered forms remains a viable choice but innovative solutions, for instance filtration through media loaded with enzymes, are advancing toward commercialization. In fact, Gonzalez-Gil et al. (2020) suggest that enzymatic pathways might provide viable solutions to treat emissions of pharmaceuticals. While wastewater treatment technologies are available, their efficacy varies substantially across the spectrum of physicochemical properties of pharmaceuticals and numerous compounds show recalcitrance to even the most effective solutions.

In general, pharmaceuticals are considered ubiquitous in aquatic environments (Kümmerer, 2019; OECD, 2019). Among the most commonly detected are the antiepileptic carbamazepine, NSAIDs diclofenac and ibuprofen, the antibiotic sulfamethoxazole and the antidepressant fluoxetine. Furthermore, numerous biotic and abiotic transformation products from wastewater treatment processes are known to be persistent in the environment. In the water column, most pharmaceuticals are susceptible to natural degradation mechanisms such as sorption, photolysis and hydrolysis with varying dissipation half-life depending on physicochemical characteristics (Peake et al., 2015). Nevertheless, the unremitting flux of pharmaceuticals in aquatic environments causes a pseudo-persistence effect.

Environmental impact and potential risk to human health

As affirmed by the WHO (2012), risk to human health via ingestion of contaminated drinking water is very low, with concentrations generally 1000-fold lower than minimum therapeutic doses. While assumed to be well within safety exposure limits, trace levels in drinking water are continuously changing according to utilization patterns (Oosterhuis et al., 2013) and variations in national formularies. An important example is the increased treatment of cancer patients with antineoplastic drugs as outpatients, leading to discharge of potent drug residues into municipal wastewater treatment systems that are largely inadequate to remove these chemicals (Mompelat et al., 2009). Consequently, research on the potential ramifications of chronic human exposure to trace levels of pharmaceuticals and their mixtures in drinking water remain a priority.

While outside the context of aquatic environment, the principal case of environmental impact relates to the near extinction (>95%) of the Asian *Gyps* vulture population caused by diclofenac. The NSAID, administered as a veterinary drug, caused liver damage to the scavengers feeding on carcasses of medicated livestock (Arnold et al., 2014; Peake et al., 2015). Within the aquatic environment, the impact of pharmaceutical emissions takes numerous facets. For instance, behavioral change, namely the inhibition to hazard perception, in fish species has been linked to exposure to psychiatric drugs (Arnold et al., 2014; OECD, 2019). Yet, the most acute impact is caused by estrogenic compounds. While endogenous oestrogens are excreted by humans and can also occur naturally in the environment, emissions of synthetic steroid hormones 17β-estradiol (E2) and 17α-ethinylestradiol (EE2), administered as sex-hormones, account for most of the estrogenicity of receiving aquatic environments. Rapid biodegradation (0.2–9 days at 20 °C) transforms E2 to estrogen in the water column whereas EE2 is primarily broken down by photolysis. Nonetheless, both compounds are liable to bioaccumulation and biomagnification (Stasinakis and Gatidou, 2019). Furthermore, the toxicity of these oestrogens expresses in the production of vitellogenin in fish, causing the feminisation of male fish (Peake et al., 2015), where trace concentrations of 5–6 μg L^{-1} are sufficient to cause crashes in fathead minnow's populations (Arnold et al., 2014; OECD, 2019). With the exception of estrogens E2 and EE2, based on the current body of knowledge bioaccumulation in aquatic biota does not appear to be a cause of concern even for the most ubiquitous pharmaceutical substances. With regards to human health, the ED characteristics of EE2 are certainly of concern to the European Commission as the substance will be added to the first watchlist for drinking water by 12 January 2022 for the purpose of informing human health risk assessment (European Union, 2020).

Surfactants and personal care products

Among the environmental contaminants present in cosmetics, personal hygiene products and detergents, the compounds causing most reason for concern are triclosan, nonylphenol and the parabens. Endocrine disrupting characteristics are the primary toxicity hazard across all of these compounds (Stasinakis and Gatidou, 2019).

Both detergents and Personal Care Products (PCPs) reach the aquatic environment primarily through influent to wastewater treatment or disposal to municipal refuse and subsequent landfill (Fig. 1). Analogous to pharmaceuticals, surfactants and PCP, at least where wastewater treatment removal is not completely effective, are prone to the pseudo-persistence effect caused by continuous environmental loading.

Personal care products: Triclosan

Triclosan, an halogenated microbial disinfectant used in PCPs, is designed to permeate cell walls of bacteria and target various cell organs, including synthesis of RNA (Hontela and Habibi, 2013). Wastewater is the main pathway of environmental loading of triclosan; removal rates vary from 50% to 80% by conventional treatment technologies (Petrie et al., 2015). However, disinfection processes can lead to the formation of chlorinated triclosan derivatives, potentially augmenting the antimicrobial and ED characteristics of this universal product (Evgenidou et al., 2015). Another concerning aspect of the environmental fate of triclosan is the degradation by photolysis. Stasinakis and Gatidou (2019) report that this natural degradation process on triclosan can cause

the generation of dioxins, toxic organic compounds with high persistence properties, high bioaccumulation potential along the food chain and substantial human health impact, including carcinogenicity.

Personal care products: Parabens

The parabens, a class of preservatives inhibiting growth of fungi and yeast in cosmetics, are primarily represented by four substances, ethyl-, butyl-, propyl- and methyl-paraben. Petrie et al. (2015) reports presence of all four parabens in wastewater influent streams in the United Kingdom but high removal rates (>80%) by conventional wastewater treatment. The potential impact of parabens to receiving aquatic environments is due to their, albeit weak, ED characteristics. Furthermore, parabens react strongly with chlorine in disinfection processes, forming chlorinated by-products with higher acute toxicity than their ED potential (Evgenidou et al., 2015). Essentially, despite the extensive reliance on parabens for preservation of PCP, paucity of knowledge on their potential impact to chronic exposure prevents accurate risk assessment.

Surfactants: Nonylphenol

Nonylphenol derives from detergents. Alkylphenol ethoxylates, some of the most widely used surfactants, are primarily constituted of nonylphenol ethoxylates. Microbial breakdown of the latter results in the release of nonylphenol (Kennedy et al., 2013; Stasinakis and Gatidou, 2019). Occurrence of nonylphenol in wastewater effluent from activated sludge plants (0–35 $\mu g\ L^{-1}$), as well as river water (3.0 $\mu g\ L^{-1}$) and groundwater (2.0 $\mu g\ L^{-1}$) has been documented for four decades (Commission of the European Communities, 1981). Although nonylphenol is rapidly degraded in the aquatic environment by photolysis (10–15 h half-life), it partitions strongly to sediment (Stasinakis and Gatidou, 2019). Furthermore, because of continuous discharge to wastewater, the substance is subject to pseudo-persistence effects. Bioaccumulation of nonylphenol in mussels (*Mytilus edulis*) has also been known for at least three decades (Commission of the European Communities, 1991). More recent research demonstrated bioaccumulation by freshwater macroalgae (*Cladophora glomerata*) and microalgae (*Chlorella vulgaris*) and consequent biomagnification in fathead minnow and subsequent trophic levels (Sun et al., 2014). Endocrine disruption characteristics are the primary cause of concern relating to nonylphenol (Kennedy et al., 2013; European Union, 2020).

Among the most researched surfactants and PCPs, nonylphenol is the only substance currently regulated in Europe by the Priority Substances Directive, stipulating a maximum allowable concentration of 2.0 $\mu g\ L^{-1}$ for inland surface waters (European Union, 2013). While the WHO proposed the consideration of nonylphenol (at a value of 3.0 $\mu g\ L^{-1}$) as a benchmark substance for ED risk assessment for drinking water, at this time the European Commission opted for the inclusion of the substance to the first watch list of contaminants of emerging concern. The watch list, to be formalized by 12 January 2022, will indicate guidance values for nonylphenol. Furthermore, Member States operating drinking water supplies exceeding the established guidance value will be required to initiate corrective measures (European Union, 2020).

Global regulatory framework

Perhaps the most significant problem in the regulation of emission of organic micropollutants is the sheer number of chemical substances present on the market. Exacerbating the challenge even further, the applications for these substances vary immensely, from endless functions in the case of PFCs to specific utilization for pharmaceutical ingredients. Aiming to achieve unity in responsibility across the planet, Multilateral Environmental Agreements (MEA) offer mechanisms for Parties—generally States or International Organisations—to conform on the regulatory front, particularly important where the fate of micropollutants has transboundary characteristics. These Treaties, brokered under the aegis of the United Nations Environment Programme (UNEP), are widely ratified across the world (Diamond et al., 2015).

Chemical legislation regulating emissions to the environment expands substantially at regional jurisdiction levels. For instance, in Europe, the Priority Substances Directive (European Union, 2013) governs policy action necessary to manage chemical pollution to the environment. Further, on 16 December 2020, the European Parliament adopted a recast of the Drinking Water Directive (European Union, 2020), which formalizes the inclusion of micropollutants to a watch list mechanism aimed at informing further policy decisions. The latter legislation clearly demonstrates the growing concern on emerging chemical pollutants. Nonetheless, this abridged appraisal focuses on global coverage only with particular emphasis on one specific MEA, more pertinent to micropollutants, the Stockholm Convention on Persistent Organic Pollutants (POPs).

Persistent organic pollutants: Original 12 chemicals and recent additions to the Stockholm convention annexes

Growing concerns about environmental and human health risk posed by organic chemicals showing high persistency in the environment, high partitioning to sediment and biota, bioaccumulation and biomagnification, extended range of atmospheric transport and, most importantly, high toxicity warranted the devising of a global response. On 25 May 1995, the UNEP Governing Council (1995) issued Decision 18/32, inviting a series of assessments for 12 POPs to be carried out under the direction of the Intergovernmental Forum on Chemical Safety. The resulting recommendations issued by the Forum led to the adoption of the Stockholm Convention on 23 May 2001. However, in order to enter into force, the Treaty required a minimum of 50 statutory

instruments of ratification, acceptance, approval or accession submitted by Parties to the Convention. On 17 May 2004 the Treaty became legally binding to the Parties and, as at January 2021, the Stockholm Convention had 152 Parties and 184 Signatories.

Undoubtedly, in addition to the socio-economic aspects, the formulation of international conventions necessitates exhaustive assessments of the hazard posed by chemical substances. In the case of the Stockholm Convention, 9 years passed before the Treaty became legally binding, despite the fact that substantial knowledge on the environmental and human health risk was already available for the original 12 POPs. While the lengthy process is necessary to guarantee the effectiveness of these global policies, the delayed action meant that, because of the persistent nature of POPs, legacy emission and accumulation in sediment and biota sinks continued uninterrupted during the legislative period (Hung et al., 2016).

The initial 12 POPs consisted of nine pesticides, two industrial chemicals, one of which is also used as a pesticide, and two incomplete combustion by-products (Table 2). The listing of chemicals is based on a three-tier system: Annex A lists prohibited substances and Annex B stipulates restriction of production and use. Whereas Annex A and Annex B address intentional production, Annex C calls for (i) the formulation of action plans at regional levels to address unintentional production from anthropogenic sources, and (ii) the application of Best Available Techniques (BAT) to abate emissions of these by-products.

Periodical reviews of POPs, conducted by the appointed POP Review Committee, are requested by Parties to the Conventions for listing of new chemicals based on the criteria specified in Annex D. To date, a further 18 chemicals have been added to the list; interestingly, all but one, PFOS and PFOS-F, are listed in Annex A (Table 2). Another criterion of considerable relevance to

Table 2 List of Persistent Organic Pollutants (POPs) under the Stockholm Convention as at January 2021 categorized by usage and Annex listing. Note that substances may be listed under multiple application categories.

	Pesticide by-products	Pesticides	Flame retardants	Insulation coating, plasticisers, solvents and lubricants	Incomplete combustion by-products
Initial 12 (legacy) POPs				HCB	PCDD
				PCB	PCDF
		DDT			
		Dieldrin			
		Endrin			
		Heptachlor			
		HCB			
		Mirex			
		Toxaphene			
Subsequent additions	alpha-HCH	Chlordecone	c-decaBDE	HBCDD	
	beta-HCH	Dicofol	HBCDD	HCBD	
		Endosulfan	hexaBDE and heptaBDE	PCNs	
		Lindane	Hexabromobiphenyl	PCP	
		PeCB	PeCB	SCCPs	
		PCP	PFOA		
			PFOS and PFOS-F		
			SCCPs		
			tetraBDE and pentaBDE		
Under review		Methoxychlor	Dechlorane Plus	UV-328	

Keys:

Annex A listed chemical (prohibited chemical)

Annex B listed chemical (restricted production and use of a chemical)

Annex C listed chemical (by-product chemical to be reduced or eliminated by BAT means)

Chemical listed under Annex A and Annex C

Acronyms: Alpha-HCH, alpha hexachlorocyclohexane; BAT, best available techniques; beta-HCH, beta hexachlorocyclohexane; c-decaBDE, decabromodiphenyl ether; DDT, dichloro-diphenyl-trichloroethane; HBCDD, hexabromocyclododecane; HCB, hexachlorobenzene; HCBD, hexachlorobutadiene; heptaBDE, heptabromodiphenyl ether; hexaBDE, hexabromodiphenyl ether; PCB, polychlorinated biphenyls; PCDD, polychlorinated dibenzo-*p*-dioxins; PCDF, polychlorinated dibenzofurans; PCNs, polychlorinated naphthalenes: PCP, pentachlorophenol, its salts and esters; PeCB, pentachlorobenzene; pentaBDE, pentabromodiphenyl ether; PFOA, perfluorooctanoic acid, its salts and PFOA-related compounds; PFOS, perfluorooctane sulfonic acid and its salts; PFOS-F, perfluorooctane sulfonyl fluoride; SCCPs, short-chained chlorinated paraffins; tetraBDE, tetrabromodiphenyl ether.

Sources: Secretariat of the Stockholm Convention (2018) *Stockholm Conventionon Persistent Organic Pollutants (POPs), Texts and Annexes-Revised in 2017*. Geneva: United Nations.

micropollutants is stipulated in Part [b] of Annex E, namely the profiling of risk caused by simultaneous exposure to multiple chemicals. As knowledge on toxicological interaction and ED potential of mixtures expands, more micropollutants will be proposed for review.

The Stockholm Convention provided a concerted action to address the global risk posed by legacy POPs. Despite the challenges associated by a Global Monitoring Plan (Magulova and Priceputu, 2016), the second global monitoring report (UNEP, 2017) shows declining environmental concentrations of legacy POPs, a clear demonstration of the success of this MEA.

PFOS and PFOA inclusion in the Stockholm convention annexes

Although not present in the initial set of POPs, flame retardants featured extensively in the subsequent 18 additions to the Stockholm Convention. A total of nine flame retardants were included since 2009, all but one becoming prohibited substances under Annex A (Table 2). Whereas PFOS and PFOS-F were listed in Annex B in 2009 (UNEP, 2009), the decision to add PFOA compounds to Annex A was reached in 2019, albeit with abundant exemptions (UNEP, 2019).

In the context of water pollution, the content of PFOA in firefighting foams is of primary importance. As part of the listing of PFOA, the Convention of the Parties included and addendum stipulating that, no later than 2025, the use of PFOA containing firefighting foams must be restricted to sites providing surface water drainage containment. Another amendment to the Convention relevant to water pollution was implement in 2011. The amendment, addressing the Global Monitoring Plan, called for the establishment of a monitoring program for PFOS in surface water with the aim of informing future evaluations (UNEP, 2011).

Synthesis

The intricacy of sources, applications and pathways of emission of organic micropollutants to the aquatic environment was presented in this article. Due to the wide diversity among organic micropollutants, environmental impacts and the hazard posed to human health vary substantially and are poorly understood for many compounds. Table 3 provides a succinct summary of these

Table 3 Summary of primary sources, pathways of emission, environmental fate and human health hazard for four classes of organic micropollutants.

Class	*Applications and sources*	*Pathways of emission*	*Fate*	*Environmental impact*	*Human health hazard*
PFAS (PFOS and PFOA)	Firefighting (aqueous film-forming foams), flame retardant additives, plasticisers, textile coating (stain-resistant and water-resistant coatings) pesticides, fluoropolymers, greaseproof paper	Dispersal of aqueous film-forming foams via urban drainage to WWT or storm overflow Discharge in WWT treated effluent WWT sludge spreading to land Textile coating is a primary source of legacy emissions	Prone to negative removal efficiency effect Highly persistent in the aquatic environment and resistant to natural degradation processes	Classed as POPs, with numerous potential impacts to receiving aquatic environments. Groundwater contamination difficult to treat	Tolerable weekly intakes of 6 and 13 ng kg^{-1} bodyweight for PFOA and PFOS[a] Serum total cholesterol levels (PFOA and PFOS) and attenuation of immune response in children's vaccinations (PFOS)
Biocides	Diffuse application to land or spot application	Runoff from land and urban areas Urban drainage to WWT or storm overflow Discharge in WWT treated effluent	Persistence and degradation vary, governed by substance physicochemical characteristics	Bioaccumulation and toxicity vary, governed by substance physicochemical characteristics	Toxicity varies, governed by substance physicochemical characteristics. Primary route of exposure through the food chain
Pharmaceuticals	Over the counter sales and prescription of human pharmaceuticals. Veterinary drugs administration to livestock	Discharge to wastewater Disposal of unused medicines to wastewater or landfill Discharge in WWT treated effluent WWT sludge spreading to land Runoff containing animal excreta from medicated livestock	Persistence generally low. Both persistence and degradation governed by substance physicochemical characteristics Subject to pseudo-persistence effect Negative removal efficiency effect known for some compounds	Bioaccumulation and toxicity vary but evidence of widespread impact is lacking. ED impact on fish by estrogenic compounds remains the primary concern	Acute exposure via drinking water unlikely. However, knowledge on effect of chronic exposure to trace concentrations is lacking

Table 3 (Continued)

Class	*Applications and sources*	*Pathways of emission*	*Fate*	*Environmental impact*	*Human health hazard*
Surfactants (nonylphenol)	Detergents, industrial and household applications	Discharge to wastewater WWT sludge spreading to land Disposal to landfill	Rapidly photodegraded (10–15 h half-life) but partitions strongly to sediments[b]. Subject to pseudo-persistence effect	Substantial evidence of bioaccumulation, biomagnification and ED properties. Maximum allowable concentration of 2.0 $\mu g\ L^{-1}$ for inland surface waters[c]	Recommended benchmark substance for ED risk assessment for drinking water by the WHO[d]
PCPs (triclosan and parabens)	Beautification and personal hygiene	Discharge to wastewater WWT sludge spreading to land Disposal to landfill	High removal by conventional WWT. PCPs can generate by-products with greater ED or toxicity potential during disinfection. Triclosan shown potential to generate dioxins by photolysis	ED characteristics. Triclosan bioaccumulates strongly	Potential exposure to triclosan, a possible carcinogen, through the food chain Information on parabens is lacking

Abbreviations: ED, endocrine disruptor; PCP, personal care product; PFAS, Per- and polyfluoroalkyl substances; PFOA, perfluorooctanoic acid, its salts and PFOA-related compounds; PFOS, perfluorooctane sulfonic acid and its salts; POP, persistent organic pollutant; WHO, World Health Organisation; WWT, wastewater treatment.

[a]Source: European Food Safety Authority (2014) Conclusion on the peer review of the pesticide risk assessment of the active substance amitrole. *EFSA Journal* 12(7): 3742.

[b]Source: Stasinakis AS and Gatidou G (2019) Micropollutants and aquatic environment. In: Virkutyte J, Varma RS and Jegatheesan V (eds.) *Treatment of Micropollutants in Water and Wastewater*. London, England: IWA Publishing.

[c]Source: European Union (2013) Council Directive 2013/39/EC of the European Parliament and of the Council of 12 August 2013, Amending Directive 2000/60/EC and 2008/105/EC as regards priority substances in the field of water policy. *Official Journal of the European Union* L226: 1–17.

[d]Source: European Union (2020) Council Directive (EU) 2020/2184 of the European Parliament and of the Council of 16 December 2020, On the quality of water intended for human consumption. *Official Journal of the European Union* L435: 1–62.

aspects of organic micropollutants. With the exemption of pharmaceutical products for human and animal utilization, knowledge of the impact on the environment in terms of PBT and ED properties has been well characterized for PFC and biocides and it is relatively well understood for the most common surfactants and PCPs. Largely because of the vast number of pharmaceuticals available on the market and the richness in their chemical structure diversity, knowledge of the potential hazard by trace levels of contamination of drugs to the aquatic environment is severely limited.

However, concern is rapidly shifting from the adverse effect caused by individual substances to potential amplifications of impacts generated by synergies and interactions of mixtures of organic micropollutants. This is a plausible concern warranted by extensive knowledge available on drug interaction. Yet, knowledge on the interactions of hundreds of pharmaceuticals emitted in unison is negligeable and the concern on chemical mixtures in the aquatic environment rightly extends to possible synergies between the various classes of organic micropollutants. Exacerbating the problem further, particularly so for aquatic environments, is the pseudo-persistence effect caused by continuous discharge of trace levels of some micropollutants, namely surfactants, PCPs, pharmaceuticals and short chain PFAS.

Because of these complexities, the problem of organic micropollutants will require an array of multifaceted solutions, among them improving removal technologies, greening chemistry and changing socio-economic models. The progress made by the Stockholm Convention demonstrates that multilateral alliances can provide systematic frameworks to achieve change; nevertheless, command and control currently remains the most viable alternative to address the emission of organic micropollutants.

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Microplastics in the Freshwater Environment

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This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Feeding guild A group of unrelated species that exploit the same environmental resources in a similar manner (e.g., detritivores, benthivores, herbivores, and so on).
Food chain: a linear network of trophic transfer links, within a food web, starting from a producer organism and ending at an apex predator species, detritivore, or decomposer.
Hazard A potential source of danger and/or harm.
Risk The likelihood that harm from a specific hazard will occur, and this is typically assessed by considering both the hazard and exposure to that hazard.
Trophic transfer The process by which constituents, including contaminants, are transferred from one trophic level to another.

Introduction

Micro-sized particles are ubiquitous in all ecosystems and, as a consequence, all living organisms are exposed to such particles. Most of these particles have a natural origin (e.g., spores, pollen, sand, silt or clay), but as a result of human activities, anthropogenic micro-sized particles are also present in the environment (e.g., particulate matter from combustion processes or microplastics) (Ogonowski et al., 2018). The threat of microplastic pollution is only starting to be recognized by the wider public (Henderson and Green, 2020). This contrasts with the public awareness of macroplastic pollution. The presence of plastic litter in the environment has caught the attention of the general public as well as policymakers. The collection of plastic debris on shores and/or in waterbodies by hand or using mechanical implements has demonstrated the extent of macroplastic pollution in the environment, as well as the dangers to wildlife through entanglement or following ingestion. Yet, a more insidious danger relates to the formation of smaller (less than 5 mm) micro- and nano-sized plastics from macroplastic waste.

Plastics are relatively new materials. Commercial production of plastics started in the early 1900s with Bakelite, and global production has increased from 5 million tonnes in the 1950s (Andrady and Neal, 2009) to 368 million tonnes in 2018 (Plastics Europe, 2020), a compound annual growth rate in production of more than 8% (Geyer et al., 2017). Characteristics such as durability, light weight, moldability and low production costs, have rapidly made plastics the key material of the current time (Thompson et al., 2009).

The term "plastic" refers to a range of synthetic materials that are mostly thermoplastic polymers of high molecular weight that can be moulded into films, fibers, filaments and other structures. Examples of commonly encountered plastics are polyethylene (PE), polypropylene (PP), polystyrene (PS), polyvinylchloride (PVC), polyethylene terephthalate (PET), and polyester, polyamide, and acrylic (PP&A). These different plastics share similar moldability and durability, but have distinct physicochemical properties,

which will determine their environmental fate and impacts on living organisms (Wang and Wang, 2018). For example, depending on its density a plastic may float or settle in the sediment, and the resulting differences in distribution will determine which organisms are exposed to these plastics. The vast majority of plastics produced are made using fossil fuels, and are not biodegradable (Geyer et al., 2017). They therefore accumulate rather than decompose in the environment unless recycled or incinerated. It has been estimated that if current production and waste management trends continue, roughly 12,000 megatonnes of plastic waste will be in landfills or in the natural environment by 2050 (Geyer et al., 2017).

Notwithstanding the environmental threat posed by macroplastics, a more insidious risk of plastics relates to small plastic particles, referred to as micro- and nanoplastics. The term microplastic was initially used rather loosely to indicate small pieces of plastics found in the natural environment (Thompson et al., 2004). A more advanced definition was proposed by Frias and Nash (2019) who described a microplastic particle as a "synthetic solid particle or polymeric matrix, with regular or irregular shape and with a size ranging from 1 μm to 5 mm, of either primary or secondary manufacturing origin, which is insoluble in water". Plastic particles smaller than 1 μm diameter are referred to as nanoplastics (Koelmans et al., 2019; Triebskorn et al., 2019).

Primary microplastics are those plastics that are manufactured as microparticles. Microbeads present in, for example, cosmetics or personal care products such as toothpaste or facial scrubs are typical primary microplastics. The majority of microbeads (93%) are made from polyethylene (UNEP, 2015). Napper et al. (2015) estimated that up to 94,500 particles can enter the environment per single use of a facial scrub. The use of microbeads in cosmetics is increasingly subject to restrictions in many countries, but it is expected that plastic microbeads, intact and/or after fragmentation into nanoparticles, will still be present in environmental samples for a long time due to their durability.

Secondary microplastics include plastic fragments and fibers, which are released when larger plastic objects disintegrate. The fragmentation of plastics into smaller pieces has been described as a slow process that is caused by exposure to UV light (i.e., photodegradation), heat (Andrady, 2011), wave-action and physical abrasion (Browne et al., 2011), or a combination of these processes. For example, due to wear-and-tear microplastics are released from tyres (Kole et al., 2017) and the artificial grass used in sports pitches (Mahon et al., 2014). Plastics and plastic fragments are highly durable and, depending on their chemical makeup, have been speculated to persist for hundreds of years, although accurate information on persistence is notably lacking (Ward and Reddy, 2020). Plastic microfibers from textiles are particularly common in environmental samples (Browne et al., 2011; Zambrano et al., 2020), including marine (Gago et al., 2018), freshwater (Miller et al., 2017), and indoor or outdoor atmospheric samples (Gasperi et al., 2018; Liu et al., 2019a). Most microfibers are released during washing and drying of textiles by consumers (Browne et al., 2011). The scope for microfiber release is subject to some debate, but it is estimated that a 6 kg wash load may release 700,000 fibers from an acrylic fabric, 500,000 fibers from a polyester fabric and 140,000 fibers from a polyester-cotton blend (Napper and Thompson, 2016). Other authors found in excess of 6 million microfibers per 5 kg wash load (De Falco et al., 2018). The former study referred to fibers between 12 and 18 μm in diameter, and 5–8 mm in length, while the latter considered fibers between 0.3 and 0.5 mm in length. Thus, small (<1 mm) microfibers in particular are generated in very large amounts during the laundry process. To make matters worse, tumble drying can subsequently release even more (three to four times) polyester microfibers than washing (Pirc et al., 2016). Notwithstanding the potential of some wastewater treatment plants to remove high percentages of microplastics, large numbers are likely to pass through filtration systems because of their small size (Horton et al., 2017). Furthermore, those microfibers (and other microplastics) contained within the sludges of wastewater treatment plants may still enter the freshwater environment at a later stage following application of the sludge as a soil improver (Horton et al., 2017). Thus, it is not surprising that microfibers are highly abundant in environmental samples (Browne et al., 2011; Zambrano et al., 2020).

It is now widely accepted that microplastics are widespread in terrestrial, marine and freshwater environments. The knowledge concerning the distribution and fate of microplastics and their impacts on the living organisms is rapidly increasing. However, major knowledge gaps remain, particularly for the freshwater environment. The aim of this chapter is to introduce some of the current understanding concerning micro- and nano-plastics in the freshwater environment, focusing on two key issues: Monitoring of distribution and assessment of biological impacts.

Monitoring microplastic in the freshwater environment

A prerequisite for understanding the ecological impacts of plastics is good quantitative knowledge of the distribution of plastics in the environment. Here we will discuss some of the current microplastic monitoring approaches and their shortfalls, but also the important finding that microplastics are ubiquitous in the natural environment.

The technology to monitor microplastics in the environment is not yet standardized

Notwithstanding a drive to recycle and/or incinerate plastic waste, plastic litter is now pervasive in the environment (Gall and Thompson, 2015). Indeed, plastics are so prevalent that they are now referred to as a stratigraphic indicator for the Anthropocene (Waters et al., 2016). The visible presence of macroplastic waste has become an issue of public and policy concern. Plastics are predominantly of terrestrial origin, and enter the freshwater environment either as diffuse, general litter, or through specific point sources such as wastewater treatment discharges (Horton et al., 2017). In the environment, plastics tend to fragment, resulting in the formation of smaller, secondary plastics, including micro- and nanoplastics. These small plastic particles are now considered ubiquitous in the environment (Rochman, 2018). Indeed, multiple studies have reported the presence of microplastics in air, food

and drinking water samples (Koelmans et al., 2019), as well as in far flung places such as the deep sea (Van Cauwenberghe et al., 2013) and the Arctic (Cózar et al., 2017). Based on their pervasive presence in the freshwater environment, the ability to adsorb other pollutants and the potential to cause negative impacts when ingested by organisms, Wagner et al. (2014) proposed to categorize microplastics as Contaminants of Emerging Concern (CECs) for the freshwater environment.

Actual concentrations of microplastics in the freshwater environment can vary dramatically, depending on factors such as water depth, currents, and wind exposure (Horton et al., 2017). Tens to hundreds of microplastic particles have been found per kg of dry sediment (Horton et al., 2017), while water samples can contain anything between 1×10^{-2} and 1×10^{8} particles per m^3, with highest concentrations found in wastewater treatment effluent (Koelmans et al., 2019). High microplastic concentrations tend to be associated with urbanization (Horton et al., 2017). However, it is likely that a major determinant of the variation in microplastic concentration is the sampling technology. Monitoring of microplastics in the environment is still under development, and standardized monitoring protocols and units of measurement are lacking (Rodrigues et al., 2018; Koelmans et al., 2019). Sampling of microplastics in the water column typically involves the use of filters with mesh sizes varying between 50 μm and 500 μm. Not surprisingly, the abundance of plastics is far greater when filters with a small mesh size are used; however, such filters easily clog up with non-plastic microparticles (Stock et al., 2019; Lindeque et al., 2020). As a consequence, most environmental monitoring studies fail to monitor microplastics in the sub-200 μm range (O'Connor et al., 2020). Thus, information on the presence of nanoplastics in natural environments is substantially lacking.

Surface layer plastics are sampled using a variety of implements, including rotating drum samplers, while sediment samples are taken using grabbers, box or drill corers (Stock et al., 2019). Sample preparation (e.g., the separation of microplastics, water, sediment and organic material) using density and/or electrostatic separation techniques and chemical or enzymatic digestion is followed by characterization of particles using specialized analytical techniques such as Fourier-transform infrared spectroscopy, Raman microscopy, and pyrolysis gas chromatography (Stock et al., 2019). Yet, in practice the determination of polymer identity is often lacking (Li et al., 2018; Koelmans et al., 2019). Identifying the chemical composition of plastic particles is critical from an impact perspective. However, it is also a complex and expensive challenge because the various plastic polymers used in commercial plastics are complemented by additives such as plasticizers, fillers, flame retardants and dyes (Geyer et al., 2017; Rochman et al., 2019). Due to the lack of standardized microplastic measurement and analysis protocols, extreme care is required when interpreting quantitative data on the prevalence of microplastic pollution. Furthermore, data on the perceived ecotoxicological risks associated with microplastics in the freshwater environment should be interpreted against a background of limited information on environmental concentrations and polymer identity (Triebskorn et al., 2019).

Microplastics are ubiquitous in the freshwater environment

Monitoring has, up to now, focused disproportionally on marine plastics. In contrast, studies on the presence of microplastics in freshwaters are relatively scarce. It appears that some of the early studies on microplastics perceived streams and rivers simply as channels that transfer terrestrial plastics to the marine sink, ignoring the vital ecological, economic, cultural, and aesthetic importance of freshwater environments. In sharp contrast, a host of recent studies has revealed that freshwater systems do not just transport plastics from land to marine environments, but are microplastic pollution sinks (Ballent et al., 2016; Wagner and Lambert, 2018), as well as a starting point for the transfer of plastics through food webs (Gouin, 2020) (Fig. 1). Rivers near urban and industrial centers are now considered hotspots of microplastics pollution (Horton et al., 2017), while lakes may act as microplastic sinks (Free et al., 2014). Microplastics can be found on the freshwater surface, in the water column (Lechner et al., 2014; Mani et al., 2015; Miller et al., 2017), and in benthic sediments (Castañeda et al., 2014; Klein et al., 2015; Tan et al., 2016; Pomeroy et al., 2017; Hurley et al., 2018). Polyethylene, polystyrene and polypropylene based plastics are most frequently found in freshwater samples, and this finding is likely to reflect plastic production and use, as well as the actual polymer density. The most common plastic forms observed in freshwater samples are microfibers and fragments, with lesser numbers of films and microbeads (Horton et al., 2017; Hurley et al., 2018; Koelmans et al., 2019). Water samples from rivers and lakes contain both small and medium size microparticles (<1 mm). Yet, the lack of standardized microplastic monitoring protocols, makes quantitative comparisons across different studies using different protocols problematic (Koelmans et al., 2019).

Notwithstanding uncertainties with respect to the quantification of microplastics in the freshwater environment, there is no doubt that such plastics are ubiquitous. Given the rapid progress in the development of monitoring technology, it can reasonably be expected that more accurate quantitative information on microplastics in the freshwater environment will increasingly become available in the coming years. However, major challenges remain with respect to the quantification of nanoplastics and the chemical characterization of nano- and microplastics. Nevertheless, such information is critically needed to inform impact studies and risk assessments.

Effects of microplastics on freshwater organisms

Substantial research efforts are being made to analyze the impacts of microplastics on freshwater organisms. Yet, there is still a lack of consensus regarding the biological effects of micro- and nanoplastics on organisms, and especially ecological communities. Here we consider the uptake by, and presence of microplastics in freshwater organisms, as well as the evidence for impacts on these species.

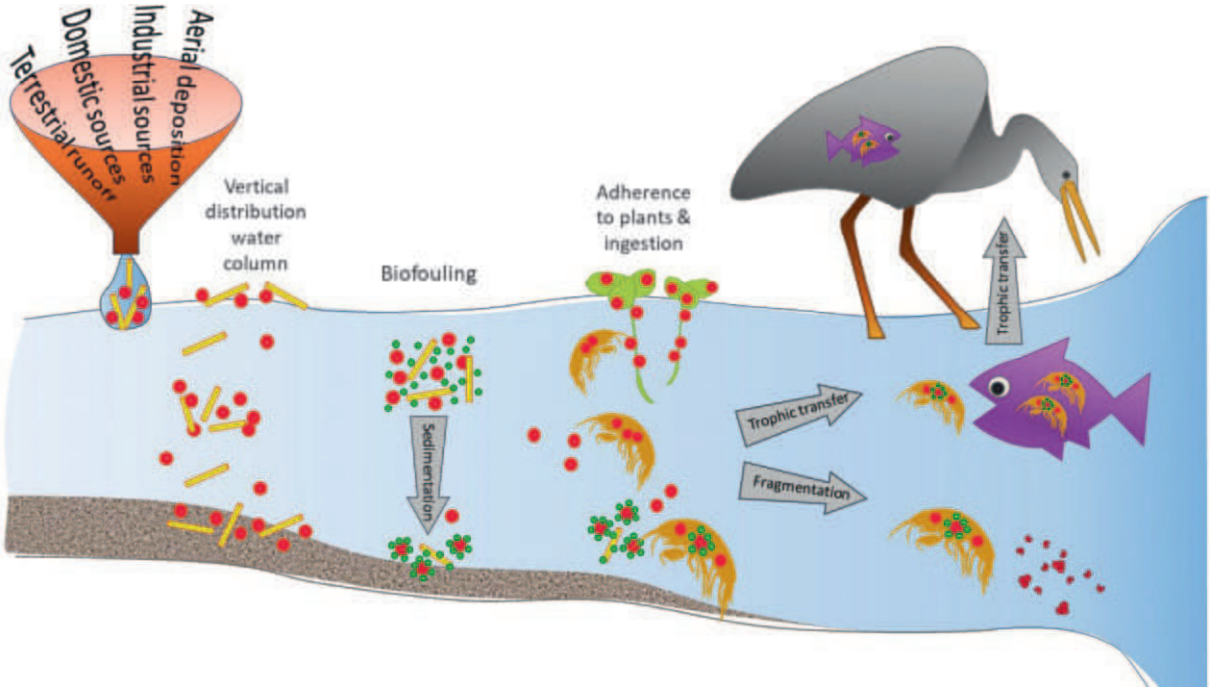

Fig. 1 Conceptual graphic showing key aspects of microplastic pollution in the freshwater environment. Micro- and nanoplastics enter the freshwater environment from a potentially large variety of different terrestrial sources. Depending amongst others on the density of the specific plastic polymer, microplastics float, are suspended in the water column, or settle in the sediment, resulting in a particular vertical distribution that will have consequences for the type of organisms exposed to these plastics. Biofouling of microplastics, and formation of aggregates with organic or inorganic detritus will accelerate sedimentation, but may also increase "accidental" ingestion by various organisms. Ingestion of microplastics may also relate to the adherence of plastics to plants and macroalgae. Once ingested, microplastics may be fragmented into nanoplastics, which are thought to be potentially more hazardous than microplastics. Furthermore, trophic transfer of ingested plastics will result in large numbers of species being exposed to plastics.

Microplastics are found inside organisms

Given the presence of micro- and nanoplastics in the freshwater environment, organisms will unavoidably be exposed to these polymers (Fig. 1). Indeed, microplastics have been identified inside a variety of freshwater organisms. For example, 75% of all sampled bayflies (*Chironomus* spp.) collected in the summer from South African rivers were found to contain microplastics, and this increased to 98% in the winter (Nel et al., 2018). The reported microplastic load varied between 0 and 1.4 particles per mg body weight during the summer, but increased up to 5.04 particles per mg in the winter (Nel et al., 2018). The microplastic load in the bayflies was positively correlated with the microplastic load in the sediment, indicating the lack of an organismal avoidance response. Rather, seasonal flow dynamics were found to be the major determinant of concentrations of microplastics in the sediment, and hence organismal plastic loads. Mayflies (*Baetidae* spp. and *Heptageniidae* spp.) and caddisflies (*Hydropsychidae* spp.) were similarly found to have ingested microplastic particles (Windsor et al., 2019), while Hurley et al. (2017) noted microplastic concentrations of 0.13 particles mg^{-1} body weight in sediment dwelling sludge worms (*Tubifex tubifex*). Microplastic ingestion is not limited to invertebrates. Microplastics have been identified in more than 200 freshwater species (Azevedo-Santos et al., 2021), including species of riverine fish (Collard et al., 2018; McNeish et al., 2018) and amphibians (Azevedo-Santos et al., 2021), in faecal samples of birds (D'Souza et al., 2020) and mammals (Smiroldo et al., 2019), as well as attached to plant surfaces (Mateos-Cárdenas et al., 2019). These data emphasize the apparent lack of a microplastic avoidance response, i.e., once present in the environment, it is likely that all parts of the aquatic food web will be exposed to these particles.

Impacts of microplastics on biota

A pertinent question concerns the effects of plastic particles on organisms. There is currently no consensus regarding the impacts of micro- and nanoplastics on living organisms, although a range of potential effects have been proposed. For example, and depending on attributes such as size and chemical composition (Carbery et al., 2018), ingested plastic particles can cause lacerations, inflammations, and immune responses. Plastics can also accumulate in organisms and interfere with feeding, leading to starvation, although there is currently no evidence for substantial bioaccumulation of microplastics in organisms. Some studies have shown that plastics can cross the gut wall and enter internal tissues (Farrell and Nelson, 2013) and this would be particularly the case for smaller plastics, i.e., nanoplastics. Understanding of the toxicology of nanoplastics is still limited, but cytotoxicity is associated with nanoplastic-induced oxidative stress, protein modification, DNA fragmentation, membrane damage and alterations in gene expression (Kihara et al., 2020).

Thus, plastics may impact on cells, tissues and/or organisms in a number of ways, through direct physical interactions, as vehicles for surface adhering contaminants or through direct toxicity of the plastic and its constituents themselves. Yet, while some studies have revealed negative impacts, others failed to do so. There are several reasons underlying the lack of agreement among studies. Firstly, microplastics comprise a bewildering assortment of different materials with different physicochemical characteristics, including polymer type, size, shape and presence of additives and contaminants (Triebskorn et al., 2019). Additives in particular have received considerable attention. Potentially, toxic effects can be related to additives, such as dyes, UV stabilizers or plasticizers, all of which may leach out of plastics. For example, phthalates are plasticizers that are also endocrine disruptors (Sheikh and Beg, 2017). Furthermore, the physical and chemical properties of micro- and nanoplastics, including their high surface area-to-volume compared with macroplastics, can facilitate adherence of further pollutants. In particular, hydrophobic contaminants can easily adhere to the hydrophobic surfaces of plastics (Hartmann et al., 2017). Marine studies have demonstrated adherence of polyaromatic hydrocarbons (PAHs), and polychlorinated biphenyls (PCBs) to polypropylene and polyethylene pellets (Frias et al., 2010), as well as adherence of cadmium and lead to plastic pellets collected from beaches (Ashton et al., 2010). It has been argued that such adherence results in the creation of a vector for contaminants, with release of pollutants inside organisms as a result of exposure to acidic gut conditions as shown by Batel et al. (2016). Yet, the environmental evidence for such adherence and release processes is not conclusive (Triebskorn et al., 2019). In summary, it appears that micro- and nanoplastics can cause direct, rather generic effects (e.g., lacerations, inflammations, impediments of feed intake) once ingested by organisms. These effects may be complemented by impacts related to the specific type of plastic, used additives, and adhering pollutants. Thus, the question is not whether microplastics are toxic, but rather which plastics are toxic under which environmental conditions (Triebskorn et al., 2019).

At present, the number of toxicological studies quantifying impacts of microplastics on freshwater organisms is limited, particularly in comparison with the extensive knowledge describing impacts of microplastics on marine species (Wegner et al., 2012; Cole et al., 2015). Most studied are impacts of plastics on daphnids, a common freshwater model species for toxicological testing. Acute exposure of the filter feeder *Daphnia magna* to polyethylene microbeads (size 1–100 μm) resulted in immobilization (Rehse et al., 2016), while exposure to polyester microfibers (length 300 μm) negatively impacted *D. magna* survival in the absence of food (Jemec et al., 2016). Acute exposure of *D. pulex* to a high concentration of polystyrene nanoplastics caused mortality with a 48-h median lethal concentration of 77 mg nanoplastic per liter (Liu et al., 2019b). Conversely, exposure of *D. pulex* over three 21-day generations to a more environmentally relevant concentration of polystyrene nanoplastics did not affect survival, although a range of subtle physiological changes were noted (Liu et al., 2020). Apart from concentration, size is a key determinant of toxicity to daphnids. While 50 nm polystyrene nanoplastics are highly toxic for *D. magna* in acute exposure studies, no mortality was caused by 200–500 nm nanoplastics (Frankel et al., 2020). Another important determinant of toxicity is nanoplastic surface structure. Polystyrene nanoparticles with added surface groups (amine- and carboxylate-groups) are less toxic to *D. magna* compared with the non-modified nanoplastics (Lin et al., 2019).

These daphnid studies demonstrate a broad range of biological effects of nano- and microplastics. Older studies were typically performed using pristine (non-weathered) microplastics (>5–10 μm) which are less likely to be taken up in the tissues or cells of exposed organisms, compared with nanoplastics. More recent studies have focused on nanoplastics which can potentially enter cells and tissues through processes ranging from diffusion to endocytosis (Triebskorn et al., 2019), and, therefore, pose a greater threat. By and large, observed effects refer to potential hazards, resulting from short-term (i.e., acute) exposure to an excessively high concentration of pristine plastics under laboratory conditions. In contrast, in the natural environment, exposure of organisms involves two important differences. Firstly, organisms are more likely to be chronically exposed to much lower concentrations of plastics. Secondly, it has been argued that plastics in the natural environment may act as vectors of adhering pollutants already present in the environment. At present, there is an urgent need to improve our understanding of how low concentrations of nanoplastics affect freshwater organisms, as well as their communities. This, in combination with advanced environmental monitoring of plastics, can lead to an informed risk analysis concerning plastics in the environment.

Biota alter microplastics in the freshwater environment

Microplastics can affect a broad range of organisms. However, the reverse is also true, biota can affect microplastic distribution, fate and fragmentation. Here we consider three specific processes: biofouling of plastics by microorganisms, adherence to plant structures and fragmentation by consumer species.

Biofouling of plastics

Depending on specific density, a substantial part of plastic waste entering the aquatic environment will sink and end up in sediments. Relatively dense plastics, such as polystyrene, will sink readily. However, less dense plastics often sink as well because of biofouling by microorganisms, sometimes in combination with larger organisms such as plants, macroalgae and small animals. Kaiser et al. (2017) demonstrated how the formation of a biofilm accelerated sinking of polystyrene and polyethylene microplastics in marine and estuarine waters. Investigating the sedimentation of low-density plastics in a freshwater system, Leiser et al. (2021) observed how phototrophic cyanobacteria (*Chamaesiphon* spp. and *Leptolyngbya* spp.) precipitated calcite while forming biofilms on microplastics, leading to increased sinking of polyethylene particles. Analyses of microplastics isolated from sediment attributed the relative high density to a combination of biofouling and adherence of inorganic minerals (Wu et al., 2020). Apart from increasing

the density, biofilms can secrete sticky polymeric substances which aid in the formation of larger aggregates of microplastic particles with organic and inorganic detritus that alter the density and therefore the distribution of plastics in the environment (Besseling et al., 2017).

Consequences of biofouling are far reaching. The presence of a biofilm, as well as the resulting sedimentation, may shield plastics from UV radiation, slowing down light-dependent fragmentation of macroplastics into micro- and nanoplastics (Gerritse et al., 2020). Furthermore, the altered vertical distribution of particles in the water column will alter the exposure of specific feeding guilds to these particles. It has also been reported that the formation of a biofilm may actually attract organisms that use olfactory and gustatory cues to select feed (Carbery et al., 2018). Thus, biofouling may contribute to feeding by organisms on plastic (Kooi et al., 2017).

Fragmentation of plastics

Plastics in the natural environment are subject to weathering, fragmentation and mineralization, with rates that differ for different types of plastics (Gerritse et al., 2020). Fragmentation results in the formation of smaller particles, i.e., micro- and nanoplastics, and has been largely associated with a combination of mechanical processes, including abrasion, and photodegradation following exposure to UV wavelengths. Recently, the role of biota in fragmentation has been highlighted. Microorganisms such as bacteria and fungi have long been implicated in plastic degradation (Horton et al., 2017), but it was shown that common freshwater invertebrates can also fragment some microplastics (Mateos-Cárdenas et al., 2020; Hasegawa and Nakaoka, 2021). Mateos-Cárdenas et al. (2020) demonstrated the generation and accumulation of polyethylene nanoplastics from microplastics in the digestive tracts of *Gammarus duebeni* following just a few days of plastic exposure (Figs. 1 and 2). Similarly, Hasegawa and Nakaoka (2021) showed that mysids (*Neomysis* spp.) fragment polyethylene microplastics, and that these fragments are ingested by the benthic fish *Myoxocephalus brandti* when it feeds on these crustaceans. Such nanoplastics are perceived as a greater environmental hazard than microplastics, as they can cross into cells and cause adverse effects in microalgae (Besseling et al., 2014), macrophytes

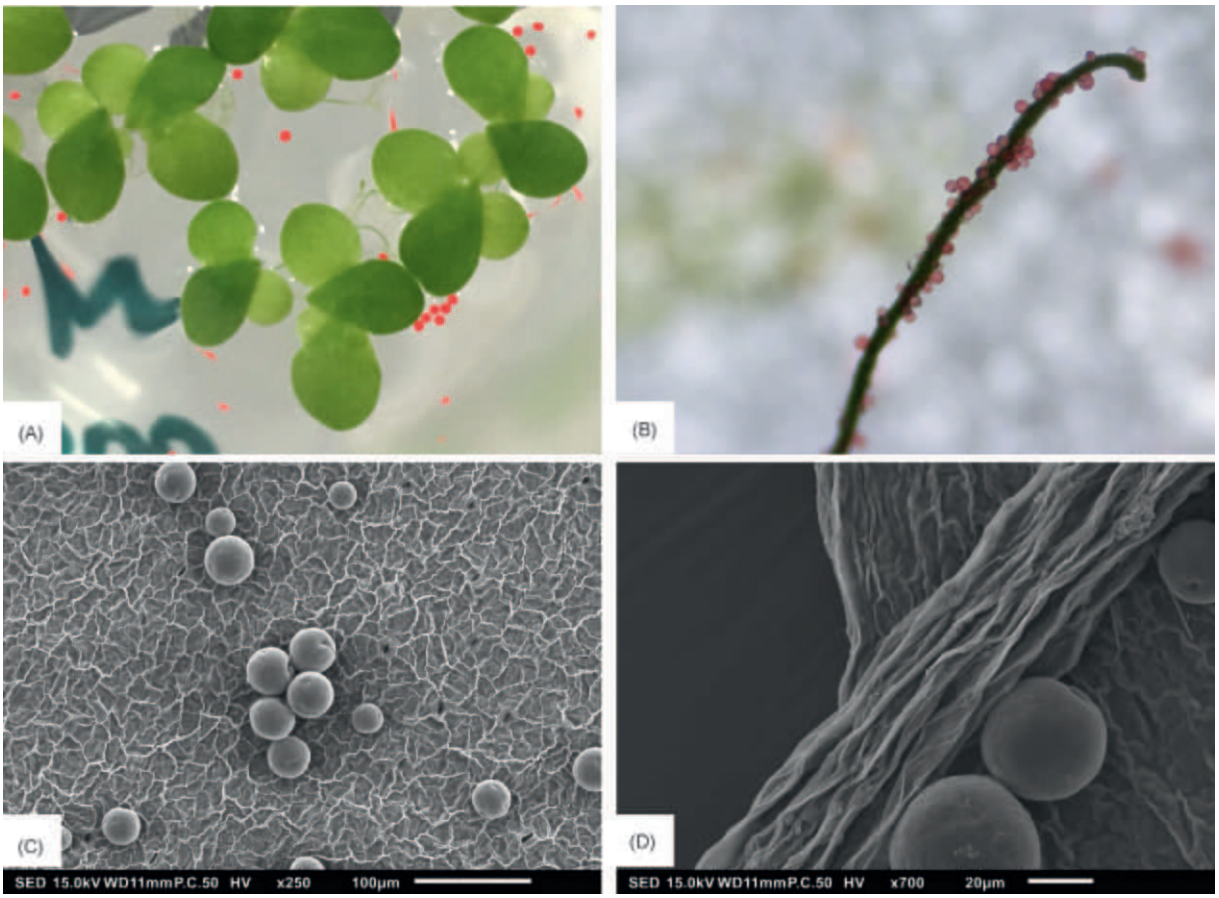

Fig. 2 Adherence of microplastics to plants and microalgae can be a step towards ingestion by herbivores and detritivores. Here, 30 µm diameter brightly stained polyethylene beads are seen to adhere to the duckweed *Lemna minor* (panels A and B, respectively). Using Scanning Electron Microscopy, adherence of 30 µm microplastics to the adaxial surface of the duckweed frond, and to the root can be seen (panel C and D). Size bars are shown for panels C and D. Full details in Mateos-Cárdenas et al. (2019).

(van Weert et al., 2019) and invertebrates (Cui et al., 2017). These discoveries reveal that once larger plastics are allowed to accumulate in the environment, the formation of more hazardous nanoplastics is almost unavoidable due to mechanical, photochemical and biological fragmentation processes. This, in turn, implies that prevention and/or capture of polluting macroplastics is essential to avert formation of micro- and nanoplastics.

Adherence of plastics to aquatic plants

There is a striking lack of studies on the effects of micro- and nanoplastics on freshwater plants and macroalgae. Those studies that explored potential effects did, in general, identify at most minor effects on growth and development. For example, Mateos-Cárdenas et al. (2019) found that exposure of the duckweed *Lemna minor* to polyethylene microbeads did not affect growth, biomass accumulation and photosynthesis. Kalčíková et al. (2017) also found no effects of polyethylene microplastic particles on *Lemna minor* leaf growth and photosynthetic pigments, but reported that sharp-shaped particles caused some root damage. However, a remarkable find was that microbeads were adsorbed to the roots of aquatic duckweed (*Lemna minor*). Mateos-Cárdenas et al. (2019) showed that a single *L. minor* colony can adsorb as many as 125 polyethylene microplastic particles after 72 h exposure (Fig. 3). Similarly, it was found that nanosized plastic particles adsorbed externally to the duckweed *Spirodela polyrhiza*, although no nanoplastics were observed inside plant tissues (Dovidat et al., 2020). However, other studies have shown that nanoplastics can be taken up in the tissues of exposed plants (Ma et al., 2010; Chae and An, 2020).

The mechanisms of microplastic adsorption onto plant surfaces are unclear. It is speculated that absorbance is the result of the affinity of some microplastics for hydrophobic substances (Xia et al., 2020), such as waxy plant cuticles. Irrespective of the mechanism, the relevance of adherence of plastics to plant and algal surfaces is substantial even when they may have no impact on plant health. Plants and algae are at the bottom of the food web, and therefore adsorption of microplastics is directly relevant for trophic transfer of plastics to herbivorous organisms, and further up the food chain, potentially to human consumers.

Trophic mobility of plastics

The transfer of microplastics through the food web is of serious concern and may, among others, result in exposure of human consumers to microplastics. Here we consider some of the evidence that indicates that trophic transfer of microplastics in the freshwater environment is likely to be widespread.

The literature contains ample evidence that microplastics are commonly present inside freshwater macroinvertebrates (Fig. 4) (Windsor et al., 2019; Triebskorn et al., 2019; Li et al., 2020). Micro- and nanoplastics are also present on plant surfaces (Kalčíková et al., 2017; Mateos-Cárdenas et al., 2019). Given that these organisms constitute basal trophic resources, there is a potential risk of transfer of plastics to organisms higher up in the food web by trophic transfer. Indeed, microplastics have been identified in riverine fish (Collard et al., 2018; McNeish et al., 2018) and amphibians (Azevedo-Santos et al., 2021), as well as faecal samples of birds (D'Souza et al., 2020) and mammals (Smiroldo et al., 2019). Hasegawa and Nakaoka (2021) compared microplastic ingestion directly from the water column with ingestion through feed, and concluded that trophic transfer of plastics from mysids to the benthic fish *Myoxocephalus brandti* considerably exceeds direct uptake from the water column. It was concluded that trophic transfer of microplastics is a key exposure route for organisms at higher trophic levels.

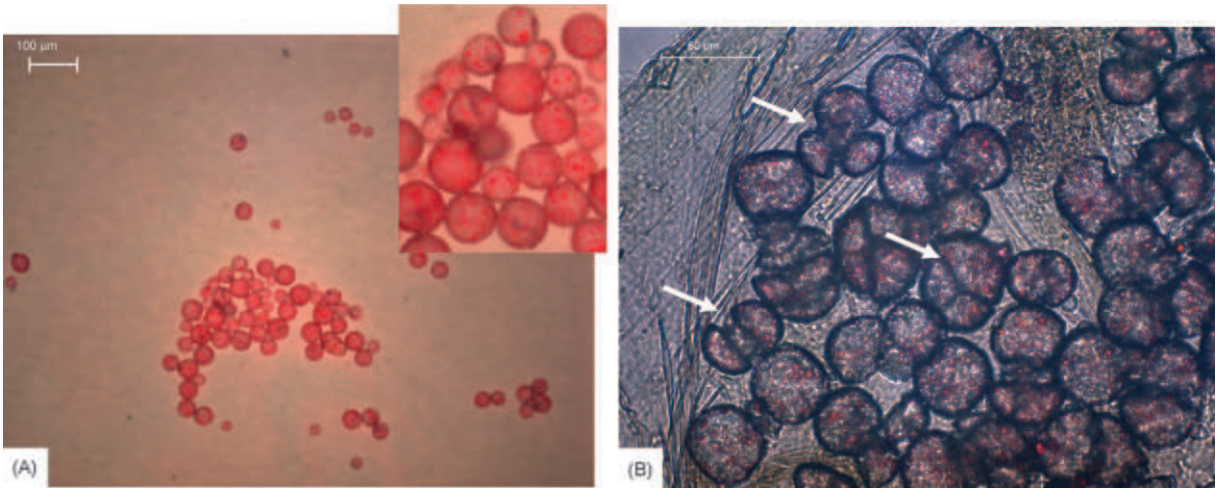

Fig. 3 Ingestion of microplastics by the invertebrate *Gammarus duebeni* can lead to fragmentation, and generation of nano-sized fragments. Here, a suspension of 30 µm diameter stained polyethylene beads are visualized using fluorescent microscopy (panel A). The same microplastics visualized using light microscopy in the gut of *G. duebeni*, display distinct cracks, leading to fragmentation (panel B). Size bars are shown. Full details in Mateos-Cárdenas et al. (2020).

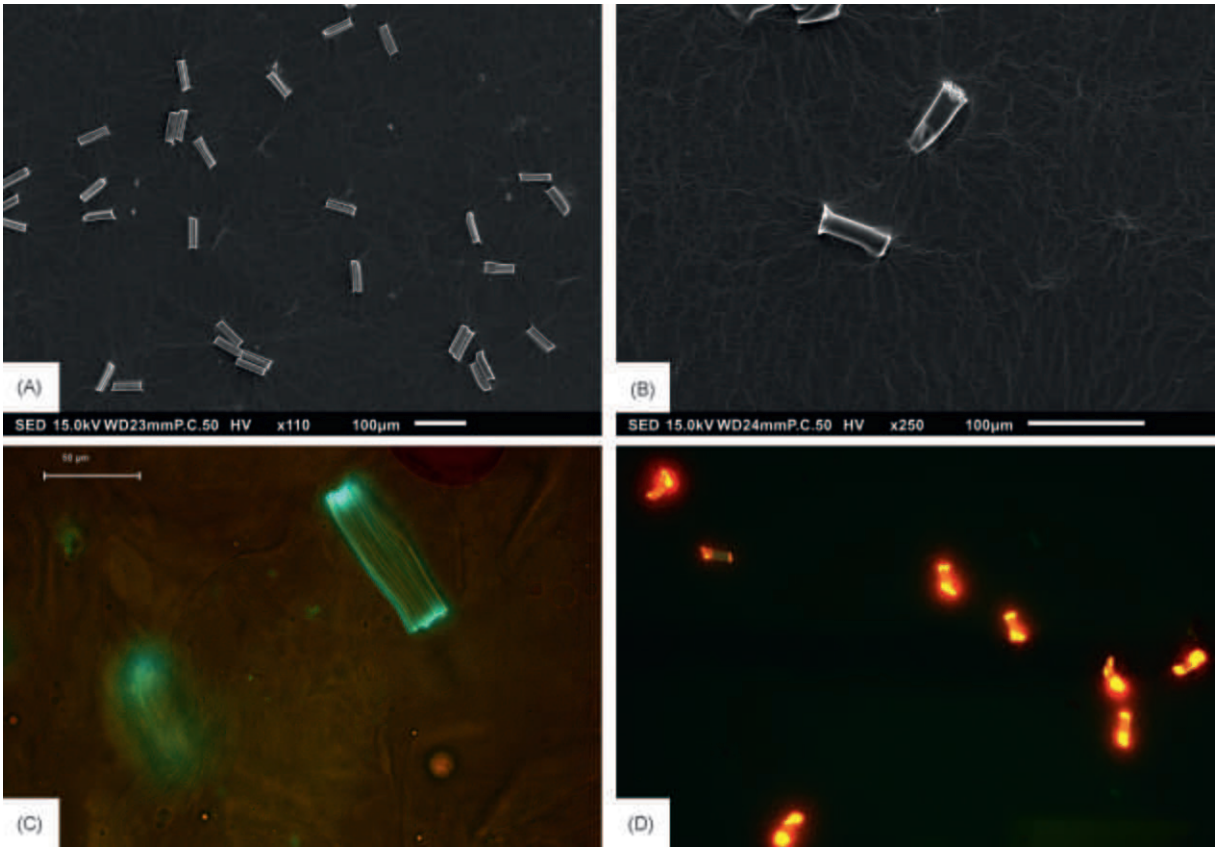

Fig. 4 Plastic microfibers are amongst the most common type of microplastics in the natural environment. Here, short cellulose and polyester fibers are visualized using Scanning Electron Microscopy (panel A and B, respectively). Using fluorescent microscopy, cellulose (panel C) and polyester (panel D) microfibers were also visualized to accumulate in the digestive tract of *G. duebeni*. Size bars are shown in panels A, B, and C. Full details in Mateos-Cárdenas et al. (2021).

The importance of trophic transfer was confirmed by a recent study which demonstrated the ingestion of microplastics by the Eurasian dipper (*Cinclus cinclus*). Modelling indicates that some 200 plastic particles can typically be ingested per day by these birds. Plastics were identified in some 50% of regurgitates and 45% of fecal samples, and concentrations in these samples were positively linked to local environmental concentrations (D'Souza et al., 2020). Plastic uptake by the dipper was directly associated with ingestion of microplastic-containing prey. Indeed, freshwater macroinvertebrates such as gammarids are a key staple of the dipper (Taylor and O'Halloran, 1997), but also for a range of other species such as brown trout *Salmo trutta* (MacNeil et al., 1999), implying that trophic transfer of plastics is likely to be widespread in the freshwater environment.

So far, microplastic trophic transfer studies have predominantly investigated prey-predator interactions, studied either under controlled experimental conditions (Athey et al., 2020; Hasegawa and Nakaoka, 2021) or in the natural environment (Nelms et al., 2018), with less attention to primary producers like plants. Nevertheless, adsorption of microplastics to plant surfaces is of concern given the role of plant biomass as food for herbivores, omnivores and detritivores. A recent study shows quantitative transfer of microplastics from the primary producers *L. minor* to the consumer *G. duebeni* in a model freshwater food chain (Mateos-Cárdenas et al., 2019). The implications of the finding of trophic transfer from *L. minor* to *G. duebeni* go beyond the actual species and are relevant for entire ecosystems. While the trophic transfer of microplastics in freshwater systems remains less well understood than that in marine environments (e.g., Carbery et al., 2018), it can be speculated that such transfer will result in all parts of the aquatic food web being exposed to micro- and nanoplastics.

Conclusion—synthesis

Technology to monitor microplastics in the natural environment is developing rapidly. However, at present there are no agreed standardized monitoring protocols to determine microplastic concentrations and analyze plastic composition, and as a result it is difficult to compare data generated by different research groups. Furthermore, current technology mostly monitors macroplastics, and larger microplastics, but fails to assess the presence of potentially more hazardous nanoplastics in the natural environment. Nevertheless, it is clear that both micro- and nanoplastics are ubiquitous throughout terrestrial, marine and freshwater environments.

Microplastics in the freshwater environment remain insufficiently studied. Yet, it has become evident that freshwater systems are not just a conduit for transport of plastics from terrestrial sources to the marine sink. Rather, freshwater systems themselves are important sinks for plastics, with widely reported observations on the presence of microplastics in the sediment as well as inside freshwater invertebrates, fish, amphibians, birds and mammals, as well as adherence to plant and algal surfaces (Fig. 1). Despite the pervasive presence of microplastics inside freshwater organisms, there is lack of consensus concerning the impacts of micro- and nanoplastics on these organisms. It is likely that nanoplastics are more hazardous than microplastics, while additives (e.g., plasticizers, dyes and UV-stabilizers) and adhering pollutants (e.g., polyaromatic hydrocarbons) further add to their hazard potential. Nevertheless, given the level of uncertainty with respect to actual microplastic concentrations in the environment, it remains unknown to what extent these potential hazards pose a real risk to freshwater species and communities. While there is a strong extent of uncertainty with respect to the impacts of microplastics on freshwater organisms, the opposite is becoming quite clear: Biota can impact on microplastics in the freshwater environment. Biofouling can increase the density of plastics resulting in increased sedimentation. Ingestion by invertebrates may result in fragmentation into smaller plastics, including potentially more hazardous nanoplastics. Adherence to plant surfaces does remove some of the freely suspended plastics from the water column, but may result in increased ingestion by herbivorous species. Indeed, an important finding is the trophic transfer of microplastics throughout the freshwater food web.

In conclusion, once macroplastics are discharged into the aquatic environment, processes such as fragmentation, ingestion and trophic transfer will spread these plastics in the form of micro- and nanoplastics throughout the aquatic food web (Fig. 1). Currently, no effective techniques are available to remove micro- and nanoplastics from the natural environment. Therefore, the emphasis in water management needs to be on prevention of plastic pollution rather than remediation.

Knowledge gaps

- There is a lack of quantitative data on the presence of microplastics in the freshwater environment, and this relates to a lack of standardized protocols for monitoring the presence of plastic particles.
- There is a need to develop novel methods to detect and quantify nano-, and possible even smaller, plastics in the environment.
- The environmental fate of plastics in the freshwater environment, including distribution, transport, sedimentation, fragmentation, ingestion and adsorption, remains to be fully established.
- The hazards, and especially risks, posed by micro- and especially nanoplastics to freshwater species and communities remain unclear.
- The roles of additives and adhering pollutants in microplastic toxicity remain to be fully established.

See Also: ; Human pressures and management of Inland Waters: Case Studies of (Semi)Constructed Wetlands Treating Point and Non-point Pollutant Loads to Protect Downstream Natural Ecosystems; Emerging and Less Commonly Recognized Chemical Contaminants: Organic Micropollutants; The Role of Wetlands in Mitigating Impacts From Diffuse Agricultural Loads

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Constructed Wetlands for Urban Wastewater Treatment: An Overview

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Constructed wetland Manmade wetland ecosystems, engineered in such a way that they make optimal use of the biological, physical and chemical processes offered by wetland vegetation, microorganisms and soil/filling media to purify water.
Ecological engineering Design, construction and management of ecosystems that have value to both humans and the environment.
Intensified constructed wetlands CWs with extra engineering features such as active aeration or recirculation or special filling media, typically with the aim of improving treatment efficiency and thus reducing the area needed.
Population or Person Equivalent—PE The water based organic biodegradable pollutant load produced per capita per day. In EU legislation, 1 PE = 60 gBOD/cap/day. Actual numbers vary however based on water and food consumption patterns.
Primary treatment The removal of undissolved particles and preparation for secondary treatment.
Secondary treatment The treatment of waste water, generally through a biological process, to remove the largest part of the biological oxygen demand.
Subsurface flow constructed wetlands CWs where the water flows either vertically or horizontally below the ground surface through a porous medium such as sand or gravel.
Surface flow constructed wetlands CWs where the water flows above the ground surface and where there is direct contact between the water and the atmosphere.
Tertiary treatment Also called 'polishing' or 'advanced treatment'. The treatment of secondary treated wastewater to further improve quality for discharge into the receiving water body.
Urban wastewater Usually a mix of domestic wastewater, stormwater and (possibly already partially treated) artisanal/industrial wastewater.

Introduction and aim of the chapter

Most domestic, industrial and agricultural activities generate wastewater streams which, depending on the specific activity, contain varying concentrations of organic matter, nutrients, inorganic (e.g., heavy metals) and organic (e.g., pesticides, pharmaceutical residues) micropollutants and pathogenic microorganisms. According to estimations from the United Nations (UN Water, 2017), more than 80% of all wastewater generated globally is discharged to the environment without adequate treatment. This threatens not only ecosystem health through phenomena such as oxygen depletion, eutrophication, ecotoxicity, but also threatens human health of those people depending on the water resources where the wastewaters are discharged. In addition, valuable and non-renewable resources such as phosphorus and metals are in this way lost to the environment.

In a reaction to these problems, wastewater treatment technologies were developed from the late 1800s onwards (Lofrano and Brown, 2010). While originally focused on improving hygienic conditions, through time the focus shifted to environmental protection and in recent years to resource recovery, each time posing more stringent demands on effluent quality. Many of the commonly used wastewater treatment technologies are, however, very resource intensive, both during the building phase (construction materials) and during their operational life (energy for pumping and aeration, sludge conditioning chemicals) (Garfí et al., 2017). In the 1960s, German researchers developed a new, resource-extensive technology which was entirely based on the self-purification capacity of nature: constructed wetlands (CWs). CWs are defined as manmade wetland ecosystems, engineered in such a way that they make optimal use of the biological, physical and chemical processes offered by wetland vegetation, microorganisms and soil to purify water. An alternative term is treatment wetlands, to distinguish them from other "constructed" (i.e., artificial) wetlands whose primary purpose is nature restoration rather than water purification.

Apart from wastewater treatment, CWs potentially also offer other ecosystem and circular economy services such as biomass production, wildlife habitat provision, evaporative cooling and even recreational possibilities (Masi et al., 2018). In this way, CWs are a prime example of ecological engineering, a term coined in 1962 by the American ecologist Howard T. Odum, and defined as "design, construction and management of ecosystems that have value to both humans and the environment". Likewise, CWs can be considered as green infrastructure under the umbrella concept of nature-based solutions, which are equally defined as "working with nature to address societal challenges, providing benefits for both human well-being and biodiversity" (Nature-based Solutions Initiative, n.d.).

From their initial conceptualization for domestic wastewater treatment, the use of CWs has been expanding rapidly, and CWs are now being used across the globe, in every possible type of climate (desert to arctic, e.g., Stefanakis et al. (2018) and Yates et al. (2012)), for a wide range of wastewater types, i.e., domestic, urban, industrial and agricultural, and at scales varying from a few m^2 to several km^2. This expansion is chiefly due to the positive balance between investment and operation costs on the one hand, which are typically lower than other wastewater treatment technologies, and the obtained treatment efficiencies on the other hand, which are competitive with other biological treatment technologies, though obviously cannot reach similar quality levels as energy-intensive systems like membrane filtration. The major drawback of CWs—when ignoring other ecosystem services apart from wastewater treatment—is the rather large area they occupy compared with conventional industrial plants. For this reason, CWs are mainly applied in rural and semi-urban areas, although recent developments (see section "Alternative lay-outs") have triggered urban applications as well.

This chapter gives an overview on the use of constructed wetlands for urban wastewater treatment. Urban wastewater consists at least of domestic wastewater, in many cases mixed with (possibly already partially treated) industrial wastewater and/or stormwater runoff (Fig. 1). To this end, the different types of constructed wetlands and their characteristics will be summarized, the most important treatment processes occurring in CWs will be discussed, and the essential criteria for choosing, designing and operating CWs will be listed.

Types of constructed wetlands

Over the years, various types of CWs have been created which, just as their natural counterparts, vary in terms of vegetation, soil, water levels etc. In this chapter only the most widely applied CW types are discussed (Table 1). For a more comprehensive overview, the reader is referred to Fonder and Headley (2013).

Based on the hydrology and vegetation, four main types of CWs are differentiated. The first two are surface flow systems and the last two are mainly subsurface flow systems.

Surface flow (SF), free water surface (FWS) or free-floating macrophyte wetland (FFM)

These CWs have a water level that is set above the substrate, allowing for a larger available water volume than their subsurface CW counterparts where only the pore spaces are available. Aboveground water entails higher risks of odor, insects and contact of wildlife with the wastewater, hence such CWs are more often used for tertiary treatment or polishing. The upper water layers in contact with the atmosphere tend to be aerobic unless they are completely covered by floating macrophytes. Lower water layers tend to be anoxic or anaerobic.

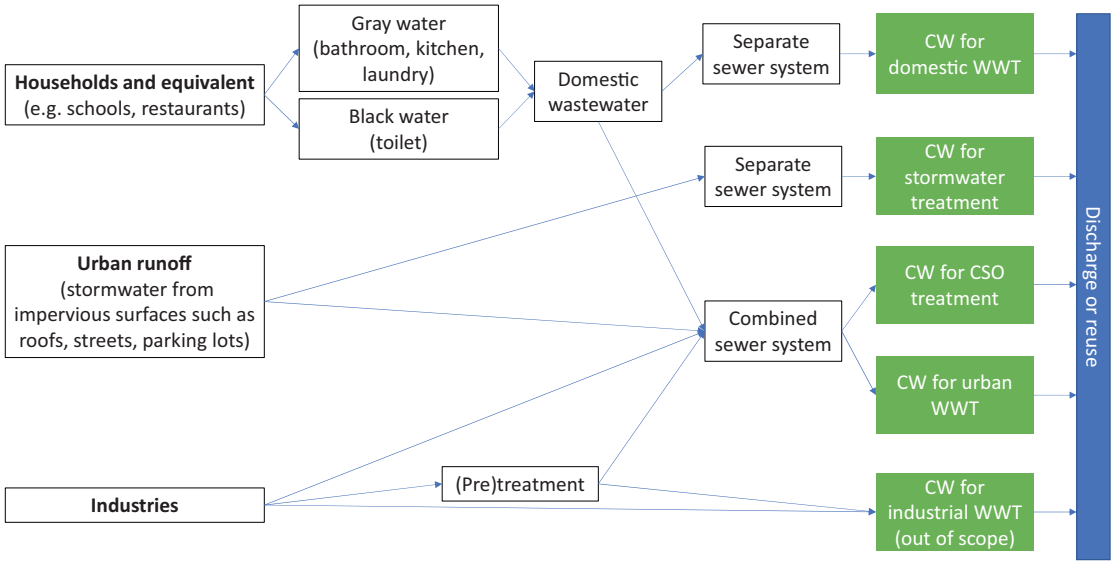


Fig. 1 Concept of urban wastewater (*WWT*, wastewater treatment; *CW*, constructed wetland; *CSO*, combined sewer overflow).

The macrophytes dominating these systems are emergent or free-floating (Table 2). When free-floating macrophytes are used, the recommended minimum water depth is considered 0.8–1.0 m, to prevent roots growing into the sediment and losing the free-floating character (Headley and Tanner, 2012). Emergent macrophytes require lower water depths, in the order of 0.5 m. Apart from the treatment processes discussed in section "Important treatment processes in constructed wetlands", macrophytes also play a role in reducing harmful algal blooms by lowering the amount of sunlight that reaches the water.

Floating emergent macrophyte (FEM) CW or floating CW

Similar to SF CWs, the FEM CWs have a substrate-free upper water column. The main difference is that the macrophytes are anchored in buoyant structures with or without growing media. The FEM CWs are very suitable for stormwater applications because the water level is not constrained so these systems can deal with sudden high inflow rates (Headley and Tanner, 2012). The buoyant structures provide shading, reducing algae growth.

Horizontal subsurface flow (HSSF) CW

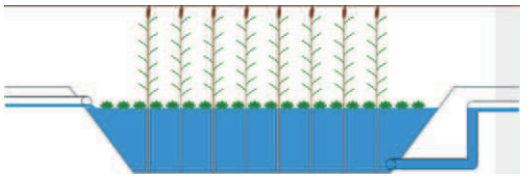
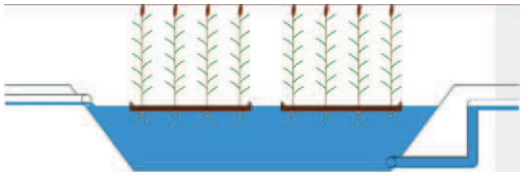
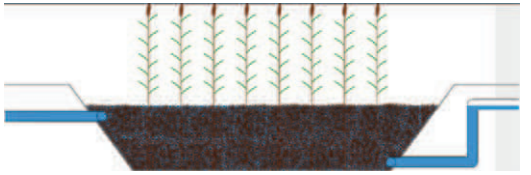
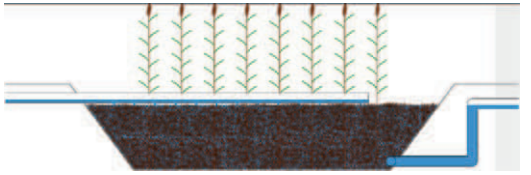
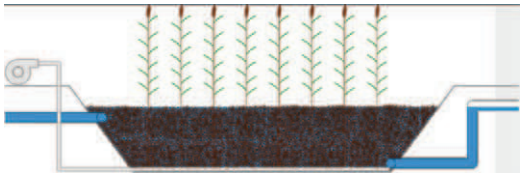
Wastewater is fed through the buried inlet zone and flows horizontally through the substrate until it reaches the outlet zone for collection and discharge. The water level is typically regulated with an elbow-like effluent pipe, and is maintained 5–10 cm below the surface. Oxygen transfer is, therefore, restricted, and HSSF CW are typically anoxic or anaerobic environments. The substrate generally consists of porous materials like gravel, sand or soil. HSSF CW are typically planted with emergent plants which are usually herbaceous (Table 2). A rule of thumb for design is 5 m^2 PE^{-1}, when treating domestic wastewater (Vymazal, 2010).

Vertical down flow (VDF) or vertical subsurface (VSSF) CW

Primary treated wastewater is intermittently fed on top of the wetland and migrates down through the substrate. This intermittent feeding enhances oxygen transfer and ensures aerobic conditions. The upper substrate surface consists of fine material to distribute the water. The bottom layer of the substrate consists of coarser material to enhance the draining capacity (Fonder and Headley, 2013). Similar macrophytes as in HSSF are used. A rule of thumb for design when treating domestic wastewater is 1–3 m^2 PE^{-1} (Vymazal, 2010).

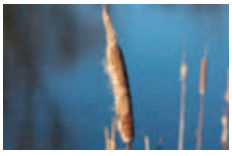
A modification where raw (untreated) wastewater instead of primary treated wastewater is fed on a VDF is usually referred to as a French-type CW. These French-type CWs consist in essence of two stages of several parallel VDF CWs, which are operated in a rotational manner, i.e., some beds are loaded while others are resting. The first stage VDF CWs receive raw wastewater and as a result a sludge layer quickly accumulates on top. This sludge layer is biologically very active and enhances treatment efficiency, but on the other hand it also reduces water infiltration rates. During the resting periods, this layer dries out and the accumulated organic matter is being mineralized, thus restoring the infiltration capacity. This results in an overall increase of the sludge layer of only 1–2 cm $year^{-1}$. A second stage VDF CW is needed for further nitrification and carbon removal (Morvannou et al., 2015).

Table 1 Overview of different types of CWs and their main characteristics.

Wetland name and abbreviation	*Water level relative to substrate*	*Flow direction*	*Vegetation type*	*Type of treatment*[d]	*Typical removal efficiencies*	*Scheme*
Surface flow (SF) or free water surface (FWS) and free-floating macrophyte (FFM)	Above	Horizontal	Emergent, floating or submerged	(II), III and stormwaters	BOD > 80%[a] NH_4^+ –*N* > 80%[a] TN 30–50%[a] TP 10–20%[a] TSS > 90%[a]	
Floating emergent macrophyte (FEM)	Above	Horizontal	Emergent on buoyant structure	(II), III and stormwaters	BOD > 80%[a] NH_4^+ –*N* > 80%[a] TN 30–50%[a] TP 10–20%[a] TSS > 90%[a]	
Horizontal subsurface (HSSF)	Below	Horizontal	Emergent	II, III	BOD > 80%[a] NH_4^+ –N 20–30%[a] TN 30–50%[a] TP 10–20%[a] TSS > 80%[a]	
Vertical down flow (VDF)	Below	Vertical up or down	Emergent	I, II	BOD > 90%[a] NH_4^+ –*N* > 90%[a] TN < 20%[a] TP 10–20%[a] TSS > 90%[a]	
Fill and drain (FaD), tidal flow or batch operated	Periodically below and empty	Vertical	Emergent	I, II	COD > 90%[b] NH_4^+ –N > 80%[b] T*N* > 80%[b] TSS > 90%[b]	
Aerated (AE)	Below	Horizontal or vertical	Emergent	I, II	COD ±85.6%[c] TKN ± 85.4%[c] NH_4^+ –N ± 86.7%[c] TSS > 85%[b]	

[a]Based on Dotro et al. (2017).
[b]Based on Ilyas and Masih (2017)
[c]Based on Rous et al. (2019).
[d]I, primary treatment; II, secondary treatment; III, tertiary treatment.

Table 2 Examples of typical species of vegetation used in constructed wetlands.

Classification	*Name*			
Emergent plants—herbaceous	Reed *Phragmites australis*	Bulrush *Typha latifolia*	Papyrus *Cyperus papyrus*	Golden torch *Heliconia psittacorum*
				
Emergent plants—woody	Mangroves *Rhizophoraceae*	Pond cypress *Taxodium distichum*		
				
Floating-leaved plants	Water lilies *Nymphaea*	Water caltrops *Trapa bicornis*		
				
Floating plants	Water hyacinth *Eichhornia crassipes*	Duckweed *Spirodela polyrhiza*	Water lettuce *Pistia stratiotes*	
				

Hybrid wetlands

It is also perfectly possible to combine several of the above-described CW types into one single treatment plant. Such wetlands are then called hybrid wetlands. A popular combination is for instance VDF followed by HSSF CWs because the sequence of aerobic and anoxic conditions allows to optimize nitrogen removal.

Important treatment processes in constructed wetlands

Solids

From an operational point of view, solids (Total Suspended Solids—TSS) in wastewater are a prime concern, especially in subsurface flow CWs, as they can cause clogging of the porous media. CWs therefore rely on a preceding primary treatment step, such as a septic tank or Imhoff tank, to remove most solids. The only exception are the French-type CWs (see section "Types of constructed wetlands") which treat raw wastewater. Any remaining particles are then removed efficiently by CWs (Table 1). In subsurface flow CWs, this mainly happens through filtration, governed not only by the pore characteristics of the porous media, but also by the density and penetration depth of the plant root biomass. In SF CWs, filtration depends mainly on aboveground vegetation density, and is complemented by settling of particles in the slow-flowing water. In both cases, filtration is aided by the "sticky" biofilms that develop on any hard surface in the CWs (porous materials, plant stems and basin walls) which capture suspended solids. Retained materials, if biodegradable in nature, can be hydrolyzed and mineralized by microorganisms and will thus liberate dissolved components (e.g., C, N, P) to the water; non-biodegradable organic matter and inorganic materials will accumulate in the system and will have to be removed eventually to avoid water flow blockage. This is usually needed after 8–10 years (Knowles et al., 2011; Nivala et al., 2012). Protozoans (e.g., ciliates) and metazoans (e.g., worms) also play a role in capturing and processing particles (Decamp and Warren, 1998; Ye et al., 2018).

Dissolved organic matter

Dissolved organic matter (designated as BOD, Biochemical Oxygen Demand or COD, Chemical Oxygen Demand) is mainly processed by the ubiquitous biofilms. Depending on the type of wetland, position within the CW (top vs. bottom, inlet compared with outlet) and loading conditions, these biofilms may be exposed to aerobic, anoxic or even anaerobic conditions, which allows a wide range of concurrent removal processes. Even within one section of biofilm, different redox conditions may exist simultaneously due to the oxygen gradients that are formed. Of particular note here is the concept of root oxygen loss, which concerns oxygen leakage by wetland plant roots as a mechanism to survive the typical anoxic wetland soil environments. Root oxygen loss creates aerobic conditions in the biofilm layers in closest contact with the plant roots. For a while, it was considered that this oxygen supply was sufficient to cover a large part of the oxygen demand (for BOD removal and nitrification), but more recent insights have refuted this idea (Liu et al., 2016).

Biodegradable organic matter can be removed by aerobic or anaerobic respiration, typically leading to high removal efficiencies (Table 1). Notwithstanding, this also results in CO_2 and/or CH_4 greenhouse gas emissions. As the vegetation also fixes atmospheric carbon by photosynthesis, most CWs still act as a net sink for greenhouse gases, and they typically emit less greenhouse gases per unit of BOD or COD removed than conventional wastewater treatment plants (Maucieri et al., 2017).

Nitrogenous compounds

The dominant nitrogenous compounds in urban wastewater are mostly organic nitrogen and NH_4^+. As for organic material, nitrogen cycling is dominated by microbial processes in the biofilm. Microbial nitrogen conversions typically involve ammonification, nitrification and denitrification, although other biological N-conversions such as nitrogen fixation, ANAMMOX and dissimilatory nitrate reduction have also been shown to play a role in CWs (Fig. 2). Only denitrification and ANAMMOX result in nitrogen removal, as the final product N_2 escapes to the atmosphere. All other processes simply convert one form into another. This may still be beneficial as for instance nitrate is less toxic to aquatic life than ammonia. Next to microbial conversions, there are also uptake processes. N-uptake by the microorganisms is insignificant, because N taken up by the bacteria in biofilms is liberated again when the bacteria decay. Plant uptake is more significant, and can be a permanent sink of N when aboveground biomass is harvested and removed from the CW. N removal efficiency by CWs is usually 40–80%, depending on the type and operation of the CW (Table 1). Finally, certain N-compounds can also be adsorbed to the porous media, soil particles or dead organic matter, but this process is typically also insignificant over longer periods as saturation limits are rapidly reached.

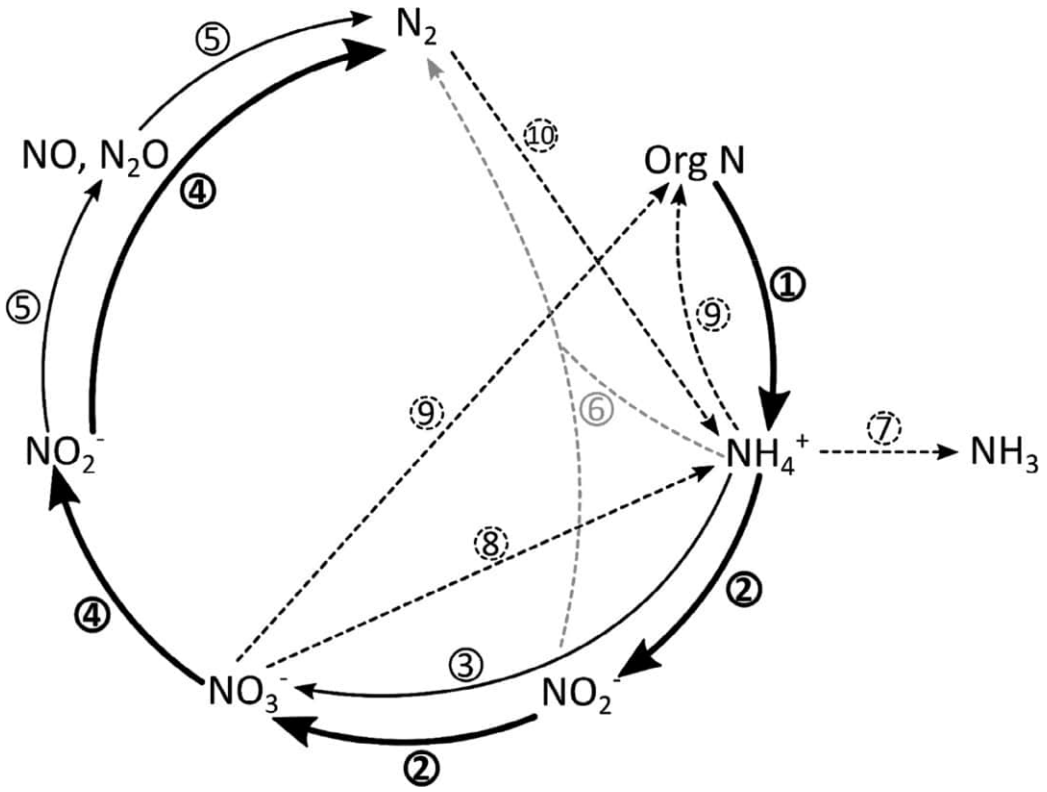


Fig. 2 Nitrogen cycle in constructed wetlands with following processes: 1 ammonification, 2 nitrification, 3 comammox, 4 complete denitrification, 5 partial denitrification, 6 ANAMMOX, 7 volatilization, 8 dissimilatory nitrate reduction, 9 assimilation and 10 nitrogen fixation.

Phosphorus compounds

The main phosphorus removal mechanisms in CWs are typically adsorption and precipitation by porous media (SSF CW) or soil (SF CW). Unfortunately, these are by nature finite processes, limited by the maximal adsorption capacity of the applied material, or the maximal amount of ions liberated that can precipitate phosphates. Both largely depend on the content of iron, calcium and aluminum, as well as on the specific surface (area per volume) of the applied materials. Therefore, recent research aims to apply new substrates that have a high phosphorus removal capacity in CWs (see section "New substrates"). To avoid having to refurbish the entire CW once the substrate is saturated, P-adsorbing materials can also be added as a separate filter behind the CW.

In addition, as for nitrogen, plants also take up P, but the quantity stored in the plant biomass is usually insignificant versus the amount of P delivered to the CW by the urban wastewater, hence this is not an important removal mechanism. Likewise, P-uptake by the bacteria is at best a temporary phenomenon during biofilm development, which very quickly evolves to an equilibrium between uptake and decay.

Pathogens

Pathogens are the main vector for the spread of diseases. In urban wastewater, pathogens mainly include viruses, bacteria, pathogenic protozoa and pathogenic helminths stemming from human and animal feces. Currently, their presence in wastewater is assessed by routine monitoring of indicator microorganisms such as *Escherichia coli* (*E. coli*), total coliforms, fecal coliforms, fecal streptococci and *Clostridium perfringens*. The removal of pathogens in CWs depends on mechanisms which include sedimentation, filtration, adsorption, predation, and natural death (Wu et al., 2016). Sedimentation and filtration in CWs (discussed above) plays a major role in the removal of pathogens. Adsorption of pathogens in CWs is also partially a mechanism of filtration as pathogens are adsorbed by the substrates, plant roots or biofilms and thus trapped in the CWs. Predation is another important process as both protozoans such as ciliates, and metazoans such as nematodes and copepods have been reported to be an important factor in the removal of bacteria. Finally, natural death of pathogens is a complex process that may involve a variety of physical and chemical factors such as pH, oxygen levels etc. The overall pathogen removal capacity is dependent on various factors such as flow pattern, matrix, vegetation and hydraulic retention time. Also, natural factors such as temperature and solar intensity are of importance. Generally, subsurface flow CWs have better capacity than surface flow CWs (Table 1).

Micropollutants

Micropollutants encompass a massive range of organic and inorganic pollutants of anthropogenic origin, whose presence at even very low concentrations (ng to μg/L) in the environment can have negative effects on living organisms. Urban wastewater contains a wide variety of micropollutants including metals, pharmaceuticals and personal care products (PPCPs) and microplastics, which have gradually received attention in CWs.

Adsorption and precipitation are the main physical and chemical processes that stimulate metal retention and removal in CWs. Metals can either be adsorbed by ion exchange, or they can form insoluble compounds through redox reactions. Plants can also play a major role in extracting metals and metabolizing them (Marchand et al., 2010).

CWs also possess the ability to remove some pharmaceuticals and personal care products (PPCPs). As for other wastewater components, the micro-environments formed by microbiological communities in CWs are able to offer different metabolic pathway for their degradation (Ilyas and van Hullebusch, 2020a,b).

The removal and fate of microplastics as a persistent pollutant is also gaining attention in CWs. Current studies indicate that CWs can effectively remove microplastics by filtration, but further research is needed on removal mechanisms and influencing factors (Wang et al., 2020a; Wei et al., 2020).

Alternative lay-outs

The search for smaller area and higher performance CWs in the past decades has led to "intensification" of CWs (Ilyas and Masih, 2017). The tradeoff here is that the low-tech, low-maintenance, low-cost and natural character of traditional CWs is (partially) lost for higher efficiency treatment of wastewater. The recently developed CWs are generally designed to enhance a certain treatment process or as a crossover with other environmental technologies.

Enhanced nitrogen removal by hybrid wetlands and recirculation

Hybrid CWs are a combination of two or more standard CW types with sometimes partial recirculation. The most used hybrid combination is a VDF CW followed by a HSSF CW, where the VDF CW promotes nitrification and the HSSF denitrification (Vymazal, 2013; Ilyas and Masih, 2017). Removal of BOD, COD, TSS and TP are less affected by such hybrid configurations.

In an effluent recirculation system, part of the effluent is returned to the influent zone of the CW. The goal is to improve effluent quality, by making only minor changes to the design of the CW. Nitrate-rich effluent can be denitrified in the presence of fresh carbon-rich wastewater, with a higher hydraulic load promoting less oxygen transfer due to shorter atmospheric contact time. Recirculation can also be used as a strategy to dilute influent with a high toxicity and hence to reduce toxic effects on the (micro) biota of the CW. Recirculation is mainly carried out in subsurface flow CWs and recirculation ratios vary from 0.5 to 2.5. The total CW area can be reduced to 1.1–1.6 m^2 PE^{-1}, depending on the CW type, but the hydraulic conductivity must be taken into account to prevent flooding of the CW (Prost-Boucle and Molle, 2012; Wu et al., 2014, 2015).

Oxygen enhancement

Low oxygen concentrations reduce the removal rate of BOD and COD and inhibit the conversion of ammonium to nitrate. This can be countered by artificial aeration in the form of compressed air addition. The aeration regime must be balanced to allow for anoxic conditions for nitrate removal. Aeration efficiency is still being researched (Rous et al., 2019). Ouellet-Plamondon et al. (2006) found that aeration cannot replace macrophytes, pointing out that macrophytes have more functions in relation to treatment efficiency than only oxygen addition to the root zone. Aeration however leads to additional operation and maintenance costs (Wu et al., 2014; Ilyas and Masih, 2017).

Alternatively, a passive aeration strategy can be applied by designing a two or multiple stage CW. When water travels gravitationally to the next stage, a waterfall is created and oxygen is being dissolved (White, 1995). This waterfall aeration is however limited to a one-time spike of 7–14 mg L^{-1}, depending on environment temperature. Vertical baffles, spanning the whole CW length, can be inserted to promote water mixing and subsequent oxygen transfer. Another passive aeration strategy is to use vertical perforated pipes, that suck in air when water is draining due to negative pressure (Wu et al., 2014).

A tidal flow or FaD CW is considered a separate category of CWs (Table 1), but has recently gained more attention. Tidal flow CWs are batch operated, in contrast to all other standard CW types. A cycle consists of filling, contact phase, draining and resting, where the emphasis lies on the alternation of saturated/unsaturated substrate. This regime pulls in oxygen for nitrification when filling and resting, while anaerobic conditions are reached during the contact phase. The energy requirements for a FaD CW are about half as much as for actively aerated CWs (Austin and Nivala, 2009).

New substrates

Substrates such as gravel, sand and soil have been used for decades in CWs, with the primary functions of supporting macrophyte growth and providing surfaces for microbial growth. Recent research has started to focus more on improvements of substrates for CWs, in areas such as waste material reuse, nutrient removal and prevention of clogging (Wang et al., 2020b). A number of materials that have been tried as newer substrates in CWs include:

I. Zeolites, a group of minerals rich in micro and macro pores, with high sorption capacity of cations such as heavy metals and ammonium. Phosphorus removal is, however, moderate to low. Zeolites are relatively easy to obtain and the price is reasonably low, making them suitable for use in CWs;
II. Woodchips, bark chips or wood shavings are an abundant by-product of the timber industry. The woodchips can be implemented in a CW substrate for better denitrification and thus nitrogen removal, as it acts as a slow-release carbon source;
III. Biochar is produced through pyrolysis of agricultural biomass and is intended as a soil-improving substance. Biochar is similar to activated carbon, but is not specifically activated. Yet, biochar has a large surface area and high sorption capacity, yielding removal of heavy metals and ammonium. Biochar also is a slow-release carbon source, suitable for denitrification;
IV. Oyster shells mainly consist of $CaCO_3$ and have a great potential for phosphorus removal through adsorption and precipitation;
V. Construction wastes consist of bricks, gravel, concrete, fly-ash, etc. Some construction wastes facilitate phosphorus removal, similar to oyster shells; and
VI. Slag is an industrial by-product from the steel industry, with practically no other uses, making it cheap to use. Slag has a high phosphorus sorption capacity, but can leach other metals and can negatively affect macrophyte growing conditions.

Crossover with other environmental technologies

Microbial fuel cell (MFC): MFCs are bioelectrochemical systems that generate current by means of electrochemically active microorganisms as catalysts. In a wastewater MFC, organic substrates present in the wastewater are hydrolyzed and oxidized by bacteria. The electrons are transferred to an anode from where they flow through a conductive material and a resistor to an electron acceptor, such as oxygen, at the cathode (Logan et al., 2006; Rabaey et al., 2007). Such processes require a redox gradient. A CW has aerobic and anoxic zones and is therefore suitable for embedding MFCs (Ji et al., 2021). The technology is still in its infancy and needs more research before upscaling. The power output is low and ranges from a few to several thousands of milliWatts, however the combination of a standard type of CW with an MFC yields better COD and nitrogen removal compared with a standalone CW (Ebrahimi et al., 2021; Gupta et al., 2021). An MFC can also be used as an alarm-like biosensor for detecting high COD influent concentrations, as the voltage of an MFC is correlated with the COD concentration (Corbella et al., 2019).

Green roofs: Green roofs are typically used to reduce stormwater flows by storing rainwater, and in addition provide air filtration, cooling in urban areas and better building insulation. However, they can also be constructed or converted into CWs for treating domestic wastewater (Vo et al., 2019). The design generally consists of a standard type HSSF or VDF CW. Surface flow CWs are not recommended as they are prone to odor nuisances and mosquito growth. The depth of the CW is reduced and lighter substrate material is required to reduce structural load on the roof. The treated water can be reused for flushing toilets or irrigation as this poses less health and safety issues than reuse for other purposes.

Green walls: Green walls or living walls have become popular to improve the aesthetic appearance of buildings and to introduce patches of green in dense urban environments. Similar to green roofs, they also provide some insulation in terms of heat and noise, provide a habitat for insects and can improve air quality by capturing fine dust. Whereas most green walls are maintained with tap water or rainwater and chemical fertilizers, it has also been shown that such systems can treat wastewater (Pradhan et al., 2019). Flipping a CW 90° obviously saves a great deal of space.

A CW project from A-Z

Opting to use CWs for wastewater treatment and consequently designing the system, typically involves several steps (Fig. 3). The decision whether or not to use CWs in a new wastewater treatment project, mainly depends on three criteria:

- Available space: depending on the selected type and climate, conventional CWs require an absolute minimum of 1 m^2 PE^{-1} up to >5 m^2 PE^{-1}. With aerated wetland technology, 0.5–1 m^2 PE^{-1} is possible. If even that amount of space is not available, alternative spaces such as roofs or walls may be used, or other technologies need to be considered.
- Toxicity of the wastewater: like any biological wastewater treatment plant, the bacteria and in the case of CWs also the vegetation can only function within certain ecotoxicological boundaries. If toxicity is an issue, CWs can only be used further down in the treatment train, after having removed most of the toxic substances with other technologies. For urban wastewater, this would rarely be the case.
- Effluent requirements: as discussed above (Table 1). CWs are very effective in removing BOD, COD and TSS, reasonably effective in removing N and pathogens, and rather inefficient in removing phosphorus, unless using special porous media or additional P-removal techniques. Micropollutant removal is highly variable and depends on the individual components. Applying CWs thus depends on the requirements of the receiving water bodies or on the intended reuse purposes.

In a next step, the appropriate type(s) of CWs should be selected. Apart from the treatment performance which varies between types (Table 1), other points of attention are:

- Is a good primary treatment feasible or not? If not, subsurface flow CWs will not be appropriate.
- When applied for secondary treatment, odor and insect nuisance is typically lower in subsurface flow CWs. When using SF CWs, a reasonable distance between CW and nearest houses should be foreseen. For tertiary treatment, this is less a point of attention as concentrations are already much lower.
- Health and safety issues: open water surfaces as in SF CWs promote contact between wastewater and wildlife, and if not properly fenced entail drowning risks.

The next step is then to calculate the required CW area. For VF CWs, this still involves very simple rules of thumbs (e.g., x m^2 PE^{-1}), complemented in several countries with national standards detailing required pretreatment technology, filter depth and filter materials (grain size distribution, different layers) (Dotro et al., 2017). For FWS and HSSF CW, the most widespread design model is the P-k-C^* model. This model takes into account mixing conditions in the wetlands (P), weathering of pollutants (e.g., the phenomenon that bacteria will rapidly degrade easily biodegradable material, but be more slow in degrading more recalcitrant materials) (P), removal rates as affected by temperature (k), and a background concentration (C^*) which considers for instance that due to the decay of plants and microorganisms or due to droppings from wildlife, concentrations in the water never really go down to zero. For aerated wetlands, the design mainly involves a balance between the oxygen demand and the oxygen supply that can be provided through aeration. For a more detailed discussion, see Dotro et al. (2017).

For larger FWS wetlands, and for any HSSF wetland, translating the obtained area to an appropriate LxW further involves hydraulic calculations, in FWS according to a Manning-type equation, and in HSSF wetlands according to the Darcy equation (Dotro et al., 2017). The obtained area can also be split over several cells which gives some flexibility in terms of maintenance.

Most CWs are built with a plastic liner (PE, PP, etc.) to ensure water tightness. Alternatively, basins can be sealed with clay or concrete.

For SSF CW, choosing the correct porous media is essential. This involves firstly considering properties such as grain size distribution, porosity and hydraulic conductivity which will be of importance in the above-mentioned Darcy equation. Secondly, sorption capacity (for N, P, metals, etc.) should be taken into account if relevant. Finally, another important factor is the cost of the material and its transport, which in part depends on local availability.

The final step is to vegetate the wetland. It is highly recommended, and in some cases legally required, to use native plant species. *Phragmites australis* for instance is commonly used in Europe in CWs, but is considered an invasive species in the United States. Next, plants should be selected which can survive in hydric soils and in nutrient-rich conditions, and which preferably form a dense and deep root system. An overview is given by Vymazal (2013). Another potential criterion is the subsequent use of harvested plant materials (e.g., ornamental plants, for roof thatching) which may also influence the selection. From an aesthetic point of view, it may be desirable to select evergreen species, but this is not essential from a treatment point of view as the root systems keep supporting the biofilms also during winter. In temperate and cold climates, it is advised to harvest in spring, just before the plants start growing again. The dead biomass will provide some insulation during winter time, conserving heat inside the CW. In tropical climates, multiple harvests may be possible within 1 year, leading to higher nutrient exports.

Once in operation, a CW requires minimal maintenance. Apart from plant harvesting discussed above, this mainly involves maintenance of pumps, cleaning of water distribution systems, and sludge removal from the primary treatment step when applicable.

Synthesis

Since their conception in the 1960s, CWs have become a standard option for urban wastewater treatment. These manmade wetlands make optimal use of the physical, biological and chemical treatment processes offered by vegetation, (micro)organisms and soil/filling media. In addition, CWs can provide other important ecosystem services such as biomass production, habitat provision and cooling.

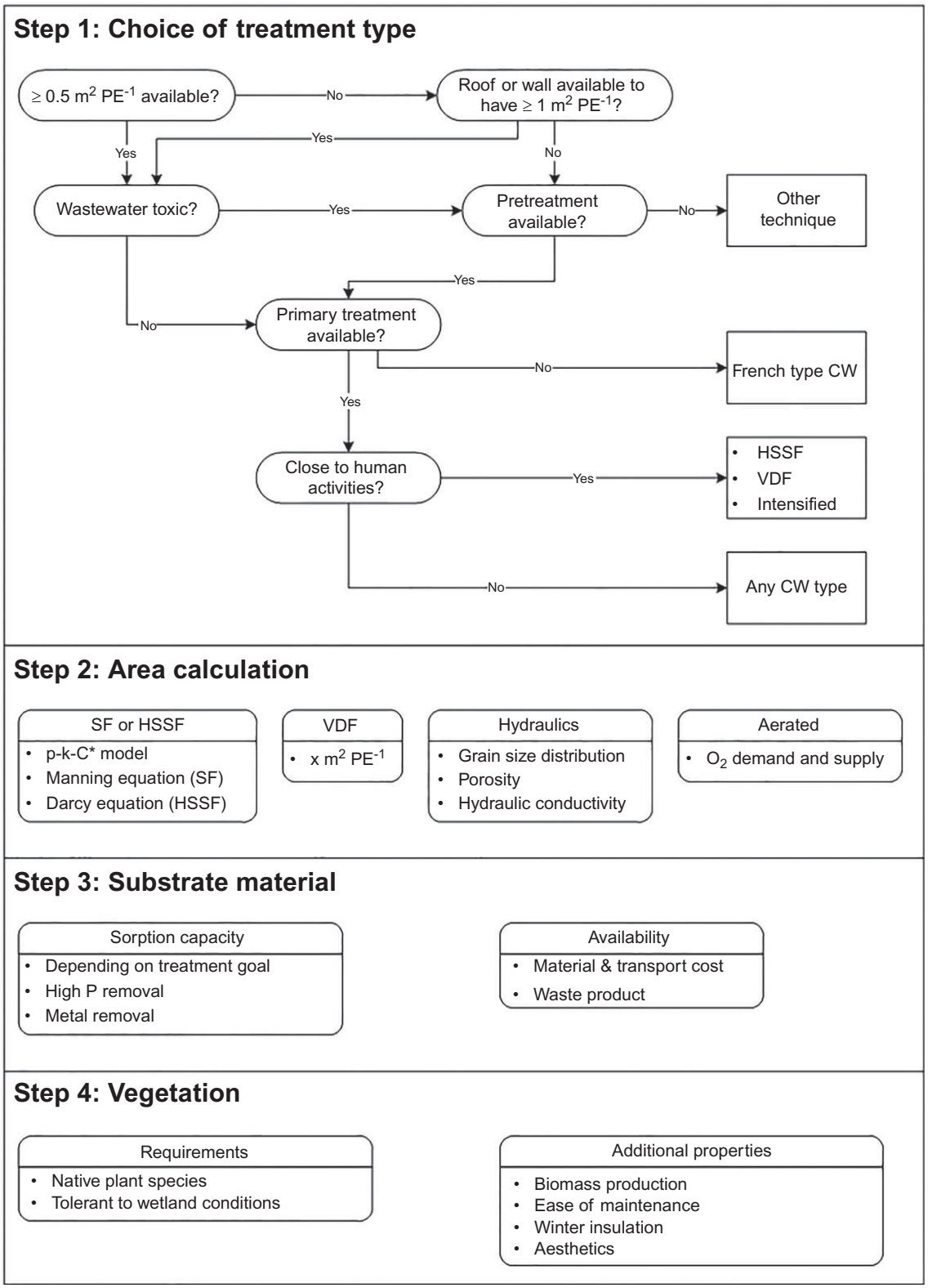


Fig. 3 Flowchart showing the essential steps in selecting and designing constructed wetlands.

The first generations of CWs mainly consisted of surface flow and subsurface flow types with traditional filling media such as gravel, sand and soil. The search for more efficient and less area-demanding technologies has paved the way for intensified wetlands and cross-over technologies, with a higher degree of engineering interventions. Especially in terms of urban wastewater treatment, this has resulted in an increasing application of CWs in more densely populated areas.

Knowledge gaps

- *Modelling*: Process-based models are an essential tool to guide design and operation of wastewater treatment plants. Despite many efforts (e.g., Langergraber et al., 2009; Samsó et al., 2015), CW models have not surpassed the research stage yet and are thus far not available as straightforward tools for consultants and engineers. This is one of the key aspects that hampers further uptake of CWs, unlike for instance the wide-spread activated sludge wastewater treatment systems for which the activated sludge models have become standard tools (Henze et al., 2000).
- *Emerging pollutants*: through time, various groups of emerging pollutants have become the focus of attention. There is a large body of evidence now on for instance the removal of pesticides, pharmaceuticals and personal care products, but researchers have only recently started to tackle other pollutants of concern such microplastics, PFAS (*Per-* and polyfluoroalkyl substances) and metallic nanoparticles.
- *Practical and full-scale applications*: a large majority of research papers on CWs are based on short-term laboratory-scale studies. Although such studies have undeniable merits, they also have many disadvantages such as ignoring meteorological influences, seasonal influences, wastewater variability. Longer-term, pilot-scale or full-scale studies are needed to irrefutably demonstrate the success of new concepts.
- *Ecosystem service valuation and accounting*: CWs, and to a wider extent all nature-based solutions, struggle to valuate and account for the less tangible ecosystem services such as aesthetics, evaporative cooling, air quality improvement, habitat provision etc. Ignoring such benefits when comparing green (nature-based) and grey (non-nature-based) solutions results in distorted cost-benefit analyses often favoring the grey solutions. Standardized methods remain to be developed that take such aspects into account.
- *Circular economy perspective*: It has become a commonplace to consider (urban) wastewater as an interesting resource rather than as a nuisance. Hence, rather than the classic linear approach of collecting—treating—discharging, the circular approach attempts to recover water, nutrients and other components contained in the wastewater, and energy. CWs can surely play a role in this model by delivering for example, effluents suitable for toilet flushing or even irrigation and by producing plant biomass that can serve as biofuel or can be converted into compost or even building materials. As rightfully pointed out by Masi et al. (2018), most research is still aimed at improving the treatment efficiency within a linear approach, and a paradigm shift is needed towards the circular approach.

Important case studies

Name of site	*Country*	*Coordinates*	*Main topic/concept covered*	*Key references*
Zemst-Kesterbeek	Belgium	50°59′39.0"N 4°25′44.6″E	Removal and accumulation of metals in an HSSF CW treating municipal wastewater	Lesage et al. (2007)
Inwald	Poland	n/a	Long-term behavior of a rather rare soil-based HSSF CW	Mucha et al. (2018)
Quaid-i-Azam University, Islamabad	Pakistan	33°44′43.28″N 73° 7′4.09″E	Compares treatment efficiencies of various full-scale hybrid CWs	Ali et al. (2018)
Constructed wetroof, van Helvoirt Groenprojecten, Tilburg	The Netherlands	51°34′00.7"N 5°08′01.6″E	Subsurface flow wetland conceived as a green roof treats wastewater from an office building	Zapater-Pereyra et al. (2016)
Linyi	China	34°52′14″ N 118°20′53″ E	Large SF CW for secondary treated urban wastewater	Wu et al. (2018)
Bribie Island, Queensland	Australia	27°03′55.5"S 153°09′50.1″E	FEM CW treating stormwater	Nichols et al. (2016)
Coral Harbour, Nunavut	Canada	64° 08′ 13″ N 83° 09′ 51″ W	Arctic tundra wetland receiving primary treated municipal wastewater	Hayward et al. (2014)
Rongcheng, Shandong Province	PR China	n/a	A full scale large urban CW with a total area of 80 ha	Song et al. (2006)
Orhei	Moldova	n/a	One of the largest CW systems for secondary treatment worldwide, based on French-type CW	Masi et al. (2017)

See Also: Human pressures and management of Inland Waters: Emerging and Less Commonly Recognized Chemical Contaminants: Organic Micropollutants; Case Studies of (Semi)Constructed Wetlands Treating Point and Non-point Pollutant Loads to Protect Downstream Natural Ecosystems; Microplastics in the Freshwater Environment; The Role of Wetlands in Mitigating Impacts From Diffuse Agricultural Loads; Structures and functions of Inland Waters - Lakes: Protists: Flagellates and Amoebae

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Relevant websites

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https://encyclopedia.pub/3798—Scholarly Community Encyclopedia - Wetland Systems.
http://www.cwetlands.net/learn/—UNU-FLORES CWetlands training material.
https://www.youtube.com/watch?v=deKenkkhMuY—Constructed Wetland Design.
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https://ocw.un-ihe.org/course/view.php?id=43—Constructed wetlands for wastewater treatment. Open Courseware UN-IHE.
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http://ioev.de/ch/fallbeispiele/pflanzenklaeranlagen.html—Ingenieurökologische Vereinigung e.V. Show cases of constructed wetlands in Germany, UK and China.

The Role of Wetlands in Mitigating Impacts From Diffuse Agricultural Loads

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This article was reviewed for the *Encyclopedia of Inland Waters*, Second Edition by Section Editors Ken Irvine, Deborah V Chapman and Stuart Warner.

Glossary

"Black box" concept Studying the system in terms of its inputs and outputs, without detailed consideration of its internal processes.
Agricultural loads/pollution Sediment load caused by soil degradation and erosion, chemical pollution by application of fertilizers and pesticides, discharge from animal farms.
Catchment Geographical area of land within which all precipitation falling and all water flowing in streams drains into a common outlet.
Diffuse pollution Differs from direct pollution originating from point sources since there is no specific point of discharge and hence are more difficult to control. Main pathways are surface runoff, subsurface flow, and soil loss. Agriculture is a key source of diffuse pollution, but urban land, forestry, atmospheric deposition and rural dwellings can also be important sources.
Ecosystem service The resources and benefits that humans derive from an ecosystem directly or indirectly.
Ecotone Transition area between two ecosystems, more specifically also border zones separating different land use types.
Eutrophication Enrichment of water by inorganic nutrients which results in intensive growth of plants (algae, macrophytes).
Interstream divide A terrain that separates drainage basins.
Nutrient load retention Difference between inflow and outflow of nutrients within the system boundary.
Urbanization Increasing proportion of human population living in urban areas.

Introduction

The importance of natural wetlands has been appreciated by numerous cultures throughout history, e.g., the economic basis of the culture of the Marsh Arabs (inhabitants of the Tigris-Euphrates marshlands, Southern Iraq) is based upon the marshes as a natural sustainable resource. Wetlands also received particular interest in terms of its role as a natural "filtering/purification-system" of freshwater in the second half of the 20th century (e.g., Mitsch et al. (1979), and more recently have received attention as engineered semi-natural systems in the treatment of diffuse loads of nutrients originating from agricultural areas (Mitsch, 1992; Vymazal and Dvořáková Březinová, 2018).

Until the 1950s, on a global scale, farming was primarily carried out on smaller, family farm units, as opposed to large monocultural and intensively managed units common today. Previously, therefore, the amount of farming waste produced was smaller and it was more easily assimilated by soil and receiving water bodies (Novotny, 1999). Between 1961 and 2009, however, there was a 12% increase in the extent of cultivated land to 1.6 billion ha (almost the size of Russia), mostly at the expense of wetlands, natural grasslands, and forest,s while, irrigated land increased by about 120% Dubois (2011). Together, these processes have resulted in the loss of about 35% of all natural wetlands (primarily inland wetlands) since the 1970s, mostly due to the encroachment of agricultural, residential and industrial land uses. This worrying trend continues, also affecting extensive areas of internationally renowned wetlands, e.g., the loss of the whole Matogrossense National Park (Brazil), or the oil exploration plans in the Okavango delta (Botswana) (Editorial, 2021). In addition, with the increase of the area under cultivation or intensification of grasslands, the amount of nonpoint (diffuse) pollution of nutrients arriving in surface waters has also increased. This has reached such an extent that in industrialized countries, agriculture has become one of the major sources of nutrient loss to surface waters (Mateo-Sagasta et al., 2018).

Diffuse pollution from agriculture may be defined as pollution without an obvious single point of discharge. Contaminants are indirectly discharged into receiving water bodies and cannot be easily traced back to a single source. Moreover, it may also mask effluents from minor point sources. While the term is not exclusive to loads deriving from agricultural activity and the transformation of land use, agricultural loads (consisting of, among others, phosphorus (P) and nitrogen (N) compounds) may indeed be considered primarily as non-point in origin and diffuse in transport. Since P and N compounds are the primary limiting factor for algal growth (Yang et al., 2008), agricultural diffuse loads are responsible for the eutrophication and degradation of inland surface waters across the globe (Carpenter et al., 1998), e.g., in Europe (Csathó et al., 2007), North America (Daniel et al., 1998), and Asia (Agrawal, 1999; Jiang et al., 2007). In Europe, nutrient run-off from agriculture is a critical obstacle to the achievement of the "good chemical and ecological status" of surface waters required by the Water Framework Directive (EC, 2000; Vymazal et al., 2020).

Retaining such loads and protecting surface waters in a non-urban environment requires complex catchment-wide approaches and should be achieved in the most 'natural way' possible. In this context one of the most effective tools for mitigation of risk of pollution to surface waters are (semi-)constructed wetlands.

This chapter provides an overview of the most important characteristics of (semi-)constructed wetlands in their capacity to retain agricultural diffuse loads from ever reaching inland surface waters. Due to their complex nature, the basics of wetland typology, the design criteria, and their possible location in the landscape (including riparian wetlands) require a multi-faceted discussion. Furthermore, agricultural diffuse loads of nonpoint source-nature, will also be introduced. We do not provide a detailed technical description of the underlying processes operating in wetlands, rather give an overview of the key concept and functionality of wetlands.

Wetlands

Up to date, there is no single scientific definition of what specifically constitutes a wetland (Box 1). Instead, depending on the discipline, there is a range of characterizations of the water bodies that might be defined as "wetlands." Despite this constrain, a commonly agreed characteristic of wetlands is that they are permanently or seasonally saturated by water, with soils distinct from those found in uplands, and whose flora (and fauna) is adapted to saturated conditions (Scholz and Lee, 2005). Wetlands can be found on every continent, with the most recent global area estimated as around 12.1×10^6 km^2 (Davidson et al., 2018). At the same time, there has been a loss of 64–71% in wetland area since 1900, while the total loss since 1700 may be as high as 87% (Davidson, 2014).

Box 1 Wetlands.

The term "wetland" refers to a wide set of primarily aquatic habitats that usually have a number of common features; thus, one route to a comprehensive definition is via the consideration of numerous definitions.

Wetlands represent a transient world existing between two which are easily recognizable, terrestrial and aquatic ecosystems, serving as an interface/ecotone (Holland et al., 1990) between the two, displaying some of the characteristics and depending on both, yet still remaining distinct (Smith et al., 1996; Mitsch and Gosselink, 2011; Scholz and Lee, 2005). It was the Ramsar Convention on Wetlands (1971) that brought the question of wetland conservation into the limelight. It represented a move towards a more specific wetland-definition (Gardner and Davidson, 2011): "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters."

In contrast to fully natural wetlands, which are gravity-fed and have a fully natural vegetation, and thus found at the most natural, low-energy end of the hydrological gradient, constructed wetlands are higher energy water bodies engineered for a given purpose (Box 2). One example would be for treatment of urban or agricultural wastewater (Kadlec, 2009; Vymazal, 2010, 2011). In this instance, the aspect of deliberate construction makes them effective measures in the removal of particulate material and nutrients lost from agriculture and reduction of their transport into water bodies. Despite being constructed, such wetlands operate in a near natural state (Kasak et al., 2018). In relation to this function, eight primary principles of wetland design to control nonpoint source (diffuse) pollution were listed by Mitsch (1992).

Box 2 Ecological Engineering.

This discipline aims to solve environmental problems via the combination of ecology and engineering, designing natural systems using the quantitative approaches of science with technology, in the form of self-designing ecosystems, to generate efficient and cost-effective alternatives to common environmental solutions. Examples might include the restoration, design, and construction of ecosystems, including wetlands, which shall contain all biological components present under natural conditions (Kangas, 2003; Mitsch and Joergensen, 1989).

The system should:

- require minimal maintenance and be developed to maximize the possibility of self-maintenance and self-design;
- utilize natural (renewable) energies;
- be embedded in the natural landscape, and not against it;
- have one major and multiple side-objectives;
- be designed as an ecotone (i.e., include a buffer strip, see Section "Riparian wetlands as buffer strips" for details);
- be given time to develop;
- be designed for function, not for form;
- mimic natural systems rather than being over-engineered.

Typology of wetlands

In the early years, typology of *natural wetlands* was primarily based on their utilization (farmable, marginal and unfarmable). The Ramsar Convention on Wetlands (1971) fundamentally changed this paradigm, placing wetlands into three main categories: marine and coastal wetlands, inland wetlands, and man-made wetlands. These were then further subdivided into 42 wetland types; see e.g., Finlayson (2016). Numerous attempts have been made to refine, standardize and/or modernize this typology to arrive at a more systematic classification and to move away from the current listing of wetlands. The modern classification of wetlands is approached by a range of highly diverse perspectives, and these are also applied at different international, national or regional levels. Even the aims vary, such as comparisons of natural value, or examinations of the functionality of a wetland. Yet, the typology agreed in the Ramsar Convention has remained one of the most frequently used typologies on a global scale.

In contrast to the discussion above, the *categorization of constructed wetlands* (Box 3) is much more straightforward, consisting of two main categories. The first one is based on the type of aquatic plants, commonly known as macrophytes. This would include

BOX 3 (Semi-)constructed wetlands.

Constructed wetlands or treatment wetlands are ecologically engineered artificial wetlands designed to harness the natural processes taking place in wetland vegetation and soils, their associated microbial assemblages and utilize these in the treatment of organic, inorganic and excess nutrient contaminants in surface water, municipal wastewater, domestic sewage, refinery effluents, or landfill leachate.

Semi-constructed wetlands represent a "compromise" between natural and constructed wetlands in terms of their purpose and functioning. They are commonly established on degraded/modified wetlands and/or in areas where the filtering capability of a natural wetland must be enhanced and directed by means of minor construction/modification (Illustration 1). At the same time, semi-natural wetlands may be considered as those which are constructed but do not need any energy input and have a minimum of artificial structures, such as free water surface wetlands. Although this type is fully artificial, again, the level of construction is minimal, and therefore resembles a natural wetland. The extent to which a restored wetland resembles a natural one will ultimately define its success.

Illustration 1 The outflow of the Kis-Balaton Water Protection System to Lake Balaton (Hungary, Europe) with neighboring agricultural fields, marshes, and the wetland ecosystem in the distance. The construction shows the speedway being built crossing the inflow channel of the River Zala to Lake Balaton after passing through the Kis-Balaton Water Protection System (see e.g., Hatvani et al., 2014; Honti et al., 2020; Bhomia et al., 2022). Foto by 'LégiProjekt'.

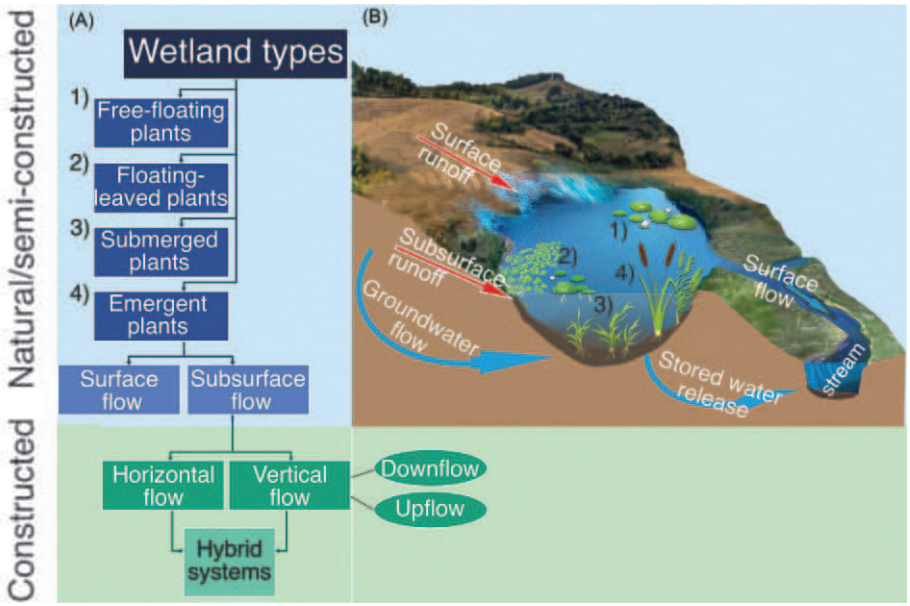

Fig. 1 Types of constructed wetlands after Vymazal (2001) (A), and the illustration of the most basic hydrological fluxes in a semi-constructed wetland (B). Red arrows indicate the direction of loading processes, blue arrows show the primary water flow directions. The numbers in the figure (B) indicate the types of vegetation based on which classification can be done (A).

species normally found growing in wetlands of any kind, either in or on the water, or where soils are flooded or saturated long enough for anaerobic conditions to develop in the root zone. In terms of growth type and morphologies, these may be described as emergent, submergent, floating-leaved, or floating species (Fig. 1A and B).

The second categorization is based on the water flow regime (Fig. 1A: green background). According to the International Water Association (2000), regimes can be subdivided into three basic types of treatment systems in constructed wetlands: free water surface, horizontal subsurface flow, and vertical flow (Fig. 1A) (Kadlec, 2009; Vymazal, 2001).[1] Wetlands with free water surface (FWS) closely resemble natural wetlands. Since semi-constructed wetlands directly exploit the remaining resources of the former natural wetlands, the FWS model reflects most of their characteristics.

Non-point source (diffuse) pollution

Great efforts have been made to handle point source pollution in the past. Unfortunately, the retention and treatment of agricultural diffuse loads has not been so successful. Several factors lie behind this. In the early years (mid-late 20th century) of recognizing and attempting to ameliorate pollution arriving to surface waters, point source pollution had an overwhelming and much more distinguishable effect on receiving waters than diffuse loads. When management measures seemed to fail, or were not as successful as anticipated, greater research effort was expended on diffuse pollution, which is harder to monitor and identify than point sources that are typically discharges of effluent from a pipe.

The main characteristics of diffuse sources of pollution according to Campbell et al. (2005) are those discharged into the receiving surface waters intermittently and in a diffuse manner. These pollutants transit across landscapes—involving complex transport and transformation routes through several media—on a catchment-scale with a spatiotemporally variable volume and concentration depending on the environmental conditions (meteorological, geological and geographical). They involve a variety of sources and pathways (Heathwaite et al., 2005). It is difficult or even impossible to monitor them at their source, due to their non-point nature and any impact assessment is performed rather on a catchment-scale, focusing primarily on nutrients, suspended solids, toxic compounds and pathogens. These, in turn, operate in certain situations superimposed on and/or parallel to point sources, in which case they are practically indistinguishable from them; e.g., Hatvani et al. (2015). The issue is further complicated since these systems may cross administrative divisions such as catchments, sub-national regions or even national borders, making their control even more difficult.

[1]For a more detailed description of the typology, the reader is referred to the Ecology of Wetlands: Classification Systems chapter of the first edition of this encyclopedia Tiner (2009) and the Constructed Wetlands for urban wastewater treatment: an overview chapter in the Human pressures and management of Inland Waters Section of this encyclopedia Rousseau et al. (2022).

Agricultural catchments

Diffuse pollution from agriculture is of different origin: (i) increased soil erosion and soil loss, (ii) chemical pollution by fertilizers and pesticides, (iii) irrigation return flow, and (iv) pollution from animal husbandry (Campbell et al., 2005). In the past there have been attempts to reduce the overall loss of nutrients with

(i) the focused measures taken to reduce point source loads;
(ii) changes in technologies (in fertilizers, sewage handling in wastewater treatment plants, etc.) and policies, e.g., the banning phosphorus from detergents;
(iii) the decline of industry and agricultural production, characteristic in the late 20th century over much of the area of Eastern European countries, e.g., Hatvani et al. (2015); and,
(iv) the implementation of directives such as the Clean Water Act in the US (US Gov, 1948), or the Water Framework Directive in Europe (EC, 2000).

Despite the foregoing, the water quality of surface water bodies remained poor, and still of major global concern; see e.g., Thornton (1999), Carvalho et al. (2019), Malone and Newton (2020). A likely cause of this somewhat paradoxical result is that, while nutrient losses from easily identified point sources have indeed been reduced in many countries, diffuse loads originating from agriculture remain significant.

Given current trends in global population growth, according to the Food and Agriculture Organization (FAO), by 2050 the current output of the food production industry must increase on average by 70% compared with 2011 (Dubois, 2011) to be able to maintain current highly wasteful consumption habits in which approximately one third of produced food is lost (FAO, 2011). Agriculture is the main source of diffuse pollution affecting surface (and subsurface) waters on a catchment-scale. Therefore, any increase in productivity presents a risk to, among others, the quality of surface water ecosystems and ecosystem services. The phenomenon can be viewed both as the loss of substances from agricultural fields and an overuse or misuse of land (Novotny, 1999), or the appearance of these substances as excess in surface waters. The primary impacts will be associated with the enrichment of nutrients derived from fertilizers, applied in agriculture and forestry, which contain phosphorus and/or nitrogen. Furthermore, sediment contamination is likely to increase, and pathogens, pesticides, salts, trace elements, dissolved organic carbon, and substances contributing to the increase in biological oxygen demand are also likely to be arriving in the receiving waters (O'Geen et al., 2010).

The management of diffuse pollution from agricultural areas is necessarily a complex operation requiring catchment-wide approaches (OEDC, 2017). It is in this context that (semi)-constructed wetlands can be efficient tools for mitigation of risk of pollution to surface waters.

Wetlands in the mitigation of agricultural diffuse pollution

Constructed wetlands in agricultural settings are very different from their urban "treatment" counterparts in terms of flow, nutrient composition, etc. Under natural conditions, the inflow rate to wetlands is characterized by a higher degree of variation over seasonal or even diurnal scales. In contrast to constructed treatment wetlands used to treat municipal wastewater, this might be due to localized meteorological events (Gopal, 1999). Not only the flow conditions, but also the composition and concentration of substances in the inflow are different.

Possible location of semi-constructed wetlands in a catchment—general considerations

The location of wetlands, whether on an interstream divide, coastal lowland, in a topographic depression, or on a slope, is a product of historical development and the regulation of surface water within the landscape. For a semi-constructed or constructed wetland to function, it must be self-sustaining. In order to achieve that, it has to be properly embedded in the catchment, because its location in the landscape influences its geographical characteristics, and should be evaluated in this context. Elements such as slope, thickness and permeability of soils, and the hydrogeological properties of the subsurface layers have to be taken into account, since all of these influence surface and subsurface flows of water. The slope of the area where the wetland is located is a key factor. In the case of slopes which have a moderate to steep gradient, similar characteristics will prevail, with any changes ocurring mainly in the flora; however, the steeper the slope, the more the functionality of the buffer strip is shifted towards erosion prevention and P retention from runoff (Stuart et al., 2022).

The question of where a wetland is located within the catchment is important. In the case of upstream wetlands (Fig. 2A), their optimal location coincides with the maximization of particle trapping, placing them close to the sediment resource areas (hot-spots), where the erosion potential is the highest within the catchment. In this way, travel distance is minimized and the likelihood of the wetland receiving intact aggregates, which have greater settling velocities than smaller particles, is higher (O'Geen et al., 2010). If, however, the aim is to maximize the retention of agricultural diffuse loads within the landscape (i.e., collect as much of the effluents as possible), the ultimate receiving water bodies must be located at an elevation relatively lower in the catchment than the contributing upland hot-spots (Fig. 2B–D). The essential point is that, the closer the wetland to the source, the more sediment it retains, while the further downstream it is—and therefore the more extensive the catchment upstream of it—the greater amount of diffuse loads it can retain.

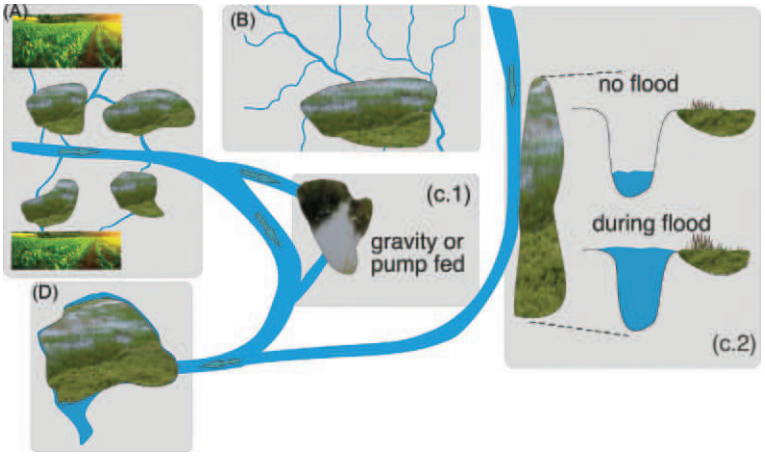

Fig. 2 Possible locations of (semi-)constructed and/or natural wetlands in a landscape for controlling nonpoint source pollution. Upstream (A); isolated wetlands with their own catchment (B); riparian (C) including gravity/pump fed (c.1) and flood fed (c.2); and downstream (D) wetland locations. All of these are illustrated in a catchment of a large river receiving agricultural diffuse loads inspired by Mitsch (1992). The blue arrows indicate the water flow direction.

To evaluate the position and possible functions of wetlands created or restored for compensatory mitigation purposes, the context of the landscape itself should be considered, and that landscape is divided into catchments, by watersheds. Wetland development and/or restoration have to be drawn up with reference to the catchment in order to identify the most appropriate location for mitigation sites (NRC, 2001). Agricultural runoff (surface and/or subsurface) can reach rivers, streams and lakes via different paths across a wetland system depending on its construction and location within the landscape and a catchment (O'Geen et al., 2010). Within a catchment, wetlands can be located: (i) U*pstream*, where numerous relatively smaller wetlands independently intercept waters arriving from smaller water courses/channels before allowing these to reach the main river or stream (Fig. 2A). These, however, are not necessarily located in the streams themselves: one common location is in the restored floodplain (e.g. Fig. 2B). This then constitutes the next location: (ii) *riparian zones*. These run parallel to the river, and serve as an interface between the land and freshwater ecosystems, and thus represent transitional areas. Wetlands in the riparian zone can be further subdivided: (ii/a) pump fed (Fig. 2c.1) or (ii/b) gravity fed (Fig. 2c.2), with the latter having continuous water flow, or flow only during flood events. Lastly, (iii) *downstream* wetlands are characteristic of water courses which are mostly located instream (Fig. 2D), and are among the largest in size and runoff, usually comprising engineered control structures (Mitsch, 1992).

Design criteria and characterization of wetlands adjacent to agricultural areas intended to increase retention efficiency

(Semi-)constructed wetlands

Semi-constructed wetlands are designed to serve a variety of purposes, such as the retention of excess nutrients through the ecosystem services they provide: e.g., contribution to biological habitats and diversity, hydrologic buffering, or water filtration (for details see Section "Ecosystem services"). Their position within a catchment and the landscape involves many considerations (as seen in Section "Possible location of semi-constructed wetlands in a catchment—general considerations"; Fig. 2). Wetlands at the head of stream channels prevent further pollution by exercising their effects before the water enters the mainstream channel. The efficiency of retention is primarily determined by how evenly the arriving water is distributed across the wetland area. Therefore, the most important design parameters of constructed wetlands are (i) area and (ii) hydrologic load, which in turn, affect the (iii) retention time of the water in the system (see Section "Retention of substances" as well).

The minimal area of a wetland ((i) above), will vary between 0.1% and 7% proportionate to the size of its contributing catchment (O'Geen et al., 2010; Mander et al., 2017). If the wetland to catchment ratio is too small, the connectedness problem[2] will arise—see Mander et al. (2017) and Zedler (2003)—excessive loading rates will limit the water and substance retention times, and a significant amount of water will not flow through the wetlands. In contrast, larger wetlands will be highly sensitive to dry periods, due to the increased water surface area.

From a hydrological perspective, flow velocity, volume, seasonality and duration of flow are important factors, and will differ greatly among agricultural catchments. Therefore, all these parameters have to be considered in the design process (O'Geen et al., 2010). Depending on the spatiotemporal distribution of rainfall there is a continuous variation in the water depth, degree of water saturation and the area of the wetland. This spatiotemporal pattern affects the surface area of wetlands, which vegetation is present, the pace and degree of particle settling and resuspension, biodiversity, the redox status of the soil and its mineralogy, and last, but by no means least, the capability of the wetland to remove pollutants (Mitsch and Gosselink, 2011; O'Geen et al., 2010). Fluctuations in floods and dry periods facilitate the aerobic and anaerobic conditions, respectively, which are necessary for wetlands to retain

[2]The connectedness problem deals with the hydrological connectedness of wetlands t the stream network, which is an important factor in their phosphorus and nitrogen removal capacity, see Mander et al. (2017).

their natural functioning as much as possible; e.g., Hatvani et al. (2011). The coming and going of these aerobic and anaerobic conditions facilitates biochemical nutrient removal processes, such as denitrification and the degradation of organic carbon, as well as assisting in the transformation of phosphorus to soluble forms via Eh/pH driven reactions (O'Geen et al., 2010).

As a general principle, to calculate hydrologic loading and hydraulic retention time ((ii) and (iii) above), the flow rate has to be divided by the wetland surface area and the volume, respectively. In general, maximizing the retention time should elevate the degree of pollutant removal, and the removal efficiency correlates negatively with the hydraulic load (Mander et al., 2017). Mitsch and Gosselink (2011) suggested that (ii) hydrologic loading rates should vary between 25 and 50 mm day^{-1}. Although the manipulation of the area of a semi-constructed wetland is necessary to optimize hydraulic loading rate (O'Geen et al., 2010), this is difficult to achieve, since such wetlands can receive highly variable inflow rates originating from potentially vast areas of land in most agricultural settings.

Given that (iii) hydraulic retention time depends on the volume of a water body, the same retention time can be attributed to a wetland small in area, but deep, as to a one which is extensive, but shallow. These, however, will not have the same ecological characteristics, due to the effects of water depth on various key elements of any water body. These include plant habitats, the Secchi depth,[3] particle settling and resuspension rates and perhaps most importantly, depth is negatively correlated with the efficiency of the removal of most pollutants. The shallower the depth, the greater the surface area for a given planned volume in engineered systems, since more plant and microbial biomass can be present. For example, a wetland with a small surface area, but which is deep may have a similar retention time to a more extensive but shallow system, but the latter may well display a higher degree of efficiency in nutrient removal. This is why many studies suggest that depth should range from 15 cm to 50 cm. Thus, areal loading rate is a more accurate criterion then the load per volume (O'Geen et al., 2010).

In the case of a constructed wetland, the ratio of its length to width (as measured along the direction of flow and perpendicular to this) is a critical question in terms of the optimal proportions regarding their effect on removal efficiency (Mander et al., 2017). In order for semi-constructed wetlands to be efficient in load retention these have to be of a width sufficient to ensure the effective trapping of sediment and other particulate materials, and of a length sufficient to ensure an adequate residence time. Some argue that long, narrow wetlands are less efficient at removing contaminants than square or round ones (Scholz et al., 2007; O'Geen et al., 2010). Nevertheless, it is those wetlands with a channel-like surface flow and a length to width ratio of >20:1 that achieve the best water treatment performance (Kadlec and Wallace, 2008). In the meanwhile, in rectangular constructed wetlands, a serpentine flow-path winding along the long axis is the best way to increase hydraulic retention time (Persson et al., 1999).

Besides the abiotic design characteristics discussed above, the type of vegetation that is planted affects the effective area of the wetland, its hydraulic retention time, as well as its light conditions too. The most important task in either restoring, or designing/creating, a wetland is at least to maintain and if possible increase the diversity of flora and fauna. Diversity in terms of plants ensures a low cost, whether this is initial, operational or maintenance, and the efficient operation of any wetland system. For details on the types of vegetation, the reader is referred to Rousseau et al. (2022), and regarding the related processes to Section "Retention of substances".

Riparian wetlands as buffer strips

Riparian zones form an ecotone between anthropogenically disturbed lands and surface waters. These are one of the most effective and widely applied means to the interruption of the movement of diffuse substances from adjacent agricultural areas to surface waters (Stutter et al., 2019). This is because the processes taking place in such zones are fundamentally driven by the channel dynamics, flooding and soil moisture. In addition, and in a similar way to wetlands, these areas filter water originating from intensively managed agricultural land in the vicinity, and polluted flows which arrive by both overland and subsurface routes. They also work to protect the banks against erosion. Furthermore, the shade from the canopy of trees growing in riparian zones helps inhibit the intensive growth of aquatic macrophytes, not to mention improving the microclimate in the adjacent fields (Fig. 3) (Mander et al., 1997). Nowadays the extent of the areas adjacent to intensively cultivated agricultural zones is becoming ever more limited, often reduced to only narrow (sometimes mandatory) strips of vegetation along streams and rivers characteristic of various riparian soil water conditions, and without the prescribed management of this buffer zone between field and water body (Mander et al., 2017; Stutter et al., 2012).

That said, many riparian areas can and do function as wetlands, if the water table has a sufficient spatiotemporal presence for hydromorphic features, characteristic for wetlands to develop in the top 50 cm of the soil profile (Mitsch and Gosselink, 2011). Conversely, only those wetlands which are located along the banks of a stream or river and have at least seasonal connection to them can be rightly regarded as riparian (Fig. 2).

Riparian buffer zones frequently consist of semi-constructed wetlands. It should be borne in mind that a wetland itself can have its own buffer zone(s) (see e.g., Norman (1996)), but in such a case, this will not be riparian rather "just" a buffer zone. In the present case the focus is on semi-constructed wetlands located within the riparian zone of a larger river (Fig. 2C). Specifically, functioning as buffers between the larger river and the intensively managed adjacent agricultural fields, since these have a much higher efficiency in the retention of nutrients from the river than a vegetated buffer strip (Osborne and Kovacic, 1993). Hence, semi-constructed buffer wetlands in riparian zones have become a widely implemented and studied "edge-of-the-field" mitigation measure to provide a physical barrier against nitrogen, phosphorus, and sediment transfer (Stutter et al., 2012).

[3] "The Secchi disk in most countries is a circular white disk 30 cm in diameter that is lowered into a natural body of water by a human observer until it disappears from view. The depth of disappearance is a visual measure of the clarity of the water" Preisendorfer (1986).

The main processes mediating water quality are sediment trapping, denitrification, nutrient uptake, and the sorption of phosphate into soil particles, as is the case in natural wetlands; see review by Vymazal (1995). By example, with regard to P loads—which are typically bound to sediment—a buffer strip 10 m in width can reduce these P loads brought by surface runoff by up to 95%, but again depending on the P forms efficiency can vary; see e.g., Dorioz et al. (2006). Nitrate is more difficult to remove, because it is less likely to adsorbed in the soil and may be removed and/or transformed by soil microbial processes such as denitrification in these zones. Nonetheless, there is about 50% efficiency in its removal in these same buffer strips (Vought et al., 1995); e.g., Fig. 3 circular arrows. Efficiency may, however, vary greatly, as the relationship between pollutant removal and buffer width is nonlinear with wider buffers tend to remove more N (Mayer et al., 2007). To reach a similar level of retention as in the previously mentioned case, in a coastal setting for P, a 250 m width is needed, while for N this figure is only 3.5 m. In any case, generally optimal buffer efficiency occurs at approximately 80% removal (Desbonnet et al., 1995). It should be noted that *there is no "one-size-fits-all solution"* in this regard.

In order to exploit the retention capability of a riparian wetland, its integrated embedding into the landscape is suggested, and as close to the stream as practicable. Moreover, besides engineering and landscape considerations, when wetlands are designed and placed within a catchment, a balance should be reached between the primary drivers of nutrient removal rates (e.g., the hydraulic loading rate and inflow concentration), so the wetland is capable of achieving peak retention capacity of the total transport of nutrients. This balance is, as in many natural systems, delicate, and subject to tipping into imbalance as a result of only small changes in any of its elements. In terms of the likely effects of climate change, loads of N (Jeppesen et al., 2011) and P (Jeppesen et al., 2009) from cultivated areas to surface waters will probably increase, rendering efficient functioning even more important.

Proceeding from the agricultural fields towards the stream, the following sequence is suggested: First, a narrow grass strip at the upland edge of the zone for runoff control and which will retain suspended solids and phosphorus. Next, an area of shrubs and a wider area of primarily deciduous trees; this should be capable of retaining nitrate, providing organic matter and shade under the canopy (Mander et al., 2017). Heading towards the stream, the riparian trees will achieve bigger and more robust growth as the shallow groundwater table (replenished by the stream) approaches approximately the level of the ground surface. The final zone is defined by the saturated condition of the soil, and it is only here that the riparian wetland ecosystem proper can be said to begin, and it is this zone that forms the ultimate "defense against" the excess substances lost from agricultural fields reaching the stream or river Fig. 3).[4]

Retention of substances

In agricultural settings, wetlands serve as filters and transformers of water-quality constituents. In terms of the mass balance, they may function as either sinks or sources, depending on the wetland type, hydrological conditions and the duration and temporal variability of input nutrient flow. The latter may adversely affect both the rates and pathways of removal mechanisms by the transfer of contaminants from one compartment of the system (water column) to another (sediment). Such transfers are the result of a combination of hydrological and biogeochemical processes which control how they are mobilized in an agricultural landscape and subsequently delivered by land or water. Due to the complexity of agricultural landscapes, these processes might as well be difficult to understand and to model (Dupas et al., 2015).

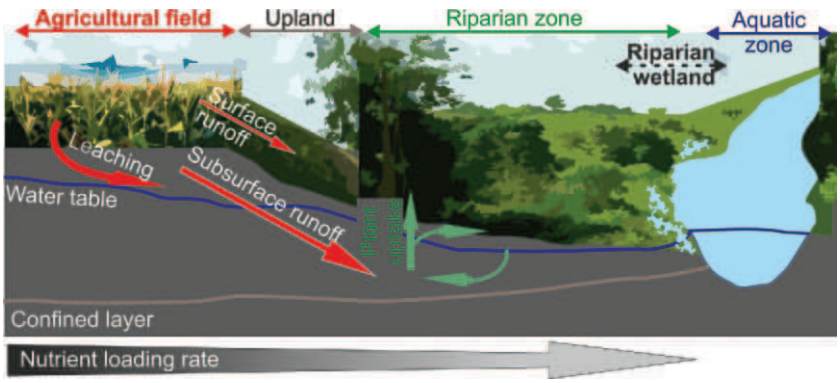

Fig. 3 Cross-section of a riparian zone including a riparian wetland area, showing the primary hydrological fluxes responsible for nutrient transport from agricultural land. The arrowed divisions at the top of the figure indicate the various areas of a (simplified) riparian zone. Red arrows indicate the direction of nutrient loading processes, with the shaded arrow at the bottom indicates the loading rate as it decreases towards the stream, the shading reflecting the intensity of these from dark (higher) to light (lower). Green arrows indicate main processes retaining and reprocessing nutrient loads arriving from the agricultural field.

[4]For a more detailed description of the three-zone structure, the reader is referred to the Constructed Wetlands for urban wastewater treatment: an overview Chapter in the Human pressures and management of Inland Waters Section of this encyclopedia (Stuart et al., 2022).

In constructed wetlands, the removal of contaminants can take place via various mechanisms. These primarily include: the biotic uptake of nutrients, including, in some cases, salts; pesticides and organic matter undergoing microbial degradation; biogeochemical transformations, for example, methanogenesis and denitrification; the sedimentation of substances like phosphorus, pesticides, particulate organic carbon and pathogens, and their subsequent burial; biogeochemical transformations, such as denitrification and methanogenesis; redox transformations, which in turn, affect qualities like solubility, sorption, and even toxicity; pathogen predation; pesticides and organic matter undergoing photodegradation (Zedler, 2003).

Wetland flora is the major element of such a system through which these mechanisms operate for the retention of nutrients. The most essential component in this regard are the micro-biomes in the sediment/soil in the vicinity of the roots. As might be expected, it is most active in the growing season, due to higher rates of microbial activity and macrophyte productivity. An increased plant presence increases the nutrient removal efficiency; though the quantity removed will depend on the choice of plant species used to vegetate the area; for a comprehensive review see Vymazal (2007). Whatever exceptions and caveats might be made, it is possible to make the following general points concerning wetland plants:

- They influence water chemistry in two directions: through their uptake of nutrients, acting as nutrient sinks, and through input, as nutrient pumps transferring compounds from the sediment to the water column (Fig. 3: plant uptake). The relationship of emergent vegetation to contaminant removal is not a simple, straightforward one.While vital in the translocation and transformation of nutrients, the vegetation can only remove these excess materials from the system if the vegetation itself is harvested and removed (or in the case of nitrogen, burned). That said, however, if this is not the case, wetland vegetation can and does still contribute to nutrient removal in a variety of ways, but indirectly: simply by impeding water flow, which in turn, promotes particle settling and the prevention of sediment resuspension, on account of the mere presence of stems and leaves within the water column (Fig. 1B) (Johnston, 1991).
- Wetland plants also perform vital functions in the wetland ecosystem by providing habitat for other taxonomic groups. Apart from the living plants themselves, their litter and stems increase the surface area of the substrate available for microbial attachment, as also for biofilm communities, and these two are in the front line of many transformation processes. What is more, the death and decay of plants recycles P and N to the system, while supplying organic carbon which then plays a central role in many microbial transformations, a key example in the current context being denitrification. Parallel to this, the carbon content of plant litter functions as the energy source for heterotrophic denitrifiers (Brix, 1994).
- Plants also influence hydrologic conditions, like transpiration and water shading; and they also stabilize the banks by modifying currents and sedimentation, as well as mitigating the effects of flooding. In addition, the composition of such vegetation may serve as an indicator of the health of a wetland (Cronk and Fennessy, 2009).
- Wetland plants intercept solar radiation, thus reducing the penetration of UV light into the water column, thereby reducing pathogen attenuation and the process of photodegradation. However, light interception also "shades out" algae, resulting in fewer phytoplankton which, in excessive numbers might cause high biological oxygen demand and hypoxia (O'Geen et al., 2010).

Nutrients: Phosphorus and nitrogen

Looking at the number of influencing factors, the question may arise of what might in fact be expected of semi-constructed / natural wetland systems in terms of their retention of agricultural diffuse loads. The degree of efficiency in nutrient removal of semi-constructed wetlands has been discussed from innumerable angles over recent decades; e.g., Fisher and Acreman (2004), Land et al. (2016). A thorough review of the topic in 2016 looked at more than 200 wetlands (primarily in N America and Europe) which were assessed in 93 different papers (Land et al., 2016). Despite this potentially baffling variety, one general and overarching truth can be established: the greater the amount of nutrients (total phosphorus (TP) and total nitrogen (TN)) received by the wetland, so, proportionately, the greater percentage of that total will the wetland be capable of removing, see e.g., Hatvani et al., 2014. It is, however, important to impose a qualification on this general point: the specific degree of the efficiency of the removal of a given amount of nutrients will vary greatly across different sites depending on factors such as the structure and functioning of the particular wetland, inflow concentration, load variations, hydraulic retention time, the temperature regime (Kadlec and Reddy, 2001), hydraulic efficiency, and the type of wetland in the first place (Land et al., 2016; Kadlec, 2009). It is for this reason that making any comparison or any generalization at all is fraught with difficulty. Taking all of this into account, it is no wonder that there has been widespread confusion over the relationship between nutrient reduction within wetlands and the quantity of nutrient loads arriving in them.

Wetlands play a crucial role in the retention of phosphorus and nitrogen compounds from agricultural fields, thus retaining the degradation and eutrophication of freshwater ecosystems. Temporary storage via plant uptake retains both P and N, while inorganic soil adsorption, and in peatlands, incorporation of organic matter into the peat, both reduce P loads. N, meanwhile, is retained by microbial activity, specifically, its immobilization and storage in the soil as organic N and its conversion to gaseous N-forms (Mander et al., 1997).

Before presenting some figures for removal rates, it is important to note that the removal rates of nutrients loads are commonly expressed either in g m^{-2} $year^{-1}$ or in %, and referred to as *removal efficiency*. (In certain cases, the former is also expressed in kg ha^{-1} $year^{-1}$, which basically gives values one order of magnitude larger). It is also necessary to note that, as a general principle, in wetlands' nutrient retention, the variability of diffuse inflow in terms of its occurrence and concentration is quite problematic. The

more balanced the inflow of nutrients, the more the system can retain (Tanner and Kadlec, 2013). Thus, there is a strong tendency in the numerous reviews of nutrient retention to treat wetland systems as 'black boxes', for which the internal workings are not always explored.

Nevertheless, turning to the figures, it can be stated that in the last 25 years of the 20th century, sustainable removal rates for constructed wetlands were typically 10–40 g N m^{-2} $year^{-1}$ and 0.5–5 g P m^{-2} $year^{-1}$ (Mitsch et al., 2000). These may be compared with figures from a review of the first 20 years of the 21st century, which suggests a wider range for N and P removal from agricultural drainage and runoff by free water surface constructed wetlands: approximately 1 to 1.125 g N m^{-2} $year^{-1}$ (avg. 117.5 g N m^{-2} $year^{-1}$) and approximately 0.2 to 115 g P m^{-2} $year^{-1}$ (avg. 15.7 g P m^{-2} $year^{-1}$) (Vymazal and Dvořáková Březinová, 2018). The most comprehensive study reviewed 203 wetlands of all types (Fig. 1A), with various inflow types (e.g., agricultural runoff, secondary domestic wastewater, etc.). The average removal rates for TN and TP were 184 and 15 g m^{-2} $year^{-1}$, respectively; that is, these were of the same magnitude as in the case of the wetlands discussed previously, or those reviewed by Weisner et al. (2015), although it must be emphasized that these were mostly (about 80%) free water surface wetlands, and about 50% of the wetlands had agricultural runoff inflow (Land et al., 2016). It should also be emphasized that within the bounds of natural variability, the removal efficiency of TN and TP (among others) increases with hydraulic loading rate (mm day^{-1}) and inflow concentration (mg L^{-1}); note that there is a steeper increase in removal rate at concentrations higher than about 20 mg L^{-1} and about 0.5 mg L^{-1}, respectively (Land et al., 2016).

Outlook on retaining pesticides

The number of products registered as pesticides are already in the thousands and in 2017 approximately 4.1 million tons were *reportedly* applied globally (FAO, 2020). These are substances or their mixtures, primarily used to control weeds, pests and pathogens in agriculture to increase crop yields, and used to protect humans from vector-borne diseases (Nicolopoulou-Stamati et al., 2016). Unfortunately, after playing their role in the fields such compounds enter surface and subsurface water bodies primarily via diffuse pollution (see Section "Non-point source (diffuse) pollution"). The mechanisms of this process are as follows: surface runoff and erosion; spray-drift[5]; leaching; drainflow, or as it is sometimes called, preferential flow; various other atmospheric routes, such as deposition and atmospheric transport of soil eroded by the wind (Reichenberger et al., 2007). Although there are various highly important negative aspects of pesticides and their residues, in the present subsection we focus on their presence and more importantly retention via wetland systems from surface waters.

In surface waters pesticide concentrations are primarily related to soil management practices and agriculture, and their most effective control is with the application of edge-of-field and riparian buffer strips (see Section "Riparian wetlands as buffer strips"), vegetated ditches (which may replace the grass strip of a riparian buffer strip), and constructed wetlands. However, removal efficiency varies across different pesticides, grouped based on the chemical basis of their compounds between approximately 25% (triazinone) to approximately 100% (e.g., organochloride, organophosphate), or based on the pesticides' physicochemical parameters (Vymazal and Březinová, 2015). It is a common characteristic, however, that removal efficiency increases with retention time in all cases, although not in a linear fashion. Depending on whether the environment is aerobic or anaerobic, the following processes will be operating in pesticide mitigation: hydrolysis, photolysis, sedimentation, adsorption, microbial degradation or plant uptake. However, the extent and intensity of these processes will depend on local conditions, making an a priori decision regarding the importance of any one of them difficult. One thing does appear to be definite, and that is the evidence that the presence of vegetation enhances pesticide retention: as one study found, plant uptake and sorption of systemic herbicides could reach up to 80% in some cases (Vymazal and Březinová, 2015). This however raises the question, how much of these pesticides will be accumulated in the sediments, or their residues over time?

Although there are trends emerging to reduce the use of pesticides, this might lead to a serious drop in crop yields. Therefore, new approaches and technologies, and a change in paradigm are needed, especially in the view of the aforementioned ever greater need for produced food (see Section "Introduction") (Chen and Wong, 2016).

Ecological considerations

Ecosystem services

In the first decades of the 21st century the global monetary value of ecosystem services provided by wetlands reached almost Int$50 trillion a year (Davidson et al., 2018). In terms of Green infrastructure, then, it is clear that constructed wetlands in a catchment and riparian buffer zones (including when a buffer zone comprises the wetland) are important and valuable elements of such infrastructure in intensively farmed landscapes (Mander et al., 2017). While for centuries constructed and restored wetlands had played a crucial role in improving wildlife habitats in agricultural settings, with the rise of awareness of the problems of pollution and the importance of environmental protection in the 1970s, they came to be recognized as zones capable of efficiently retaining diffuse pollution from agricultural areas arriving to freshwater rivers and lakes. Indeed, since then, wetlands have come to be seen as the 'kidneys' (although with a limited capacity) of the hydrological cycle, providing a wide variety of ecosystem services working in

[5]Spray drift can occur during the application of plant protection products. It is defined as the transfer of small spray droplets by wind from the target area due to poor calibration or application practices.

favor of the mitigation of agricultural diffuse loads. These wetlands act as biodiversity hot-spots by providing shade, wind buffering, protection from floods and a habitat for birds, thus sustaining the natural functioning of the wetland. In the meanwhile, these factors can only enhance their functioning as carbon sinks. Completing and complementing these defenses and protections, wetlands support the formation of fertile soils, thus helping further in decreasing nutrient and sediment loss from agricultural areas.

The foregoing does not, however, exhaust the ways in which wetland ecosystem services are beneficial. Wetlands act as areas of flood protection, and are a valuable resource in terms of drought resistance. They support grazing and aquaculture and they provide raw materials such as timber, peat and firewood. Wetlands are also a source of drinking water for livestock. Last, but not least, wetlands have an aesthetic and cultural value as well (Zedler, 2003). When the extent and/or functioning of wetlands is degraded for the benefit of the extension of agriculture or urbanization, all of the above-mentioned services are also degraded, or even completely lost. However, at sites where farming is not profitable, the restoration of former wetlands could revitalize these ecosystem services, via rethinking existing landscape-design models and attuning them to agricultural landscapes (Zedler, 2003).

A practical demonstration of the potential ecological and economic value of wetland restoration is the case of the Nakivubo wetland system in Kampala (Uganda, Africa), which has been used as part of the nutrient management by Kampala and reducing loads to Lake Victoria. This wetland system is hemmed in by urban and agricultural land, and runs from the central industrial district of Kampala, entering Lake Victoria. About one third of its original area has been used for agriculture and further part for industry and housing in the past decades (Emerton et al., 1999). The interesting part in the case study—from the perspective of this chapter—is that there has been a detailed estimation of the overall costs of the restoration and its benefits in ecosystem services. The capital cost of the project alone was Int$53 million, approximately 20% of which was used to handle nonpoint source pollution and focused on wetland rehabilitation; measures to control agricultural activity comprised <0.1% of the total budget. Even in the case of the worst estimates, the internal rate of return over a period of 15 years was projected to be 4% per year, reaching up to 34% in the best-case scenario (Turpie et al., 2017).

This case study emphasizes the importance of integrating wetland values into land use and development decisions, and provides examples of the estimated economic value of important wetland 'goods' and services. However, the proportionately low level of planned expenditure designated for the handling of related agricultural problems seems to be associated with the lower priority historically given to such phenomena (see Section "Non-point source (diffuse) pollution").

Eutrophication and trophic state

The process of eutrophication in any wetland is not essentially different from other water bodies. Natural or anthropogenic input/load of inorganic elements, primarily phosphorus and nitrogen among many others (Naeem et al., 2014), can lead to internal enrichment of nutrients in the system. The resulting excessive growth of macrophytes or algae enhancing primary productivity, net accumulation and decomposition of organic matter differ little from symptoms in shallow lakes (Scheffer, 2013). Although there is still a controversy about the role and magnitude of nitrogen and phosphorus in limiting the productivity of aquatic ecosystems. Nitrogen is often the most limiting element in flooded soils of wetlands and not phosphorus. Soil microbial biomass, however, reacts positively to phosphorus enrichment. Consequently, internal phosphorus loading from the sediment/flooded soil regulates the eutrophic status of wetlands particularly at low or reduced external loading (Sánchez-Carrillo et al., 2011). All processes associated with eutrophication will be intensified by climate warming, reinforced weather variability, population growth, changes in land use and agricultural pollution (Dokulil and Teubner, 2011; Dokulil, 2014) with severe effects on biodiversity of macrophytes and freshwater algae (Dokulil, 2003, 2017).

One of the main direct effects of discharge of the anthropogenically-driven excess nutrients into aquatic ecosystems from agricultural runoff is the dramatic shift towards less desirable trophic status, which represents the most widespread challenge to water quality globally. The oxygen depletion and algal blooms caused by this process lead to the serious degradation of freshwater biodiversity, ecosystem services and water quality. A cause for concern is that examples of the adverse effects of algae blooms on shallow lakes have been, and continue to be, reported all over the world, for example: in Asia (Qin et al., 2007); North America (López-López et al., 2016; Oberholster et al., 2006); Europe (Hatvani et al., 2020); South America (Oliveira and Machado, 2013) and Africa (Muli, 1996). Furthermore, it appears that the nutrient (and especially P) enrichment of surface waters is reaching such levels that it will be extremely difficult to reverse, or even that it is no longer possible (Carpenter and Bennett, 2011). The timescale in which this problem is unfolding is measured in generations: it has taken a whole generation to recognize the gravity of agricultural diffuse loads arriving to surface waters, and it will most likely take another to resolve its impacts (Withers et al., 2014).

Conclusion/synthesis

This chapter gives an overview on the most important characteristics of (semi-) constructed wetlands in retaining agricultural diffuse loads from inland surface waters. The basics of their typology and possible location in the landscape, and most important design criteria are discussed while keeping the focus on nutrient retention.

The preservation of water bodies of all sorts for future generations is a global need. At first it may seem that the satisfaction of human demands, the provision of enough food for the ever-growing human population, stands in opposition to the necessity of mitigating the negative effects of expanding agricultural production. This is not, however, an either/or choice, but rather a problem of finding nature-based solutions capable of meeting both the socio-economic and environmental challenges.

Wetlands of all kinds in the right position in the landscape and the catchment are one of the most capable tools of handling catchment-scale pollution from agricultural areas. (Semi-)constructed wetlands in this context can be a "compromise" between natural and constructed wetlands in terms of their purpose and functioning, while not requiring any energy input (unlike constructed ones) and have a minimum of artificial structures. Semi-constructed wetlands are designed to serve a variety of purposes, such as the retention of excess nutrients, pesticides, etc. through the ecosystem services they provide, e.g., contribution to biological habitats and diversity, hydrologic buffering, or water filtration.

It is, however, strongly preferable to preserve and protect existing wetlands rather than to let them degrade and then create artificial wetlands. It has taken decades to recognize and begin to understand the complex nature of agricultural diffuse pollution and its adverse effects in continental waters. It will take considerably global, and collaborative, effort across multiple sectors to mitigate these negative changes. With cross-disciplinary research and good policies made in due time, conserved and semi-constructed wetlands can play an important role as nature-based solutions in reducing transport and mitigating impact of inland agricultural diffuse pollutant loads.

Knowledge gaps

- There remains major *uncertainty* about the retention of certain substances (*material fluxes*) by wetlands, despite many experiences and strong knowledge of the underlying processes. In our review, we did not cover in detail heavy metals (Matagi et al., 1998) and, other micropollutants related to agricultural origin (e.g. livestock farming), such as the removal of pharmaceuticals, e.g. antibiotics (Liu et al., 2019).
- *Lifespan of wetlands*: one of the main benefits of natural systems compared to artificial treatment is their long lifespan. However, in this review the question is not discussed, how does efficiency and functionality change over time? Furthermore, how will natural wetlands respond to changing external loading and/or changing climatic conditions (Honti et al., 2020)? There is quite a lot of uncertainty, for example regarding sediment accumulation, changes in the wetland ecosystem, and decreasing adsorption capacity (Dugan and Dugan, 1990).
- *Legislative issues*: the management of natural wetlands raises legal issues (Smardon, 2009), for example, harmonization with agricultural regulations (Shine and De Klemm, 1999). Property rights need to be clarified: who is the owner and who is responsible for the maintenance of wetlands? More general, a main question is how farmers may be persuaded (and supported) to establish a wetland on their land? This can be achieved through the proper application of subsidies.

Important case studies

- Case study chapter of the same Book Section (under planning); leading author Rupesh Bhomia.
- Kis-Balaton Water Protection System (Hungary, Europe; adjacent to Lake Balaton) (Hatvani et al., 2014; Honti et al., 2020; Rupesh Bhomia et al., 2022).
- Nakivubo wetland system in Kampala (Uganda, Africa; adjacent to Lake Victoria) (Emerton et al., 1999; Turpie et al., 2017).
- Heavy metal retention by constructed wetlands (case study) (Vymazal and Březinová, 2016).
- Case study on the mitigatind diffuse loads with a field wetland (Ockenden et al., 2012).
- Case study on how low nutrient removal efficiency can be from agricultural diffuse loads (Kasak et al., 2018).

See Also: Human pressures and management of Inland Waters: Agricultural Pressures on Inland Waters; Case Studies of (Semi)Constructed Wetlands Treating Point and Non-point Pollutant Loads to Protect Downstream Natural Ecosystems; Constructed Wetlands for Urban Wastewater Treatment: An Overview; Emerging and Less Commonly Recognized Chemical Contaminants: Organic Micropollutants; The Best Management Practices in Agriculture for Protection of Inland Water Ecosystems; Structures and functions of Inland Waters - Lakes: Lacustrine Phosphorus Cycling

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Case Studies of (Semi)Constructed Wetlands Treating Point and Non-point Pollutant Loads to Protect Downstream Natural Ecosystems

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Biomass The mass of animals and plants within a habitat measured at a given time.
Emergy The amount of energy that was consumed in direct and indirect transformations to make a product or service.
Eutrophication Enrichment of water by inorganic nutrients which results in intensive growth of plants (algae, macrophytes).
Heavy metals Metalliferous elements and their derivatives including zinc, lead, copper, iron, mercury, cadmium, cobalt, manganese and nickel.
Input output analysis The statistical assessment and visualization of the difference between inflow and outflow nutrient fluxes within the system boundary.; see Box 1 for further details.
Medium Soil, gravel or other material used in a constructed wetland in which to grow plants and support micro-organisms; also known as support matrix.
Nutrient load retention Difference between inflow and outflow nutrient fluxes within the system boundary.

 https://doi.org/10.1016/B978-0-12-819166-8.00150-X

Nutrients These are essential for the survival of an organism. In aquatic environments, nitrogen (N) and phosphorus (P) are key nutrients that affect the growth rate of plants. Although N and P are vital in natural systems, they are also fertilizer components. These nutrients leave the landscape as stormwater runoff (urban and agricultural) and harm natural areas by promoting algae growth and an overabundance of non-native plants disrupting food sources and habitats used by native wildlife.
Population equivalent (PE) Amount of degradable matter (expressed as BOD or something other) or volume of wastewater produced per capita (1 pe <150 LD^{-1} <0.15 m^3 D^{-1}).
Primary treatment Physical separation of solids, usually by settlement, before secondary biological sewage treatment.
Secondary treatment First biological stage of treatment for sewage.
Tertiary treatment Treatment following the biological stage of treatment for sewage, which may incorporate removal of nitrate and removal of surplus suspended solids.

Introduction

Wetlands are used as cost-effective nature-based solutions that provide environmental and socio-economic benefits to people locally and regionally. However, increased demand for, and exploitation of, wetland ecosystem services have placed stress on wetlands worldwide (Zedler and Kercher, 2005; Mitsch and Gosselink, 2011; Hatvani et al., 2022). Wetlands have often been treated in ways that results in pressures such as pollution, eutrophication, overexploitation of resources, and introduction of alien species. In a natural water body (lakes, ponds, wetlands), phosphorus (P) and nitrogen (N) compounds are primary limiting factors for algal growth (Yang et al., 2008), and addition of P and N through agricultural diffuse loads have been primarily responsible for eutrophication and degradation of inland surface waters across the globe (Carpenter et al., 1998), e.g., in Europe (Csathó et al., 2007), N. America (Daniel et al., 1998), and Asia (Jiang et al., 2007; Agrawal, 1999).

While more attention is needed to conserve wetlands and prevent rapid disappearance of existing natural wetlands, this chapter is aimed to highlight the role of wetlands as natural solutions to improve the quality of water which has been deteriorated due to anthropogenic activities. By availing natural biogeochemical processes, constructed wetlands have been widely used to remove excessive nutrients and other pollutants and improve water quality before it is discharged downstream (Langergraber et al., 2019; Rousseau et al., 2022).

Constructed wetlands (CW) utilized specifically for water treatment benefits serve as buffers in the catchment to retain nutrients, sediments, and contaminants (Kadlec and Wallace, 2009; Callaway et al., 2012; DeLaune et al., 2013, 2018; Bhomia et al., 2015; Morris et al., 2016; Qualls and Heyvaert, 2017). These CWs are designed to take advantage of many of the same biogeochemical processes that occur in natural wetlands, but do so within a more controlled manner. Constructed wetlands are used for reduction of nutrient loads in surface runoff to protect downstream ecosystems. Impacts from excess nutrient availability are known to degrade the natural balance of aquatic ecosystems (Smith, 2003; Verhoeven et al., 2006), hence CWs are specifically designed and strategically positioned on the landscape to transform and assimilate excess nutrients (Solano et al., 2004; Vymazal, 2007; Hatvani et al., 2022). Given their ability to 'treat' water, constructed wetlands specifically created for water quality enhancement are referred to as 'treatment wetlands'.

Constructed and semi-constructed wetlands are used to manage point and nonpoint sources of water pollution, including stormwater runoff (e.g., Rizzo et al., 2020; Sharma et al., 2021), domestic wastewater (e.g., Stefanakis et al., 2014; Auvinen et al., 2016), and agricultural wastewater (e.g., Hatvani et al., 2022). Constructed wetlands are mechanically simple, require low energy inputs, and generally have low operational and management costs. Additionally, wetlands can be designed across a broad realm of operational scales ranging in size from smaller units capable of treating wastewaters from a single household to large systems covering many hectares and treating high volumes of agricultural or stormwater runoff (Chen et al., 2009). These constructed treatment wetlands offer relatively natural and sustainable solutions to the more technological and resource intensive options for improving water quality and can operate for a long period of time.

This chapter provides four case studies where constructed (and semi-constructed) wetlands have been employed to reduce pollutants (and nutrients) originating from both point and non-point sources from having an impact on downstream waterbodies. These case studies not only highlights the successful utilization of natural biogeochemical processes for pollutant abatement but also demonstrates how constructed wetlands led also to significant improvement in our knowledge and understanding of these biological systems. These examples also indicate the wide acceptance of treatment wetlands as a functional ecological solution to effluent treatment across broad range of operational parameters. The first case study focuses on Florida Everglades (United States) which represents a semi-tropical system where constructed wetlands play a crucial role in ecological restoration of Everglades. The second case study focusses on Lake Balaton (Hungary), the largest shallow freshwater lake in Central Europe, and the important service these wetlands provides in reducing excessive nutrients to downstream ecosystems. The third case study provides details of a constructed wetland close to the capital city of New Delhi (India) treating effluent from domestic and small scale industrial/commercial units to generate treated water for irrigation. The fourth and last case study is based on a hybrid constructed wetland for decentralized treatment of municipal wastewater in De Pinte (Belgium) as an alternative to a large-scale conventional wastewater treatment plant.

Case study 1

The Everglades: Background

The Everglades system can be defined as the watershed beginning at the Kissimmee Chain of Lakes in central Florida, running south through Lake Okeechobee, the Everglades Agricultural Area, Water Conservation Areas, the ridges and sloughs of South Florida, the Shark River Slough, and ending at Florida Bay (Fig. 1). The Everglades system also includes the Caloosahatchee River and the St. Lucie Canal, flowing west and east, respectively from Lake Okeechobee.

Historically, distinct wet and dry seasons brought varying rain throughout the year, and annual fluctuations in rainfall overtime contributed to the ever-changing landscape of the Everglades, but the system remained oligotrophic in absence of any significant external inputs of nutrients. Interconnected small and large wetlands, the unique ridge and slough system, and limestone bedrock worked in concert with the volatile weather patterns and provided ideal conditions for water storage. Though slow moving for much of the year, water flowed through this landscape creating near perfect habitat for wetland populations of migrating birds, as well as terrestrial and marine wildlife.

This system was never a static ecosystem, but the rate of ecological and landscape change dramatically increased over the past 125 years. Drivers of these changes were from a set of predominately natural sources to a complex interplay of anthropogenic sources. This transformation of the historic Everglades was accelerated by an unprecedented input of phosphorus (P) as a byproduct of agricultural and urban development during mid-twentieth century (Richardson, 2010). The impacts due to excessive P influx have been widely documented for the greater Everglades ecosystem (Noe et al., 2001; Reddy et al., 1999). These impacts include reduced productivity of submerged plants and benthic periphyton, depletion of dissolved oxygen in the water, and changes in invertebrate and vertebrate community structure (Smith et al., 2009). The most conspicuous change in the Everglades has been the expansion of monotypic stands of cattail (*Typha* spp.) that displaced the indigenous sawgrass community (*Cladium jamaicense Crantz*) (Daoust and Childers, 2004).

Phosphorus is included in fertilizers and feed supplements to meet the requirement of agricultural crops and livestock and enable continued high yields, but unutilized P is lost from the agricultural fields or livestock feed lots. Because P in all its various forms is non-volatile, it follows hydrologic pathways and often gets concentrated in wetlands and inland water bodies after being introduced in the environment (Reddy et al., 1999). This excessive P in the Everglades system has been responsible for disrupting historical natural balance and unwanted impacts on flora and fauna of the system. In the past two decades much effort has gone into restoring the Everglades to its original hydrologic flow and ecological condition (Chimney, 2020).

Everglades restoration

Restoration of the Everglades is currently underway, with the aim to improve water quality, quantity, timing, and flow for both human needs and ecological integrity. Restoration efforts are steered by plans outlined in the Comprehensive Everglades

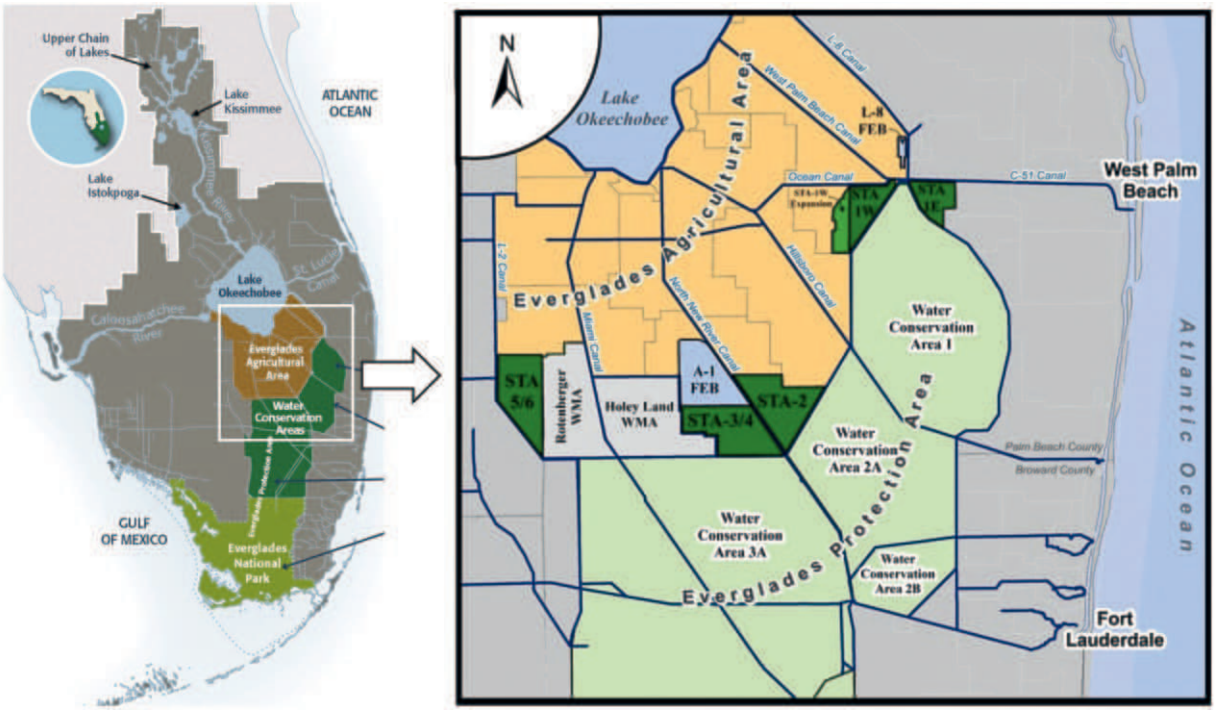

Fig. 1 Everglades ecosystem and location of six treatment wetlands intercepting agricultural and stormwater runoff originating from Everglades Agricultural Area. Map source: South Florida Water Management District.

Restoration Plan. A major component of this plan, water quality improvement, includes reduction of P inputs by implementing best management practices in the Everglades agriculture area (Diaz et al., 2005; Rice et al., 2002) and subsequent treatment of agricultural drainage waters (ADW) running off farmlands. A network of constructed treatment wetlands established to intercept ADW and stormwater runoff forms a crucial component of the Comprehensive Everglades Restoration Plan.

These constructed wetlands referred to as the Everglades stormwater treatment areas (STAs) are designed to reduce total P (TP) concentrations in surface runoff to reduce risk to receiving ecosystems. Six STAs (Fig. 1) with different sizes and configurations with a combined treatment area of 23,000 ha have been in operation for different time periods. The strategic location of these STAs has allowed them to retain over 2882 tons of P between WY1993 (Water Year 1993: May 1992–April 1993) and WY2020 (Chimney, 2020) which has resulted in a considerable load reduction of P to the Everglades. The overall outflow flow-weighted mean total P concentration from these treatment wetlands during this period has been 31 μg/L (Chimney, 2020) (Fig. 2). Although some of this retained P is in the vegetation and thriving biota (birds, fishes and alligators), a significant proportion of removed P is accumulated in soils and stored in both organic and inorganic forms (Reddy et al., 2020).

Complexity of STA operations

Although the STAs have sequestered a substantial amount of P during their operational history, they are known to exhibit variable treatment performance in terms of P removal efficiency over time (Chen et al., 2015). The spatio-temporal variability in STA treatment performance has been attributed to factors such as antecedent land use, vegetation condition and species composition, nutrient and hydraulic loading, hydraulic residence time, hydroperiod, soil characteristics and P content, flow way topography and configuration, extreme weather events, construction activities and regional operations (Germain and Pietro, 2011).

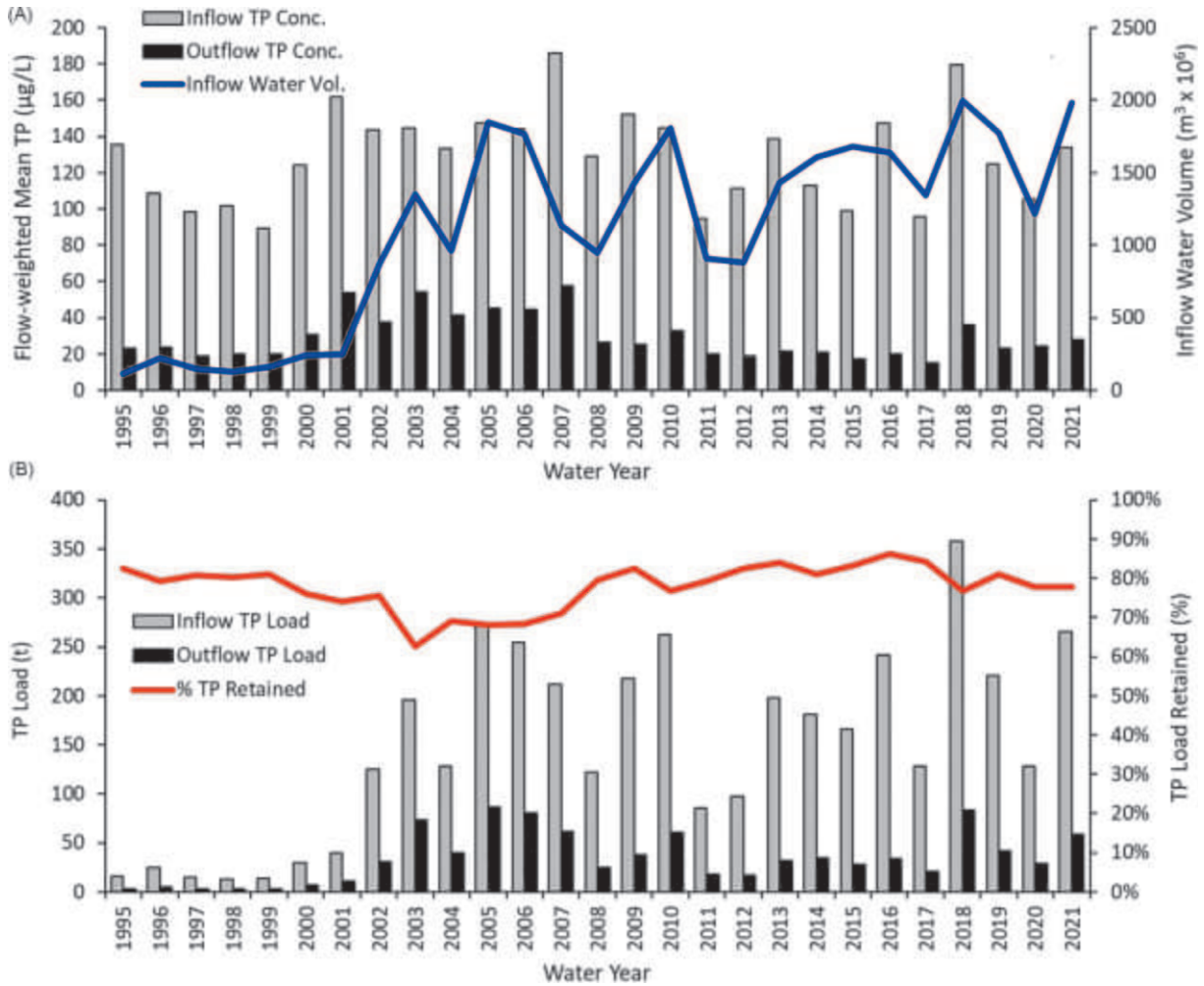

Fig. 2 Period of record time series of water quality enhancement (phosphorus removal by Everglades Stormwater areas. (A) Annual inflow and outflow flow weighted mean total P concentrations with corresponding inflow water volumes. (B) Annual inflow and outflow total P loads with percent total P load retained in the system (Chimney, 2020).

Performance of the STAs for regulatory compliance is quantified by measuring hydrologic parameters, i.e., volume and chemical characteristics of inflow and outflow waters to and from STAs. This approach, however, overlooks the complex biogeochemical processes that regulate P removal from the water column and controls the stability of sequestered P pools in the STAs. With continued STA operation, P removed from the water column accumulates as recently accreted soil and contributes to the incremental enrichment of the surficial layer of soil, potentially leading to the saturation of internal P storage compartments. Recently accreted soils (RAS) share an active interface with floc (unconsolidated detritus that is deposited on the consolidated wetland surface layer) and the overlying water column, and depending on the existing biogeochemical factors, nutrient concentrations in the RAS layer could potentially influence STA TP outflows (White et al., 2006; Bhomia, 2013). Therefore, an understanding of the complex processes that regulate long-term sustainable P removal in the STAs is desired for effective management and for meeting Everglades restoration goals.

Future outlook

The Everglades STAs are unique because of their large size and low target outflow TP concentrations (~13–19 μg/L). The general range of inflow P concentrations in many other treatment wetlands are 1–2 orders of magnitude greater than the STAs. The large expanse of STAs, past land use (agricultural farm or historic wetland), extreme weather events (e.g., droughts, storms), and suspension of operations due to nesting of migratory bird species, are only a few examples of the complex challenges encountered during the management of the STAs. The status of STA operational phases (start-up, routine operation, or recovery) and management activities (e.g., drawdown, cell rehabilitation, vegetation conversion and control) also influence outflow P concentrations from the STAs. For STAs to meet the desired outflow TP concentrations, it is important to understand the chemical composition and stability of accreted soil and implement sustainable management strategies for long-term performance of STAs. In addition, P storage, transformation, and transport are linked to cycling of other associated elements including C, N, K, and S. All these cycles are mutually dependent on each other and ultimately influence stability of stored P in soils and export of P into surface water. These interactions among key elemental cycles need further study and proper assessment before new management strategies are planned and implemented. Each of these factors has some bearing on the overall treatment performance of the STAs, and detailed understanding of the fate and transformation of sequestered P in STA soils may help in adaptive management to optimize STA efficiency.

Case study 2

The Kis-Balaton water protection system—Background

The Kis-Balaton Water Protection System (KBWPS) is a semi-constructed wetland (for a definition, see Hatvani et al., 2022) constructed on the remains of a once fully natural wetland—Kis-Balaton—to retain the nutrient loads brought to Lake Balaton by the River Zala (Fig. 3). The Zala accounts for about 50% of Lake Balaton's water and ~40% of its nutrient input (Hatvani et al., 2014). Lake Balaton is the largest shallow freshwater lake in Europe (surface area = 596 km^2), with an average water depth of 3.2 m, and its catchment extends over an area about 10 times that of its surface (~5180 km^2; Somlyódy and van Straten, 1986). Besides its role in the protection of water quality, the KBWPS is a protected nature conservation and NATURA 2000 area and has been under the de-jure protection of the Ramsar Convention since 1979 (Convention on Wetlands, 1971).

Brief history of the Kis-Balaton Wetland and the KBWPS

Prior to the 18th century, the area where the KBWPS is now located formed a part of the water body of Lake Balaton (Fig. 3A). However, due to deforestation, river control measures (primarily the regulation of the River Zala), and erosion, excess sediment was delivered to the western basin of the lake, resulting in the separation of the area and the formation of the Kis-Balaton Wetland (Erdélyi, 1963). It was first mentioned in historical documents as a separate water body in 1805 (Lovász and Baranyai, 2019; Lotz, 1988). In the 19th century, the River Zala was further regulated, and the wetland areas were drained to create arable land. Simultaneously, the water level of Lake Balaton was regulated (resulting in a drop in water level of 2–2.5 m by the mid-19th century) to protect the then-newly built railways. Thus, by the turn of the 20th century, the River Zala entered lake Balaton directly in its westernmost basin bringing nutrient-rich sediment to the lake without the KBW filtering or retaining it. Over the course of the 20th century, with increased agricultural activity, the growth of towns, and the rise of modern tourism with its concomitant expansion of the built environment expanding urbanization (the number of holiday homes along the shores quadrupled between 1920 and 1960), deterioration of Balaton's water quality continued (Hatvani et al., 2014; Somlyódy et al., 1983). Comprehensive measures to halt and reverse these negative trends were taken (details in Section "Construction and current setup of the KBWPS" and Hatvani et al. (2020) and Istvánovics et al. (2007) alongside the plans to reverse the adverse effects of agriculture and urbanization on the lower reaches of the Zala through the restoration of the former wetland in the form of the Kis-Balaton Water Protection System (Tátrai et al., 2000).

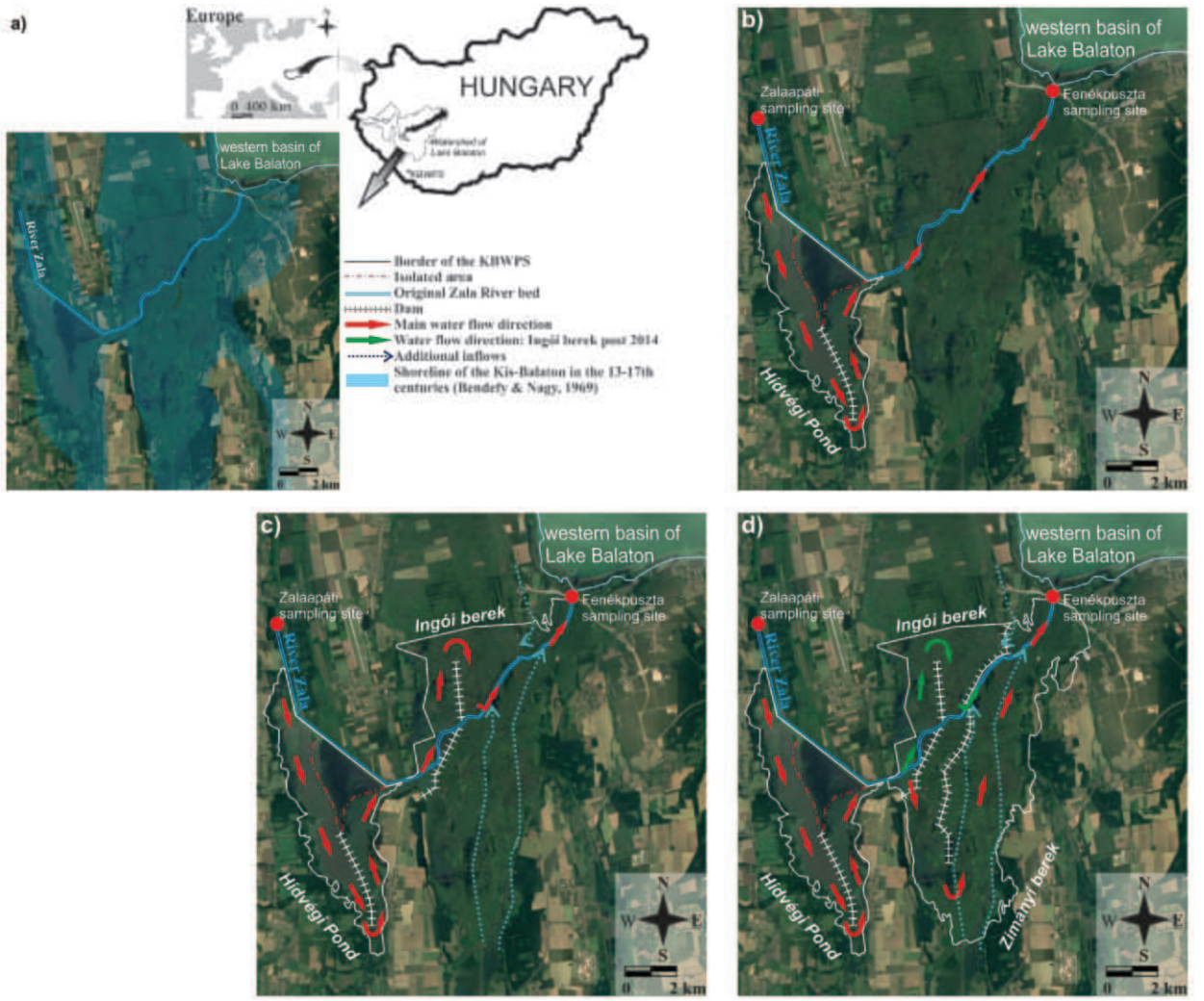

Fig. 3 Location and historical changes in the structure of the Kis-Balaton Water Protection System. (A) Pre-18th century catchment; (B) inundated 1985–1992 state of Phase I (Hídvégi Pond); (C) partial completion of Phase II (Ingói-berek inundated) (1992–2014); and (D) the current state of the system (post-2015). The names in italics indicate geographic names of different areas of the system; the area of former Kis-Balaton Wetland was drawn based on Bendefy and Nagy (1969); illustrative map based on Hatvani et al. (2017); basemap: Google map imagery taken on 14 August, 2021.

Restoration of the wetland

Construction and current setup of the KBWPS

The original plan (from 1976) was (i) to remove nutrients—primarily P—already in the KBWPS area using macrophytes before the nutrients ever entered Lake Balaton (Tátrai et al., 2000) and (ii) to move the eutrophication processes upstream of Lake Balaton into the reservoir(s) of the KBWPS to prevent further deterioration in water quality, with the aim that by 2005–2010, a return to the trophic conditions typical of the early 1960s would be achieved (Istvánovics et al., 2007). We now know that this was approximated in the mid-2010s (Hatvani et al., 2020).

The construction of the KBWPS was planned in two phases. The area of Phase I was formerly grassland and partially forested, that was inundated in 1985 (the 18 km^2 Hídvégi Pond; Fig. 3B). However, instead of becoming a wetland populated by macrophytes, became an algae dominated pond. Phase II (total area 51 km^2) was partially inundated (Ingói-berek: 16 km^2) at the end of 1992 (Fig. 3C), and became an area covered by macrophytes, predominantly reeds/reed-beds. The remaining area (Zimányi-berek: ~35 km^2) was inundated in 2014, when a new operating approach was introduced and the main water flow direction was changed, so that loads no longer affected the Ingói-berek on a daily basis (Fig. 3D); it only receives water for natural protection purposes from the Zala. The system is operated utilizing multi-directional water management options that can be adapted to ecological, water quality and water quantity conditions.

Operation and management of the system

The operation of the system is maintained by 26 engineered structures (e.g., sluices, dams (Fig. 3), pumping stations) per multiple parallel requirements of the policies of the General Directorate of Water Management, the Ministry of Interior, and the National Park governing water quality and other aspects. Thus, the water level in the system is dynamically managed to mimic natural water level in the areas to maintain wetland habitats (Kovács et al., 2010; Hatvani et al., 2017), to keep up with the recreational use-needs of Lake Balaton, both in terms of quality and quantity (Istvánovics et al., 2007; Kutics, 2019) and provide for other economic needs (e.g., inland water pumping). Because of several adverse changes made in the system over the decades, it difficult to compare its functioning to other semi-constructed wetlands on a decadal timescale.

Retention capacity

In natural (and semi-natural) systems, retention is influenced by many factors; see e.g., Dupas et al. (2015), Zedler (2003), Hatvani et al. (2022). Uncertainties regarding the KBWPS are, therefore, not surprising, especially due to the numerous interventions this system has been subjected to over time. In order to improve water quality and achieve good ecological status, as prescribed by Water Framework Directive (EC, 2000), and support the oligotrophication of Lake Balaton, phosphorus retention is crucial (Tátrai et al., 2000; Istvánovics et al., 2007). Thus, the storage of P has the highest importance in the KBWPS, both in the short-term (uptake and release by vegetation, microorganisms, periphyton and detritus) and long-term (deposition in soil and accretion of organic matter; Reddy et al., 1999).

The retention capacity of the system can be viewed from two perspectives. In the first, if only the input from catchment of River Zala into KBWPS is considered (Zalaapáti sampling site) (Fig. 4A), and in the second, if full input to KBWPS is estimated including the system's direct catchments between Zalaapáti and Fenékpuszta (Figs. 3 and 4B). The former accounts for about 60% of the total load arriving to Lake Balaton, important in long-term historical comparisons with the literature, while the latter is of practical significance for achieving management objectives (Nyuduvizig, 2020).

Prior to the inundation of Phase I (1985), an excess amount of P left the area of former Kis-Balaton Wetland into Lake Balaton (Fig. 4A: blue ellipse), while after being inundated in 1985, the Hídvégi Pond removed about 50% of the external P loads annually (Fig. 4A: yellow ellipse) up to 1991. However, after the reduction of external loads from the Zala catchment, the TP retention efficiency highly decreased (Hatvani et al., 2014); Fig. 4A: green ellipse). Between 1981 and 1990 an annual average of ~92 t of TP load arrived into the KBWPS, while this value dropped to only ~42 t in the 1990s (Hatvani et al., 2014).

At the turn of 1990s, Hungarian agriculture and heavy industry were thoroughly restructured following political and economic changes, and high state subsidies to mineral fertilizers were withdrawn, and this ran parallel to a drastic reduction in fertilizer usage (Hatvani et al., 2015). These changes contributed to the significant reduction in diffuse pollution arriving in the system. Continuing the load reduction measures, in the late 1990s additional nutrient removal was implemented, i.e., phosphorus removal began at wastewater treatment plants in the Balaton region, resulting in reduced TP inputs to Lake Balaton compared to the 1980s (Somlyódy, 1998) (Figs. 4B and 5). This reduction was not, however, as great as anticipated, due to the increased contribution of internal loading as a response to the reduction in external loads (Clement et al., 1998; Sas, 1990). This resulted in decreased retention (Fig. 4A: green ellipse). It is understood that if input decreases, rate of retention (%) does not decrease proportionately, but to a much greater degree. In the years following 2010, the TP input to the KBWPS reached its lowest, thus its retention efficiency further decreased (Fig. 4A: red ellipse). Nevertheless, taking the system and the input to Lake Balaton as a whole, this was not a major issue because of the already low inputs (<20 t TP a^{-1}) to the KBWPS, and outputs to Lake Balaton (<7 t TP a^{-1}), equivalent to a calculated annual average TP input of approximately 0.13 mg/L and 0.003 mg/L annual average TP output from the KBWPS for 2010–2019.

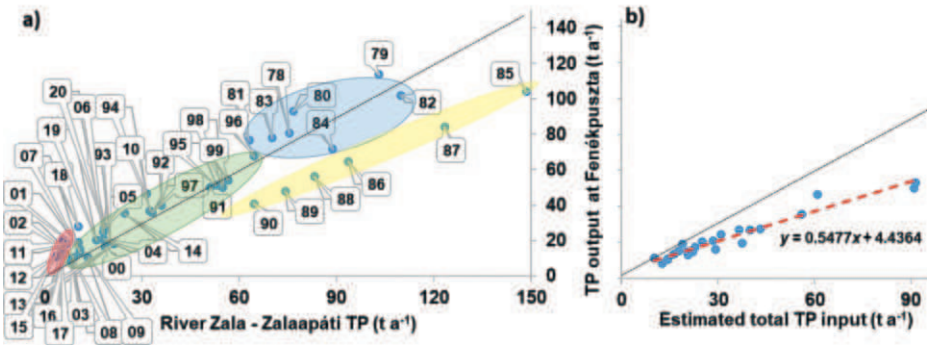

Fig. 4 Total phosphorus input-output graph of the KBWPS. Input from the upstream catchment of the River Zala (Zalaapáti sampling site; see Fig. 1) and output to Lake Balaton at Fenékpuszta sampling site (1978–2020; for locations see Fig. 1), updated from Hatvani et al. (2014). (A) Calculated TP input-output between the upstream and direct catchment of the KBWPS and Lake Balaton at Fenékpuszta (1998–2020). The ellipses with different colors indicate the arbitrarily chosen clusters of years. The years themselves are marked as data labels next to the points. (B) The red dashed line is the linear regression between input and output. The dashed 1:1 line represents the points along which the same amount of TP is entering KBWPS as leaving it; for details see Box 1. Data: Nyuduvizig (2020).

Box 1

Input-output analysis in water quality protection explores the mass of substances entering and leaving a system, revealing systems capacity to retain or transform a given proportion of these substances. In some cases, larger mass leaves a system then being added', this additional amount is due to internal loadings, e.g., when phosphorous is released from the sediment of the given water body. In its most typical visualization, a graph is presented on which the output values are scattered along the ordinate and the input amounts along the ordinate. Therefore, if a 1:1 line is drawn, the values above it will indicate excess output, and the ones below it will indicate retention. See Fig. 4 and e.g., Chen et al. (2009).

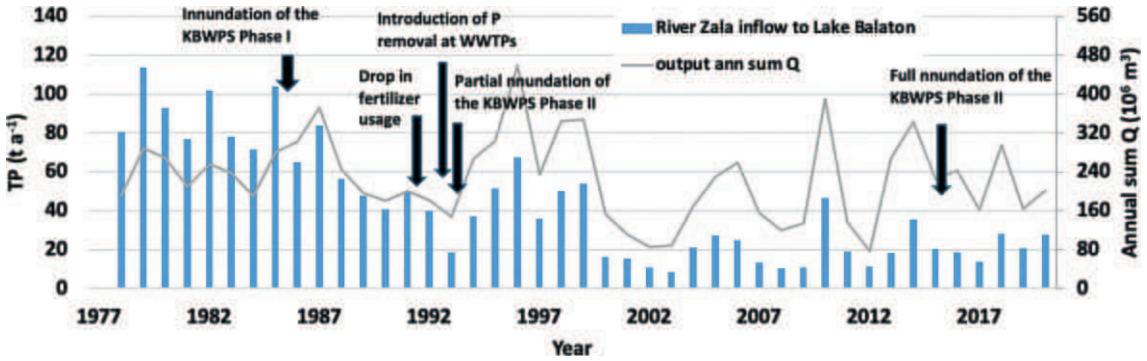

Fig. 5 Annual TP loads and volume of water arriving in Lake Balaton from the KBWPS at Fenékpuszta (Fig. 1B–D) between 1978 and 2020. The historical milestones of the system are indicated above the graphs.

Considering entire inflow and outflow data (available after 1998), it is visible that if input increases, the amount of output (t nutrient per year) from the system increases in a way which is close to linear ($r_{\text{calculated input - output load}}$ (23) = 0.94, $p < .00001$), while overall the system is working efficiently (Fig. 4B). The total load carried by the River Zala directly into Lake Balaton has changed dramatically, with the inter-annual variation depending to a significant degree on the rate of flow ($r_{\text{TP—Q outflow}}$ (41) = 0.60, $p = .000034$) (Fig. 5). Examining the overall operation of the system, P retention is smaller than originally anticipated (Tátrai et al., 2000), but always positive on an annual basis, except for 2 years during last two decades (Fig. 4B). The system, therefore, fulfills its function in protecting the water quality of Lake Balaton.

Given that abiotic processes controlling P retention are dominated by sediment sorption and chemical precipitation (see e.g., Hatvani et al. (2022), Vymazal (2007)), if external P loads are low, wetlands may export P instead of retaining it. This is significantly different from wetlands which are constructed as buffers or for the treatment of domestic or industrial waste waters, since in such systems the concentration ranges of nutrients and organic matter are several orders of magnitude higher; e.g., He et al. (2007). As a result, these do not lend themselves readily to comparison with those treating surface waters (low P levels) (Hatvani et al., 2014). As the KBWPS's retention capacity is strongly influenced by inflow concentrations, the P resuspension from the sediment of the system depends to a great extent on the current water levels and the amount of sediment brought by the river, again influencing the retention capacity of the system. Thus, any changes in the Zala catchment (Fig. 5) will affect its efficiency (Hatvani et al., 2014; Clement et al., 1998). Nevertheless, proper maintenance (e.g., dredging and vegetation removal) and operation are of paramount importance to the retention of P and then its removal from the sediment of the KBWPS.

Future outlook

In conjunction with other measures, the KBWPS can be considered a success story in ameliorating the water quality of Lake Balaton, a process leading to changes in the trophic state and the restructuring of the lake's ecosystem (Istvánovics et al., 2007). The construction of the KBWPS was an important measure—albeit not the only one taken—to facilitate these oligotrophization processes. However, in addition to its major role in diminishing the loads carried by the Zala River through natural filtration, the KBWPS has also proven capable of thoroughly modifying river load conditions in its role as a pre-reservoir system. As such, the water governance and water level management of the system is of great importance because of its multiple habitats with different ecological needs.

In future, the most important task will be to apply research concerning the operational experience and monitoring studies of the KBWPS. Solutions continue to be sought for the optimization of the operation of the KBWPS in the interests of the economically and ecologically efficient regeneration of the system, and ensuring good water quality of Lake Balaton. In the long term it is anticipated that the experience gained, and conclusions drawn from the monitoring at KBWPS can serve as a basis for construction of other living waters and reservoirs, and for addressing any operational difficulties (Lovász et al., 2020). In comparison with international case studies the "story" of the KBWPS once again underlines that such semi-constructed wetland systems can only be successful in retaining external nutrient loads if continuous monitoring and event-specific operation is maintained, the focus being on the achievement of a close to natural state.

Case study 3

Indian Agricultural Research Institute Wastewater Treatment System: Background

The Indian Agricultural Research Institute (IARI)- a micro-watershed located at the heart of the National Capital Territory (NCT)—Delhi (India) comprises about 290-ha ground water-irrigated farm area and a network of storm water drains, responsible for annually discharging about 700 ha-m (or 20-Million Liters per Day, MLD) of wastewaters (besides storm waters) received from the domestic and small scale industrial/commercial units located within IARI micro-watershed and its adjoining areas. The untreated urban wastewater stream (originating from nearby residential colonies—Krishi Kunj and Loha Mandi) used to pass through IARI farm area to into the Loha Mandi drain—a branch of the main Najafgarh (storm water) drain of the NCT-Delhi, which discharges runoff and domestic/industrial effluents from the entire Delhi catchment area into the Yamuna River.

Detailed physical and chemical analysis of this wastewater stream showed that it was associated with extensive inter-seasonal turbidity of 200 to 1000 NTU and increased biological oxygen demand (BOD) from 230 to 730 mg/L, along with elevated nutrients (0.1–12 mg/L nitrates; 3–28 mg/L phosphates, 11–99 mg/L sulphates) and heavy metals (0.1–1.3 mg/L nickel, 1.5–2.3 mg/L chromium, 0.41–23.60 mg/L iron and 0.31–4.65 mg/L zinc). As a result, the wastewater (apart from being a habitat for mosquito breeding and a source of offensive smell) contributed to the extensive soil and groundwater degradation in the farm area (Fig. 6A). A detailed analysis of total soil heavy metal pollution load at the local farm site indicated 1.23 times more than permissible level(PL) of copper (Actual value: 122 mg/kg, PL: 100 mg/kg), 1.57 times more zinc (Actual value: 393 mg/kg, PL: 250 mg/kg), 4.3 times more nickel (Actual value: 42.8 mg/kg; PL: 20 mg/kg) and about 11.5 times more chromium (Actual value: 252 mg/kg; PL: 100 mg/kg), as per international agricultural soil standards (Alloway, 1990).

The agricultural activity within the IARI micro-watershed had been experiencing an annual irrigation water deficit of about 101.5 ha-m (or 2.78 MLD), while wastewater was passing through this system as it was unfit for use. Hence against the backdrop of an acute water shortage in the farm area on one hand and the availability of an appreciable quantity of urban wastewaters that could be treated, recycled, and re-used for safe farm irrigations on the other hand; a need to utilize and operationalize low-cost energy efficient constructed wetland at the project site was felt.

Implementation process

The first step in designing appropriate wastewater treatment system at the proposed farm site, with 1.42 ha land area was to obtain detailed temporal information on the quantity and quality of the wastewaters and assess their impact on the soil and ground water quality at the site (2010–2011). The land and water quality information were used to design a unique decentralized urban wastewater treatment facility (during February–March 2011), based on the optimized hydraulic loading rates (HLR) and hydraulic retention times (HRT), for effective remediation and safe re-use of about 2.2 MLD wastewaters at the site. The developed wastewater treatment facility (Figs. 6B and 7) comprised two wastewater collection wells and one grit chamber (for reducing unintentional solid's spill-over due to any upstream processes) besides three treatment beds and one treated water collection tank, along with a conduit for bypassing excess flows. The construction of the optimized design began in September 2011 and was completed by 2013 after observing satisfactory performance of the first treatment cell. To make the whole treatment process energy intensive, a complete gravity flow of the wastewater, from the grit chamber to each of the treatment beds and thereafter up to the treated water collection tank was ensured.

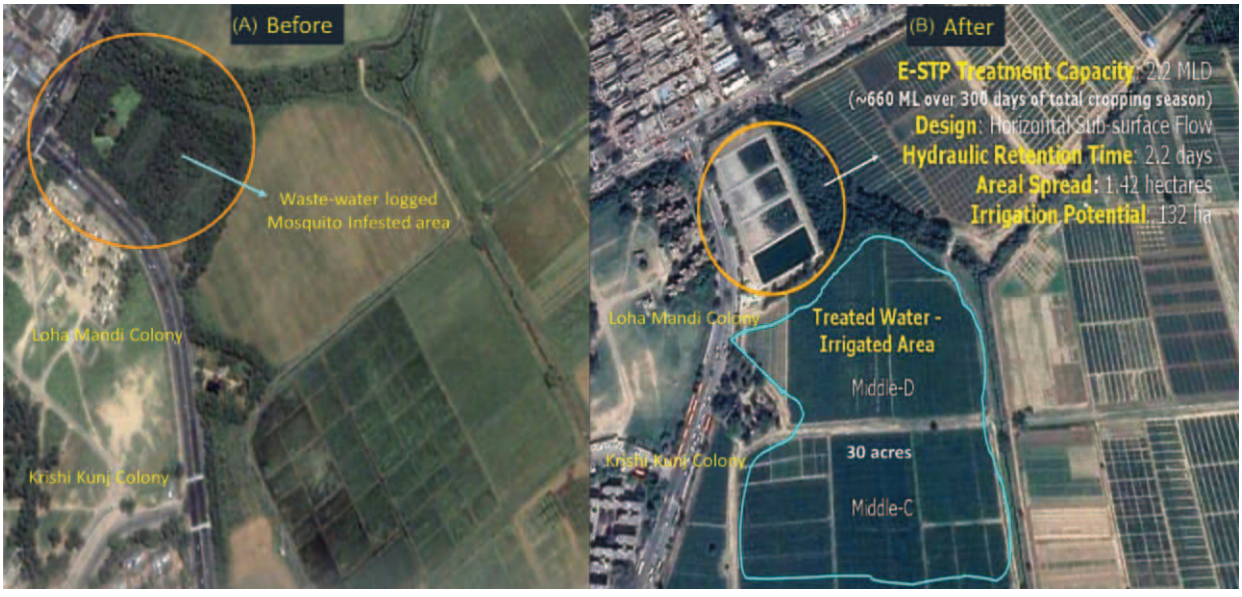

Fig. 6 Satellite view of the project site (A) before and (B) after implementation of the wastewater treatment technology.

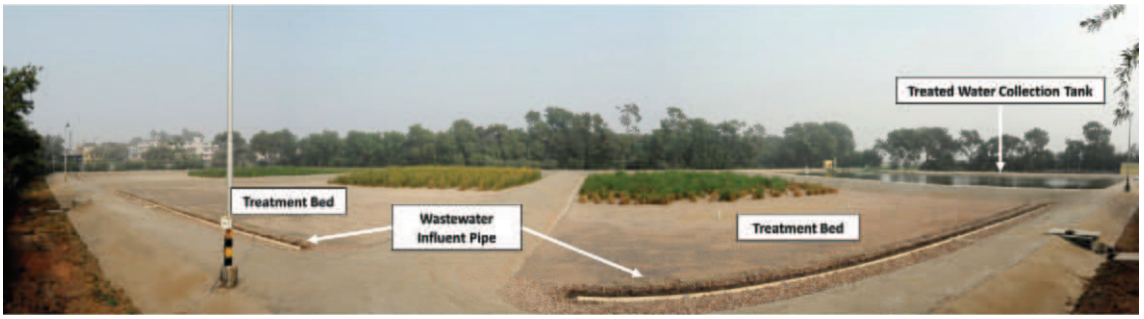

Fig. 7 Panoramic view of eco-friendly wastewater treatment facility at Indian Agricultural Research Institute farm.

The treatment process works on the Plant—Microbe—Media interactions and thus utilizes natural biogeochemical processes triggered by the emergent vegetation (*Typha latifolia*), planted at design depth and inter-spacing on the appropriately sized stratified-media and the native microbial assemblages present in the influent wastewaters. Unlike the conventional subsurface flow wetland systems, wherein clogging is the major operational and maintenance issue, the proposed technology solution took care of the system clogging by completely eliminating the incorporation of any sand/soil in the treatment beds and ensuring intermittent uniform sheet-distribution of the influent wastewaters over the entire treatment zone through the use of multi-perforated influent discharge pipes.

Hence, with the wastewater moving at design depth and flow rate through the root-zone of the planted emergent vegetation and its interaction with the native micro-organisms and the planting media, various organic/inorganic pollutants and heavy metals in the wastewater got adsorbed, transformed, sequestered, and thus removed from the influent—wastewaters. The treated water was finally collected in a 2 m deep treated water collection tank, from where it is being regularly pumped into the irrigation network of the Indian Agricultural Research Institute farm, through a riser and a set of hydrants. The system is in operation since September 2012 and is regularly monitored for its nutrient and metal reduction efficiencies.

Treatment efficiency and impact

Monitoring of long-term pollutant reduction efficiency of the facility has shown that it is capable of yielding treated wastewaters with 97.62% reduction in turbidity, 99.9% lower pathogen loads, 83.6% reduction in BOD levels, 39.5–87.9% reduction in heavy metals and 38.5–53.5% reduction in phosphate and nitrate concentrations (Table 1).

The treated wastewaters were used for aquaculture as an alternative business model, in collaboration with the Regional Research Centre, ICAR-CIFA, Kolkata and ICAR-Central Institute of Freshwater Aquaculture, Bhubaneswar. As a part of this intervention, 2315 *Pangas pungas* fish fry of 5 g each were stocked in the treated sewage water pond of 0.3 ha area. Regular monitoring of pond ecology and water quality revealed its moderate natural productivity (GPP: 340–425 mg C/m^3/h and NPP: 150–350 mg C/m^3/h), high DO (8.8–14.2 mg/L), low BOD (<30 ppm) and normal pH (7.2). In such condition, fish growth was recorded in the range of 200–300 g (from an initial 5.0 g), over 3.5 months of culture and with 80% survival. The pond was harvested with an exceptional fish catch of about 580 kg in 3.5 months (equivalent to 4 tons/ha/9 months). Noteworthy feature of this intervention was that this could be achieved through just 115 kg of supplementary feed, which is below 50% of the normal feed requirement. It was further observed that the heavy metals (viz. Cu: 0.09–0.14 ppm, Fe: 0.97–1.1 ppm; Mn: 0.13–0.17 ppm; Zn: 0.54–0.68 ppm; Ni: 0.38–0.42 ppm; Pb: 0.10–0.44 ppm) as recorded from fish muscle (Table 2, Kaur, 2020) were completely within designated safe limits, from the point of view of both fish growth and consumer health.

Ecological efficiency and sustainability

Emergy analysis, a comprehensive environmental accounting technique (Odum II, 1996), was applied in terms of several Emergy indices (Table 3; Kaur, 2020) for comparing the ecological efficiency and sustainability of the developed solution vs. a comparable conventional sewage treatment plant (STP). The analysis showed that the implemented solution utilizes 27 times more renewable resources than a conventional STP and is, thus, 1500 times more sustainable (as evident from Emergy Sustainability Index in Table 3). The implemented solution was in fact found to cause about 31 times lesser environmental stress (as evident from the environment loading ratio in Table 3), than a comparable conventional Sewage treatment plant.

Economic considerations

In terms of standard cost-accounting, as per 2011–2012 cost estimates, the implemented solution was found to be associated with about 76,300 USD per MLD of capital expenditure (CAPEX), with civil works and media demanding (80–90%), electrical works demanding (8–15%) and purchase/incorporation of appropriate vegetation demanding the remaining (2–5%) of the total capital requirement. The operational and maintenance expenditure (OPEX) on the implemented solution, on the other hand, was

Table 1 Long-term pollutant reduction efficiency of the commissioned wastewater treatment facility at the Agricultural Research Institute farm, New Delhi.

Facility Specifications	*Pollutant Load*											*Microbial Load*	
	Turbidity(NTU)	*BOD(ppm)*	*NO_3(ppm)*	*PO_4(ppm)*	*Cu(ppm)*	*Fe(ppm)*	*Mn(ppm)*	*Zn(ppm)*	*Ni(ppm)*	*Cr(ppm)*	*Pb(ppm)*	*Total heterotrophs (cfu/mL)*	*Total coliforms (cfu/mL)*
Influent Quality	318.2	317.3	12.2	11.1	0.18	10.99	0.56	1.05	0.17	0.63	0.25	3.0×10^6	1.9×10^6
Treatment Efficiency (%)	97.6	83.6	53.5	38.5	58.4	82.19	47.45	87.86	51.72	57.05	39.5	99.96	99.94
Permissible Levels[a]	NA (<=20)	<=30	<= 5–30	<=0.5–50	<=0.2	<=5	<=0.2	<=2	<=0.2	<=0.1	<=5	NA	10^3 to 10^4 MPN/ 100 mL

[a]As prescribed by BIS (1986) and Ayres and Westcot (1985).

Table 2 Heavy metal load of fish grown in treated waters generated by IARI wastewater treatment facility.

Fish body part/Organ	*Heavy metal concentration (ppm)*					
	Copper (Cu)	*Iron (Fe)*	*Manganese (Mn)*	*Zinc (Zn)*	*Nickel (Ni)*	*Lead (Pb)*
Upper part Muscle	0.09	0.97	0.17	0.54	0.42	0.22
Middle part Muscle	0.09	1.05	0.13	0.58	0.34	0.44
Lower part Muscle	0.14	1.05	0.17	0.68	0.38	0.10
Gills	0.18	2.13	0.95	1.98	0.47	0.48
Lower Gut	0.15	1.92	0.90	0.96	0.35	0.14
Liver	0.18	2.14	0.18	0.87	0.42	0.25
Permissible Limits	30[a]	100[a]	1[a]	100[a]	70–80[b]	NA

[a]As prescribed by NRC (1989).
[b]As prescribed by USFDA (1993).

Table 3 Ecological efficiency and sustainability of proposed initiative compared with conventional STP.

Emergy Indices	*Implemented Solution*	*Conventional STP*
Emergy Yield Ratio	0.70	0.01
Environment Loading Ratio	1.37	42.19
Renewable Percentage	0.54	0.02
Emergy Sustainability Index	0.51	0.00034

evaluated to be around 0.85 US cents per Kiloliter (KL) that primarily constituted expenditure on energy of around 0.35 cents, for pumping and incorporating 1-KL wastewaters into the treatment beds of the facility, and on unskilled manpower, of about 0.49 cents.

Comparison of the implemented solution with a comparable conventional wastewater treatment technology thus revealed that the developed solution is associated with zero-chemical application and zero energy demand for treatment, besides having no skilled manpower requirement. Hence the implemented technology was observed to be associated with about 50–65% reduced treatment costs than the conventional wastewater treatment technologies.

Revenue generation potential

The vegetation planted in the treatment beds of the fully operational wastewater treatment facility could be harvested (once every 3–4 months) to annually yield about 30 tons of dry biomass. The harvested biomass could be either sold to the local particle board manufacturing units (@USD 28 per ton, as dry biomass) or be transformed into the (termite- and water—proof) particle boards (16,000 sq. ft. per annum @USD 0.168/sq. ft.) or the energy-pellets (24,000 kg @USD 0.112/kg) thereby demonstrating an annual revenue generation potential of around USD 2688 through the *Cash from Trash* wastewater treatment intervention.

Conclusions

The proposed initiative was able to generate good-quality local surface water resource of about 660 million liters per annum and led to avoidance of applying contaminated drain waters (@ USD 25,900 per annum) for meeting irrigation water demand of IARI farmland. The initiative could thus, in addition to resulting in an annual saving of about USD 25,900 and bridging the annual gap (of 520 ML) in the irrigation water supply and demand of the IARI farmland, could also lead to effective urban wastewater management and sanitation (including reduction in offensive smell and mosquito breeding areas). In fact, the project site that used to be completely unapproachable (Fig. 6A) got transformed into an eco-park (Figs. 6B and 7) after the establishment of this constructed treatment wetland.

Case study 4

Zevergem waste-water treatment plant: Background

Flanders is a densely populated region in Belgium with 487 inhabitants km^{-2} and a total area of 13,625 km^2. Yet, only 85.5% of all household wastewater is treated. This is largely due to the fragmented spatial planning (StatBel, 2020; VMM, 2021) which makes it not always economically feasible for smaller communities or single homes to connect to large centralized wastewater treatment plants. Constructed wetlands (CW) for wastewater treatment generally meet discharge standards, are cost effective and require low maintenance. In 2014, there were 338 constructed wetlands in use in Flanders, designed as systems for $\leq$2500 person equivalent (PE) (Auvinen et al., 2016).

One of those systems is the constructed wetland from the village of Zevergem, which is part of the municipality of De Pinte. The system was designed for 750 PE and has been in operation since, 2000. The municipal wastewater first receives primary treatment in a simple settling tank. Secondary treatment is accomplished by a hybrid system comprised of two vertical down flow constructed wetlands (VSSF = vertical subsurface flow) followed by two horizontal subsurface flow (HSSF) constructed wetlands, each in parallel (Fig. 8). The CWs are planted with *Phragmites australis*. No tertiary treatment is applied, and the treated water is discharged in the Toutefaisbeek, a small brook, which leads to the river Scheldt.

Removal of organic matter and nutrients

Flemish discharge standards for urban wastewater treatment plants state that every parameter given in Table 4 should be lower than the concentration limit and should have a minimal reduction percentage relative to the incoming wastewater. Analysis results (Flemish Environment Agency, geoloket.vmm.be) show that for biological oxygen demand (BOD), chemical oxygen demand (COD) and total suspended solids (TSS), respectively, 99.5%, 99% and 99% of samples ($n \geq 215$, data available since 2002) meet the discharge standards (Fig. 9).

Discharge limits for other water quality parameters such as nutrients are yet nonexistent for small-scale wastewater treatment plants (<2000 PE) in Flanders. Notwithstanding, more parameters than required are being monitored and give insight on nitrogen and phosphorus removal.

The largest part of total N enters and exits the system as ammonium. Ammonium removal requires aerobic conditions for nitrification, but as Fig. 10 shows, ammonium effluent concentrations are generally high. It can be concluded that oxygen transfer to the system is not sufficient for nitrogen removal. The VSSF should be the main supplier of oxygen but is in this case not able to provide sufficient oxygen for complete nitrification. In addition, nitrate requires anoxic conditions and a carbon source for denitrification. Denitrification is clearly happening as 90% of effluent NO_3^--values are below 7 mg N L^{-1}, which leads to the conclusion that the HSSF can remove nitrate well in the current setting.

Phosphorus removal is very low (Fig. 11), because the main removal mechanisms are precipitation and adsorption. The substrate of a CW quickly becomes saturated with phosphorus compounds over time, and P-removal therefore ceases.

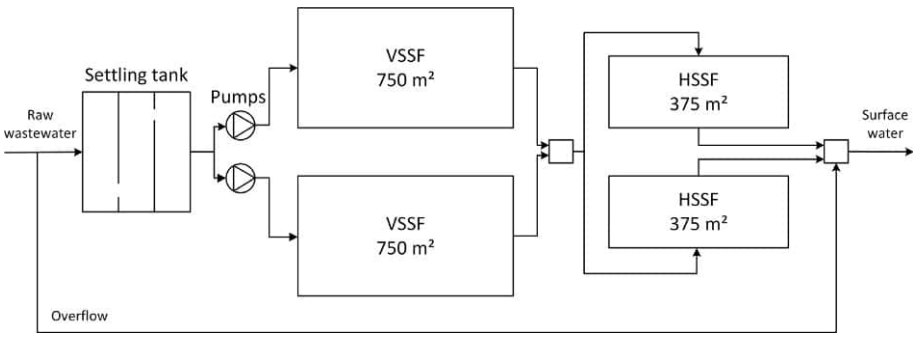

Fig. 8 Process scheme of the constructed wetland in Zevergem. [VSSF, vertical subsurface flow; HSSF, horizontal subsurface flow].

Table 4 Flemish discharge limits for urban wastewater treatment plants, receiving wastewater from agglomerations smaller than 2000 population equivalent (PE).

Parameter	*Concentration limit (mg/L)*	*Minimal reduction percentage (%)*
BOD_5^{20}	25	90
COD	125	75
TSS	35	70

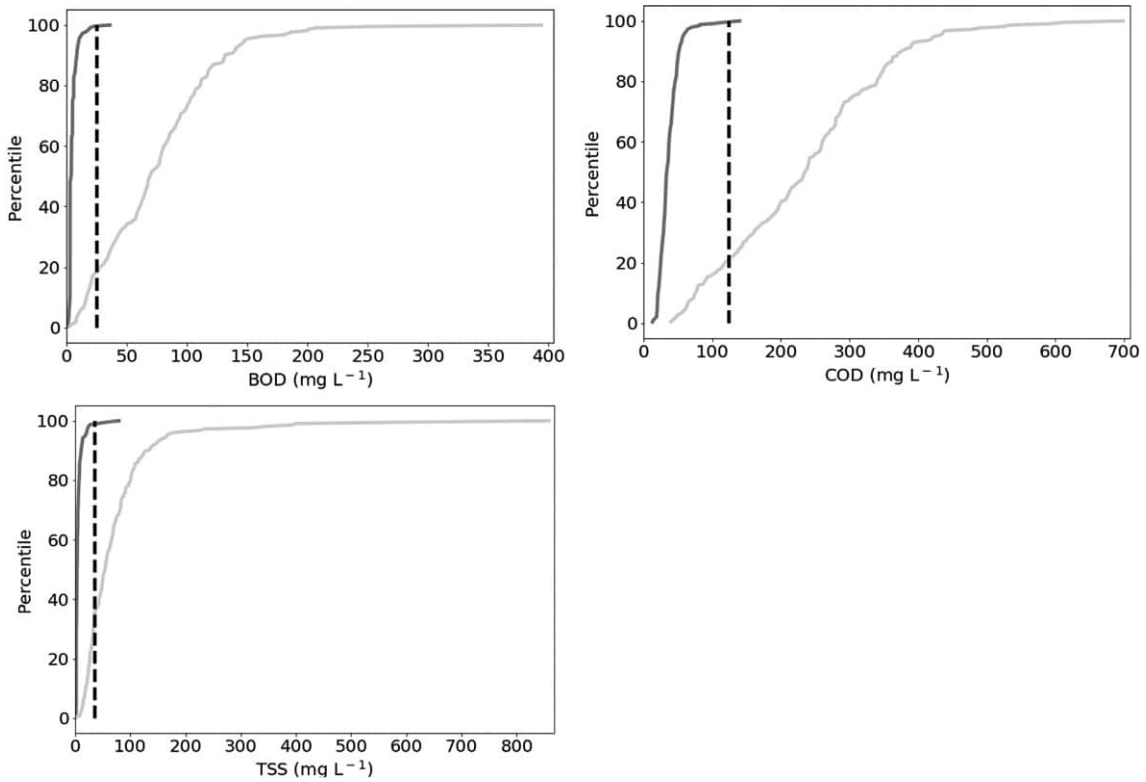

Fig. 9 Cumulative frequency of BOD, COD and TSS concentrations between 2002 and 2021 from the wastewater treatment plant in Zevergem. Inflow and effluent are represented by the light and dark grey lines respectively, the black dashed line is the discharge limit. Data from VMM (geoloket.vmm.be).

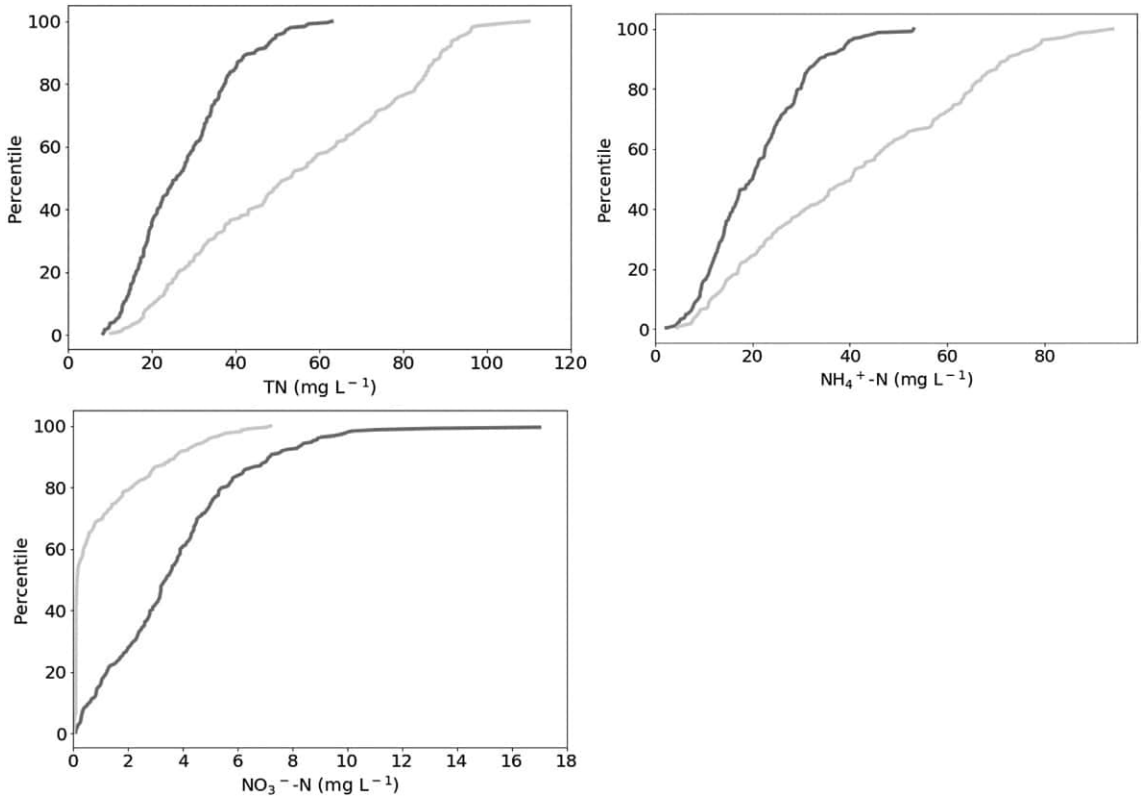

Fig. 10 The cumulative frequency of TN, NH_4^+ and NO_3^- concentrations between 2002 and 2021 from the wastewater treatment plant in Zevergem. Inflow and effluent are represented by the light and dark grey lines respectively. Data from VMM (geoloket.vmm.be).

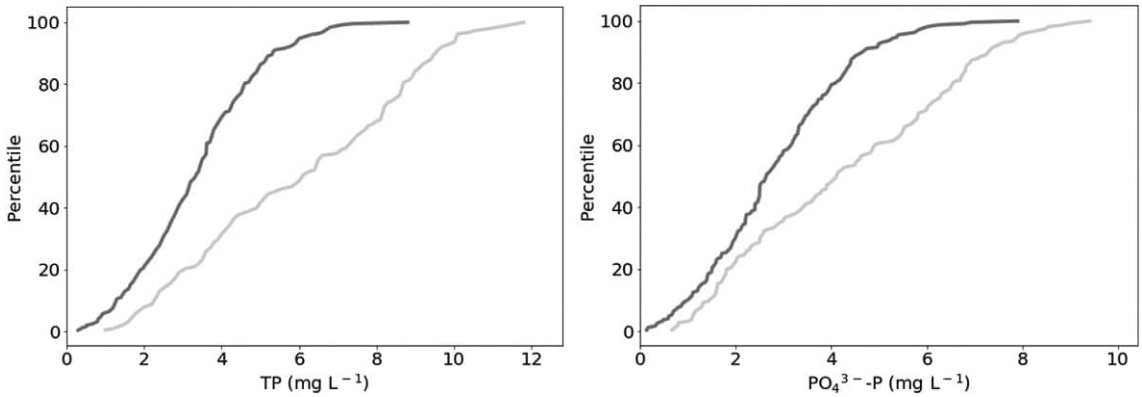

Fig. 11 The cumulative frequency of TP and PO_4^{3-} concentrations between 2002 and 2021 from the wastewater treatment plant in Zevergem. Inflow and effluent are represented by the light and dark grey lines respectively. Data from VMM (geoloket.vmm.be).

Removal of micropollutants

Metals

Apart from organic matter and nutrients, municipal wastewater typically also contains micropollutants. The treatment system in Zevergem has been monitored also in that respect, looking at metals and at microplastics.

In 2004, the system was studied in detail in terms of metal removal and metal accumulation (Lesage et al., 2007). Al, Cd, Cr, Cu, Fe, Mn, Ni and Zn were measured in the influent and effluent, in the sediment and in the macrophytes (Table 5). Sediment was defined here as everything that was not roots or gravel (i.e., organic and inorganic matter accumulated on the wetland and in the pore spaces).

Only Cu and Zn were encountered in the influent of the system in concentrations above the detection limit. The removal of Zn and Cu by the CW was 72% and at least 64% respectively. Notwithstanding, other metals were also retained in the wetlands, as proven by elevated concentrations especially in sediments and to a much lesser extent also in plants. Indeed, uptake of metals by *P. australis* aboveground biomass was found to be very low, which was also confirmed by many other studies. A mass balance indicated that *P. australis* was responsible for less than 2% of Cu and Zn removal from the influent, the largest amounts were thus retained in the sediment.

The Cd, Cu, Pb and Zn concentrations in the sediment decreased along the treatment path, being highest in the VSSF and lowest at the end of the HSSF. The other sampled metals were highest in the HSSF inlet area, except for Mn, which was highest at the HSSF outlet. An explanation for this behavior was found in the redox conditions. A sludge layer had formed on top of the VSSF wetland and flooding was observed during the monitoring period. These events indicate low oxygen transfer and consequently anaerobic and reducing conditions inside the VSSF, which are not desirable. Reducing conditions can increase the mobility of Al, Cr, Fe, Mn and Ni, allowing them to enter the second stage HSSF CW. There the metals encounter oxidizing conditions around the roots of *P. australis* (root oxygen loss) and this in turn leads to metal precipitation. However, the most important conclusion of the study was that all metals remained far below any threshold level for soil pollution and soil remediation.

Microplastics

In 2020–2021, the inflows and outflows of the different unit processes have been monitored for microplastics (MP) (Wang et al., in preparation). The system in Zevergem removed 96% of all MPs entering the system, thereby reducing the MPs concentration in the raw wastewater of 15.0 particles L^{-1} to 0.6 particles L^{-1} in the final effluent (Fig. 12). The primary treatment removed more than 50% of all MPs, and the CWs removed another 91% of the microplastics that were still left after the primary treatment.

Table 5 Estimation of the yearly metal mass removal from *P. australis* in the CW system in Zevergem (mg m^{-2} y^{-1}).

	Cd	*Cu*	*Pb*	*Zn*	*Cr*	*Ni*	*Al*	*Fe*	*Mn*
VSSF	0.014	7.5	0.44	90	0.6	0.91	9.4	64	91
HSSF	0.038	2.9	0.36	30	0.57	0.57	8.7	42	58

Data from Lesage E et al. (2007).

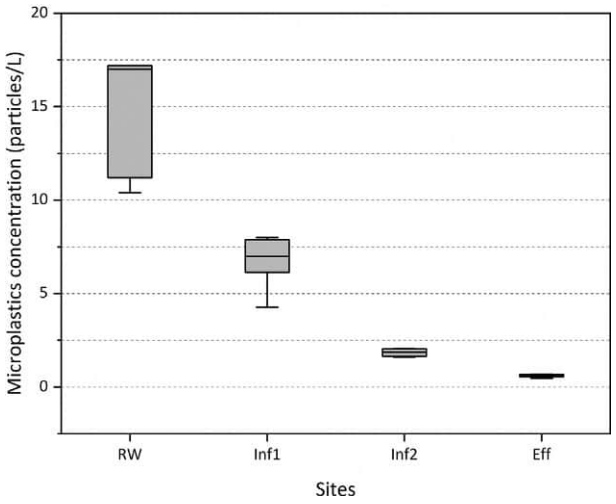

Fig. 12 Microplastics concentration (particles/L) from different sites in the Zevergem CW.

Future outlook

The CW at Zevergem is a perfect example of a good functioning wastewater treatment solution for a small community (750 PE). All discharge limits are met with averages of >99%. However, it should be noted that this configuration of VSSF-HSSF is not capable of protecting sensitive water courses from eutrophication, as nutrient removal is rather low. Additional solutions are needed in that case, such as "intensification" of the wetlands (Rousseau et al., 2022). Micropollutants such as metals and microplastics are retained as well and end up mostly in the sediments. Their accumulation should be assessed on a case-by-case base to verify whether or not any toxic threshold levels are reached.

Summary and conclusions

Constructed and semi-constructed wetlands have played an important role in offering simple and cost-effective solutions for wastewater treatment worldwide. These systems are effective in treating a wide variety of pollutants and have been utilized to treat both point and non-point sources of pollution. The four case studies discussed here demonstrates functional constructed wetlands employed for treating agricultural drainage waters and stormwater runoff, domestic wastewater and semi-industrial effluent as well as municipal waste waters. These constructed treatment wetlands offer natural and sustainable solutions in comparison to the more technological and resource intensive options and are known to also provide some economic benefits on top of ecological services.

The examples included in this chapter highlights marked improvement in our understanding of these biological systems and growing experience in operating, managing and running these systems across a broad range of climatic and operational parameters strengthens their wide acceptance as a functional ecological solution to effluent treatment around the world. As a special case of inland wetlands, constructed wetlands have played an important role in human society, and we have greatly benefitted from their functional roles either by treating our waste waters, or reducing harmful pollutants, or offering a habitat for biodiversity.

See Also: Human pressures and management of Inland Waters: Constructed Wetlands for Urban Wastewater Treatment: An Overview; The Role of Wetlands in Mitigating Impacts From Diffuse Agricultural Loads

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Inland Fisheries Management - Exploitation and Livelihoods

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Age at sexual maturity The expected age that fish of a given species will be able to reproduce.
Aquaculture Farmed fish.
Capture fisheries Wild harvest of fish from the natural environment, rather than farmed or produced through breeding methods controlled by humans.
Fecundity Ability to produce offspring and/or the quantity of eggs or off-spring an individual fish will produce either in a single breeding period or over their life.
Fermented fish products Fish that is preserved using the technique of fermentation, which is a method that makes fish muscle more acidic and thus prevents microbials from making the fish spoil.
Fin-fish Fish with fins and tail as opposed to shellfish.
Fishery production The amount of fish that is present in the waterbody being fished, roughly equivalent to the fish resource availability.
Gillnet A type of fishing gear made of fine cord (e.g. string or nylon) tied together to create a mesh of squares that form a net. The net is hung vertically in the water column with weights at the bottom and floats and the top. Fish are caught by their opercula and heads as they try to swim through. The space between squares can vary to allow capture of smaller or larger fish.
Harvest The quantity of fish that is gathered by one or more fishers.
Indiscriminate fishery A fishery in which no particular fish or species are specifically targeted, and all species and individuals are harvested, as opposed to fisheries in which only selected individuals (sizes) or species are harvested through specific gears used or by throwing back individuals that are not targeted.
Inland aquatic ecosystems Any environment that is inside land borders having no or low salinity. They include some brackish estuarine areas and a variety of natural (streams, rivers, floodplains, lakes, swamps, etc.) and manmade (reservoirs, rice fields, irrigation canals, etc.) inland water bodies.
Landed Brought on land to be processed or sold.
Landing sites Areas where fish can be brought to land. They are often associated with the first sale of fish from fishers to the middle-men or processing institutions. They can vary from well-established formal docks or ports, where fish are brought to shore in large numbers to small mud banks where fish are sold locally.
Middle-men Middle-men generally do not buy for their own consumption or processing but will sell the fish onto another buyer.

 https://doi.org/10.1016/B978-0-12-819166-8.00189-4

Post-harvest production The use of fish once extracted from the water body to make fish products, ranging from dried fish to fish sauces.
Quota A set amount allocated to an individual or group.
Seine net A type of fishing gear made of a fine mesh that is used to encircle fish so that they cannot escape. The mesh size can vary to allow capture of smaller or larger fish.
Subsistence fishery The capture of low quantities of fish with the primary purpose of feeding an individual, family or group. It can also include harvests large enough to sell locally in order to buy other staples. The primary purpose of the fishing activity is not for sale and the fish does not formally enter the market. Almost exclusively small-scale (using simple technology and of limited amount).
Sustainability/sustainable catch limits See panel.

Introduction

Inland fisheries rely on both wild capture and cultured fish resources from a variety of water bodies, including rivers, streams, lakes, wetlands, rice-fields, reservoirs, and natural or man-made ponds. Inland fisheries are an important resource for communities the world over (Lynch et al., 2017). Many poor communities are especially reliant on them to provide food, nutrition, employment and income (Funge-Smith and Bennett, 2019). In some places, inland fisheries supplement other primary livelihoods, in others they are the only regular source of protein and income available (Martin et al., 2013).

In this chapter the inland fisheries livelihoods are described through a series of case studies taken from different perspectives around the globe. They illustrate how important inland fisheries are to people for a variety of livelihoods and discuss how with improved management a resource that is heavily exploited has the potential to be sustained into the future.

Livelihoods

Livelihoods supported by inland fisheries can be diverse. They not only encompass subsistence, recreational, commercial, and aquaculture fisheries (Cooke et al., 2016a,b), but also extend to a myriad of post-harvest production and trade opportunities provided by the fishery (Zelasney et al., 2020). While subsistence fishing is often considered synonymous with inland fisheries, and poor communities in developing nations frequently rely on them as their only livelihood option (Cooke et al., 2016b; Smith et al., 2005), inland aquatic ecosystems also support important post-harvest livelihoods (Allison and Horemans, 2006). Market traders, middle-men, and aquarium traders, among others, rely on fresh inland fish to provide them with income and employment. Livelihoods are also supported along the value chain of post-harvest production. As fresh inland fish are processed into dried, smoked, or fermented fish products, employment options for packaging, processing, transporting and selling arise (Fig. 1). Similarly, inland fish are increasingly supporting an expanding canned and fish sauce industry (Loring et al., 2019).

Fig. 1 Dried and fermented fish products at a market in Kampong Khleang, Cambodia. Image credit: Vittoria Elliott.

Exploitation of inland resources and sustainability

As in marine environments, fish resources in inland waters are hidden under water and thus hard to quantify (Welcomme, 2011). They are often also characterized by high species diversity (Darwall et al., 2009), high mobility (Deinet et al., 2020) and seasonality (Winemiller and Jepsen, 1998). These innate challenges of inland fish for managing and regulating harvests are compounded by the following specific characteristics of inland fisheries. Although some inland fisheries target a handful of species, or individual fishers within the fishery might be somewhat selective (e.g. snakehead, trout), in the majority of inland environments wild capture will include most species, which will be harvested indiscriminately (McCann et al., 2016). This makes it extremely difficult to monitor species-specific harvests and set associated quotas. Inland fisheries are largely dominated by numerous small-scale operators, so fish may be taken directly to a fisher's household, landed at commercially operated landing sites (Fig. 2), or taken directly abroad through inland waterways (Fluet-Chouinard et al., 2018). These diverse landing options, again, make it hard to monitor what catch is being withdrawn and to set limits. Consequently, defining resource availability by estimating production, setting sustainable catch limits, and regulating harvests is challenging.

Historically, marine harvest has largely been regulated at the species level, with catch limits being calculated based on models of sustainability (Hilborn, 2004; Kinzey and Punt, 2009). These models generally incorporate life-history characteristics (e.g. fecundity, age at sexual maturity) that indicate how often the harvested fish will be replenished by reproduction, combined with reasonably accurate estimates of the amount of fish being removed from the system (Sissenwine and Shepherd, 1987). These models calculate exploitation levels that should enable the stock to replenish, while allowing regular harvest; generating, what is known as, a maximum sustainable yield (MSY) (Fig. 3). These models require fairly accurate predictions of the productivity of the fishery and reasonably precise estimates of the on-going levels of exploitation (Funge-Smith and Bennett, 2019). However, in biodiverse inland fisheries, obtaining accurate life-history information on numerous species, while keeping track of the fish being caught and landed at a variety of sites, makes using these models to calculate an MSY virtually impossible (Lorenzen et al., 2016). More recently, models have been developed specifically for data-limited fisheries (Walsh et al., 2018). Models use a range of alternative approaches as surrogates for detailed life-history and catch statistics. Some use size-based approaches, others use indicator-based systems, with the aim of determining harvest levels that can be expected to be sustained (De Graaf et al., 2015; Lorenzen et al., 2016; Kindong et al., 2019; Mildenberger et al., 2021). However, the accuracy of these approaches is also limited (Chrysafi and Kuparinen, 2016).

Increasing human populations and the accessibility of inland fisheries resources has led some people to assume that inland fisheries are being over-exploited and suggest that inland fisheries livelihoods are just not sustainable. However, on-going global efforts to improve management and overcome or circumvent some of the challenges of monitoring and managing fisheries, bring hope to the many peoples who rely on these resources, and who often have no viable alternatives.

Fig. 2 (A) A medium-sized operator carries his fish to the landing site in a basket for sale to middle men, (B) small-scale operators land small fish, (C) a large-scale operator lands containers full of fish for sale, (D) fish are sorted and weighed for sale by commercial middlemen. Image combined includes (A) photo credit World Fish, (B) photo credit: Vittoria Elliott, (C) photo credit: Jason South, and (D) photo credit: Vittoria Elliott. Combined image Courtesy of Vittoria Elliott.

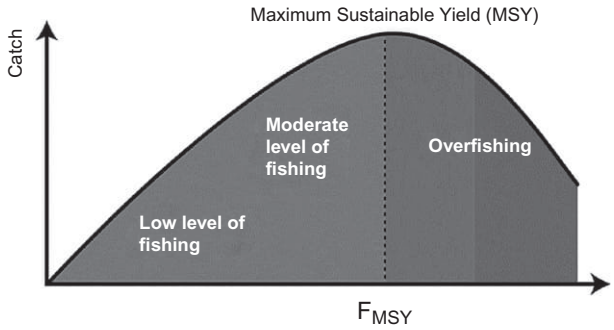

Fig. 3 Illustration of Maximum Sustainable yields (MSY). Maximum Sustainable yield is derived from estimates of population biomass of fish or the amount of fish (in number or weight) that can be produced by the system given the biology of the fish and the environmental conditions, and the fishing pressure or amount of fish being removed by fishers. The purpose is to understand the system well enough to have accurate estimates of the quantity of fish being produced, and to have an accurate estimate of how much fish is being harvested, to define an amount that can be removed while allowing the fish to reproduce and replace the individuals that have been removed by fishing or that die from other causes. This is called the maximum sustainable yield or the maximum amount of fish that can be removed without resulting in a net reduction in total fish availability. The number of individuals that can be taken without compromising the ability of a species to replace the individuals taken through reproduction is dependent on the biology of the individual species (the number of individuals that are produced, the number that will survive to be reproductive, the number of years before the individuals will be reproductively capable). These characteristics can be highly variable from species to species making it challenging to define values of sustainable harvest in biodiverse systems. The number of individuals harvested of each species is often not recorded when fishing behavior is indiscriminate, compounding the challenge for setting and adhering to maximum yields.

Case studies

Case studies are presented here from across the globe, showing how local fishermen and fishing communities are working with governments to combat some of the challenges of inland fisheries livelihoods. From the Murray-Darling basin in Southern Australia, where environmental performance indicators are being used to overcome the challenge of stock assessments, to the Mekong River in South-east Asia, where widespread community-managed fish conservation zones are being endorsed by the government to provide a network for migratory fish. Along Costa Rica's Di Crí river, communities are combining traditional knowledge with science to improve fisheries management, while in the Midwest territories of North America, Tribes are working with state governments to rehabilitate the walleye (*Sander vitreus)* fishery. Finally, in Lake Victoria in East Africa, rights-based fisheries options are being explored to overcome the challenges of open-access over-exploitation, and local fishers are exploring opportunities to enhance profits without increasing fishing pressure by exploring product enhancement techniques, while at the same time exploring alternative livelihood options. Building on local knowledge combined with evidence-based management and strong support from the government, local fishers and communities are working together to overcome some of the challenges facing fishery-based livelihoods in inland waters.

Case study: The south Australian Lakes and Coorong fishery

The Lakes and Coorong Fishery (LCF) is a small-scale, semi-artisanal commercial fishery that operates at the terminus of Australia's longest river system, the Murray-Darling Basin (MDB) (Fig. 4). The Lower Lakes and Coorong region is recognized as a Wetland of International Importance under the Ramsar Convention due to its unique ecological character and is a place of significant cultural value, particularly to the local indigenous people, the Ngarrindjeri (Phillips and Muller, 2006).

In operation since 1846, the LCF is a multi-species, multi-method fishery, primarily targeting finfish in freshwater and estuarine habitats (Olsen and Evans, 1991). The fishery is a regionally important source of fresh fish and employment. The average annual catch for 2016–2021 was ~1700 t, with a gross value of ~AU$11.5 M/year, supporting a fleet of 36 licensed vessels, and directly employing ~70 skippers and crew (EconSearch, 2019; Earl and Bailleul, 2021). Like many small-scale fisheries, the LCF is characterized by 'sole-operator' local fishers that use small vessels and basic methods, primarily gillnets of varying mesh size. As mandated by regulations, all gillnets are 50 m long, and each vessel has a daily entitlement of up to 100 gillnets.

Different species are targeted in freshwater and estuarine waters. In freshwaters, golden perch (*Macquaria ambigua ambigua*), bony herring (*Nematalosa erebi*) and non-native common carp (*Cyprinus carpio*) are key species. Whereas, mulloway (*Argyrosomus japonicus*), yelloweye mullet (*Aldrichetta forsteri*), greenback flounder (*Rhombosolea tapirina*) and black bream (*Acanthopagrus butcheri*) comprise the majority of the estuarine harvest. With the exception of common carp and bony herring, which are primarily supplied as bait to local commercial crustacean fisheries, catches support high-value domestic human consumption markets (Ferguson et al., 2018). The Ngarrindjeri way of life is inextricably linked with the fishes of the Lower Lakes and Coorong region, several of which represent Ngarrindjeri *njartis* (totems – friends) and have provided important food sources for thousands of years (Berndt et al., 1993). More recently, several species, notably mulloway, form the basis of an important recreational fishery (Ferguson et al., 2018). Total harvest by indigenous and recreational sectors is unquantified but is an important consideration for management of the LCF and the environment.

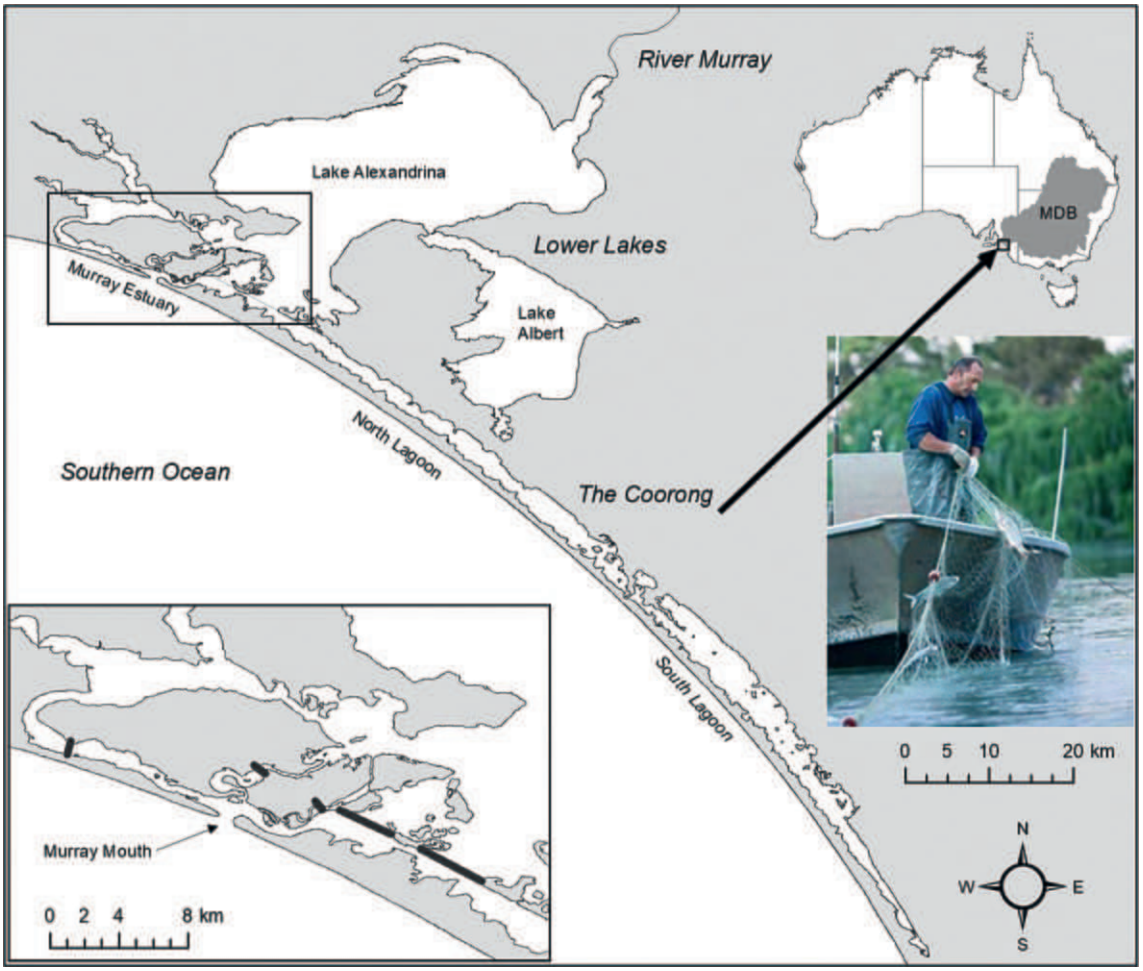

Fig. 4 Map of the Coorong (Murray Estuary, North Lagoon and Southern Lagoon) and Lower Lakes (Lakes Alexandrina and Albert) at the terminus of the Murray-Darling Basin (MDB), southern Australia. Inset shows the Murray Estuary, highlighting the Murray Mouth and the five tidal barrages (dark thick lines) that separate freshwater (Lower Lakes) and estuarine (Coorong) environments of the region. Insert LCF Fisher. Photo credit: Randy Larcombe, Southern Fishermen's Association.

A critical aspect of the LCF is the influence of river flow on target species abundance. The MDB is known as Australia's food bowl, supporting 70% of the country's irrigated agriculture (ABS/ABARE/BRS, 2009). Consequently, end-of-system freshwater flow is on average approximately only a third of its natural potential, while a series of tidal barrages separate freshwater and estuarine environments of the LCF. These changes have resulted in disruption to population dynamics and historic declines in species critical to the LCF (Bice et al., 2018). The ecological value of the region and legislative responsibility associated with the Ramsar convention and the *Murray-Darling Basin Plan* have recently prompted considerable management action to promote ecosystem rehabilitation. This has involved the delivery of environmental flows that seek, in part, to promote connectivity, and salinity regimes that support ecologically and commercially important fish species (Bice et al., 2018). Thus, there is a nexus between environmental and fishery management that is critical to the production and sustainability of the LCF.

Fisheries management for the LCF has been gradually established since the 1970s, including a minimum legal length for most target species, as well as input controls that include limited entry (restrictions in the time or seasonal access), gear restrictions (only specified types of fishing gears can be used), and spatial closures (some locations are off-bounds for fishing permanently or seasonally) (Ferguson et al., 2018). A compliance program, with cost-recovery through commercial fishery license fees, is in place to educate fishers, deter opportunistic and financially motivated fishery-related crimes and enforce the rules and regulations.

In 2015, a review of the fisheries management arrangements for the LCF exposed several operational shortfalls. This included a lack of quantitative indicators and defined management responses to varying environmental conditions; no limit reference point that defined an unacceptable risk of fishing pressure; and no formal mechanism to control the level of exploitation should any reference point be approached (Knuckey et al., 2015). This led to the development of a harvest strategy for finfish and the introduction of specific output controls in the form of a total allowable commercial gillnet effort (TACE) for the freshwater and estuarine fishery. In the absence of quantitative stock assessments, often infeasible for multi-species fisheries (Newman et al., 2018),

the harvest strategy aims to manage the sustainable harvest of target species relative to the condition of the environment within which the fishery operates using environmental performance indicators (e.g. lake water levels) as surrogate metrics for fishable biomass (Knuckey et al., 2015). The harvest strategy could, however, be improved for key species by integrating biological performance indicators, such as population age structure, to inform on the influence of fishing pressure, environmental variability and demographic processes (i.e. recruitment and movement) on stock status. Consideration of trends in commercial fishery catch and effort statistics for key species (e.g. standardized catch rates) may also improve the capacity for effective management at the species level. Such integration will strengthen the sustainability of the LCF and contribute to maintaining the rich cultural, ecological and social values of the Lower Lakes and Coorong into the future.

Case study: Community-based fisheries management at Kengmai rapids on the Mekong River in northern Lao PDR

The Mekong River is the largest river in Southeast Asia and flows through six countries from its headwaters in the Tibetan Plateau to the Mekong Delta in Vietnam. At Kengmai Rapids, there is a 5-km section of the Mekong River in northern Lao People's Democratic Republic (Lao PDR) that is bordered by the villages of Donsok, Phalath, Donmen, and Houayla (Fig. 5). The principal livelihood practiced by over 90% of the people is farming for rice and other agricultural products. Fishing is primarily opportunistic for household consumption, with the largest number of full or part-time fishers found in Houayla. Fishing is typically conducted by men from wooden boats, primarily using gillnets, cast nets, hook and line, and traps. Women participate in fish processing activities, such as drying and fermenting. The catch is diverse, with key species consisting of catfishes (e.g., *Bagarius yarrelli*., *Clarias* spp., *Hemibagrus* spp., *Micronema* spp., *Pangasius* spp.) and cyprinids (e.g., *Cyclocheilichthys* spp., *Hypsibarbus* spp., *Morulius chrysophekadion*, *Mystacoleucus* spp.).

The fishery is largely indiscriminate with the notable exceptions of the critically endangered Jullien's golden carp (*Probarbus jullieni*) and the endangered thick-lipped barb (*Probarbus labeamajor*). Historically, the villages would target these species when the fish congregate to spawn at sand bars and rapids during the dry season (December–February). The fish splash at the surface during their spawning displays, making them vulnerable to fishing activity. *Probarbus* are economically prized and are sold to fish traders. As a result of overfishing and loss of habitat, these highly migratory fish have declined significantly in number and size.

Based on interviews with local communities in 2014, Kengmai Rapids was identified as a potential *Probarbus* spawning habitat and proposed as the location for a community-managed protected area. Villages in Lao PDR are authorized to set their own

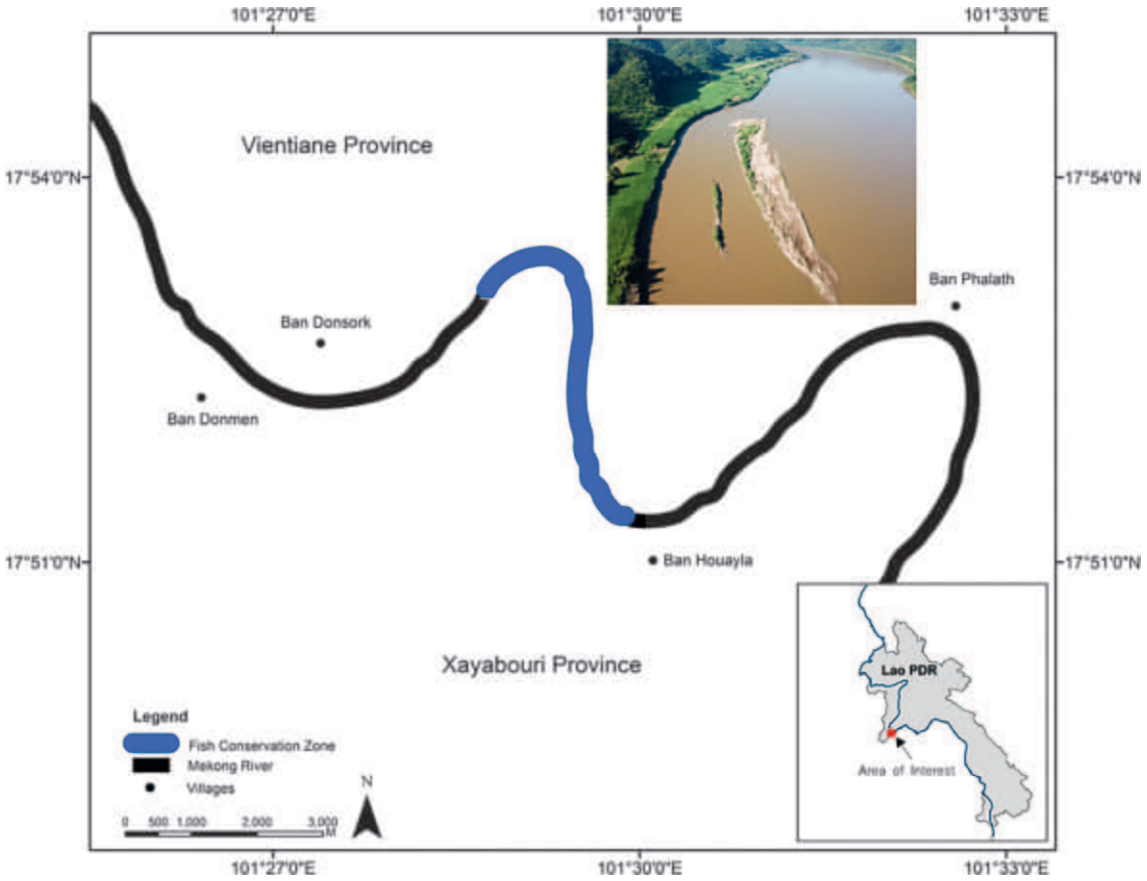

Fig. 5 Map of communities at Kengmai Rapids, Lao PDR. Courtesy of Erin Loury, FISHBIO.

regulations for fisheries management under the Lao fisheries law. In 2015, the four villages formally established a community-managed Fish Conservation Zone (FCZ) at Kengmai Rapids, one of over 1300 such FCZs recognized by the Lao government. The Kengmai Rapids FCZ supports biodiversity conservation, local livelihoods and food security by protecting spawning *Probarbus* and key breeding and feeding habitats for other species. Enforcement of the FCZ regulations also addresses the threat from destructive dynamite and electrofishing. Fish sampling surveys have documented juvenile *Probarbus* inside the FCZ, confirming the importance of the location as a spawning and rearing area.

The FCZ prohibits all fishing along a 5-km stretch of the Mekong River, and represents one of the largest freshwater protected areas on the mainstem Mekong in Lao PDR. Although the size of the area presents logistical challenges for patrolling and enforcement, the villages share responsibility for enforcing the FCZ regulations, and communities are generally supportive of the FCZ. Illegal fishing does still occur in the area; however, communities believe that the FCZ has helped increase compliance with regulations and decrease the extent of illegal and destructive practices. Given adequate support, local communities are able to effectively manage fish resources to both sustain food security and to conserve freshwater biodiversity. Government recognition of FCZs is a major contributing factor that has enabled this model to be adopted by communities throughout Lao PDR. Although dam construction on the Mekong River threatens the habitat and the migratory fishes protected by the Kengmai Rapids FCZ, increased coordination of community enforcement at FCZs across Lao PDR could help support a network of refuges for aquatic biodiversity at a landscape scale, while providing resilience to local fisheries.

Case study: Fisheries in the indigenous territory of Rey Curré, Costa Rica

Rey Curré is an indigenous territory (10,600 ha) in the Puntarenas province of Costa Rica, inhabited by the Bruncaj people. The territory is located close to Costa Rica's largest (160 km) river, the Térraba river, known locally as Dí Crí, meaning big water (Fig. 6). The river flows 50 km from the center of Rey Curré downstream toward the Pacific Ocean, passing through the Térraba-Sierpe wetlands RAMSAR site, the largest mangrove system in the country.

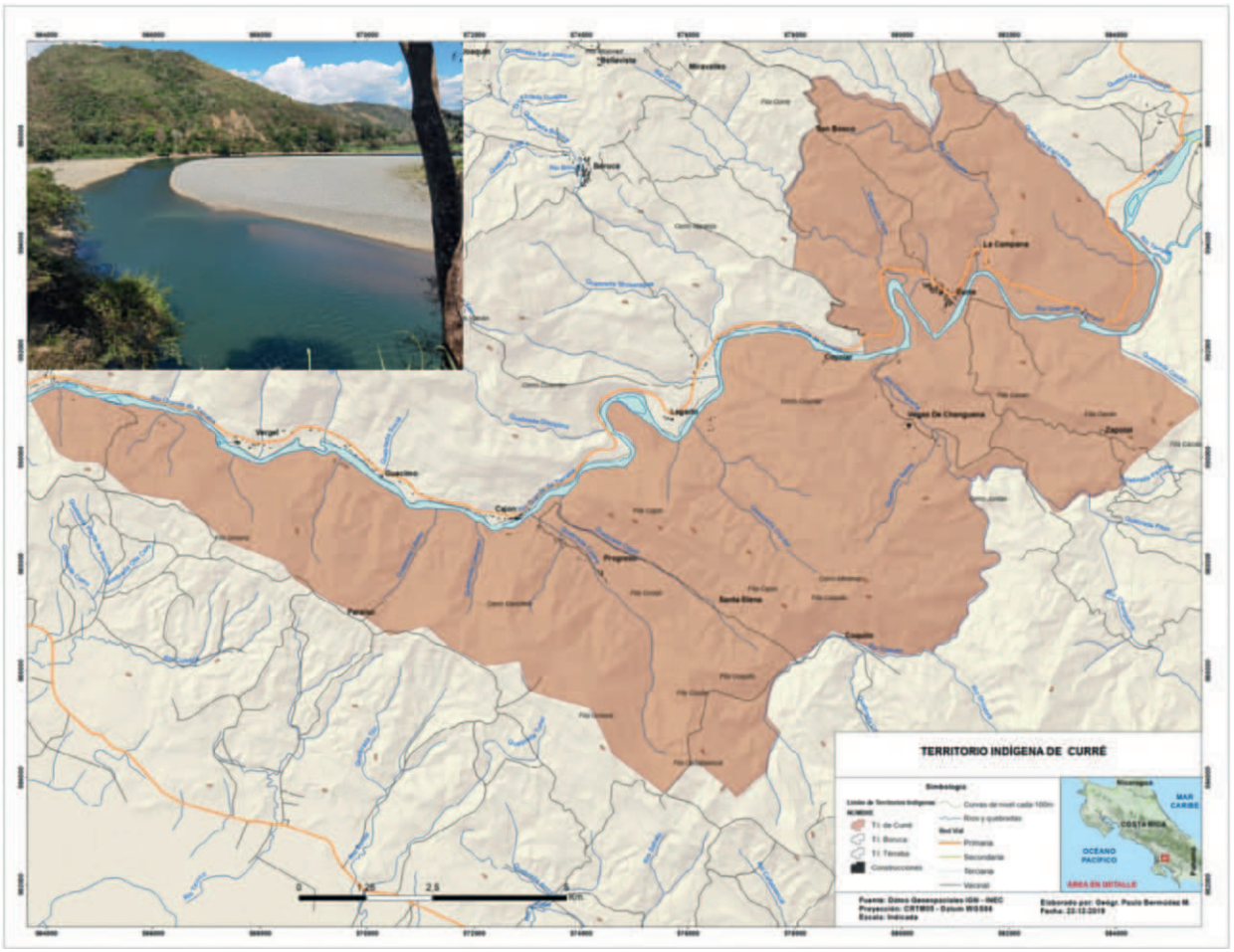

Fig. 6 Fishing communities in Rey Curré. Courtesy of Eva Salas, FISHBIO.

The inland fishery provides an important source of protein for these low-income communities and has historically been important to the culture of Rey Curré and nearby indigenous territories. In particular, the Di Crí river is considered a sacred place, of spiritual, recreational and cultural value. The multispecies subsistence fishery is largely shore-based and is most active during the dry season. Although the most common and abundant catch is machaca (*Brycon beherae*), the diverse fishery includes various shrimp species, especially *Macrobrachium* spp. and maruchas (*Atya spp*), as well as coastal fish species, such as snooks (Centropomidae), grunts (Haemulidae) and snappers (Lutjanidae).

The only legal fishing gear in Costa Rican inland waters is the hook and line, but other gears, such as cast nets, gillnets, seine nets, and spear guns are also frequently used, because regulations are rarely enforced. Of even greater concern is the use of poisons for harvesting shrimp. Although there is work in progress to establish additional local management, as well as an interest in establishing freshwater protected areas, there are currently no other regulations, such as size, season or species restrictions, and no freshwater protected areas. The lack of regulations and increasing fishing pressure have prompted local fears that the fishery is being over-exploited. Local ecological knowledge surveys suggest that shrimp in particular, are being over harvested as a result of the use of poisons.

Despite providing an important source of local protein and a pressing need for improved fishery management, inland fisheries are not a national priority, due to the greater economic importance of marine fisheries. As a result of this lack of attention, there is insufficient funding available for patrolling and other management needs, including establishing the critical regulations and other interventions to enhance the fishery and the environment.

Pineapple crops, deforestation and climate change are making conditions drier and threatening downstream ecosystems, such as the wetlands of the Terraba-Sierpe, affecting the whole watershed and having far-reaching consequences for fish health, productivity and life-history. To protect and manage their valuable resources, Rey Curré and the neighboring territories of Boruca and Térraba need more support. Through the development of local management plans led by local communities and informed by science, there are opportunities to combine traditional knowledge with western science to guide management and conservation goals that will help restore the river, protect its species, and unite the communities around the same goals.

Acknowledgements

We want to thank Daniel Leiva of the Instancia de Consulta, and over 40 people of the territory that have shared fishery information. The information used to build the profile of Rey Curré comes from the collective knowledge of over 40 people of the territory that have participated in FISHBIO project workshops, and it was validated by José Rigoberto Leiva, the current president of Rey Curré's Asociación de Desarrollo Integral (ADI Curré).

Case study: Co-management of fisheries in the ceded territories of the upper Midwest, USA

Harvest of *Ogaa* (Walleye; *Sander vitreus*) is an essential subsistence and cultural activity among the Ojibwe Tribes of the northern glaciated region of the states, now known as Wisconsin, Michigan, and Minnesota in the United States of America. During the early spring when *Ogaa* are spawning in nearshore areas (BIA, 1991), harvesters spear or net *Ogaa* and share the harvest with members of their extended families, elders, and throughout the community. These fish form an important part of ceremonies and community feasts. Harvest season brings the tribal community together and provides sustenance for the coming months.

Ogaa also contribute to the sportfishing economy of the midwestern region (BIA, 1991). It rates as one of the most popular fish targeted by anglers for recreation and harvest, and draws tourists to the region throughout most of the year. As the most abundant predator in most of the lakes and rivers in the region, *Ogaa* is also important ecologically.

In the mid-1800s, Ojibwe ceded large tracts of land to the USA in a series of treaties (Fig. 7) in which tribes reserved the right to hunt, fish, and gather on the lands. In Wisconsin and Minnesota, Tribes regulate their harvests according to court mandates. Although not formalized in Michigan, Tribes in these territories have set up similar systems to regulate harvest. The Great Lakes Indian Fish and Wildlife Commission (GLIFWC) is a tribal natural resource agency that was formed by, and assists, its 11 member Ojibwe Tribes in implementing the federal court orders and intergovernmental arrangements governing treaty rights. In these systems, Tribes and GLIFWC work with the State Department of Natural Resources (DNR) to co-manage and set annual quotas in accordance with the best available population data for individual lakes (Hansen et al., 1991, 2015; Schmalz et al., 2011). These decisions are made based on science generated by all partners and traditional knowledge held by the Tribes. The available annual harvest is allocated between tribal subsistence fisheries and state-regulated angling fisheries, implicitly based on the method of harvest (i.e. Wisconsin Lakes, Staggs et al., 1990), or explicitly (i.e. Mille Lacs Lake, MN) based on an agreement between the parties (Schmalz et al., 2011). In all territories, the goal of the Tribes is to allow walleye populations to be sustained and provide harvest opportunities for current members and for the next seven generations.

Despite these goals and careful consideration, *Ogaa* are declining in many of these waters. Habitat destruction, invasive species, continued harvest of declining populations (Embke et al., 2019), and climate change pose major threats to walleye populations in this region (Hansen et al., 2017). Extra coordination between Tribes, States, and others will be required to rehabilitate declining stocks and protect resilient populations. In some lakes where *Ogaa* populations are declining, Tribes are working with state agencies and nongovernmental organizations to create and implement rehabilitation plans. These plans have primarily focused on resisting fish community transformations that may be caused by ecosystem change, but recent discussions have included accepting or directing these transformations. Typically harvest reductions, stocking, and frequent population monitoring are the main tools used for rehabilitation. More recently, plans have attempted to account for climate change when projecting fish populations

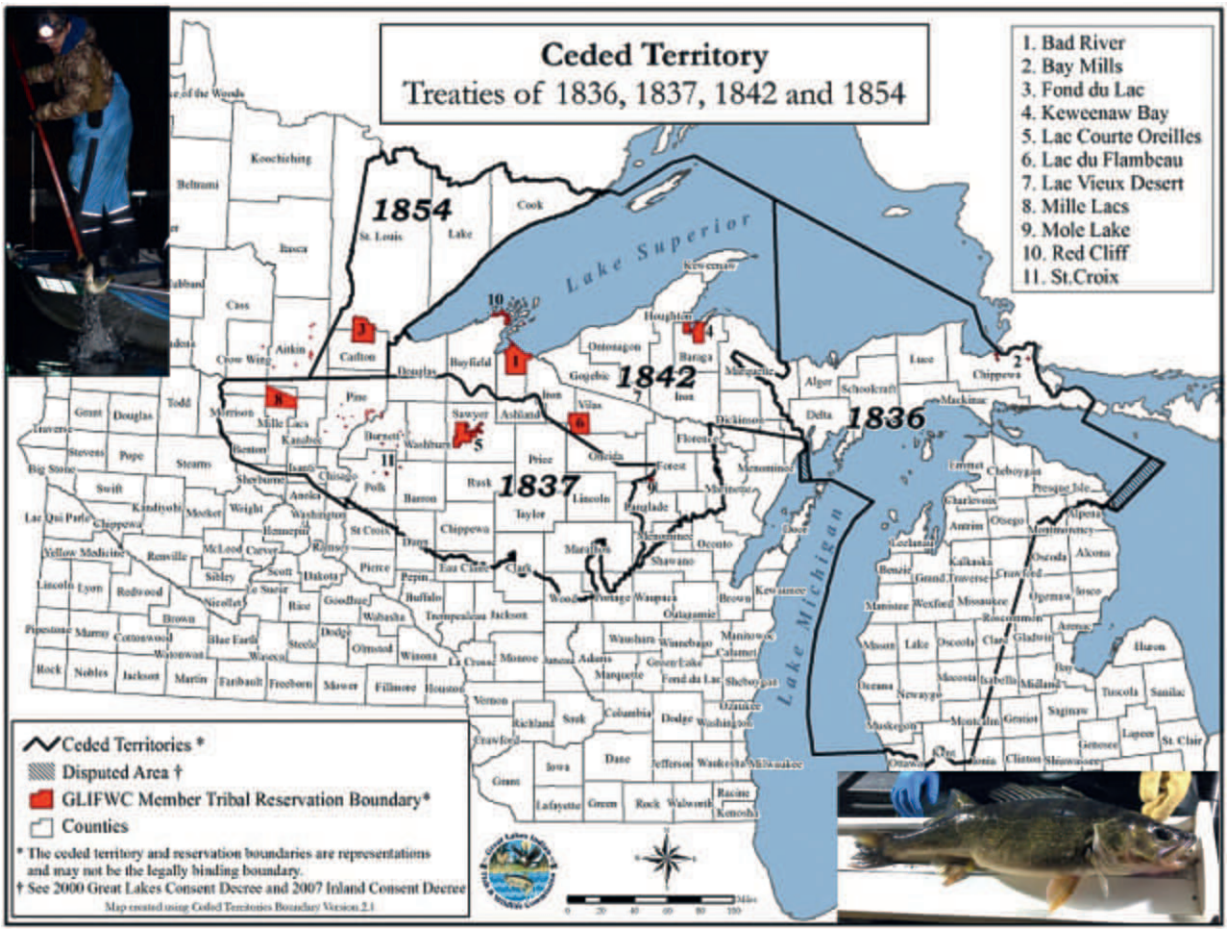

Fig. 7 Map of the Ceded Territories in the Upper Midwest, USA. Image credit: Great Lakes Indian Fish & Wildlife Commission.

(e.g. Hansen et al., 2017), evaluating future habitat, and implementing potential mitigation efforts, such as those proposed in the Midwest Glacial Lakes Partnership Conservation Plan, 2019.

Overall, *Ogaa* remain an important species for subsistence harvest and recreational angling in the Ceded Territories of the Upper Midwest. Additional protection and rehabilitation efforts will be required to ensure that fisheries livelihoods can be sustained in the area for the long term.

Acknowledgements

Ann McCammon-Soltis provided valuable edits to earlier versions of this case study. Dara Unglaube supplied us with the map of the Ceded Territories in the Upper Midwest.

Case study: Human pressure and management of Lake Victoria resource use

Lake Victoria (2°3′S 33°4′E) is the largest (about 68,800 km^2) inland tropical lake. The main lake is shared between Kenya (6% of coastline), Uganda (43%) and Tanzania (51%) with a catchment that extends to Burundi and Rwanda (Fig. 8). The Lake Victoria Basin supports the lives of about 51 million inhabitants with more than 500 persons per km^2, which makes it one of the most densely populated basins globally (Kimani et al., 2018a). The fishery is estimated to directly employ about 200,000 fishers, and 700,000 people along the value chain, while supporting the livelihoods of 3–4 million people (Mkumbo and Marshall, 2015).

Since the 1950s, the fishery has transformed from a multispecies, native fishery to focus on three species of commercial importance: *Lates niloticus* (Nile perch), *Oreochromis niloticus* (Nile tilapia) and *Rastrineobola argentea* (Dagaa or Omena). The Nile perch, together with four Tilapiines: *O. niloticus* (L), *O. leucosticus* (Trewavas), *Coptodon rendalli* (Boulenger) and *Coptodon zillii* (Gervais) were introduced in the 1950s and 1960s (Powell, 2020). The introduction of these exotic fish species placed endemic cichlids in grave danger of extinction and is thought to have led to the explosion of Nile perch population (although there is some debate) and a dramatic decrease in the species diversity and fish biomass in the lake (Marshall, 2018; Downing et al., 2013). Nile perch has been credited with the disappearance of more than 200 species of haplochromine cichlids, one of the most biodiverse and locally adapted Tribe of cichlids, and the decline of other native species (Nyamweya et al., 2016).

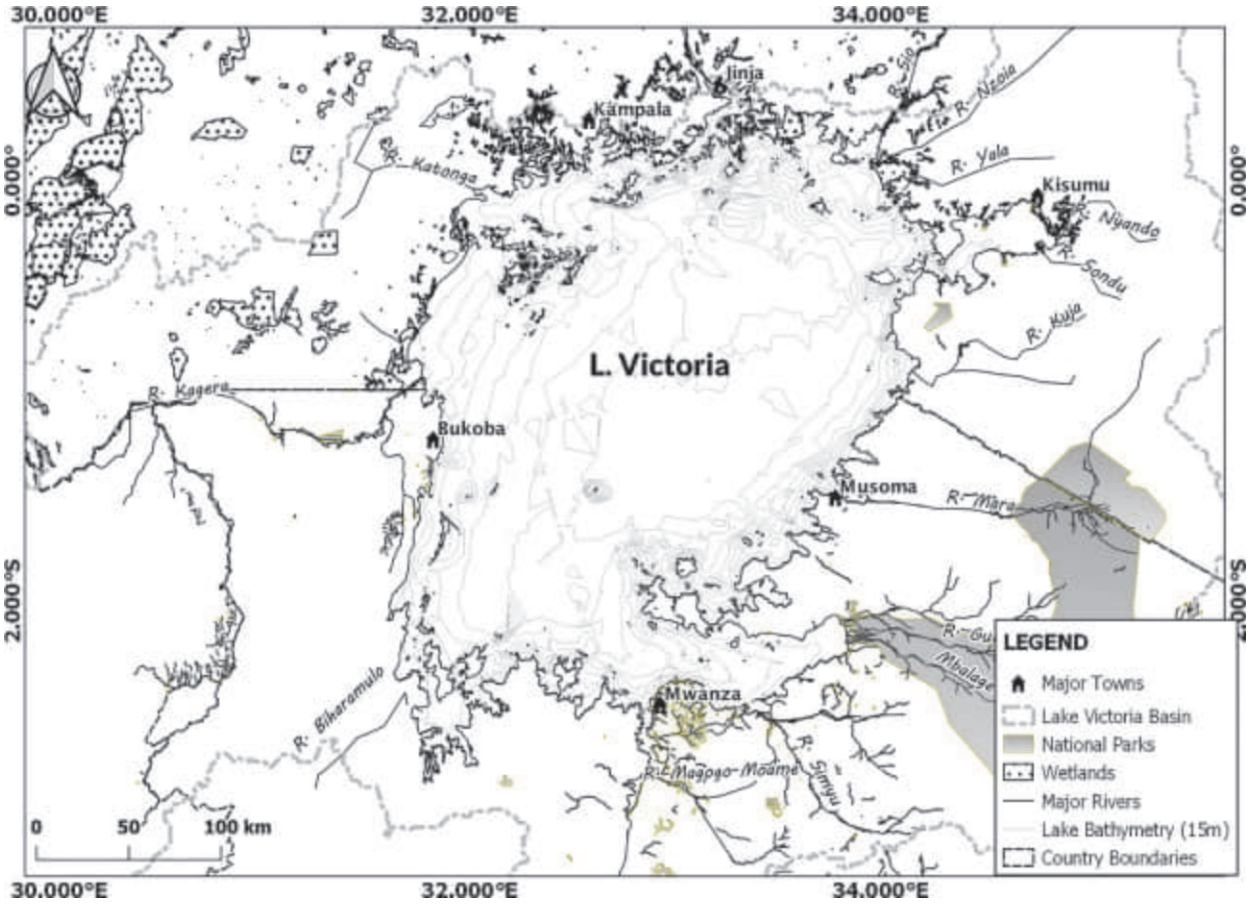

Fig. 8 Lake Vitoria Fisheries with major rivers, towns and other natural resources. Image credit Christopher Aura.

While Nile perch decimated native biodiversity, it has also expanded commercial opportunities within the lake, with international exports of Nile perch reaching Europe and the Middle East (Odongkara et al., 2005). The lake provides a blended artisanal-commercial fishery, which is largely traditional in terms of fishing methods and vessels, but supports a large Nile perch fish export industry, coupled with substantial domestic trade in many endemic species. Fisheries production from Lake Victoria increased tenfold from 1980 to 2016 (98,250 tons in 1980 to 918,000 tons in 2016) (Aura et al., 2020). About 1 million metric tons of fish are harvested annually from Lake Victoria, generating >840 million US$ at the beach and > 300 million US$ in exports (van Zwieten et al., 2016; Aura et al., 2020). Further processing and marketing of the catch is valued at US$ 60 million. However, the fishery has recorded a steady decline in fish harvests since the year 2000, and continues to exhibit this trend, provoking fears that the lake is being over-harvested and requires better management to support sustainable harvests (Nyamweya et al., 2020). Aside from the transformation of the aquatic food web, the Lake Victoria region has experienced an accelerated rate of population growth, land cover change, and ecosystem change, which has put increasing pressure on the fishery, challenging its sustainability (Ongore et al., 2018).

The lake is co-managed by local associations (Beach Management Units, BMUs), national management and research institutions and regional institutions consisting of Lake Victoria Fisheries Organization (LVFO), the East African Community (EAC), and the Lake Victoria Basin Commission (LVBC); with several international, regional and national regulations, policies and laws also guiding the exploitation and management of fisheries resources (Aura et al., 2019). The BMUs are intended to bring together everyone involved in fisheries, in particular fishers, boat owners, traders, processors, boat builders, net menders, and others - to work together with the government in an attempt to manage the fisheries resources more holistically. Despite the extensive co-management efforts, there have been many challenges, including Uganda suspending its BMU activity (Etiegni et al., 2020) and Lake Victoria largely continues to operate as an open-access system (Nunan, 2010). This poses a serious challenge to managing fishing effort sustainably. Exploration of rights-based fisheries to delimit local fishing areas as an alternative to open-access, and being more cognizant of community priorities, biases and limitations, could improve the existing co-management (Edward et al., 2011; Mgaya and Mahongo, 2017). Increased investment in Monitoring Control and Surveillance (MCS) and identifying ways of determining sustainable fishing effort for the Lake, would also be beneficial.

Options for expanding livelihood opportunities within the fishery are few. However, with improved management and regulation, cage culture, which integrates fisheries knowledge with entrepreneurship skills could be a particularly attractive option,

increasing productivity and offering employment (Kizza et al., 2009; Aura et al., 2018). Expansion of trading opportunities in the local and international markets through post-harvest production has the potential to enhance the value of the same catch, helping to reduce fishing pressure. With appropriate technology and investment, trade in fish products and aquatic plants could also offer a viable alternative. Nile perch swim bladder (fish maw), which is largely exported to China through Hong Kong fetches a higher price than fish itself. Fish maw are used as a source of collagen, proteins and nutrients, which are believed to improve skin tissues and tone and promote healing of weak lungs and kidneys (Kimani et al., 2018b). If the Nile perch maw trade is formalized and optimized, it could improve the socio-economic benefits for the region. Careful exploration of the potential use of selected endemic and small indigenous species like Dagaa by the animal feed industries, could ease pressure on the preferred Nile tilapia food-fish, but they play a critical role in local food security and thus should be approached with caution (Matsuishi et al., 2006).

Unrestricted fisheries have few entry demands and a rather quick repayment period, providing significant advantages over many livelihood alternatives (e.g., farming) (Edward et al., 2011). Nevertheless, Lake Victoria's 7000 km shoreline provides great potential for fisheries tourism and a fledgling hospitality industry (McCarthy, 2004; Hamilton, 2016). The shoreline and the lake could also offer unique and unexploited recreational opportunities like sport fishing, boat racing, and wind surfing in the expansive open waters, snorkeling and diving in aquatic diversity hotspots, and holidaying in its many exotic islands. Fish, plants and other local resources could also be turned into souvenirs and sold to the tourists. Invasive aquatic weeds, such as the water hyacinth, which have gained much attention for their undesirable socio-ecological impacts could, for example, be used for energy production; to make mats and furniture; for fish feeds; for biodegradable paper; and to produce charcoal (Ongore et al., 2018). With declining fisheries, fishers are being forced to consider alternatives and finding livelihood opportunities outside the fishery is becoming essential to ensure the sustainability of the Lake Victoria ecosystem and its resources.

Conclusions

While coasts offer many marine fishery landing opportunities, inland waters are integrated into the landscape as wetlands, ponds, agri-fisheries, and networks of rivers and streams, all offering the possibility to bring fish on land. Thus, the challenge of monitoring and regulating exploitation with so many opportunities, becomes insurmountable. Inland fisheries, more so than marine, must rely on the integrity and interest of fishers to harvest sustainably in order for exploitation of inland resources to remain a viable livelihood option. Inland fishers, fishing communities and governments around the world are working together to make fishing practices more sustainable and to ensure that inland fisheries remain a feasible livelihood in the future.

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Relevant Website

https://infish.org—Overview of inland fisheries | Inland Fisheries.
fao.org—Food and Agriculture Organization of the United Nations.

Implications of Climate Change for Freshwater Fisheries

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Adaptive capacity The capacity of a species to adapt to changing environmental conditions, such as increased temperature. This can involve behavioral, physiological, morphological and phenological change.
Critical thermal maxima/minima Thermal endpoint following a constant change in water temperature at which a loss of equilibrium occurs. Used to assess the tolerance of fish species and populations to upper and lower temperature extremes.
Degree-days The accumulated thermal units, measured as mean daily temperature, experienced by a fish over time (e.g. a fish held for 1 day at 10 °C and a fish held for 2 days at 5 °C have both experienced 10 degree-days).
Diadromous Species that migrate between marine and freshwater habitats.
Eurytherm Species that can function over a wide temperature range.
Freshwater fish A fish species that spends all or part of its life-cycle in freshwater bodies, such as lakes or rivers.
Inland fisheries Includes all types of fisheries (artisanal, subsistence, recreational and commercial) in freshwater and brackish waterbodies.
Lentic Still or slow-moving freshwater habitat (lakes, reservoirs, ponds, floodplains).
Lotic Fast-flowing freshwater habitat (rivers and streams).
Potamodromous Species that migrate within freshwater habitats (e.g. between rivers and lakes).
Riparian zone A transitional interface between aquatic and terrestrial environments, characterized by a zone of vegetation bordering water bodies.
Stenotherm Species that typically can only function over a narrower temperature range.

Introduction - climate change as a threat for freshwater fish

The diversity and widespread distribution of *freshwater fishes* illustrates an extraordinary adaptability to a range of environmental conditions, from small mountain streams to vast lowland river basins and from shallow ponds to the world's deepest lakes. Even the natural range of a single fish species may be spread across a considerable climatic gradient. For example, the native distributions of the American eel (*Anguilla rostrata*) and European eel (*Anguilla anguilla*) cover drainage basins that occur along latitudinal extremes on western and eastern Atlantic coastlines. Throughout the long evolutionary history of freshwater fish they have experienced, and have successfully adapted to, shifts in climatic and environmental conditions. Recent and rapidly changing human-influenced climate change is a novel form of climatic variability that fish populations have not experienced previously. Substantial increases in atmospheric greenhouse gases over the past two centuries have occurred due to human activities (IPCC, 2021) and the primary relevance to freshwater fisheries involves changes to the temperature and precipitation climatology at the Earth's surface.

Additional factors, often arising through complex feedback loops, involve increased frequency, duration, and intensity of episodic and extreme climatic events such as storms, floods, heatwaves, and droughts. The need to understand climate-induced changes in freshwater fish habitat and resulting ecological consequences is clear - half of all current freshwater fish species are predicted to be potentially at risk of climate-induced extinctions in the coming century (Manjarrés-Hernández et al., 2021) and over a third of species may have over a half of their current geographic range exposed to climatic extremes (Barbarossa et al., 2021).

The aim of this chapter is to provide a general overview of predicted climate-induced impacts on freshwater fish species, their habitats and fisheries and to review potential ecological consequences. Specific *lentic* and *lotic* responses to climate change pertinent to fish populations are discussed. Furthermore, the unequal vulnerability of individual fish species and inland fisheries to climate change is considered, which depends not only on the magnitude of change occurring across a species' natural range but also on each species' biological tolerance and capacity to adapt. The emerging threat of climate change for freshwater fish and their habitats is much more formidable combined with multiple additional existing and emergent stressors, with direct climate change effects potentially accentuating existing pressures faced by fish populations. While an exhaustive account of human impacts on freshwater fish is beyond the scope of this article, the potential for climatic and other specific anthropogenic environmental pressures to interact and create compounding stressors is considered. The chapter is concluded by highlighting some important knowledge gaps and potential mitigation strategies aimed at increasing the resilience of freshwater fish to climate change.

Climate change effects on freshwater fish environments

Thermal habitat

At a global scale, the net outcome of excess radiative energy being trapped in the atmosphere due to increased greenhouse gas concentrations is an increase in heat uptake in inland waters through modification of the surface energy budget (Vanderkelen et al., 2020). This will inevitably lead to thermal regimes in lakes and rivers worldwide becoming warmer on average, which has major ecological consequences for fish.

As obligate ectotherms, the body temperature of almost all fish is dictated by the surrounding water temperature (Haesemeyer, 2020). Therefore, the ambient temperature affects various physiological processes such as blood circulation, respiration, hormonal activity, the immune system, and behavior. It also affects movement, reproduction, growth, and life span. Unable to thermoregulate to any significant degree through internal physiological processes, fish must inhabit thermal environments that allow them to maintain a body temperature necessary for physiological and metabolic functioning.

Individual fish species have evolved a set of critical upper and lower thermal limits that allows them to adapt to their environment (see Section "Vulnerability and resiliency of freshwater fish to climate change"). Thermal tolerances within each species can be further categorized, as different life-stages (adults, juveniles, spawning adults and developing embryos) generally have a different set of critical thermal limits (Dahlke et al., 2020). Spawning adults and the developing egg stage are the least thermally tolerant, with a much narrower set of thermal limits compared with juveniles and adults during the growth stage (e.g. Elliott and Elliott, 2010). Therefore, reproductive phases potentially represent a thermal bottleneck in the life stage of freshwater fish and could be the most important determinant for whether a temperature increase in their native habitat will be tolerable. In this regard, temperature increases during the spawning season and subsequent incubation period are of particular concern. The rudimentary cardio-respiratory system, and inability to produce heat shock proteins in response to direct heat stress, leaves the egg stage at highest risk for warming-related mortality. Furthermore, development at the egg stage is highly temperature dependent and warmer average temperatures during the developmental stage cause *degree-days* to be accumulated at a more rapid pace. This can cause the overall developmental time (in degree-days but not necessarily in calendar days) to be longer, depleting the yolk sac and resulting in smaller, poorer conditioned fry upon hatching (Mari et al., 2021). Total incubation length in calendar days however may still be shorter at warmer temperatures as the increased number of degree-days are accumulated more rapidly. This could lead many species to undergo shifts in timing of reproductive life-history events, with spawning and hatching events in spring and summer spawning species likely to occur earlier in the year. In addition, changes in hatching phenology could lead to possible timing mismatches between emergence of fry and peak food availability (e.g. Jonsson and Setzer, 2015).

The global distribution of freshwater fish across climatic gradients reflects the thermal tolerances of individual species. Fish living in warm tropical rivers and lakes (e.g. cichlids) have a relatively high 'critical thermal maximum' while fish in northern temperate and polar environments (e.g. salmonids) have a 'lower critical thermal minimum', allowing them to tolerate cold, ice-covered waters. *Stenothermal* species (e.g. Arctic charr, (*Salvelinus alpinus*)) have a narrow thermal tolerance limit, while 'eurythermal' species can tolerate a wider range of water temperatures and generally illustrate a wide latitudinal distribution reflecting this (e.g. freshwater eels in the genus *Anguilla* (Froese and Pauly, 2000). However, stenothermal species may be able to exploit extreme freshwater habitat types uninhabitable to most other species (Klemetsen et al., 2003). Furthermore, while fish can survive within a sublethal temperature range bounded by their upper and lower critical limits, each species is defined typically by an optimal temperature range for growth (Elliott and Elliott, 2010). This optimal range is even narrower than the critical thermal range and fish exposed to warmer temperatures outside of this optimal range may cease to grow efficiently, primarily due to more energy being invested into cellular repair related to heat damage. This decreases energy allotment for somatic growth (e.g. muscle, skeletal, organ) and reproductive growth as well as activity, which inevitably leads to reduced feeding. Thus, given the critical role of water temperature

in shaping the ecology and contemporary global distribution of freshwater fish, climate-induced warming could necessitate range shifts and change the overall extent of species' distributions (Comte et al., 2013). The different critical thermal limits and thermal optima of freshwater fish could also lead to a competitive edge for warm-adapted species, which could alter fish species assemblages in river and lake ecosystems.

Freshwater heatwaves are projected to become an increasingly common, longer-lasting phenomenon over the coming century (Woolway et al., 2021). This will greatly increase the risk of fish die-offs and major fish kills (Till et al., 2019). If the water temperature exceeds the critical thermal maxima of fish in river or lake environments, physiological functioning ceases and mortality follows. While fish kills due to extreme heat events have always occurred, the increased risk associated with ongoing climate change is related to the frequency and intensity of such heat events. The specific thermal response of rivers and their fish populations to heatwaves strongly depends on factors such as altitude (e.g. rivers fed by snowmelt may show a damped thermal response (Piccolroaz et al., 2018)). Shading from catchment features and riparian cover may alleviate heatwave conditions (Garner et al., 2017). Physical factors that govern the severity of heatwave events in lakes and wetlands may include morphometry, as large shallow bodies with a high surface area to volume ratio are more exposed to direct atmospheric heating across their surface and have a reduced capacity to store cool subsurface water, leaving less suitable thermal habitat for fish to occupy.

Dissolved oxygen depletion

Along with direct thermal stress, one of the most important consequences of increased water temperature for fish is the effect on dissolved oxygen. The solubility of oxygen in water decreases with temperature. For most fish, dissolved oxygen is fundamental for controlling elements of behavior, growth and reproductive functioning (Claireaux and Chabot, 2016). A scenario combining lower dissolved oxygen and warmer water temperatures represents a dire combination for fish, as increased temperature elevates metabolic rate and oxygen consumption. This combination has the potential to severely reduce growth rate and reproductive potential. Alarmingly, evidence of a global decline in dissolved oxygen in freshwater ecosystems as a response to climate change is beginning to emerge (Jane et al., 2021). However, as the oxygen budget in lotic and lentic systems depends upon additional biogeochemical processes, land-use and catchment-scale factors play a key role in determining rates of aquatic oxygen consumption in freshwater environments (Jenny et al., 2016). In systems that receive large quantities of organic matter input, oxygen consumption through respiration is likely to be high, and when superimposed on lower dissolved oxygen solubility due to warming, there is a greater deoxygenation risk compared with systems that have a net positive production of oxygen. In addition, physical limnology plays an important role in determining the areal extent of deoxygenation (see Section "Lakes").

Climate change effects on specific freshwater fish habitat

Rivers and streams

In addition to the direct warming effects discussed above, climate-induced changes in precipitation and evaporation will also impact lotic environments by modifying hydrologic regimes. For riverine fish species, current velocity is a major environmental variable that exerts considerable influence over habitat selection and availability (Maddock, 1999). The energetic cost of holding in-stream position and swimming against currents can vary dramatically depending upon the velocity and resulting drag forces associated with river flow. River flow also mediates predator-prey interactions and food availability (Turschwell et al., 2019) and provides a supply of oxygen-rich water to developing embryos in spawning sites.

Decreased precipitation and increased evaporation associated with climate change could lead to decreased river water levels and reduced current velocities, also accentuated by other water user demands. Regions most acutely at risk include arid and tropical regions during the dry season, where increased drought intensity, frequency and duration during the 20th century has been attributed to anthropogenic climate change (Chiang et al., 2021). Many tropical river basins may experience significant habitat loss and fragmentation owing to reduced hydrological connectivity associated with low flows and water levels (e.g. Pettit et al., 2017). This will create a reduction in wetted area and a decrease in suitable fish habitat. Furthermore, drastically decreased flow velocities tend to create homogeneous river flows, as turbulent, heterogenous flow created by fast river flow interacting with instream bed features and channel morphology decreases. While the role of turbulence in riverine fish ecology is complex, turbulent patches, and hydraulic variability in general, benefit fish bioenergetics (Tullos and Walter, 2015). Shallow, turbulent riffle zones, an important source of invertebrate prey items, may undergo partial drying during prolonged periods of low flow. Lower water levels could lead to increased competition for pools, mainly during concurrent warming phases. If decreased flow occurs during spawning season, shallow gravel spawning sites may become partially or entirely desiccated.

In addition to periods of decreased river flow, episodic periods of increased rainfall intensity and duration may cause extreme flood events, with several geographic regions (e.g. southeast Asia) anticipated to experience larger peak flows (Dankers et al., 2014). Fast current velocities typically invoke a high energetic demand for riverine fish and this could particularly have an impact on overwintering juvenile fish attempting to minimize energy loss during a period of low food intake (Finstad et al., 2004). Higher flows in combination with warmer temperatures may invoke a high metabolic cost and result in decreased body condition and overall survival.

Another cause for concern in relation to hydrologic change and fish ecology is not necessarily change in mean annual discharge, but rather changes in how discharge is distributed over the course of the year (e.g. Bunn and Arthington, 2002). The freshwater fish

groups most likely to be affected by this are the *diadromous* and *potamodromous* species. Rivers provide the necessary migration routes for fluvial-adfluvial, fluvial-lacustrine and fluvial-marine migrations that characterize the life cycles of some of the most ecologically and economically important freshwater fish, including the salmonids, eels and sturgeons. However, migratory freshwater fish populations have declined by an estimated 76% on average since the 1970s (Deinet et al., 2020). Climate-induced alteration of flows has the potential to impede migration if adverse flow conditions coincide with migration timing. The phenology of migration is a complicated process depending upon remote-scale cues (e.g. conditions in marine feeding grounds and antecedent freshwater conditions during the growth phase) and local-scale cues (e.g. water temperature, timing of adequate water flow, daylight hours and lunar phase) (Carr-Harris et al., 2018). Widespread declines in diadromous Atlantic and Pacific salmon (*Salmo salar* and *Oncorhynchus* spp.) have coincided with the changing climate, and multiple climate change threats in conjunction with existing pressures have been identified in the marine and freshwater life stages of salmon (Thorstad et al., 2021). Changing hydrological regimes and increasing temperatures have led to concern that phenological mismatches may occur between migrating salmonid smolts and favorable survival conditions as fish move into the marine environment (Kennedy and Crozier, 2010). For example, the direct effects of climate and local-scale river conditions on salmonid migration timing were apparent during the 2020 smolt migration downstream from the Erriff river system, Ireland's National Salmonid Index Catchment (Fig. 1). Such adverse flow conditions during the annual migratory phase can decrease migration success and highlight the heightened sensitivity of diadromous fish to changing climatic conditions.

Lakes

The summer warming response of lakes to climate change has been well documented (e.g. O'Reilly et al., 2015). For lake and potamodromous fish ecology in temperate regions, a key period for feeding and growth occurs from spring through summer, when high primary productivity fuels the lake food web. Warming lake temperatures and changes in the stratification regime may negate some of the bioenergetic benefits of lake productivity (Fig. 2). Warm surface summer lake temperatures can restrict suitable fish thermal habitat. Like rivers, cool spots associated with groundwater seeps may become prime thermal refugia for fish, although groundwater levels may also decrease in some regions (Wu et al., 2020). For many cold-preferring fish, the deep, cooler hypolimnion can provide an escape from excessively warm surface water (Morrissey-McCaffrey et al., 2019). However, one effect of increased length and intensity of stratification is a depletion of hypolimnetic oxygen. The longer the stratification duration, the greater the severity of oxygen depletion and the stronger the stratification (i.e. the greater the temperature difference between surface and bottom waters) the more limited the rates of deep-water ventilation.

Nutrient enrichment can exacerbate the problem of deoxygenation as excessive primary production leads to heightened oxygen consumption (Müller et al., 2019). Lake fish could be faced with a contraction of habitat – warm unhabitable conditions at the surface and deoxygenated water near the bottom (Fig. 2). In addition, wind-driven upwelling of low oxygen deep water into shallower nearshore oxygenated areas may occur, which can effectively compress usable fish habitat even further (e.g. Kelly et al., 2018).

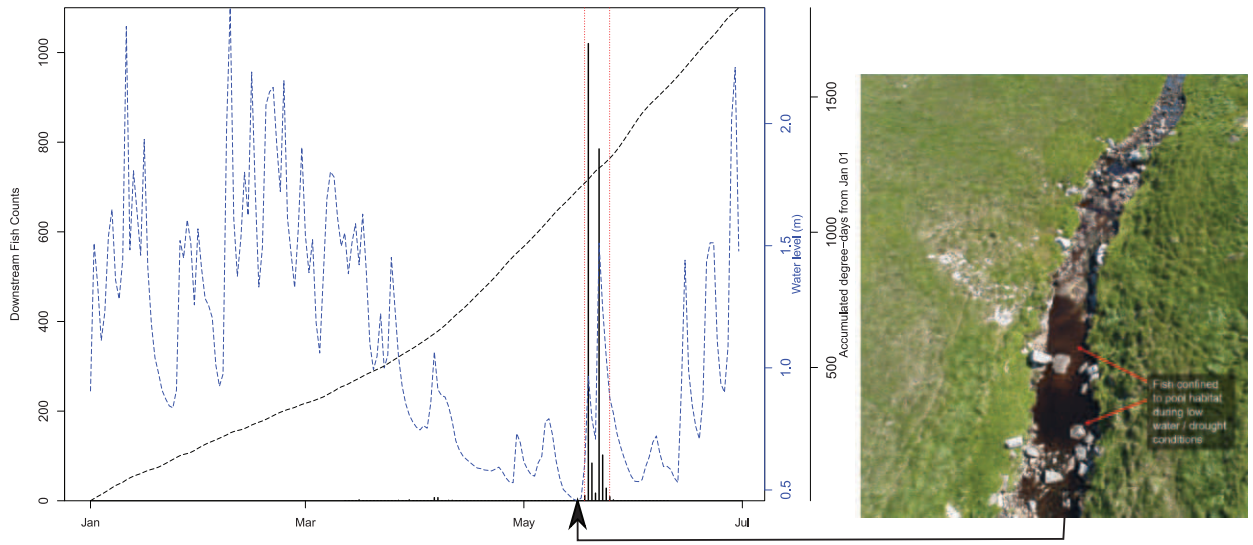

Fig. 1 (A) Timeseries showing the importance of climatic cues for the seaward migration of Sea trout (*Salmo trutta*) from the Erriff river (Ireland). Trout normally enter seawater during the spring period, with onset of migration mainly triggered by temperature accumulation (black dashed line) and photoperiod (daylength). However, a prolonged dry period without rainfall from April to May meant that extremely low river levels (blue dashed line) held up migrating smolts and 98% of the migration (black vertical bars) occurred within a narrow five-day window following rainfall. (B) Fish are confined to river pools during such low water conditions, which can increase predation risk and lead to a phenological mismatch between timing of outmigration from freshwater and optimal coastal conditions (Unpublished data, Inland Fisheries Ireland).

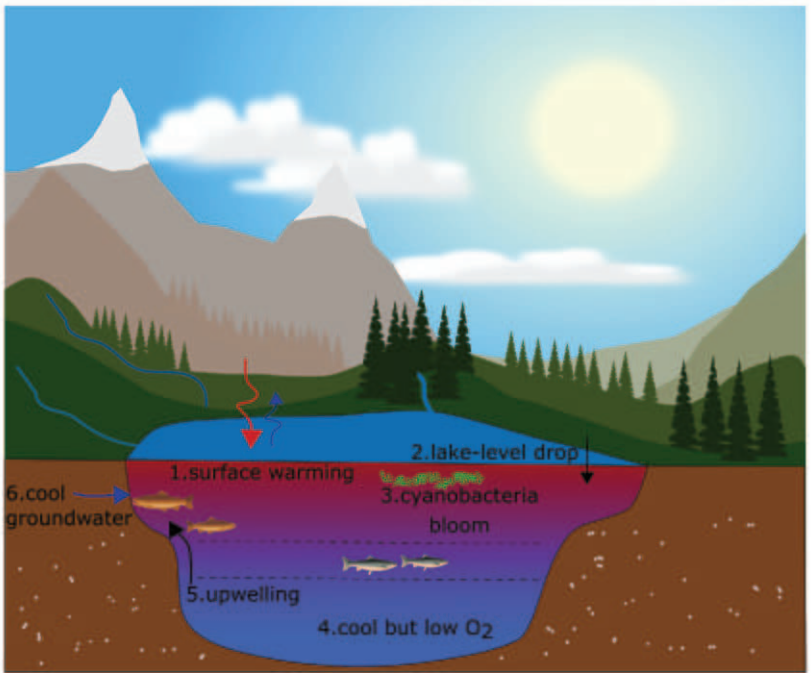

Fig. 2 Some examples of a typical lake response to summer climate warming relevant to fish ecology. 1. Excessive near-surface warming will avert many fish species away from this zone entirely; 2. Decreased river inflows, low rainfall and high evaporative cooling leads to reduced lake volume; 3. Warm conditions and stable thermal stratification during calm wind conditions, favors formation of cyanobacterial blooms; 4. Long periods of stable stratification prevent ventilation of lake bottom water – fish habitat contracts if cooler, deep water deoxygenates; 5. Upwelling events may pump deoxygenated deep water into shallower nearshore zones; 6. Sites of cool groundwater inflow become increasingly important as thermal refugia.

While the direct effects of climate change on tropical lakes and their fish populations is understudied compared to temperate lakes, climate-mediated changes in physical limnology and deep-water deoxygenation may be most severe in such ecosystems. In many large, deep tropical lakes, intensified surface warming experienced at low latitudes reduces the extent of vertical mixing not just during a seasonal stratified period but often year-round. This can result in decreased algal productivity in the nutrient-depleted sunlit surface zone (Verburg and Hecky, 2009) and a contraction in oxygenated benthic habitat in nearshore zones (Cohen et al., 2016), both of which have the capacity to negatively impact fishery productivity.

Prolonged periods of warm, stratified lake conditions are also conducive to the formation of algal blooms. When wind forcing is also weak, suppressed water column turbulence and upwelling of nutrient-rich hypolimnetic water favors cyanobacterial blooms owing to their competitive advantage in these conditions (O'Neil et al., 2012). However, cyanobacteria-dominant phytoplankton blooms can be unfavorable for fish as they provide a poor food source for most zooplankton grazers and may also lead to the accumulation of toxins in fish tissues (Flores et al., 2018).

For lake-spawning fish, the role of water temperature, water level, oxygen concentration and current speeds at spawning sites are all important components of spawning success. Warmer temperatures at lake spawning sites are projected for many lakes (Kelly et al., 2020), which are likely to impede subsequent embryo survival and fry condition (Farmer et al., 2015). Furthermore, warmer temperatures and siltation related to phosphorus loading can have a compounding effect, significantly reducing rates of embryonic survival (Mari et al., 2021). Wind-swept shoreline habitats are critical for lake spawning success as they provide a flow of oxygen-rich water and may disturb predators on fish eggs; in contrast, excessive current speeds may cause a loss of eggs and wash-out of spawning sites entirely (Callaghan et al., 2016). Climate-mediated changes in wind speed could affect current dynamics in some lakes, although the precise mechanisms are complex and depend upon lake characteristics (fetch and shoreline sheltering). Increased frequency of winter-time storm events related to climate change may negatively impact lake spawning sites for example.

Reductions in the thickness and extent of lake ice, and timing of ice onset and break-up, are pertinent signals of climate warming in boreal and polar lakes (Sharma et al., 2019). Potential effects on fish ecology include reduced anadromy rates (with a longer ice-free season potentially encouraging freshwater residency (Reist et al., 2006)) and a shorter winter torpor phase (Curry et al., 2005). The effects of winter warming for fish in high latitude lakes are complex, as overwintering fish are faced with low winter productivity and food abundance, minimal under-ice light conditions and very cold temperatures, which often results in high winter mortality and overall poor body condition (Amundsen and Knudsen, 2009). Thus, an increase in temperature, and a decrease in ice cover duration and thickness, may aid fish survival initially. However, longer-term adverse impacts may be that these lakes eventually become hospitable to non-cold stenothermic fish species (e.g. Hein et al., 2012). This could mean that extreme cold-adapted species such as Arctic Charr, that previously persisted in isolation in the northernmost lakes on Earth, could face competition from existing competitors or new interloping species such as pike or trout (e.g. Svenning et al., 2021), should corridors to range expansion become available (Connor et al., 2019).

Wetlands and floodplains

In many regions, wetland and floodplain ecosystems provide valuable natural fish habitat, yet are highly vulnerable to changes in rainfall patterns and increasing temperatures. Yet, relative to rivers and lakes in ***temperate*** regions, monitoring of thermal and hydrological dynamics, and especially long-term temperature timeseries, are lacking for floodplain ecosystems (Hamilton, 2010).

Sufficient water depth is necessary to sustain wetland fisheries, which support a critical and highly productive component of natural fishery resources in regions such as southern Asia (e.g. Sarkar et al., 2020), south-eastern United States (e.g. Hupp, 2000), central and southern Africa (e.g. Mosepele et al., 2009) and South America (Junk et al., 2011). High water during the wet season creates vast river floodplains and leaves behind floodplain lakes during subsequent lower water stages, which provide critical nursery habitat for juvenile fish. Owing to their intrinsic seasonal fluctuations in water level, many floodplain ecosystems depend upon low and predictable inter-annual variation in seasonal water cycles. Thus, a future climate scenario with a reduction in rainfall and high evaporation due to warmer, drier atmospheric conditions could reduce the extent and connectivity of floodplain lakes and lead to a decline in fish species abundance. An increase in the length of the dry season may be further exacerbated by a decrease in the amount of rainfall during the wet season. An extreme drought in the Brazilian Amazon in 2005 led to isolation of floodplain lakes and large reductions in wetted area, causing mass fish kills and a reduction in the abundance of economically valuable species (Freitas et al., 2013).

In addition, river floodplain waters typically experience the highest temperatures in tropical freshwater systems (Hamilton, 2010). This is related to their shallow, slow-flowing nature and occurrence at low elevations, exposing them to intense daytime atmospheric heating. Water temperatures may remain elevated above 30 °C year-round in tropical floodplain lakes (e.g. de Melo and Huszar, 2000). A decrease in water level due to drier, warmer atmospheric conditions could escalate daytime water heating for resident fish, as shallower floodplains concentrate heat accumulation from direct solar radiation over a smaller volume of water. An additional concern in many tropical basins and their floodplain ecosystems relates to large-scale changes in terrestrial vegetation associated with climate-induced changes in hydroclimate and the severity and intensity of wildfires (e.g. Flores and Holmgren, 2021). This could have profound effects on hydrological and thermal regimes in floodplains, given the role of floodplain forests in regional precipitation dynamics and their provision of canopy cover from direct solar heating.

Vulnerability and resilience of freshwater fish and inland fisheries to climate change

Vulnerability and resilience of freshwater fish to climate change

The impacts of climate change will not affect all freshwater fish equally – some species will experience more severe impacts and some species will be more resilient to changes compared with others. This will depend ultimately upon the severity of climatic changes that occur within the geographical range of individual species, as well as their phenotypic and genetic response to rapidly changing environmental conditions. Consider the foremost example of climate-induced changes relevant to freshwater fish discussed thus far - increased water temperatures. Each freshwater fish species has evolved a physiological capacity to acclimatize to a specific range of water temperatures, that typically correspond with their contemporary thermal habitat. The upper limit of species' thermal tolerance range and the 'adaptive capacity' of their response to warming environmental temperatures differs between species. These are largely constrained by evolutionary conservatism of ancestral traits as well as the degree to which environmental conditions fluctuate across their current geographic range.

Owing to the naturally fragmented landscape of freshwater ecosystems and the abundance of unnatural barriers and waterway modification, behavioral adaptation to changing environmental conditions may be difficult, as dispersal and range shift opportunities are often severely limited (Woodward et al., 2010). Some behavioral adaptations that may alleviate direct effects of warming include migrating to cooler waters, groundwater-fed streams or deep, stratified lentic waters. Diadromous species may be able to move along coastlines and colonize watersheds characterized by cooler thermal regimes. Landscape features unique to each watershed, such as large amounts of riparian and topographical shading of direct sunlight or a large proportion of wetlands and lakes can increase the availability of thermal refugia. In this regard, euryhaline migratory fish that display straying behavior in their selection of spawning rivers rather than homing to their natal stream of origin may have greater innate behavioral flexibility for adapting to climate change. Phenological adaptation, such as modifying timing of key life-history events such as spawning or migration, may be an especially important resiliency strategy in freshwater fish. Climate change may alter seasonal timing and dynamics (e.g. later onset of cold-season, early onset of warm-season) and in many fish such as salmonids, phenological traits have a high degree of heritability, implying that they may be a likely source of evolutionary adaptation to changing environmental cues (Manhard et al., 2017). Both Atlantic (Kennedy and Crozier, 2010) and Pacific (Kovach et al., 2015) salmonid populations have shown indication of earlier seaward migration timing, consistent with springtime warming trends.

Perhaps most vulnerable to the direct effects of warming are obligate freshwater resident fishes, especially populations that reside permanently within a single lake and have little or no potential to colonize other lentic or lotic ecosystems. Tragically, many such vulnerable 'land-locked' species are often endemic, such as the cichlid species of the African Great Lakes (Nyboer et al., 2019). The loss of such endemic species would represent a substantial loss of total global freshwater fish biodiversity. For riverine fish, moving upstream to higher altitude, cooler streams is one viable behavioral modification although dams and other barriers to dispersal may severely limit such range shifts (Woodward et al., 2010). Thus, physiological adaptation to warmer temperatures is a critical consideration when assessing the capacity of fish species to adapt to climate warming.

How well individual fish species can adapt physiologically to increasingly warmer temperatures will depend upon their thermal tolerance range, capacity to acclimatize and how close they currently live to their critical thermal maximum. For example, tropical fish inhabiting lakes and rivers at low, warm latitudes are typically more heat-tolerant and have higher critical thermal maxima compared with fish species at colder latitudes. In contrast, fish at temperate and polar latitudes experience a larger thermal range, with greater seasonal variation and, although not as heat tolerant as tropical fish, very often the warmest annual water temperatures they experience are much higher than their upper thermal limits. As tropical freshwater fish species are generally closer to their critical thermal maxima under contemporary climatic conditions (Comte and Olden, 2017), they may have reduced physiological scope for continually buffering against ongoing temperature increases, leaving little opportunity to adapt. Thus, despite the magnitude of climate-induced warming being greater toward the poles (Stuecker et al., 2018), and tropical fish having a higher warm tolerance compared with high latitude fish, populations near the tropics may be more acutely vulnerable to climate warming. The same dynamic can also be illustrated within a single species complex (Fig. 3). Peripheral populations near the latitudinal limit of a species natural geographic distribution routinely survive in, and have adapted to, warmer temperatures compared with other populations of the same species. Nevertheless, they may also be the most vulnerable to climate change, given that they are already close to their upper physiological thermal limit. This is likely, given that upper thermal limits among populations of the same

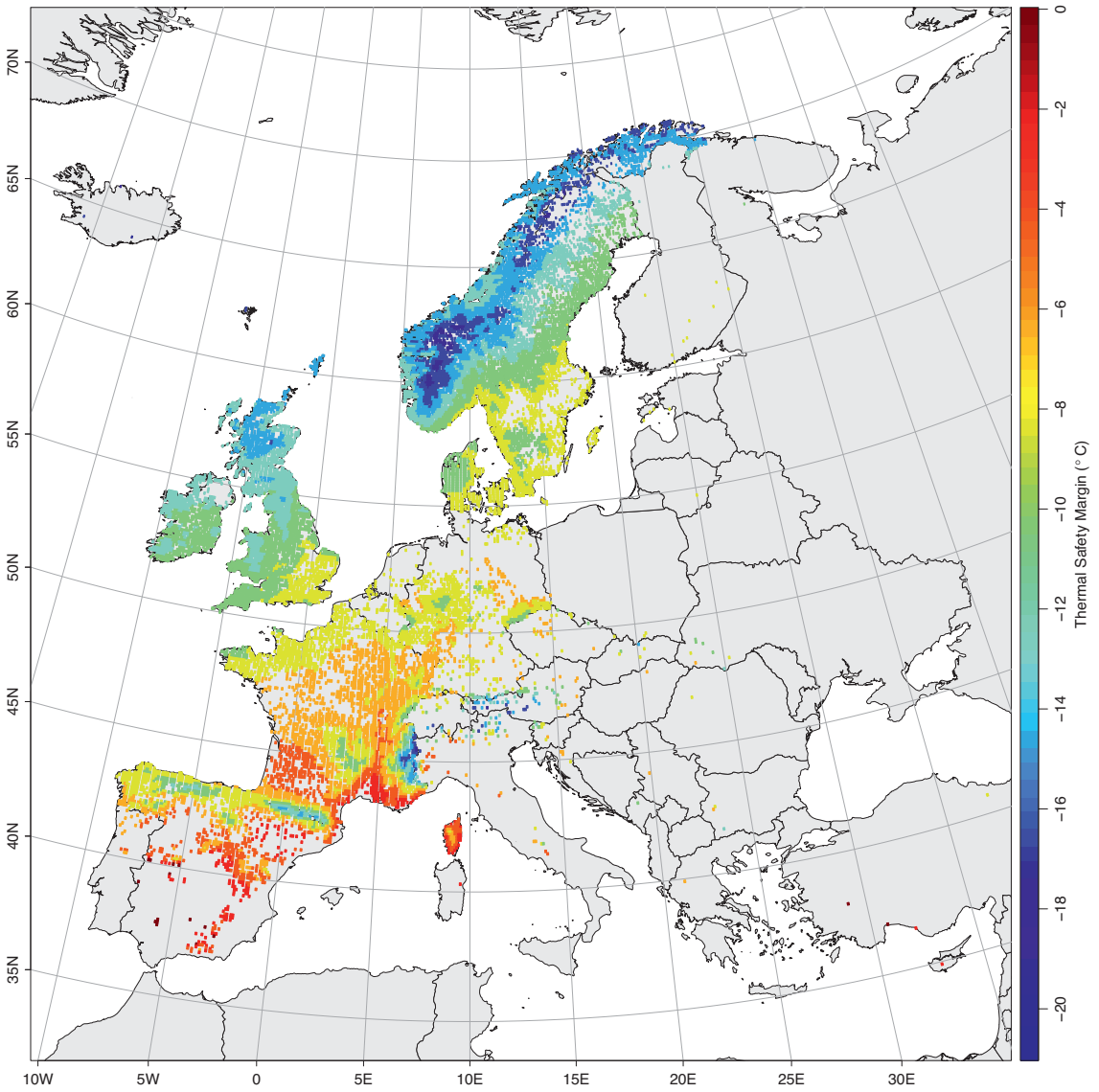

Fig. 3 Vulnerability to warming among Brown trout (*Salmo trutta*) populations across its native European range. Thermal safety margin represents the difference between mean July stream temperature for the 30-year climate period 1991–2020 and the critical thermal maximum of trout (estimated as 28 °C, Elliott and Elliott, 2010). Southern peripheral populations in low-elevation regions seemingly have minimal buffering capacity to tolerate continued warming (Unpublished data, Inland Fisheries Ireland). Species occurrences, which are incomplete, were obtained from www.gbif.org and matched with temperature data from the ERA5-Land reanalysis product (Muñoz-Sabater et al., 2021). Surface temperatures were converted to stream temperature in each 0.1° grid cell following (Punzet et al., 2012).

species, and between closely related species, seem to be a highly conserved trait compared with lower thermal limits (Bennett et al., 2021). A similar, comparatively understudied, set of evolutionary and environmental determinants are also likely to dictate how resilient specific fish species and sub-populations are to other climate-induced impacts, such as flow regime and dissolved oxygen concentrations, making climate-induced extinctions, range shifts and future distributions of freshwater fish especially difficult to predict.

Vulnerability and resilience of inland fisheries to climate change

Given profound effects on freshwater fish species and their habitats, climate change will likely have outcomes for inland fisheries on every continent, particularly those that are already heavily impacted by non-climatic pressures. Many inland fisheries throughout the world provide a range of important ecosystem services to human populations including food and livelihoods. In many such populations, inland fisheries provide the primary or secondary source of income and fish provides critical nutritional security (e.g. African Great Lakes, Lower Mekong Basin, Peruvian, Brazilian Amazon) (FAO, 2020). In 2018 it was estimated that the world's inland fisheries had an estimated value of $26 billion (USD), but the value could be as high as $35 billion (USD) (Funge-Smith, 2018; FAO, 2020). Their significance varies worldwide and is highest in Asia (66%) and Africa (25%). In contrast, the value of recreational fisheries worldwide is higher and has been estimated to be more than $64 billion (USD) (Funge-Smith, 2018).

Inland fisheries most at risk occur in areas that experience water stress and competition for water resources (Seggel and De Young, 2016). Several regions and countries that are highly dependent on inland fisheries including central and western Africa, north-western South America and tropical Asia have been identified as most vulnerable to potential climate change impacts (Allison et al., 2009). Fisheries that already experience severe threats from anthropogenic and natural environmental pressures from agriculture (e.g. irrigation), urbanization, industry and damming are likely to be most affected.

It is crucial to identify those at risk and to prioritize conservation measures and maximize resilience of threatened fisheries sectors. Through altered growth rates and inter-species competition, climate change could cause an increase or decrease in productivity and in biodiversity, which will affect harvests in a fishery or region (Harrod, 2015). Fishers may gain access to new fisheries or lose access to traditional ones, efficiency of fishing gear may change and become ineffective, and additional pressures from contaminants or parasites may mean that fish are unsuitable for sale. Fishers living in or close to poverty are likely to be particularly vulnerable because they may be unable to adapt to the changes caused by climate change. Additionally, extreme weather events such as storms and floods may damage gear, risk lives, and restrict fishery operations.

It is estimated that 20% of recreationally-targeted fish species (including diadromous fishes) are vulnerable to climate change, with a higher proportion of recreationally targeted freshwater species at risk from climate change compared with marine species (Nyboer et al., 2021). Furthermore, 72% of freshwater fishes and 33% of diadromous fishes have no conservation measures in place, despite their high vulnerability and cultural value. Clearly, a multi-faceted approach toward managing recreational inland fisheries in the context of climate change is required that links together climate impacts, vulnerable species and angling behavior toward targeted or prized recreational species.

Interaction between climate change and additional environmental stressors

The threat of climate change for freshwater fish is magnified given the array of pre-existing and emerging environmental stressors. Of particular concern is the potential for direct climate change effects to interact with additional anthropogenic stressors faced by species and populations (Staudt et al., 2013). This phenomenon is difficult to identify and predict for freshwater fisheries. As outlined so far in this chapter, multiple pathways exist for climate change to impact fish and their habitats, and inland waterways are generally rife with additional environmental stressors for fish including habitat modification and fragmentation, pollution and non-native species introductions. Much of the challenge associated with understanding these interactions relates to the dimensionality - a single climate impact may interact with one or many additional climatic or environmental stressors simultaneously. Multiple stressors may co-occur and have an additive effect, or they may act synergistically whereby the combined effects have a compounding impact. Future climate change may invoke increasing demands on water resources, or alter land-use practices that further intensify direct climate impacts on fish habitat (e.g. increased water abstractions during drought).

An integral aspect of assessing climatic vulnerability of specific fish populations is identifying concurrent stressors that decrease resiliency to climatic changes. Given the site-specific nature of non-climatic pressures and interaction with climate change, Fig. 4 conceptualizes some examples of a direct climate change effect on freshwater fish habitat with associated impacts and potential adaptations, while highlighting potential interaction pathways with additional anthropogenic factors that may exacerbate the situation for freshwater fish populations.

Adaptation and mitigation

Understanding the factors through which climate change can affect freshwater fish species and subpopulations, and the fisheries they support, will aid enormously with adaptation and mitigation strategies aimed at increasing the resiliency of climatically vulnerable fish populations. While the most ambitious mitigation strategy is to reduce greenhouse gas emissions sufficiently on a global scale, local strategies to decrease climate vulnerability of freshwater fish populations and inland fisheries can represent a pragmatic approach.

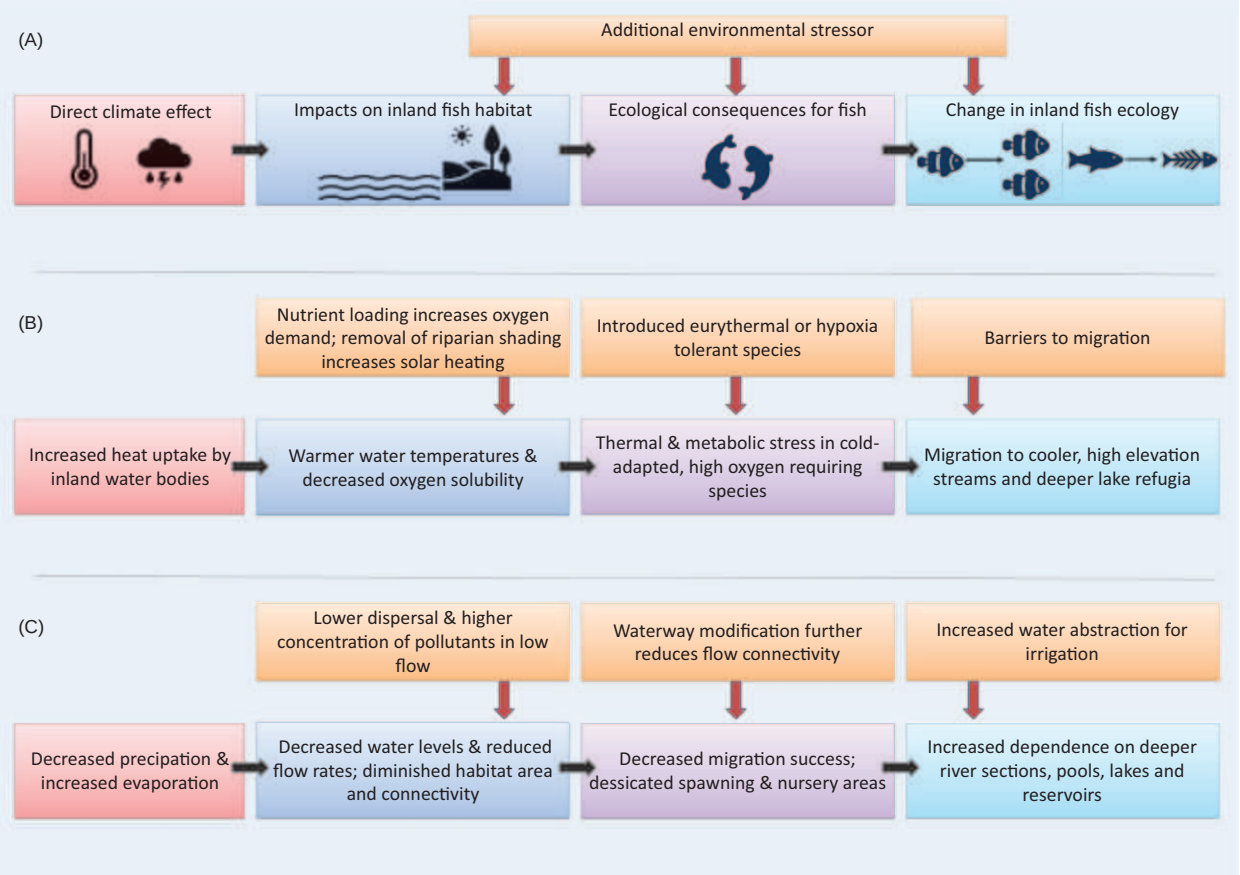

Fig. 4 (A) Conceptualization of the pathways through which a direct climate effect and additional anthropogenic or environmental stressors may impact freshwater fish. Additional stressors may have an interactive effect with a climate stressor by simultaneously impacting fish habitat, intensifying ecological consequences of climate-induced habitat changes or compromising the capacity of affected species to overcome the climate impact. A single climate change effect may also interact with other climate change effects and the interaction between a climate effect and an additional environmental stressor can work both ways (i.e. the climate change impact can intensify a pre-existing environmental stressor). Example of this simplified multi-pressure conceptualization for (B) water temperature increases and (C) decreased precipitation and increased evaporation rates associated with climate change.

Fish species and their habitats

Management and mitigation measures need to follow an ecosystem-based approach toward conserving overall biodiversity and should not focus solely on fish species of interest (capture fisheries). Potential approaches include:

- Mitigation strategies to decrease thermal vulnerability include: ensuring riparian cover is maintained or increased along sun-exposed shallow streams; improving both longitudinal and lateral river connectivity; restoring pools which act as a thermal refuge for fish species in modified channels; and tighter regulation surrounding introductions of non-native species adapted to warmer temperatures in sensitive regions.
- Mitigation strategies to protect against climate-induced flow alterations (droughts and floods) include minimizing extensive channel modification that directly intensifies flow-related stress and ensuring suitable flow regimes resilient to climate impacts are reconstructed in heavily modified rivers.
- To alleviate climate-induced deoxygenation it is imperative that good water quality is maintained, and poor water quality improved, in sensitive habitats and during warm spells with low water conditions.
- Identifying populations (e.g. peripheral; isolated), species (e.g. cold-water-adapted; migratory), regions (e.g. with severe warming projections) and local habitats (e.g. shallow lakes; low-lying unshaded streams) that are most vulnerable to warmer water temperatures could facilitate a focusing of fishery management practices.

Inland fisheries ecosystem services

Vulnerability of inland fisheries to climate change can be reduced through adaptive strategies that allow for management of unexpected results and to exploit any positive opportunities that may arise. It is important that governments worldwide understand the anticipated risks of climate change for inland fisheries and attempt to identify vulnerable systems through:

- Incorporating adaptive strategies for the inland fisheries sector into climate adaptation policies to ensure sustainability.
- Fish biologists, fishery managers and fishery scientists need to consider climate change in their activities, policies and future management. For example, a review of ethics of angling practices during warm periods or the closing of heavily impacted fisheries to conserve stocks may be required for many recreational fisheries.
- Measures could include diversification of livelihoods for the most vulnerable fisheries and fishers, management of stocks in response to projected climate change impacts and catch declines, advances in technology and planning for vulnerable areas.

Such mitigation strategies must be supported by evidence-based research to maximize their efficacy. There is a need for investment in science education strategies for fishers, fishery managers and the public encompassing climate-related impacts.

Conclusion and knowledge gaps

Given the multiple climate effects, interaction pathways with additional stressors and nuanced response of freshwater fish populations and inland fisheries to combined climatic and environmental changes, there are considerable requirements for further research to address critical questions. The future status of freshwater fish will largely depend upon how climatic, environmental, biological and socio-economic factors integrate. Some prospective avenues for further research include:

- Assessing the linkage between past climate dynamics and historical changes in freshwater fish abundance and distributions, which if understood will provide insight into how future fish populations will respond to specific climate projections.
- Disentangling the compounding effects of direct climate change and additional anthropogenic stressors such as introduced non-native species, water quality decline and habitat modification and fragmentation. There is a need to understand explicitly how multiple stressors interact and which specific combinations generate additive impacts or compounding impacts.
- Identifying proposed or conceivable alterations to land-use and water resource management related to climate adaptation strategies that could jeopardize freshwater fish populations.
- Understanding the resilience of different fish species and populations to changing climatic and hydrologic conditions. This would facilitate identification of the most acutely vulnerable populations.
- Informed by each of the prior suggestions, use of coupled climate-fish habitat models, that consider biological and ecological dynamics as well as inland fishery management practices where necessary. Applications could allow for robust predictions on the future status of freshwater fish abundance and distribution and allow adoption of guided management strategies.

This article has outlined some of the general pathways through which climate change can affect riverine and lake fish, and consequently global inland fisheries. Climate change consequences will be unique to individual species and their subpopulations and specific to their local environment. The immense ecological, economical and societal value of freshwater fish and inland fisheries demands that monitoring and research programs dedicated to sensing their vulnerability to climatic and environmental change are implemented and continued. By neglecting this component of freshwater fish conservation, we invite irreversible biodiversity loss and the continued decline of one the world's most imperiled vertebrate groups.

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Inland Fisheries Management - Case Studies of Inland Fish

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Algal bloom The rapid and excessive growth of microscopic, unicellular algae that produce toxins; often as a consequence of eutrophication (the excessive richness of nutrients in a body of water, often as a result of run-off).
Anerobic Without air.
Bioaccumulate To collect or become concentrated in the tissues of organisms.
Evidence-based limits Restrictions or maximum quantities of a given resource (e.g. fish) based on some scientific evidence or knowledge to verify the reasonableness of the limit.
Harvest regulations A series of instructions or restrictions associated with the amount of fish that can be removed; often linked to specific time periods and associated with permits or quota.
Licensing schemes A fishery system regulated by the use of a permit or license for a vessel, gear or fishing activity to allow its use. Often associated with a particular timeframe, season or location.
Precautionary principal In the absence of sufficient information to make an evidence-based informed decision the least consequential action should be followed to reduce harms (for example, to the environment or organisms) but the lack of information should not lead to inaction.
Psychosocial balance Maintaining an equilibrium between mental health and social interaction.
Quota-based management Management linked to setting limits of fish catch and allocating them among individuals or groups who are given or can purchase a portion of the total available catch.
Resource stewards Individuals who often voluntarily advocate for particular resources (e.g., fish), ensuring their sustainability.
Rights-based approaches Based on the principle that everyone has the right to participate in decisions, these approaches focus on trying to establish an equity among the holders of rights to the resource.
Sediment transport Movement of particles (including sand and silt) in the water flow that helps distribute nutrients through the aquatic ecosystem.
Smelt Small silvery food fish, usually consumed whole or with the head removed.
Sustainability/sustainable fishery The ability of a system or fishery to have a certain quantity of individuals withdrawn while retaining the capacity of the remaining individuals to reproduce and replenish stocks (fish numbers).

Introduction

The importance of inland fisheries for food security and livelihoods is often overlooked because of the higher profile of marine fisheries (Funge-Smith and Bennett, 2019). While the contribution of inland fisheries to global commercial fish production may be overshadowed by marine outputs, inland fish play an important role in sustaining local and small-scale operations, providing valuable recreational opportunities, and contributing to global biodiversity (Lynch et al., 2017). Importantly, inland fish support the food security and livelihoods of some of the most vulnerable communities (Cooke et al., 2016). Freshwaters form a network of connected ecosystems that weave their way among terrestrial landscapes from icy mountain streams, through vast turbulent rivers to seasonally flooded wetlands and brackish estuaries. Inland aquatic environments are also extremely diverse, ranging from tiny streams, brooks, ponds, reservoirs, and canals to large lakes, floodplains, wetlands, inland seas, and vast rivers. They even include the mosaic habitats found in estuaries and rice fields, with fish thriving in almost all of these environments (Moyle and Leidy, 1992). Their accessibility and connectivity, however, make them vulnerable to diverse threats from pollution to infrastructure development; the impacts of which can often be detected many miles downstream (Reid et al., 2019). Despite their importance for nature and humans, rapid development continues to threaten freshwater ecosystems and the fisheries resources that rely on them (Youn et al., 2014).

This chapter covers important but often overlooked aspects of inland aquatic ecosystems and highlights their major contributions to livelihoods and food security. It comprises five case studies:

Case Study 1: Inland Recreational Fisheries
Case Study 2: Rights in Inland Fisheries
Case Study 3: Threats to Inland Capture Fisheries: Hydropower, Mining, Agriculture, and Aquaculture
Case Study 4: Welfare Considerations of Aquaculture and Fisheries
Case Study 5: Freshwater Elasmobranchs.

Case study 1: Inland recreational fisheries

From flyfishing for rainbow trout in the headwater streams of the Pacific northwest, to ice fishing for smelt in lakes on the Korean Peninsula, to catching tigerfish in the Zambezi River of south-central Africa, inland recreational fisheries span the globe and represent diverse intersections between humans and freshwater ecosystems (Cooke et al., 2016; Funge-Smith and Bennett, 2019). Recreational fishing is defined by the Food and Agriculture Organization (FAO) of the United Nations (UN) as the "fishing of aquatic animals (mainly fish) that doesn't constitute the individual's primary resource to meet basic nutrition needs and are not generally sold or otherwise traded on export, domestic or black markets." (FAO, 2012). Recreational fishers mostly use rod and reel (i.e., angling), although other gear such as nets are also commonly used in some regions (Arlinghaus et al., 2007; Arlinghaus and Cooke, 2009). While recreational fishing can certainly be consumptive, catch and release is common, with release rates exceeding 95% for some species (Fayram, 2003). The reasons people engage in recreational fishing is as diverse as the fish targeted, and spans beyond the desire to catch and/or harvest fish (Fedler and Ditton, 1994). Many people derive satisfaction from spending time in nature, and/or fishing with friends and family, and therefore benefit from increases in wellbeing because of recreational fishing (Hunt and McManus, 2016; Wheeler et al., 2020).

Recreational inland fisheries are most common in developed countries where there is disposable income, which can be devoted to leisure and fishing for fun (Arlinghaus et al., 2021). Yet, there is also evidence that at some point during the development cycle, interest in recreational fishing declines as recreational fishing is supplanted by conservation values (Arlinghaus et al., 2021). It is estimated that, on average, around 10% of the human population engages in recreational fishing, although participation rates are highly variable around the world (Arlinghaus et al., 2015). Inland recreational fisheries generate a variety of benefits, including economic returns from fees for example, in the tens of billions of USD (Lynch et al., 2016), psychosocial balance (Hunt and McManus, 2016; Wheeler et al., 2020), and nutritional security (Cooke et al., 2018). In most developed countries, recreational fishing is intensively managed through harvest regulations and licensing schemes (Arlinghaus and Cooke, 2009). By contrast, recreational fisheries in developing countries frequently have no active monitoring or management and are often ignored and undervalued (Bower et al., 2020). Recreational anglers can be important resource stewards. Not only do many anglers offset their environmental impacts through conservation-minded actions on the water, but many also actively engage in directly managing, and protecting water resources and aquatic environments, or they contribute their voice to advocacy for aquatic species or habitats at risk (Granek et al., 2008).

While recreational fisheries are of socio-economic importance and can foster conservation-minded actions directed at aquatic ecosystems, recreational fishing can also have negative impacts on the sustainability of resources and the environment. Recreational fishing has been implicated in the collapse of some inland fish populations in Canada (Post et al., 2002) for several reasons. For one, overfishing can occur if systems are not adequately monitored. Even when release rates are high, fishing mortality can occur in the form of release mortality (Bartholomew and Bohnsack, 2005). Secondly, many non-native fish have been introduced by recreational fishers or managers to enhance fishing opportunities with negative consequences for native biodiversity (Gozlan et al., 2010; Mickle and Higgs, 2018). In addition, recreational fisheries can lead to other undesirable consequences, such as disturbances from boat noise (Whitfield and Becker, 2014), trampling of habitats while wading (O'Toole et al., 2009), and the entanglement or hooking of non-target species (e.g. birds and turtles; Lloret et al., 2020). Fortunately, most of these issues can be addressed through regulation and encouragement of responsible fishing behavior (Cooke et al., 2019). Moving forward, there is much potential for recreational fisheries to be conducted in a responsible and sustainable manner that connects people to freshwater ecosystems. Climate change will require the sector to adapt, as fish, freshwater ecosystems, and anglers experience additional external pressures (Holder et al., 2020). Nonetheless, there is evidence that inland recreational fisheries can be resilient or adapt if managers and fishers are proactive (Jeanson et al., 2021). For example, simple changes in angler behavior (e.g., following best practices for handling and releasing fish) will reduce the negative impacts of climate change on fishing mortality. Recreational fisheries create opportunities for interactions with freshwater organisms, increasing awareness of the value of freshwater ecosystems, enhancing respect for the environment and encouraging people to be more active advocates for, and stewards of, freshwater ecosystems.

Case study 2: Rights in inland fisheries

Recognizing the need to secure equality in access and withdrawal rights for fishers has lagged well behind securing rights and tenure on land (Ruddle et al., 1992). Capture fisheries have historically been an open-access resource throughout the world (Arthur, 2020). The ease of access and challenges for control and regulation have meant, that in large areas of the globe, open-access rights to fishing have prevailed, despite recognition of their issues. This has resulted in several problems, including fishing industry over-capacity, challenges in monitoring and control of exploitation, negative environmental impacts, inequities in access to resources, and insecure tenure rights. In some regions, licenses for commercial operations have been granted to improve control over the fishery and harvest, but has generally exacerbated over-fishing, inequality, conflict, and food insecurity (Arthur, 2020).

Determining how to define access rights that are equitable is not an easy challenge to resolve. Further, the ecological implications of establishing property rights have historically not always been positive (Brubaker, 1997). Increasingly, rights-based approaches have been explored to reduce food insecurity and reduce stakeholder conflicts.

Some guidelines to help improve equity in fishery rights have been outlined by the FAO (e.g. Small-Scale Fisheries Guidelines (FAO, 2015) or the Rome declaration (FAO and MSU, 2016)), but challenges remain for the best ways to implement them in diverse global fisheries, which are already showing signs of over-exploitation. Adopting rights-based approaches has been suggested by FAO and others, to be an equitable solution for meeting combined objectives for conservation, food security and livelihoods (FAO, 2015; Allison et al., 2012; Willmann et al., 2017a,b). Rights-based approaches have been adopted in many countries in an effort to

increase equity, however, enforcement and implementation are often lacking, limiting the opportunities for the benefits of rights-based approaches to be realized (Willmann et al., 2017a,b).

The conditions for access and removal of fish need to be clearly defined, evidence-based limits need to be set, and fishers need to agree and commit to access agreements. While rights-based approaches can help to allocate resources more fairly, the existence of multiple fishing rights holders in a single waterbody (in contrast to ownership by the State) and high mobility of fish resources, complicate the situation. Such circumstances disincentivize investment in management of resources because investment by one rights-holder is just as likely to support the harvest of another rights-holder. The use of quota-based management and resource sharing can help to distribute access and withdrawal rights equitably (Bellanger et al., 2019; Bradley et al., 2019). For example, the Japanese catch-share system has a long history of equitable catch-sharing success (McIlwain, 2013). However, careful management of quotas and restriction of quota transfers, are needed to prevent aggregation of quotas by large industry resulting in the exclusion of smaller operators (Delaney, 2015).

By ensuring access and rights to withdraw, manage and protect fisheries, people in communities reliant on fisheries can retain greater ownership and responsibility for the fishery. As a result, they can implement approaches that help them to respond to sustainability needs, increasing fishing pressure, development, and climate change. Co-operative management and regimes that build trust among collectives have the potential to improve equity in fishery rights. However, caution must be taken to avoid pitfalls experienced when cooperatives become too big and commercial operations start to dominate, reducing equity for smaller operators.

Case study 3: Threats to capture fisheries

Many of the exploited populations of inland fisheries can be found in floodplains and seasonal waterbodies. The geographic conditions associated with inland capture fisheries, subject them to a variety of threats, including hydropower development and agriculture, mining and aquaculture. The inherent restrictions of freshwater ecosystems, i.e., being constrained by land, being widely distributed, having a relatively small volume of water that is subject to climatic conditions (e.g., flood and drought), and being forced to follow a path through human-dominated landscapes, make inland aquatic organisms extremely vulnerable to habitat changes (Compagno and Cook, 1995). Inland capture fisheries provide important contributions to food and nutrition security, especially in developing regions, where there are often few livelihood alternatives. The following examples describe a cross-section of industrial developments that are increasingly threatening the viability of inland capture fisheries and the communities that rely upon them for nutrition and food security, and commercial and livelihood opportunities.

Example 1: Hydropower development

The impact of hydropower development on fish has garnered a lot of recent attention, especially regarding large and highly migratory species found in the Amazon, Columbia, Congo, Nile, and Mekong rivers (Winemiller et al., 2016; Jager et al., 2001). Hydropower dams block fish movement, change hydrology and water flows, disrupt seasonal patterns on which fish rely for behavioral cues, and block the movement of sediments, thus preventing the distribution of nutrients (Clarke et al., 2008). These impacts are being felt to a greater or lesser degree in watersheds the world over (Wu et al., 2019). In developed regions, many dams are being removed and waterways are being opened up (Ding et al., 2019), with both positive and negative impacts on the ecosystem and fish (Bednarek, 2001). In developing nations, sustainable development makes hydropower (a renewable energy source) a very attractive option (Fearnside, 2014). Recent attention to the problem of dams for fish has seen the development of tools and approaches to help mitigate impacts, including moving dams into less vulnerable locations (Opperman et al., 2019), managing flows for fish (Sabo et al., 2017), helping fish circumnavigate dams through alternative tributaries (Schmitt et al., 2019), or developing fish passages (Schilt, 2007).

Example 2: Mining and mercury

Mercury contamination is one of the main reasons that caution is advised for consumption of large quantities of fish. Mercury 'bioaccumulates' in the tissues of fish (Johnsson et al., 2005), and when the fish are eaten can rapidly lead to mercury poisoning (Ha et al., 2017). The mining industry, especially artisanal miners, use mercury in the extraction process, leading to the leaching of mercury into the environment (Veiga et al., 2006). Mercury is also a bi-product of coal-fired power generation (Kuiken and Stadler, 2003). Aside from the human health impacts, mercury poisoning also leads to neurological conditions (Morcillo et al., 2017) and reproductive problems in fish (Scheuhammer et al., 2015; Crump and Trudeau, 2009). Increased awareness of the impacts and research investigations have led to the use of mercury alternatives in industry, improved waste treatment, the development of guidelines and regulation for reducing leeching into the environment, and recommendations for consumers to reduce their intake of some high-risk species (EPA-FDA, 2021). Mercury in fish tissues and waterways is still problematic (Kolipinski et al., 2020; Evers and Sunderland, 2019; Wang et al., 2004) and further investigations are required to determine effective ways to reduce or remove mercury from fish tissues and waterbodies (Jezierska and Witeska, 2006; Cuvin-Aralar and Furness, 1991).

Example 3: Agriculture

The impacts of agriculture on fisheries are often considered to be quite localized but agriculture can have extreme and far-reaching consequences (Blann et al., 2009). The modified landscape leads to changes in drainage and hydrologic dynamics, transforming the structure and function of stream and wetland ecosystems and impeding connectivity, limiting access to key habitats, disrupting nutrient cycling, and interfering with sediment transport (Carpenter et al., 2011). The consequent changes to nutrient transport, and quantity and configuration of waterflows, can both directly and indirectly affect fish and their behavior (Bunn and Arthington, 2002).

The impacts of agricultural development in flood plains and wetlands can also reach far beyond the floodplains and inland waters. Pesticides and fertilizers, used to enhance crops both in the floodplain and in the watershed beyond, are often directly toxic for fish (Klemick and Lichtenberg, 2008). Chemicals, such as phosphorus found in runoff from agriculture, can also indirectly impact fish by transforming the nutrient and trophic dynamics of the aquatic ecosystem. The increased availability of phosphorus can lead to over-production of aquatic microorganisms, such as cyanobacterial algae. The increased production of algae (or algal bloom) reduces the availability of oxygen in the water below concentrations tolerated by fish. Some cyanobacteria algae also release toxins into the water that have a poisonous effect on fish. Sudden low oxygen levels combined with high levels of toxins in the water can result in mass fish die-offs (Paerl et al., 2001).

Transformations in the floodplain and conversion of wetlands from flooded forest and submerged vegetation can remove important habitats. Wetlands are frequently drained, so that land can be 'reclaimed' for property or agricultural development, with barriers erected to prevent flooding. Conversely, barriers might be erected to retain water for rice crops or water might be diverted to irrigate other crops, consequently reducing natural flows, preventing fish passage, and limiting access to important habitats.

Recently, positive interactions between farming and fisheries have increased. In the floodplains of South-east and South Asia, complementary management of rice-field fisheries has led to mutual benefits for the farmers and fishers (Freed et al., 2020). In lieu of pesticides and fertilizers, farmers help retain access passages for fish to breed and feed in their rice-fields. The fish then contribute important fertilizing nutrients in their feces and feed on agricultural pests. The fish grow and develop in the rice-fields and are then harvested as the waters recede (Ahmed and Garnett, 2011). Such examples can serve as a positive model for finding complementary management solutions in a variety of inland aquatic ecosystems.

Example 4: Aquaculture

Negative environmental impacts of aquaculture are well-documented (Fernandes et al., 2001), but most of them occur in marine environments where the majority of aquaculture occurs. Recent development of inland aquaculture in both developed (Gooley et al., 2000) and developing regions (Musinguzi et al., 2019), has given rise to many of these same impacts in inland waters (Telfer et al., 2009; Beveridge and Phillips, 1993). Typically, aquaculture uses substances that can become pollutants, for example phosphorus and nitrogen, which are used in feeds and chemical maintenance of aquaculture ponds. These chemicals when released into the environment can result in algal blooms by over-stimulating algal growth. As well as depleting the oxygen concentrations below the tolerance of fish, some algae (e.g. cyanobacteria) also release toxins into the water, which can be toxic to fish (Brooks et al., 2016; Herath and Satoh, 2015). Other impacts include the release of non-native species, e.g., Tilapia, that outcompete natives for resources; and selective breeding that can contaminate the natural gene pool (Ansah et al., 2014; Canonico et al., 2005).

As well as the above more obvious environmental concerns, increasing harvest of small fish from inland waters to feed the growing marine aquaculture industry (Edwards et al., 2004) is putting additional pressure on the inland capture fishery (Nunoo et al., 2009). Although there are now more feed options available, the aquaculture industry still relies heavily on small "feed fish" from capture fisheries to supply farmed fish with vital nutrient inputs (Tacon and Metian, 2008). Both whole fish and fish processed into fishmeal, that are fed to the farmed fish rely on low value "trash fish," harvested from the wild (Goldburg and Naylor, 2005). In developing countries, in particular, where small fish species are often an essential source of protein and nutrients (Allan, 2004), the rerouting of these fish from human consumption to feeding the farmed fish, has a negative impact on food and nutrition security (Belton and Thilsted, 2014; Tacon and Metian, 2009). Small individuals of larger species are also harvested and sold to the aquaculture industry as 'trash-fish,' often removing the young-of-the-year and constraining production of commercially important species (Huntington and Hasan, 2009).

Case study 4: Welfare considerations of aquaculture and fisheries

The methods used in fisheries that result in the death of fish are some of the harshest and often thoughtless of all methods used in animal production. Although sentience of fish is still debated (e.g., Kristopher et al., 2004; Rose et al., 2014) the awareness and consciousness of some fish including elasmobranchs, that lack nociceptors (or pain receptors) is increasingly being documented (Brown, 2015). The difference in the way that fish apparently experience pain has led to the generally dispassionate way that harvest of fish in fisheries is handled, and a lack of consideration of the need to use more humane methods (Fernö et al., 2020). Irrespective of the reality, the precautionary principal dictates that we should give the benefit of the doubt to fish and assume that they are suffering when death is prolonged or dramatic, or when experimental procedures require invasive procedures (JWD, 2016; Cooke et al., 2013a,b; Browman et al., 2019).

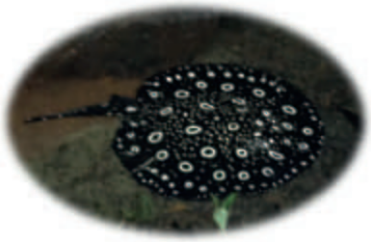
In experimental work, increasingly more humane methods are being adopted, such as the use of clove oils and other temporary sedatives for the capture, killing or tagging of experimental animals (Cooke et al., 2013a,b). In captive and aquarium contexts, the care and welfare needs of fish are increasingly being considered. But fisheries lag behind. Aquaculture ponds are essentially large industrial aquaria where the objective is to harvest and sell the fish for food rather than for display. However, the conditions in which they are kept in fish farms, and the process by which they are killed, presents a stark contrast to aquarium conditions. Of greatest welfare concern is the prevalence of diseases and over-crowding that result in negative welfare conditions (Barreto et al., 2021). Even more extreme, the conditions experienced by fish in the mass hauls of global capture fisheries, during which fish experience prolonged death by suffocation, crushing, decompression, asphyxiation, or exsanguination (bleeding to death), make the sometimes-unpleasant conditions and harvest practices used in aquaculture seem benign (Breen et al., 2020). While the capture techniques of recreational fisheries, are often considered more humane, they can also present welfare concerns for fish. Recently increased attention and an increased understanding of fish experiences have led researchers and anglers to consider the welfare and physiological experiences of fish more carefully (Cooke et al., 2013a,b). It is also worth noting that, improvement in the management of wild populations, where behavioral and physiological indicators suggest that welfare can vary depending on environmental and ecological factors, such as turbidity and predation risk, could also be beneficial (Freeling and Connell, 2021).

As recently noted by Lugert et al. (2020) "Lack of knowledge does not justify a lack of action." Irrespective of whether fish are sentient and feel pain or not, we have a responsibility to consider their welfare. The regulations and concern for inland aquatic organisms lag well behind that of terrestrial animals, despite the much greater harvest of individuals and use across industries. Increasing awareness and a sense of connection to wildlife, felt by recreational anglers, has led to welfare improvements in the capture techniques being used in recreational fisheries. Recognition of the benefits to the product quality and individual survival, of addressing welfare for fish sold as ornamentals, has led to improvements in conditions in the aquarium trade, such as preventing over-crowding, providing enrichments, and keeping the water clean (Stevens, 2019). Aquaculture and capture fisheries could benefit from more humane capture techniques and better holding conditions (e.g. water quality and enrichments), increasingly being used due to recognition of fish welfare in recreational fisheries and the aquarium trade, respectively. Recreational anglers may in fact, be particularly inclined to advocate for improved welfare consideration of inland fish (Cooke et al., 2013a,b), and may lead the way in drawing greater attention to the need for improved methods used for the harvest of fish by fisheries.

Case study 5: Freshwater elasmobranchs

Freshwater elasmobranchs are often overlooked when considering inland aquatic biodiversity, likely because the vast majority of cartilaginous fish species are associated with coastal and high seas marine environments. They are, however, particularly vulnerable and will need careful management to protect key habitats that support their life-cycles in order to persist. Freshwater elasmobranchs or stenohaline species (those that have a low tolerance for changes in salinity), have successfully adapted to freshwater environments and have developed the ability to complete their life cycles in streams, rivers, and lakes without depending on marine waters.

There are also species of freshwater elasmobranchs found in rivers, lakes and estuaries that conduct only part of their life cycle in fresh or brackish waters (euryhaline). These species can tolerate low salinity levels (<32 psu) during brief incursions, up to several months, in freshwater or during specific life development stages (mainly pupping and juvenile development). It is estimated that at least 171 species (15%) of elasmobranchs inhabit areas with reduced salinity (Martin, 2005).



The stenohaline elasmobranch species belong mainly to a group of stingrays (Potamotrygoninae). This chondrichthyan lineage, mainly of sharks and rays, successfully colonized South American freshwater environments. The subfamily Potamotrygoninae, or Neotropical Freshwater Stingrays, comprises 39 described species (Last et al., 2016; Roberts, 2020; Loboda et al., 2021), distributed in the main water basins and sub-basins of South America. Most potamotrygonin species are endemic to a single basin, sometimes even to a single river, which contrasts to bony-fish species, that are widely distributed in multiple watersheds (Lasso et al., 2016). Known as 'river jewels,' some species have attractive and striking dorsal color patterns that make them a target for the ornamental trade. This trade threatens the conservation and sustainability of the group (Araújo et al., 2004).

Stenohaline chondrichthyan ray species are also found in other freshwater ecosystems around the world. Two species, Smooth Stingray (*Fontitrygon gaurouensis*) and Thorny Stingray (*F. ukpam*) are present in West Africa. Another six species, Roughback Whipray (*Fluvitrygon kittipongi*), Marbled Whipray (*F. oxyrhynchus*), White-edge Whipray (*F. signifer*), Mekong Stingray (*Hemitrygon laosensis*), Chindwin Cowtail Ray (*Makararaja chindwinensis*), and the Giant Freshwater Whipray (*Urogymnus polylepis*) are found in various water bodies of Southeast Asia. While most of the stenohaline chondrichthyan species are rays, there are also sharks from the genus *Glyphis* that exclusively inhabit freshwater habitats in Australia, Papua New Guinea, India and Myanmar.

Several other ray species including, *Hypanus* spp., *Fontitrygon colarensis, F. geijskesi, and Styracura* spp., are euryhaline and depend on inland waters to complete their life cycle, using estuarine habitats as a nursery and for pupping. Several euryhaline shark species can also be found in estuaries and inland waters around the world, while many other sharks are classified as marginal species, tolerating the lower salinities found in estuaries but not venturing into true freshwater environments (Martin, 2005). Six species of sawfish from the Pristidae family, five in the genus *Pristis* and one in the genus *Anoxypristis*, and three species of requiem shark, two from the genus *Glyphis* and one Carcharhinus are also euryhaline. Among them the iconic Bull Shark (*Carcharhinus leucas*) has been recorded worldwide making extensive migrations hundreds of kilometers inland through rivers in Africa, Asia, Australia, and the Americas (Gaussman, 2018), including an infamous migration 80 km up the Mississippi River (Shell and Gardner, 2021) and even more extraordinary, sightings 4000 km up the Amazon River (Thorson, 1972). This is, however, not the rule for most species that generally occupy more restricted habitats.

The freshwater elasmobranchs face several threats from fisheries, including uncontrolled harvest for consumption, and for the aquarium trade, particularly of several species of South American freshwater stingray in the family Potamotrygonidae. They are also threatened by bycatch, especially by the use of trawling operations (Araújo et al., 2004). Some countries are now applying species quotas, but most of the harvest and the market is unregulated. Recreational fishing is a particular concern for the large-bodied species found in South America (*Potamotrygon brachyura*) and Southeast Asia (*Urogymnus polylepis*), where they are targeted for their prestige and often mishandled (Vidthayanon et al., 2016). Due to accidents, mainly with stingrays, elasmobranchs have a reputation for being dangerous. As a result, mainly to avoid conflicts in tourist areas (Rosa et al., 2010), "negative fishing" has developed, which targets elasmobranch species with the aim of eliminating them in some areas (Araújo et al., 2004).

Freshwater elasmobranchs are subject to a number of threats, with the constraints of freshwater ecosystems making them even more vulnerable to environmental changes (Compagno and Cook, 1995). For example, the life cycles of inland elasmobranchs are closely tied to cycles of droughts and floods (Charvet-Almeida et al., 2005). Across the globe climate change is altering the hydrology of inland aquatic ecosystems, disrupting these seasonal dynamics and interfering with fish lifecycles. They are also threatened by pollution from a number of sources, including mining, sewage discharge, agricultural or industrial runoff (Carpenter et al., 2011), as well as by damming and silting. Damming of the upper Paraná River (Brazil), for example, has altered the distribution of freshwater stingray species in the Paraná Basin providing favorable conditions for some species in the genus Potamotrygon to become invasive (Garrone-Neto et al., 2014). These impacts are heightened by rising human populations and their predilection to concentrate along freshwater bodies (Martin, 2005). Most of the freshwater elasmobranch species are concentrated in tropical regions, which face strong human population growth and habitat degradation (Bradshaw et al., 2009).

The management and protection of important nursery and pupping habitats is important to ensure their persistence, particularly of elasmobranch species that are dependent on these environments.

Developing management strategies for freshwater elasmobranchs is essential but challenging. Like many other elasmobranchs, freshwater elasmobranchs are typical K-strategists with low fertility, late maturity, and long lifespans, making them more susceptible to exploitation (Charvet-Almeida et al., 2005). The restrictions created by their life history characteristics, combined with the constraints of freshwater environments, make them particularly vulnerable species, for which careful management is required. Currently, there are very few conservation measures in place to protect them. There is an optional recommendation for Potamotrygoninae species to be listed on the CITES Appendix III, which is a list of species recognizing them as being of some conservation concern (CITES, n.d.). However, most agreements are at the national level (e.g., ornamental trade export quotas), and the risk of

extinction for most species has not yet been evaluated. A lack of basic biological knowledge for most freshwater elasmobranchs has been an obstacle for developing effective assessments and management strategies (Martin, 2005). Thus, filling knowledge gaps and ensuring that socio-economic considerations are included, will be essential for developing adequate strategies. To preserve elasmobranch species in their natural environments, careful and coordinated management will be needed both globally in the form of legislation controlling trade, and locally to ensure that interventions address their specific context.

Future research needs

While much is understood about the needs for sustainable fish harvest (Hilborn, 2011), critical knowledge gaps remain, impeding sustainable fisheries management by limiting the potential for setting effective regulations (Funge-Smith and Bennett, 2019). Both an improved understanding of inland aquatic ecosystems, and greater knowledge of the ecology of particular fish species, are needed to identify management strategies that will lead to sustainable harvests, and that can address the various challenges outlined in this chapter (Cooke et al., 2021). Inland fish life-histories are closely tied to environmental conditions (Bergerot et al., 2015; Mims and Olden, 2013) and as such, are especially vulnerable to climate changes (Myers et al., 2017). Expanding the knowledge base, through research and monitoring that targets these critical knowledge gaps (Loury et al., 2021), can help equip managers and fishers with the necessary tools to improve management and respond to climate change (Myers et al., 2017). Understanding fish welfare and how we can improve their quality of life, also requires greater emphasis on research. Through targeted welfare studies of fish behavior and physiology, it is possible to increase awareness and understanding of fish sentience, capacity for pain and critical thinking. By gaining a better understanding of the impacts of threats to inland fisheries, outlined in this chapter, fisheries managers can improve management approaches and adapt to changing conditions. Particular research priorities for the future include understanding climate change impacts on hydrology, filling critical knowledge gaps in fish ecology, improving our understanding of fish welfare and cognition, and investigating the links between fishing practices and resource sustainability.

Conclusions

Inland aquatic ecosystems are diverse and widespread. They provide key habitats to a high diversity of aquatic organisms and sustain the livelihoods of many human communities around the globe (Funge-Smith and Bennett, 2019). Their integration into the landscape makes them vital for ecosystem function and at the same time extremely vulnerable to increasing threats from development and agriculture (Reid et al., 2019). The fisheries that they sustain are at the same time biodiverse and important for supporting food security, livelihoods and recreation (Funge-Smith and Bennett, 2019). Some freshwater fish species are highly attractive and sought after, making them very important to the aquarium trade (Stevens, 2019). The effective management of fisheries is increasingly important as human populations continue to increase and demands on the fisheries and the ecosystems they rely on grow more numerous and diverse (Youn et al., 2014). Consideration of the welfare of individual fish in a growing industry, and recognition of the benefits that ensure care is taken when handling them, is a recent development in fisheries (Breen et al., 2020), one that builds on centuries of awareness that the well-being of animals is of moral and practical concern.

A diverse set of case studies has been presented, describing a range of themes within freshwater fisheries. While representing various perspectives, they are all areas that have been overlooked to some degree. A common theme identified in the case studies is the need for effective management, which, in many cases, requires addressing critical knowledge gaps. Together the case studies highlight that changes to the way we consider fish, and approach and manage fisheries are needed to ensure that recreational fisheries, rights of fishers, and elasmobranch species can be sustained in the face of diverse threats.

See Also: Human pressures and management of Inland Waters: Inland Fisheries Management - Exploitation and Livelihoods; Evolving Perspectives on Hydropower: Balancing Societal Benefits and Environmental Impacts; Hydropower in the Danube River Basin: Current Status and Emerging Challenges; Hydropeaking: Processes, Effects, and Mitigation

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Biological Invasions: Introduction, Establishment and Spread

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Alien species See "non-native species."

Colonization pressure The number of species introduced to a given location (Lockwood et al., 2009). Colonization pressure should be discriminated from "propagule pressure" (see below).

Impact A change or effect of a non-native species on either the environment (i.e., biodiversity) or socio-economics in the broad sense (i.e., including culture, religion, human health, safety, livelihoods and other aspects of human well-being), whether positive or negative (Jeschke et al., 2014).

Introduction pathways The processes and mechanisms behind the human-mediated introduction of non-native species from one geographic location to another (Hulme et al., 2008). These introductions can be either intended by humans or unintentional.

Invasion process See "invasive species."

Invasive species Species that have successfully completed the invasion process, i.e., they have: (i) been intentionally or unintentionally transported by human action from their native range to a new range; (ii) been released there or escaped into the wild; (iii) have established one or more self-sustaining populations; and (iv) have spread substantially beyond their point(s) of release or escape (Blackburn et al., 2011; Jeschke et al., 2013, see also Fig. 1). The stages i and ii of the process are jointly called "introduction," and an alternative name for the invasion process is the "introduction-naturalization-invasion continuum" (Richardson and Pyšek, 2012). Synonyms of invasive species are "invasive alien species" or "invasive non-native species."

Naturalized species Species that have reached the third stage of the invasion process, i.e., they have: (i) been intentionally or unintentionally transported by human action from their native range to a new range; (ii) been released there or escaped into the wild; and (iii) have established one or more self-sustaining populations (Blackburn et al., 2011, see also Fig. 1).

Non-native species Species that have been intentionally or unintentionally transported by human action from their native range to a new range (Blackburn et al., 2011). Non-native species are also called "alien species," "exotic species" or "non-indigenous species." Therefore, non-native species are not necessarily invasive, but invasive species as defined above are always non-native.

Phenotypic plasticity The ability of a genotype to have variable phenotypes in different environments. Phenotypic plasticity is widespread, but the degree of plasticity varies among species and genotypes (DeWitt and Scheiner, 2004; Engel et al., 2011; Jeschke and Heger, 2018).

Propagule pressure A composite measure of introduction effort consisting of: (i) the frequency of introduction events (propagule frequency or number); (ii) the number of individuals or propagules introduced per introduction event (propagule size); and (iii) the type of individuals (life stage, genotype, phenotype) introduced per introduction even (propagule composition) (Lockwood et al., 2005; Simberloff, 2009; Ricciardi et al., 2013; Jeschke and Heger, 2018). Propagule pressure should be discriminated from "colonization pressure" (see above). While propagule pressure refers to the number of introduced individuals or propagules of the same species, colonization pressure considers the number of introduced species.

Species distribution models (SDMs) Empirical models that are developed on the basis of niche theory by fitting the relationship between observed species distributions and environmental variables with a wide range of statistical algorithms and machine-learning methods to understand the drivers of biodiversity patterns and forecast species distributions across space and time (Guisan and Thuiller, 2005), e.g., in the context of climate change.

Introduction to the topic

Biological invasions have been a research topic for a long time, and even the probably most famous biologist of all times, Charles Darwin, thought and wrote about them back in the 19th century (Darwin, 1859; Ludsin and Wolfe, 2001; Cadotte, 2006). However, neither Darwin nor other influential researchers before the 20th century *focused* their investigations on biological invasions. After World War II, Charles Elton published *The ecology of invasions by animals and plants* (Elton, 1958), which laid the foundation for the discipline of invasion biology. Yet it took until the 1990s that this discipline really started to rise. Research on biological invasions has intensified rapidly since then, indicated by the strong increase in the number of relevant publications (Richardson and Pyšek, 2008; Enders et al., 2019). The number and impacts of non-native species translocated across the globe have seen a similar rise (Seebens et al., 2017, Pyšek et al., 2020).

Biological invasions are thus an important component of how ecological communities form and are being formed in the Anthropocene (Crutzen, 2002; Waters et al., 2016). While investigating invasions, we learn a lot about biotic interactions, community and evolutionary dynamics, dispersal and species distributions (Sax et al., 2005). In addition, it is a highly interdisciplinary research topic related to socio-ecological systems, the values of nature and its contributions to people. Therefore, biological invasions not only unify efforts from various ecological and related disciplines, but also from other natural sciences, economics and social sciences.

An important concept in this research field is the invasion process which consists of the consecutive stages that invasive species go through: transport, release/escape, establishment and spread (Fig. 1, Glossary, Blackburn et al., 2011; Jeschke et al., 2013). This definition also specifies what invasion biologists mean when talking or writing about "non-native", "alien" or "invasive" species: the latter are only those species that reached the final stage of the process, while "non-native" (or "alien"; these are synonyms) species are all those that completed at least the first stage (Fig. 1, Glossary and Blackburn et al., 2011). In other words, invasive species are a subgroup of non-native species.

The invasion process also guides the structure of the current chapter which consists of two main sections. The first main section focuses on the stages transport and release/escape, which are frequently summarized as "introduction". This section outlines (1a) historical dynamics of species introductions and (1b) how pathways of species introductions can be categorized and analyzed. The second main section focuses on the establishment and spread of non-native species, featuring (2a) major hypotheses about non-native species, which largely focus on their establishment and spread; and (2b) species distribution models, which are an

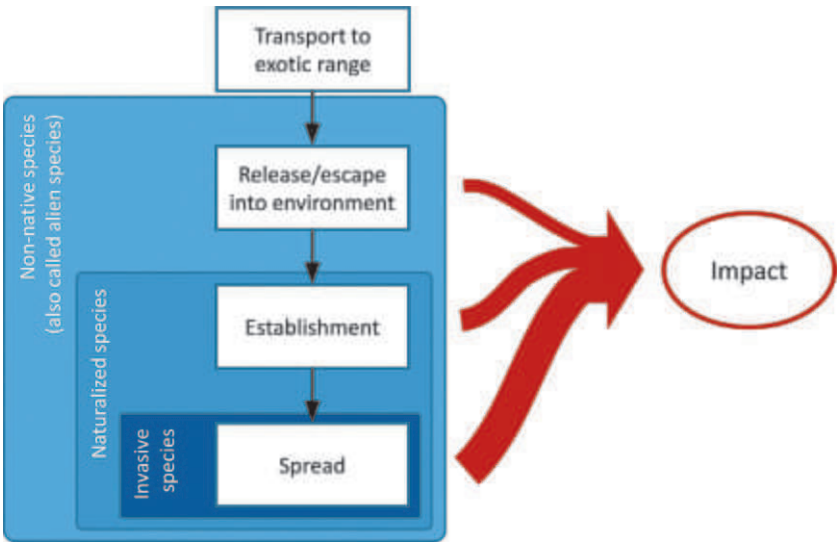

Fig. 1 The invasion process consists of four consecutive stages (indicated by rectangular boxes; see Blackburn et al., 2011 and Jeschke et al., 2013). Only those non-native species that reached the final stage (spread) are termed "invasive species." The first two stages of the process are sometimes summarized as "introduction." "Impact" itself is not considered a stage of the invasion process, as non-native species can have impacts at any stage. Impact magnitude typically increases as non-native species progress through the invasion process (indicated by increasingly thicker red arrows).

important and widely used tool to predict where non-native species are able to establish themselves and spread. The present chapter is complemented by two other chapters on biological invasions in this encyclopedia, which outline the impact and management of non-native species and feature case studies, respectively.

Introductions of non-native species

Historical dynamics of species introductions

The introduction (i.e., transport and escape/release, cf. Fig. 1) of non-native species by humans has a very long history, spanning hundreds to thousands of years. Indications of early non-native species introductions exist from all over the world, including for example during the time of the Pharaohs in ancient Egypt and within areas in Central America 3000 years ago (Sanchéz, 1997; Janick, 2007), by the Polynesians in the Pacific region, the Greeks and Romans in the Mediterranean and the Han dynasty in China (di Castri, 1989; Cox and Banack, 1991; Keller, 1994; Sanchéz, 1997). However, nearly all of these cases represent terrestrial species, with the vast majority being agricultural or ornamental plant species (see the following section for details on introduction pathways). An exception represents the well documented introductions of ornamental fishes in China, where for instance common carp (*Cyprinus carpio*) have been raised and dispersed already 1000–2000 years ago (Ma et al., 2003).

Overall, reports of freshwater species introductions are largely lacking from before 1500 and are still low before 1800 (Fig. 2). Outside China, a few reports of early introductions of freshwater species exist for the 16th century. In most cases, these were introductions of fishes, such as common carp introduced to the United Kingdom (Jackson and Grey, 2013) or common bream (*Abramis brama*) to Ireland (O'Flynn et al., 2014). Integrating the First Records Database (Seebens et al., 2017) with habitat types of species obtained from WoRMS Editorial Board (2020) revealed that the earliest introduction of a non-native freshwater plant species was recorded for European water-plantain (*Alisma plantago-aquatica*), which was found in 1672 in the USA (Pyšek et al., 2015). Among invertebrates, one of the few early records denote the introduction of the zebra mussel (*Dreissena polymorpha*), which was already recorded in 1619 as being introduced to North America from Europe or Central Asia, and is now widespread and abundant in large parts of the United States and Canada (Mangiante et al., 2018).

After 1800, the total number of non-native freshwater species shows a clear rising trend until today (Fig. 2). According to the First Records Database, a total of 645 non-native freshwater species have been introduced worldwide until 2010. As the time of first detection is not available for most introduction events, many species are lacking from this database and the true number of non-native freshwater species is likely much higher. For example, a comparison of non-native species occurrences reported in the online database FishBase (Froese and Pauly, 2019) and the First Records Database revealed that for most regions of the world the proportion of entries with available dates of first record is often below 50% (Seebens et al., 2021). For less investigated taxonomic groups such as invertebrates, the proportion is certainly even lower. While the absolute numbers of introduced non-native species must be higher, sensitivity analyzes revealed that the trends are robust (Seebens et al., 2018).

The overall rise in the number of non-native freshwater species has been consistently reported from all over the world, across habitats such as lakes and rivers, and across a large range of taxonomic groups (Cowie, 1998; Kumar, 2000; Ricciardi, 2001; Roll et al., 2009; Hussner et al., 2010; Jackson and Grey, 2013; Rabitsch and Nehring, 2017; Mangiante et al., 2018; Muñoz-Mas and García-Berthou, 2020). Although comprehensive analyzes of long-term trends of non-native freshwater species are still missing at the global scale, the consistency of reported trends across taxonomic groups, habitats and regions indicates that similar trends can also be expected for less investigated taxa and regions.

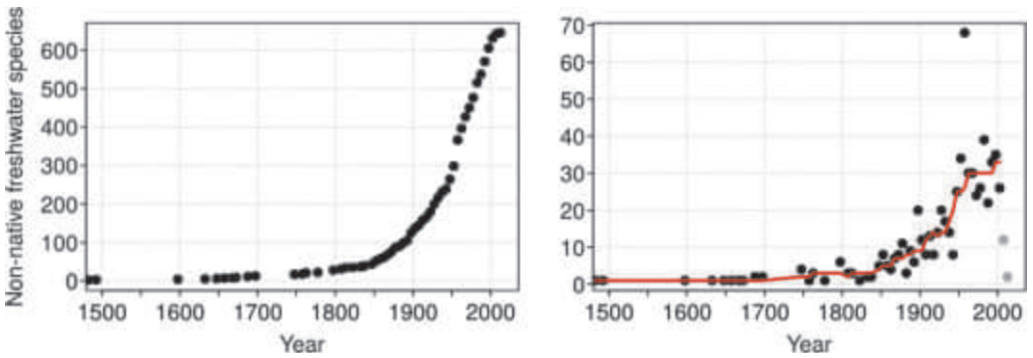

Fig. 2 Temporal development of the number of non-native freshwater species globally shown as total numbers (left panel) and the number of new non-native species per five-year interval (right panel). The red line indicates the overall trend calculated as a running median until 2005. Records after 2005 (grey dots) are prone to time lags in detection and recording, and were thus not considered for the trend calculation. Sources: First Records Database, https://doi.org/10.5281/zenodo.3690748, Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T and Essl F (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435; WoRMS Editorial Board (2020) *World Register of Marine Species*. Available from https://www.marinespecies.org at VLIZ. (Accessed 10 October 2020). https://doi.org/10.14284/170.

In addition to increases in total numbers, also the rate of new records per time has risen continuously (Fig. 2; Ricciardi, 2001, Jackson and Grey, 2013, Muñoz-Mas and García-Berthou, 2020). This rise may indicate an acceleration of introductions, although such dynamics may also result from increased sampling intensity (Costello and Solow, 2003; Belmaker et al., 2009). A few studies reported declines in rates of new non-native species records in most recent years (i.e., after 2005), which is also apparent in Fig. 2 (grey dots). However, it has been repeatedly concluded that such apparently declining trends in recent years are most likely a consequence of delays in detection and reporting of new non-native species rather than the reflection of true trends (Seebens et al., 2017, Mangiante et al., 2018, Muñoz-Mas and García-Berthou, 2020).

Within the coming decades, the observed rise in the number of non-native freshwater species is very likely to continue for two reasons: First, numbers of non-native species consistently increased during the last decades for nearly all taxonomic groups and regions without signs of saturation (Seebens et al., 2017). As there are no indications for upcoming major policy changes to mitigate further introductions, it seems unlikely that trends will change distinctly in the near future. Second, drivers of introduction and establishment of non-native freshwater species are expected to increase likewise. For instance, the intensity of shipping, tourism or fishing, but also the number of pets and the interconnectivity among freshwater systems through canals—which are all pathways of introduction (see above and Cowie, 1998, Ricciardi, 2001, Galil et al., 2007, Jackson and Grey, 2013)—are expected to increase. If dynamics continue as observed during the last decades, further increases in the number of new non-native species in inland waters are very likely. Indeed, such increases are predicted to occur until 2050, although the dynamics may vary among taxonomic groups (Seebens et al., 2021): While a clear increase is predicted for non-native freshwater plants, introductions of non-native freshwater arthropods are predicted to slow down, which can be partly attributed to the depletion of source pools (Liebhold et al., 2017). Finally, climate change will increasingly affect the establishment and spatial distribution of non-native freshwater species in manifold ways (e.g., Bellard et al., 2013, 2018).

Introduction pathways of non-native species

Non-native species can be introduced from one geographic location to another, intentionally or unintentionally, by various processes and mechanisms which are called introduction pathways. As mentioned above, "introduction" refers to the first two stages of the invasion process, namely "transport" and "escape/release" (Fig. 1). To make the large variety of pathways easier to grasp and more effectively manageable, efforts have been made to standardize pathway terminology and categorization. Based on foundational work by Hulme et al. (2008), the Convention on Biological Diversity proposed a unified pathway categorization (CBD, 2014; IUCN, 2017; Table 1) which differentiates between three general mechanisms (importation as or with a commodity, arrival via a transport vector, natural spread from a neighboring region where the species is alien) and six main pathway categories: Release in nature; Escape from confinement; Transport—Contaminant; Transport—Stowaway; Corridor; and Unaided. Each of these main pathways comprises several subcategories (Table 1; Faulkner et al., 2020; Pergl et al., 2020 discuss potential improvements to this standard scheme). The categories Release and Escape relate to the intentional transportation of non-native species outside of their native range, whereas the other categories describe unintentional transportation.

The relevance of many introduction pathways is linked directly to the strong increase in global trade and transport in the last centuries. Differences in their importance relative to each other, however, can be seen when considering different habitat types and taxonomic groups. Combined pathway data from two major IAS databases, IUCN's Global Invasive Species Database (GISD) and the DAISIE European Invasive Alien Species Gateway, show that the pathway Escape is responsible for most introductions of freshwater species (Fig. 3A, modified from Saul et al., 2017). For instance, many species of fish, crustaceans and mollusks were transported outside of their native areas for aquaculture and escaped from the respective facilities into the wild. Freshwater species used in aquarium trade or for ornamental purposes (animals as well as plants) often escape with or without their owner's knowledge (Keller et al., 2011; Fig. 3B). Release is the second most important pathway in freshwater habitats, comprising such widespread activities as stocking of fish and crustaceans as a means to improve commercial and recreational fisheries or introductions for biocontrol (e.g., mosquitofish *Gambusia* spp. for mosquito control, or herbivorous weevils to control aquatic invaders like water hyacinth *Eichhornia crassipes* and giant salvinia *Salvinia molesta*). The pooled pathway category "Transport— Contaminant & Stowaway" (a differentiation between the two individual transport categories is not possible with sufficient certainty in the global dataset from Saul et al., 2017) comes third, with contaminated bait and stowaways in angling/fishing equipment, ballast water and "hitchhikers" on ship or boat hulls (hull fouling) being of particular relevance for freshwater introductions. Finally, many freshwater introductions have been facilitated through the creation of canals (pathway Corridor), such as the Rhine-Main-Danube canal in Europe, which is effectively connecting the Black Sea with the North Sea, or the Chicago Sanitary and Ship Canal in North America connecting the Great Lakes with the Mississippi River. The Corridor pathway is particularly important for introductions of freshwater invertebrates (Fig. 3B).

The prevalence of pathways for species introductions may change over time due to changes in human activities, such as trade, tourism or fashion (see e.g., Ricciardi, 2006; Hulme et al., 2008; Essl et al., 2015; Pagnucco et al., 2015). Likewise, the relative importance of pathways varies among freshwater systems of different regions. For example, the proportions of pathways responsible for freshwater introductions in Europe (see e.g., Gherardi et al., 2009; Nunes et al., 2015) align well with the overall pattern found in the combined dataset described above. By contrast, in the Laurentian Great Lake basin in North America, one of the world's most invaded freshwater system, until recently ballast water (pathway Transport—Contaminant) was the overwhelmingly dominant pathway (Ricciardi, 2006; Pagnucco et al., 2015). In South Africa, important introduction pathways of freshwater fish are related to stocking for sport fishing and food (pathway Release) as well as aquaculture and aquarium trade (pathway Escape) (Richardson et al., 2003).

Table 1 CBD pathway categorization (CBD, 2014; IUCN, 2017).

Mechanism	*Category*	*Subcategory*
Importation as or with a commodity	Release in nature	Biological control
		Erosion control/dune stabilization
		Fishery in the wild
		Hunting in the wild
		Landscape/flora/fauna "improvement"
		Introduction for conservation purposes
		Release in nature for use
		Other intentional release
	Escape from confinement	Agriculture
		Aquaculture/mariculture
		Botanical garden/zoo/aquaria
		Pet/aquarium/terrarium species
		Farmed animals
		Forestry
		Fur farms
		Horticulture
		Ornamental purpose (not horticulture)
		Research and ex-situ breeding
		Live food & live bait
		Other escape from confinement
	Transport—Contaminant	Contaminant nursery material
		Contaminated bait
		Food contaminant
		Contaminant on animals
		Parasites on animals
		Contaminant on plants
		Parasites on plants
		Seed contaminant
		Timber trade
		Transportation of habitat material
Arrival via a transport vector	Transport—Stowaway	Angling/fishing equipment
		Container/bulk
		Hitchhikers in or on airplane
		Hitchhikers on ship/boat
		Machinery/equipment
		People & their luggage/equipment
		Organic packing material
		Ship/boat ballast water
		Ship/boat hull fouling
		Vehicles
		Other means of transport
Spread	Corridor	Interconnected waterways/basins/seas
		Tunnels & land bridges
	Unaided	Natural dispersal across borders
		(from an area to which the species was introduced by human mediation)

The categories Release and Escape relate to the intentional transportation of non-native species outside of their native range, whereas the other categories relate to unintentional transportation.

Establishment and spread of non-native species: Hypotheses and models about invasion success

While the previous section focused on the first two stages of the invasion process, stages three and four refer to establishment and spread. These two stages have received more attention in invasion biology than the early stages, particularly in the 20th and early 21st century. For example, the SCOPE program in the 1980s formulated the following central research questions for biological invasions, which have remained highly influential for the field until today: "What are the characteristics of a successful invader species? What characteristics determine the susceptibility to invasions of a natural ecosystem? How successful are attempts to predict in a quantitative manner the outcome of a particular introduction, or the effect of an invading organism on ecosystem structure and function? What particular implications are there for the management and conservation of natural or semi-natural ecosystems?" (pp. 8–9 in Huenneke, 1988).

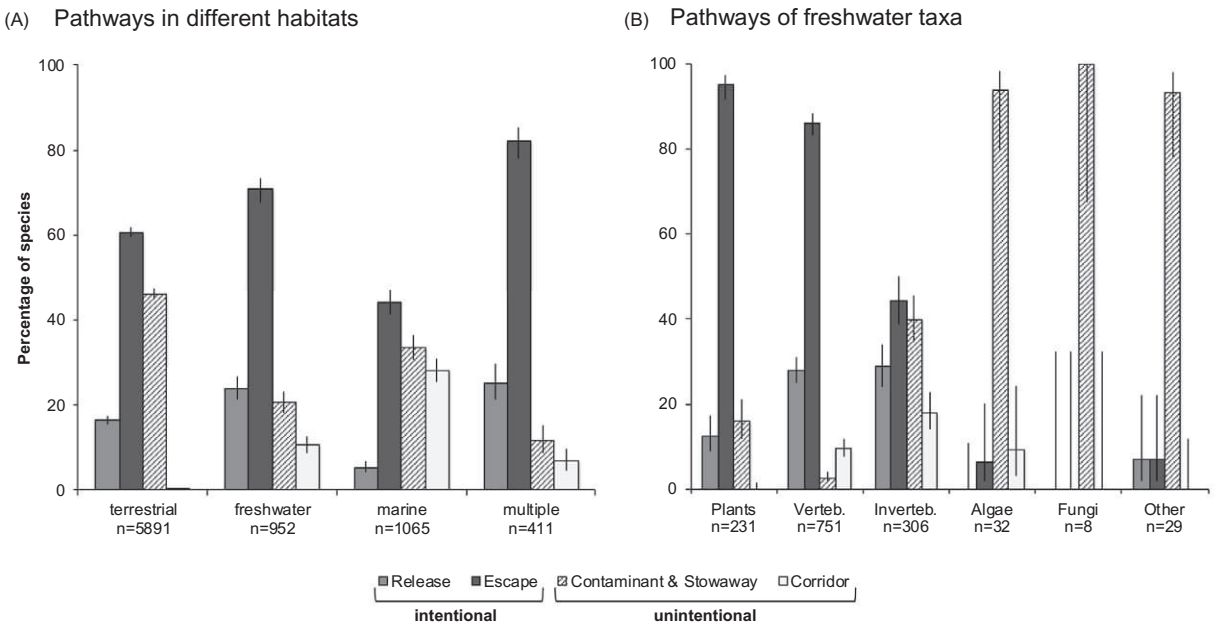

Fig. 3 Main introduction pathways recorded in a large dataset that combines global data from GISD/IASPMR with European data from DAISIE, comparing among (A) different habitat types (8319 spp.) and (B) different taxonomic groups of freshwater species (1357 spp.). Species in (B) include those that occur in freshwater alongside other habitat types (part of "multiple" in (A)). The pathways Transport—Contaminant and Transport—Stowaway were pooled ("Contaminant & Stowaway") since their differentiation was not possible with sufficient certainty for many of the species in the dataset. The sum of pathway proportions is larger than 100% for each habitat and taxonomic group since species can be introduced via more than one pathway. Error bars indicate 95% Wilson confidence intervals; (B) uses the combined dataset provided therein. Strongly modified from a previous publication by the authors who own the copyright: Saul W-C, Roy HE, Booy O, Carnevali L, Chen H-J, Genovesi P, Harrower CA, Hulme PE, Pagad S, Pergl J and Jeschke JM (2017) Assessing patterns in introduction pathways of alien species by linking major invasion databases. *Journal of Applied Ecology* 54: 657–669.

These questions largely focus on invasion success (i.e., which factors are responsible that invasive species have completed the invasion process?), emphasizing the relevance of identifying the characteristics of invasive species and invaded ecosystems. It could be argued that in order to answer these questions, the complete invasion process should be considered, including the first stages. However, the importance of considering the role of humans in the introduction of non-native species to improve our understanding on the invasion success has only become clear to the field in the 2000s. In this decade, Richardson (2004; see also Richardson and Pyšek, 2008) declared understanding propagule pressure, and generally the role of the early stages of the invasion process, as the new frontier in invasion biology. Taking into account propagule pressure, a composite measure of (human-driven) introduction effort (see Glossary for details), has been eye-opening: it turned out that it is often more important for the success of non-native species than the biological characteristics of these species or the ecosystems to which they were introduced (reviewed in e.g., Simberloff, 2009, Keller et al., 2011).

The following sub-sections focus on invasion success of non-native species, particularly their establishment and spread, from two different perspectives: The first one highlights major hypotheses in the field of invasion biology about the reasons for invasion success (or failure); and the second sub-section outlines species distribution models (SDMs), which are widely used for predicting where non-native species are able to establish and spread.

Major hypotheses on the invasion success of non-native species

Major hypotheses of a research field are typically a rich source of knowledge reflecting the combined conceptual understanding of the field. In a thriving discipline such as invasion biology, it is quite challenging to get and keep on overview of existing hypotheses. In their review "Fifty years of invasion ecology—the legacy of Charles Elton", Richardson and Pyšek (2008) wrote: "The literature on invasion ecology contains a growing number of theories and generalizations, with much duplication, redundancy and reinventing of the wheel. There is a need to distill the fundamental issues from the different theories, while realizing that invasions are context specific summarizing the state of the field" (p. 166). Only a year later, Catford et al. (2009) tackled exactly this issue by publishing their seminal paper "Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework."

More recently, the first author of this article teamed up with Martin Enders, Tina Heger and colleagues to create interactive conceptual maps of invasion biology by constructing zoomable networks of common invasion hypotheses (Jeschke, 2014; Enders

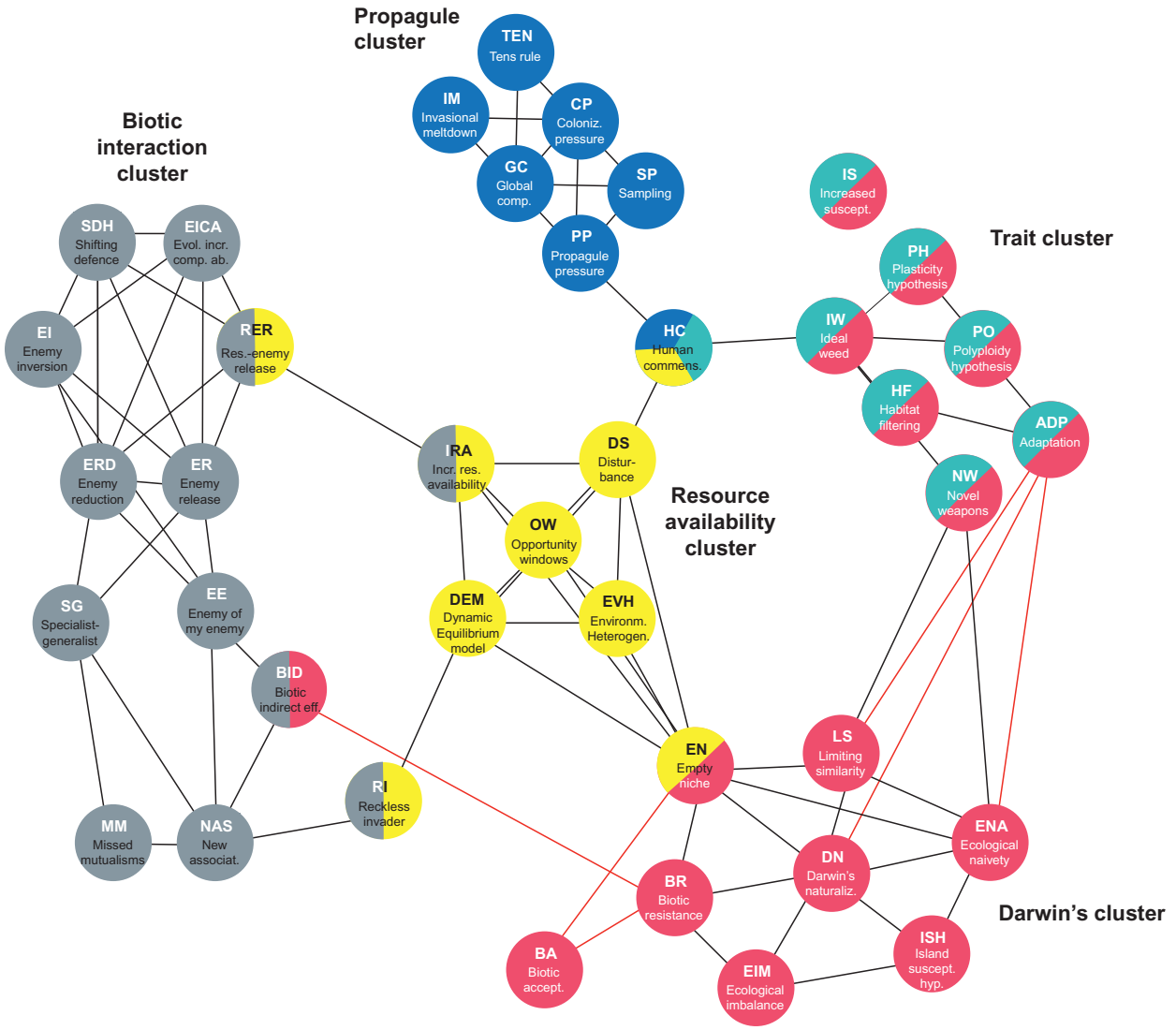

Fig. 4 Hypothesis network consisting of 39 invasion hypotheses grouped in five topical clusters. The color of each hypothesis illustrates to which cluster it belongs. Multi-color hypotheses belong to more than one cluster—they conceptually connect clusters. A black line connecting two hypotheses indicates that they are logically similar, whereas a red line indicates contradictory hypotheses. More information on each hypothesis is provided at https://hi-knowledge.org and in: Enders M, Havemann F, Ruland F, Bernard-Verdier M, Catford JA, Gómez-Aparicio L, Haider S, Heger T, Kueffer C, Kühn I, Meyerson LA, Musseau C, Novoa A, Ricciardi A, Sagouis A, Schittko C, Strayer DL, Vilà M, Essl F, Hulme PE, van Kleunen M, Kumschick S, Lockwood JL, Mabey AL, McGeoch M, Palma E, Pyšek P, Saul W-C, Yannelli FA and Jeschke JM (2020) A conceptual map of invasion biology: integrating hypotheses into a consensus network. *Global Ecology and Biogeography* 29: 978–991.

et al., 2018, 2019, 2020; Jeschke and Heger, 2018). These conceptual maps provide a visual overview of existing key hypotheses of the field as well as how they are related to each other, and are freely available online at https://hi-knowledge.org. Taking the most recent conceptual map (Enders et al., 2020), 39 invasion hypotheses are connected in five topical clusters that each represent a different perspective on biological invasions (Fig. 4).

Specifically, the propagule cluster includes hypotheses that highlight the role of humans and the importance of propagule and colonization pressure (Lockwood et al., 2009) for invasion success. The best known hypothesis in this cluster (according to a survey performed by Enders et al., 2018) is the propagule pressure hypothesis which posits that non-native species with a high propagule pressure have a higher invasion success than non-native species with a low propagule pressure (Lockwood et al., 2005; Jeschke and Heger, 2018). It is one of the best supported hypotheses in the field. More than 80% of the studies addressing this hypothesis reported evidence in its support (Jeschke and Heger, 2018). Another hypothesis in this cluster is the tens rule, which says that about 10% of species will pass from one stage of the invasion process to the next. For example, if 100 species have been introduced to an exotic range, the tens rule predicts that 10 of these species will establish themselves and 1 species will spread. According to Jeschke

and Heger (2018), the overall percentage of species passing from one stage of the invasion process to the next was 38% ($n = 66$ studies), thus almost four times more than predicted. For freshwater species, this percentage was even 54% ($n = 5$) which is significantly higher than the 34% observed for terrestrial species ($n = 52$). Thus for freshwater species, about five times more species pass from one invasion stage to the next one than predicted by the tens rule. On the other side, the sample size for freshwater species was low, so more studies are needed to allow for a more robust conclusion.

The resource-availability cluster includes hypotheses on the characteristics of ecosystems into which non-native species were introduced. One well-known hypothesis in this cluster is the disturbance hypothesis, which posits that the invasion success of non-native species is higher in disturbed than undisturbed ecosystems (Elton, 1958; Hobbs and Huenneke, 1992; Jeschke and Heger, 2018; Enders et al., 2020). "Disturbance" can be measured in different ways, but empirical support for the disturbance hypothesis is high across almost all disturbance measures, having an overall level of support of about 60% of the studies addressing it (Jeschke and Heger, 2018). As for other invasion hypotheses, though, most studies addressing the disturbance hypothesis were done in terrestrial systems; in this case, only 4% of all studies focused on fresh waters (Jeschke and Heger, 2018).

Darwin's cluster includes the oldest major invasion hypothesis, Darwin's naturalization hypothesis, which states that the invasion success of non-native species is higher in areas that are poor in closely related species than in areas that are rich in closely related species (Darwin, 1859; Daehler, 2001; Schaefer et al., 2011; Jeschke and Heger, 2018; Enders et al., 2020). This hypothesis is well supported by evidence if phylogenetic distance is measured between the non-native species and the phylogenetically closest native species (phylogenetic nearest neighbor distance), whereas it is poorly supported if a taxonomic measure is used (non-membership in the same genus or family; Jeschke and Heger, 2018). Other hypotheses in this cluster also focus on eco-evolutionary factors to explain the invasion success (or failure) and impacts (or lack thereof) of non-native species. Specifically, the ecological naivety hypothesis posits that the invasion success and impact of non-native species on biodiversity is influenced by the eco-evolutionary experience of the resident community. Thus, invasion success and impacts are particularly high if no phylogenetically or functionally similar species exist in the resident community (Diamond and Case, 1986; Ricciardi and Atkinson, 2004; Saul and Jeschke, 2015; Enders et al., 2020). Another hypothesis in this cluster is the biotic resistance hypothesis, which posits that an ecosystem with high biodiversity is more resistant against non-native species than an ecosystem with lower biodiversity (Elton, 1958; Levine and D'Antonio 1999; Jeschke and Heger, 2018, Enders et al., 2020). This hypothesis is also known as diversity-invasibility hypothesis and is poorly supported by empirical evidence, particularly if "resistance" is implied simply from the number of non-native species in an ecosystem: if resistance is high, there should be few non-native species in the ecosystem, whereas if it is low, there should be many. If the biodiversity of ecosystems is measured as the number of native species in a system, a simple test of the resistance hypothesis is if the number of native and non-native species found in comparable ecosystems are negatively related to each other: such a negative correlation would be expected based on this hypothesis, as a high biodiversity (i.e., many native species) is predicted to result in high resistance (i.e., few non-native species). However, most studies testing this relationship did not find this pattern, which led to the formulation of the acceptance hypothesis (Stohlgren et al., 2006; Enders et al., 2020), which predicts the opposite pattern and is also included in Darwin's cluster.

The trait cluster is nested in Darwin's cluster and includes hypotheses with a focus on species characteristics. In particular, the ideal weed hypothesis posits that the invasion success of a non-native species depends on its specific traits (e.g., life-history traits) (Baker, 1965; Rejmánek and Richardson, 1996; Enders et al., 2020). The plasticity hypothesis states that a particular characteristic of non-native species, phenotypic plasticity, often makes them successful invaders (Richards et al., 2006; Jeschke and Heger, 2018; Enders et al., 2020). This hypothesis has been empirically supported by more than 60% of the studies addressing it, similar to the propagule pressure and disturbance hypotheses and, therefore, is among the best supported invasion hypotheses (Jeschke and Heger, 2018).

Finally, the biotic interaction cluster features hypotheses that emphasize the importance of species interactions for invasion success. A central hypothesis in this cluster is the enemy release hypothesis, which says that the absence of enemies in the exotic range is a cause of invasion success (Keane and Crawley, 2002; Heger and Jeschke, 2014; Jeschke and Heger, 2018; Enders et al., 2020). According to the survey by Enders et al. (2018), this is altogether the best known invasion hypothesis. Its empirical support is mixed, though: while invaders indeed seem to be frequently released from their enemies, they rarely showed an enhanced performance if released from enemies (Heger and Jeschke, 2014; Jeschke and Heger, 2018; Ryo et al., 2020).

Predicting establishment and spread of non-native species using species distribution models (SDMs)

Much research has been devoted to accurately predicting the potential distributions of non-native species in exotic ranges, for example to design cost-effective strategies for managing invasions (Vander Zanden and Olden, 2008; Bellard et al., 2013; Liu et al., 2019). Species distribution models (SDMs) have emerged as one of the most promising and popular tools to forecast the invasion risks of non-native species and the vulnerability of recipient ecosystems (Jeschke and Strayer, 2008; Liu et al., 2020a). The development of SDMs is based on the realized ecological niche, which defines the set of environmental conditions occupied by species in nature as a consequence of negative biotic interactions and dispersal limitations (rather than the fundamental niche, i.e., the set of environmental conditions that species can in principle occupy based on their physiological tolerance). Specifically, SDMs are first developed with statistical or machine-learning algorithms using the observed data of species distributions and environmental predictors to delineate the conditions in which species can survive (Guisan and Thuiller, 2005; Liu et al., 2020a). Models are then applied to new environmental layers to predict habitat suitability for species in new geographic ranges and/or within certain

time frames (Yates et al., 2018). Recent years have seen a proliferation of data on species distributions and environmental factors, and a rapid development of modeling algorithms, greatly facilitating the application of SDMs to forecast invasion risks of non-native species (Guisan and Thuiller, 2005; Werkowska et al., 2017).

For non-native species in inland waters, many studies have employed SDMs to anticipate their potential establishment and spread at global (e.g., Larson and Olden, 2012), national (e.g., Liu et al., 2019) and local (e.g., Vander Zanden and Olden, 2008) scales. Bellard et al. (2013) predicted the global distributions of 100 of the worst invaders (i.e., invasive species that are very successful and have a high impact) and found that range size would increase by 12% for aquatic plants and by 59% for aquatic invertebrates under upcoming climates.

To better predict species distributions, considerable efforts have been made for improving the predictive performance of SDMs (Guisan and Thuiller, 2005; Qiao et al., 2015; Werkowska et al., 2017). A recent synthesis documented that the predictability of SDMs in new ranges was positively correlated with the number of presence points used for developing models, but negatively with the number of predictors (Liu et al., 2020a). Therefore, selecting appropriate presence and predictor data is a key step to improve model performance in exotic ranges (Liu et al., 2020a). Developing SDMs should also account for the physiological characters of focal species, as species-environment relationships are remarkably different among functional groups (Yates et al., 2018; Norberg et al., 2019). Previous studies reported that distributions of species with larger body size, lower dispersal capacity or smaller range size could be predicted with greater accuracy (Soininen and Luoto, 2014). Huang et al. (2016) evaluated model performance for 16 freshwater fish species in the eastern USA and found a higher performance for species endemic in cool waters and species with small population sizes. Biotic interactions are another important factor, because the distributions of species are strongly shaped by their interactions with other species (e.g., competition and predation; Guisan and Thuiller, 2005, Yates et al., 2018). Also, biotic interactions regulating species distributions in the native range are often absent in the exotic range, yet biotic interactions are not considered in most SDM studies (Guisan and Thuiller, 2005; Jeschke and Strayer, 2008). In addition, better model performance has been found for non-native species with shorter residence times and for species introduced both intentionally and unintentionally (Liu et al., 2020a). Given the substantial heterogeneity in the ways of species being introduced, it is necessary to integrate the history and intentionality of species introductions into SDMs.

Several sources of uncertainty underlie the prediction of spatial distributions for non-native species (Jeschke and Strayer, 2008). One key premise of applying SDMs is that species should be in equilibrium with the environment (i.e., present in all suitable conditions and absent in all unsuitable conditions, Guisan and Thuiller, 2005). But this premise is often violated by non-native species, as it takes time until a non-native species is more or less in equilibrium with its exotic environment (Václavík and Meentemeyer, 2012). For example, Prussian carp (*Carassius gibelio*) showed an eightfold expansion of its range from 2000 to 2014 in Canada, and will likely continue to spread into the United States (Docherty et al., 2017). There are no signs yet that this species has reached equilibrium, and its expansion is further facilitated by additional human introductions and artificial waterways. For non-native species in a non-equilibrium state, many introduced populations might be observed in sink habitats (i.e., environmental conditions under which species can survive, but cannot maintain a population; Jeschke and Strayer, 2008, Liu et al., 2020b), reducing the performance of SDMs to predict species distributions in their exotic range (Zhu et al., 2014). Another key premise is that species do not or only slowly change their niche (i.e., niche conservatism), so that they can occupy similar environmental conditions in new regions and time periods (Liu et al., 2020b). However, non-native species may actually rapidly change their realized niches in exotic ranges due to new biotic interactions, dispersal limitations or rapid evolution (Guisan et al., 2014; Liu et al., 2020b). Changes in the realized niche have, for example, been reported for eastern mosquitofish *Gambusia holbrooki* introduced to Europe (Strubbe et al., 2015) and for freshwater invertebrates introduced to New Zealand (Torres et al., 2018). Niche changes cause SDMs to incorrectly assess species-environment relationships, leading to decreased reliability of predicted distributions (Liu et al., 2020a). A deteriorating effect of niche change on model performance has been found for multiple taxonomic groups, such as plants (Petitpierre et al., 2017) and vertebrates (Strubbe et al., 2015). Despite being rarely investigated for freshwater species, such an effect has been found for freshwater fishes in Brazil (Frederico et al., 2019) and crayfish in the United States (Morehouse and Tobler, 2013). Incorporating equilibrium status and niche changes into SDMs can be an effective way to increase model performance for non-native species (Pearman et al., 2008; Václavík and Meentemeyer, 2012).

Conclusions

Although classic studies about non-native species exist, the modern discipline of invasion biology did not emerge before the 1990s. An important conceptual strength that the discipline has developed over time is the invasion process, which consists of the consecutive stages that invasive species go through: transport, release/escape, establishment and spread. Research on biological invasions in the 1990s focused mainly on establishment and spread, and thus on those stages that are not as strongly connected to human actions as species transport and release/escape. This initial focus is unsurprising, as invasion biology emerged as an ecological subdiscipline and first focused on interactions between species and their environment without usually considering humans as an explicit part of this environment. Until today, most hypotheses in the field focus on establishment and spread, and do not put a strong focus on the role of humans. Since the 21st century, however, humans and their actions have become increasingly recognized as important to the field. Introduction pathways of non-native species are now more frequently studied, including their past and potential future dynamics. Similarly, propagule and colonization pressure, that is the number of individuals and species being globally translocated by humans, either intentionally or unintentionally, have become key concepts. These are also

empirically well supported, in contrast to some classic hypotheses that have received relatively little empirical support. The trend of the discipline to increasingly incorporate humans and their actions needs to continue in order to allow for a better understanding of biological invasions in the Anthropocene (cf. Kueffer, 2017; Archibald et al., 2020). Indeed, the importance of factors not classically investigated by biologists and ecologists has been predicted to further rise in the future, particularly transport, climate change and socio-economic change (Essl et al., 2020). Forecasting future distributions of non-native species has also become a stronger research focus, for which species distribution models (SDMs) are frequently applied. Novel synthesis tools that, for example, apply interactive visualization techniques to allow researchers and other stakeholders to get and keep an overview of the field's vast and further growing literature are becoming increasingly important as well (cf. Jeschke et al., 2020). Finally, there is a rise in research effort on the impacts and management of non-native species, which is the focus of the second chapter on biological invasions in this encyclopedia.

Knowledge gaps

- Information about biological invasions is strongly biased spatially towards large economies, temporally towards very recent data and taxonomically towards vertebrates and plants. Thus, large knowledge gaps exist, particularly for invertebrates in the aquatic realm in the global South (Pyšek et al., 2008; Jeschke et al., 2012; Bellard and Jeschke, 2016). There is a similar research bias in the application of species distribution models (SDMs), which also have mainly been applied in terrestrial systems (Soininen and Luoto, 2014; Liu et al., 2020a).
- There is a lack of general hypotheses about species introduction pathways.
- Our capacity to differentiate between pathways of primary introduction (e.g., intercontinental introductions to major ports) and of subsequent secondary introduction (e.g., intracontinental transport to smaller towns or natural spread of introduced species) needs to be increased to use limited management resources more efficiently. In particular, information about unaided introductions, i.e., secondary natural dispersal across borders, is very incomplete.
- Pathway information is still often scattered across databases that utilize disparate terminology and pathway categorisations. Databases need to be harmonized to exploit the full potential of accumulating pathway data.
- The influence of non-equilibrium status and niche changes on the performance of SDMs is not yet understood.
- We currently do not know to which degree the performance of SDMs can be improved by considering biotic interactions or the physiological characteristics and introduction history of the focal non-native species.

Acknowledgments

We thank Ken Irvine for the invitation to contribute this article. His comments on the chapter and those of Thomas Mehner and an anonymous reviewer are also highly appreciated. HS, JMJ and WCS acknowledge support by the Belmont-Forum-BiodivERsA project AlienScenarios through the national funder German Federal Ministry of Education and Research (BMBF; grants 01LC1807A and 01LC1807B). CL was sponsored by the PRIME program of the German Academic Exchange Service (DAAD) with funds from the BMBF. This chapter is a contribution of the Invasion Dynamics Network (InDyNet).

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Relevant websites

https://www.cabi.org/isc—CABI Invasive Species Compendium.
https://easin.jrc.ec.europa.eu—European Alien Species Information Network (EASIN).
https://www.nobanis.org—European Network on Invasive Alien Species (NOBANIS).
http://www.fao.org/fishery/dias/en—FAO Database on Introductions of Aquatic Species (DIAS).
Global Register of Introduced and Invasive Species (GRIIS): http://www.griis.org
https://hi-knowledge.org—Interactive visualisation tools to dive into invasion biology.
www.corpi.ku.lt/databases/index.php/aquanis—Information system on aquatic non-indigenous and cryptogenic species (AquaNIS).
http://www.iucngisd.org—IUCN Global Invasive Species Database (GISD).
https://nas.er.usgs.gov—USGS Nonindigenous Aquatic Species (NAS).
http://www.marinespecies.org/introduced—World Register of Introduced Marine Species (WRiMS).

Biological Invasions: Impact and Management

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Alien species See 'non-native species.'

EICAT Short for Environmental Impact Classification for Alien Taxa, a standardized system to assess biodiversity impacts of non-native species (Blackburn et al., 2014; Hawkins et al., 2015) that has been adopted by the International Union for Conservation of Nature (IUCN, 2020a, b).

Impact A change or effect of a non-native species on either the environment (i.e. biodiversity) or socio-economics in the broad sense (i.e. including culture, religion, human health, safety, livelihoods and other aspects of human well-being), whether positive or negative (Jeschke et al., 2014).

Introduction pathways The processes and mechanisms behind the human-mediated transportation and introduction of non-native species from one geographic location to another (Hulme et al., 2008). These introductions can be either intended by humans or unintentional.

Invasion process See 'invasive species.'

Invasion syndrome A combination of pathways, alien species traits and characteristics of the recipient ecosystem that collectively result in predictable dynamics and impacts, and that can be managed effectively using specific policy and management actions (Novoa et al., 2020).

Invasive species Species that have successfully completed the invasion process, i.e. they have: (i) been intentionally or unintentionally transported by human action from their native range to a new range; (ii) been released there or escaped into the wild; (iii) have established one or more self-sustaining populations; and (iv) have spread substantially beyond their point(s) of release or escape (Blackburn et al., 2011; Jeschke et al., 2013). Synonyms of invasive species are 'invasive alien species' or 'invasive non-native species.'

Management of biological invasions Actions that reduce the presence, abundance or impact of non-native species. These actions may: (1) prevent a non-native species from entering a new area (prevention and captive management); (2) if introduced, may remove it before it becomes widely established (eradication); and (3) if it becomes widely established, may limit its impact by reducing spread and abundance (long-term management). Management may also include actions that reduce impact without affecting the presence or abundance of non-native species. These actions include: (4) impact adaptation; and (5) environmental restoration after species removal (Robertson et al., 2020).

Non-native species Species that have been intentionally or unintentionally transported by human action from their native range to a new range (Blackburn et al., 2011). Non-native species are also called 'alien species,' 'exotic species' or 'non-indigenous species.' Therefore, non-native species are not necessarily invasive, but invasive species as defined above are always non-native.

SEICAT Short for Socio-Economic Impact Classification for Alien Taxa, a standardized system to assess socio-economic impacts of non-native species (Bacher et al., 2018) that complements EICAT (which focuses on environmental impacts, see above).

Introduction to the topic

Biological invasions are a key stressor of biodiversity (IPBES, 2019; Pyšek et al., 2020) and have important impacts on socio-economics in a broad sense (including culture, religion, human health, safety, livelihoods and other aspects of human well-being) (Pyšek et al., 2020). There is often confusion about what is meant by 'impact' in the context of biological invasions, which is why we start the main part of this chapter with an outline of the different meanings of this term. We also outline how impacts of non-native species can be categorized and assessed, using the IUCN EICAT scheme as an example (which assesses biodiversity impacts; Blackburn et al., 2014; Hawkins et al., 2015; IUCN, 2020a, b), together with the associated SEICAT scheme (which assesses socio-economic impacts; Bacher et al., 2018). A key benefit of such schemes is that they help identify non-native species that have particularly severe impacts in order to prioritize management actions. The management of non-native species is the second focus of this chapter. We provide a detailed description of a management framework and each of its components.

This chapter is complementary to two other chapters on biological invasions in this encyclopedia. These give a general introduction to biological invasions with a focus on their introduction, establishment and spread, and feature case studies of freshwater invaders, respectively.

Defining the impact of non-native species

As for many other key terms in ecology and related disciplines, the term 'impact' is widely used in the context of biological invasions, and often with quite different meanings. This is unsurprising, as an array of people with various backgrounds and perspectives are interested in invader impacts. Often, the definition of impact is not explicitly provided, which can make interpretation difficult. Unclear terminology hampers the progress of science, the growth of knowledge and the translation of scientific findings into practical applications (Jeschke et al., 2019), for example to manage the impacts of non-native species.

What are the different meanings of 'impact' in the context of biological invasions? Fig. 1 (modified from Jeschke et al., 2014) gives an overview. First, some authors only consider unidirectional effects, focusing on either the negative or positive consequences of the presence of non-native species. In contrast, others consider bidirectional effects, i.e. both negative and positive consequences. The IUCN EICAT scheme outlined below is an example of a framework that only considers unidirectional effects, in this case negative effects on the environment (Blackburn et al., 2014; Hawkins et al., 2015; IUCN, 2020a, b). A complementary scheme that also considers positive effects on the environment is currently in preparation.

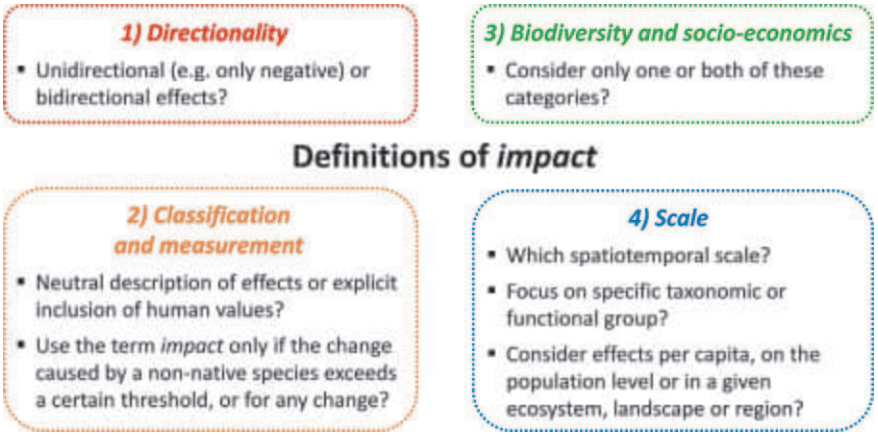

Fig. 1 To clearly define *impact* in the context of biological invasions, several questions need to be addressed. These fall into four categories: (1) directionality, (2) classification and measurement, (3) biodiversity and socio-economics and (4) scale. Modified from Jeschke JM, Bacher S, Blackburn TM, Dick JTA, Essl F, Evans T, Gaertner M, Hulme PE, Kühn I, Mrugała A, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Winter M, and Kumschick S (2014) Defining the impact of non-native species. *Conservation Biology* 28: 1188–1194.

Second, some authors aim to define and measure the impacts of non-native species in a way that excludes human values as far as possible. In contrast, others intentionally and explicitly include human values. The former typically focus on measures such as absolute or relative changes caused by non-native species (e.g. percentage decrease in the population size of a native species). They aim to describe changes caused by non-native species, but not to evaluate if they are desirable ('good') or undesirable ('bad') from a certain perspective or for different stakeholders. Other authors explicitly aim for such an evaluation (cf. Bartz et al., 2010). Indeed, different stakeholders often have contradictory perspectives on the impacts of non-native species. For example, while anglers often consider it desirable to have the opportunity to catch exotic fish species in their local water bodies, conservationists are concerned about the detrimental impacts that these fishes can have on native species (see e.g. the rainbow trout (*Oncorhynchus mykiss*) conflict, Woodford et al., 2016). When discussing the classification and measurement of impacts caused by non-native species, an important aspect is the extent of the impact. That is, whether the change caused by a non-native species needs to exceed a certain threshold to be called an 'impact' or whether any change (including a very small one, as long as it is detectable) is sufficient.

Third, some authors focus on biodiversity impacts of non-native species (e.g. Blackburn et al., 2014 when developing the EICAT scheme), others on socio-economic impacts (e.g. Bacher et al., 2018 when developing the SEICAT scheme, and see the next section for details about these schemes). Included in this second group are impacts that can be monetized (i.e. they are quantifiable in euros, dollars or other financial currencies; e.g. Pimentel et al., 2005; Lovell et al., 2006; Diagne et al., 2020). Regulations on biological invasions also focus on different types of impacts. For instance, the EU Regulation 1143/2014 (EU, 2014) concentrates on biodiversity impacts of non-native species, which is why the list of 'Invasive Alien Species of Union concern' (EU, 2016, 2017, 2019) is mainly composed of species with such impacts (still, socio-economic impacts are not completely ignored by this regulation).

Fourth and finally, the scale used to define the impacts of non-native species can also vary. Spatial scale can range from local to global. The EICAT scheme, for instance, is typically applied at the global level, but it can also be applied at continental, national, regional or local levels. Regarding the temporal scale, relatively few studies about biological invasions have a mid- to long-term perspective, while the majority of studies cover short timespans (Strayer et al., 2006). Further, some authors focus on certain taxonomic or functional groups. Traditionally, the field of invasion biology has a strong focus on terrestrial species, mainly plants and, to a lesser degree, vertebrates and invertebrates, whereas aquatic species are only considered in a relatively small number of studies (Pyšek et al., 2008; Jeschke et al., 2012; Jeschke and Heger, 2018). Finally, some authors refer to per-capita impact, others to impacts of a non-native species' population or in a given ecosystem, landscape or larger geographic or political region, such as a county or country. According to Parker et al.'s (1999) widely used impact equation, the total impact of a given non-native species in a geographic region is the product of its range size, its average population density and its per-capita impact. However, a linear relationship between impact and population density cannot usually be expected (Thiele et al., 2010; Strayer, 2020).

Assessing the impact of non-native species

The environmental and socio-economic impacts of non-native species can be severe. For example, they have caused native species extinctions (Blackburn et al., 2019) and threaten human livelihoods in developing countries by adversely affecting agricultural production and hence food security (Perrings, 2005). Unfortunately, comprehensive data on biological invasions is often lacking, making it difficult to identify their causes and consequences, and the non-native species we should prioritize for management (Kumschick et al., 2015; Hoffmann and Courchamp, 2016; Wilson et al., 2016). A current challenge for invasion science is to find ways to quantify and categorize the impacts of non-native species in a standardized manner, to support comparisons across geographic regions, habitats and taxonomic groups (Nentwig et al., 2010). To this end, numerous schemes have been developed (see e.g. González-Moreno et al., 2019; Vimercati et al., 2020). We highlight two of them here, the Environmental Impact Classification for Alien Taxa (EICAT) (Blackburn et al., 2014; Hawkins et al., 2015; IUCN, 2020a, b) and the Socio-Economic Impact Classification for Alien Taxa (SEICAT) (Bacher et al., 2018) (Fig. 2).

Environmental impact classification for alien taxa (EICAT)

The main aim of EICAT is to enable research scientists and other stakeholders to identify variation in the severity and type of environmental impacts caused by different non-native species. EICAT facilitates clear comparisons regarding the severity and type of these impacts occurring in different regions of the world and caused by different taxonomic groups of non-native species. Following published guidelines (IUCN, 2020a, b), semi-quantitative impact descriptions are used to allocate a non-native species to one of five impact categories, depending on the most severe documented impacts it has caused. The categories are: Minimal Concern (MC – meaning that while the non-native species interacts with a native species, it causes no discernible impacts); Minor (MN – the non-native species causes impacts that affected the performance of individual native species); Moderate (MO – the non-native species causes declining populations of one or more native species); Major (MR – the non-native species causes native species extirpations that would be reversible if the non-native species was removed); and Massive (MV – the non-native species causes irreversible native species extinctions).

Each non-native species is also categorized by the type of impacts it causes according to 12 mechanisms: (1) competition, (2) predation, (3) hybridization, (4) transmission of disease, (5) parasitism, (6) poisoning/toxicity, (7) bio-fouling or other direct physical disturbance, (8) grazing/herbivory/browsing, (9, 10, 11) chemical, physical, or structural impact on ecosystem, and (12) indirect impacts through interactions with other species.

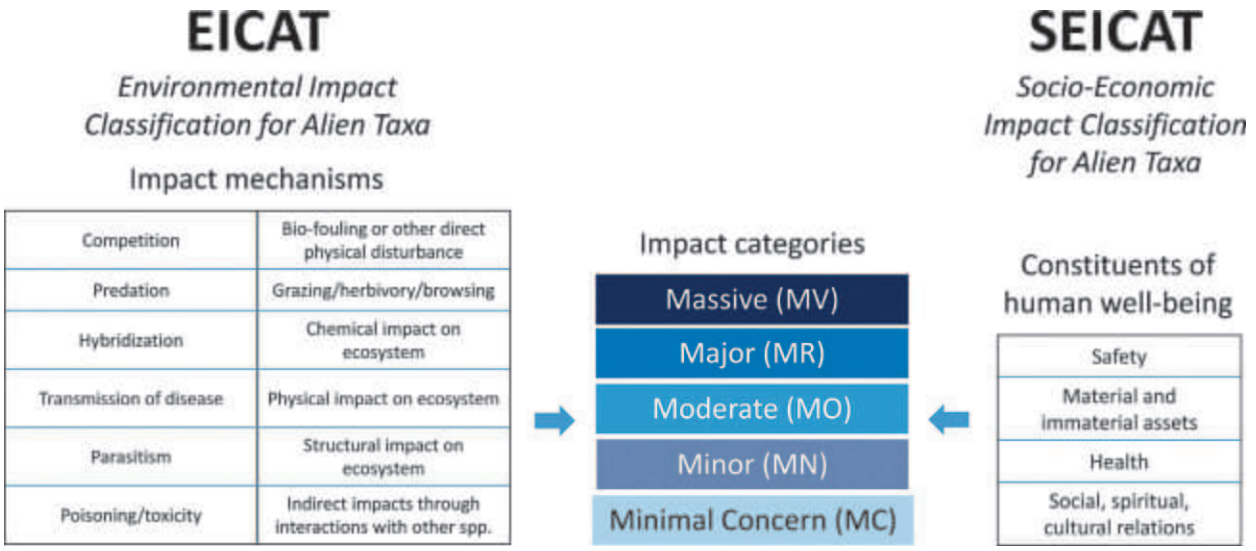

Fig. 2 The EICAT and SEICAT impact classification schemes focus on environmental and socio-economic impacts, respectively. Both schemes can be used to classify non-native species according to the severity of their impacts into one of five impact categories, from Minimal concern (MC) to Massive (MV). EICAT thereby discriminates 12 impact mechanisms, while SEICAT considers four constituents of human well-being and how these are affected by non-native species. See main text for details and references.

EICAT was adopted by the IUCN in 2020 as its formal method for categorizing and assessing the impacts of non-native species. It has been applied to various taxonomic groups including non-native birds (Evans et al., 2016), amphibians (Kumschick et al., 2017), fishes (Galanidi et al., 2018), gastropods (Kesner and Kumschick, 2018) and bamboos (Canavan et al., 2019). Data from EICAT assessments have been used to identify the characteristics of non-native bird species that have the most severe impacts (Evans et al., 2018a) and the characteristics of native bird species that make them vulnerable to the impacts of non-native bird species (Evans et al., 2021). EICAT assessments have also been used to identify the factors that influence why we have impact data for some non-native bird species (Evans et al., 2018b) and for some regions of the world (Evans and Blackburn, 2020), but not others. EICAT may therefore be used to direct research to identify impacts associated with data-deficient species and regions.

Socio-economic impact classification for alien taxa (SEICAT)

SEICAT has been developed analogously to EICAT to provide a standardized method for categorizing and assessing the wide-ranging socio-economic impacts caused by non-native species. It is based on the capability approach from welfare economics and uses changes in human activities that result from the impacts of non-native species to assess the severity of these impacts. SEICAT enables direct comparisons to be made regarding the severity of impacts to human well-being occurring in different regions of the world and caused by different taxonomic groups of non-native species.

As with EICAT, a series of impact descriptions are used to allocate a non-native species to one of five impact categories, depending on the most severe documented impacts it has caused. The categories are: Minimal Concern (MC – meaning that the impacts caused by a non-native species do not affect human well-being); Minor (MN – the non-native species causes impacts that make it difficult for people to participate in their normal activities and individuals suffer in at least one constituent of human well-being (e.g. security, material assets, health)); Moderate (MO – the non-native species causes impacts that result in a reduction in the size of an activity, with fewer people participating in it (e.g. the partial abandonment of an activity)); Major (MR – the non-native species causes impacts that result in the local disappearance of an activity from all or part of an area it has invaded (e.g. people switch to other activities), but this impact is considered to be reversible if the non-native species is controlled or removed); and Massive (MV – the non-native species causes impacts that result in the local disappearance of an activity, and this change is likely to persist for at least a decade, even if the non-native species is controlled or removed).

Unlike EICAT, SECIAT does not include a standardized set of impact mechanisms through which to categorize the types of impacts caused by a non-native species. Instead, these are determined during the SEICAT assessment by the assessor, taking into account different constituents of human well-being (based on MEA, 2005). These include safety (e.g. personal safety, secure resource access, security from disasters), material and immaterial assets (adequate livelihoods, sufficient food, shelter, access to goods), health (strength, feeling well, access to clean air and water) and social, spiritual and cultural relations (social, spiritual and cultural practice, mutual respect, friendship). For example, a SEICAT assessment undertaken for non-native birds (Evans et al., 2020) identified impacts to human safety (resulting from bird strikes with aircraft), livelihoods (through impacts to agriculture such as damage to soft fruit crops), and social and cultural assets (for example through the fouling of sports pitches and recreational facilities). Aside from non-native birds, SEICAT assessments have so far been undertaken for amphibians (Bacher et al., 2018), gastropods (Kesner and Kumschick, 2018) and fishes (Galanidi et al., 2018).

Freshwater invaders on high-impact lists

Several lists have been produced that identify non-native species with particularly high known impacts. We focus on two of these lists here – one at the global level, the other specific to continental European level; highlighting the freshwater invaders included in both.

At the global level, a well-known list of high-impact invaders has been compiled by IUCN's Invasive Species Specialist Group (ISSG). This list is called '100 of the World's Worst Invasive Alien Species' and is accessible online at the Global Invasive Species Database (GISD): http://www.iucngisd.org/gisd/100_worst.php. Importantly and as the name implies, this list does not claim to include *the* 100 worst invasive species. Instead, it includes 100 invasive species that are *among* the worst. Rather than following a particular impact assessment, the ISSG selected species for this list based on the following criteria: "their serious impact on biological diversity and/or human activities, and their illustration of important issues surrounding biological invasion. To ensure the inclusion of a wide variety of examples, only one species from each genus was selected" (quote from above-given website, accessed 17 October 2020). The list was first compiled in 2000 and updated in 2004 and 2013. Of the 100 species in this list, 24 can be considered freshwater species (including those that partly live in fresh waters, e.g. amphibians) (Table 1). Once more invasive species have been assessed with the new IUCN EICAT standard, the IUCN list of high-impact invaders might be updated again.

At the continental level, we highlight the EU list of 'Invasive Alien Species of Union concern': https://ec.europa.eu/environment/nature/invasivealien/list/index_en.htm (EU, 2016, 2017, 2019). This list relates to EU Regulation 1143/2014 (EU, 2014) which focuses on the biodiversity impacts of non-native species. As such, these species have been listed from a conservation perspective. The European Commission and EU member states can propose species to be listed. These proposals are supported by scientific risk assessments, which are reviewed by the Scientific Forum established under the regulation. Final decisions on the listing of species

Table 1 Freshwater species included in IUCN's list '100 of the World's Worst Invasive Alien Species' and the EU list of 'Invasive Alien Species of Union concern' (which currently includes 66 species altogether).

100 of the World's Worst Invasive Alien Species	*Invasive Alien Species of European Union concern*
Vertebrates	
Clarias batrachus (walking catfish)	*Alopochen aegyptiacus* (Egyptian goose)
Cyprinus carpio (common carp)	*Lepomis gibbosus* (pumpkinseed)
Eleutherodactylus coqui (common coquí)	***Lithobates catesbeianus* (American bullfrog)**
Gambusia affinis (western mosquitofish)	***Myocastor coypus* (coypu, nutria)**
Lates niloticus (Nile perch)	*Ondatra zibethicus* (muskrat)
***Lithobates catesbeianus* (American bullfrog)**	*Oxyura jamaicensis* (ruddy duck)
Micropterus salmoides (largemouth bass)	*Perccottus glenii* (Amur sleeper)
***Myocastor coypus* (coypu, nutria)**	*Plotosus lineatus* (striped eel catfish)
Oncorhynchus mykiss (rainbow trout)	*Pseudorasbora parva* (stone moroko)
Oreochromis mossambicus (Mozambique tilapia)	***Trachemys scripta* (red-eared, yellow-bellied and Cumberland sliders)**
Rhinella marina (cane toad)	
Salmo trutta (brown trout)	
***Trachemys scripta elegans* (red-eared slider)**	
Invertebrates	
Aedes albopictus (Asian tiger mosquito)	***Eriocheir sinensis* (Chinese mitten crab)**
Anopheles quadrimaculatus (malaria mosquito)	*Faxonius limosus* (spiny-cheek crayfish)
Carcinus maenas (European green crab)	*Orconectes virilis* (virile crayfish)
Cercopagis pengoi (fishhook waterflea)	*Pacifastacus leniusculus* (signal crayfish)
Dreissena polymorpha (zebra mussel)	*Procambarus clarkii* (red swamp crayfish)
***Eriocheir sinensis* (Chinese mitten crab)**	*Procambarus virginalis* (marbled crayfish)
Pomacea canaliculata (golden apple snail)	
Plants	
***Eichhornia crassipes* (water hyacinth)**	*Alternanthera philoxeroides* (Alligator weed)
***Salvinia molesta* (giant salvinia)**	*Cabomba caroliniana* (Carolina fanwort)
Other taxonomic groups	***Eichhornia crassipes* (water hyacinth)**
Aphanomyces astaci (crayfish plague pathogen)	*Elodea nuttallii* (Nuttall's waterweed)
Batrachochytrium dendrobatidis (amphibian chytrid fungus)	*Gymnocoronis spilanthoides* (Senegal tea plant)
	Hydrocotyle ranunculoides (floating pennywort)
	Lagarosiphon major (curly waterweed)
	Ludwigia grandiflora (water primrose)
	Ludwigia peploides (floating primrose-willow)
	Myriophyllum aquaticum (parrot's feather)
	Myriophyllum heterophyllum (broadleaf watermilfoil)
	***Salvinia molesta* (giant salvinia)**

Six freshwater species (highlighted in bold) are included in both lists.

are political, being made by the European Commission and the IAS Committee, which includes representatives from all EU member states. This list is of high practical importance, as the listed species are the focus of management actions in the EU member states. The list focuses on the EU as a whole, and species can only be listed if they are non-native to the entire EU region. This means that, for example, Ponto-Caspian invaders such as the round goby (*Neogobius melanostomus*) cannot be included (such species could be listed as invasive alien species of regional concern). The list was first published in 2016 and included 37 species (EU, 2016); the first update in 2017 added 12 species (EU, 2017) and the second update in 2019 added another 17 species (EU, 2019). Given it is a dynamic list, the number of species it includes will continue to vary over time. Of the 66 currently listed species, 28 (42%) can be considered freshwater species (Table 1). This is a strikingly high number, as freshwater invaders are much less frequently researched than terrestrial ones (Pyšek et al., 2008; Jeschke et al., 2012; Jeschke and Heger, 2018).

Management of non-native species

Framework for the management of non-native species

As a species enters, establishes and spreads within a new environment, the opportunities and objectives of management change. Our main focus here is on active management – actions taken that directly influence the presence or abundance of the focal non-native species. Active management can help achieve the following specific goals: (1) it may prevent a non-native species from entering a new area; (2) if the species is introduced, active management may remove it before it becomes widely established; and (3) if it becomes widely established, active management may limit its impact by reducing spread and abundance. Robertson et al. (2020) provide a framework for the management of non-native species, based on changing species status during the invasion process, and the different forms of management that apply to each stage (Fig. 3). Management may also include actions that reduce impact without affecting the presence or abundance of the focal non-native species, in particular through (4) impact adaptation or (5) environmental restoration after species removal. Finally, we also outline how identifying invasion syndromes (see Glossary) may improve the future management of non-native species.

A range of supporting methods are widely used to guide active management, but do not in themselves involve any form of intervention. These include informing the public and raising awareness (Eiswerth et al., 2011); early detection and monitoring (Trebitz et al., 2017); risk analysis, which includes risk assessment (Mandrak and Cudmore, 2015), risk management (Booy et al., 2017) and risk communication (Verbrugge et al., 2014); contingency planning (Wittenberg and Cock, 2005); and analysis of costs (Oreska and Aldridge, 2011). All of these support active management and help ensure that it is well targeted, feasible and cost-effective.

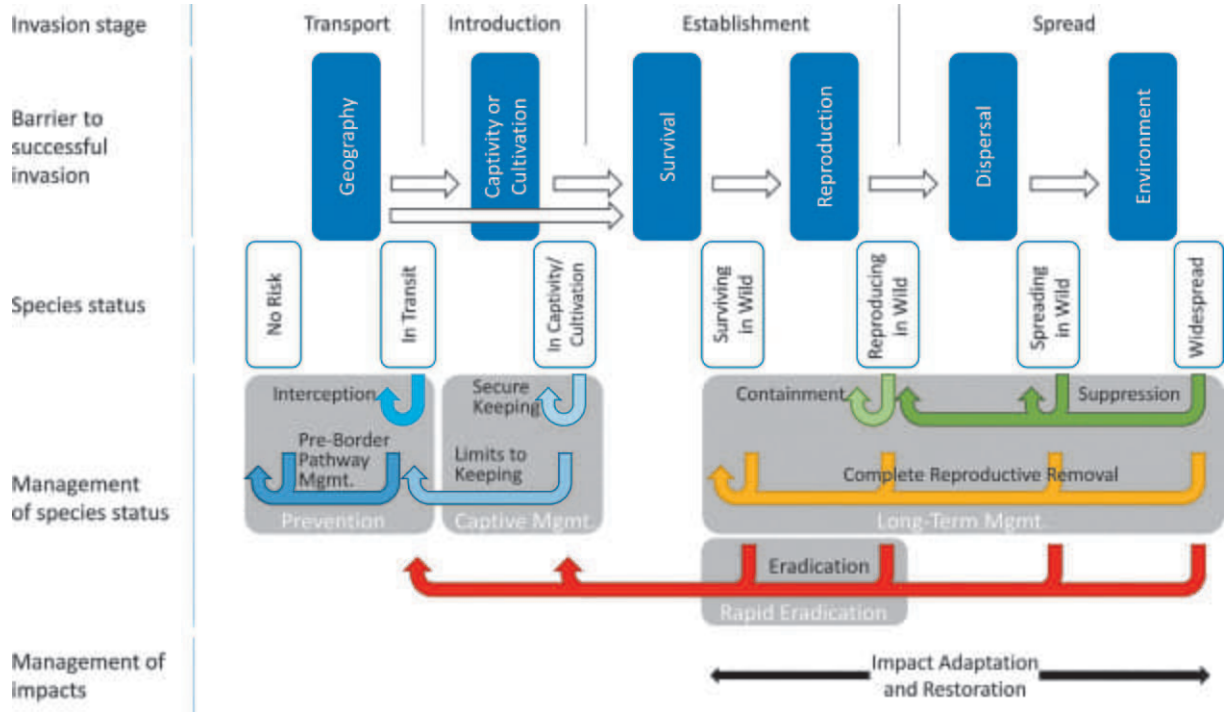

Fig. 3 Framework of the possible management actions during a biological invasion (Robertson et al., 2020). The barriers to successful invasion described by Blackburn et al. (2011) are represented by blue bars. The descriptions of species status associated with the barriers are presented as white boxes. The different forms of management and their associated changes in species status are represented by colored arrows. Four groups of related management actions are represented by grey boxes with white labels.

Some regions, particularly in the Southern Hemisphere, have well developed systems to apply the full range of management options. The New Zealand archipelago has the largest number of established non-native plants compared with other islands (Hulme, 2020). As such, New Zealand is a global leader in tackling plant invasions through stringent biosecurity measures. New Zealand's intended appropriate level of protection is strict compared with that of most other developed countries and operates pre-border control with a 'guilty until proven innocent' approach (Brenton-Rule et al., 2016). Investment in invader management in New Zealand, Australia and South Africa is highly prioritized. In New Zealand, this is supported by legislation (Biosecurity Act 1993, http://www.legislation.govt.nz/act/public/1993/0095/latest/DLM314623.html), particularly for aquatic non-native species, which are generally understudied (Champion, 2018). In South Africa, efforts to manage and regulate invasions began in the 19th century, leading to a wealth of knowledge on the management of non-native species (van Wilgen et al., 2020). In the following sections, we review the different forms of management.

Prevention

Preventing the introduction of non-native species is usually considered a preferable option in management, as the costs for doing so are often significantly lower than those for eradication and long-term control measures necessary once a species is established and spreading. The focus lies on pre-border pathway management, i.e. on reducing the uptake of non-native species and their transport, as well as on the interception of individuals when they first enter a country or other area of interest (Robertson et al., 2020). Successful prevention of non-native species introductions thus critically depends on identifying the relevant introduction pathways. Subsequent to the identification of relevant pathways, these need to be prioritized (e.g. according to the total number of species introduced by each pathway) to maximize management effectiveness in view of the generally limited available resources. Following this approach, management may target pathways shared by several non-native species or shared attributes of different pathways (Hulme et al., 2008).

Pathway identification and prioritization is increasingly integrated into international goals of biodiversity conservation, such as Aichi Target 9 (CBD, 2010), as well as in invasion policy, such as EU regulation No 1143/2014 on invasive alien species (EU, 2014; Rabitsch et al., 2018). In this context, a working collaboration and coordination between countries (especially when they have shared borders) and/or with private companies (e.g. when non-native species of economic interest need to be managed) is another challenge for successful management. Furthermore, pathways and their prioritization need to be regularly updated, as the importance of introduction pathways changes over time, for example due to changes in trade activities (Ricciardi, 2006; Hulme et al., 2008; Essl et al., 2015; Pagnucco et al., 2015).

Despite increasing efforts, our knowledge about the specific pathways used by different non-native species (and about potential regional differences) is still incomplete. This is especially true in regard to unaided introductions, i.e. the secondary natural dispersal of non-native species across borders (e.g. Saul et al., 2017), which may be of particular importance for freshwater species using the large number and extent of continental waterways. So far, shipping ballast water has been identified as a major pathway for the transport of aquatic species (Werschkun et al., 2014), which is why international agreements have introduced measures to reduce the risks of invasive species transport by this route (i.e. pre-border management; Tsolaki and Diamadopoulos, 2010). For the interception of individuals of non-native species, many countries rely on processes of inspection on entry, but this faces many challenges. It mostly applies to formal imports, yet the growth of international online trade has led to alternative routes of entry for species such as aquatic weeds (Kay and Hoyle, 2001). Further, given the diversity of aquatic species and their often cryptic nature, identification can be challenging, although modern genetic barcoding offers a potential solution in some circumstances (Collins et al., 2012).

Captive management

Species may be introduced to an area but held in captivity or under controlled conditions without free-living populations. Such captive populations, however, can provide a route of entry to the wild. With regard to inland waters, this applies especially to species occurring in garden ponds, in aquaria or aquaculture. Two forms of management are available to reduce the risk of these captive species establishing free-living populations in the wild: (1) limits to keeping, and (2) secure keeping. Keeping of a species may be limited by way of legislation. For example, all species listed as Invasive Alien Species of Union concern under EU regulation (EU, 2014) are prohibited from being kept, bred, transported, sold, used or exchanged, allowed to reproduce, to be grown or cultivated, or released into the environment (EU, 2014). Secure keeping, on the other hand, involves intensified measures to reduce the risk that captive species may escape control and establish in the wild. This may include increased biosecurity (e.g. quarantine) and licensing approaches.

Despite the potential use of captive management, escapes from captivity remain an important introduction pathway for freshwater invaders. They include accidental and intentional escapes of species from the aquarium trade (Padilla and Williams, 2004; Magalhães et al., 2017; Banha et al., 2019) and the aquaculture trade (the farming of fish, shellfish and aquatic plants), which is considered a key vector for aquatic invasive species worldwide (Naylor et al., 2001). Here, biosecurity measures exist that aim to protect managed or cultured populations of aquatic species, as well as the wider environment, from disease and pests (Hine et al., 2012), but ensuring their effectiveness can be challenging as there are a wide range of species cultured under a variety of conditions (regarding e.g. containment, intensity of practice, type of management) (Subasinghe, 2005). The main introduction pathways by aquaculture activities are escape via effluent water, inappropriate management and rupture or overflow of ponds after floods

(Forneck et al., 2016). In freshwater systems, which feature high levels of connectivity between water bodies, this leads to the repeated spread of invaders. For example, Nile tilapia (*Oreochromis niloticus*) originating from fish aquaculture in Brazil are now widespread and established from North to South America. This invasive species changes community structure, reduces abundance of planktonic microcrustaceans, lowers water transparency, and increases the abundance of microalgae (Vitule et al., 2009). Aquaculture is a very efficient way of producing proteins for human consumption, and the rapid expansion of this sector warrants special care to avoid the spread of even more invasive species.

Eradication

If an invasive species has established itself in a new environment, then eradication is a favored option. Eradication has been defined as the complete and permanent removal of all wild populations from a defined area by a time-limited campaign (Bomford and O'Brien, 1995). The objective of this approach is clear – complete and permanent removal – but care is needed to define the area involved. Scale is also a significant challenge for the use of this approach. This can be particularly difficult in aquatic environments. Connectivity among water bodies and the flow of water through landscapes increases opportunities for species dispersal, thereby increasing the area of invasion to be addressed. This creates unique challenges for the control and management of aquatic invaders. Detection of non-native species in aquatic habitats is also difficult due to lack of visibility, and control options are often limited. Successful eradication of aquatic species has mainly been achieved at small spatial scales, predominantly in ponds and lakes. Examples include the eradication of the invasive fish species top-mouth gudgeon (*Pseudorasbora parva)* from small fishing lakes (Britton et al., 2008) and of the invasive aquatic plant giant salvinia (*Salvinia molesta)* from ponds in South Carolina, USA (Mack and Lonsdale, 2002). In both cases was the invasive species detected soon after arrival, established in a small area and was removed prior to further spread into neighboring river systems.

Eradication in aquatic habitats often involves extreme measures such as chemical spraying and water draining. In order to remove signal crayfish (*Pacifastacus leniusculus*) from five small water bodies in the North Esk catchment, Scotland, biocide treatment was applied to both the aquatic and adjacent terrestrial habitats. Prior to treatment, through flow was stopped and fish had to be removed, followed by lengthy biomonitoring to test water-quality conditions (Peay et al., 2006). Eradications from open river systems are scarcer, although work in Norway has included the eradication of the salmonid parasite *Gyrodactylus salaris* from entire river systems by treatment with rotenone to temporarily remove their fish hosts (Sandodden et al., 2018). Many documented success stories of eradication within aquatic environments have targeted non-discrete invader populations, and would be better described as complete reproductive removal, as they will need ongoing management to maintain the areas as clear of the species (Robertson et al., 2020). While eradication of some species may be possible in small enclosed water bodies, the feasibility and cost change rapidly as the size of the water body increases, and become particularly challenging in open water systems. Risk management methods are available to help assess and prioritize cases where eradication may or may not be feasible (Booy et al., 2017). As a consequence, considering eradication in aquatic systems is often focused on a rapid response, detecting and removing the species before it has had a chance to spread (Vander Zanden et al., 2010).

Long-term management

If a non-native species has established and eradication is not feasible, then the population will remain and has the potential to spread. In this case, the objective of management is typically driven by the need to reduce the impacts of the species and will require continued management inputs for the foreseeable future. Long-term management of this sort includes three different management approaches: (1) complete reproductive removal; (2) containment; and (3) suppression.

Complete reproductive removal aims to eliminate the entire reproductive population of a species from the area of interest. This management method has similarities to eradication, but requires an on-going effort to maintain the area in the face of dormant life stages such as seeds, or the continued influx of new individuals from neighboring areas. If not, there remains the risk of re-invasion, further reproduction or the remaining presence of non-breeding forms. Examples of this approach include the removal of semi-aquatic American mink (*Neovison vison*) from a large area in Northern Scotland. Although mink populations remain in neighboring areas, ongoing management aims to prevent the re-establishment of breeding mink populations in the cleared area (Bryce et al., 2011). The ruddy duck (*Oxyura jamaicensis*) has been removed as a breeding species from the United Kingdom, and work is ongoing in neighboring countries to remove the species from Europe (Robertson et al., 2015). However, until eradication is complete at a continental scale, ongoing management is required to prevent the species from re-establishing.

Containment includes measures to limit the spread of a reproducing population. This approach includes any action aimed at creating barriers that minimize the risk of an invader population to disperse and spread beyond the invaded area (EU, 2014). Networks of connected inland waters offer opportunities for species spread, and methods to assess the risks and routes of spread are used to prioritize action (Vander Zanden and Olden, 2008). This can be particularly important when new developments such as canals (Leuven et al., 2009) or bulk water transfer (Gallardo and Aldridge, 2018) allow spread between previously isolated catchments. Management can include methods to reduce the risks of local spread through the movement of boats or equipment (Anderson et al., 2015), or the construction of barriers to limit species spread (Lavis et al., 2003; Robinson et al., 2019).

Suppression includes measures to reduce the distribution or abundance of a population within the area of interest. Suppression is a widely used form of management, and its objectives are typically defined in terms of the degree of suppression or the reduction of impact needed to meet socio-economic or conservation goals (e.g. Pinto et al., 2005). There is a large literature describing

management methods to control different aquatic invasive species including the trapping or shooting of animals (Roy et al., 2015; Robertson et al., 2015), cutting of vegetation (Kettenring and Adams, 2011), excavation and dredging of the substrate, water-level manipulation and desiccation (Coughlan et al., 2018), use of toxins or other chemicals (Christie et al., 2003), biological control (Hill et al., 2020), jets of water or steam (Coughlan et al., 2020) or genetic methods to reduce reproduction of the target species (Twohey et al., 2003). Detailed accounts and reviews are available that describe the options for managing different taxa, including aquatic plants (Hussner et al., 2017), crayfish (Manfrin et al., 2019) and fish (Donaldson and Cooke, 2016).

Suppression of impacts often requires balancing the costs of management with the benefits in terms of reduced impacts. Understanding the form of the relationship between effort and benefit is important to rationalize the choices inherent in long-term management (Norbury et al., 2015). However, as biological systems contain great complexity and uncertainty, adaptive management (Williams, 2011) can be of particular benefit in these circumstances. Adaptive management systems learn through management, applying a sequence of predicting the effects of management based on the best available data, implementing management, monitoring the effects, reviewing the results and updating future predictions based on improved understanding. This approach has particular value for guiding rational management given the uncertainties inherent in natural systems.

Impact adaptation (managing impacts without directly intervening with the invader)

The examples above describe the different forms of direct intervention to manage non-native species. However, in many situations the management objective is to reduce impacts, and this can also be achieved without direct intervention with the respective species. Examples include responding to increased erosion risk by mechanically stabilizing habitats (Bendoricchio et al., 2000), altering human behavior to adapt to the presence of the invasive species (Havel et al., 2015) or compensating landowners for damage caused (Panzacchi et al., 2007).

Restoration

Restoration is the management of the environment following its degradation, for example due to an invasive species. Related terms describing different forms and intensities of management include regeneration, revegetation, replacement, rehabilitation and remediation of a habitat favoring native communities (van Andel and Aronson, 2012). Definitions include 'restoring ecosystems following the removal of invasive species' (van Wilgen et al., 2014) or to 'restore or rehabilitate degraded areas to their proper ecological function [. . .] after invasive species removal' (USDA, 2004).

Restoration of freshwater habitats can be particularly challenging, as they are typically highly connected (river catchments), heavily impacted by humans and difficult to monitor, as most changes occur below the water surface. There are a limited number of successful restoration examples of invaded freshwater habitats (Havel et al., 2015). When restoration efforts are successful, the benefits can be tangible. For example, water hyacinth (*Eichornia crassipes*) is an aquatic plant that can form dense floating mats on the surface of water bodies. These mats alter processes of respiration and primary production, with flow-on effects to food webs; they also reduce connectivity between adjacent water bodies (Perna et al., 2012). Restoration of the heavily invaded Burdekin River floodplain, Australia, following removal of water hyacinth, led to improved water quality and increased connectivity between adjacent lagoons. This resulted in the re-establishment of many native fish populations (Perna et al., 2012).

A lack of funding often prevents the long-term monitoring of restoration sites following the removal of non-native species (Geist and Hawkins, 2016). However, without monitoring it is difficult to deduce the efficacy and longevity of restoration practices in freshwater systems. The Working for Water program was established in South Africa in 1995. In coordination with local communities, the scheme aims to remove invasive species in order to restore water supplies (Binns et al., 2001). Ongoing monitoring and treatments are carried out to maintain restoration sites, which also provides employment opportunities for local communities. Plant invaders in riparian zones can use significantly more water than native species: clearing 25,000 m^2 of invasive trees from river banks within the Western Cape, South Africa, led to an increase in streamflow of an estimated 30,480 l of water per day (Binns et al., 2001), illustrating the links between restoring invaded sites and livelihoods.

Thus, targeted approaches can aid in the success of restoration practices. Restoration projects should also be properly monitored to assess success, thus enabling adaptive management and learning for the future from both successful and unsuccessful restorations (Janssen et al., 2007).

Invasion syndromes

The management framework presented above greatly helps to determine the appropriate management response to individual cases of invasion. Novoa et al. (2020) argue that for being able to deal with the continuously growing number of non-native species, we need to determine groups of invasion events for which similar management goals and responses apply. They propose to delineate invasion syndromes by identifying congruence among invasions regarding the introduction pathways used, the traits of the non-native species, the characteristics of the area of introduction and the invasion outcomes. The expectation is that congruence in these aspects will also lead to congruence in the set of response options that are suitable for managing the respective invasions. By identifying a species as a member of an invasion syndrome, we would know which management measures are likely to be most effective without having to consider a multitude of case-specific details first. Thus, we can act faster and with a higher probability of success, based on sharing of management lessons learnt from previous invasion events. Novoa et al. (2020) describe introduced

piscivorous freshwater fish as an example for a freshwater invasion syndrome. They are often introduced intentionally (e.g. for enhancing fisheries) and primarily invade connected inland waters. Impacts include hybridization with native species, introduction of disease and extirpations of native species by direct predation. The management of invasive freshwater fish turns out to be challenging: they are difficult to eradicate once established, and conflicting values of stakeholders may interfere (see above, e.g. the rainbow trout (*Oncorhynchus mykiss*) conflict, Woodford et al., 2016). Therefore, active management may in this case focus on prevention and long-term management.

Summary

The impact of non-native species has been defined in different ways and from different perspectives. It is therefore important to be aware of the various possible meanings of 'impact' in the context of biological invasions. Similarly, numerous schemes have been developed to assess the impacts of non-native species The EICAT scheme for assessing environmental impacts has recently been adopted as an IUCN standard (Blackburn et al., 2014; Hawkins et al., 2015; IUCN, 2020a, b), and the SEICAT scheme can be analogously used to assess the socio-economic impacts of non-native species (Bacher et al., 2018). These and other schemes have been widely applied, yet freshwater species have been under-assessed when compared with terrestrial species. There are numerous lists of high-impact invasive species, some are legally binding (e.g. the European Union list of 'Invasive Alien Species of Union concern'), while others are not (e.g. the IUCN list of '100 of the World's Worst Invasive Alien Species'). Freshwater species that often appear on high-impact lists include the coypu (*Myocastor coypu*), American bullfrog (*Lithobates catesbeianus*), red-eared slider (*Trachemys scripta elegans*), Chinese mitten crab (*Eriocheir sinensis*), water hyacinth (*Eichhornia crassipes*) and giant salvinia (*Salvinia molesta*).

As for impact, the terminology referring to the management of non-native species is often confusing. However, a standard framework has recently been developed which we outlined above (Robertson et al., 2020). This framework aligns with the invasion process and its consecutive stages (see Glossary and Blackburn et al., 2011). It includes various management actions that either actively target the focal non-native species (prevention, captive management, eradication and long-term management) or reduce impact without affecting the presence or abundance of the focal non-native species (impact adaptation and restoration). Invasion syndromes (Novoa et al., 2020) may be an efficient way of dealing with the continuously growing number of non-native species.

Different stakeholders are involved in the impact and management of non-native species: impact assessment is mainly done by researchers; decisions which species should be listed on legally binding lists of high-impact invaders are mainly made by policy makers; decisions which invaders should be targeted by which management actions are mainly made by national, regional and local authorities; and on-the-ground management is mainly carried out by paid practitioners and unpaid volunteers. All stakeholders have an important role and collaboration is recommended. However, there are often conflicts, and a lack of understanding and communication between stakeholders can hamper effective research, decision-making and management (e.g. Heger et al., 2013; Matzek et al., 2015). Platforms and networks such as the RISCC Network in the Northeast USA (www.risccnetwork.org) are important for bringing stakeholders together and improving mutual understanding.

Knowledge gaps

- Freshwater invasive species are known for their high potential to have strong harmful impacts (see e.g. Vilà et al., 2010 and the EU list of Invasive Alien Species of Union Concern, which includes a high proportion of freshwater invaders, see Table 1), yet only few studies in invasion biology focus on freshwater habitats (Pyšek et al., 2008; Jeschke et al., 2012; Jeschke and Heger, 2018).
- Knowledge about the mid- to long-term impacts of non-native species is critical, yet the majority of studies about biological invasions only cover short timespans (Strayer et al., 2006; Pergl et al., 2020).
- Evidence that is available for those few freshwater invaders that have been investigated in a high number of systems and for longer time periods suggests that their population dynamics and impacts can be highly variable and context-dependent (see e.g. Strayer et al., 2019 for zebra and quagga mussels, *Dreissena polymorpha* and *D. rostriformis*). Better understanding this context-dependency is critical.
- The standardized EICAT and SEICAT schemes for assessing negative impacts of non-native species on biodiversity and socio-economics (as outlined above) do not yet have parallel schemes for assessing positive impacts of non-native species. Such schemes are currently being developed. Schemes assessing positive impacts of non-native species are generally rare compared to those assessing negative impacts (Vimercati et al., 2020). Once they are available, careful evaluation is needed how non-native species with both positive and negative impacts should be managed.
- Since escapes from captivity remain an important introduction pathway for freshwater invaders, more effective ways for captive management need to be found, taking into account the wide range of species cultured under a variety of conditions.
- The number of successful eradications in freshwater systems remain limited. As experience grows and further methods are developed, there is a need to increase the number and scale of eradication programs.

- For many established invasive species, long-term management will be crucial to reduce their impacts. There is a need to develop new and more cost-effective methods of reducing impacts, together with recording and sharing information on costs and best practice.
- Restoration of invaded freshwater habitats is difficult and relies on long-term monitoring which is often limited by lack of funding. Clear restoration targets and assessment of success can aid progression towards better restorations in the future.
- More invasion syndromes (Novoa et al., 2020) have yet to be identified and existing ones need to be refined, so that their full potential for a more effective management can be exploited.

Acknowledgments

We thank Ken Irvine for the invitation to contribute this chapter. His comments on the chapter and those of Thomas Mehner and an anonymous reviewer are highly appreciated as well. JMJ and WCS acknowledge support by the Belmont-Forum-BiodivERsA project InvasiBES through the national funder German Federal Ministry of Education and Research (BMBF; grant 01LC1803A). TE was supported by the Alexander von Humboldt Foundation. This chapter is a contribution of the Invasion Dynamics Network (InDyNet).

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Relevant websites

https://www.cabi.org/isc—CABI Invasive Species Compendium.
https://ec.europa.eu/environment/nature/invasivealien/list/index_en.htm—EU List of Invasive Alien Species of Union concern.
https://easin.jrc.ec.europa.eu—European Alien Species Information Network (EASIN).
http://www.fao.org/fishery/dias/en—FAO Database on Introductions of Aquatic Species (DIAS).
www.corpi.ku.lt/databases/index.php/aquanis—Information system on aquatic non-indigenous and cryptogenic species (AquaNIS).
https://www.invasivesnet.org—International Association for Open Knowledge on Invasive Alien Species (INVASIVESNET).
https://indynet.de—Invasion Dynamics Network (InDyNet).
http://www.iucngisd.org—IUCN Global Invasive Species Database (GISD).
http://www.issg.org—IUCN Invasive Species Specialist Group (ISSG).
https://www.risccnetwork.org—Northeast RISCC Network.

Biological Invasions: Case Studies

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Alien species See 'non-native species.'

Impact A change or effect of a non-native species on either the environment (i.e. biodiversity) or socio-economics in the broad sense (i.e. including culture, religion, human health, safety, livelihoods and other aspects of human well-being), whether positive or negative (Jeschke et al., 2014).

Introduction pathways The processes and mechanisms behind the human-mediated transportation and introduction of non-native species from one geographic location to another. They can be either intended by humans or unintentional (Hulme et al., 2008).

Invasive species Species that have successfully completed the invasion process, i.e. they have: (i) been intentionally or unintentionally transported by human action from their native range to a new range; (ii) been released there or escaped into the wild; (iii) have established one or more self-sustaining populations; and (iv) have spread substantially beyond their point(s) of release or escape (Blackburn et al., 2011; Jeschke et al., 2013). Synonyms of invasive species are 'invasive alien species' or 'invasive non-native species.'

Management of biological invasions Actions that reduce the presence, abundance or impact of non-native species. These actions may: (1) prevent a non-native species from entering a new area (prevention and captive management); (2) if introduced, may remove it before it becomes widely established (eradication); and (3) if it becomes widely established, may limit its impact by reducing spread and abundance (long-term management). Management may also include actions that reduce impact without affecting the presence or abundance of non-native species. These actions include: (4) impact adaptation; and (5) environmental restoration after species removal (Robertson et al., 2020).

Non-native species Species that have been intentionally or unintentionally transported by human action from their native range to a new range. Non-native species are also called 'alien species,' 'exotic species' or 'non-indigenous species' (Blackburn et al., 2011). Therefore, non-native species are not necessarily invasive, but invasive species as defined above are always non-native.

Introduction to the topic

Biological invasions are a major research focus of ecologists, conservation biologists and scientists in related fields. This is particularly true for terrestrial invaders, but increasingly also for freshwater species. Comparing studies in freshwater and terrestrial habitats suggests that non-native freshwater species have both particularly high invasion success and particularly high impacts in their exotic ranges (Vilà et al., 2010; Jeschke and Heger, 2018). Thus, research insights are clearly needed to allow for a better understanding and more effective management of freshwater invasive species.

This chapter builds on and complements the two previous chapters on biological invasions in this encyclopedia, which focused on (i) the introduction, establishment and spread of non-native species, and (ii) on their impact and management. In the current chapter, case studies of invasive species in different taxonomic groups are featured. The compilation we present here cannot be exhaustive, as that would need an encyclopedia in itself.

 https://doi.org/10.1016/B978-0-12-819166-8.00035-9

We highlight taxonomic groups that either (1) include particularly well-known freshwater invaders (bivalves; crustaceans, here with a focus on crayfish; and fish) or (2) are often overlooked when it comes to freshwater invaders, as they are mainly investigated in terrestrial habitats (plants and mammals). For each taxonomic group, we provide a brief general introduction to their biology and ecology. We also give examples of invasive species within each taxon, particularly high-impact invaders, and indicate where on the globe they are invasive. The main introduction pathways are outlined as well, including a brief description of major events in the taxonomic group's invasion history, and the main ecological and socio-economic impacts. Finally, we describe possible management actions.

Aquatic plants

Aquatic plants (macrophytes) are important components of freshwater ecosystems, affecting diverse ecosystem functions and services (Hilt et al., 2017). Many aquatic macrophyte species have a high invasion potential due to their high propagule pressure, rapid growth, wide environmental tolerance, high phenotypic plasticity and ability to produce allelopathic compounds (Riis et al., 2010; Heidbüchel et al., 2020; Hussner et al., 2021). Biological interactions such as competition, mutual facilitation, invasional meltdown and novel weapons can also be crucial for their invasion success (e.g. Fleming and Dibble, 2015; Wegner et al., 2019). Climate change is expected to result in a range expansion of macrophytes from warmer climates into formerly cooler regions. In general, global warming and habitat disturbance by hydrological and trophic alterations can accelerate the invasion success of non-native aquatic macrophytes. In contrast, the presence of native vegetation can decrease the establishment success of non-native macrophytes (Petruzzella et al., 2018).

Ornamental trade is considered to be the main introduction pathway for invasive aquatic plants (Maki and Galatowitsch, 2004; Peres et al., 2018; Hill et al., 2020). Most traded aquatic plant species are characterized by a low sensitivity to mechanical and handling damage, easy propagation and the ability to grow under a large variety of environmental conditions; traits that are related to their invasiveness in freshwater ecosystems (Azan et al., 2015). Once introduced into a new region, invasive macrophytes spread via sexual and asexual propagules (i.e. stem fragments and tubers or turions; Hussner et al., 2021). Within connected water bodies, these propagules are usually transported by water movement (Heidbüchel et al., 2016, 2020). Overland transport to new water bodies can occur through attachment to water sport equipment (Johnstone et al., 1985; Bruckerhoff et al., 2015) or animals (Van Leeuwen, 2018).

Once established, non-native aquatic plants often rapidly grow and spread, and can cause various significant ecological and socio-economic impacts. Ecosystem functions and services can be hampered, such as fishing, boating and diving, and the aesthetic values of infested waters can be reduced (Janssen et al., 2021). A well-known example is the invasion of the free-floating water hyacinth (*Eichhornia crassipes*, Fig. 1A) into Lake Victoria (Africa). It directly and indirectly affected 30 million people through the

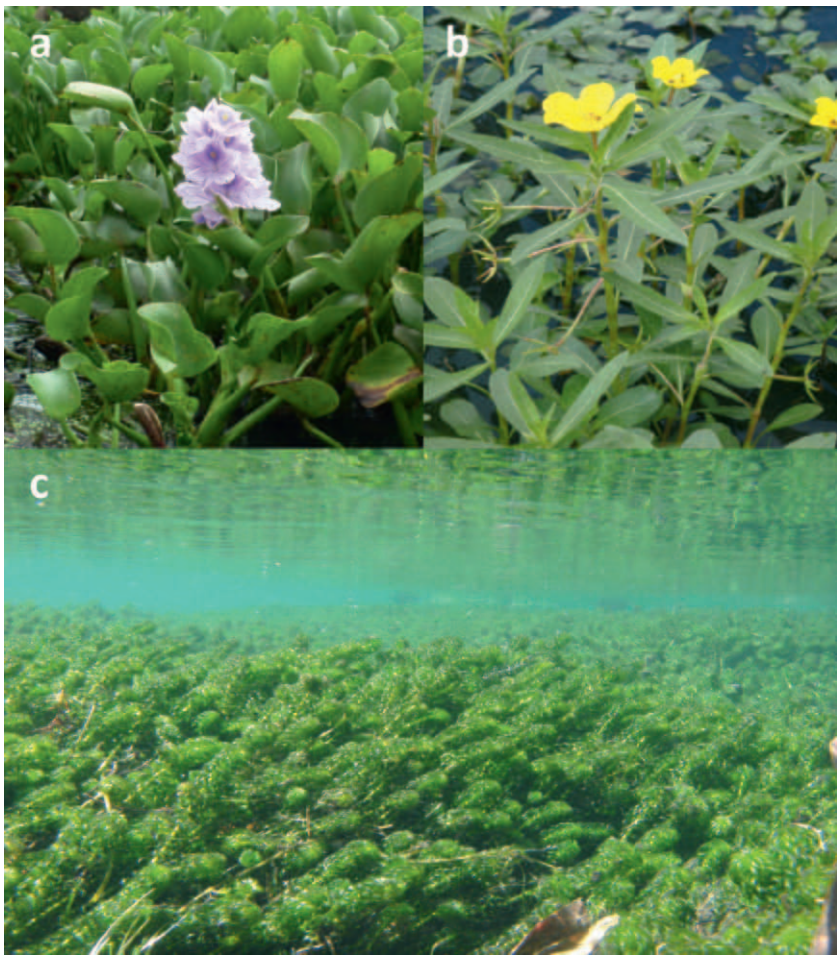


Fig. 1 Three types of invasive aquatic plants: (A) free-floating *Eichhornia crassipes* (water hyacinth), (B) sediment rooted, emerged and floating-leaved *Ludwigia grandiflora* (water primrose) and (C) submerged rooted *Lagarosiphon major* (curly waterweed). Photos: Andreas Hussner.

loss of fisheries, water supply and transport, environmental health and power generation (Aloo et al., 2013). Invasive macrophytes are recognized as a major biodiversity threat. They can change the structure and composition of native macrophyte, zooplankton (Stiers and Triest, 2017), macroinvertebrate (Houston and Duivenvoorden, 2002) and fish communities (Carniatto et al., 2013). Invasive macrophytes can grow in dense mats that limit water flow and light penetration, cause hypoxia or anoxia in the water column and alter nutrient cycling (Urban et al., 2006; Thomaz et al., 2015), productivity and food-web dynamics. Dense stands of invasive macrophytes can trigger stable stratification events and can be involved in a change in the metabolism of ecosystems, resulting in a net nutrient release towards the water column, concurrently with a net increase in carbon emission towards the atmosphere, as recently demonstrated for large infestations of *Lagarosiphon major* (Fig. 1C) and *Egeria densa* in France (Ribaudo et al., 2018). On the other hand, non-native macrophytes can also provide habitat to animals or remove nitrogen from inland waters (Strayer et al., 2003; Tall et al., 2011). Overall, current knowledge on the impacts of non-native macrophytes is restricted to a few species (e.g. Table 1).

The most effective management action against invasive macrophytes is preventing their introduction (Hussner et al., 2017). Trading bans are a major tool and should be based on Pest Risk Assessment scorings of plant characteristics, such as habitat versatility, competitive ability, reproductive output, dispersal mechanisms and the range of potential impacts. The Aquatic Weed Risk Assessment Model (AWRAM, Champion and Clayton, 2000) has been successfully established in New Zealand and Australia (see Table 1 for AWRAM scores of invasive macrophytes in New Zealand and the USA) to guide the import control and management of invasive and potentially invasive macrophytes. Early detection and rapid response increase the likelihood of eradication of invasive macrophytes. Maintenance of invasive macrophyte stands, however, often only come into play after a species has spread and causes nuisance, or if eradication measures have failed (Hussner et al., 2017; Simberloff, 2021). The eradication and management of invasive macrophytes comprise a range of biological, chemical and mechanical control methods that are either applied alone or in combination, and which must be tailored towards the focal species and habitat characteristics (Hussner et al., 2017).

Table 1 Status (native or non-native) and classification of invasiveness of 21 selected macrophyte species in the USA (www.plants.usda.gov; Gordon et al., 2012), South Africa (Coetzee et al., 2011; Hill et al., 2020), China (Wu and Ding, 2019) and New Zealand (Champion and Clayton, 2001); additional information was taken from CABI (2020).

	Species	*USA*	*South Africa*	*China*	*New Zealand*	*EU*
Free-floating	*Azolla filiculoides*	Native	Non-native, invasive	Non-native, invasive	Non-native	Non-native
	Eichhornia crassipes	Non-native (81/100)	Non-native, invasive	Non-native, invasive	Non-native (67/100)	Non-native Union list
	Pistia stratiotes	Non-native (72)	Non-native, invasive	Non-native, invasive	Non-native (42)	Non-native
	Salvinia molesta	Non-native, invasive	Non-native, invasive	Not present	Non-native (57)	Non-native Union list
Sediment rooted, emerged/floating-leaved	*Alternanthera philoxeroides*	Non-native (75)	Not present	Non-native, invasive	Non-native (63)	Non-native Union list
	Crassula helmsii	Non-native	Not present	Not present	Native	Non-native
	Hydrocotyle ranunculoides	Native	Not present	not present	Not present	Non-native Union list
	Hygrophila polysperma	Non-native (53)	Not present	Native	Not present (44)	Non-native
	Ludwigia grandiflora	Partly native and non-native	Not present	Not present	Not present	Non-native Union list
	Ludwigia peploides	Partly native and non-native	Not present	Not present	Non-native (51)	Non-native Union list
	Myriophyllum aquaticum	Non-native (75)	Non-native, invasive	Non-native, invasive	Non-native (56)	Non-native Union list
	Trapa natans	Non-native	Native	Native	Not present (63)	Native
Sediment rooted, submerged	*Cabomba caroliniana*	Partly native and non-native	Non-native, not invasive	Non-native, invasive	Non-native (58)	Non-native Union list
	Ceratophyllum demersum	Native	Native	Native	Non-native (67)	Native
	Egeria densa	Non-native (71)	Non-native, invasive	Non-native	Non-native (64)	Non-native
	Elodea canadensis	Native	Not present	Non-native	Non-native	Non-native
	Elodea nuttallii	Native	Not present	Non-native	Not present	Non-native Union list
	Hydrilla verticillata	Non-native (79)	Non-native, invasive	Native	Non-native (74)	Partly native and non-native
	Lagarosiphon major	Not present	native	Not present	Non-native (60)	Non-native Union list
	Myriophyllum heterophyllum	Partly native and non-native	not present	Non-native	Not present	Non-native Union list
	Myriophyllum spicatum	Non-native (81)	native	Native	Not present 73	native

Invasiveness is based on the Aquatic Weed Risk Assessment score (in parenthesis for the USA and New Zealand; maximum score = 100) and for the EU on the List of Invasive Alien Species of Union concern (EU, 2016, 2017, 2019).

Adapted from Hussner A, Stiers I, Verhofstad M, Bakker ES, Grutters B, Haury J, Van Valkenburg J, Brundu G, Newman J, Clayton J, Anderson L, and Hofstra D (2017) Management and control methods of invasive alien freshwater aquatic plants: A review. *Aquatic Botany* 136: 112–137.

Bivalves

Although just a few of the world's ca. 1200 species of freshwater bivalves have become invasive, they include some of the world's most widespread, well known, and problematic invaders. The five selected species discussed here come from four widely divergent groups of bivalves, and so have different origins, affinities, biological characteristics and histories of spread. Specifically, two species of Dreissenidae, the zebra mussel (*Dreissena polymorpha*, Fig. 2A) and the quagga mussel (*Dreissena bugensis*), have spread widely from their native ranges in the Black, Caspian and Aral Sea basins. Both are now common and widespread in Europe and North America. Dreissenids have separate sexes, free-swimming planktonic larvae that live for a few weeks and sessile adults that live for 1–10 years (Nalepa and Schloesser, 2014). The golden mussel *Limnoperna fortunei* (Mytilidae, Fig. 2B) is native to south China and perhaps elsewhere in southeastern Asia. It has spread widely elsewhere in Asia and in South America. Its life cycle and general biology are broadly similar to the dreissenids (Boltovskoy, 2015). The Asian clam *Corbicula* (Cyrenidae, Fig. 2C), native to East Asia, is now common and widespread in the Americas and Europe, and recently appeared in Morocco (Crespo et al., 2015). The taxonomy of *Corbicula* is poorly understood, and perhaps two to four species of *Corbicula* are spreading around the world (Lydeard and Cummings, 2019). Most invasive populations of *Corbicula* apparently consist of hermaphrodites reproducing asexually by androgenesis (in which only male nuclear DNA is inherited; Pigneur et al., 2012). Adults typically live for 1–5 years. Finally, the Chinese pond mussel *Sinanodonta woodiana* (Fig. 2D) is a pearly mussel (Unionidae) native to East Asia that is now common and widespread across Europe. Non-native populations have also established outside its native range in Asia, and in Central America and the USA (from which it was apparently eradicated). Larvae of the Chinese pond mussel are parasites on fish. Following this parasitic phase, the burrowing juvenile and adult live in sediments, and may live for 10–15 years (Cummings, 2011).

Invasive bivalves spread through a combination of long-distance leaps across continents and drainage basins via human activities, plus short-distance spread within drainage basins via both natural and human-aided means (see references cited in the previous paragraph). The main human-aided introduction pathways depend on the biology of each species. For species with free-living larvae (all of the species treated here except the Chinese pond mussel), the movement of ship ballast water between continents has been of primary importance. The larvae or small juveniles and adults of these species are also readily transported on recreational boats. The chief pathway for the Chinese pond mussel was the transport of infested carps in aquaculture. The Chinese pond mussel and *Corbicula* are sold as 'biofilters' in the aquarium and water-garden trade.

Most long-distance leaps in freshwater bivalve distributions occurred since 1900, reflecting large increases in intercontinental trade. Zebra mussels spread westward across Europe beginning in 1825 with the opening of new canals, and both zebra and quagga mussels appeared in North America in the 1980s via ballast water introductions. The golden mussel moved into new areas of Asia between 1965 and 1990, and was first seen in South America in 1991. *Corbicula* appeared in western North America in 1924, in the

Fig. 2 Four important invasive freshwater bivalves: (A) a cluster of zebra mussels (*Dreissena polymorpha*); (B) the golden mussel (*Limnoperna fortunei*); (C) the Asian clam (*Corbicula fluminea*); (D) the Chinese pond mussel (*Sinanodonta woodiana*). (A) Photo: Heather Malcom. (B) Photo: Demetrio Boltovskoy. (C) Photo: Björn S., via Wikipedia. (D) Photo: Welter Schultes, from http://www.animalbase.uni-goettingen.de/zooweb/servlet/AnimalBase/home/species?id=2919.

eastern and central United States in the 1950s, and in South America and Europe in the 1970s. The Chinese pond mussel came into Europe in the 1960s. All of these bivalves are spreading so rapidly that the ranges given here will soon be out of date. Future range expansions will probably include spread into continents and drainage basins not yet occupied, as well as range-filling within already-occupied regions (e.g. Strayer, 2010; Gama et al., 2017; Petsch et al., 2021).

The impacts of invasive bivalves stem from three major mechanisms: (1) removal of phytoplankton and consequent effects on the food web; (2) fouling of human-made structures and animals; and (3) habitat engineering by shell-building (Strayer, 2009, 2010; Higgins and Vander Zanden, 2010; Nalepa and Schloesser, 2014; Sousa et al., 2014; Boltovskoy, 2015). *Sinanodonta* also competes for fish hosts with native unionid mussels (Donrovich et al., 2017). All of the bivalves discussed here feed on phytoplankton and other small particles in the water column. Because they often form dense populations, their feeding can substantially reduce phytoplankton populations, often by 50% or more. Bivalve-caused losses of phytoplankton have led to strong impacts on freshwater ecosystems, including increased water clarity, increased concentrations of soluble nitrogen and phosphorus, declines in zooplankton, native bivalves and suspension-feeders in general, increased growth and coverage of aquatic plants, and changes in fish abundance, growth and distribution. *Dreissena* and *Limnoperna* attach to hard surfaces, including shells of living native bivalves, a process called 'fouling.' They and *Corbicula* block pipes and other water infrastructure, leading to problems for power plants, water intakes and irrigation systems (Nakano and Strayer, 2014). Fouling by *Dreissena* has extirpated or greatly reduced many populations of unionid mussels (Lucy et al., 2014). Finally, both the shells of living bivalves and their empty shells, which may persist for decades after death, change the physical character of aquatic habitats, affecting both their value as habitat for other animals and exchanges of materials between the sediments and water column. Large windrows of shells and decaying animals on beaches may reduce their recreational value.

It is easier and more cost-effective to prevent new invasions by freshwater bivalves than to manage established populations. New invasions can be reduced by managing the vectors that carry bivalves from place to place. For example, regulations, public education and application of better practices can prevent movement of larvae in ballast water, live wells and bait buckets, or of older animals on boat hulls and trailers; it can stop sale of living bivalves in the pet and water-garden trade, reduce deliberate releases of living bivalves into lakes for food or to 'clean up the water' and reduce transport of *Sinanodonta* in contaminated aquaculture stock.

Options are fewer once a bivalve population is established. If the control area is small or isolated, it may be feasible to apply molluscicides (e.g. the bacterial toxin Zequanox® for dreissenids, or potassium chloride) to locally eradicate the bivalve (Fernald and Watson, 2014; Whitledge et al., 2015). In some cases, bivalves may be killed by installing benthic barriers or draining the body of water. In closed settings (e.g. water intakes, power plants), bivalve fouling can be managed using screening, antifouling coatings, chlorine, polyquaternary ammonium compounds, heat, dewatering or mechanical scraping (Mackie and Claudi, 2009; Nalepa and Schloesser, 2014). Because of concerns about feasibility, cost and harmful side-effects, post-establishment control is used widely only in closed settings and not in open waters. If it is not possible to control or eradicate the population of the invasive bivalve itself, it may be possible to reduce some of its harmful effects. For example, imperiled native bivalves can be moved into uninfested waters or propagated in hatcheries or zoos, nuisance aquatic plants that flourish in the newly clearer waters can be cut and oxygen-depleted waters can be aerated. These options have rarely been pursued.

Crayfish

Freshwater crayfish are a diverse group of decapod crustaceans in temperate and subtropical regions that can be found in lotic, lentic and terrestrial habitats. They are native to all continents except continental Africa (seven species occur in Madagascar) and Antarctica. Over 660 species have been described, with hotspots of diversity in the south-eastern USA (>400 species) and south-eastern Australia (>170 species) (Crandall and De Grave, 2017). Many crayfish species, including invasive ones, are able to construct burrows that ensure their survival during droughts (Reynolds et al., 2013). They are 'ecosystem engineers' (see Jones et al., 1994, 2010) that can fundamentally alter the structure and functioning of aquatic ecosystems. As generalist omnivores, crayfish also influence the rates and pathways of nutrient and energy flows (Reynolds et al., 2013).

The economic significance of freshwater crayfish led to their successful introductions around the world (Hobbs et al., 1989; Kouba et al., 2014; Madzivanzira et al., 2021). Their tolerance to a broad range of environmental conditions and high fecundity predisposed them to establish and spread in new ranges (Hobbs and Lodge, 2010; Lodge et al., 2012; Twardochleb et al., 2013). Freshwater crayfish have been traded for direct consumption, aquaculture and stocking for centuries, with documented translocations dating back to the 18th century (Hobbs et al., 1989). More recent introductions are also related to the pet trade and the use of crayfish as fish bait (Souty-Grosset et al., 2006; Oficialdegui et al., 2020; Madzivanzira et al., 2021). As a result, Europe currently harbors the highest number of non-native crayfish species of North American and Australian origin (Kouba et al., 2014), and all crayfish species occurring in continental Africa are of foreign origin (Madzivanzira et al., 2021). North American crayfish species are most frequently introduced, particularly the genera *Faxonius, Pacifastacus* and *Procambarus*. For example, the originally North American red swamp crayfish (*Procambarus clarkii*, Fig. 3A) is now the most widely introduced crayfish species worldwide (Loureiro et al., 2015; shown for Europe in Fig. 3D). Due to its high growth rate and commercial value, it has become established all over the USA (far beyond its native range), in Europe, South America, Africa and Asia (Hobbs et al., 1989; Loureiro et al., 2015; Oficialdegui et al., 2020).

More recently, introductions of *P. clarkii* and many other freshwater crayfish were linked to the pet trade, specifically aquarium releases and garden-pond escapes (Peay, 2009; Patoka et al., 2014; Faulkes, 2015). For more than a decade, trade in ornamental

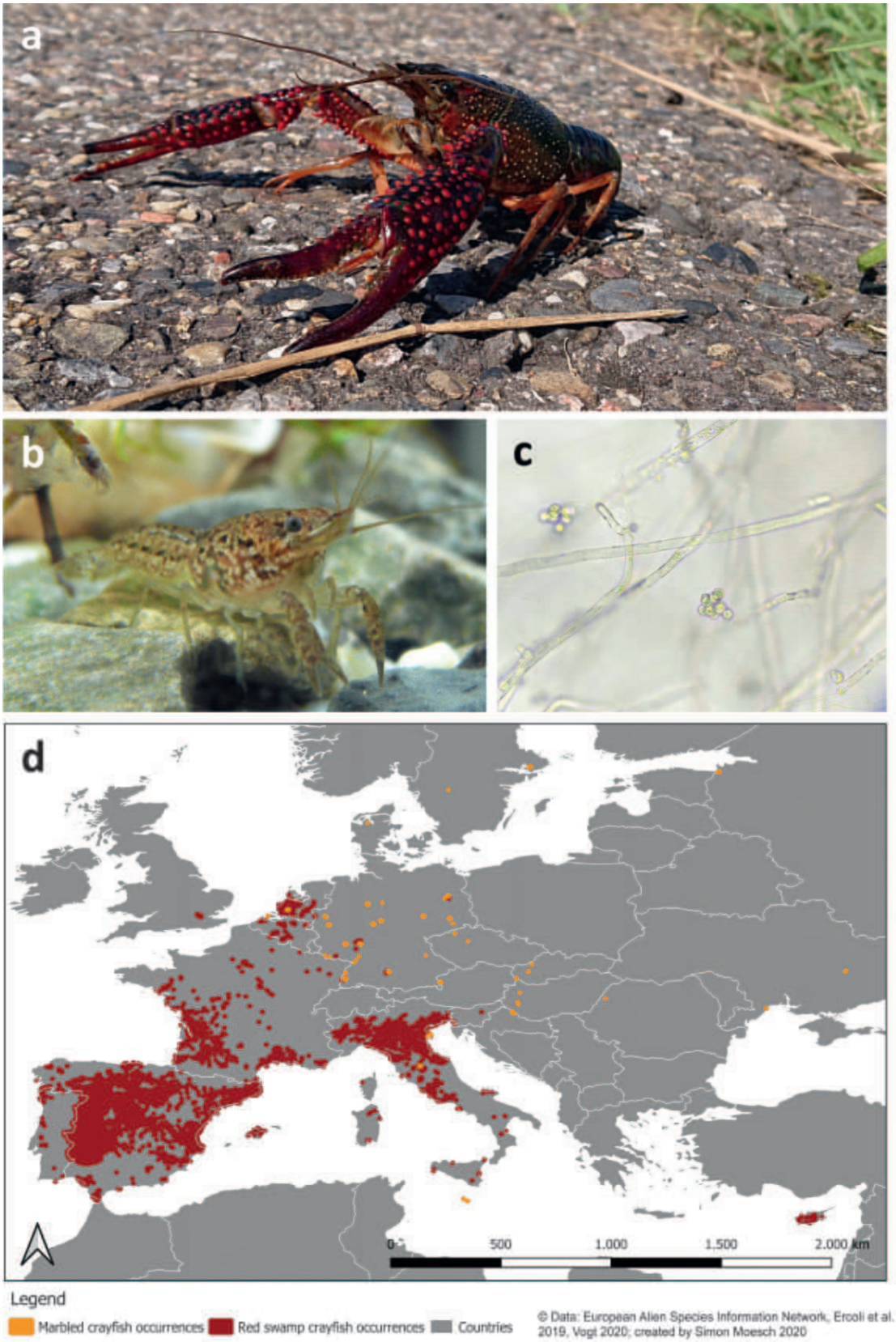


Fig. 3 The invasive (A) red swamp crayfish (*Procambarus clarkii*) and (B) marbled crayfish (*Procambarus virginalis*) can both transmit the (C) crayfish plague pathogen (*Aphanomyces astaci*) and occur in (D) many European countries (see the main text for other occurrences on the globe). Photos A–C by Bram Koese.

crayfish has acted as the most prominent introduction pathway of these crustaceans in Europe (Peay, 2009), including the marbled crayfish (*Procambarus virginalis*, Fig. 3B), the only known parthenogenetic crayfish, which appeared in the German pet trade in the mid-1990s (Scholtz et al., 2003). Due to the fact that a single individual is able to establish a population, this species has high potential to become a widespread invader. In fact, it has already managed to establish populations in many European countries (Fig. 3D, Ercoli et al., 2019; Vogt, 2020 and references therein) and to spread rapidly across Madagascar (Andriantsoa et al., 2020).

The socio-economic benefits through stocking and aquaculture are the main reasons for most crayfish introductions. However, introduced crayfish can cause negative ecological and socio-economic impacts that often surpass these benefits (Lodge et al., 2012; Twardochleb et al., 2013). For example, non-native crayfish can interfere with fisheries by damaging fishing gear, scavenging on caught fish, competing with fish and negatively affecting their recruitment. As prominent burrowers, they may increase bank erosion and siltation of waterways as well as damage earth dams and irrigation canals that may lead to drying of the rice fields (Lodge et al., 2012; Madzivanzira et al., 2021). They can also substantially alter freshwater food webs by negatively affecting the biomass and abundance of macrophytes, invertebrates, fish and amphibians (Twardochleb et al., 2013). Moreover, many native crayfish are threatened through competition and predation, which often leads to their replacement and disappearance from water catchments.

Non-native crayfish may also act as vectors of harmful pathogens, parasites and epibionts. The most infamous example is the crayfish plague pathogen (*Aphanomyces astaci*, Fig. 3C; Souty-Grosset et al., 2006). It was introduced to Europe in the mid-19th century and since then has caused severe declines of European crayfish populations (Alderman, 1996) that led to its inclusion among '100 of the World's Worst Invasive Alien Species' (http://www.iucngisd.org/gisd/100_worst.php). North American crayfish exhibit higher resistance to this pathogen, but act as asymptomatic carriers. Therefore, their global spread threatens crayfish species outside of North America, for which infection with this pathogen is usually lethal (Svoboda et al., 2017). The relation between North American crayfish and the formerly 'mysterious' disease in Europe wasonly discovered after the introductions of North American crayfish to compensate for the loss of European stocks. Beyond Europe, *A. astaci* caused mass mortalities of *Cambaroides japonicus,* endemic to Japan (Martín-Torrijos et al., 2018), and of the Australian *Cherax quadricarinatus,* farmed in Taiwan (Hsieh et al., 2016). The pathogen was also introduced to Brazil and Indonesia with infected *P. clarkii* (Peiró et al., 2016; Putra et al., 2018).

The growing concern about negative impacts caused by non-native crayfish species led to restrictions on their import and use. In the European Union, five non-native crayfish species (including *P. clarkii* and *P. virginalis*) are included in the List of Invasive Alien Species of Union concern that prohibits import, breeding, commercial production and keeping of these species (EU 2016, 2017, 2019). However, the regulations differ across countries in Europe as a whole and in other continents, which often hinders successful control of introduced species Souty-Grosset et al., 2016). Populations of non-native crayfish can be eradicated or controlled through physical measures (intensive trapping, draining of ponds, construction of barriers), chemicals (use of biocides) and biological measures (e.g. predators) (Gherardi et al., 2001; Manfrin et al., 2019). Complete eradication of crayfish populations is, however, rarely feasible. Prevention of their introduction is, therefore, typically more cost-effective and environmentally more desirable (Gherardi et al., 2001).

Fish

More than 34,000 species of fish live in marine and inland waters worldwide. Fish can be found in most freshwater systems including wetlands, ponds, lakes, streams, rivers and estuaries in which they occupy a wide range of ecological niches and trophic positions.

Fish are among the organisms most commonly introduced outside their native range (Gozlan et al., 2010). In particular, the Salmonidae family (charr, salmon and trout) includes some of the most widely introduced species (Cucherousset and Olden, 2011), including the rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) which are both listed among '100 of the World's Worst Invasive Alien Species' (http://www.iucngisd.org/gisd/100_worst.php) (Fig. 4). These two species, originally from western North America and Eurasia/northern Africa, respectively, have been widely introduced and are considered as global invaders. Centrarchidae (sunfishes, black basses) are native to North America, but can now be found in most other continents in vegetated lakes, ponds and rivers. The Poeciliidae (mosquitofish, guppy) are among the most frequently introduced fish species. This family originally comes from the southeastern USA, southeastern South America and Africa. An important invader in this

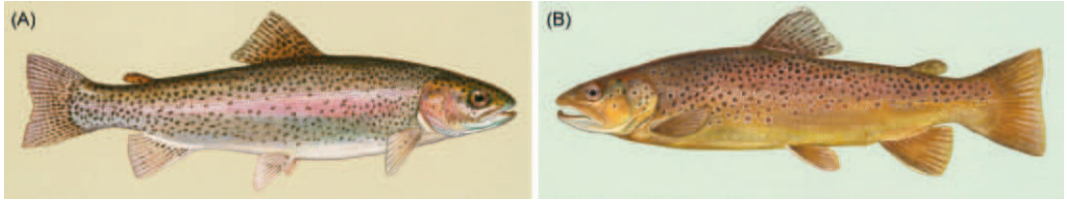


Fig. 4 The (A) rainbow trout (*Oncorhynchus mykiss*) is native to western North America and has been introduced to many areas worldwide including Europe where the (B) brown trout (*Salmo trutta*) is native, which has in turn been introduced to North America and elsewhere. This species pair is thus an interesting example of a crosswise introduction. Both species are also included in the IUCN's list of '100 of the World's Worst Invasive Alien Species.' Illustrations: Duane Raver, U.S. Fish and Wildlife Service.

family is the mosquitofish (*Gambusia affinis*) which is also included in the list of '100 of the World's Worst Invasive Alien Species.' It has been introduced around the world, starting early last century as a biological control agent for mosquitoes, and is now established in Europe, Asia, Australasia, South America, North America and Africa. While introductions have vastly increased the spatial distribution of many fish species, they are usually restricted to the type of ecosystem they are adapted to, such as well oxygenated fast-flowing waters for Salmonidae. On the contrary, more generalist species dwelling in both lotic and lentic, pristine or disturbed ecosystems develop and expand without further human intervention. It is also interesting to note that beyond the spatial extent that some species reached because of human activities, some species such as *Cyprinus carpio* (common carp) from the Cyprinidae family (carps, tenchs) were introduced to natural ecosystems centuries or even millennia ago (Balon, 1995; Ma et al., 2003). For species that were introduced such a long time ago, it depends on the time period that is considered to still call a species non-native. For example, if using the threshold of 1492 or 1500, carp would be called native in many countries where they were historically introduced (cf. Essl et al., 2018).

Non-native fish species have been introduced worldwide through human activities, either intentionally or unintentionally. To enhance aquaculture production and performance of commercial fisheries, invasive fish such as the Nile perch (*Lates niloticus*) have been stocked in artificial and natural ecosystems for centuries, and still are (Gozlan et al., 2010). Besides pisciculture, invasive fish are still stocked to support angling. This is true for piscivorous fish that are of angling interest due to their flesh or their combativity, and for fish species that these predators forage (e.g. threadfin shad or smelt) (Devries and Stein, 1990). During the second half of the 20th century, modern human activities created new introduction pathways. For instance, biocontrol became a strong motive for invasive fish introductions, either for controlling phytoplankton, macrophytes or mosquitos. Another example is the release of ornamental fish (Padilla and Williams, 2004).

Non-native fish species can have deleterious effects at all levels of biological organization from genetics to ecosystem functioning, including individual, population and community levels (Cucherousset and Olden, 2011). Hybridization with invasive species is a major threat, as native populations can be replaced by hybrids, which is particularly concerning when the native populations are rare and vulnerable. For example, the Mediterranean trout (*Salmo cettii*) in Central Italy (Splendiani et al., 2019) and the marble trout (*Salmo marmoratus*) in the Po and Soča basins (Crivelli et al., 2006) have been partly replaced in their native ranges by hybrids with introduced brown trout. Non-native fish species induce predator-avoiding adaptive mechanisms in native prey species that affect their morphology, behavior or life-history traits (Cucherousset and Olden, 2011). Such adaptations can in turn affect native predators' success and diet. Invasive fishes can severely impact native fishes through direct and indirect competition for space and food, or through transmitting pathogens (Spikmans et al., 2020). At the community level, invasive fish species can change community structure and composition, for example through extinction of resident species. One of the best-known examples is the introduction of Nile perch (*Lates niloticus*) to Lake Victoria (Africa) in the 1960s to improve fisheries production, which happened despite contrary advice from scientists and other experts (Marshall, 2018). This species caused the demise of more than 500 endemic fish species in the lake (Marshall, 2018). Introductions of invasive fish species can cause trophic cascades with severe effects at multiple levels of the food web, modifying nutrient cycles and cross-ecosystem interactions across a large landscape. The introduction of the lake trout (*Salvelinus namaycush*) in the Yellowstone Lake (USA) resulted in the addition of a new predator preying upon the native planktivorous cutthroat trout (*Oncorhynchus clarkii bouvieri*). The decline of the native trout led to changes in plankton communities, a decline in chlorophyll *a* concentration and alteration of nitrogen dynamics. Indirectly, the introduction of lake trout had far-reaching consequences, affecting neighboring ecosystems and other taxa such as predatory birds and mammals, as the loss of migrating spawning native cutthroat trout in tributary streams modified the cross-ecosystem interactions and therefore terrestrial food webs (Koel et al., 2019).

Invasive fish species have not only ecological impacts but also socio-economic ones, as they can strongly affect local fisheries and ecosystem services provided by freshwater ecosystems to human societies. For example, the Great Lakes invasion by the sea lamprey (*Petromyzon marinus*) led to an economic catastrophe after severe losses of highly valuable species in the region (Siefkies, 2017). By using their suction-cup mouth, rasping tongue and pointy teeth, parasitic sea lamprey feed on the blood and other vital fluids of their fish hosts. Native fish in the Great Lakes did not coevolve with this large and prolific parasite, thus many of them declined sharply since its arrival.

To minimize the harmful impacts of invasive fish species, diverse management strategies are used: prevention, early detection, rapid response and eradication, and control methods for reducing invasive populations. For example, the invasive common carp was successfully removed from a reservoir in South Africa using rotenone, and the removal was followed by an improvement of the water quality and recovery of invertebrates and zooplankton communities (Dalu et al., 2020). However, this successful removal is an exception, as most attempts to remove invasive fish fail or have unexpected effects. Removal attempts also incur high environmental and financial costs which might exceed the focal invader's impacts. In addition, such management actions may face opposition, as anglers and other interest groups often value the presence of exotic fish, even if they have detrimental impacts on resident species (e.g. McIntosh et al., 2012). The general public can also oppose management against invasive fish species, particularly piscivores which are charismatic for many people (see Jarić et al., 2020 for a general treatment on the role of species charisma in biological invasions). New technologies, such as environmental DNA metabarcoding, are promising to allow for better monitoring, early detection and thus rapid response against invasive fish (and other invasive aquatic) species (Hinlo et al., 2017). Such rapid responses are less costly for the environment and the taxpayer, and they also face less opposition from the public.

Mammals

There are about 6500 known species of mammals (Mammal Diversity Database, 2020). This group includes high-impact invaders such as rats (*Rattus* spp.), cats (*Felis catus*) and pigs (*Sus scrofa*) (cf. Bellard et al., 2016, http://www.iucngisd.org/gisd/100_worst.php). Since most mammals are terrestrial, this section is structured with a focus on five selected invasive mammal species (three from the order Rodentia, two from the order Carnivora) that are often found in or around inland waters.

Beavers (Fig. 5A) are semi-aquatic rodents whose dam-building activities alter freshwater systems; they are therefore 'ecosystem engineers' (Jones et al., 1994, 2010; Rosell et al., 2005). North American beavers (*Castor canadensis*) are native to the USA and Canada where they are official state symbols (Jernelöv, 2017). Eurasian beavers (*Castor fiber*) were almost hunted to extinction in the 19th century (Sjöberg et al., 2011), but were successfully reintroduced in Bavaria (Germany) in 1966 (Schwab and Schmidbauer, 2003), Hungary in 1996 (Bajomi, 2011) and the UK in 2009 (Stringer and Gaywood, 2016). In Finland, 17 Eurasian beavers from

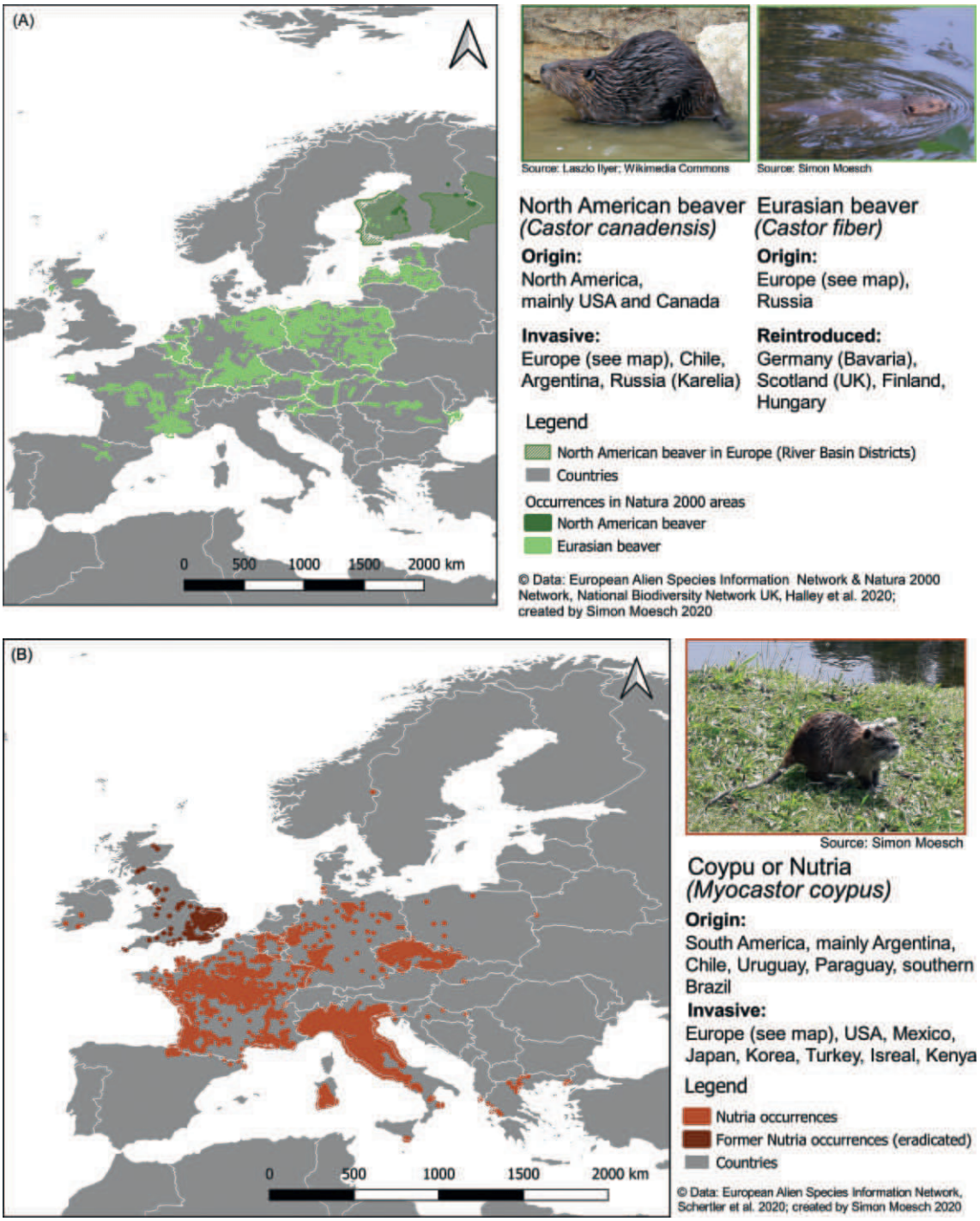
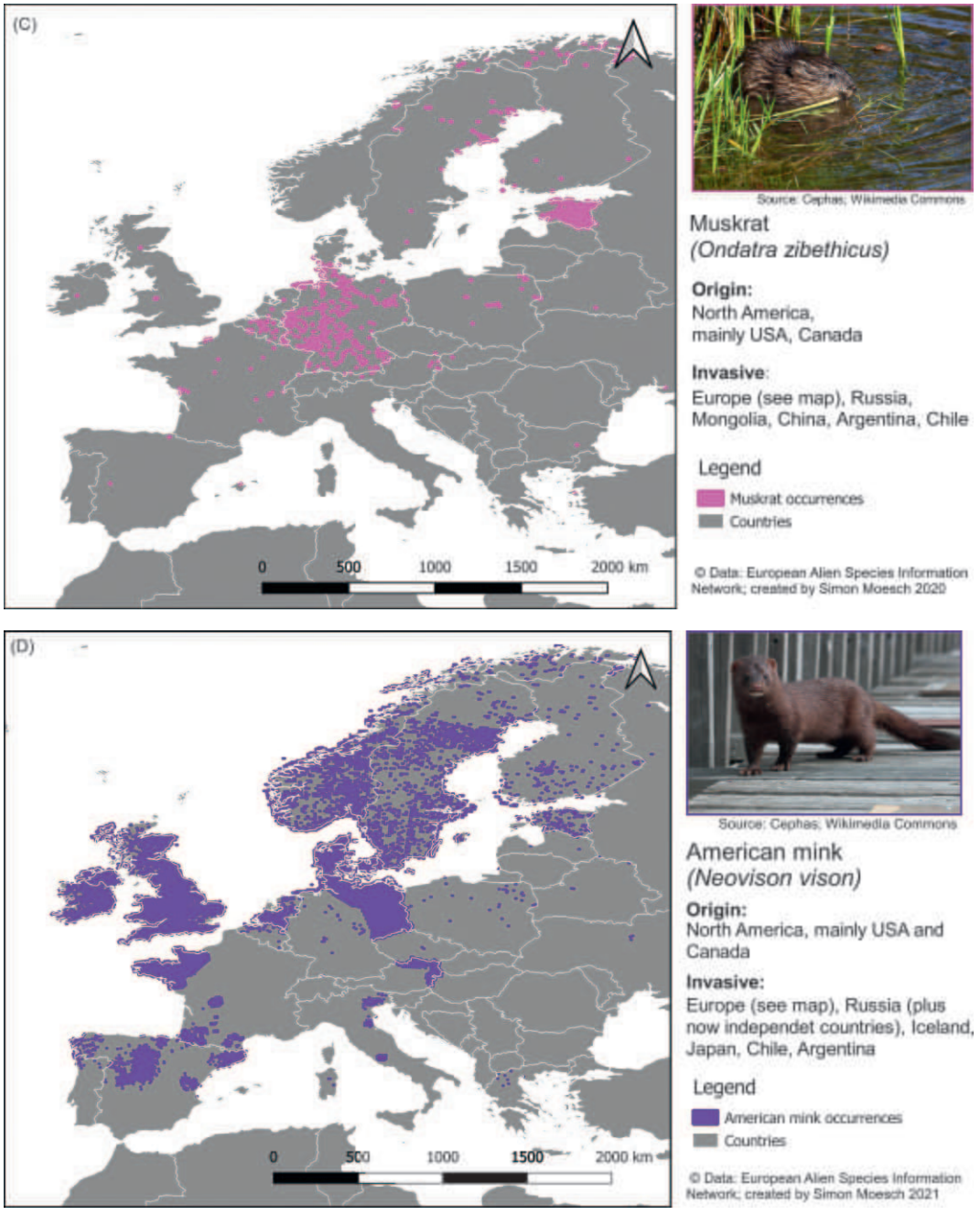


Fig. 5 European occurrences of (A) North American and Eurasian beavers (*Castor canadensis*, *Castor fiber*), (B) the coypu or nutria (*Myocastor coypus*), (C) muskrat (*Ondatra zibethicus*), (D) American mink (*Neovison vison*) and (E) raccoon (*Procyon lotor*).



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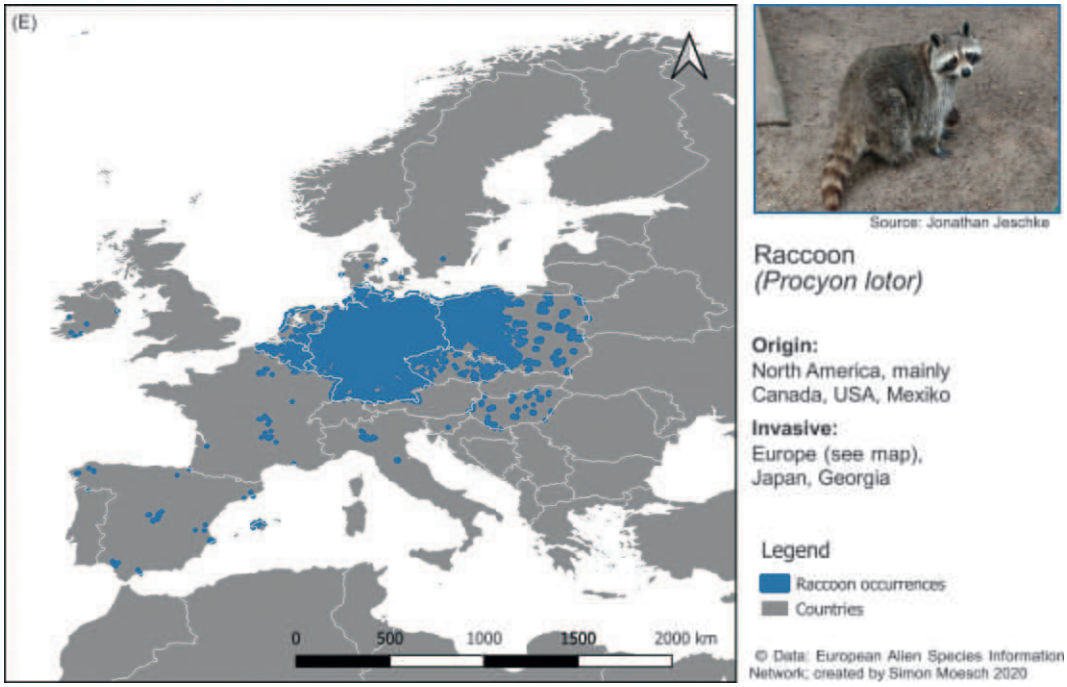

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Norway and seven North American beavers from the USA were reintroduced at around 1930 (Härkönen, 1999a). Until 1973, North American and Eurasian beavers were often believed to be the same species until chromosome counts showed a difference (Parker et al., 2012). North American beavers are spreading faster in Europe than Eurasian beavers (Halley et al., 2021). In South America, 25 pairs of North American beavers from Manitoba (Canada) were introduced in 1946 to Tierra del Fuego by the Secretary of the Navy of Argentina to enrich the community and for fur trading (Pietrek and Fasola, 2014). Since then, they have vastly altered the ecosystem there (Anderson et al., 2009; Henn et al., 2016), caused the establishment of non-native plants (Martínez Pastur et al., 2006) and are beneficial for native but also non-native fish species (Malmierca et al., 2011). Beaver impacts include those on agriculture through flooding and erosion due to dam building and burrowing into flood banks, on forestry through tree damage, on fishery due to beaver dams being migration barriers and raising water temperatures, and on infrastructure due to dam failure (Butler and Malanson, 1994; Härkönen, 1999b; Collen and Gibson, 2000; Müller-Schwarze, 2011). To reduce such impacts, invasive North American beavers are now being hunted and trapped in both South America and Europe (Worth, 2014; Brommer et al., 2017).

The coypu, which is alternatively called nutria (*Myocastor coypus*, Fig. 5B), is also a semi-aquatic rodent and often mistaken for a beaver or muskrat (see below). It is native to South America and was introduced to Europe in the 19th century for fur farming where individuals escaped confinement and established wild populations (Carter and Leonard, 2002; Schertler et al., 2020). Other invasive populations exist in the USA, Mexico, Japan, Korea, Kenya and the Middle East (Bertolino et al., 2012). The coypu is widely recognized as a high-impact invader. It is on the lists of '100 of the World's Worst Invasive Alien Species' (http://www.iucngisd.org/gisd/100_worst.php) and 'Invasive Alien Species of Union concern' (EU, 2016). Specifically, the coypu is responsible for the loss of freshwater marshes through the 'eat-out effect' where aboveground biomass is washed away due to root foraging (Linscombe and Kinler, 1997; Carter et al., 1999). It threatens various species, e.g. hygrophilic plants (Prigioni et al., 2005) and freshwater mussels (Stemmer, 2017), reduces water quality in urban areas (Nehring et al., 2015), and its burrowing reduces dam stability (Reinhardt et al., 2003; Nehring et al., 2015). Due to successful eradication programs, the UK and the Chesapeake Bay (USA) are now believed to be coypu-free (Kil et al., 2015). Eradication programs only work where re-immigration is impossible (Robertson et al., 2017). Therefore, successful management requires cost-benefit analysis plus long-term measures at the local (e.g. fencing off waterways) and national level (e.g. hunting, water-level adjustment) (Gethöffer and Siebert, 2020).

The final semi-aquatic rodent highlighted here is the muskrat (*Ondatra zibethicus*). This species is native to North America and invasive in Europe (Fig. 5C), Asia (Russia, Mongolia, China) and South America (Argentina, Chile) (Skyrienė and Paulauskas, 2012). It is listed as Invasive Alien Species of Union concern (EU, 2017) and its successful invasion in Eurasia resulted from multiple releases at numerous sites (Danell, 1996; Skyrienė and Paulauskas, 2012). Muskrats damage watercourse embankments through burrowing and forage on crops (Bayoumi and Meguid, 2011; Skyrienė and Paulauskas, 2012). They also alter aquatic plant communities (Smirnov and Tretyakov, 1998) and negatively affect freshwater mussels (Zahner-Meike and Hanson, 2001). Trapping is currently the most effective management action to control the spread of muskrats (Bos et al., 2019).

The American mink (*Neovison vison*, Fig. 5D) is a high-impact invader from the family of Mustelidae within the order Carnivora (Genovesi et al., 2012). A semi-aquatic generalist predator native to North America, this species is now invasive in Europe, Asia and South America (Reid et al., 2016). Mink were trapped in North America for commercial fur trade since the 17th century (Spraakman and Wilkie, 2000). Starting in the late 1920s when populations declined and trapping was less profitable, large numbers were transported to Europe to be released (Heptner et al., 1967) and kept in fur farms (Macdonald and Harrington, 2003). Many individuals escaped or were released from farms in years of bad business, so that by 1969 the American mink was naturalized in at least 16 European countries (Bonesi and Palazon, 2007). High propagule pressure and multiple introductions increase fitness and resilience of mink populations in Europe (Bevanger and Henriksen, 1995). The spread is ongoing (e.g. Brzeziński et al., 2019), as are impacts on native species such as the European mink (*Mustela lutreola*, Macdonald et al., 2017), the water vole (*Arvicola amphibius*, Defra, 2005) and waterfowl (Dunstone, 1993; Magnusdottir et al., 2012). American mink can also be infected with SARS-CoV-2 and can infect humans with it, and infected mink have been found both on farms and in the wild (Oude Munnink et al., 2021, https://promedmail.org/promed-post/?id=8015608). Controlling mink populations by hunting and trapping is costly (Stefansson et al., 2016), which is why programs of complete eradication are discussed (see e.g. Martin and Lea, 2020 for the UK).

Finally, the raccoon (*Procyon lotor*) is a medium-sized, nocturnal and omnivorous mammal from the family Procyonidae, order Carnivora, that is recognizable by its grey fur, bushy tail and 'bandit's mask' fur pattern around the eyes (Hohmann et al., 2001). It is native to North America and invasive in Europe and Asia (Fig. 5E, Zeveloff, 2002; Ikeda et al., 2004; Salgado, 2018). Its introduction in Japan resulted from zoo escapes in 1962 (Ikeda et al., 2004) and releases and escapes of pets promoted through a children's book and its TV adaptation (Clark, 2015). Hence, the raccoon is another good example of an invasive species that benefited from its charisma (Jarić et al., 2020). In Europe, raccoons can be traced back to releases in the 1930s in Germany and are now found especially in urban regions such as Kassel, Hamburg, Frankfurt, Berlin, Madrid, Milan and Prague (Jernelöv, 2017). Raccoons are known for inspecting food in water (Zeveloff, 2002) and are frequently found in the vicinity of inland waters. They are listed as an Invasive Alien Species of Union concern (EU, 2016), and negative influences on e.g. breeding birds (García et al., 2012; Tolkmitt et al., 2012), crayfish and salamanders have been recognized (Ikeda et al., 2004). They have significant socio-economic impacts, particularly due to their high abundance in cities: raccoons damage attics and gardens, and are potential transmitters of diseases (Michler, 2004). Management actions include trapping, hunting, fencing off areas, making buildings inaccessible and raising public awareness about raccoon impacts (Suzuki and Ikeda, 2020, https://neobiota.bfn.de/unionsliste/art-19-management.html). As the raccoon population tripled in Europe since 1980, long-term management strategies are needed (Salgado, 2018).

Conclusions

Invasive freshwater species can be found in many taxonomic groups, some of which were featured here. An exhaustive overview of freshwater invaders could not be provided in this chapter, and examples of other important taxonomic groups are snails, e.g. *Cipangopaludina chinensis* (Chinese mystery snail), *Pomacea canaliculata* (golden apple snail) and *Potamopyrgus antipodarum* (New Zealand mud snail); crustaceans other than crayfish, e.g. the waterfleas *Cercopagis pengoi* and *Daphnia lumholtzi*, or the Chinese mitten crab (*Eriocheir sinensis*); insects, e.g. the mosquito species *Aedes albopictus* (Asian tiger mosquito), *Aedes japonicas* (Asian bush mosquito) and *Anopheles quadrimaculatus* (common malaria mosquito); amphibians, e.g. *Lithobates catesbeianus* (American bullfrog) and *Rhinella marina* (cane toad); reptiles, e.g. *Python bivittatus* (Burmese python) and *Trachemys scripta* (red-eared, yellow-bellied and Cumberland sliders); birds, e.g. *Alopochen aegyptiacus* (Egyptian goose), *Branta canadensis* (Canada goose) and *Oxyura jamaicensis* (ruddy duck); and different taxonomic groups of pathogens, e.g. chytrids (for example, *Batrachochytrium dendrobatidis* and *Batrachochytrium salamandrivorans* affecting amphibians).

This list and the whole chapter illustrate the huge variety of freshwater invaders that can now be found across the globe. They are being either intentionally or unintentionally introduced through different pathways, have various impacts and can be managed in multiple ways, but more research is clearly needed to better understand their ecology and impacts in order to improve current policy and management practices.

Knowledge gaps

- Compared with terrestrial invasive species, relatively little is known about freshwater invaders.
- Current knowledge on invasive macrophyte impacts is particularly restricted and focused on a few species.
- We do not fully understand how the alteration of habitat properties could facilitate or limit the establishment and spread of invasive species.
- Estimates of the economic impacts of freshwater invaders are scarce, incomplete and imprecise.
- We still need to identify the strategies that are most effective in raising awareness of the impacts of freshwater invaders, so that introduction rates of invaders are reduced and management efforts improved.
- The interplay between invasive species and other biodiversity drivers (such as habitat change, climate change, pollution, overexploitation artificial light at night etc.) is still poorly understood, as most studies focus on one of these factors only (Mazor et al., 2018).

Acknowledgments

We thank Ken Irvine for the invitation to contribute this chapter. His comments and those of Thomas Mehner and an anonymous reviewer are also highly appreciated. We acknowledge financial support from the Federal Agency for Nature Conservation (FKZ: 3519892014) to AH, the Alexander von Humboldt Foundation to AM, the German Federal Ministry of Education and Research (BMBF) within the Collaborative Project 'Bridging in Biodiversity Science - BIBS' (funding number 01LC1501A-H) to CLM and the German Research Foundation (DFG–FZT 118, 202548816) within iDiv to AS. This chapter is a contribution of the Invasion Dynamics Network (InDyNet).

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Relevant Websites

https://www.cabi.org/isc—CABI Invasive Species Compendium.
https://ec.europa.eu/environment/nature/invasivealien/list/index_en.htm—EU List of Invasive Alien Species of Union concern.
https://easin.jrc.ec.europa.eu—European Alien Species Information Network (EASIN).
http://www.fao.org/fishery/dias/en—FAO Database on Introductions of Aquatic Species (DIAS).
www.corpi.ku.lt/databases/index.php/aquanis—Information system on aquatic non-indigenous and cryptogenic species (AquaNIS).
https://indynet.de—Invasion Dynamics Network (InDyNet).
http://www.iucngisd.org—IUCN Global Invasive Species Database (GISD).
http://www.issg.org—IUCN Invasive Species Specialist Group (ISSG).
https://nas.er.usgs.gov—USGS Nonindigenous Aquatic Species (NAS).
http://www.marinespecies.org/introduced—World Register of Introduced Marine Species (WRiMS).

Moving Towards Water Sensitive Cities: A Planning Framework, Underlying Principles, and Technologies—Case Study Kunshan Sponge City

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Ken Irvine, Debbie Chapman and Stuart Warner.

Glossary

Blue infrastructure Refers to water elements, like rivers, canals, ponds, wetlands, floodplains, can be used to connect the benefits of green and gray infrastructure.

Cultural eutrophication The impact of an increase in the concentration of phosphorus, nitrogen, and other plant nutrients in an aquatic ecosystem due to human activities. Water blooms, or great concentrations of algae and microscopic organisms, often develop on the surface, preventing the light penetration and oxygen absorption necessary for underwater life. Eutrophic waters are often murky and may support fewer large animals, such as fish and birds, than non-eutrophic waters.

Detention and retention Detention and retention are two conventional methods to manage pluvial and/or fluvial flooding. Retention systems are designed to always have water in it and detention systems only detain the water during rainy periods or flood events. Retention systems usually capture water from its original path and release it for other usages (e.g., supplementing groundwater, stormwater utilization). Detention systems usually capture water from its original path and release it into the same path (e.g., to the drainage network, to the canals).

Green infrastructure Is the strategic use of networks of natural lands, working landscapes, and other open spaces to conserve ecosystem values and functions and provide associated benefits to human populations (Benedict and McMahon, 2006; Gartner et al., 2013), which are generally decentralized. The 2013 European Commission (2013) defines GI as a "strategically planned network of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ecosystem services."

Gray infrastructure Refers to the human-engineered infrastructure for water resources such as water and wastewater treatment plants, pipelines, and reservoirs, which is generally a centralized approach for water management.

Livable city Is conceptualized as a city which is "safe, attractive, socially cohesive and inclusive, and environmentally sustainable."

Nature-based solution Interventions (technologies and designs) which are inspired, supported by, or copied from nature to address the ecological, social, and economic challenges our society are facing in a sustainable way.

Polder area Tract of lowland reclaimed from a body of water, often the sea or main rivers, by the construction of dikes roughly parallel to the shoreline, followed by drainage of the area between the dikes and the natural waterbody (Britannica, 2015).
Sponge City An emerging approach developed in China which refers to a city that functions like a sponge to absorb, store, and purify rainwater and to release water for replenishing ground water or reuse when necessary, now and in future. Hence, it aims to alleviate waterlogging, water resource shortages, and improves the ecological environment and biodiversity in cities by absorbing, capturing utilizing rainwater. Similar concepts developed outside China include low-impact development (North America), nature-based solutions (European Union), and water sensitive urban design (Australia).

Introduction

Globally, cities are increasingly under pressure as they have to adapt to rapidly changing environmental conditions as well as to socio-economic development. Cities are vulnerable to water- related hazards such as flooding, water pollution and droughts. As the intensity and frequency of extreme weather events increase due to climate change, cities need to embrace integrated and decentralized urban water management approaches. These challenges are particularly felt in "yesterday's cities" that require transformation of the existing urban fabric to ensure a city is created that is more sustainable, livable and disaster resilient.

Blue-green infrastructure (BGI) is advocated as one of the key solutions for resolving water and environmental-related challenges and is particularly relevant for cities. However, mainstreaming BGI in urban redevelopment projects is still constrained. While current upscaling efforts of pilot projects are important steps towards broader implementation, in many cities BGI projects still have limited impact due to their small size and scattered distribution (Albert et al., 2021). BGIs ultimate focus is on residents' health and well-being and on reducing the city's environmental impact. A sustainable urban water system is a prerequisite to achieve these objectives.

China is experiencing unprecedented urban expansion and growth in wealth since the 1980s. In 2020, about 64% of the total population in China lives in cities, which is higher than the global average of 55%. Many cities in China are experiencing regular flooding and severe pollution of urban waterbodies. China is currently making the transition towards Sponge Cities enforced by a new vision coined as "ecological civilization" (Gare, 2020). Laid down in the Chinese constitution in 2018, the vision of "ecological civilization construction" has become the major ideological principle for environmental and climate policy action at different levels of government and across policy sectors in China. This vision is driving the uptake of BGI projects in urban and infrastructure planning of new built-up areas and in redevelopment programs of the existing urban fabric.

In 2014, China adopted a National Policy referred to as the Sponge Cities Program. In line with other emerging concepts of holistic urban water management (Fletcher et al., 2014), the Chinese concept of Sponge Cities calls for an integrative approach acknowledging that the urban water system is a dynamic part of a larger water catchment. Only recently, China has shifted its emphasis from traditional gray infrastructure towards blue-green and blue-green-gray infrastructure to improve the capacity of cities to capture, convey and purify urban water.

In these cities, BGI is currently being implemented at a rapid pace to replace and/or upgrade existing gray infrastructure with the objective to expand capacity and increase resilience. At the same time there is a growing recognition that BGI solutions are conditional to improve the livability of cities. This shift in focus from largely mono-functional to multi-functional approaches is also reflected in the planning, design and engineering process of urban water infrastructure in many other countries (Wong, 2006; Gersonius et al., 2012; Zevenbergen et al., 2018). It is increasingly recognized that the process of BGI uptake requires engagement of a broad range of disciplines, such as architecture, landscape design, planning, ecology, engineering and social science (Wong, 2006; Fletcher et al., 2014).

As part of the Sponge Cities Program, numerous BGI projects in the first batch of 30 'pilot cities' across the country have been implemented and are currently being monitored (Li et al., 2017; Jiang et al., 2017; Chan et al., 2018). One of these pilot cities is Kunshan, a low-lying city located in China's Jiangsu Province. A typical hydrological feature of Kunshan is its location in a low-lying polder area. Polder cities can be found in many regions across the globe, particularly in deltas. Typical examples of polder cities are Rotterdam (The Netherlands), Surabaya (Indonesia) and Bangkok (Thailand) (Hooimeijer, 2011). They are prone to flooding, experiencing subsidence and their surface waters generally have a poor water quality. Indeed, Kunshan experienced frequent flooding in the past and suffered from severe water pollution.

Kunshan is one of the vanguard sponge cities of China. In 2015, the city has launched its "Kunshan Sponge City Implementation Plan." An area of 23 km^2 was designated to be transformed into a Sponge City area which was accomplished in 2018. In that same year, the city launched a follow-up program referred to as "Kunshan Sponge City Special Plan," which targets the transformation of the remainder 80% of the urbanized area (233 km^2) into a Sponge City by 2030.

In this chapter, the underlying principles, methodologies and technologies of this new sponge city program will be given, which eventually aims to result in the transformation of Kunshan into a water sensitive city referred to as a Sponge City. A selection of projects which have already been implemented under this program will be presented.

Sponge cities program and technologies

The Sponge City program aims to restore the city's capacity to infiltrate, detain, store, purify, drain, and utilize rainwater and regulate the water cycle as much as possible to mimic the natural hydrological cycle. To achieve these objectives, three types of interventions (referred to as Sponge Cities Technologies (SPTs)) are being proposed (Li et al., 2017): (i) implementation of BGI to effectively retain and store peak run off and to purify rainwater (regular rainfall), (ii) upgrading of the existing (gray) infrastructure to collect, transport and discharge rainwater, and (iii) (re)introduction of natural waterbodies and deployment of multifunctional storage facilities and underground tunnels to deal with extreme events (to cope with excess run off beyond the design standard). China's ambition is to transform 80% of the urban areas of Chinese cities into a sponge city to absorb, retain and reuse 70% of rainwater by 2030.

An overview of the various BGI technologies and their application in China is shown in Fig. 1 and Table 1. These technologies are also used in many other countries across the globe (Balmforth, 2006; Woods-Ballard et al., 2007; Hoyer and Al, 2011). Their effectiveness depends on several factors, such as the prevailing climatological and geophysical conditions.

An expanding polder city: Example of Kunshan

Development of polder cities

In China, the first polders were mostly formed in coastal zones and lower river catchments for agricultural and flood protection. This can be traced back to the Pre-Qin Period (before 221 B.C.), whereas in Europe the first polders date back to the 11th century. The oldest extant polder is the Achtermeer polder in the Netherlands (from 1533). Urban settlements and villages expanded rapidly in polder areas resulting in densely populated areas over the past decades (Su and Luo, 2019). Due to their manmade nature, they have a unique water system comprising embankments (or dikes), canals, pumps, sluices and sewer systems to provide flood protection (dikes) drainage. The drainage system removes surplus rain and seepage water, and is made up of a network of field drains. These field drains are connected to the main drainage system and an outlet structure to evacuate the water from the area (Schultz, 1983). Hence, typical features of a polder city are: (i) controlled high water levels which may fluctuate depending on the season through groundwater extraction and/or surface water discharge; (ii) a hydrological regime and water table which are independent from their surrounding environment; and (iii) soil subsidence due to continuous groundwater extraction (Segeren, 1983).

Before the onset of the economic growth and urbanization in the 1980s and 1990s, the pollutants discharged from agricultural runoff and domestic wastewater to the aquatic environment were limited and counterbalanced by the self-purification capacity of the receiving waterbodies in the polder (Fig. 2).

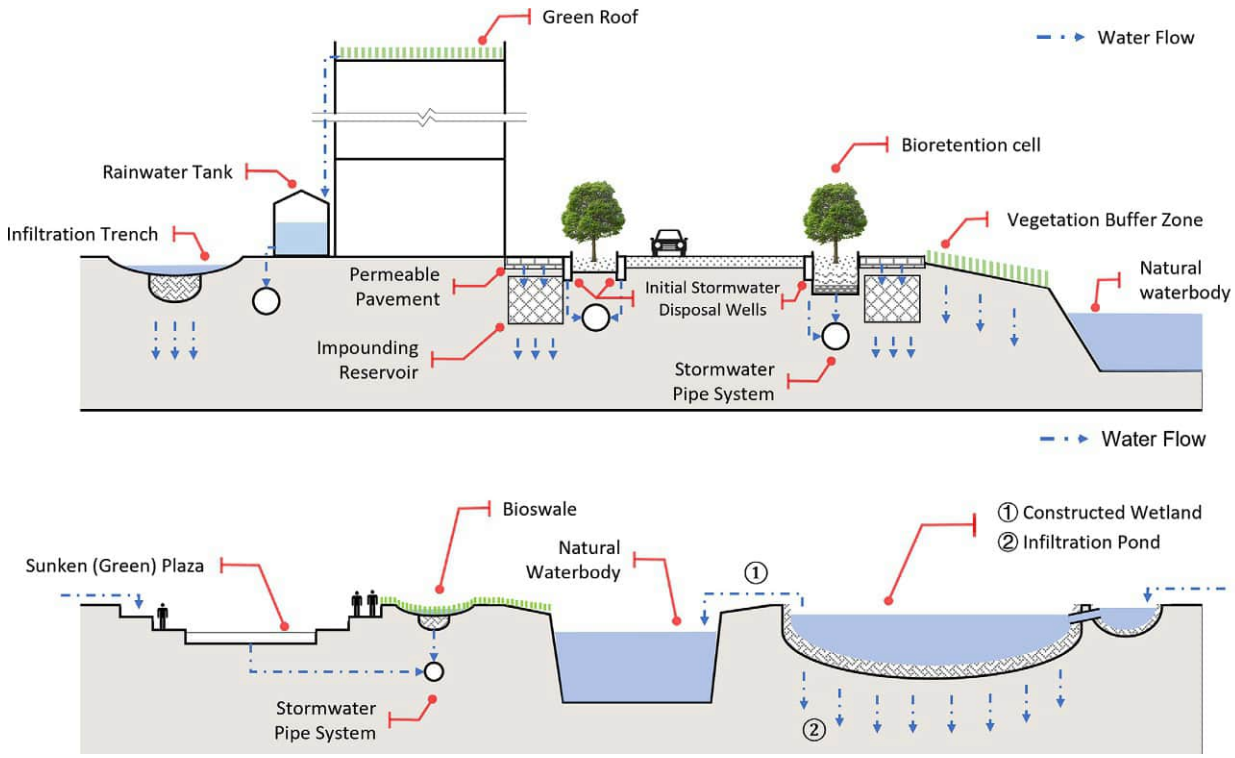

Fig. 1 Illustration of BGI applications.

Table 1 Recommendation of SPT technologies for different land uses.

	Land use						*Function*					
Technology	*Buildings*	*Urban road*	*Urban open space*	*Urban river system*	*Example*	*Type of intervention*	*Infiltrate*	*Detain*	*Store*	*Purify*	*Drain*	*Utilize*
Permeable pavement	●	●	●	○		Upgrading existing infrastructure	●	○	×	○	×	×
Green roof	●	×	×	×		Installation of BGI	×	○	○	○	×	×
Sunken green space	●	●	●	○		Deployment of multifunctional storage facilities	○	●	×	○	×	×
Bioretention system	●	●	○	○		Installation of BGI	●	○	○	●	×	○
Infiltration pond	●	○	●	×		Deployment of natural waterbodies	●	●	●	○	×	○
Constructed wetland	●	●	●	●		Deployment of multifunctional storage facilities	●	○	○	●	○	×

Table 1 (Continued)

	Land use						*Function*					
Technology	*Buildings*	*Urban road*	*Urban open space*	*Urban river system*	*Example*	*Type of intervention*	*Infiltrate*	*Detain*	*Store*	*Purify*	*Drain*	*Utilize*
Impounding reservoir	○	×	○	×		Deployment of underground tunnels	○	○	●	×	×	○
Rainwater tank	●	×	×	×		Installation of BGI	×	○	●	×	×	●
Bioswale	●	●	●	○		Installation of BGI	○	○	×	○	●	×
Infiltration trench	●	●	●	×		Installation of BGI	●	○	×	×	○	×
Vegetation Buffer Zone	●	●	●	●		Installation of BGI	○	×	×	●	×	×
Initial stormwater disposal facilities	●	○	○	×		Upgrading existing infrastructure	×	×	×	●	○	×

●, recommended; ○, applicable; ×, not applicable.

Translated and modified from Ministry of Housing and Urban-Rural Development of the People's Republic of China: 'Technical Guideline for Sponge City Construction (Trial)', 2014.

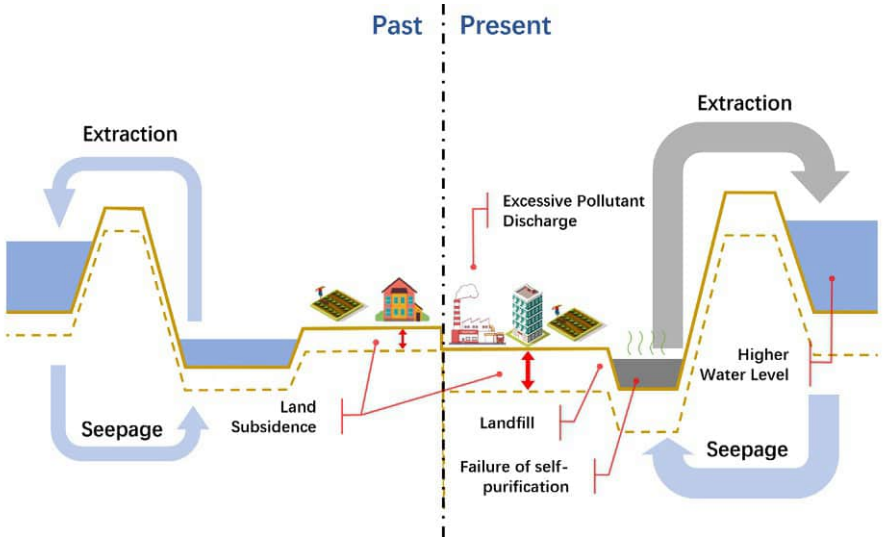

Fig. 2 Cross section of the polder system before and after urbanization showing its impact on water quality (population growth and industrial development led to excessive pollution), water quantity (expansion of the city led to landfill of channels), and regional vulnerability (global climate change led to an increase of the water level outside the polder, resulting in an increase of the seepage, extraction and land subsidence rate).

The rapid process of urbanization leads to competing land use claims to accommodate residential, industrial, and commercial development, and associated water demands and subsequent pressures on water circulation and storage. In polder cities, the total area of land available for urbanization is physically constrained by the surrounding embankments, canals and other open waterbodies. Moreover, continued land reclamation by landfilling has transformed these waterbodies into dry land to allow expansion of the urban areas. This in turn has led to an intensification of the hydrological cycle. A sharp reduction of farmland and grassland areas leads to an increase of the surface runoff coefficient and runoff volume. Meanwhile, increasing pollution loads from urbanization and industrial activities are discharged into water systems without any prior treatment (Jeon et al., 2006; Gagrani et al., 2013; Yadav et al., 2019), with impact on the quality of life of the citizens and aquatic ecosystem health (Huang et al., 2016).

These land-use changes often lead to more frequent urban waterlogging and even to severe pluvial flooding after heavy rainfall events when the volume of floodwater exceeds the capacity of the existing infrastructure. The floodwater is eventually discharged into the water system of the polder. This floodwater is often contaminated with nitrogen and phosphorus from domestic sewage, industrial wastewater, and surface runoff. In order to prevent further deterioration of the water quality, more water from outside the polder is pumped into the water system of the polder to reduce the concentration of the pollutants. In addition, continuous surface water and groundwater extraction to remove seepage water often leads to land subsidence and salinity intrusion.

The planning framework and underlying principles

The planning framework used in the Kunshan Sponge City program is based on three general principles which have been derived from water management practices developed in the Netherlands (see Chen et al., 2021). This framework is used in the selection, final design and engineering of the individual SPT interventions of the program. These principles are:

(i) Interventions should mimic natural processes as much as possible. By introducing BGI, the capacity of the city to deal with water stress such as drought, flood and water pollution will increase. BGI can also provide important additional ecosystem services and socio-cultural benefits and enhance the adaptability of the water system to future (uncertain) changes in climate and land use.

(ii) Interventions should foster or contribute to the preservation or restoration of the indigenous (man-made) water system. In many cases these systems do not exist anymore in modern cities as the huge demand for land has resulted in landfilling of indigenous canals and detention ponds to allow these landfilled areas to be used for urban development. These indigenous water systems have evolved over many decades and even centuries. They function well and sustainably under the prevailing (slow changing) geophysical and climatological conditions. In this context the indigenous water system refers to the polder water system before urbanization and offers important directions to better manage current water challenges.

(iii) Interventions should contribute to the overall performance of the city. Hence, these interventions should not be conceived as isolated, ad hoc interventions, but as ones that are interacting and impacting the urban water system as a whole. Applying this principle to manage stormwater sustainably results in an intervention which is not shifting its problem to a neighboring area. Adopting this principle requires a strategic, integrated approach at the city-scale and is based on an understanding of the function of the water system.

The last two principles are also reflected in the so called "Layer Approach," used in landscape planning and management. The Layer Approach provides guidance to identify, select, prioritize, plan and design interventions based on their impact on the water system and on the opportunities of an intervention arising from the dynamics (end-of-life cycle) of and interdependencies (incl. synergies) among the various components of the urban landscape. These components consist of: (i) surface and subsurface infrastructure; (ii) other engineered elements of the urban fabric such as buildings and public spaces; and (iii) the top and deeper soil layer; and (iv) the natural water system. The Layer Approach originates from the shearing layers concept of Duffy (1992) used in architecture and later adopted by van Schaick and Klaasen (2011) in landscape planning. This approach recognizes that buildings and landscapes can be conceived as a multi-layered system. Each layer of the system accommodates a collection of components with specific temporal features. The components of each layer have a confined and distinct time window. The performance and functions of each layer change over time, but at different rates depending on the substitution rate of the components. Components with the highest substitution rate and thus the highest adaptability are found in the upper layer, while components with the lowest substitution rate are confined to the bottom layer. When the Layer Approach is applied to the context of the polders of Kunshan, three distinct layers based on their dynamics can be defined (Fig. 3):

1. *The Occupation Layer*—This layer hosts the buildings, public spaces and all SPT (above ground) interventions. The lifetime of the components is between 10 to max 20 years.
2. *The Network Layer*—This layer consists of road infrastructure, an underground urban drainage system and other infrastructure such as bridges and pipes with lifetimes between 20 and 50 years. The capacity to adapt to changing conditions (such as driven by densification) of this layer is lower than of the Occupation Layer.

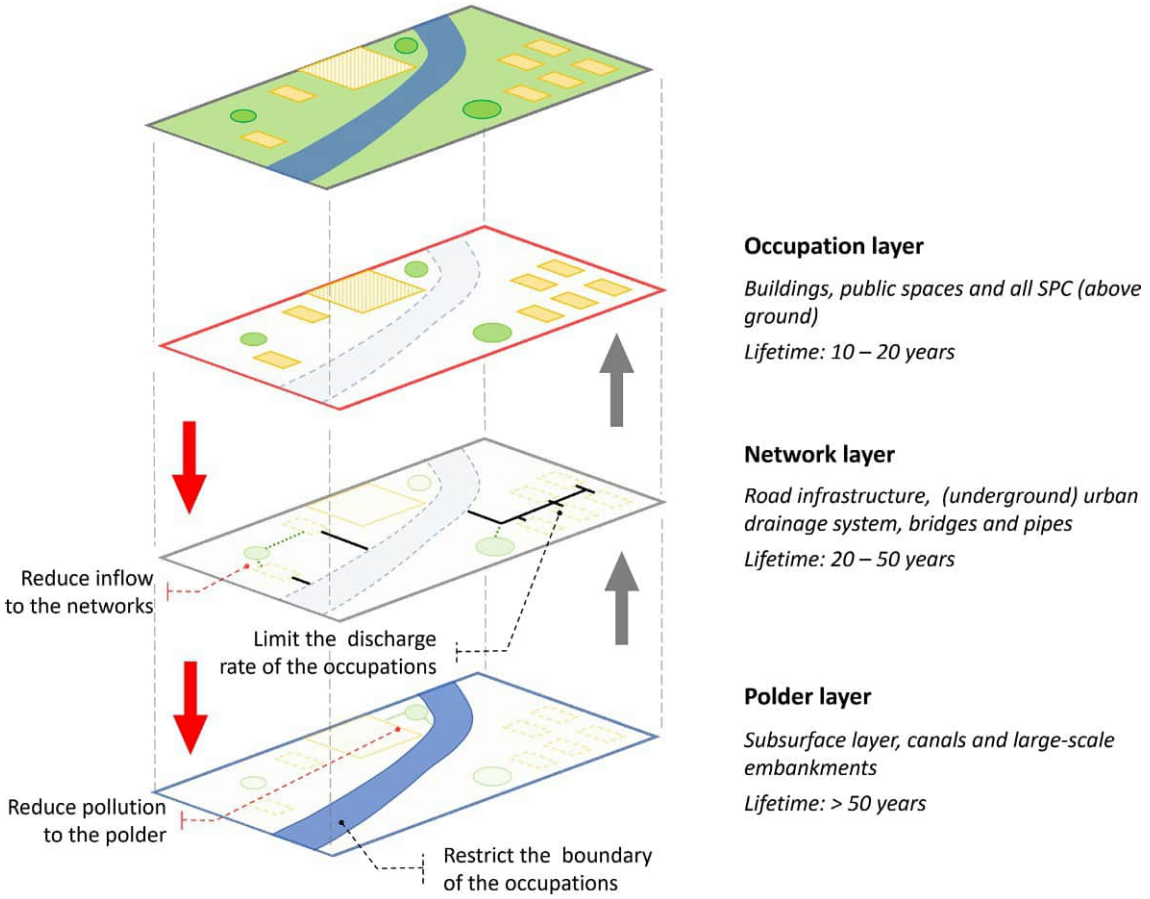

Fig. 3 The Layer approach for sponge polder management. The gray arrows indicate the hierarchy between the three layers based on the dynamics of the components of each layer. The Polder Layer with the lowest rate of change imposes restrictions on the Network Layer situated above, which in turn, imposes restrictions on the Occupation Layer. The SPT interventions are confined to the Occupation Layer. The red arrows indicate the potential impacts ranging from adverse to highly positive (synergies) of an intervention taken at the Occupation Layer on the layers below. The selection, design, and engineering of SPT interventions should be based on the opportunities that arise from the differences in dynamics (gray arrow) between the three layers, and the synergies (red arrow) of interventions on the Polder Layer and Network Layer.

3. *The Polder Layer*—This layer comprises the subsurface layer and the long lifetime man-made structures typically associated with the polder system, including large scale embankments and canals. These components have lifetimes of more than 50 years. The indigenous water system of the polder is part of this layer.

The visualization of the Polder System in layers reveals the inter-connections and the hierarchy between the layers. For example, replacing a (subsurface) drainage system to expand its capacity in the Network Layer is opportune when it has reached its end of lifetime. As these gray infrastructure systems have lifetimes of 40–50 years, in many cities they will not be replaced in the coming decade(s). Expanding their capacity by adding BGI in the Occupation Layer to the existing gray systems is an alternative option to increase the capacity but at much lower cost. Moreover, introducing BGI is an opportunity to bring additional benefits to the area. Hence, the strength of the Layer Approach is that it provides guidance in prioritizing SPT interventions (which occur in the Occupation Layer) based on restrictions imposed by the dynamics of the components in the Network and Polder Layer. At the same time, understanding and mapping the rate of change of components in the Network and even in the Polder layer will provide crucial information for strategic (longer term) planning as it will assist in identifying opportunities to intervene and synergies across the three layers.

The process steps

The overall design process of transformation is depicted in Fig. 4. Each step of the process has a specific emphasis and objective.

Step 1. System analysis

A comprehensive assessment of the water quality and quantity is conducted at polder level to establish a detailed understanding of hydrology and environmental quality, and the challenges for implementing the plans. The assessment focused on the main aspects of pollution and flooding.

To understand the challenges related to pollution, an assessment of the water quality and potential pollution sources are carried out with the aim to identify the dominant sources of pollution (e.g., farmland, industries.). Attention is also paid to pollutants in runoff which could also contaminate waterbodies in the polder. A series of control measures at the source are then implemented to reduce pollution. To assess the flood risk (stormwater), flood maps will be developed. Based on these maps, areas vulnerable to flooding will be identified to assist in the selection and location of SPT interventions in step 2.

Step 2. SPT interventions

Based on the results of the water quality and quantity assessment of step 1, SPT interventions in the occupation layer are identified and prioritized for the whole polder system Only those measures were selected which provided multiple benefits: notably flood risk reduction (reduced waterlogging) and emission reduction of contaminants to the inland waterbodies (see also Table 1). Principle (i) (mimic natural processes) is the guiding principle in this step.

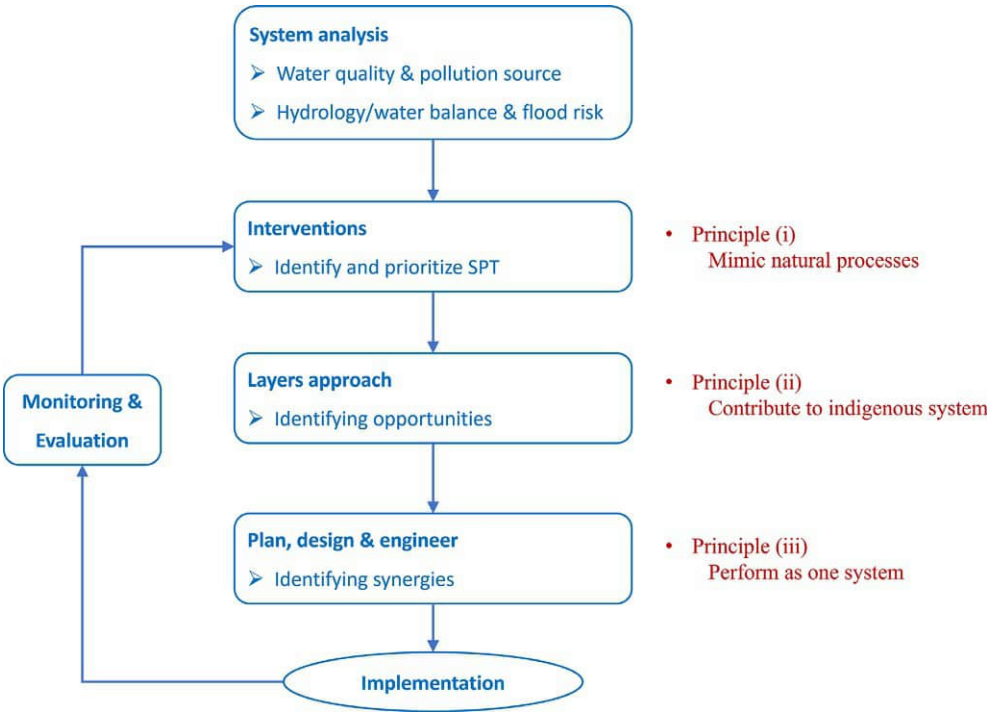

Fig. 4 The process steps of Kunshan's Sponge City Special Plan.

Step 3. Layers approach

In step 3, the selection, customization and planning of the candidate interventions are further elaborated and defined based on an understanding of the interactions and water flows among the three layers. Opportunities of when and where to intervene are identified by mapping the remaining lifetime of each component of an individual system (largely involving buildings and gray infrastructure in the occupation and network layer, respectively). Based on this information, candidate SPT interventions are selected which could coexist with, or adaptively replace these components. Principle (ii) (contribute to the indigenous system) is the guiding principle in this step.

For example, the allocation of a new bioretention cell (Occupation Layer) is constrained by other buildings in the area (Occupation Layer). The maximum depth of the cell is subject to the depth of the underground systems such as pipe networks or metros (Network Layer), as well as the water level of the nearby canals (Polder Layer). In return, the implementation of a bioretention cell could enlarge the flood protection capacity of an outdated drainage network (Network Layer), or reduce contaminant discharged into the canals (Polder Layer). In this case, opportunities will be identified to offer choices such as small new bioretention cell with preservation of the outdated drainage network, large new bioretention cell with dismantling of the drainage network. . .

Step 4. Plan, design and engineer

For the design and customization (engineering) of SPT interventions, and in particular, for a cluster of facilities in the large-scale polder cities, much attention is paid to the social/environmental functions they provide and the risk of failure, in case of exceedance of the design standard of an individual facility.

To achieve that, synergies between individual SPT interventions or different layers are identified (e.g., the conventional pumping system in the outlet of a constructed wetland could contribute to the discharge capacity of the receiving canal, the connection of nearby detention facilities could help to balance the load during flood events). Depending on the results of the assessments, adjustments of the design are made to increase the robustness of the final design. Such robustness refers here to the capacity of the design to deal with failure in case the design standard of an individual SPT intervention of the design is exceeded. If failure of an individual SPT intervention will have a minimum impact on the total performance of the design, as other interventions will take over the burden resulting from failure of that individual SPT intervention, the design is considered to be robust. This iterative process eventually results in a blend of SPT interventions contributing to a blue-green and gray infrastructure network servicing a relatively large area (>5 km^2). Principle (iii) (perform as one system) is the guiding principle in this step.

Step 5. Monitoring and evaluation

After implementation of the interventions, a monitoring scheme is set up to assess and evaluate the performance of individual interventions as well as of the polder system. These insights are required to optimize the maintenance and operation schemes.

An expanding polder city: Application in the design of Kunshan

Kunshan, a city in China's Jiangsu Province, is located in a low-lying polder landscape. These polders have been reclaimed in the 7th century and onwards. Throughout the centuries farmers managed to adapt their agricultural system to soil subsidence and occasional flooding. In the past decades the original rural landscape transformed into an urban landscape (Fig. 5). The rapid urban development of the polders around the city of Kunshan started in the 1980s. This resulted in the creation of the present-day Kunshan polder city (928 km^2) which consists of 51% rural area and 32% urban area. The city expansion developed on a paddy soil which is drained by means of a network of indigenous drainage channels interconnected to the neighboring canals and lakes (17%). By the 2000s, nearly half of the canals became black and odorous, seriously impacting the residents' health.

In addition, to human-induced soil subsidence, an increase of the impervious area has led to a further reduction of the water retention capacity. As a result, less rainwater is detained or retained in periods of excessive rainfall. If this trend will continue (following a business as unusual scenario), Kunshan will experience more frequent inundations.

"Kunshan Sponge City Special Plan"

After the implementation and evaluation of the first batch of pilot projects (2015–2018), which largely consists of isolated, small-scale (SPT) interventions, the Kunshan government adopted a comprehensive, integrated approach for the second batch of projects in a new Sponge City planning program (the Kunshan Sponge City Special Plan). This new program, launched in 2018, aims to address both the water challenges Kunshan is currently facing as well as the poor living conditions in the city. In order to accomplish this ambition, BGI is envisioned as a mechanism to foster urban regeneration: the full range of BGI benefits needs to be considered both at the level of a single intervention as well as the polder system as a whole. This requires that these benefits have to be understood, valued, and used in the planning, design and engineering process of the program. A new integrated planning framework and institutional arrangements have been adopted to identify these benefits arising from the interactions between multiple spatial scales, and cross-departmental cooperation between policy domains and sectoral planning processes, such as transportation (road infrastructure) and water resource management, respectively (Jiang et al., 2018).

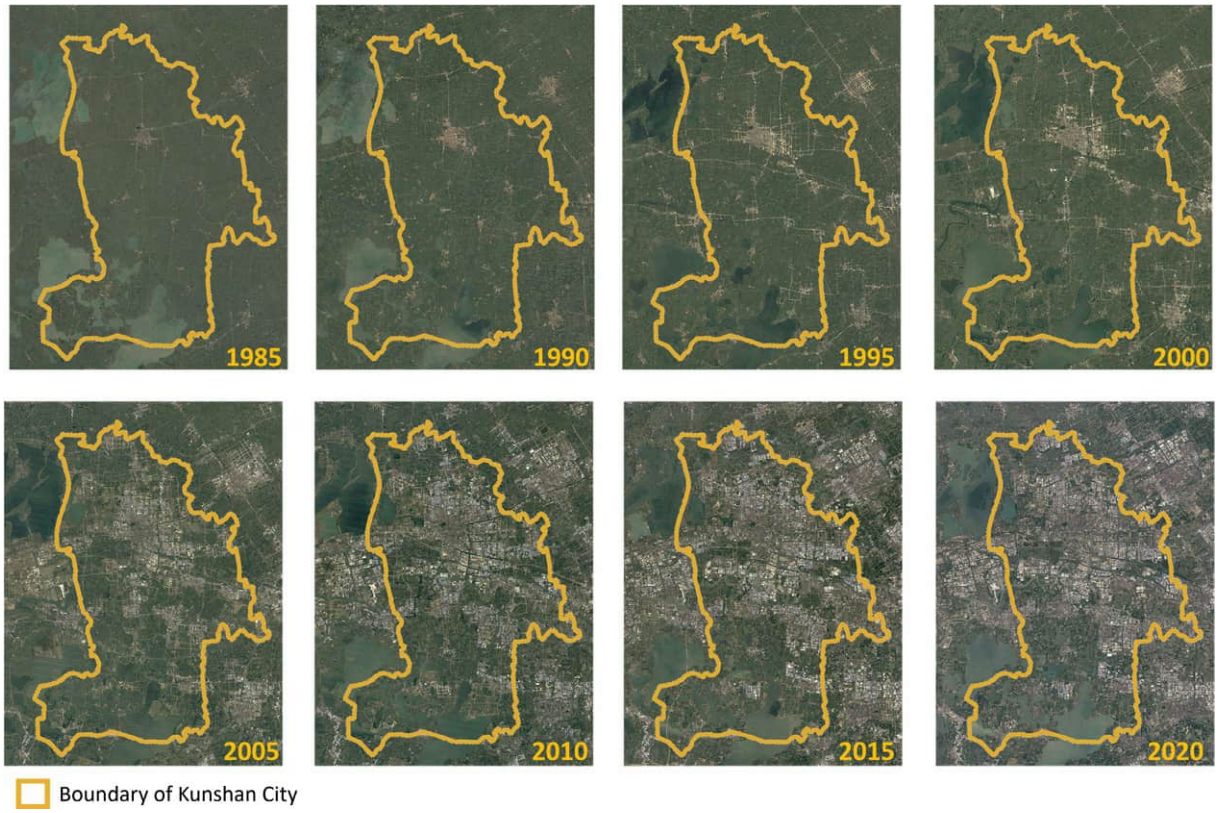

Fig. 5 Change of land use in Kunshan (1985–2020). The city originally consisted of polders used for farming. In the last 25 years, rapid development has significantly changed its land use, and consequently its water quality and flood protection capacity. Based on the remote sensing data from Kunshan government.

Table 2 Annual average water quality of some monitored canals in Kunshan (2017).

	Ammonia-N[a] *(mg L^{-1})*	*Phosphate-P (mg L^{-1})*
1#	9.77	0.78
2#	4.23	0.47
3#	4.92	0.26
4#	5.26	0.54
5#	6.08	0.32
6#	13.36	1.35
7#	18.1	2.29
Class III	1.0	0.2
Class V	2.0	0.4

Only Ammonia-N and Phosphate-P were reported as they were the dominant excessive pollutants.
[a]There is no requirement for nitrate-N or total nitrogen in the standard for surface water not serving as water sources, because the testing result of nitrate-N or total nitrogen is sensitive to nitrate-N which could bring large uncertainties in the assessment.

Implementing Kunshan's Sponge City Special Plan

Step 1. System analysis

The water quality of Kunshan was evaluated using monitoring data since early 2017. Hundreds of canals were identified as" black and odorous rivers" according to China's national Environmental Quality Standards for Surface Water (Table 2). In this standard, Class III is the minimum requirement for surface water which is accessible to citizens (e.g., swimming, fishery, or serving as water sources) and Class V is the minimum requirement for surface water to be utilized in cities (e.g., irrigation, inaccessible waterscape). The monitoring data indicate that the excessive pollutants in Kunshan comprising ammonia-N and phosphate-P originate predominantly from combined sewage system and agricultural runoff.

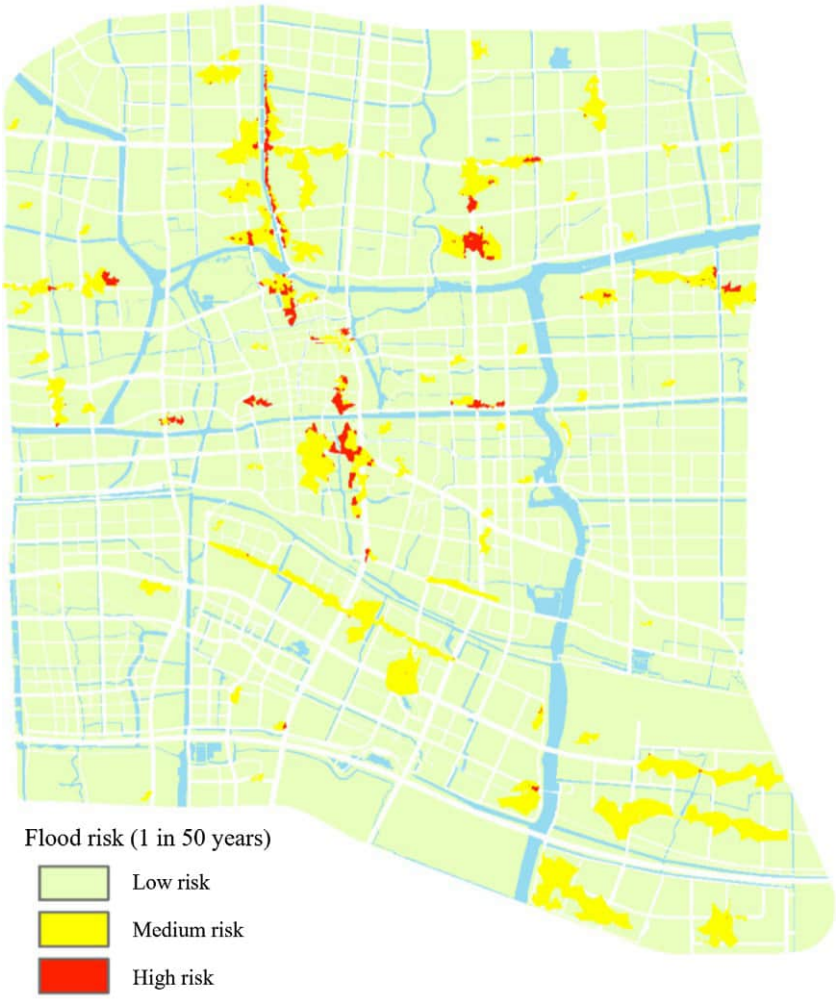

Fig. 6 Flood risk map of the city center of Kunshan indicating areas at risk in a situation after extreme rainfall (50-year rainfall event). Reproduced with permission from Stormwater system planning of Kunshan City.

Hydrological modelling was carried out to assess the extent and depth of flooding resulting from extreme rainfall events (one in 50-year rainfall event) of Kunshan. The results reveal a scattered distribution of highly localized inundated areas across the city. The total flooded area comprises 1.9%, with different flood depths (15–29 cm, 47%; 30–49 cm, 50%; $\geq$50 cm, 3%). A flood risk map was constructed using these data in combination with an assessment of the flood duration and potential loss (see Fig. 6).

Step 2. SPT interventions

SPT interventions which have been selected in step 2 are constructed wetlands, detention plazas and bioswales (Table 1).

Constructed wetlands are artificial wetlands to treat sewage, greywater, stormwater runoff and industrial wastewater. All water flows through a settling basin (where large particles settle), a treating basin (where biological processes take place) and a drainage basin. The treatment basin is the dominant section of the wetland. In this section different water velocities and dissolved oxygen in the basin enable natural purification and mimic natural processes to foster various kinds bio-chemical processes such as micro-biome or biocenosis in the same infrastructure facility. Other water sources than stormwater, such as river water or treated water from wastewater treatment plants, have been considered in the wetland designs to assure permanent saturation of the system. Constructed wetlands provide multiple benefits: runoff mitigation and purification on rainy days, improve local water environment and micro-climate on non-rainy days. Typical examples of constructed wetlands in Kunshan are depicted in Fig. 7.

Detention plazas are designed to retain/store stormwater rather than provide water quality improvement. They are usually constructed in new land development projects in residential or commercial areas, providing flood protection capacity as well as a social function.

Typical design allows large flow of water to enter but limits the outflow by having small openings at the lowest point of the structure. The size of the opening is determined by the capacity of underground and downstream culverts to handle the release of the contained water (Dykehouse and Edmunds, 2010). Typical examples of detention plazas in Kunshan are depicted in Fig. 8.

Fig. 7 Constructed wetlands in Kunshan: (left) a constructed wetland in industrial park; (right) a roadside wetland landscape.

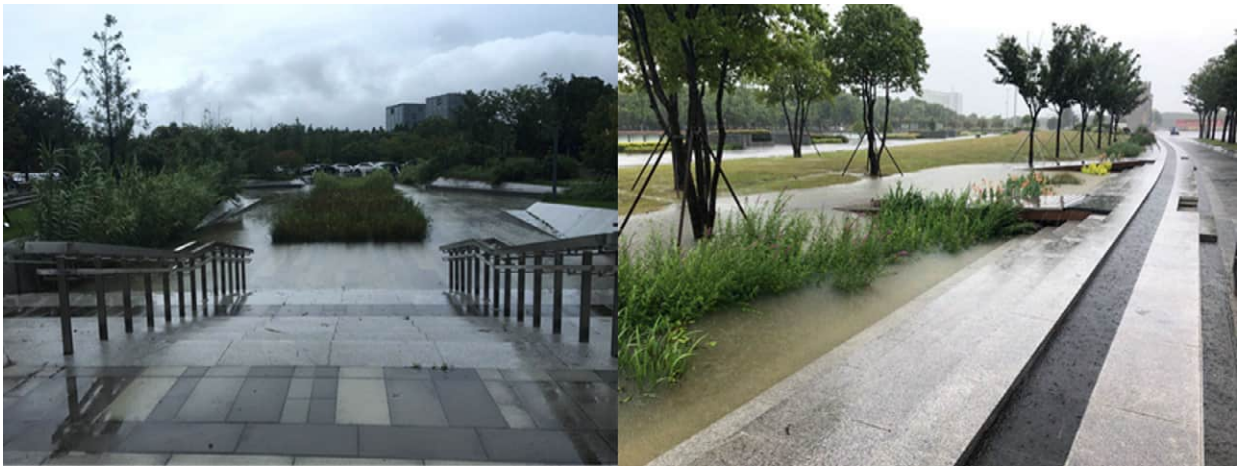

Fig. 8 A detention plaza in Kunshan: (left) plaza during normal days; (right) plaza during rainfall events.

*Bioswale*s consist of a ditch with vegetation and a porous bottom. They can be regarded as a smaller and decentralized version of the bioretention cell with a limited pollution removal capacity. Stormwater (from roofs and roads) does not flow into sewers but instead is directed into the bioswale. As bioswales are much smaller in size than bioretention cells and wetlands, they fit more easily into most of the existing green spaces than the other SPT technologies. Typical examples of bioswales in Kunshan are depicted in Fig. 9.

Step 3. Layers approach

After selecting the candidate SPT interventions, opportunities are identified to integrate these interventions into the design of the existing system. An example project is the upgrading of the existing combined sewage system (CSS) of Kunshan. In 2016, 94 communities in Kunshan's downtown area used CSS (Fig. 10). The capacity of the CSS system could no longer meet the needs of the growing population and accommodate the volumes of stormwater during extreme rainfall. To expand its capacity and separate the drainage network from the existing CSS, the SPT interventions comprised a stepwise and opportunity driven approach (Fig. 11). This involved short, medium and long-term initiatives. In the short-term, highly permeable pavement (roads, public spaces) were deployed to allow direct infiltration of stormwater to the natural water system and detention of runoff in above ground facilities such as plazas, bioswales, constructed wetlands. In the medium term, large scale (gray infrastructure) interventions such as underground water storage facilities will be implemented when components of the existing CSS infrastructure have reached their end of life (Xi, 2020). In the long-term, this will result in the total replacement of the existing CSS system to deliver sufficient capacity, to treat domestic wastewater in non-rainy days for the growing population.

Fig. 9 Bioswales in Kunshan: (left) a bioswale in a closed housing district; (right) a bioswale in public space.

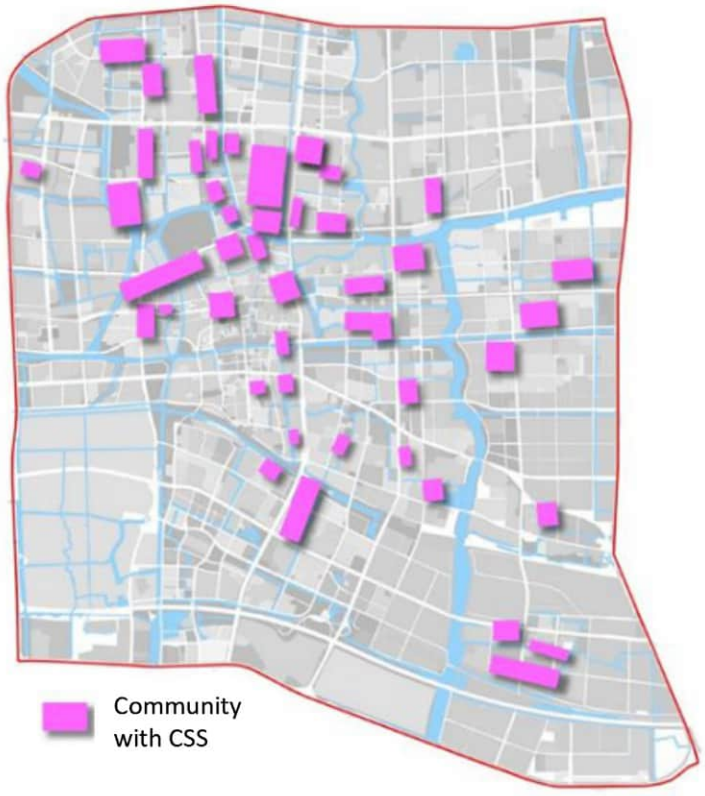

Fig. 10 Communities with CSS in Kunshan downtown, 2016. Reproduced with permission from Stormwater system planning of Kunshan City.

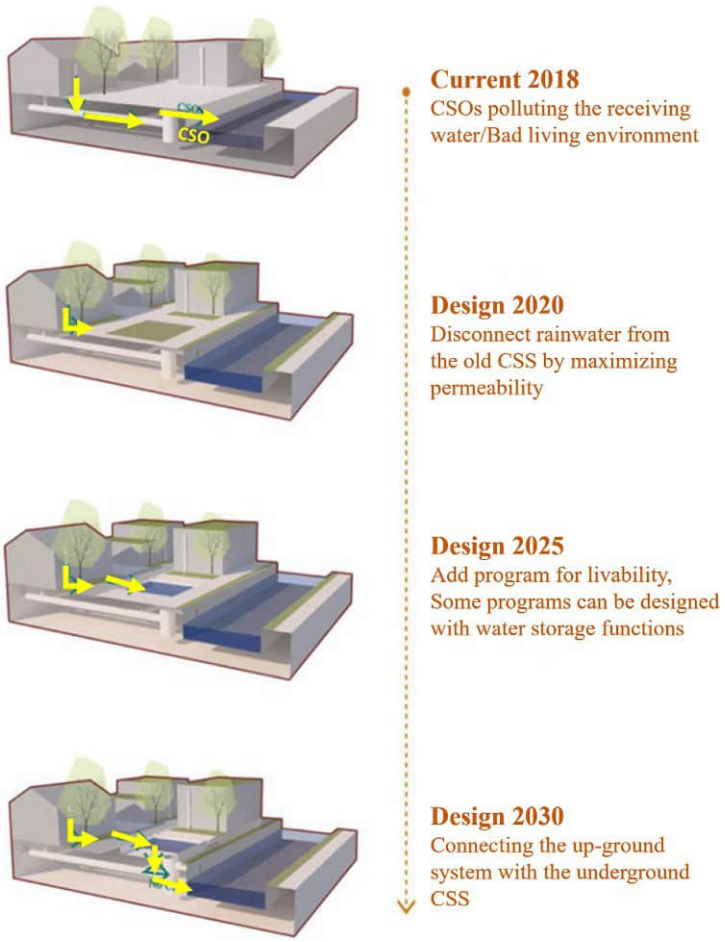

Fig. 11 Opportunity-based design for CSS upgrade through SPT interventions. Reproduced with permission from Xi F (2020) A multi-layered approach to rapid transitioning of high- density Chinese urban areas to water sensitive neighbourhoods in Kunshan. Unpublished master's thesis, IHE Delft Institution for Water Education, Delft, Netherlands.

Step 4. Plan, design and engineer

Based upon the timeline of implementation of the interventions, in this step the design process is used to appraise the synergies among SPT interventions and the robustness of the resulting system. Via an iterative process the final design (and engineering) is delivered. One typical example of this step comprises a large-scale blue-green and gray infrastructure network (covering 10 ha which equals the surface area of 14 standard soccer fields), the Qingsong Wetland Park project in Kunshan. This project consists of a collection of SPT interventions to support urban agriculture targeting to maximize synergies resulting from an integrated design. In China, and many other countries, the potential of urban agriculture to provide fresh food, generate employment, enhance livability and recycle of urban wastewater are increasingly recognized. Only in recent years, urban agriculture has been acknowledged and promoted as a new generation of BGI to play a role in strengthening cities' resilience to climate change. The Qingsong project aims to introduce a new, urban agricultural function into one of Kunshan's urban redevelopment programs. The programs serve at least two objectives: (i) to comply with the Sponge Cities requirements to enhance pollutants removal and water retention while maintaining its original land use function such as basic farmland and green space; and (ii) to enhance the livability and attractiveness of the redeveloped urban area for its citizens.

In Figs. 12 and 13, the layout of the project is given together with impressions of its multiple functions. An important design criterion for the park is its capacity to remove nitrogen from the surrounding surface waters (canals).

There are three SPT interventions and three city components which have been integrated to create synergies between the individual parts in this project (see Fig. 14). The CSS in the residential area was connected to the farmland to prevent excessive ammonia and phosphate pollution of the canal. The farmland was designed as a bioretention cell with extra submerged layers to store nutrients from either fertilization or CSS discharging while maintaining its agricultural function. Wetland A detain stormwater from Road & Highway as well as overflow from Farmland, and release irrigation water for Farmland when needed. The water in the canal was pumped into Wetland A and B from the west and north side while the treated water was released into the canal from the south side.

Fig. 12 Layout of the Qingsong Wetland Park, Kunshan.

Fig. 13 Qingsong Wetland Park: (Left) Harvesting paddy rice field; (Middle) information provided to visitors; (Right) monitoring of the wetland system.

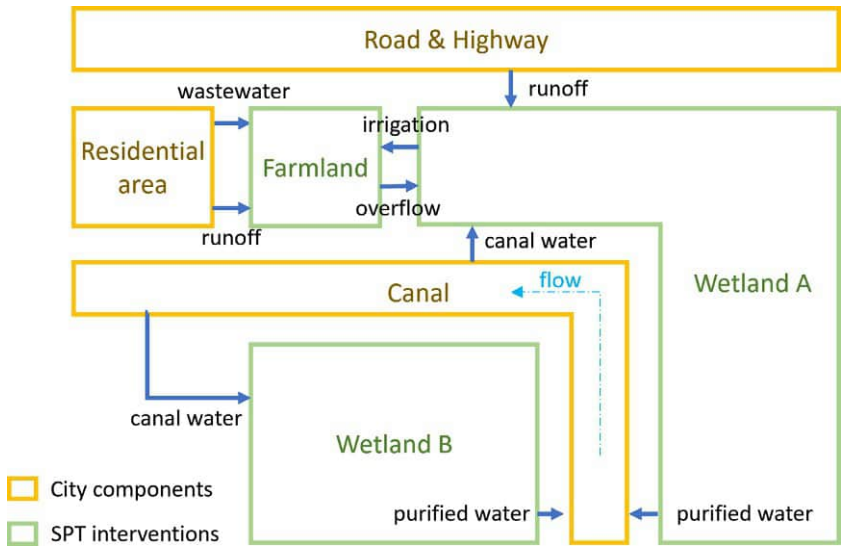

Fig. 14 Synergistical design in the Qingsong Wetland Park.

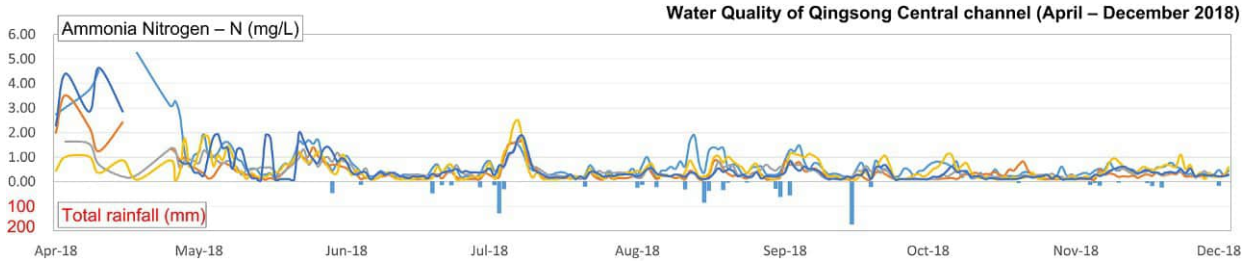

Fig. 15 Monitoring data for total rainfall and ammonia nitrogen in April 2017–December 2017 (the starting period of sponge city transformation). The transformation significantly reduces the nitrogen concentration in the river. Rainfall events could cause the increase of nitrogen in the river due to the runoff from farmland, road, etc.

When failure occurs in any part of the project, the design of the park always assures that the receiving waters are being well detained and treated. E.g., Wetland A is designed to treat domestic wastewater and retain runoff from the residential area when the farmland area fails; Wetland A and B will function as a substitution when one of the two fails; When the CSS leaks into the canal, Wetland B will partially treat and retain the wastewater; Runoff water from the roads and highway will always take a D-tour through the residential area of the farmland before it is arriving in Wetland A.

Through continuous circulation, the contaminants that originally are being discharged into the canal are captured and utilized by the farmland and/or degraded by the wetland, resulting in a gradual improvement of the water quality of the canal system in the polder. In particular, the citizens are benefiting from the park as many of them engage in the urban farming activities of the park of which its environment is gradually improving.

Step 5. Monitoring and evaluation

An example of the results of the monitoring is given in Fig. 15. Total rainfall and ammonia and nitrogen concentrations of surface water are given, which illustrate the effect of the Qingsong Wetland Park on the water quality (starting from April 2018 (before implementation) to December 2018 (after implementation)). The concentration and its fluctuation of these components gradually decrease over time to a stable level.

Conclusions

Cities both in the developed and developing world are facing complex challenges associated with urban growth, aging infrastructure, and degraded environments, exacerbated by climate change. Urban planning is urgently required to address these challenges and to transform cities into livable and resilient cities. Water is playing a pivotal and steering role in this transformation process. It calls for a broad, integrated approach to urban water infrastructure planning as our current urban water related challenges cannot be resolved in isolation. This will require to have in place the capacities at the various governmental institutions and stakeholders to work together. To capturing the multiple benefits of blue-green infrastructure as well as the interdependencies over the entire water infrastructure system comprising water supply, storm water runoff drainage, sewerage wastewater management.

Current practice tends to focus on individual (sectoral) projects and specific neighborhoods of the city, often resulting in (institutional) fragmentation and disconnected activities neglecting synergies and lacking consideration for wider societal benefits from human-nature relations. It also may lead to a sectoral approach which forgoes the opportunity to make the link with other domains (such as sustainable energy and circular economy).

The aim of the Sponge City concept is to address both the current water challenges, such as a poor water quality, floods and droughts, and to improve the livability of cities. In China, an ambitious program has been launched to accelerate this transformation process towards a water sensitive or sponge city. BGI technologies are a crucial component in this program to foster this transformation to become a Sponge City. The polder city Kunshan is one of the frontrunner cities in this program. Kunshan is following an integrated, strategic approach which is stepwise and opportunity-driven, with short, medium and long-term interventions that are planned, designed and engineered using the Layer Approach. This approach fosters to maximize synergies between the different interventions and to seize opportunities that arise from autonomous urban renewal activities outside the water domain in the city.

Most of the technologies to build a sponge city are already widely available, but they lack a historical track record (on their long-term performance, operation and maintenance) and are often not embedded in an integrated plan. Cities in other regions of the world can benefit from the experiences of Kunshan, which is now building that evidence base through its Sponge City program and application of various SPT technologies following a dynamic-based planning approach.

Knowledge gaps

Knowledge on Sponge City performance is still limited, because of a lack of understanding on the functioning of BGI under different conditions and their long-term behavior as they age. Moreover, it is a challenge to design a meaningful monitoring program and to select key performance indicators for monitoring.

Nevertheless, local stakeholder involvement and alignment is generally more important for BGI than for gray infrastructure. However, stakeholders' expertise, knowledge and perspectives are still underutilized. The way to effectively involve stakeholders in the Sponge City program is still a challenge and requires further study.

Acknowledgments

We thank Ken Irvine for the invitation to contribute this chapter. His comments on the chapter and those of an anonymous reviewer are also highly appreciated.

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Resources on Sponge City

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https://www.chinadaily.com.cn/a/202108/16/WS6119af4fa310efa1bd668e82.html—After the flood.
https://global.chinadaily.com.cn/a/202110/29/WS617b41bca310cdd39bc71fea_1.html—Sponge city—Shanghai.
https://global.chinadaily.com.cn/a/202108/24/WS61245ea5a310efa1bd66ac3c.html—Sponge park—Shanghai.
https://www.chinadaily.com.cn/a/202010/15/WS5f88128da31024ad0ba7eea9.html—Binhai's ecological system overcomes salinity.
https://www.chinadaily.com.cn/a/202103/17/WS60515b59a31024ad0baafa81.html—Smelly Beijing lake transformed into vibrant bird habitat.
https://www.chinadaily.com.cn/a/202110/04/WS615a3a38a310cdd39bc6d00f_1.html—Extreme weather events a challenge to city management.

Resources on Relevant Concepts

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https://watersensitivecities.org.au/—CRC for Water sensitive cities.
https://watersensitivecities.org.au/solutions/case-studies/kunshan-ring-road-case-study/—Kunshan Ring Road—CRC for Water sensitive cities.
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Section Introduction: Societal Values and Other Human Dimensions in the Science and Management of Inland Waters: For Whom? By Whom?

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Glossary

Biocultural dimensions As defined by the Convention on Biological Diversity (2018), this term broadly links biological diversity with cultural dimensions, reflecting a holistic approach of many Indigenous peoples and local communities.
Human dimensions The broad range of ways that humans are in relationship with fresh water, and particularly as they relate to the science and management of inland freshwater ecosystems at a range of scales.
Societal values One example of human dimensions as they relate to inland freshwater, referring to how local communities and society place priority over an attribute of fresh water. This can include cultural, recreational, fishery, ecosystem provisioning, etc., and can elicit or necessitate efforts to place value on aspects of fresh water.
Socio-ecological system Linked social and ecological units as one system of study or management.

Introduction

The link between humans and freshwater is inextricable. Humans are drivers of degradation and critical to ensuring a more sustainable freshwater future. Freshwater is so widely recognized as being vital to human life and societal well-being that many Indigenous and local cultures have a common saying: Water is life. Despite being responsible for the degradation and stress placed on inland freshwater ecosystems, humans play a central role in the study, stewardship and management of freshwater. As drivers of the Anthropocene (Lewis and Maslin, 2015), humans are also critical in reversing further declines in biodiversity and ecosystem functioning to ensure planetary sustainability for future generations (Bennett et al., 2016). Unfortunately, the intentional inclusion of human dimensions in freshwater science and especially policy- and management-relevant science is not yet commonplace. In the current 'code red' state of emergency when it comes to climate change (IPCC, 2021), it is almost impossible to imagine that the science and management of inland waters can proceed without accelerated efforts to incorporate societal values and other human dimensions related to fresh water.

Freshwater biodiversity has been in crisis globally (Dudgeon, 2010; Dudgeon et al., 2006; Jenny et al., 2020; Reid et al., 2019) which intersects with threats to human water security (Vorosmarty et al., 2010). Thus, freshwater and human dimensions are inextricable. Human dimensions refer to the multiplicity of ways in which society interacts with and benefits from a relationship with water. The term is inherently diverse in scope, nature, geography and thus necessitate a pluralistic view and set of approaches when dealing with incorporation in science-based pursuits and management. One of the more common operational frameworks for linking humans and ecosystems is the *ecosystem services* concept which provided a way to encode economically valuable services provided by freshwater alongside other societal benefits (e.g., health and well-being) (Millenium Ecosystem Assessment, 2005). For freshwater specifically, there is a growing global recognition that water is a finite human resource that must be managed to address economic, social, environmental and basic needs of society. This has necessitated strategic partnerships at a range of scales, including across multiple nations (e.g., European Union's Water Framework Directive) (European Commission, 2000) and increasing awareness of the

importance of different knowledge systems (Ban et al., 2018; Whaanga et al., 2018). Thus, societal values are highly variable, context-dependent that can inform how water is prioritized in and across communities (e.g., recreation, culture, biodiversity, etc.) but also in practically assessing preferences through exercises in valuation (e.g., economic) (Tadaki et al., 2017). While examples of human dimensions are varied across inland ecosystems and contexts, considerable progress has been made in better understanding how to gather, harness and amplify societal values in research and management. It is not our intention to capture all of the examples in this chapter but to provide a broad overview on recent work and highlight the opportunities that are on the horizon.

Looking back

Along the same vein, looking to the future requires an effort to consider what has been done to date. As one example, the aim of the 1st Edition of the Encyclopedia of Inland Waters (2009) was to bring together the most recent and comprehensive overview of knowledge for scientists to study and manage? inland freshwater ecosystems. Additionally, the resource was developed to provide critical information for water-related decision-makers to effectively manage and protect inland ecosystems for future generations. The initial offering covered the suite of physical, biological and ecological attributes of inland ecosystems globally across all levels of taxa and across ecosystems. Notably, human dimensions were featured in an analysis of water as a human resource (Dudgeon, 2010; Reid et al., 2019), in terms of water ecosystem services (Limburg, 2009), relationship to human health (McNinch et al., 2009), agriculture (Jones and Downing, 2009), aquaculture (Boyd, 2009), aesthetic values (Corrigan et al., 2009), management (Cardoso et al., 2009), bioassessment (Norris and Barbour, 2009), to name a few. Varied human dimensions were also woven across chapters that were geographical in focus.

For further context, we explored and broadly quantified the growing literature that explores inland ecosystems and some human dimension (Supplementary Material 1 in the online version at https://doi.org/10.1016/B978-0-12-819166-8.00216-4). More than 100,000 peer-reviewed publications have appeared with direct use of inland freshwater ecosystems alongside social dimensions (Fig. 1). These offerings have more than doubled in the last decade since the publication of the 1st edition.

Current examples integrating human dimensions in science

Collaborations between science and management have been incredibly fruitful but still have a far way to go to successfully restoring inland waters globally as coupled environmental and human dimensions are rarely assessed (Padowski et al., 2015).

Inland fisheries have been a classic motivation for collaboration between science and management. Lynch et al. (in press) provide a global overview of inland fisheries and provide examples for nine societal services provided by inland waters. From livelihoods to subsistence income, food and nutrition, recreational, cultural, economic and ecosystem provisioning services, they are all under threat due to human-induced pressures. Despite case studies globally showing how science and management have

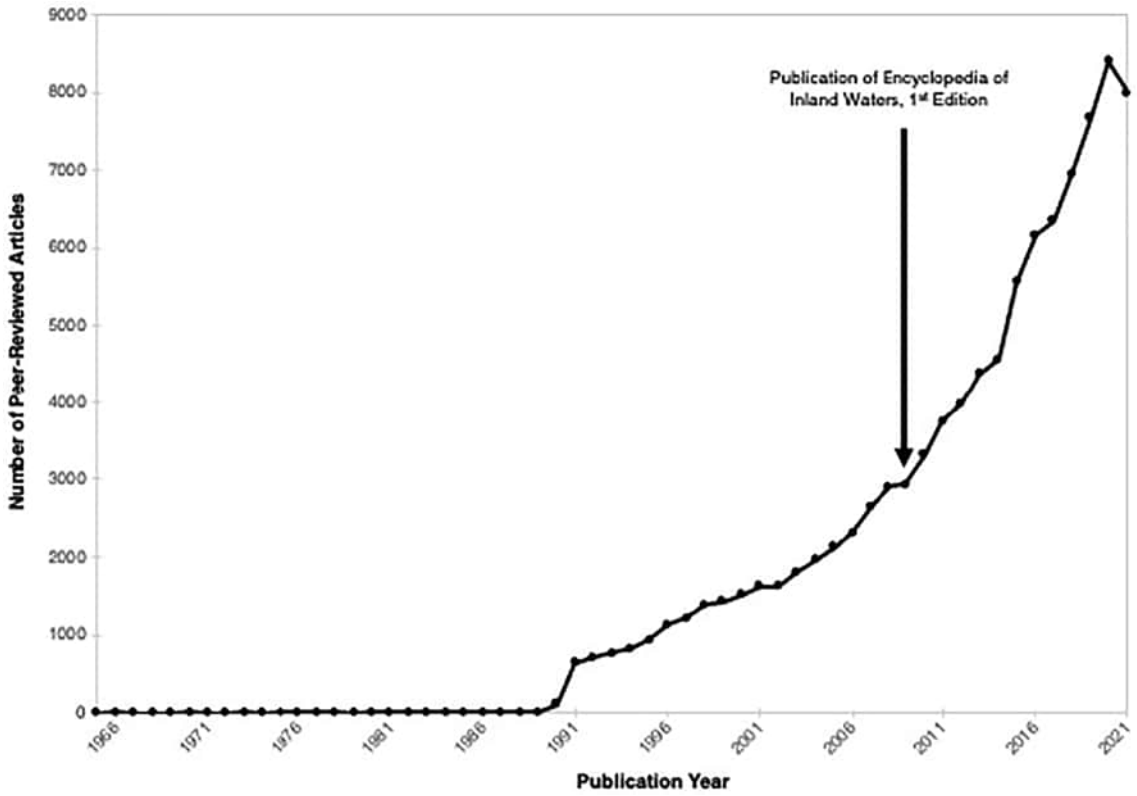

Fig. 1 Published peer-reviewed articles over time since 1965 covering societal dimensions of inland, freshwater ecosystems globally. See Supplementary Material 1 for broad search terms employed and thematic analysis.

come together to support local needs and interests, there are many gaps to be filled to ensure that the incredible biodiversity found in inland systems can be sustainably stewarded and managed.

Situated at the science-management nexus is the protection of inland waterways through the restoration of land-water/aquatic-terrestrial interface via the implementation of riparian buffers at range of scales. Stokes and Smidt (in press) applied a land cover change analysis of riparian buffers in the United States to illustrate the diverse values and support further valuation of riparian zones in decision-making. Their analysis confirms the importance of considering transitional aquatic habitats (e.g., wetlands) as well as terrestrial species in riparian buffers as part of the science required to advance management in the United States but likely also globally. Krantzberg (in press) catalogues the intense efforts of communities and governments of all orders place on restoration of ecosystem function to achieve desired human and non-human uses of the Great Lakes basin geographic Areas of Concern.

To illustrate the diverse set of values placed on inland waters, we look to the Global South where societal implications to effective science and management are essential for addressing multiple stressors and supporting livelihoods at a range of complex and interacting scales. Obiero et al. (in press) provide an overview of the challenges and opportunities facing Kenya, a riparian country in the African Great Lakes basin. Top of mind is the harnessing of societal dimensions to enhance sustainable management of inland resources for current and future generations. An emphasis on the blue economy, or economic activities linked to the sustainable use of freshwater, has the potential to offer the most significant contribution to Kenya's economic growth. To balance the societal dimensions with ecological challenges and opportunities, a driver-pressure-state-impact-response (DPSIR) framework is offered to bring Kenya into the future in a people-centered, equitable and just way.

Centering human dimensions—For whom?

It is critical that those engaged in scientific research on inland waters—especially the next generation of leaders—understand the social or governance structures that connect research with management and practice to anticipate, integrate and co-design work that can be implemented more rapidly. Farhad and Baird (in press) draw on resilience principles and perspectives to illustrate the role that governance places on inland systems. Invoking socio-ecological systems thinking, the authors describe how freshwater management and governance can incorporate attributes to ensure good outcomes when resilience principles are incorporated. Resilience as an ecological concept should be familiar to most scientific undertakings; however, translated to social realms, it becomes clear that decision-making can be more effectively supported when social dimensions are intentionally incorporated.

This theme is echoed in Johns' offering and consideration of how societal values are reflected in public policy (Johns in press). Drawing on rich case studies from the North American/Laurentian Great Lakes system, the author illustrates how conflicts in values can be addressed using alternative approaches. A key example in Canada and other countries is the values shared by Indigenous communities, the original stewards of water resources prior to European colonization and settlement of North America. Contrasting current and Indigenous laws, this offering illustrates the interconnectedness of water as a guiding principle or new water ethic. Underpinning this is that water is a basic human right, which despite offering an alternative path for water valuation, remains an ongoing challenge. Other alternatives, such as re-framing values placed on built environments, and economic mechanisms to support sustainable water management are discussed using the North American/Laurentian Great Lakes as a regional example (Krantzberg in press). Efforts in the Laurentian Great Lakes are built upon decades of an Ecosystem approach (Alsip et al., 2021; Hartig et al., 1998), which has offered a collaborative governance framework for considering the interrelationships between the Great Lakes ecosystem and various actors around the basin. Building on decades of efforts focused on Areas of Concern (AOC) and remedial action plans (RAPs), much insight is offered by Krantzberg (in press) (Krantzberg, 2018) on how this approach may offer a path for the management of inland waters elsewhere.

More broadly, legal and institutional frameworks vary within and across nations that share boundary waters. In the Global South, Achieng et al. (in press) examine how cross-nation watershed management in Africa might be approached to engage national and regional social and biophysical elements. Finding common ground within a shared watershed, the biodiversity and values found therein, the authors provide examples for how a more decentralized approach may facilitate greater engagement at the local level in more effective watershed management.

Given the varied examples across the globe, Nagabhatla et al. (in press) offer a framework for addressing societal values through the general idea of 'Valuing Water' as a multifaceted effort to operationalize terms and concepts for the benefit of multiple actors, from research to policy and stakeholders involved in water decisions. A key motivation for valuing water is to enable and accelerate change to ensure that the UN Sustainable Development Goals (SDGs) can be achieved. Reframing water values is their proposed solution, and drawing on examples globally, they highlight the importance of pluralistic approaches to valuing water through economic and non-economic lenses to facilitate more equitable access to the management of water.

Centering human dimensions—By whom?

Notions of just, equitable and fair access to, distribution of and research on inland fresh water are a common theme in this thematic section and the growing body of literature. Not often discussed is the human dimension of those engaging in research, management and stewardship of inland waters, i.e., who is conducting this work?

In this thematic section, Penaluna and Arismendi (in press) pull the curtain back on those engaging in published work related to fisheries. Focusing on the period of time just prior to the publication of the 1st edition of this Encyclopedia (i.e., 2006–2020), the authors examined the gap in women vs. men in fisheries. The trends observed in this global analysis confer similar patterns found at national and sub-regional scales: women are consistently disproportionately represented in publications, are cited less than men, which all contribute to a lack of recruitment and retention in research-related and leadership positions. Given the central role than

women play in water stewardship globally, the authors make visible a 'productivity' vs. 'impact' gap in fisheries and highlight the need for a systemic shift in how we value women and non-binary individuals who engage in fisheries work.

We acknowledge that the global community of researchers and decision-makers are in a period of incredible flux. At the time of writing, the global COVID-19 pandemic—which took hold in March 2020—continues to exert prolonged stress on society. When it comes to the inland research and management community, the impacts are most deeply felt by historically underrepresented groups, notably women, early-career, Black, Indigenous and People of Colour (BIPOC). Despite a lengthy period of invitations and interactions with potential authors, many invitations were declined or remained unanswered. Our analyses of publications (Fig. 1) provide reveal a levelling off in 2020–2021, likely due to widespread disruptions due to the pandemic. Societal impacts are multi-fold, particularly when we consider countries of the Global South where freshwater is already a limited resource. Women often play central roles in terms of local scale water stewardship. Early reports suggest a magnification of inequity when it comes to women and water because of the pandemic (Parry and Gordon, 2021; Stoler et al., 2020). Moreover, women in the research community are also experiencing inequities due to intersecting, underrepresented identities in academia that include parenthood (Gewin, 2020; Kramer, 2020). As we continue to navigate a multitude of stressors, there are opportunities to re-think, re-frame and rebuild opportunities to support a richer, more inclusive and impactful global freshwater community (Fulweiler et al., 2021; Gewin, 2020; Nocco et al., 2021).

Looking forward and moving towards connectedness

Inland waters have long been recognized as being hotspots of biodiversity (Dudgeon et al., 2006), inextricably connected to their surrounding catchment (i.e., the stream and its valley) (Hynes, 1975) however in practice local management units often focus on land or water separately. Multiple efforts have promoted more integrated social-ecological systems approaches to water restoration or management (Naiman, 2013; Ostrom, 2009). Falkenmark (2004) suggested that moving beyond land-water dichotomies in freshwater management was essential to achieving global targets for global freshwater sustainability. In particular, balancing local-scale with catchment-scale efforts. In the recent decade, growing efforts have sought to move beyond freshwater units alone but connectivity with terrestrial units, the interface or ecotone in between, and as discussed in this thematic section, human perspectives and dimensions.

Consideration of human dimensions and how they may be more effectively incorporated in freshwater research and management have long been pursued, discussed and conceptualized (Fig. 2). Moving forward, it seems essential that intentional engagement of human dimensions must be incorporated from the start both conceptually (e.g., socio-ecological systems) (Naiman, 2013; Ostrom, 2009; Parsons et al., 2016), by engaging and maximizing diverse knowledge systems (Febria et al., 2022; Suding et al., 2015), and operationally through engagement and partnership as part of a larger process of knowledge co-production (Ban et al., 2018; Norström et al., 2020).

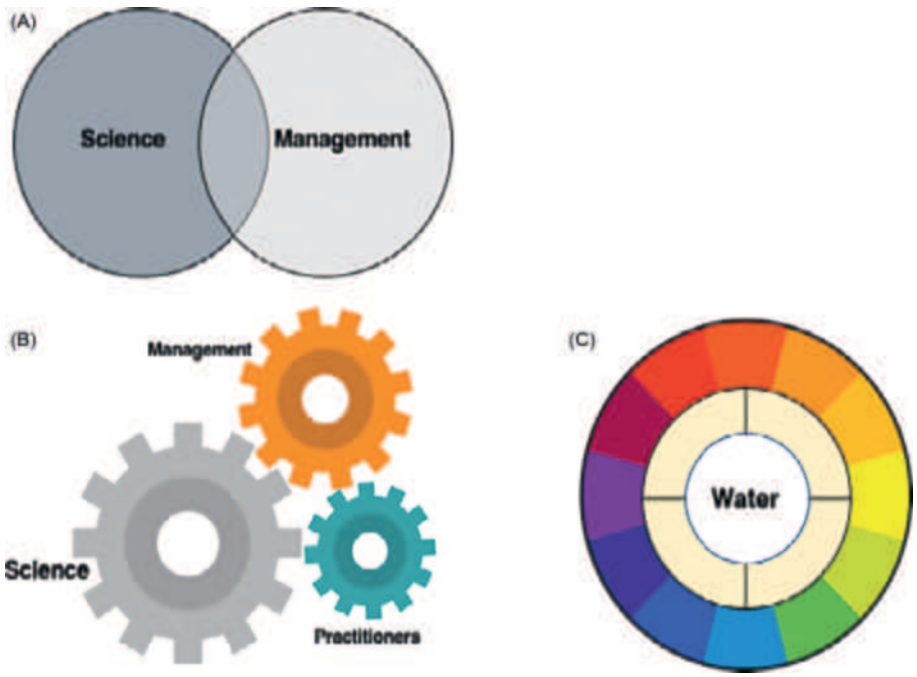

Fig. 2 Conceptual shift in approach in inland freshwater science and management from (A) to (B) that attempt to recognize complementary components leading to more innovative outcomes, or (C) more pluralistic, inclusive and holistic approaches that engage human dimensions, Indigenous and local knowledge systems, values and ways of knowing.

Ko au te awa, ko te awa ko au (I am the River and the River is me)—Māori proverb

There are increasing examples of change in the ways that inland research and management is taking place globally. Notably, growing awareness of a connectedness with nature, and the inseparability of society and nature has been best exemplified by greater amplification of Indigenous knowledge systems alongside western science-led efforts in various examples globally (Ban et al., 2018; Collier, 2017; Rayne et al., 2020; Reid et al., 2021; Suding et al., 2015). For example, in Aotearoa New Zealand, the Whanganui River was recently granted legal person status, a first for rivers globally. Empowering Indigenous communities as the guardians of the river offers a framework for connecting the river from mountains to the sea, its' tributaries and catchment into a more holistic, integrated view of the river as a living ancestor. Similar efforts are underfoot elsewhere, such as the Ganges River (India), the Magpie River (Canada) and to varying extents in South America (Ecuador, Bolivia).

Knowledge gaps

To effectively bridge science with human dimensions, the offerings presented here and across the literature demonstrate how the approach is shifting towards a more innovative knowledge co-creation process (Hallett et al., 2017; Krantzberg, 2018; Norström et al., 2020), including the prioritization of collaborations, partnerships and workforce training. Outcomes of collaborative co-design of research and management can lead to shared benefits/co-benefits and enrichened trust-based collaborations in governance and decision-making at a range of scales (Alsip et al., 2021; Febria et al., 2020, 2022). Therefore, this thematic section provides rich and varied examples such as locally-implemented river restoration and riparian planting (Stokes et al. 2022), watershed management (Achieng et al. 2022), to legal and social mechanisms (Lynch et al. 2022; Johns 2022). As important is how different sectors of society in this work (Penualuna and Arismendi 2022). Thus, evidence is building towards more equitable, inclusive and just approaches to research and management of inland waters, the advancement, operationalization and testing of frameworks that can be tailored to societal values and systems, that will be truly impactful if they can address and alleviate existing disparities and inequities in inland water research and management.

Conclusions

Now is the time to consider the plurality of connections between inland ecosystems and humans. In related efforts, such as biodiversity conservation, it has become clear that efforts to achieve sustainability at local to global scales must consider new approaches to co-produce knowledge and co-innovate science-based innovations to improve management and sustainability. Notably, a more just and inclusive approach in these efforts—which also centers Indigenous and local knowledge systems—alongside western science may also help to address apparent cultural and gender-based gaps in the inland freshwater science and management work thus far. Reflecting on the decade in between the first and second offering of this holistic and comprehensive resource, the sheer number of efforts that span disciplines, ecosystem and geographical scales have increased. We anticipate that the decade ahead will reflect the growing awareness and importance of linking science, management and human dimensions as the status quo approach for the benefit of future generations.

See Also: Social/societal values of Inland waters: Freshwater Governance and Resilience; Great Lakes Revitalization and Renewal; Riparian Buffers and Land Cover Change; Societal Implications of Kenya's Inland and Marine Waters; Societal Values of Inland Fishes; Societal Values, Water and Public Policy; The Gender Gap: Women as Authors and Leaders in International Publications in Fisheries Science; Value Proposal in Freshwater Systems-Theoretical Frameworks and Operational Measures; Watershed Management in Kenya; Societal Implications, Drivers of Change and Governance Needs

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Great Lakes Revitalization and Renewal

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This contribution is a compilation of publications that I co-authored on large lakes, and particularly, Great Lakes resilience and restoration. It consists of sections adapted from published works. The reference list includes literature cited herein as well as other relevant readings.

This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Editor in Chief Klement Tockner.

Glossary

Area of Concern Locations within the *Great Lakes* identified as having experienced high levels of environmental harm.
Beneficial uses A change in the chemical, physical or biological integrity of the Great Lakes system sufficient to cause significant environmental degradation.
Ecosystem services The transformation of a set of natural assets (soil, plants and animals, air and water) into things that we value as humans.
Eutrophication Excessive richness of nutrients in a lake or other body of water, frequently due to runoff from the land, which causes a dense growth of plant life and death of animal life from lack of oxygen.
GLWQA The Great Lakes Water Quality Agreement (GLWQA) is a commitment between the United States and Canada to restore and protect the waters of the Great Lakes.
Invasive species An organism that causes ecological or economic harm in a new environment where it is not native.
Microplastics Extremely small pieces of plastic debris in the environment resulting from the disposal and breakdown of consumer products and industrial waste.
Regeneration Restored to a better state.
Revival An improvement in the condition or strength of something, here, ecosystems and communities.
Stressors Physical, chemical, and biological constraints on the productivity of species and on the development of *ecosystems*.

Introduction

Fresh waters are the most valuable natural reserves on Earth. Lakes provide ecosystem services not only to humans, but also on broader scales: provisioning, regulating, supporting and cultural integrity (Table 1). Large lakes provide drinking water to hundreds of millions of people, a crucial matter considering that the drinking water insecurity faced by many populations might even be reinforced with the potential increase in drought due to a changing climate. Food harvested from large lakes is also of cultural and economic importance, and includes fish, invertebrates such as crayfish, and aquatic plants. Large lakes also provide important shipping corridors for trade, as is the case with the Laurentian Great Lakes. Regulating services—benefits obtained by regulating ecosystem processes—provided by large lakes include safe harbors (protection from storms), erosion and sedimentation regulation, water storage, hydroelectric power generation potential, water quality regulation, and waste assimilation. In terms of non-material benefits or societal services, large lakes offer extraordinary aesthetic experiences (viewscapes), recreational (boating, fishing, beach use) and tourist opportunities, and places of spiritual interludes that humans value immeasurably (Jenny et al., 2020). The variability in ecosystem services provided by large lakes depends on their underlying ecology and the current state of their environment that is closely connected to the surrounding watershed (de Groot et al., 2012).

Table. 1 List of services provided by large lakes, and specific examples of services.

	Ecosystem services	*Examples*
1	Provisioning services	Food, drinking water, industrial water and hydroelectricity, water for navigation, genetic resources, medicinal resources
2	Regulating services	Water flow regulation, local climate regulation, water quality regulation, regulation of natural risks, transfers or sequestration of elements . . .
3	Supporting services	Habitats for nursery and reproduction (plant and animal), maintenance of aquatic fauna and flora from micro-organisms to macro-organisms, sustain migratory species and wildlife, hot spots of biodiversity
4	Cultural services	Aesthetics, recreation, inspiration for culture and art, spiritual experience, cognitive and scientific development

Most of these services are provided by lakes of all sizes and are not restricted to large lakes. However, large lakes represent 90% of the total lake surface area and hence contribute the major portion of these services.

Modified from de Groot R, Brander L, van der Ploeg S, Costanza R, Bernard F, Braat L, Christie M, Crossman N, Ghermandi A, Hein L, Hussain S, Kumar P, McVittie A, Portela R, Rodriguez LC, ten Brink P, van Beukering P (2012). Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services* 1: 50–61. https://doi.org/10.1016/j.ecoser.2012.07.005.

Degradation of lake ecosystems is evident worldwide, threatening the functioning of these ecosystems and the essential services they provide at a global scale (Fig. 1, Keeler et al., 2012). Future threats to large lakes include the overexploitation of resources, inputs of excess nutrients and harmful algal blooms, changing climate, overfishing, species invasions, infectious diseases, expanding hydropower, acidification, contaminants, emerging contaminants, engineered nanomaterials, microplastic pollution, and cumulative stressors.

Past alteration of large lakes is also reducing their capability to resist new threats, and degradation of water quality will continue because of the cumulative impact of ongoing local pressures, synergies among stressors, and the imposition of global stressors (climate, volatile compounds, and invasive species). Even in regions that successfully combatted environmental degradation such as eutrophication, new threats are emerging, with consequences for large lakes and their ecosystem services that are difficult to fully predict. These impacts are altering large lake ecosystems and services in unprecedented ways, causing widespread concern among freshwater scientists.

Long-term ecosystem services of large lakes: Their role for humanity

The contribution of lakes to human assets and to the regulation of nutrient and biological cycles is particularly important to society. Over the last centuries, societal awareness and value of provisioning, regulating or cultural ecosystem services (Table 1) provided by large lakes have shifted, often in response to a growing human population and after those services were degraded. Large lakes provide critically important benefits to all people (Table 2), and they need increasing care and attention to meet the growing demands for their ecosystem services at a time of increasing threats of ecosystem degradation.

Large lakes are sentinels of local human pressure, pollution and ecological impacts, particularly large lakes, which integrate the impacts of human activities on land use, mass fluxes, pollutant transfers and management interventions. Large lakes therefore provide evidence of socio-ecological resilience, and an integrative measure of the humanity's willingness to protect and sustain the surrounding environment (Jenny et al., 2020). Many of large lakes are transboundary, necessitating international policy frameworks. Several examples of international policy frameworks and programs geared toward large lakes are described in Table 3.

Major disturbances and threats

Stressors can change physical and chemical conditions in a lake to enhance or limit plant and animal growth, alter hormone function, operate as toxic element by increasing mortality, or change the behavior and seasonal timing of plant and animal development. In addition to the direct effects, stressors can operate indirectly through prey, predation, competition and non-trophic interactions, resulting in profound impacts on water quality and ecosystem services (Fig. 4). The most widespread stressors with strong impacts on human society and a description of the main impacts are summarized below.

– Increased nutrient loading as a result of human activities results in eutrophication. Cultural eutrophication is historically associated with an oversupply of phosphorus (P) (Carpenter, 2008; Carpenter et al., 2018; Schindler, 1977, 2012). Most common symptoms of cultural eutrophication also include changes in species composition, decrease in water transparency, anoxia and biodiversity loss (Carpenter, 2005). Adverse impacts include the development of cyanobacterial blooms. Consequently, eutrophication impairs ecosystem services such as fishing, water supply, and recreation. In Lake Erie, external loading of nutrients has become a more significant threat, particularly due to increased delivery of soluble reactive phosphorus delivery from nonpoint sources via tributaries (Jarvie et al., 2017). Since the 1950s, excess nutrient concentrations of nitrogen and phosphorus

Table 2 List of services provided by large lakes, related lake properties in each service class, and specific examples of services.

	Services related to observation and warning	*Related characteristics*	*Examples*
1	Earth system integrators	Lake area, volume, depth lakeshore length; lake:watershed; position within fluvial systems, and Earth system, sensitivity to climate variability	Climate and atmospheric regulation (local and regional), mitigation (buffer) of water volumes and quality and hydric-pollutions transfer to the sea: storage of particulates matters, bio-geochemical reactors (erosion, carbon circulation, water-storage), mostly equivalent to "regulating services"
2	Natural laboratories	Depth, age, origin, morphology, basin/lake ratio; water renewal time, salinity, chemistry, microbiology, endemism, species colonization	Lake system functioning, basic processes (water chemistry interface, chemotrophic microbiota, speciation, paleo-limnology, ecological responses to natural or anthropogenic perturbations, etc.)
3	Sentinels of global and local changes	Length of hydrological, thermal, chemical and ecological records; position within biomes; paleo-limnological records	Surveillance of climate and human impacts on biota, habitat, physics and geochemical cycles
4	Natural archives of human history	Riparian population, drinking water supply, other irreplaceable economic resources; documented historical records; evidence of past/present spiritual value, land cover and uses	Anthropocene, witness of human history, interaction of human with nature, changes in how humans value lakes, but also land ecosystems

have been changing the trophic state of Lake Erie's ecosystem, leading to reduced water quality and shifting environmental structures and functions within the lake ecosystem (Steffen et al., 2014). Eutrophication coupled with climate change appear to be resulting in cyanobacteria blooms, including dominance by *Microcystis* spp. (Steffen et al., 2014; Brittain et al., 2000; Chaffin and Bridgeman, 2014; Rinta-Kanto et al., 2005). Phosphorus has been considered the primary driver of the biological productivity of freshwater ecosystems (Schindler, 1974, 1977), however, the precise nutrient regime that favors toxigenic, non-nitrogen fixing cyanobacteria is complicated and needs to be better understood (Carey et al., 2012). Several studies suggest that nitrogen chemistry may shape the biological diversity of the system (e.g., Wilhelm et al., 2003). Still, the vast majority of nutrient management plans target the reduction of phosphorus loads into the watersheds of Lake Erie, not nitrogen loads (United States Environmental Protection Agency, 2015, 2017). As such, management measures are still ineffective and inadequate in mitigating the resurgence of cyanobacterial blooms of *Microcystis* (Gobler et al., 2016; Harke et al., 2016).

- Climate change is considered to be one of the most important challenges facing humanity today (Feulner, 2017; IPCC, 2018). Responses of lakes to climate change are well documented with increases in surface water temperature and water masses stability (O'Reilly et al., 2015; Schneider and Hook, 2010), loss of ice cover (Magnuson et al., 1990; Sharma et al., 2019), alterations in distribution of freshwater fishes, or decrease in deep-water oxygen concentrations (Zhang et al., 2020). The largest lakes in the world are most vulnerable to losing ice cover (Sharma et al., 2019) and are warming at the fastest rates, even as high as 1.0 °C per decade (O'Reilly et al., 2015; Schneider and Hook, 2010). Further, climate change interactions with additional stressors can lead to ecological surprises (Christensen et al., 2016). For example, changes in precipitation levels and increased potential evaporation rates have contributed to some lakes experiencing historically low water levels, whereas others are facing high water levels because of increasing runoff (Rodell et al., 2018; Wurtsbaugh et al., 2019), contributing to alterations in water quantity, water quality, and consequently water scarcity (Vörösmarty et al., 2000).
- Littoral shoreline modification is a direct consequence of the development of human societies. Human settlement on the coast, nutrients and pollutants inputs, creation of harbors and beaches strongly influence local shorelines habitats, which represent the engines of lake biodiversity (Schmieder, 2004; Vadeboncoeur et al., 2011). Shoreline transformations modify the physical impact of waves and littoral slopes, and create sheltered areas with higher nutrient accumulation, enhancing the development of phytoplankton do the detriment of macrophyte communities (Weisner et al., 1997). This affects habitats for fishes and macroinvertebrates, and can disrupt the trophic relationships of the whole ecosystem.
- Invasive species have drastically altered large lake ecosystems, resulting in significant economic losses to society. Dreissenid mussels have changed nutrient pathways in the Laurentian Great Lakes (Hecky et al., 2004), altering benthic invertebrate and plankton communities (Madenjian et al., 2015) and leading to population changes felt by the commercial fishery (Fera et al., 2015, 2017). The threat from invasive species will likely be exacerbated as climate change pushes species boundaries to new areas. Further, transoceanic shipping networks (such as in the Laurentian Great Lakes, Holeck et al., 2004) combined with ship ballast represent an open door to invasive species if not managed aggressively.

Table 3 Examples of some international and national frameworks to manage large lakes.

Programs	*Year*	*Countries/lakes*	*Description*
International/multi-national			
Global Lake Temperature Collaboration (GLTC)	2010	15 countries in the world	Working group that analyzed global lake water temperature records
Laurentian Great Lakes Coastal Wetland Monitoring Program		USA, Canada	Assess coastal wetlands (Cooper et al., 2018; Uzarski et al., 2017)
Cooperative Science and Monitoring Initiative (CSMI)		USA, Canada—Laurentian GL	CSMI coordinates research activities and focuses resources on a few key issues (Foley et al., 2009)
EU Water Framework Directive (WFD)	2000	European Union countries	Legislative framework for assessing and protecting ecological status of all aquatic ecosystems (Directive 2000/60/EC; WFD, n.d.)
The Great Lakes Water Quality Agreement (GLWQA)	1972, 2012	USA and Canada	Commitment to restore and maintain the integrity of the Laurentian GL waters
Global Lake Ecological Observatory Network (GLEON)		34 countries on 6 continents	Network that conducts innovative science by sharing and interpreting long-term or/and high-resolution sensor data
Commission Internationale pour la Protection des Eaux du Léman (CIPEL)	1963	Switzerland and France	Commission responsible for monitoring the quality of the water in Lake Geneva, in the Rhône and in their tributaries
International Commission for the Protection of Lake Constance (IGKB)	1959	Germany, Austria, Switzerland and Liechtenstein	Observation, recommendation for coordinated preventive measures, and discussion of planned utilization of the lake
Long-Term Ecological Research (LTER)—e.g., North Temperate Lakes (NTL)	1980	Many countries world-wide	Studying ecological processes over extended temporal and spatial scales
The Great Lakes Basin Compact (GLC)	1955	Eight US states and Ontario and Quebec, Canada	Enable transboundary cooperation on lake management
National/domestic			
US Clean Water Act (CWA)	1972	USA	Primarily, regulating discharges of pollutants into the waters
Canada Ontario Agreement (COA)		Canada	Restore, protect, conserve Laurentian Great Lakes water quality and ecosystem health
Water Pollution Prevention and Control (WPPC)		China	Water management to ensure emergency and back-up water resources are available in cities
Single large lake policies			
Aral Sea Wetland Restoration Project (ASWRP)		Aral Sea	Ecosystem rehabilitation via creation of artificial ponds and wetlands in the delta, and dry bed
Aral Sea Program	1995	Aral Sea	Restoring the Aral Sea to its former level
Convention on the Legal Status of the Caspian Sea	2018	Caspian Sea	How to divide up the potentially huge oil and gas resources
Framework Convention for the Protection of the Marine Environment of the Caspian Sea	2006	Caspian Sea	Protection of the Caspian environment from all sources of pollution
Lake Victoria Environmental Management Program (LVEMP)	2011	Lake Victoria, Africa	Tackle environmental challenges of lake basin over the long-term and improve welfare of inhabitants that depend on its resources
Canada-Ontario Lake Erie Action Plan, Under Large Lakes Protection Act	2018	Lake Erie	Reducing P loads to the western and central basins of Lake Erie by 40% by 2025
Convention on the Sustainable Management of Lake Tanganyika	2003	Lake Tanganyika	Objective to ensure the protection and conservation of the biological diversity and the sustainable use of the natural resources

The story of sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes is a rare example of the successful, ecosystem-scale control of an invasive aquatic vertebrate. The sea lamprey, native to the Atlantic Ocean, was first recorded in Lake Ontario in 1835 and, after improvements to the Welland Canal, spread throughout the remaining Laurentian Great Lakes by the 1920s–30s (Christie and Goddard, 2003). This species invasion was catastrophic both ecologically and economically, decimating lake trout stocks and other native species and contributing to the collapse of commercial fisheries (Siefkes et al., 2013). Sea lamprey adults are parasitic, attaching to a fish host with their suction cup mouth, using a rasping tongue to pierce the host's flesh, and feeding on blood and body fluids. A breakthrough was made in the 1950s, when it was discovered that a compound, 3-trifluoromethyl-4′-nitrophenol (TFM), could selectively kill sea lamprey larvae (Applegate et al., 1957). The treatment of Great Lakes' tributaries with TFM is the cornerstone of an extensive binational, science-based control program administered by the Great Lakes Fishery Commission. Sea

lamprey populations have been suppressed by as much as approximately 90% compared to pre-control levels (Heinrich et al., 2003; Smith and Tibbles, 1980), resulting in the recovery of key fish populations and the restoration of the 7-billion-dollar recreational fishery (Siefkes et al., 2013). The sea lamprey example highlights the success of a science-based invasive species control program, but is also a cautionary tale for the importance of preventing exotic species introductions in the first place to avoid costly control programs to mitigate negative effects.

New challenges and future threats to large lakes

Ecosystem health and ecosystem services provided by large lakes are vulnerable to emerging threats such as microplastics, micropollutants, and the cumulative effects of threats including climate change, eutrophication, over-harvesting, and invasive species. Among contaminants, microplastics are an emerging issue for freshwaters, but studies of microplastics in freshwaters are still rare, fragmented and include little quantitative data (Mani et al., 2015; Helm, 2020). Emerging threats and the challenges associated with cumulative effects of multiple stressors in large lakes follow.

- Microplastics: Since the start of plastics mass production in the 1940s, microplastic contamination of aquatic environments has been a growing problem. Microplastics can be ingested by organisms, accumulate in specific tissues, and be transported along the food chains. Moreover, they sorb and transfer chemicals and persistent, bioaccumulative substances into the food web (Krantzberg, 2020; Eerkes-Medrano et al., 2015). As these polymers are highly resistant to degradation, quantities of microplastics in aquatic environments will most likely continue to increase over time (Galloway and Lewis, 2016).

  Although marine microplastic research remains at the forefront, in recent years researchers, recognizing the comparative lack of studies on microplastics in freshwater environments, have begun to address this field as a matter of priority (Horton et al., 2017). Tributaries and point source effluents have been identified as major pathways for microplastics of terrestrial sources (Mani et al., 2015). Recent research now shows large lakes also contain microplastic pollution, with the highest concentrations in heavily urbanized regions, such as Toronto (Canada) and Detroit (USA) (Eriksen et al., 2013). For example, Castañeda et al. (2014) found that a liter of sediment from the St. Lawrence River contained up to 1000 spherical microplastics—on par with the world's most polluted marine sediments. Plans to combat and curtail plastic debris pollution (i.e., by reducing debris input, but also tracking and removal efforts) in large lakes will come at a significant economic cost, likely in excess of $400 million annually (Driedger et al., 2015).

- Micropollutants: Micropollutants, including heavy metals, pesticides, pharmaceuticals, and cosmetics pose significant threats for aquatic ecosystems (Blair et al., 2013; Codling et al., 2018; Metcalfe et al., 2019; Schwarzenbach et al., 2006). Endocrine-disrupting compounds mimic natural hormones and interfere with the endocrine systems of animals and humans. Pharmaceuticals and personal care products are discharged into surface waters as they are not degraded by wastewater treatment plants (Kümmerer, 2008).

Micropollutants can affect the survival and behavior of aquatic species, alter the reproductive system of aquatic organisms, and promote the development of resistant bacterial strains representing a health risk to humans (Uslu, 2012). In the future, increasing human populations will exacerbate the release of micropollutants to aquatic systems. This is particularly true for large lakes as their huge catchments make them the final sink of pollution. Regulation of the release of micropollutants is essential (Uslu, 2012). This suggests that regional and international cooperation must be forged to ensure lake water quality.

Summary on threats and management of large lakes

The demands of a growing global population with rapidly changing consumption patterns for food, mobility and energy are exerting ever-increasing pressure on the Earth's ecosystems and their life-supporting services. In combination with climate change, these changes raise concerns about current large lakes ecological status and the services they can provide. In addition, increasing threats to large lakes include the overexploitation of resources (water and food), inputs of excess nutrients and contaminants, reduction of habitats, species introduction or invasion, and cumulative stressors.

Restoration efforts can achieve success. Complete restoration to historic condition or pristine condition is hard to achieve, sometimes it even fails, but the Remedial Action Plan (RAP) examples below show that the regeneration of ecosystem function is attainable. The RAP process is a method to determine restoration targets to recognize the recovery of self-functioning freshwater ecosystems. Establishing systems for efficient management may be expensive but the future cost of inaction may be too high.

Plans to combat and curtail emerging threats, such as plastic debris pollution in large lakes, will come at significant economic cost (Driedger et al., 2015). The large costs associated with conservation efforts are legitimate concerns by the citizens who bear those costs, and who need to understand the pertinence and sustainability of such programs. Further, decisions about long-term strategies will have to be supported by future generations. As such, lake managers need to consider if these strategies can be supported in the future, at what cost, and be able to demonstrate the costs and social, cultural, economic and ecological implications from temporal or permanent interruptions in ecosystem services due to inadequate investment in policies and programs for large lake monitoring, restoration, and protection.

A deeper look into the Laurentian Great Lakes

The Great Lakes and other lakes and rivers in the Basin provide drinking water to tens of millions of people. On both sides of the border, the Basin supports multibillion-dollar manufacturing, service, tourism and outdoor recreation industries as well as strong maritime transportation systems and diversified agricultural sectors. It provides the foundation for trade between Canada and the United States, equaling 50% of Canada's annual trade with the United States. Each year, the Great Lakes region contributes $180 billion to Canada-US trade. In 2012, the Great Lakes region had a combined GDP of $5.2 trillion among the two provinces and eight states (ECCC (Environment and Climate Change Canada), 2016).

Unfortunately, degradation of environmental quality directly damages the viability and vigor of the region. The reliance of the economy on a healthy Great Lakes Basin Ecosystem is unequivocal and the imperative to restore ecosystem health is clear. To strive for a sustainable future, social and ecological and economic interests must be integrated. As Costanza (1992) asserts, sustainability can be defined as a balanced relationship between the dynamic human economic systems and the dynamic, but generally slower-changing ecological systems in which: (1) human life can continue indefinitely; (2) people can flourish, (3) cultures can develop, but within bounds such that human activities do not destroy the diversity, complexity, and function of the ecological life-support system.

As consumerism and industrial production are on the rise, non-renewable and renewable natural resources are being used more frequently in order to satisfy human desires. As described by deBoer and Krantzberg (2013)

> Robert Hennigan (1970) at the Thirteenth Conference on Great Lakes Research expressed that there is a requirement for understanding and reform of the Great Lakes institutional ecosystem to establish an attainable and workable system for effective water management. Incorporation of the action elements of persuasion and education, legal action and economic incentives were noted as being particularly necessary for the success of this system.

This prophetic insight still holds and calls on stakeholders to regard the water management issue as an integrated governance challenge and not a compilation of programs and policies applied reactively to address insults to the system.

Binational accords and events

> The United States of America and His Majesty the King of the United Kingdom of Great Britain and Ireland and of the British Dominions beyond the Seas, Emperor of India, being equally desirous to prevent disputes regarding the use of boundary waters and to settle all questions which are now pending between the United States and the Dominion of Canada involving the rights, obligations, or interests of either in relation to the other or to the inhabitants of the other, along their common frontier, and to make provision for the adjustment and settlement of all such questions as may hereafter arise, have resolved to conclude a treaty in furtherance of these ends, and for that purpose have appointed as their respective plenipotentiaries
>
> BWT (Boundary Waters Treaty) (1909)

The 1909 Boundary Waters Treaty stated that "boundary waters and water flowing across the boundary shall not be polluted on either side to the injury of health or property on the other." The Treaty created the International Joint Commission to prevent and resolve disputes over the use of boundary waters and to deal with boundary tensions between the two nations.

A 1966 detailed investigation of pollution problems in Lakes Erie and Ontario and the St. Lawrence River resulted in an in-depth report on water quality and the recommendation for an international lower lakes clean-up effort focused on the role of phosphorus in eutrophication. The report resulted in the signing of the Great Lakes Water Quality Agreement in 1972. The Agreement coordinated an international clean-up effort to enhance the water quality of the Great Lakes. The International Joint Commission became actively involved in analyzing and disseminating information. The Commission advised both governments on effectiveness of programs and provided water quality updates.

In 1978, the Canadian and US governments reviewed the Agreement of 1972 and revised it to re-affirm the commitment of each country to restore and maintain the chemical, physical and biological integrity of the Great Lakes Basin Ecosystem. Even more comprehensive than the original agreement, the 1978 Great Lakes Water Quality Agreement placed greater emphasis on toxic substance management, dredging and shipping regulations, and continuation of the phosphorus control program started in 1972.

The Great Lakes Water Quality Board (the principal policy advisors to the IJC), in its 1977 Annual report, listed the problem geographic locations, described the nature of the problem, identified dischargers of substances that were probably causing the problem, and commented on progress toward compliance with jurisdictional enforcement programs. The report also described remedial programs in the drainage basin of each problem area and progress toward meeting boundary water quality objectives. The Board developed a procedure for data assessment and identification of Areas of Concern. The unique experiment in place-based remediation and protection called for in the 1987 Protocol emerged directly from recommendations of the WQB (Water Quality Board, 1985; Krantzberg et al., 2006).

In 1987, a Protocol was signed amending the 1978 Agreement. The amendments were aimed at strengthening the programs, practices and technology described in the 1978 Agreement and to increase accountability for their implementation. Timetables were set for implementation of specific programs. New annexes address atmospheric deposition of toxic pollutants, contaminated sediment, groundwater, and nonpoint sources of pollution. Annexes were also added to incorporate the development and implementation of Remedial Action Plans for Areas of Concern and Lakewide management plans to control critical pollutants.

In 1985, the Water Quality Board reported that a clear manner to measure progress in AOC implement or how to remove one from the AOC list (delisting) was absent. The Water Quality Board created a process for AOC development and implementation with categories that identify the status of the information database, ongoing programs to fill in information gaps, and the extent of remedial efforts directed at to addressing specific use impairments. Hartig and Thomas (1988) pointed out early in the program establishment that the development of RAPs represents a challenging departure from most historical pollution control efforts, where separate programs for regulation of municipal and industrial discharge, urban runoff, and agriculture runoff were implemented without considering overlapping responsibilities or whether they would be adequate to restore beneficial uses. This new process will thus call upon the talents available in a wide array of programs far beyond those traditionally associated with water pollution control, including the involvement of local communities and a wide range of agencies at all government levels. All programs, agencies, and communities affecting an Area of Concern must come together to work on common goals and objectives in the RAP.

The location of the geographic Areas of Concern is present in Fig. 4. Originally, the Province of Ontario had 17 AOCs, the State of Michigan had 14 AOCs, the State of Wisconsin had 4 AOCs, St. Louis River/Bay is the only Area of Concern in Minnesota, Waukegan Harbor is the only AOC in Illinois, Ohio had 4 AOCs, The Grand Calumet River/Indiana Harbor is the only AOC in Indiana, and New York had 6 AOCs.

Annex 1 in the Great Lakes Water Quality Agreement 2012 Protocol identifies 14 beneficial use impairments and initiated programs to restore these uses to the Great Lakes. These are:

(i) restrictions on fish and wildlife consumption;
(ii) tainting of fish and wildlife flavor;
(iii) degradation of fish wildlife populations;
(iv) fish tumors or other deformities;
(v) bird or animal deformities or reproduction problems;
(vi) degradation of benthos;
(vii) restrictions on dredging activities;
(viii) eutrophication or undesirable algae;
(ix) restrictions on drinking water consumption, or taste and odor problems
(x) beach closings;
(xi) degradation of aesthetics;
(xii) added costs to agriculture or industry;
(xiii) degradation of phytoplankton and zooplankton populations; and
(xiv) loss of fish and wildlife habitat (GLWQA, Canada and the United States, 1987).

As Krantzberg et al. (2006) described, the Agreement calls for the federal governments, in cooperation with state and provincial governments, to ensure the public is consulted throughout the development and implementation of the RAPs. Despite organizational and fiscal resource hurdles, several RAPs are being applied and as a result, there are notable advances in remediation and prevention programs. Essential elements that characterize successful initiatives include true participatory decision making, a clearly articulated and shared vision, and focused and deliberate leadership (Krantzberg, 2003).

Vallentyne and Beeton (1988) instructed that an "Ecosystem approach" means an integrated set of policies and managerial practices that relate people to "ecosystems" of which they are part-rather than to external resources or environments with which they interact. The identifying characteristics include: synthesis (integrated knowledge); a holistic perspective interrelating systems at different levels of integration; and actions that are ecological, anticipatory, and ethical in respect of other systems of Nature.

Adopting an ecosystem approach would require three changes: reframing the planning problem, creating an integrative knowledge base, and institutionalizing multi-stakeholder participation in decision making (Kellog, 1998). RAPs were a departure from water quality remediation plans to a watershed-based management context that would consider a broad array of human actions that affect water and ecosystem quality. Ecosystem-based action plans address remedial actions to restore degraded conditions, and would also inquire into the human dimensions that consider changing human behaviors that enable long term functionality and sustainability of the ecosystem. Discovering such methods necessitated an integrative understanding of the watershed's bio-chemical-physical functions and their susceptibility to anthropogenic stresses.

Hartig (1997) points out that there is no single best way to implement an ecosystem approach, since each defined AOCs involves a distinct physicochemical and biological factors, stakeholders, institutional frameworks, regulatory complexity and more. An implementation framework that is guided by eight criteria should include:

- stakeholder involvement;
- leadership;
- information and interpretation;
- action planning within a strategic framework;
- human resource development;
- results and indicators;
- review and feedback; and
- stakeholder satisfaction

The experiment in collaboration aimed at aquatic ecosystem health, as Sproule-Jones (2002) asserted, provided an innovative approach in which resource users, regulators, and those in an interest in regenerating resilience for the local ecosystem can collaborate toward a common purpose. They promise to empower local stakeholders to determine their own solutions to ecological degradation, and open new venues for collaboration.

With the assistance of governments, residents in most AOCs formed an advisory council/committee to work with federal/state/provincial technical and scientific experts. Citizen advisory committees were used as the focal point of public involvement for RAPs in 75% of the Areas of Concern. Known in various jurisdictions as public advisory committees (PACs), basin committees, or stakeholder groups, the IJC contends that such mechanisms are the key to implementing the ecosystem approach in remedial action planning. In citizen advisory committees, diverse interests come to the same table to participate in the planning process in an interactive manner, advising the planning agency throughout the preparation of the RAP. These committees typically have or had representatives from diverse community sectors, including, agriculture, business and industry, citizens-at-large, community groups, conservation and environment, education, fisheries, health, labor, municipal governments, native peoples, shipping, tourism and recreation (Landre and Knuth, 1993).

Engaging stakeholder groups in the plan design minimizes the risk of future polarization (Samy et al., 2003). Advisory Committee participants possess unique knowledge and represent the interests of their particular stakeholder groups. A key premise is that community residents poses important knowledge, and can provide an informed perspective of the social impacts of the decisions (Harris et al., 2003). The importance of involving communities in the management of water resources was one of the strongest and most consistent messages coming forward from an international conference in interjurisdictional water programs (Managing Shared Waters, 2002). Important is recognizing the value of traditional knowledge and the local public's anecdotal and experiential intellect. Best practices in public engagement processes use plain language to communicate clearly, are supported by commitments in institutional programs and policies, demonstrate early and often how the public input will be used, include mechanisms to resolve disputes, provide the community with access to technical experts, celebrate successes to nurture momentum and train community leaders thereby building capacity to sustain progress.

Jetoo et al. (2015) note that governance can be difficult to define as it is used in a multitude of different ways. While different interpretations abound, most agree that the basic characteristic of governance is the migration of power from the central state up into supranational institutions, horizontally to non-state actors, and down to sub-national levels of government and non-state actors. The collective objective is to work with governments and develop a plan to revitalize ecosystem health and implement the plan to achieve agreed-upon targets that indicate when beneficial uses are restored (Krantzberg, 2006).

Central to the successful deployment of the RAP process is clear accountability for active interventions. This is best accomplished through the open sharing of information, clear and unambiguous definition of stressors and problems (including the identification of indicators to be used in measuring when the desired state for a beneficial use is reached), agreement on the priority actions required, and the identification of who is responsible for taking what action. From this foundation, Hartig and Zarull (1992) clearly delineate the responsible institutions and individuals can be held accountable for progress.

The first stage for each Remedial Action Plan is to identify environmental problems, impaired beneficial uses, and their probable causes. The second stage is to develop a recommended set of remedial actions and preventative initiatives to improve environmental quality in support of the beneficial uses. Targets are set by which RAP practitioners can recognize that they have met their goals surrounding beneficial uses. In some AOCs, the targets set science-based and quantitative, wherever possible. In other cases, general statements guide the practitioners, making it difficult to recognize when success has been achieved.

Major successes include Collingwood Harbour, Severn Sound, and Wheatley Harbour in Ontario, Deer Lake, White Lakes, Presque Isle Bay and Oswego River in the United States, where conditions have improved to the point that these locations are no longer considered to be Areas of Concern. Spanish Harbour Jackfish Harbour in Ontario are now recognized as in a stage of recovery due to completion of all selected remedial actions, while monitoring continues to measure recovery of beneficial uses.

The Parties have completed all remedial actions at five other AOCs: Nipigon Bay in Canada; and Sheboygan River (Wisconsin), Waukegan Harbor (Illinois), Ashtabula River (Ohio), and St. Clair River (Michigan) in the United States. With remedial work completed, these five AOCs are now being monitored to determine when the beneficial use impairments have been fully addressed and delisting can occur (Progress Report of the Parties, 2016).

According to the Progress Report of the Parties (2016) improvements in Canadian AOCs include a total of 65 impairments of beneficial uses of the environment have been eliminated, with 81 impairments remaining. In 2015 construction began on the largest contaminated sediment remediation project ever undertaken in a Canadian AOC. Through a public-private partnership, the project will clean up 700,000 m^3 of severely contaminated sediment in the Hamilton Harbour AOC. Fig. 1 shows a summary of actions taken to date.

Other accomplishments in Canadian AOCs during the 2013–2016 period include improvements to approximately 4 km of shoreline habitat and approximately, 180 ha of coastal wetlands and fish spawning grounds; investments of approximately $562 million in upgrades to municipal wastewater treatment plants to significantly reduce nutrients, suspended solids and pollutants.

The US Environmental Protection Agency estimates that management actions will be completed at nine more AOCs by 2019. This pace of AOC restoration is attributed to the Great Lakes Restoration Initiative, where federal agencies have been able to apply over $650 million in GLRI funding to finance remedial action plan implementation. Fig. 2 shows a summary of actions taken to date.

The location of all the AOC are described in Fig. 3, while Fig. 4 demonstrations the process used by the International Joint Commission to monitor the progress of Canada and the United States in RAP implementation. Figs. 5 and 6 provide case studies in RAP achievements and successes.

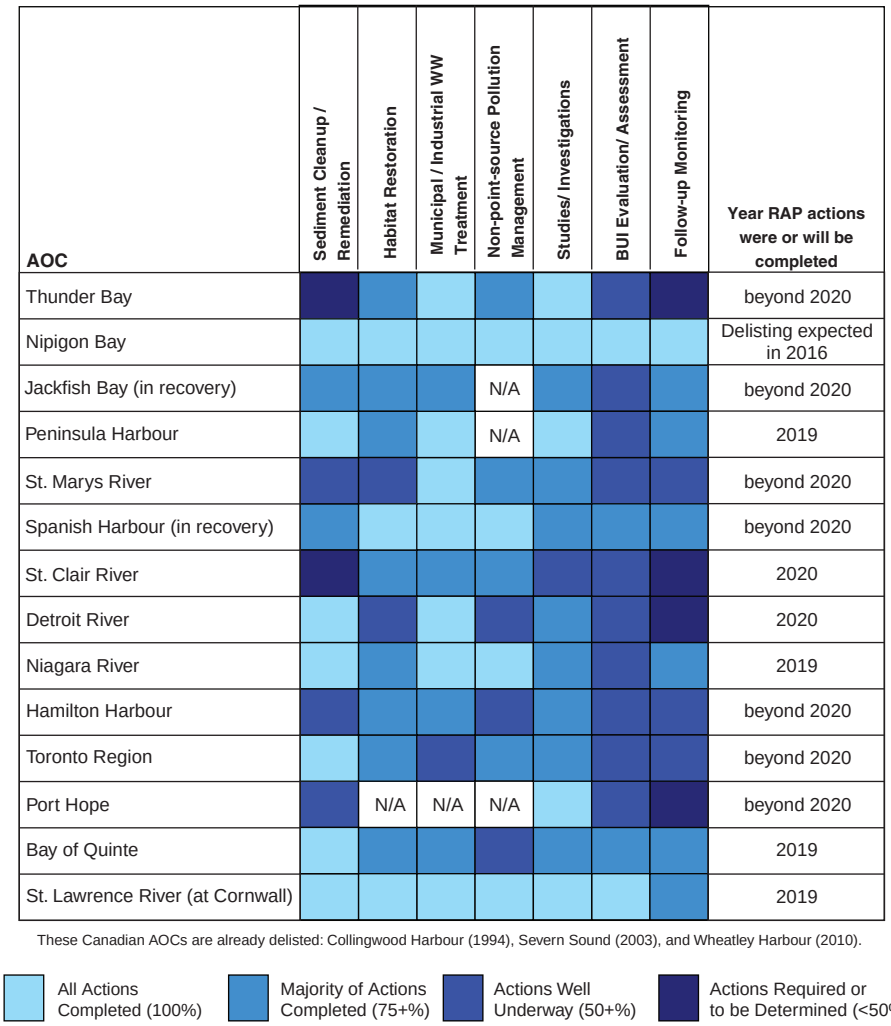

Fig. 1 Status of actions in Canada AOCs. From Progress Report of the Parties (2016) Pursuant to the Canada-United States Great Lakes Water Quality Agreement.

Working in the trenches of ecosystem-based watershed management is a challenging puzzle requiring a marathoner's discipline and perseverance. Yet the people in the 43 Great Lakes AOCs had a strong incentive to come together to clean up their communities over the past few decades. By studying their efforts, we can learn about the approaches that worked and did not work. We also can see how these efforts have paid off in the form of preventing pollution, restoring habitat for fish and wildlife, cleaning up contaminated sediment, and creating vibrant waterfronts that connect people to the water. The successes illustrated in the 10 case studies below demonstrate approaches that other waterfront communities can consider in shaping their own collaborative efforts.

Committing for the long run

It took nearly two centuries to reach the state of pollution found in the AOCs in 1985. Restoring these spots is no quick task either, considering the time it takes to build trust among stakeholders, reach agreement on problems, identify and select remedial and preventive actions, and secure funding for implementation, especially given all the competing interests for funding.

Initially, progress was slow because of the need to reach agreement on the severity and geographic extent of the problems identified in 1985; employ an ecosystem approach and involve stakeholders; align management programs; and secure commitments for implementation. Other factors included limited federal, state, and provincial funding for RAPs (Krantzberg, 2003; Botts and Muldoon, 2005), decline in the effectiveness of International Joint Commission oversight (Botts and Muldoon, 2005), and a governmental "reluctance" to accept responsibility for fulfilling obligations under the Great Lakes Water Quality Agreement (General Accounting Office (GAO), 2003, 2009). Funding commitments are an important component of the RAP program successes. Funding uncertainties in both the United States and Canada jeopardize continued progress in these important programs.

As of 2020, seven AOCs have been delisted, two have been designated as Areas of Concern in Recovery (i.e., an area where, based on community and government consensus, all scientifically feasible and economically reasonable actions have been implemented and additional time is required for the environment to recover), and six have implemented all remedial actions deemed necessary for use restoration. In addition, 75 of 146 known use impairments identified in Canadian AOCs and 73 of 255 in the United States have been eliminated. Successful RAPs have been cleanup- and prevention-driven; made existing programs and statutes work;

AOC	State	Sediment Remediation	Habitat Restoration	Hydrologic Controls/Diversions	Safe Drinking Water Provided	Engineering Design	Studies/Investigations	Other Regulatory Action	BUI Evaluation/ Assessment	Year all remediation and restoration actions were or will be completed
Waukegan Harbor	IL			N/A	N/A					2014
Grand Calumet River	IN			N/A	N/A					2020
Clinton River	MI	N/A		N/A	N/A			N/A		2017
Deer Lake	MI				N/A					Delisted 2014
Detroit River	MI			N/A	N/A					2023
Kalamazoo River	MI			N/A	N/A					2030+
Manistique River	MI		N/A	N/A	N/A			N/A		2018
Muskegon Lake	MI			N/A	N/A			N/A		2018
River Raisin	MI			N/A	N/A			N/A		2016
Rouge River	MI			N/A	N/A					2021
Saginaw River & Bay	MI									2030+
Torch Lake	MI		N/A	N/A	N/A	N/A				2030+
White Lake	MI			N/A	N/A	N/A		N/A		Delisted 2014
St. Clair River	MI/ON	N/A		N/A	N/A			N/A		2015
St. Marys River	MI/ON			N/A	N/A			N/A		2016
Menominee River	MI/WI				N/A					2016
Buffalo River	NY			N/A	N/A					2017
Eighteenmile Creek	NY		N/A		N/A					2026+
Oswego River	NY	N/A	N/A		N/A	N/A				Delisted 2006
Rochester Embayment	NY				N/A					2016
Niagara River	NY/ON			N/A	N/A					2026+
St. Lawrence River	NY/ON			N/A	N/A					2026+
Ashtabula River	OH			N/A	N/A	N/A		N/A		2013
Balck River	OH			N/A	N/A			N/A		2017
Cuyahoga River	OH			N/A	N/A					2021
Maumee River	OH			N/A	N/A			N/A		2025
Presque Isle	PA			N/A	N/A	N/A		N/A		Delisted 2013
Fox River/ S Green Bay	WI				N/A					2026+
Milwaukee Estuary	WI			N/A	N/A					2026+
Sheboygan River	WI			N/A	N/A					2013
St. Louis River & Bay	WI/MN			N/A	N/A					2020

All Actions Completed (100%) | Majority of Actions Completed (75+%) | Actions Well Underway (50+%) | Actions Required or to be Determined (<50%)

Fig. 2 Status of action in the US AOCs. From Progress Report of the Parties (2016) Pursuant to the Canada-United States Great Lakes Water Quality Agreement.

established priorities on a local basis and worked to elevate those priorities within state, provincial, and federal governments; ensured strong community-based planning processes; streamlined decision making for use restoration; and been affirming processes (Hartig, 1997).

Engaging and empowering the community

RAPs called for involving the public through use of an ecosystem approach that accounts for the interrelationships among water, air, land, and all living things, including humans, and involves all user groups in managing their communities' waterways (Vallentyne and Beeton, 1988; Hartig and Vallentyne, 1989). RAPs challenged governments and other stakeholders to transform management (McLaughlin and Krantzberg, 2018).

This commitment to an ecosystem approach and stakeholder involvement led to the establishment of a variety of institutional structures, including public advisory councils or committees (PACs), stakeholder groups, basin committees, and others. Beeker et al. (1991) identified that structuring the process to create a sense of ownership of the RAP by participants, who were the very businesses, state and local agencies, and citizens who would have to carry out the recommendations, was a critical factor in RAP acceptance by all involved. Essential elements that characterize successful initiatives include true participatory decision making, a clearly articulated and shared vision, and focused and deliberate leadership (Krantzberg, 2003).

Fig. 3 Location and status of the Areas of Concern (Progress Report of the Parties, 2016).

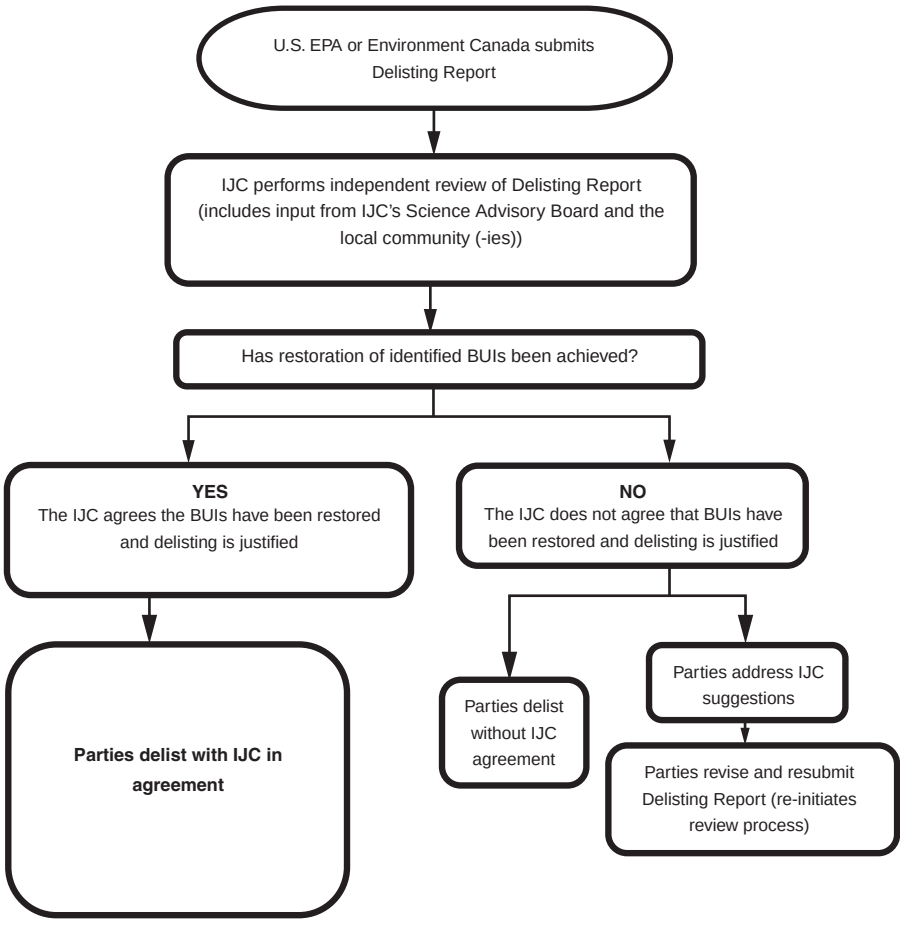

Fig. 4 A generalized process for review of RAP reports by the commission (International Joint Commission, 2003).

Randle Reef Sediment Remediation Project

Remediation is now underway at Randle Reef. The Randle Reef sediment remediation project involves constructing a 6.2 hectare engineered containment facility (ECF) on top of a portion of the most contaminated sediment, then dredging and placing the remaining contaminated sediment in the facility. The facility will be made of double steel sheet pile walls with the outer walls being driven to depths of up to 24 metres into the underlying sediment. The inner and outer walls will be sealed creating an impermeable barrier. The sediment will then be covered by a multi-layered environmental cap.

Skyway and Woodward Wastewater Treatment Plant Upgrades

Skyway (Burlington) and Woodward (Hamilton) WWTPs are currently undergoing major upgrades to improve treatment performance. At Woodward WWTP, phase 1 is now nearing completion. Future treatment process after phase 2 work is complete will employ additional methods to improve performance and reduce loadings that reach the Harbour through the effluent discharged to the Red Hill Creek.

Windermere Basin Restoration

In the summer of 2013, federal, provincial and Hamilton officials celebrated the completion of the $20.6-million rehabilitation of Windermere Basin, a 25 hectare plot of reclaimed industrial land. The purpose of the development project was to conduct restoration of the local ecosystem and provide natural wildlife areas and parklands for passive recreational use.

The project served several important environmental, social, and economic purposes. Windermere Basin:

- Enhances the Dundas Wastewater Treatment Plant's disinfection system to remove chlorine in the plant's sewage
- Increases Hamilton Harbour's visual appeal, while improving the fish and wildlife's habitat
- Creates an open body into a 13 hectare healthy Great Lakes coastal wetland that will benefit local fish and wildlife.
- Is a home to a variety of plants and animals, while offering community-based recreational opportunities.

Walleye Stocking

To create a balanced ecosystem, the presence of top predators is a necessity. In recent years, the Ministry of Natural Resources has annually stocked Hamilton Harbour with young walleye to help boost populations. In 2012, 100,000 young fish were introduced into the Harbour, followed by 10,000 in 2013, 950,000 in 2014, and another 50,000 in 2015. Along with improved water quality, the survival and eventual reproduction of walleye in Hamilton Harbour is a sign of a regenerating ecosystem.

Improvements to Public Access

With public access now restored to 28% of the Harbour shoreline, people are returning to Hamilton Harbour to enjoy recreational activities from cycling and strolling, to picnicking, sightseeing and dining. Future efforts aim to restore public access to 35% of the Harbour

Fig. 5 Hamilton Harbour, Lake Ontario, successes. Source: HHRAP (2014) 2006–2010 Stakeholder Investments. Burlington, ON, Canada.

A key concept in RAP processes has been accountability for action. This accountability is established through open sharing of information, clear definition of problems and causes, agreement on remedial and preventive actions needed, and identification of who is responsible for taking actions. From this foundation, the responsible institutions and individuals can be held accountable for progress. Indeed, increasing accountability was one RAP tenet identified in the 1987 Protocol to the Great Lakes Water Quality Agreement (Canada and the United States, 1987).

Cleaning up the legacy of toxic substances in sediment

Over many decades, toxic substances like heavy metals and organochlorine compounds were released into waterways and eventually accumulated in high concentrations in river, harbor, and embayment sediment. This buildup of toxic substances contributed to health advisories on fish, impacts on invertebrate life living in sediment, loss of habitat, restrictions on dredging activities, and more. Clearly, contaminated sediment was a major problem, yet there were no comprehensive federal, state, or provincial programs to address it. Dredging for navigational purposes was the primary means for addressing this problem at that time. Governments and RAP groups quickly discovered that the severity and geographic extent of the contaminated sediment problem was not well understood, nor was the relative importance of contaminated sediment in causing specific use impairments. In addition, stakeholders lacked a basis for determining how much sediment to clean up and what environmental/ecological improvements to expect over time.

Participatory decision-making works in the case of Presque Isle Bay for a number of reasons. First, is the relationships built over the years between the Public Advisory Council (PAC) and Pennsylvania Department of environmental Protection (PADEP) and the shared commitment to restoring the bay. That commitment is evidenced by the fact that many of the original PAC members continue to participate today nearly two decades after the bay became an AOC. Second, the citizens took ownership and exercised leadership in the decision to list the bay as an AOC. Third, both sides recognize the value of the other and appreciate the tools available to each; the PADEP understands the importance of public support and the PAC knows that government agencies are required to take or prevented from taking action due to laws, regulations, or agreements they implement. Fourth is the diversity of the PAC membership. Balancing of economic and environmental needs occurred around the PAC table as members of both communities worked hand-in-hand with regulators as part of the decision-making process. The composition of the PAC itself provided the opportunities to integrate the different yet dependent goals of economic prosperity and environmental restoration in the RAP process. While not always in agreement nor able to be equally balances, PAC members considered both perspectives. A willingness of members to compromise after being heard and the assurance of their role in decision-making prevented either perspective from bringing the RAP process to a standstill. Presque Isle Bay is a healthier ecosystem today as a direct result of the leadership and support of the community through the Coalition, Council, and PAC, as well as the vision and willingness to act exhibited by the local and state governments.

Fig. 6 Presque Isle Bay: participatory decision making. Source: Boughton (2012).

Governments, research scientists, and RAP groups had to figure out how to make decisions (e.g., on the severity and geographic extent of sediment contamination, on whether or not to remediate, on what techniques to use) and how to get the money to remediate sediment, if necessary. In many respects, both the Canadian and US contaminated sediment assessment and remediation programs came out of the RAP program.

To effectively address contaminated sediment at Canadian AOCs, the Canada-Ontario Agreement on Great Lakes Water Quality and Ecosystem Health's Sediment Assessment Decision-Making Framework was created in the early 1990s. This was a step-by-step guidance for an ecosystem approach to assess the risk of contaminated sediment. There have been nine Canadian AOCs where active remediation has been completed and the sites restored; however, additional work is still required at some AOCs where multiple sites require remediation. Remediation is currently ongoing or in the planning stages in three AOCs. One of those sites is Randle Reef in Hamilton Harbour, the largest Canadian contaminated sediment site in the Great Lakes. Remediation there is expected to cost approximately $139 million (Canadian). When completed, it is expected that water quality will improve, current restrictions on navigation will be removed, and economic returns will be generated through the creation of valuable port lands. Peninsula Harbour, a mercury- and PCB-contaminated site in Canadian waters of Lake Superior, was remediated in 2012 with the placement of the first thin layer cap. Four additional AOCs will likely continue with controlling contaminants at their source and leaving contaminated sediment in place and allowing clean sediment, over time, to effectively bury contaminated sediment; a process called monitored natural recovery.

In the United States, the US Environmental Protection Agency created the Assessment and Remediation of Contaminated Sediment (ARCS) Program in the early 1990s to measure sediment contamination at chosen sites, recommend approaches both to evaluate the effects of these contaminants on aquatic life and to assess risks to wildlife and human health posed by the contaminants, and test technologies that could be used to clean up contaminated sediment. Although the ARCS program significantly added to the scientific understanding of sediment assessment and remediation techniques, federal and state enforcement programs were primarily responsible for progress in remediating contaminated sediment in AOCs. The sediment remediation funding shortfall was then filled by the Great Lakes Legacy Act and GLRI. In total, between 2004 and 2017, US federal, state, and other partners have completed 46 contaminated sediment remediation projects in US AOCs, resulting in the remediation of more than 6.6 million cubic meters of contaminated sediment at a cost of $1 billion (US) (Tuchman et al., 2018).

Fish and wildlife habitat

Loss of fish and wildlife habitat is a common problem in most AOCs. Prior to the onset of RAPs, it was often said that "habitat had no home." Responsibility for habitat was fragmented among many stakeholders. RAPs made habitat a priority and challenged management agencies to address it explicitly. Restoration of fish and wildlife habitat had to be addressed in a systematic and

comprehensive fashion, which was particularly challenging in urban AOCs. In many cases, RAPs helped make sure that habitat was an integral part of community master plans. Early involvement of habitat experts in project planning and partnerships was essential to habitat project success.

As a result of this focus, considerable habitat rehabilitation has been undertaken in AOCs. For example, early efforts in the late 1980s and 1990s focused on the scientific assessment of "loss of fish and wildlife habitat" and its causes through RAP development. Later efforts focused on restoration options and determining how much habitat was enough to remove it as a use impairment. In general, limited habitat restoration occurred in US AOCs until the GLRI provided significant resources. Between 2011 and March 2018, more than $280 million (US) from the GLRI alone was spent on habitat restoration in US AOCs, with many projects still in the design phase (Hartig et al., 2018b). These substantial financial resources clearly accelerated habitat restoration in US AOCs.

In Canada, restoration of fish and wildlife habitat in AOCs has been a priority since the onset of RAPs. The development and implementation of Natural Heritage strategies to conserve biodiversity, as well as fish and wildlife management plans, were pioneered in AOCs. The RAP program also developed, demonstrated, and evaluated habitat restoration techniques. Since 1989, more than $500 million (Canadian) has been spent on habitat restoration in Canadian AOCs (Hartig et al., 2018a).

Restoring fish and wildlife habitat was an essential component of RAPs in each of the 10 case studies, with more than $129 million (Canadian) and more than $176 million (US) spent thus far.

Concluding remarks

Margerum and Robinson (2015) advised that partnerships operating at the organizational level require networks that support the flow of information and decisions across agencies. While such efforts predict improved better decision making, long-term efficiencies and better outcomes, there are high transaction costs, and the benefits are often not accrued until the long term. They point out that this necessitates that leaders be willing to make long-term investments and that organizations understand the need to change their culture and reward structures to support partnerships. For RAPs this is a difficult challenge if current pressures were aimed at short-term results, individual performance measures, and a focus on core organizational goals rather than collective management to attain shared goals.

Hall et al. (2006) provide an evaluation of the strengths the RAP processes. To achieve the goal of restoring environmental health requires "a dynamic process that relies heavily on research and monitoring to direct remediation efforts. Three principle means of coordinating this research and monitoring include: research and monitoring workshops; a monitoring catalogue outlining both government and nongovernment initiatives; and an annual report written by a local community group. These tools increase the effectiveness of remedial actions by: (i) improving stakeholders' ability to track trends; (ii) allowing program decision-makers to utilize adaptive management techniques to continuously modify programs based on new results; (iii) integrating interdisciplinary fields, and (iv) increasing accountability."

Together, pollution prevention, habitat restoration, contaminated sediment remediation, and other remedial and preventive actions have been a springboard for local communities to convert areas that were once a detriment to economic growth into valuable waterfront economic assets. Indeed, cleanup of AOCs is an integral and essential part of waterfront community revitalization. Good examples of where AOC cleanup has led to improved public waterfront access, followed by revitalization, include Buffalo River, Collingwood Harbour, Cuyahoga River, Detroit River, Hamilton Harbour, Muskegon Lake, River Raisin, Severn Sound, St. Louis River, and Toronto and Region. These communities are literally transforming former polluted rivers and harbors in the industrial heartland into healthier and more attractive waterfront destinations for businesses, recreation, and tourism. In many respects, this process of cleaning up AOCs, improving public access to these waters, and revitalizing waterfronts is like place making, a process that engages stakeholders in efforts to improve the quality of a public place and the lives of all who live in the community. The goal is to create a sense of place, defined as an authentic personal attachment or belonging to a particular place. Once people acquire a sense of place, this can lead to caring about their place and developing a stewardship ethic.

During the second industrial revolution, waterfronts of most communities evolved to support transportation, industry, and commerce. As such, these communities made rivers and harbors their back doors, and AOCs were no exception. In contrast, waterfronts today are viewed as magical places where the water meets the land and draws people to the shore for enjoyment and livelihood. Simply put, we have come to recognize the need to look at the water and not away from it. Experience has shown that creating waterfront vistas, reintroducing watershed residents to river history and geography, establishing unique conservation places linked by greenways and blueways (i.e., canoe and kayak trails), promoting ecotourism, and championing green developments founded on a "sense of place" help people see how they are part of an ecosystem and not separate from it. People must come to understand that what they do to their ecosystem, they do to themselves. This helps create a psychological connection that brings people to see that water is part of their life and culture. This connection also can lead to development of a stewardship ethic that builds the political base for watershed preservation and sustainability.

The Great Lakes basin ecosystem is home to 107 million people and 51 million jobs, accounts for more than 50% of all US/Canadian bilateral border trade and supports shipping of over 200 million tons of cargo annually. If it were its own country, it would have a gross domestic product of $6 trillion (US), making it the third biggest economy in the world (Desjardins, 2017).

AOCs can be considered microcosms of human impacts on the Great Lakes. After human settlement along the shores of the Great Lakes and their tributaries, these areas became centers of trade and commerce, followed by development of industry and agriculture that powered economic growth in the region. Use and abuse of these waters to power the region's mining, lumber, pulp and paper,

steel, automotive, chemical, energy, ship building, and grain industries reached a zenith in the 1960s when birds like bald eagles and peregrine falcons experienced reproductive failure because of pesticides like DDT, massive algal blooms resulted in Time magazine declaring Lake Erie dead, and indiscriminate discharge of oil and petroleum products resulted in the burning of the Buffalo, Cuyahoga, and Rouge rivers. The resulting public outcry spurred the environmental movement that led to establishment of Earth Day in 1970 and the passage of the Canada Water Act in 1970, the US Clean Water Act in 1972, the Canada-US Great Lakes Water Quality Agreement in 1972, and the US Endangered Species Act in 1973.

We continue today to clean up legacy pollution in AOCs. The development and implementation of RAPs using an ecosystem approach has opened the door to seeing how cleanup and restoration of AOCs can help catalyze waterfront revitalization. Linkages must be better established between cleanup and restoration efforts in AOCs and community revitalization efforts. Greater effort must be placed on bringing these two activities (i.e., cleanup/restoration and revitalization) into alignment and making sure that they are complementary and reinforcing to achieve a synergy for sustainable redevelopment with its substantial economic and social benefits.

Considerable evidence shows that people are willing to pay to locate in areas of high ecosystem quality (Anderson et al., 2009). People place a high value on the Great Lakes and are willing to pay a premium to live in coastal communities. Cleaning up AOCs not only improves ecosystem services (i.e., the benefits we receive from healthy ecosystems and natural resources) and makes these cities more desirable places to live, but helps businesses attract and retain employees.

The AOC designation has contributed to a negative perception of communities living in and near them. For many, the AOC designation was perceived as a "black eye" for their reputation. Cleaning up AOCs not only improves ecosystem services but can help change how communities are perceived.

The development and implementation of RAPs using an ecosystem approach has opened the door to seeing how cleanup and restoration of AOCs can help catalyze waterfront revitalization.

Where successful, RAPs clearly embrace the ecosystem approach. Here, the ecosystem approach is based on the man-in-system concept rather than a system-external-to-man concept (https://www.ijc.org/en/what/glwqa-history), where the ecosystem is composed of the interacting elements of water, air, land and living organisms including man. While there are several variants of the ecosystem approach, most share a focus on the responsiveness of ecological systems to natural and human activities, and a readiness to strike a programmatic compromise between detailed understanding and more comprehensive holistic meaning. This flexible pragmatism is perhaps the most productive feature for addressing Great Lakes environmental problems. Place-based types of restoration initiatives like RAPs are an unprecedented collaboration of international significant (Krantzberg, 1997).

Creative, distributed governance mechanisms and new institutional arrangements are needed (Krantzberg, 2003) to stimulate and sustain advances in the clean up local waterways, raise public awareness of individuals' responsibilities, unite a community around a shared purpose and need, and make the Lakes Great.

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Riparian Buffers and Land Cover Change

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Catherine Febria and Gail Krantzberg.

Glossary

Alluvial Pertaining to the deposition of sediment (e.g., clay, silt, sand, gravel) material by running water.
Ecosystem services The many and varied direct and indirect benefits obtained from ecosystems. Also, ecological contributions to human well-being. The four major categories are: provisioning, regulating, cultural and supporting services.
Emergent herbaceous wetlands A classification of vegetation characterized by herbaceous plants rooted below the surface of the water and either standing erect above the water or growing at the surface.
Floodplain The area of land, typically flat, adjacent to a river or stream, from its banks to bluff lines or valley edge.
Headwaters The initial source, or beginning location, of the water in a river. Typically, first, second, and third order streams.
Herbaceous Relating to vascular plants with non-woody stems, including grasses, sedges, rushes, and ferns.
Inland waters Freshwater aquatic ecosystems, including lakes, ponds, rivers, streams, creeks, springs, canals, reservoirs, and wetlands.
Lotic Moving, flowing or running waters, including rivers, streams, channels, creeks, and springs. Antonym is *lentic*, pertaining to low or standing waters, including lakes, ponds, swamps and marshes.
Riparian buffer The (vegetated) area near or adjacent to a stream or waterway. May be used synonymously as *stream buffer*, *riverine corridor*, or *stream corridor*.
Riparian Of, or relating to, the transitional area between aquatic and upland habitats. Frequently used broadly to describe the banks or areas surrounding a natural water area. Sometimes used interchangeably with *riverine*.
River Continuum Concept A framework describing the physical and biological gradients and longitudinal dynamics from headwaters to mouth.
Stream order A measure of the relative size of streams that assigns numerical delineations (1 through 12) according to the location of a stream segment relative to a watershed network. Streams are classified based on their number of tributaries. As such, larger orders correspond to increasing river size: first, second, and third order streams are typically considered *streams;* fourth, fifth, and sixth order streams are considered *medium streams*; and those seventh order and above are typically considered *rivers*.
Stream First to third order classification on the Strahler system for stream ordering.

Introduction

Rivers and streams cover less than 0.5% of the world's surface, yet they provide some of the most essential services for human existence, provisioning, and development (Downing et al., 2012; Allen and Pavelsky, 2018). High demand for the limited supplies of freshwater makes these ecosystems especially vulnerable to human pressures (Vörösmarty et al., 2010). Nearly 80% of the rivers important for water security and 65% of their habitat critical for biodiversity are threatened by multiple stressors from human activities including agricultural runoff, irrigation, pollution, invasive species, livestock grazing, and riparian degradation (Vörösmarty et al., 2010).

Riparian zones, at the transitional interface of terrestrial and aquatic ecosystems, encompass the low water areas of the stream channel through the surrounding upland terrestrial landscape (Naiman and Décamps, 1997). They represent a small proportion of landscape area but are more biologically diverse and productive than adjacent areas. With the majority (⅞) of the world's population living within 3 km of a river (Kummu et al., 2011) and human activities highly concentrated along rivers, riparian zones face disproportionately greater effects of human pressures on river landscapes (Naiman and Décamps, 1997).

Within riparian zones, riparian buffers are the vegetated areas most proximate to water (i.e., the areas buffering the waterway). Natural, vegetated riparian buffers provide key ecological functions, including bank stabilization, decreased erosion, flood buffering, sediment and nutrient filtration, shading and temperature moderation, and climate regulation. Buffers also provide important social services, including: (1) improved well-being from greenspaces, greenways and cultural sites along rivers; (2) improved air and water quality for human health; (3) enhanced recreational opportunities from high species richness and diversity; and (4) soil fertility and nutrient-rich soils for agriculture (Jones, 2008; Fig. 1). For example, riparian buffers support floral and faunal diversity important for human recreation, including many species of birds and ungulates (Naiman et al., 1993). Over half of adults in the U.S. hunt, fish, birdwatch or photograph wildlife, making riparian zones recreational hotspots (Jones, 2008). Proximity to riparian zones has also been shown to generate price premiums of up to 26% for residential properties adjacent to, or within, riparian zones (Jones, 2008). In Spain, approximately 4.3 million visitors enjoy riverine areas within national parks annually, and increasing numbers of urban residents are attracted to the country's river beaches and natural springs for recreational use (Gutiérrez and Alonso, 2013). In Canada, the riparian ecosystem services of just three rivers are estimated to provide 6000 Canadian dollars per hectare (Buffin-Bélanger et al., 2015). Elsewhere, riparian areas provide important intrinsic social and cultural services, including value as sacred sites or waterholes, windbreaks and hunting grounds, and in discovering a sense of place (Goldstein and DellaSala, 2020; Riis et al., 2020).

Collectively, riparian zones have considerable value to both human and natural systems (Fig. 2). Riparian buffers further serve as valuable protection for waterways from outside influences (e.g., nutrient loading). Buffers are most effective when they are contiguous along waterways and thus are often recommended as priority over broader, fragmented riparian zones (Fischer and Fischenich, 2000). Yet, by the turn of the century, the majority of riparian areas were reported to have been degraded or converted for human use; in some case studies, riparian vegetation had declined by as much as 95% (National Research Council, 2002). This is important when considering the entirety of a watershed because headwater streams have the greatest land-area ratio and are more susceptible to non-point source pollution as they are dominated by overland water flow (National Research Council, 2002). Headwater areas also have more influence on water quality than wider, downstream areas (Alexander et al., 2007). For example, removing forested buffers in smaller stream orders (i.e., size of the stream) will have a greater impact on increased water temperature than in larger rivers, where only part of the river is shaded. As such, riparian zones relative to the stream order can provide valuable opportunities for environmental management.

In the U.S., 2.65 million stream segments result in riparian areas accounting for less than 5% of total land area (National Research Council, 2002). Despite their small percentage of total land area, riparian zones are extremely important to overall

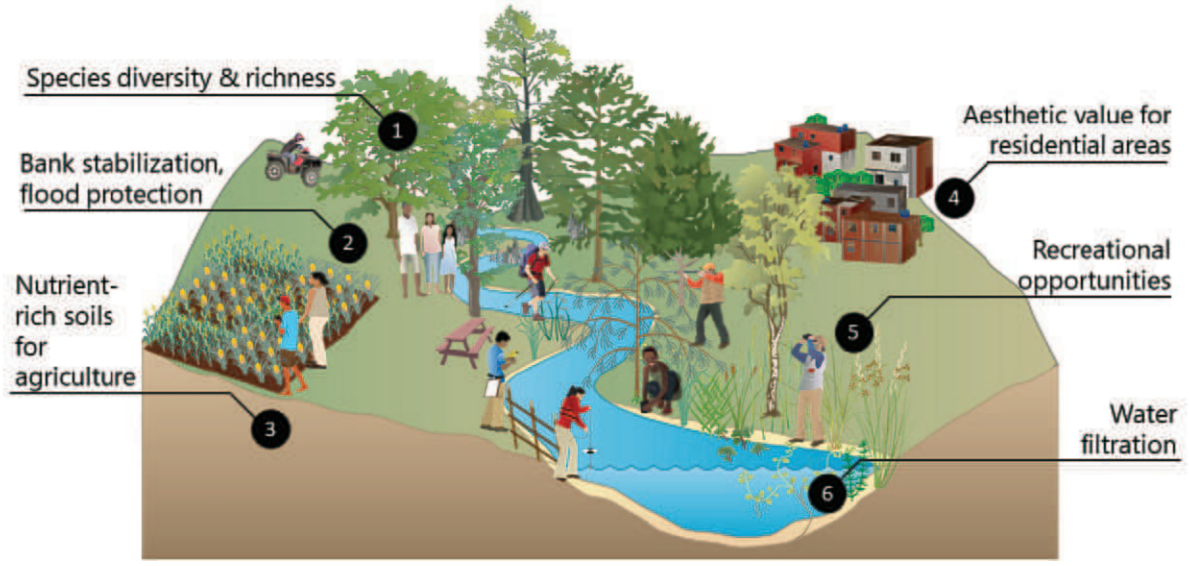

Fig. 1 Socio-economic values and uses of riparian zones: (1) species richness and diversity; (2) bank stabilization and flood control; (3) nutrient-rich soil for agricultural activities; (4) aesthetic benefits for residential properties; (5) recreational opportunities, including birdwatching, hunting, biking, and hiking (shown above); and (6) water filtration for improved water quality.

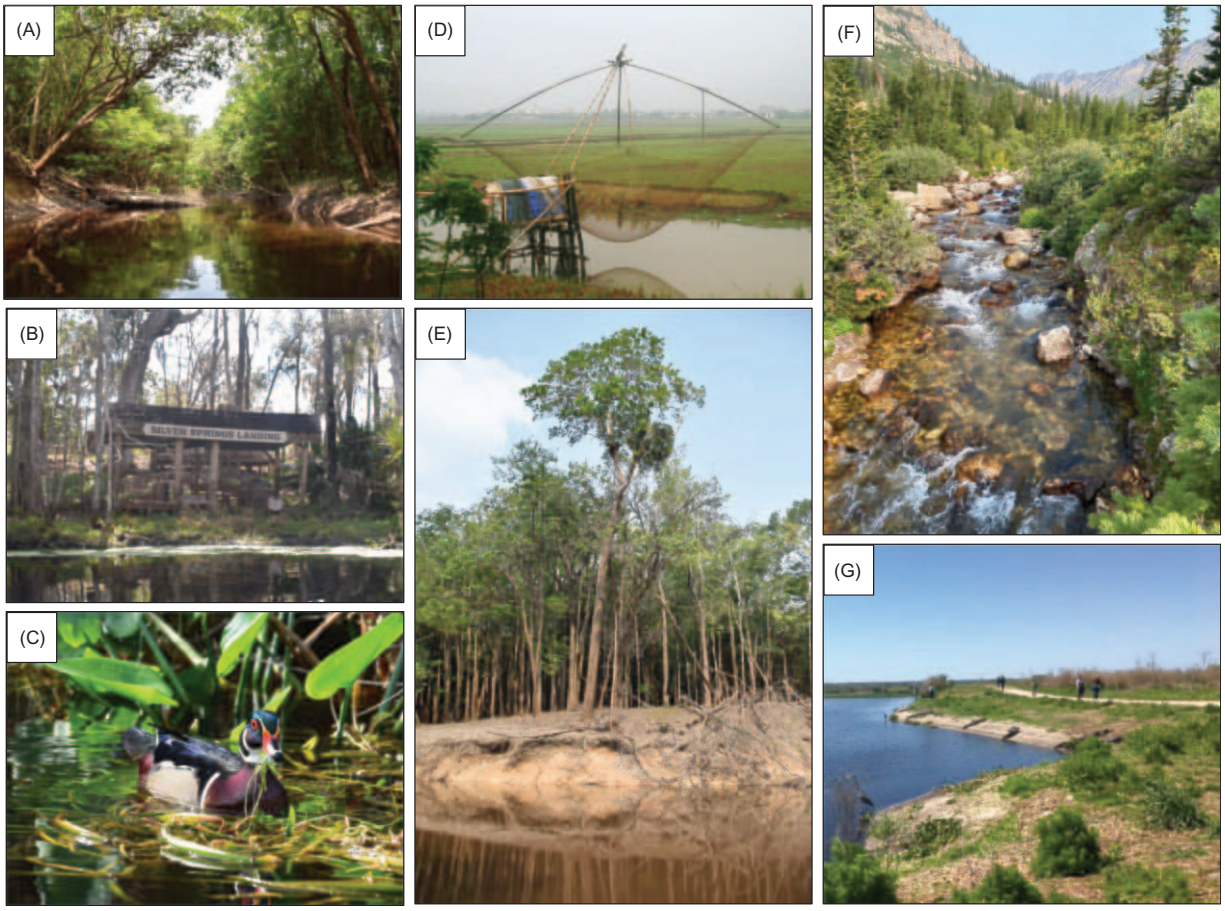

Fig. 2 Examples of riparian zone ecosystem services: (A) shading and temperature moderation, (B) enhanced residential and commercial property and aesthetic value, (C) habitat for wildlife and plant species diversity, (D) nutrient transport and nutrient-rich soils for agriculture, (E) bank stabilization, (F) water filtration, and (G) recreational use of riparian trail systems. Photo credit: Gretchen Stokes.

ecosystem function. Research is needed to understand which attributes of riparian buffers drive how people value them (Young, 2016), and historical land use trends can further be analyzed to help advance future decision-making. This chapter aims to provide a foundation for future analysis and understanding by presenting a snapshot of land cover change within riparian zone buffers classified by stream order and land cover classification. We use the U.S. from 2001 to 2020 as a case study to: (1) explore the basics of riparian zones, (2) identify trends in riparian zone land cover, (3) contribute an observational evaluation of how the U.S. has prioritized riparian zones during the 21st century, (4) provide examples of societal values placed on them and their protections, and (5) identify research gaps and needs.

Stream orders within a watershed

When water falls on the land surface, typically in the form of precipitation, some of the water drains along the land surface. As water moves along the land surface, it will flow from a location of high energy to a location of low energy; this most often results in water flowing downhill. As water flows downhill, it will establish preferential flow paths based on the path of least resistance, which ultimately results in the formation of channels for streams and rivers. As channels converge and form larger channels, the drainage pattern of water flowing across the landscape most often becomes dendritic (i.e., having a branching pattern similar to that of a tree). This is also referred to as a fractal pattern, where the drainage pattern remains the same at all spatial scales (i.e., small channels converge to form larger channels, just like larger channels converge to form even larger channels). This drainage pattern forms within a watershed, which is a topographical boundary where all surface water drainage within that boundary will exit the boundary through a single outlet (often the largest channel within the watershed as it captures all the flow).

Channels within a watershed are often a place of interest for researchers, as their surface water and channel morphology can serve as valuable indicators for the overall quality and characteristics of the watershed. There are multiple methods for classifying these

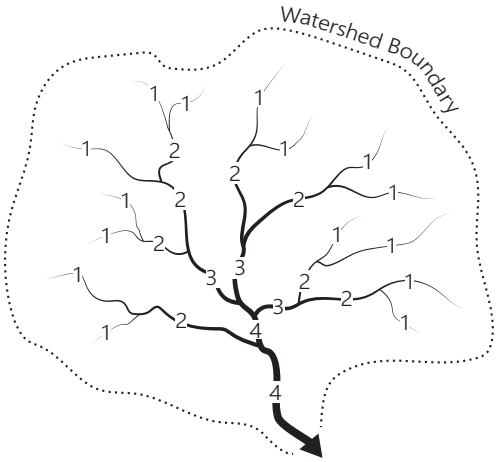

Fig. 3 Strahler stream ordering for a conceptual watershed, where stream order increases at the convergence of two segments of the same number.

channels (i.e., streams), but one of the most common is the Strahler order. The Strahler order starts with the headwaters as the first order (i.e., these are the smallest streams; the start of surface water flow). When two first order streams converge, they form a second order stream. Thereafter, whenever two streams of the same order converge, their downstream channel becomes the next higher stream order. If two streams converge of different stream orders, the highest order remains the same for the downstream channel. An example of Strahler stream ordering is available in Fig. 3, where the watershed outlet is a fourth order stream.

The U.S. has an extensive drainage network, where large mountain ranges throughout the country form the boundaries of the largest of watersheds. For example, the largest U.S. watershed is the Mississippi River watershed, where its largest channel is a 9th order stream at its outlet (Lehner and Grill, 2013; some sources have this listed as a 10th order stream; e.g., Hill et al., 2011). Bounded by the Rocky Mountains in the west and the Appalachian Mountains in the east, the Mississippi River watershed is nearly 3.2 million km^2 (Gassman and Secchi, 2006). Large stream orders (e.g., >6) are typically classified as rivers, where increasing stream number also reflects a likely increasing discharge and river power. For reference, the Amazon River is the only 12th order river in the world and has a watershed covering over 7 million km^2. Like anywhere else in the world, U.S. waterways can be divided into many smaller watersheds and subsequently many smaller stream orders (Fig. 4; Lehner and Grill, 2013). Globally, approximately 35% of all stream area is 5th order and smaller streams (Downing et al., 2012).

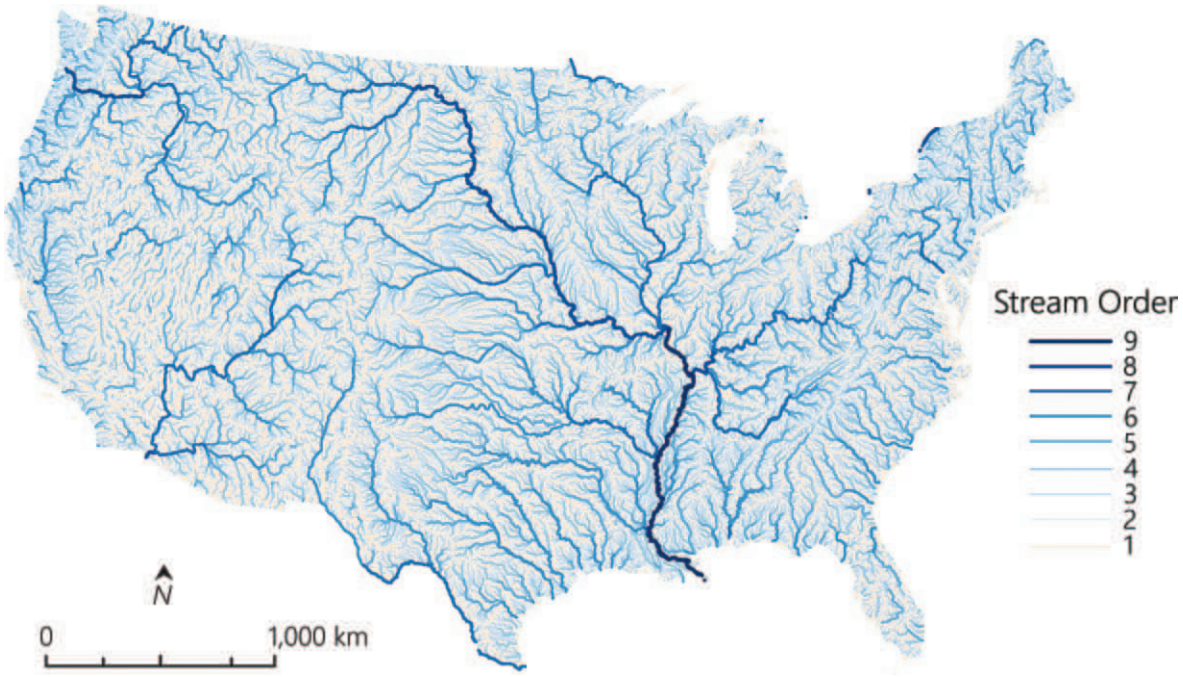

Fig. 4 U.S. streams and rivers classified by Strahler stream order (Lehner and Grill, 2013).

Land cover classifications

As water drains across the land surface, it interacts with many different land covers (e.g., urban, agriculture, forest, etc.). These land cover interactions are incredibly important for ecosystems and environmental management as draining water can inherently pick up artifacts like excess nutrients or pollutants from some of these land surfaces (e.g., urban; McGrane, 2016), while across other land surfaces (e.g., forest; Anbumozhi et al., 2005), artifacts may be removed or reduced. Likewise, different land covers (e.g., forest, grassland) generate unique environmental signals (e.g., reduced water temperatures, increased sediment load) that also have ecosystem impacts (Jones et al., 2010). Across the U.S., land cover has been divided into 8 predominant land cover classifications through the National Land Cover Database (NLCD; Homer et al., 2020). These include: (1) open water/ice, (2) developed (i.e., urban), (3) barren, (4) forest, (5) shrub/scrub, (6) grassland/herbaceous, (7) agriculture, and (8) wetlands. Each classification typically has a sub-classification that is more specific to the localized land cover. For example, forest as a classification can be subcategorized into deciduous, evergreen, or mixed. The contiguous U.S. can be summarized into 16 predominant subcategories (Fig. 5).

Riparian buffers

Riparian zones are the interfaces between waterways and adjacent lands. Riparian buffers are then often referred to as an undisrupted (i.e., vegetated) gap between a waterway and a predominant human land use (i.e., disrupted), such as a farm or urban area. Also common are buffer sequences which define the succession of vegetation within a buffer zone. For example, a common buffer sequence may consist of heavy vegetation along a waterway followed by a decrease in vegetated density away from the stream or river. An undisturbed forest, managed forest, grassland sequence is common for riparian zone management. Regardless of the sequence or vegetation, the purpose of a riparian buffer is to shelter the waterway from adjacent land use impacts while also supporting other ecosystem services, such as reduced water temperatures from the shade of a forest canopy along the stream channel. As a result, riparian buffers are often used to manage for a desirable ecosystem service; buffer sizes do not all have to be the same to achieve each service (Table 1).

The reality of human-induced land transformation is that riparian zones are often targeted for their high economic value, and historically, buffer zones have not always been respected. For example, most cities that have developed along waterways have urbanized the entirety of the buffer zone, even to the point of installing seawalls (i.e., developing right up to the water's edge). This historically has been a balance of risk versus opportunity, where development within a buffer zone opened access for trade or other economic opportunities, including crop cultivation within fertile floodplains, where the risk included the negative impacts from flood events. Human engineering has allowed for many opportunities to outweigh the flood risk, and many riparian buffers have been eliminated as a result. In recent years, the economic value of a riparian buffer has become more recognized as water quality has degraded and ecosystem services have been lost (Young, 2016). In response, there have been growing initiatives in the U.S. to protect or restore riparian buffers. For example, the Conservation Reserve Program through the United States Department of Agriculture has provided payments to landowners who have taken agricultural land out of production in riparian zones and have even subsidized landowners who have worked to establish or restore buffer zones (Sullivan et al., 2004). Similarly, financial incentives proved motivational for New Zealand farmers to install riparian fencing, for Madagascan governments to make payments for ecosystem services in critical riparian corridor areas, and for South African programs (e.g., Working for Water) to create jobs for invasive species removal and catchment protection (González et al., 2017; Wendland et al., 2010; Turpie et al., 2008). But even with these initiatives, riparian zones remain a frequently exploited region for human activities. Examples of riparian zones with varying buffer types are displayed in Fig. 6, where Panel A captures an urbanized riparian zone, Panel B an agricultural riparian zone, Panel C a forested riparian zone, and Panel D a riparian zone of wetlands.

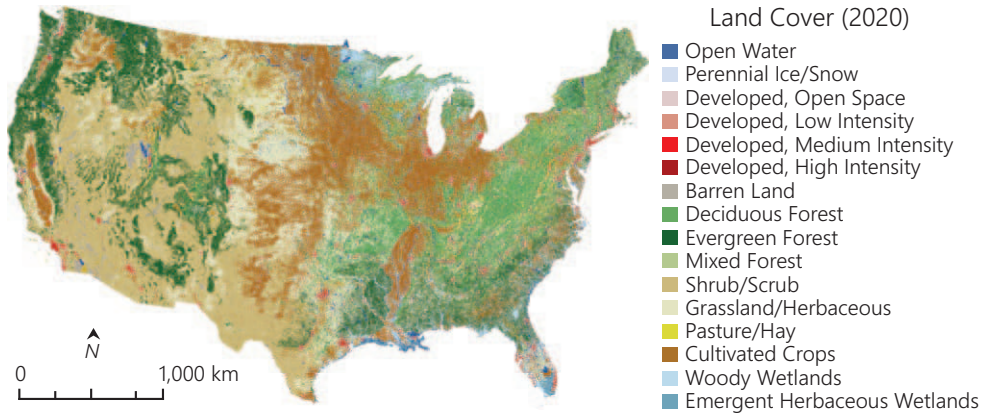

Fig. 5 U.S. land cover for the year 2020. Modified from the 2020 Cropland Data Layer; USDA (2021) *USDA National Agricultural Statistics Service Cropland Data Layer*. Washington, DC: USDA-NASS.

Table 1 Examples of recommended riparian buffer widths by ecosystem service type. Derived from Jontos (2004) and Lind et al. (2019).

Ecosystem service or management goal	*Recommended buffer width (m)*
Detrital input	3–10
Water quality protection	5–30
Sediment removal	9
Stream stabilization	10–20
Nitrogen or phosphorus reduction	11
Shading, temperature regulation	21
Floral diversity	24
Flood attenuation	20–150
Bird diversity	144
Riparian habitat	30–500+

Fig. 6 Satellite imagery of example riparian zones for (A) urban, (B) agriculture, (C) forest, and (D) wetlands. Images were extracted from Google Earth.

GIS analysis of riparian buffers

GIS analysis

A Geographic Information System (GIS) is a computer system that can display, manipulate, and analyze geographically based data. To analyze land cover within riparian zones, both the location of a stream and its adjacent land cover must be available and spatially aligned in GIS. Several databases exist for these types of geospatial data and are freely available for download. For example, we used the National Land Cover Database (NLCD) for 2001 land cover (Dewitz, 2019; Homer et al., 2020), an NLCD-summarized version of the Cropland Data Layer (CDL) for 2020 land cover (see Fig. 5; USDA, 2021), and HydroRIVERS v1.0 (Lehner and Grill, 2013) for U.S. streams and rivers. The streams and river data are a set of lines that represent the centerline of the stream and do not represent the width of the stream channel. We found a 1:100 ratio of Strahler stream order to centerline buffer size (meters) extracted a relatively consistent area (i.e., buffer zone) of land cover along the banks of streams and rivers (e.g., we used a 500-m flowline buffer for a 5th order stream; Fig. 7). We then calculated the percent change between extracted land cover from our 2001 and 2020 datasets.

Using big data

The term "big data" is typically used when referring to data files or data volumes that are so large that they are either labor or technology limited. In other words, these data require unique processing techniques that eliminate the human labor necessary to process them or higher capacity computing technologies that can handle extremely large data. For example, the 2001 and 2020 land cover datasets for the contiguous U.S. each include almost 9 billion pixels at 30 × 30-m resolution. Likewise, the HydroRIVERS flowlines data include over 400,000 unique streams. Trying to process land cover change stream-by-stream would be prohibitively time-intensive for an individual to complete by hand and attempting to process these data as a group can overwhelm the technological capacities of smaller PCs. Big data users often use both a higher performing computer and scripting language (e.g., Python) to automate computer tasks. Here, we used Python to work with ArcGIS to: (1) extract flowlines by stream order from the HydroRIVERS file, (2) create a representative buffer around those extracted flowlines, and (3) extract land cover data from the 2001 and 2020 datasets. The final data outputs of these automated processes were then stored into spreadsheets (MS Excel) for analysis.

Riparian land cover change (2001 – 2020)

The results of the land cover change analysis are available in Table 2, where the percent change was calculated using Eq. (1):

$$\%Change = \frac{LC_{2020} - LC_{2001}}{LC_{2001}} x\ 100 \quad (1)$$

where LC_{2020} are the extracted data from the 2020 land cover dataset and LC_{2001} are the extracted data from the 2001 land cover dataset.

Table 2 shows land cover change by stream order, where positive numbers suggest the addition of a land cover classification (i.e., more of that land cover), and negative numbers represent the subtraction of a land cover (i.e., less of that land cover). There are several general trends across all stream orders.

(1) Developed open space has decreased through time. Typically, urbanization patterns follow an inside-out development trend, where highest intensity is in the middle and the lowest intensity on the outside (Balk et al., 2018). Over time, the urban hub becomes more intensely developed, and new urbanization sprawls away from the urban hub in the form of open or low intensity development. Since developed open space has decreased from 2001 to 2020, this trend suggests urban sprawl has slowed within riparian zones.

The notion that new urbanization has stalled in riparian zones is further supported by (2) low intensity development that has remained fairly stable throughout this time period.

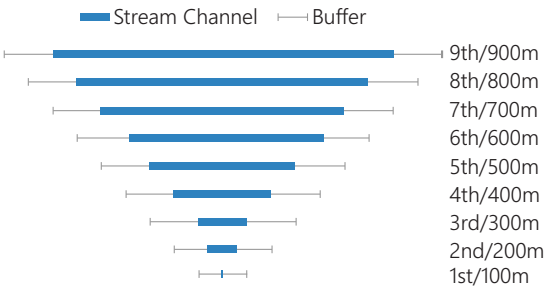

Fig. 7 Increased stream order and buffer size capture a relatively consistent width of adjacent riparian land cover.

Table 2 Land cover change in U.S. riparian zones by stream order, where change is the percent gain or loss of land area by land cover classification between 2001 and 2020.

% Change (2001–2020)									
Land Cover	*Stream Order*								
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
Developed, Open Space	–10.8	–13.5	–17.4	–19.5	–19.6	–22.4	–21.7	–26.8	–20.2
Developed, Low Intensity	3.8	2.9	1.9	–0.3	–0.2	0.2	–2.8	–0.3	–4.3
Developed, Medium Intensity	24.9	22.4	20.4	16.7	16.4	16.5	15.0	17.0	22.1
Developed, High Intensity	27.1	24.1	20.7	18.3	16.1	16.1	16.1	11.8	17.8
Barren	–12.7	–12.5	–15.6	–12.6	–6.0	–21.3	–35.9	–51.6	–75.3
Deciduous Forest	–0.9	0.0	–0.5	–4.4	–10.3	–6.3	–6.3	–12.7	–54.2
Evergreen Forest	7.1	6.5	5.5	3.5	5.1	–2.8	–16.9	21.0	–2.0
Mixed Forest	60.4	62.5	60.2	62.6	68.8	63.5	150.2	374.7	–48.6
Shrub/Scrub	9.3	11.9	14.6	15.4	14.5	2.9	4.3	–0.6	–66.1
Grassland/Herbaceous	6.9	6.4	6.2	4.7	4.0	24.5	31.4	–0.9	196.5
Pasture/Hay	–57.9	–53.0	–48.3	–41.7	–36.1	–42.0	–35.7	–56.3	–92.8
Cultivated Crops	–5.6	–7.0	–8.8	–10.7	–13.1	–11.6	–7.7	–10.4	–24.5
Woody Wetlands	1.2	0.1	1.7	4.2	5.5	6.8	–0.3	0.1	16.8
Emergent Herbaceous Wetlands	7.0	10.2	16.5	22.3	27.7	35.8	48.5	60.4	29.4

Contrarily, (3) medium and high intensity development have largely increased in riparian zones from 2001 to 2020. This trend suggests urbanization is still occurring within riparian zones, but it is from the densification of pre-existing urban areas instead of the expansion of new urban land.

(4) Barren land has greatly decreased. Barren land is where very little vegetation exists in a natural (i.e., non-urban) setting like a beach or desert. But barren land can also be classified as places that have been clear cut or drained and are awaiting a new land cover transformation. For example, barren land can also represent a clear-cut forest that is expected to become cultivated or a drained wetland that is expected to become developed. Since there is less barren land, there is less space along waterways that remains bare. This trend suggests these bare spaces have become more vegetated or have been converted into wetlands, since new urbanization was not greatly observed over the same time period (trends 1 and 2).

(5) Forests, scrublands, and grasslands have observed mixed land cover transition, where most notably deciduous forests have declined, and mixed forests have greatly increased. This trend may suggest deciduous forests have become more mixed or that deciduous forests have been removed in some areas. Regardless, forested riparian zones will make for an interesting future research trajectory given their impacts on ecosystem services and varying land cover trends. The increases in scrub and grasslands may also support the vegetation of barren land (trend 4).

(6) Agricultural land has greatly declined in riparian zones as cultivated and harvested areas were taken out of production. This trend may also contribute to the increase in grassland and forest as agricultural land is converted into other land classifications.

(7) Wetlands have increased in riparian zones which may have previously been agricultural land, barren land, or even forested land. One explanation is that floodplains have become more respected, so draining of the landscape through tiles or other engineering has decreased, and previously dry lands have been transitioned to wetlands. Likewise, there are U.S. policies that require new urbanization to also establish wetlands to offset the negative impacts of urbanization (Coker et al., 2018), so as urbanization increases throughout the country, more wetlands are likely to appear. A contrasting explanation is that increases in urbanization or urban density (both inside and outside of riparian zones) alongside changing weather patterns have made flood events more variable and common (Miller and Hutchins, 2017; Feng et al., 2021), which may result in increased wetland areas alongside waterways as floodplains become more frequently inundated.

Synthesis and conclusion

Observed patterns of riparian zones

Collectively, land cover trends suggest urban sprawl has been reduced in riparian zones, and the overall vegetation of riparian zones has increased. Likewise, intensively managed agricultural lands have also been reduced and likely replaced with less-intensive vegetated land cover (e.g., grasslands, forest) in riparian zones. From these trends, it appears the value of riparian buffers is becoming increasingly recognized in ecosystem management. However, many riparian zones remain heavily altered as evidenced by urban areas established on the banks of many waterways and agricultural lands encroaching on waterways due to the fertile soils of floodplains.

Urbanization intensity also increased the greatest in the lowest stream orders, which suggests there is an increase in human interference in headwater streams, which can be observed throughout the entirety of a watershed. It is not difficult to view satellite imagery and find many examples of limited, fragmented, or absent riparian zone buffers, and these areas certainly carry an ecological footprint that can be readily observed downstream (e.g., Novoa et al., 2018).

Future implications for riparian zones

The riparian landscape is becoming an increasingly interesting component to ecosystem management. There are clear land cover trends that document both their protection and degradation. Most urban areas within riparian zones are virtually locked in place, so their impacts will remain a foreseeable issue. Agricultural trends within riparian zones appear to be the most fluid in the 21st century, as they can easily be converted to alternate land covers. Likewise, the changes in wetland and forested environments within riparian zones should also keep attention moving forward. In terms of research and subsequent environmental management, there are several interesting questions based on the results of this chapter:

1. Why are wetlands increasing in riparian zones, and what are their impacts on human and natural systems?
2. Why are forests becoming more mixed in riparian zones, and how will this impact human and natural systems?
3. To what extent do riparian buffers need to be protected or restored to offset the inevitable impacts of increasingly dense urban areas along U.S. waterways?
4. Thinking globally, to what extent can this analysis offer insights to contexts elsewhere? What other societal dimensions may need to be considered in other contexts?

The approach described in this chapter can be applied to any geographic location globally to assess riparian changes at multiple spatial scales and across sociopolitical boundaries. It can also illuminate the global diversity of societal values of riparian areas and assist in tracking changes over time by providing a baseline metric of present and past land use.

Conclusion

Riparian zones are critically important for the overall sustainability of human and natural systems, yet these areas remain heavily degraded by human interactions. Some of this degradation is inevitable and is unlikely to change in the future, but this is largely restricted to fixed land cover like major urban areas. The rest of riparian zones can be managed and improved in a way that maximizes their ecosystem services. From 2001 to 2020, U.S. riparian zones did document more vegetation, less urban sprawl, and increased wetlands within riparian zones.

These changes suggest the value of riparian zones is influencing decision-making and environmental management during the 21st century. Going forward, there remain many important research gaps that can be addressed to help establish a thriving balance of human and natural systems within riparian zones in the U.S. and beyond. Globally, the vulnerability of riparian zones to climate impacts, biological invasions, agricultural intensification, and urbanization elevates the importance of riparian conservation and management efforts (Capon et al., 2013). Such efforts are especially needed in biomes and regions with disproportionately high riparian degradation (e.g., tropics, González et al., 2017). Consideration of the social, cultural, economic, and ecological values and services of riparian zones, including those highlighted here, will be necessary for the long-term sustainable management and restoration of local, regional, and global riparian areas.

Acknowledgments

We thank the Editors Febria and Krantzberg for their constructive feedback. This work was supported by the National Science Foundation Graduate Research Fellowship [Grant No. DGE-1842473].

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Societal Implications of Kenya's Inland and Marine Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Catherine Febria and Gail Krantzberg.

Introduction

Kenya is an emerging economy with socio-economically important inland and marine water resources that underpin the livelihoods of millions of people. The country is endowed with plenty of aquatic resources providing numerous ecological goods and services to the national economy yet classified as a lower-middle-income country (United Nations, 2019) with a rapidly growing population of over 50 million (World Bank, 2019). Kenya launched a long-term development blueprint in 2008 envisioning that by the year 2030, she will transform into a "newly-industrializing, middle-income country providing a high quality of life to all its citizens in a clean and secure environment anchored by improved services in its social, political and economic pillars." The Third Medium Term Plan (MTP III) 2018–2022 of the Vision identified the Blue Economy—including utilizing marine and freshwater fisheries resources as one of the priority sectors with a high potential to spur inclusive economic growth and development (Government of Kenya, 2018a).

Kenya has a total area of about 582,646 km^2 (square kilometers), of which 11,230 km^2 (1.9%) is covered by inland waters, while 14,300 km^2 (2.5%) is covered by territorial marine waters (NEMA, 2021). Its freshwater resources are represented by lakes, rivers, swamps, springs as well as dams, water pans and groundwater. While its territorial marine ecosystems include seagrass, mangroves, coral and river delta, and a coastline of 640 km on the Western Indian Ocean, in addition to a further 200 nautical miles Exclusive Economic Zone (EEZ). However, Kenya is a water-scarce country, with a per capita water availability of 647 cubic meters (m^3), well below the global benchmark of 1000 m^3 per capita, indicating chronic water scarcity (Government of Kenya, 2018b). The country is a chronically water scarce country with one lowest natural water replenishment rate in the world (Puzyreva and Roy, 2018). The inland waters are located in five major drainage basins (Lake Victoria, Rift Valley, Ewaso Ng'iro, Tana River and Athi River) originating from five main water towers—Cherangani Hills, Mount Kenya, Mount Elgon, the Mau Forest Complex and the Aberdares Ranges—which are the principal suppliers of water. The water towers are currently under heavy fragmentation and degraded due to human activities such as encroachment for settlement, conversion into agricultural lands owing to population pressure, grey infrastructural development and weak implementation of environmental policies (World Bank, 2019).

Presently, Kenya's aquatic resources are under immense and increasing pressure from human-related activities including rapid population growth, unsustainable agriculture, a proliferation of tourist facilities with unsustainable effluent management, deforestation and habitat degradation, water pollution, overexploitation of water resources, declining capture fishery, and the introduction of invasive non-native species (NEMA, 2021; Obiero et al., 2020; Sayer et al., 2018) with future risk from proposed dam construction, large scale irrigation and climate change. While the ecosystem faces many threats, including those in the present and those predicted for the future, the aquatic ecosystems can be resilient if management efforts focus on balancing competing user

needs. This chapter reviews the status of Kenyan inland and marine waters, major stressors and threats facing their ecological integrity and key recommendations that can be harnessed to help meet Kenya's Vision 2030 targets and sustainable development goals (SDGs).

Inland freshwater resources in Kenya

Kenya is endowed with a vast network of freshwater aquatic resources comprising lakes, rivers, dams/reservoirs, and streams. The surface water resources are distributed within five drainage basins (Fig. 1; Achieng et al., 2021): the Tana (21.7%), Athi (11.5%), Ewaso Ng'iro (36%), Rift Valley (22.7%), and Lake Victoria Basin (8%), with the highest surface water resource distribution in Lake Victoria Basin 11,672 (10^6 m^3) and lowest in Ewaso Ng'iro Basin 339 (10^6 m^3). Its groundwater resource range between 116 (10^6 m^3) and 87 (10^6 m^3) for Lake Victoria and Athi River Basin respectively (Table 1). The Lake Victoria Basin receives the highest average annual rainfall (1368 mm) while Ewaso Ng'iro receives the lowest average annual rainfall. Table 1 shows Kenya's surface and groundwater resources distribution and water abstraction levels of the five drainage basins.

Lake Victoria Basin

The Lake Victoria Basin (LVB) covers about 8% of the total area of Kenya but accounts for over 54% of the national freshwater resources (MEMR, 2012). The Kagera River which originates from Rwanda and Burundi is the largest inflow, contributing up to 33% of the surface inflow into the lake. The main inflows from the Kenyan catchment include the Sio, Nzoia, Yala, Nyando, Sondu-Miriu, North Awach, South Awach and Gucha-Migori rivers. The other major rivers are Bukora and Katonga which originate in Uganda; while the Mori, Simiyu, Grumeti, Mbalageti, Magogo-Moame, and other small streams originate from Tanzania (LVBC, 2007).

The lake basin plays major ecological, social and economic roles in the East African Community (EAC). Its drainage basin consists of rivers, streams and wetlands and supports a human population of over 42 million (Awange, 2020) by providing a variety of economic and development opportunities, including fisheries, tourism, transportation, hydropower production and trans-boundary conservation (Obiero et al., 2015). The lake is one of the most productive freshwater fisheries in the world, with an annual fish catch of 1 million tons of fish and a fishery carrying capacity of 200 million metric tons (Kimani et al., 2018; Onyango et al. 2021). The lake's fisheries support approximately 4 million people with household incomes and meet the annual fish consumption needs of almost 22 million people in the region (Onyango et al., 2021). Given the unique and diverse nature of freshwater species within the basin, the dependence of rural communities and regional economies on these species, and the high levels of threat, there is a clear need for a stronger focus on the conservation of freshwater biodiversity (Sayer et al., 2018).

Rift Valley Basin

This basin covers an area of about 130,452 km^2 and consists of a number of hydrologically closed basins. It encompasses the basins discharging into Lake Turkana in the North through the Turkwel and Kerio rivers and those draining into Lake Natron in the south through the Ewaso Ng'iro South River. The smaller lakes such as Baringo, Bogoria, Nakuru, Elementaita, Naivasha and Magadi also form individual basins (Fig. 2). In the past decade, the Great Rift Valley lakes of Kenya have recently experienced significant increases in their water levels, negatively impacting the local communities (Githaiga et al., 2021; Herrnegger et al., 2021). The increases in lake levels and consequent inundations of the riparian areas have had significant negative impacts on the local communities, since homes, schools, hospitals, roads, but also the basis for the local economy such as agricultural areas or tourism infrastructure like hotels have been submerged and rendered unusable (Githaiga et al., 2021).

Athi River Basin

The Athi Basin has an area of 66,559 km^2 and borders Tanzania to the south, the Indian Ocean coastline to the east, the Tana Basin to the north and the Rift Valley Basin to the west (NEMA, 2011). The Athi River is the main river in the Athi Basin, draining about 57% (38,170 km^2) of the basin. Although the Athi Basin only covers about 11% of Kenya's land surface area, it has high economic activity, houses a quarter of the country's population, and hosts the two largest cities in Kenya viz. Nairobi and Mombasa (Aurecon AMEI Limited, 2020). The total population of the Athi Basin is 13.43 million, which is equivalent to a population density of 202 persons/km^2. Water plays a key role in the Athi Basin and is of critical importance for economic development in the two major urban hubs of Nairobi and Mombasa. Water security is essential for industries, health, tourism and for supporting an improved standard of living. It is estimated that 63% of the urban population in the basin receives piped water provided by Water Service Providers, while 20% are dependent on unimproved water sources. The remaining 17% are supplied from groundwater, which includes protected and unimproved sources (Aurecon AMEI Limited, 2020).

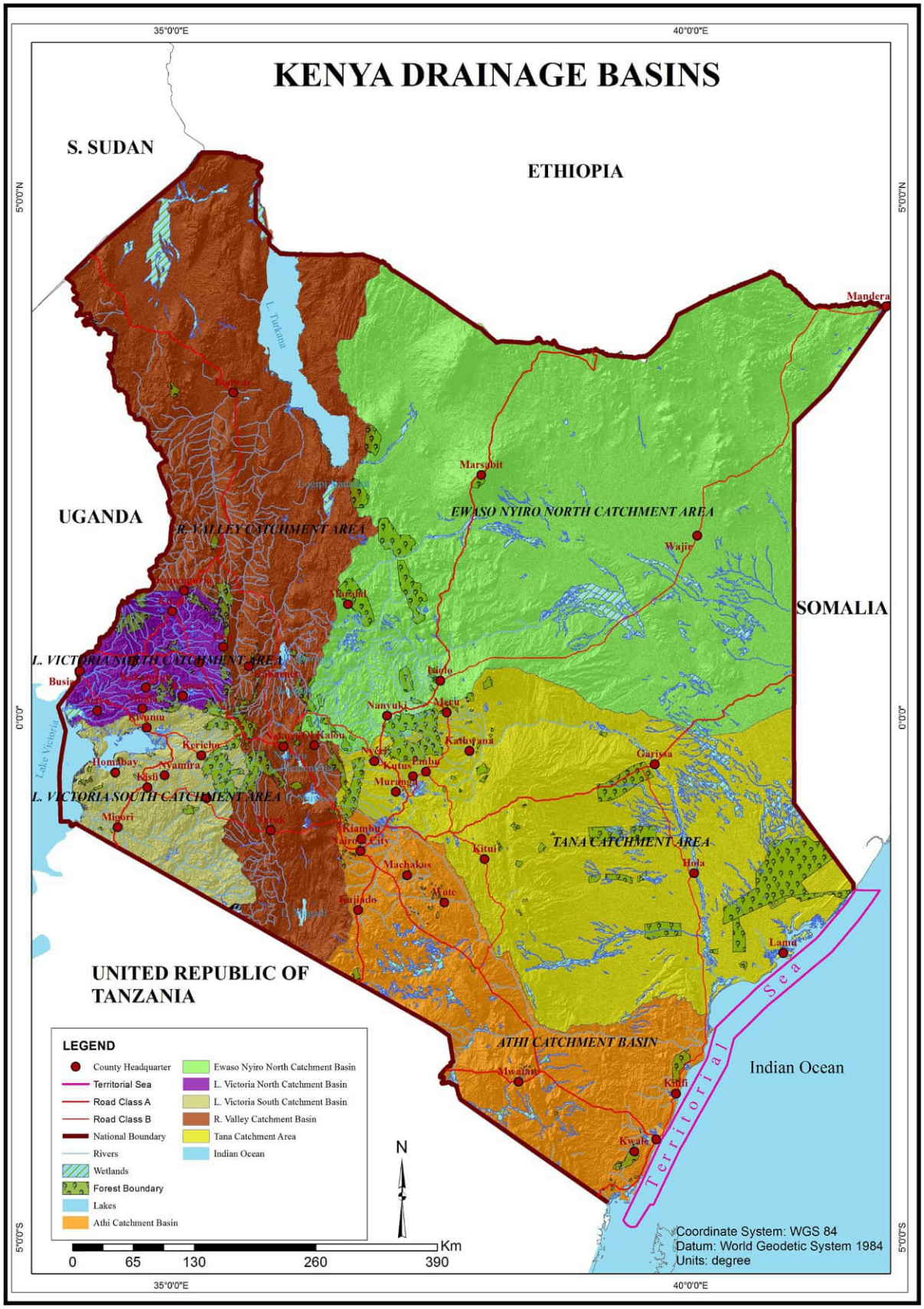

Fig. 1 Kenya's main drainage basins and surface water resources. From Achieng AO, Opaa B, Obiero KO, Osano O, and Kaunda-Arara B (2021) Watershed Management in Kenya; Societal implications, drivers of change and governance needs. *Encyclopedia of Inland Waters* (2nd edn.). doi:10.1016/B978-0-12-819166-8.00157-2.

Table 1 Average annual water availability and utilization per drainage basin in Kenya (NEMA, 2011).

Drainage basin	*Area (km^2)*	*Annual rainfall (mm)*	*Surface water (10^6 m^3)*	*Surface water abstraction*		*Groundwater (10^6 m^3)*	*Total water (10^6 m^3)*	*National freshwater resource (%)*
				10^6 m^3	*%*			
L. Victoria	46,229	1368	11,672	254.3	2.2	116	11,788	54.1
Rift Valley	130,452	562	2784	46.8	1.7	126	2910	3.4
Athi River	66,559	739	1152	133.1	11.6	87	1239	4.3
Tana River	126,026	697	3744	595.4	15.9	147	3891	32.3
Ewaso Ng'iro	210,226	411	339	42.1	12.4	142	481	5.8
Total	579,770	621	19,691	1071.1	5.44	618	20,309	99.9

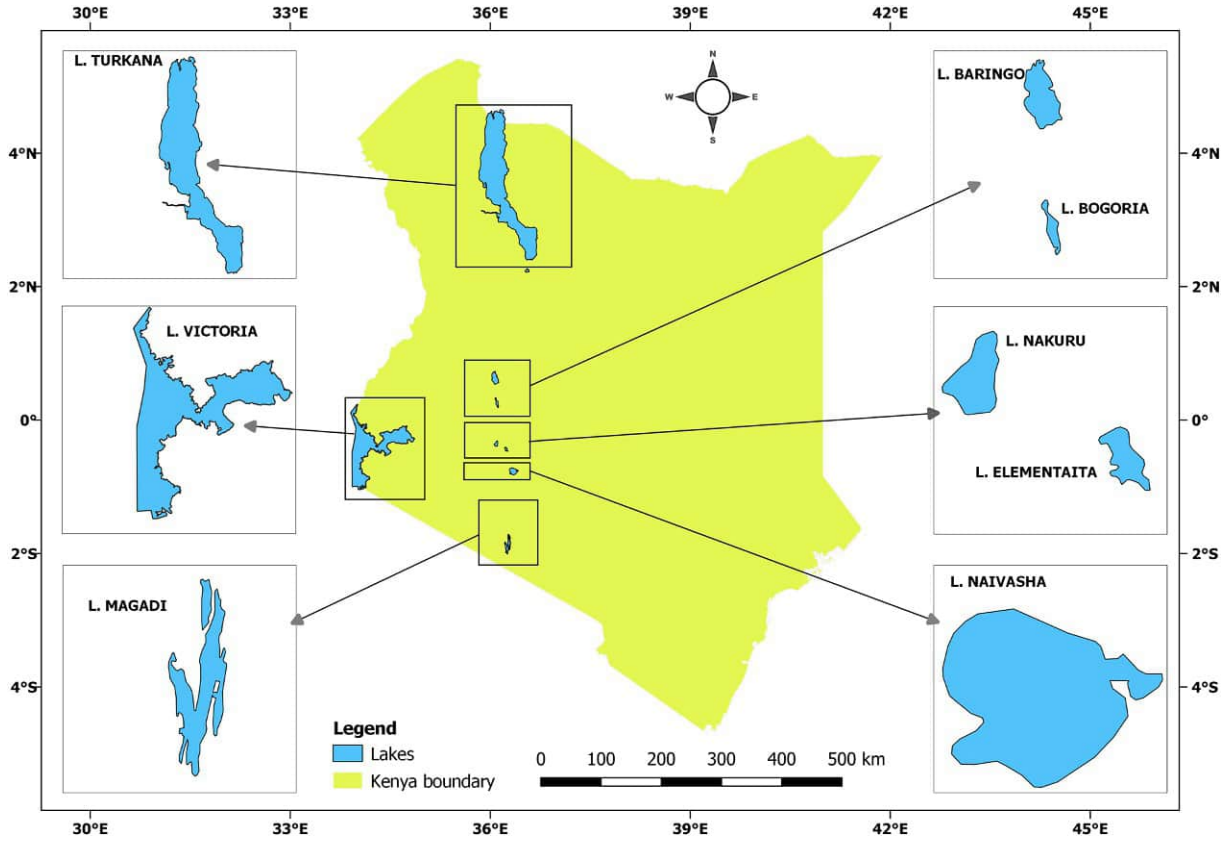

Fig. 2 Map of major lakes in Kenya. Adapted from Githaiga KB, Njuguna SM, Gituru RW, and Yan X (2021) Water quality assessment, multivariate analysis and human health risks of heavy metals in eight major lakes in Kenya Water quality assessment, multivariate analysis and human health risks of heavy metals in eight major lakes in Kenya. *Journal of Environmental Management* 297: 113410. doi: 10.1016/j.jenvman.2021.113410.

Tana River Basin

The Tana River Basin covers 22% of the country's total landmass and is home to 18% of the country's population (van Beukering and De Moel, 2015). It contributes over 50% of Kenya's river discharge to the Western Indian Ocean. The basin drains the eastern slopes of the Aberdares range, the southern slopes of Mount Kenya and the Nyambene hills before discharging into the Indian Ocean through the Tana River (NEMA, 2011). Ecosystems in the Tana River Basin including forests, arid and semiarid lands, mountain vegetation, freshwaters and wetlands, marine and coastal areas and agrosystems provide a range of ecosystem services vital for human wellbeing such as drinking water, hydro-electric power, fisheries, agriculture and biodiversity (van Beukering and De Moel, 2015). Like the Athi River Basin, the River Tana basin drains an area that is highly populated and urbanized with the Upper Tana River Basin hosting over 5.3 million people (TNC, 2015). In addition, Tana River is a major source of hydropower and has an estimated installed capacity of 480 Mega Watts (MW) out of its total estimated potential of 960 MW. For example, the basin supplies 80% of the drinking water for Kenya's capital, Nairobi. The Tana River is the country's primary source of hydroelectric power produced from five dams along the river (i.e., 70% of Kenya's hydroelectric power and 38% of Kenya power supply). Fisheries and agriculture in the basin provide a major source of food and employment for the estimated 7 million residents living in the greater basin area and other parts of the country. One of the basin's important ecosystems is the Tana Delta at the coast. This biodiversity hotspot is home to several endangered species and was designated as a Ramsar site in the year 2012—a recognized wetland of global importance (TNC, 2015).

Ewaso Ng'iro basin

The Ewaso Ng'iro North River basin covers an area of 209,000 km^2. It is found in the Northern part of Kenya and drains the northern slopes of the Aberdares Range and Mount Kenya (NEMA, 2011). It represents a typical tropical highland-lowland system characterized by humid to semi-humid conditions in the relatively small upper reaches and semi-arid to arid conditions on the plateau and in the vast lower parts of the basin (Kiteme, 2020). As a result of these conditions, the most limiting factor for human activities and development in more than 90% of the basin is water, with precipitation below the agriculturally critical 600 mm annually. In the past five decades, the Ewaso Ng'iro North basin underwent drastic socio-economic transition (Providoli et al., 2019). Large-scale ranching, immigrating small-scale farmers and recently established large-scale horticultural enterprises transformed the upper basin from its original pastoralists land use system, which still prevails in large parts of the lower basin. This transition has led to a steep increase in population densities, which in combination with the new land use systems dramatically increased the pressure on water resources, in particular on river water (Providoli et al., 2019; Kiteme, 2020).

Lacustrine ecosystems

Freshwater resources, including rivers, lakes and wetlands in Kenya are widely distributed among the five main drainage basins. The lakes provide diverse habitats ranging from the freshwater lakes of Victoria, Naivasha and Baringo to the semi-saline Lake Turkana and the alkaline lakes of Magadi, Elmentaita, Nakuru and Bogoria (Table 2). Despite their small sizes, the alkaline lakes are known for their rich biodiversity that includes bird species (both residents and migrants). The alkaline lakes also provide unique feeding habitats for East Africa's famous lesser flamingos while the freshwater lakes support important fisheries and agriculture. The semi-alkaline Lake Turkana is the world's largest permanent desert lake situated in a hydrologically closed basin that sustains indigenous fisheries, including some endemic species (Ojwang et al., 2016). Five lakes within the Rift Valley drainage basin are recognized as Wetlands of International Importance (Ramsar Sites: Table 2), and all are Important Bird Areas, with several being within UNESCO-listed World Heritage Sites (MEMR, 2012).

Riverine ecosystems

Kenya is endowed with major river systems including Athi, Tana, Nzoia, Mara, Yala, Nyando, Sondu, Kuja, Turkwel, Kerio and Ewaso Ng'iro (Table 3 and Fig. 3). Four major rivers namely Gucha-Migori, Nyando, Nzoia and Tana, discharge over 1000 m^3/day (MEMR, 2012); other rivers with a significant perennial flow are Mara, Sondu and Yala. The Tana River is Kenya's longest river and originates from two of Kenya's major water towers: Mt. Kenya and the Aberdares. River Tana measures approximately 1050 km in length and has an average width of 39.3 m, a mean depth of 2.5 m and an average flow rate of 41.98 m^3/s. Its mean annual

Table 2 Characteristics of major Kenya lakes.

Name	*River(s) draining into the lake(s)*	*Surface area (km^2)*	*Maximum depth*	*Altitude (m amsl)*	*Water quality*
1. Lakes with special categories (Ramsar sites or World Heritage Sites)					
Lake Nakuru (Ramsar/World Heritage Site)	Njoro, Makalla, Ngosur, Lamudhiak, Enderit	49	4.5	1754	45% saline (pH 10.5)
Lake Elementaita	Waseges-Sandai, Loboi, Emsos and Mogun	18	1.9	1670	40% saline (pH 9.4)
Lake Baringo (Ramsar)	Pekerra, Molo, Ndoo, Toigibe	168	8	1000	Fresh
Lake Bogoria (Ramsar/World Heritage Site)	Waseges-Sandai, Loboi, Emsos and Mogun	42.5	8.5	990	35% saline (pH 9.8–10.3)
Lake Naivasha	Malewa, Gilgil, Karati	156	7	1884	Fresh
2. Transboundary Lakes					
Lake Victoria	Nyando, Yala, Sondu, Kibis, Kija, Mara, Sio (Kenya)	68,800	84	1134	Fresh
Lake Turkana	Turkwel (Kenya), Kerio (Kenya), Omo (Ethiopia)	7560	114	360	Brackish
Lake Jipe	Umi	28	2	705	Fresh
Lake Chala	Underground seepage	6	90	880	Fresh
Lake Magadi	Ewaso Kedong	105	0.5	579	Saline pH 10.5)
3. Other lakes					
Lake Kamnarok	Kerio	1	Shallow	1064	Fresh
Lake Ol Bolossat	Ewaso Ngi'ro North	43	Shallow	2340	Fresh
Lake Amboseli	Namanga	–	Shallow	1150	Fresh
Lake Kanyaboli	Yala	15	3	1140	Fresh

Slightly modified from MEMR (2012) *Kenya Wetlands Atlas. Ministry of Environment and Mineral Resources. Nairobi, Kenya.* https://na.unep.net/siouxfalls/publications/Kenya_Wetlands.pdf. (Accessed 22nd June 2021).

Table 3 Characteristics of Kenya's 12 main river systems.

River	*Catchment area (sq.km.)*	*River length (km)*	*Drainage waterbody*
Nzoia	12,696	315	Lake Victoria
Yala	3262	261	Lake Victoria
Nyando	3450	153	Lake Victoria
Sondu	3489	173	Lake Victoria
Kuja	6868	180	Lake Victoria
Mara	9574	198	Lake Victoria
Turkwel	20,283	390	Lake Turkana
Kerio	14,172	403	Lake Turkana
Ewaso Ng'iro South	8534	213	Lake Natron
Ewaso Ng'iro North	91,428	740	Lorian Swamp
Athi	36,905	631	Indian Ocean
Tana	95,430	1050	Indian Ocean

Modified from MEMR (2012) *Kenya Wetlands Atlas. Ministry of Environment and Mineral Resources. Nairobi, Kenya.* https://na.unep.net/siouxfalls/publications/Kenya_Wetlands.pdf. (Accessed 22nd June 2021).

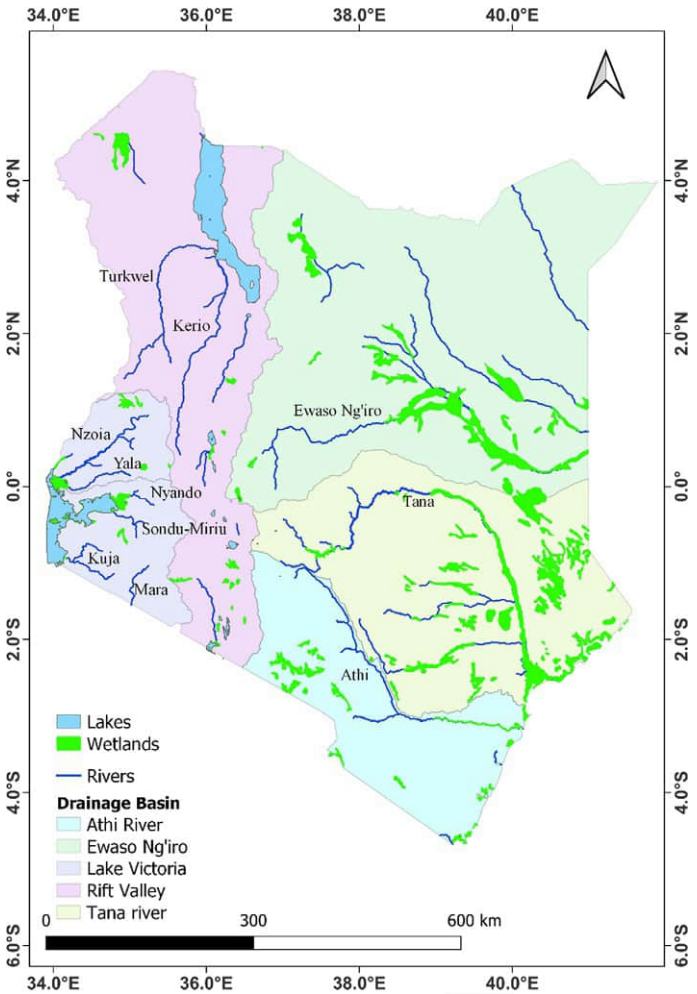

Fig. 3 Major rivers in Kenya.

discharge at Garissa is 5 billion cubic meters (BCM) (NEMA, 2011). The Athi River measures approximately 591 km and has an average width of 44.76 m, an average depth of 0.29 m and an average flow rate of 6.76 m^3/s. The Kerio River is the main river in the Rift Valley basin with a total length of 354 km. It has an average width of about 5.7 m, a mean depth of 0.21 m and the mean flow is 4.47m^3/s (NEMA, 2011).

A recent biodiversity report by World Wide Fund for Nature (WWF) in the Mara River basin identified 473 native freshwater species including four mammals, 88 waterbirds, 126 freshwater associated birds, four reptiles, 20 amphibians, 40 fishes, 50 invertebrate species and 141 vascular plants (Pringle et al., 2020). At least 10 species—equivalent to 2% of total species—are on the International Union for Conservation of Nature list of threatened species. Three—the Ningu (*Labeo victorianus*), Singida (*Oreochromis esculentus*) and Victoria tilapia (*Oreochromis variabilis*)—are "critically endangered," threatened by the introduction of non-native fish such as the Nile perch (*Lates niloticus*) (Pringle et al., 2020).

Wetland ecosystems

Kenya's wetlands are biologically productive ecosystems, rich, diverse and provide multiple goods and servises, and are critical for water purification and storage, support biodiversity, flow regulation, and flood control (Box 1; World Bank, 2019). The Kenya Environmental Management and Coordination (Wetlands, Riverbanks, Lakeshores and Sea Shores Management) Regulations 2009 define wetlands as "areas permanently or seasonally flooded by water where plants and animals have become adapted; and include swamps, areas of marsh, peatland, mountain bogs, banks of rivers, vegetation, areas of impeded drainage or brackish, salt or alkaline; including areas of marine water the depth of which at low tide does not exceed six meters". This definition includes swamps, marshes, bogs, shallow lakes, ox-bow lakes, dams, river meanders and floodplains, as well as riverbanks, lakeshores and seashores where wetland plants grow. The definition also covers marine and intertidal wetlands such as deltas, estuaries, mudflats, mangroves, salt marshes, seagrass beds and shallow reefs (MEMR, 2012).

Even though the exact extent of Kenya's wetlands is unknown owing to lack of comprehensive wetland inventory, they are estimated to occupy around 3–4%, which is approximately 14,000 km^2 of Kenya's landmass which can temporarily grow to 6% during the rainy seasons (NEMA, 2011). The Ramsar classification of wetland types contains three broad categories: inland; marine and coastal; and human-made. These are then sub-divided into 42 types (Fig. 4). Owing to Kenya's diverse climate and topography, the country is home to six wetland types: riverine; lacustrine; palustrine; estuarine; marine; and constructed wetlands. Inland freshwater wetlands cover approximately 2,641,690 ha which far outstrips the area covered by marine and coastal wetlands at 96,100 ha (MEMR, 2012). Five sites in the country have been designated as Wetlands of International Importance (Ramsar Sites) including lakes (Nakuru, Naivasha, Bogoria, Baringo and Elementaita) that are part of the Great Rift Valley system. All these lakes are important in regulating local climate, nutrient cycling, habitat for various aquatic and terrestrial species including bird, particularly renowned for their large flamingo populations and several other ecosystem servises (Box 2). As such, they are frequently visited by ornithologists, making them an important component of the tourist circuit.

Box 1 Importance of wetlands in Kenya.

Kenya is endowed with rich and diverse wetlands crucial for the provision of multiple ecosystem goods and services, beneficial to its citizens, economy and associated ecosystems. Ecologically, wetlands form the unique interface between water and land that supports a distinctive community of plants, including floating lilies and sedges, and animals including frogs, fish and turtles (MEWNR, 2015). Wetlands buffer the effects of floods, reduce erosion control, capture carbon, filter out and decontaminate pollutants and toxins, recycle nutrients and stabilize stream banks and shorelines. Wetlands store excess water and act as buffers against drought for wildlife, farmers and herders. Wetlands also provide an abundance of plant and animal produce for humans, including food, water, medicine, and material for handicrafts, furniture and construction. In recent decades wetlands have become important in irrigated farming, commercial fishing, paludiculture, carbon sequestration, flood control, wildlife conservation, tourism and recreation. Wetlands are key assets in sustainable development, poverty alleviation and the improvement of livelihoods. For instance, from horticulture alone, Lake Naivasha contributes over Kshs 5.3 billion (approximately US$ 63 million) per year while over 30,000 people derive their livelihoods from this important wetland ecosystem (MEMR, 2012). Oduor et al. (2015) revealed that Nyando Wetlands yield a flow of economic benefits from consumptive goods and services estimated at US$ 1.5 billion (US$ 62,500 ha^{-1} $year^{-1}$) with a present value of US$ 75.5 billion at a 2% discount rate. As a result, the reclamation of the wetlands would imply high economic benefits to the government and local communities. Therefore, there is a justified need to maintain the biological diversity and productivity, and to permit the wise use of Kenya's wetland resources, through development and implementation of focused management actions, and conduct regular reviews to address emerging issues in line with the changing context of the environment in the wider wetland landscape (Wetlands International, 2020).

Box 2 Importance of lakes and rivers.

Kenya's lakes and rivers contain some 20 billion cubic meters of water—which plays a critical role in local climate (MEWNR, 2015). They capture nutrients and sediments eroded from the land and so sustain a highly productive and diverse assemblage of plants and animals. Freshwater habitats support unique and specialized species, several endemics and many rare or threatened species. Lakes and rivers are important stepping stones for Palearctic migratory birds, flamingoes and shorebirds. They also supply the bulk of the water that drives the Kenyan economy, from farming and ranching to industry, commerce and settlement. Freshwater fisheries have, until recently, been dominated by traditional and artisanal fishing communities but now sustain commercial fisheries in Lake Victoria and Lake Turkana. Rivers also produce hydroelectric power, filter and provide clean water for human settlement and, together with lakes, provide transport routes for commerce and a range of amenities that attract tourists, outdoor and water-sports enthusiasts.

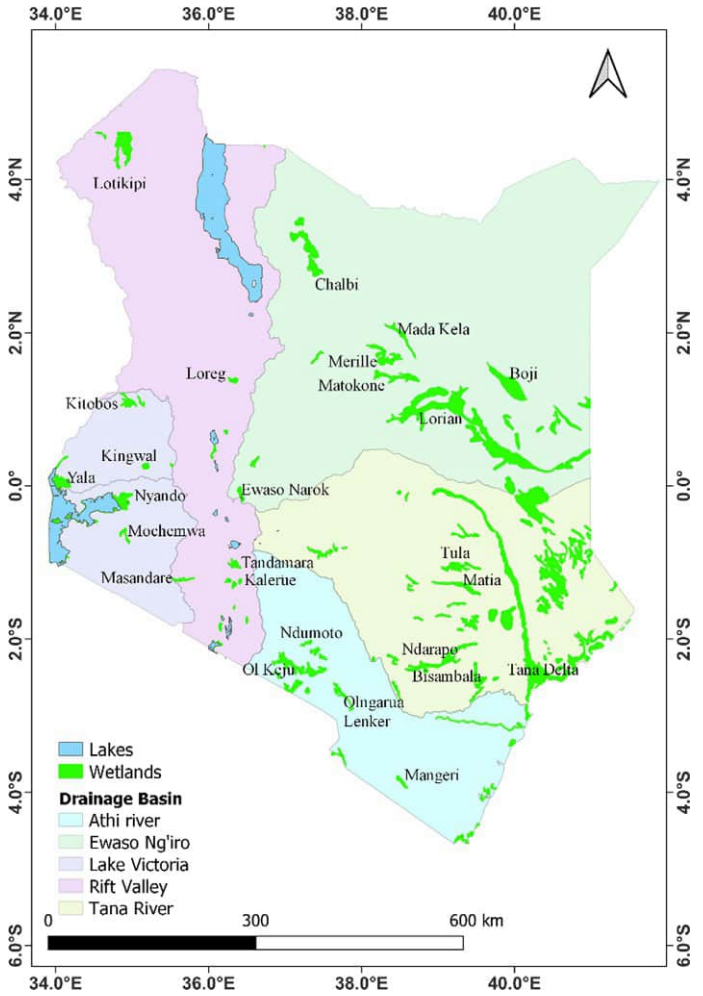

Fig. 4 Map showing the main wetlands in Kenya.

The Tana River Delta is an unprotected wetland on the Kenyan coast. The Delta, a designated Key Biodiversity Area (KBA), covers 127,000 km^2 and is Kenya's largest wetland. The Tana River Delta is also a designated Ramsar site—a recognized wetland of global importance. The Mara basin (65% of which is in Kenya and 35% in Tanzania) covers 13,750 km^2 and is home to the highest density of large herbivores on Earth (Pringle et al., 2020). The area is known globally for the annual wildebeest and zebra migration, which brings in millions of dollars in tourism.

Coastal and marine ecosystems

Kenya enjoys a marine coastline of about 640 km giving a total area of territorial waters of 9700 km^2 while the EEZ is 142,400 km^2 (Rasowo et al., 2020). The coastal region is endowed with rich natural resources that play a critical role in fostering economic development. Such resources include beaches for recreation, fisheries resources, mangrove forests and cultural diversity. Table 4 contains an overview of Kenya's coastline and marine resources including mangroves (Fig. 5A) and other coastal forests, seagrass beds (Fig. 5B), sand dunes and sandy beaches and coral reefs.

Blue economy

The World Bank defined the "blue economy" (BE) as "the sustainable use of ocean resources for economic growth, improved livelihoods, and jobs while preserving the health of ocean ecosystem" (World Bank, 2017, p.6). In the global context, the blue economy concept integrates the economic exploitation and sustainable conservation of renewable and non-renewable marine resources (UNECA, 2016). The BE sector fits within the framework of the United Nations (UN) 2030 Agenda and embraces all the sustainable development goals (SDGs) given its inclusive nature (World Bank, 2017). Kenyan has domesticated the BE concept, which is now the eighth priority sector in the Economic Pillar under the Third Medium Term Plan (MTP III) of the Kenya Vision 2030 (Third Medium Term Plan 2018–2022). The BE in Kenya encompasses activities that explore, develop and use the ocean's resources and space and protect the ocean's ecosystems. It incorporates traditional maritime industries e.g., fisheries, coastal tourism, energy and mineral production, boat building, shipping and ports as well as new and developing industries such as blue carbon (carbon stored in mangroves, seagrass and saltmarsh ecosystems, aquaculture products, marine renewable energy (i.e., wind, wave and tidal energy), bio-products (pharmaceutical and agrichemicals), and desalination.

Table 4 Kenya's coastal resources at a glance.

Coastal resource	*Description and key characteristics*
Coastal forests and mangroves	• Mangroves and coastal forests of Kenya characterize the low lying inter-tidal areas and system of low ridges between 100 and 300 m in altitude (Fig. 5) • The forests have a canopy span of up to 7 m, covering about 139,000 ha and with lowland forest patches, woodlands, bushlands and thickets • The main forests in the coastal area include Arabuko Sokoke (41,000 ha) and the Shimba Hills system (19,260 ha). Others are smaller patches ranging from 10 to 2000 ha and mainly consist of the "Kaya," sacred forests of the Mijikenda communities • Mangrove forests occur along the coast in the intertidal area between the land and the sea. The total area of mangroves in Kenya has been estimated at between 53,000–61,000 ha. It is estimated that 10,310 ha of mangrove forests have been lost due to conversion to other land uses, overexploitation and pollution • There are nine mangrove species found along the East African coast. All these occur in Kenya although the dominant ones are *Rhizophora mucronata* and *Ceriops tagal*. Other rarer species include *Heritiera littoralis and Xylocarpus moluccensis*
Seagrasses	• Seagrasses occur in extensive beds that cover the largest proportion of shallow reef slopes and form an important habitat for many species living in them and adjacent systems • Twelve seagrass species are found in Kenya. *Thalassondendron ciliatum*, which forms monospecific stands, is the dominant one. Its canopy structure provides habitats for small and juvenile fish and invertebrates • Other common seagrass species found in the country are *Halophila ovalis*, *Halophila minor, Halophila stipulacea, Halodule uninervis, Halodule wrightii, Syringodium isoetifolium, Cymodocea rotundata, C. serrulata, Thalassia hemprichii, Zostera capensis,* and *Enhalus acoroides* • Seagrass meadows are composed of submerged flowering plants that colonize shallow marine waters. The meadows settle sediment loads in the tidal zone, buffer the coastline from ocean currents, absorb suspended nutrients and sequester nitrogen. They also offer food and shelter for invertebrates and fish and are important to the subsistence, commercial and sport-fishing industry off the coast
Coral reefs	• Coral reefs are the ocean's richest ecosystems in terms of biodiversity and productivity. Kenya's reefs are particularly productive ecosystems rich in corals, sponges, sea ferns, algae, seagrasses, phytoplankton, and an extraordinary variety of invertebrates ranging from burrowing worms and bristle worms to jellyfish, anemones, shrimps, lobsters, crabs, starfish, sea urchins, sea cumbers, giant clams, bivalves, conches, sea hares, squids and octopuses

Adapted from NEMA (2011) Freshwater, Coastal and Marine Resources. In: *Kenya: State of Environment and Outlook 2010* (pp. 124–169). National Environment Management Authority and MEWNR (2015) *Kenya Biodiversity Atlas. Ministry of Environment, Natural Resources and Regional Development Authorities. Nairobi, Kenya.*

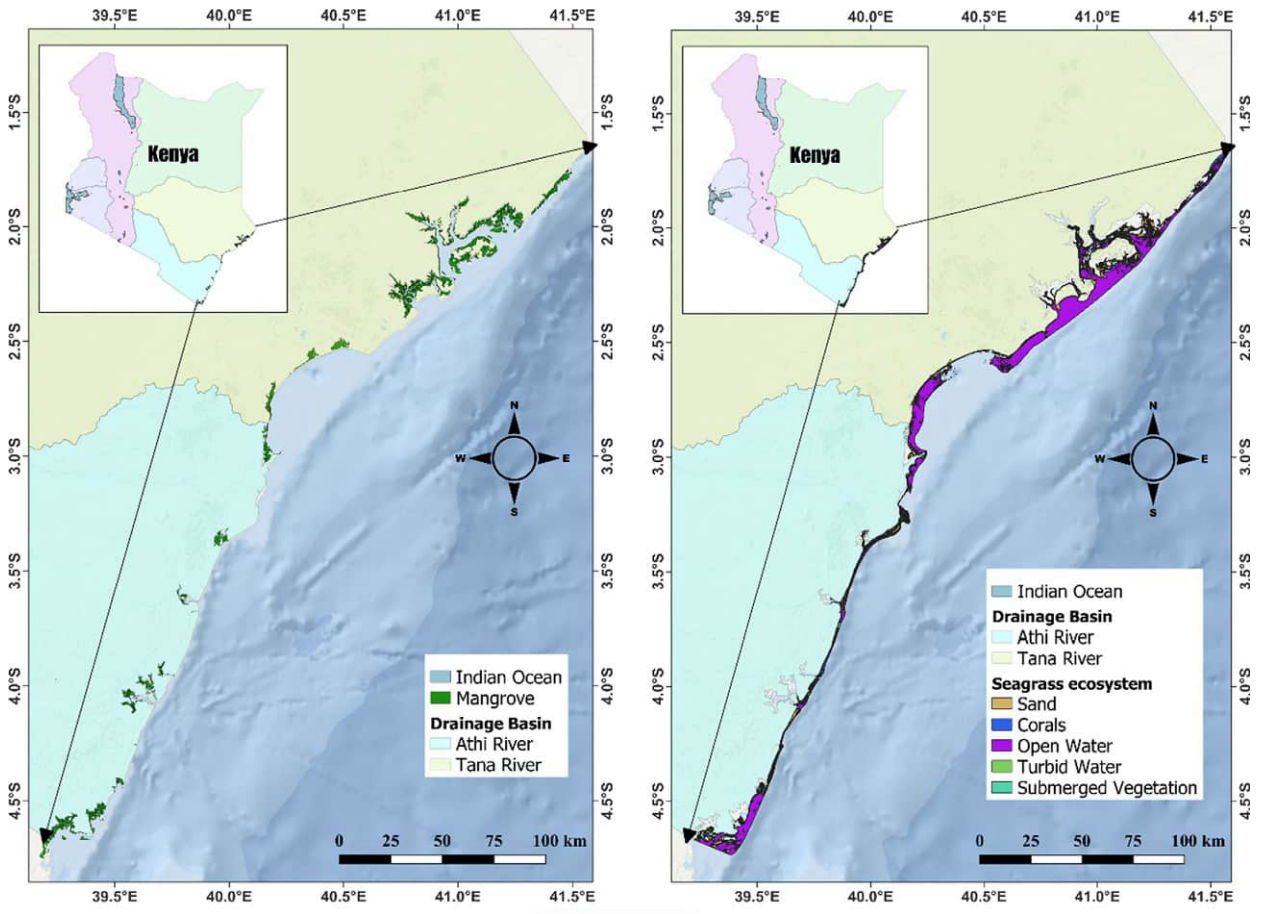

Fig. 5 Mangrove (A) and Seagrass (B) ecosystems.

Box 3 Blue Economy sector in Kenya.

The blue economy has significant value to Kenya's economy. The blue economy refers to economic activities linked to the sustainable use and economic development of all aquatic environments including oceans, seas, coasts, lakes, rivers, reservoirs, dams and underground water. Kenya's blue economy is worth about US$4.4 billion every year (World Bank, 2019). This is roughly 5.5% of gross domestic product (GDP) of which US$4.1 billion is dependent on the tourism sector (UNDP, 2018). Fisheries is another important component of the blue economy which contributes 0.8% to the country's GDP, with the inland fisheries making up about 80%, aquaculture (15%) and marine fisheries about 5% of the total national fisheries production. Close to 80% of Kenya's imports and 20% of exports are transported via sea routes. The Kenya National Bureau of Statistics (KNBS) Economic Survey estimates marine fishing had an annual fish potential of 350,000 metric tons worth over Kshs. 90 billion yet the country only harvested a paltry 25,656 metric tons worth Ksh3.3 billion in 2020 (KNBS, 2021).

The Blue Economy sector is poised to make a significant contribution to Kenya's economic growth (Box 3). In recognition of the importance of this sector to fuel Kenya's economic growth, the Kenyan Government recently allocated Kshs. 2 billion to turn around the Blue Economy sector (Ogello et al., 2021). Despite the high-level attention towards the exploitation of the BE sector in Kenya, the full economic potential of marine resources has not been exploited, yet Kenya has a maritime territory of 230,000 km^2 and a distance of 200 nautical miles offshore. Therefore, the development of Kenya's Blue Economy is expected to offer massive opportunities for sustainable growth in several traditional and emerging economic sectors.

Fisheries and aquaculture

Kenya's fishery sector can be divided into five sub-sectors: freshwater fishery, aquaculture, coastal marine capture fishery, offshore pelagic fishery and the EEZ fishery. Wild-caught fisheries play a central role in Kenya's culture, economy and food supply chain, and were valued at US$ 440 million in 2018 (Kimani et al., 2018). Overall, the fisheries sector supports about 1.2 million people working as fishers, traders, processors, suppliers and merchants of fishing accessories (Kenya Fisheries Service, 2016). The country's total fish production in 2020 is estimated at 149,678 metric tons worth US$ 256 million (Kshs. 25.6 billion) (KNBS, 2021).

The fisheries potential of Kenya's inland waters, mainly from commercial fishing is estimated between 150,000 to 300,000 metric tonnes (MT). Production from wild-caught fisheries has stagnated and declined over the past decade (Kenya Fisheries Service, 2016). Over the last 5 years, fish production from freshwater sources remained the major source of fish landed accounting for over 80% of the total fish output (Table 5). Fish output from marine sources contributed a relatively small share mainly due to inadequate technology necessary for fishing in deep waters (KNBS, 2021). Aquaculture is regarded as an alternative to bridging the widening gap between fish demand and its supply in Kenya (Obiero et al., 2019). As the industry has evolved and grown, new and promising early-stage investment opportunities to enhance sustainable aquaculture practices among young people have emerged. These have included enhanced sensing and monitoring technologies for waste pollutants; improved farm management; yield enhancement; disease control monitoring and inputs; alternative protein and feed sources (insect-based e.g., black soldier fly larvae, plant-based e.g., soy and algae), and developments in aquaculture infrastructure technologies (Munguti et al., 2021).

Table 5 Quantity (in metric tonnes) of fish production in Kenya from 2016 to 2020.

Year	*2016*	*2017*	*2018*	*2019*	*2020*
Freshwater sources					
Lake Victoria	98,666	92,727	98,150	90,743	86,659
Lake Turkana	7926	4021	7587	7031	13,190
Lake Naivasha	1064	1689	2287	3087	2216
Lake Baringo	141	155	145	203	162
Lake Jipe	106	112	131	157	197
Lake Kanyaboli	110	127	203	300	264
Lake Kenyatta	30	45	14	140	167
Tana River Dams	444	422	297	394	283
Tana River Delta	30	115	46	94	63
Turkwel Dam	39	35	34	50	107
Riverine	5	10	320	380	411.4
Small Dams	–	300	339	459	358
Aquaculture	14,952	12,356	15,320	18,542	19.945
Sub-Total	**123,513**	**112,114**	**124,673**	**121,580**	**124,021.4**
Marine sources					
Marine fish	21,190	19,357	20,133	21,647	20,201
Crustaceans	772	1646	1600	1933	1574.3
Molluscs	2203	2281	2101	2064	1909.1
Industrial fishing	–	449	1038.5	1994	1972
Sub-Total	24,165	23,733	24,872.5	27,638	25,656.4
Grand Total	**147,678**	**135,847**	**149,545.5**	**149,218**	**149,677.8**

Source of Data: Economic Survey, KNBS (Kenya National Bureau of Statistics) (2021). *Economic Survey (2020).* https://www.knbs.or.ke/wp-content/uploads/2021/09/Economic-Survey-2021.pdf (Accessed 28th July 2021).

Although Kenya's fisheries are of strategic value given the role of the sector in supporting livelihoods and contributing to food security, the resources are grossly underreported and undervalued in official statistics (Schubert et al., 2021; Onyango et al., 2021). Building on previous literature to reconstruct Kenya's marine fisheries data from 1950 (Le Manach et al., 2016; McAlpine, 2019), a new study by Schubert et al. (2021) reconstructed the freshwater catches in the country, disaggregated by major water bodies, fishing sector, taxon and reporting status. The study revealed that the total reconstructed catches in Kenya from 1950 to 2017 were 32% higher than the catches reported by the FAO on behalf of Kenya. This under-reporting was due to unmonitored water bodies, incomplete time series for monitored water bodies, and the under-representation in the officially reported data of both the catches taken with illegal gears, as well as locally consumed catches from the non-commercial subsistence sector (Schubert et al., 2021). In addition, the study showed that the subsistence fisheries sector accounted for 71% of unreported catches, compared with 29% for artisanal sector catches (small-scale, commercial), suggesting that non-commercial catches for direct local consumption are substantially under-represented in nationally reported statistics and should receive greater attention to support sustainable food security in Kenya (Onyango et al., 2021).

Major threats and challenges to water resource management in Kenya

Kenya's rich and diverse inland and marine ecosystems are under multiple threats and challenges. The Drivers-Pressure-State-Impact and Response (DPSIR) framework has been widely applied globally in assessing, addressing and communicating with regard to environmental problems (Troian et al., 2021). This framework provides a nexus between the causes of environmental problems and the resultant pressures, associated impacts and responses needed to resolve and manage specific environmental issues and challenges. This conceptual framework is used to understand, synthesize and visualize the cause-effect interactions of the threats and challenges facing water resources and to develop potential actions for improving the implementation of sustainable water resource conservation and management interventions in the country (Fig. 6). These threats vary in their severity of impacts and consequences as well as proposed mitigation measures as summarized in Table 6.

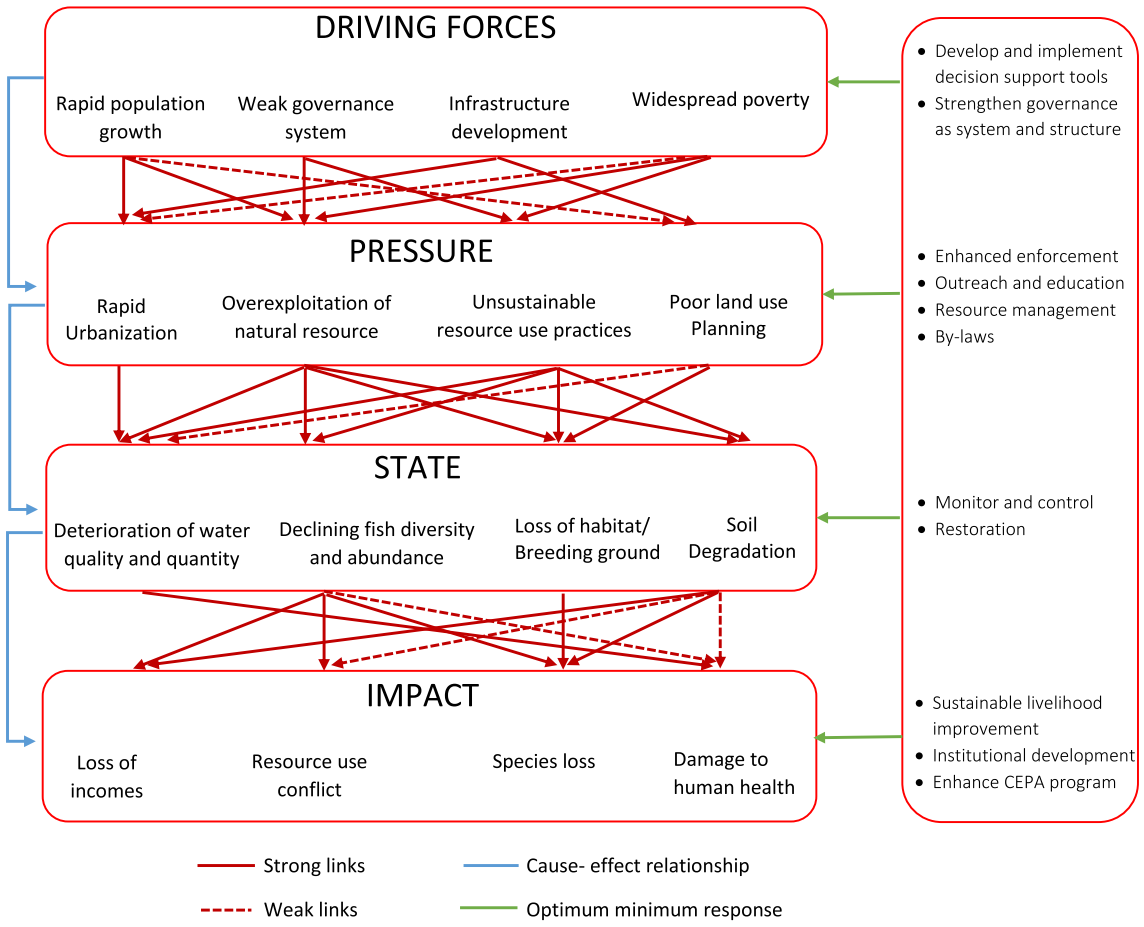

Fig. 6 Drivers-Pressure-State-Impact and Response (DPSIR) summary model of inland and marine water challenges in Kenya. Adapted from Wetlands International (2020) *Transboundary Wetland Management Plan for the Sio-Siteko Wetland Between the Republic of Kenya and the Republic of Uganda 2020–2030*. Wetlands International, Wetlands Across Borders Project, June 2020.

Table 6 Major threats and their causes, impacts, and consequences for water resources in Kenya.

Major threats and causes	*Impacts*	*Consequences*
Social drivers		
• Rapid population growth • Rural-urban migration • Infrastructural developments • Extreme poverty • Lack of education and awareness • Community alienation and marginalization	• Loss of system productivity • Resource use conflicts • Habitat fragmentation • Loss of biomass • Reduced boundaries and ecosystems • Fragmented river systems, inhibiting species movements	• Loss of revenue • Loss of livelihoods • Increased poverty • Loss of aesthetic value of resources
Environmental drivers		
• Climate change and extreme climate events • Catchment degradation due to poor agricultural practices • Urban and industrial Pollution • Extreme water level changes • Shoreline erosion and changes • Unsustainable land use management	• Increased erosion and sedimentation • More severe droughts and floods • Drying of rivers • Increased disease incidences • Coral bleaching • Reduced landscape vegetation	• Increased temperature, shifts in precipitation patterns and increase in the frequency of floods and droughts • Loss of land and property bordering water bodies • Loss of tourism opportunities • Loss of biotic integrity • Species extinctions
Ecological drivers		
• Harmful algal blooms • Eutrophication • Invasive species • Anoxia	• Biodiversity loss • Decline in aquatic species and extinction • Deteriorating of water quality and quantity • Reduced species growth, survival and reproduction	• Alteration of species size, range, phenology and survival • Loss of biotic integrity • Loss of revenue • Massive fish kills • Increased poverty
Ecosystem goods and services		
• Over abstraction of water resources • Degradation of resources • Overexploitation of fisheries resources • Unregulated harvesting of inland and marine water products	• Decline in harvestable resources • Loss of aesthetic value • Increased deforestation • Deteriorating water quantity and quality	• Decline in harvestable resources • Decreased revenue • Increased resource use conflicts • Increased poverty
Governance issues		
• Multiple and overlapping institutional mandates • Weak institutional linkages • Limited consultation of stakeholders • Inequitable resource access and control • Unilateral (often top down) decision-making • Weak monitoring, control and surveillance (MCS) • Inadequate capacity and resources at the local level to effectively manage resources	• Unsuitable exploitation of living resources • Undervaluation of ecosystem services • Limited ability to think beyond immediate needs • Diminishing livelihoods	• Decline in harvestable resources • Decreased revenue • Increased resource use conflicts • Increased poverty • Loss of aesthetic value

Modified from NEMA (2011) Freshwater, Coastal and Marine Resources. In: *Kenya: State of Environment and Outlook 2010* (pp. 124–169). National Environment Management Authority.

Key recommendations for sustainable management of inland and marine water resources

1. *Conserve, sustainably manage, restore, and remediate degraded ecosystems*: (i) consolidate and restore protected areas, landscapes, and watersheds for maximizing multiple ecosystem services; (ii) reduce deforestation rates to zero in the next decade and halt the degradation of terrestrial and aquatic ecosystems; (iii) reafforestation to improve and restore the forest cover within the gazetted areas and encourage tree plantation in uncultivated land; and (iv) implement systems to monitor, evaluate, incentivize, and hold stakeholders accountable for restoration and remediation measures.
2. *People empowerment and good governance*: (i) implement transparency and inclusive devolved governance system to improve terrestrial and aquatic resource management and strengthen human and terrestrial land and property rights; (ii) engage indigenous people and local riparian communities in planning and policy-making processes to promote their political representation at all levels of water resource governance; (iii) recognize different indigenous technical knowledge systems and promote intercultural education and information sharing through dialogs and coordinated fora where all actors convene and ventilate as well as share concerns, perspectives and ideas.

3. *Invest in a sustainable fisheries and aquaculture, lake and flowing rivers bioeconomy*: (i) invest in education, science, research, technology, and innovation; (ii) create fiscal and financial incentives to engage the private sector and multilateral institutions in innovation and sustainable fisheries and aquaculture value chains; (iii) sustainable intensification of existing aquaculture systems for increasing accessibility of aquatic foods, based on scaling of proven but infrequently adopted interventions; (iv) promote green job creation and capacity building; (v) invest in rural, urban, and peri-urban sustainable infrastructure.
4. *Expand sustainable land management interventions*: (i) diversify alternative livelihoods through climate-smart agriculture technologies, innovations and management practices; (ii) invest in sustainable land management interventions to reduce the impacts of pressures on water and land and contribute to improving food and nutrition security.
5. *Enhance compliance with environmental policies to reduce pollution and improve environmental health*: (i) strengthen environmental accountability mechanisms for industry players especially the manufacturing sector; (ii) invest in staffing and training to ensure that suitably trained government staff are dedicated to compliance are available to provide oversight on water related projects regardless of the source of funding; (iii) raise public awareness through campaigns to facilitate culture change and nationwide appreciation of the importance of environmental health for water resources.
6. *Mobilize financing and foster partnerships for water resource conservation, restoration, and sustainable development*: the current market economy and policy conditions favor deforestation over conservation or restoration. The scale of Kenya's blue economy, and the challenges it faces, call for ambitious, large-scale international finance development, and private and public financial partnerships to promote and sustain restoration, conservation, management, the development of sustainable value chains, payments for ecosystem services schemes, and investment in education, science, technology, and innovation.

Conclusion

Water is a primary life-giving resource in Kenya and across the globe. Its availability is an essential component in socioeconomic development and poverty reduction. In the face of a changing climate, rapid population growth, growing urbanization, increased deforestation and ecosystem degradation, and overexploitation of resources, water resources in Kenya could soon reach a tipping point beyond which sustainable utilization is impossible. The continuous expansion of uncontrolled agriculture, environmental degradation and extractive industries threatens freshwater and marine biodiversity. Addressing these emerging and persistent threats demands comprehensive water resource management and planning, coupled with extensive investment in climate-resilient water infrastructure. Improving the management and utilization of Kenya's rich and diverse aquatics resources will boost both growth and development in key sectors of the blue economy, such as fisheries, tourism, wave and wind energy production and bioprospecting. To safeguard the ecological integrity of freshwater and marine resources in Kenya, it is not only necessary to cease loss and degradation, but also to restore and remediate terrestrial and aquatic ecosystems. These efforts must be transboundary and support the development and implementation of landscape-level initiatives that help maintain connectivity and the health of freshwater ecosystems, ecological functions, and conserve and restore the heterogeneous biomes and their biodiversity while improving livelihoods and generating new economic activities.

See Also: Social/societal values of Inland waters: Watershed Management in Kenya; Societal Implications, Drivers of Change and Governance Needs

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Watershed Management in Kenya; Societal Implications, Drivers of Change and Governance Needs

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Catherine Febria and Gail Krantzberg.

Glossary

Catchment area The area of land bounded by watersheds draining into a river, basin or an ocean.
Conservation The care and management of a resource so that the resource maintains its ability to fulfill its functions and provide goods and services for present and future generations.
Drainage basin An area of land drained by a river and its tributaries (river system). It includes water found in the water table and surface run-off.
Ecosystem A geographic area consisting of all the organisms, as well as the non-living components of the environment with which the organisms interact, such as air, soil, water, and sunlight.
Headwater Watershed Upstream area that drains low-order streams to the main river channel.
Invasive species Non-native (or alien) species to the ecosystem under consideration and whose introduction causes or is likely to cause economic or environmental harm or harm to human health.
Land use Characterization of land based on human activities commonly practiced in a region (geographical area).
Sustainable management Present use of the environment or natural resources which does not compromise the ability to use the same by future generations or degrade the carrying capacity of supporting ecosystems.
Terminus Watershed The discharge or outflow area that drains the river system into a basin or an ocean.
Watershed An area of land that drains all the streams and rainfall to a common outlet.

Introduction

Watersheds are biophysical systems defining the land surface that drains water and waterborne sediments, nutrients, and chemical constituents in a stream channel, river, lake, or ocean specified by topographic boundaries (Brooks et al., 2012). They are the systems used to study the biogeochemical and hydrologic cycles in a region and make inference on the impact of human activities on terrestrial and aquatic ecosystem processes, structure and function. They support diverse lifeforms and are important habitats for both terrestrial and aquatic species.

Watersheds are described and mapped according to their position in the landscape, whereby, the catchment at the upper-most and unbranched streams are called headwater watersheds while at the river-outflow point are called the terminus watersheds (Duan et al., 2018). Depending on the stream size, they can be described as first order, second order or n-th order watershed. Consequently, large watersheds are a collection of many small watersheds, and every sub-catchment within a river basin is considered a watershed. The sub-catchments form local sites for river influences, socio-economic activities and anthropogenic influences that arise from various drivers of ecosystem change.

There are two categories of drivers of ecosystem change in watersheds; indirect and direct drivers. Indirect drivers include socio-economic and demographic factors affecting resource utilization, technological factors resulting in environmental degradation and cultural and government influences that affect values and decision framework on governance. In contrast, direct drivers impact on ecosystem processes and include pollution, resource exploitation, invasive species, and climate change and land-use effects among others. Major direct drivers of ecosystem change such as land-use are inextricably linked with indirect drivers. For instance, land cover conversion for agricultural use through deforestation can be linked to socio-economic and demographic

Table 1 Socioeconomic and environmental impact of land use change.

Land use change	*Socioeconomic impact*
Conversion of farmland and forests to urban development	Reduced land for food, timber, local agricultural economy, open space and environmental amenities
Agriculture and deforestation	Soil erosion, salinization, desertification, and other soil degradations hence reduced soil quality and agricultural productivity
Urban development	Organization of society, encroached rural communities, income segregation and economic disparities among communities
Land use regulations curbing development	Hinder function of market forces

Land use change	*Environmental impacts*
Agricultural run-off	Water pollution
Draining wetlands for crop production	Biodiversity loss, water diversion
Intensive farming and deforestation	Soil erosion, salinization, desertification, and other soil degradations
Deforestation	Greenhouse effect, destroys habitats that support biodiversity, affects the hydrological cycle and increases soil erosion, runoff, flooding and landslides
Urban development	Air pollution, water pollution, and urban runoff and flooding
	Habitat destruction, fragmentation, and alteration, biodiversity decline and species extinctions

Modified from Wu J (2008) Land use changes: Economic, Social, and Environmental Impacts. *Choices, Agricultural and Applied Economic Association* 23(4): 6–10, https://www.choicesmagazine.org/magazine/article.php?article=49.

changes, urbanization or settlements associated with technological developments, and change in the management of ecosystem or spatial configuration of the ecosystem affected by cultural and government influences. In this regard, land use change is a contributor to global societal challenges such as food security, climate change and biodiversity loss.

Even though land use change is necessary and essential for economic development and social progress, its socioeconomic and environmental impacts are evident (Table 1). In the last six decades, it has affected approximately a third of the global land area, especially, through deforestation and agricultural expansion in the tropics (Mwangi et al., 2015; Winkler et al., 2021). Land use is an important driver of hydrological and ecological changes (Lin et al., 2015) and has caused shrinking and fragmentation of watershed resources and modification of their natural landscapes (Rogger et al., 2017) thus impacting catchment run-off, drought and flooding. Land management practices have major influence on watershed resources including water, soil, air, nutrients, plants, and animals (Wu, 2008), with worrying trends in the developing countries (Xiong et al., 2017) where weak governance of natural resources (Arthur, 2014) and challenges with implementation of policy, institutional and legal framework are escalated by increasing population and overdependence on natural resource as primary source of livelihood.

Strengthening policy, institutional and legal frameworks and implementation of good governance for watershed resource serve as precondition for the successful watershed management and interventions especially in developing countries. This requires understanding of the hydrological basins at the watershed scale and their intersection with local populations through informed studies. We therefore review and analyze watersheds in Kenya with regards to human activities, drivers of ecosystem change, legal, policy and institutional frameworks and map land-use systems at national scale to depict the rich values of these ecosystems, their need for sustainable management and lessons to learn from a developing country grappling with conflicts between resource use demands and conservation.

Kenyan drainage basins

Kenya has five major drainage basins that water the whole country, namely, Lake Victoria, Athi, Tana, Rift Valley and Ewaso Ng'iro/Nyiro (Fig. 1), covering 8%, 11.5%, 21.7%, 22.7%, and 36% of the country, respectively (Seegers et al., 2003; Nyingi et al., 2013). They describe and depict a variety of watershed characteristics. Their headwater watersheds originate from tropical and montane rainforests in central and western parts of the country and flow eastwards to the Indian Ocean, northwards to Lake Turkana and south west into Lake Victoria (Fig. 2A). Their midstream are endowed with national parks, national reserves and conservancies teaming with terrestrial and aquatic biodiversity, while the terminus watersheds or river-outflow points that discharge into transboundary lakes or the ocean (Fig. 2B). These natural assets play a critical role in the achievement of socio-economic and ecological development in the country. They are exceptional geographical features, rich in biodiversity and endemic terrestrial and aquatic species supported by various habitats; from montane and afro-alpine highlands, forests, grasslands, rangelands to lakes, rivers, wetlands and marine environments that provide a wide variety of niches for many different species (Western et al., 2015). Like many tropical ecosystems, they are ecologically rich and with evidence of complex biotic interactions (Western et al., 2015) with fascinating theories (time, climate stability, spatial heterogeneity, competition, predation and productivity hypotheses) explaining these exclusive reservoirs of much of the world's biodiversity (Pianka, 1966; Sodhi et al., 2010; Schemske and Mittelbach, 2017).

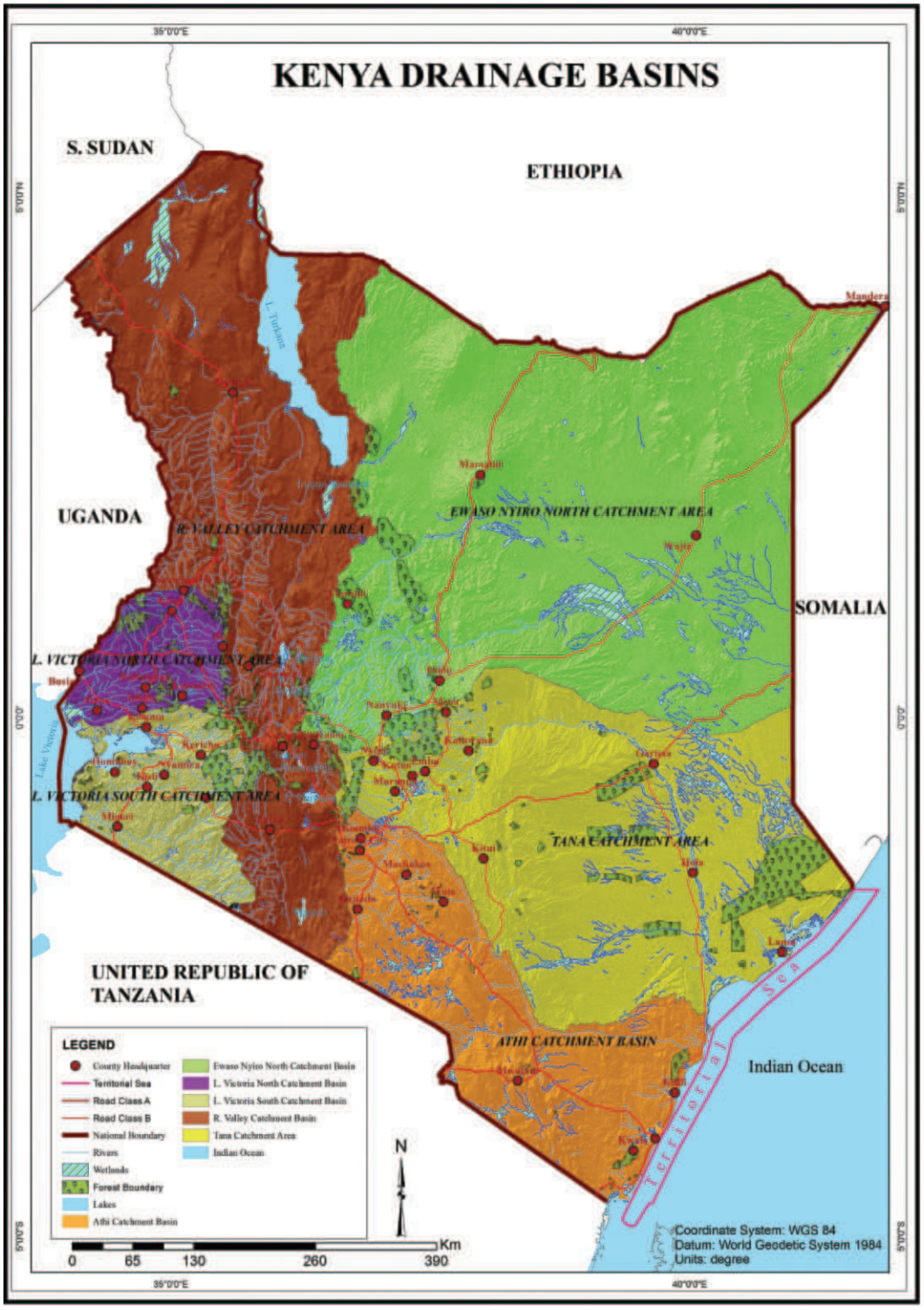

Fig. 1 Kenya's Drainage basins.

The five drainage basins differ in their environmental and socioeconomic characteristics and benefits. Ewaso Ng'iro (Fig. 2A) exhibits physical, socioeconomic and ecological diversities with high temporal and spatial variability in rainfall and has one of the steepest ecological gradients in water flow regime and temperature variations in East Africa (Kiteme et al., 2019; Providoli et al., 2019). A small fraction of the basin at the slopes and foot of Mount Kenya receives constant, periodic and reliable rainfall with fertile land for agriculture, but the rest of the basin is arid and semi-arid land with seasonal river flow and frequented by drought. Tana and Athi basins originate from Mount Kenya and Aberdare forests with fertile agricultural land at the headwaters. Athi stretches

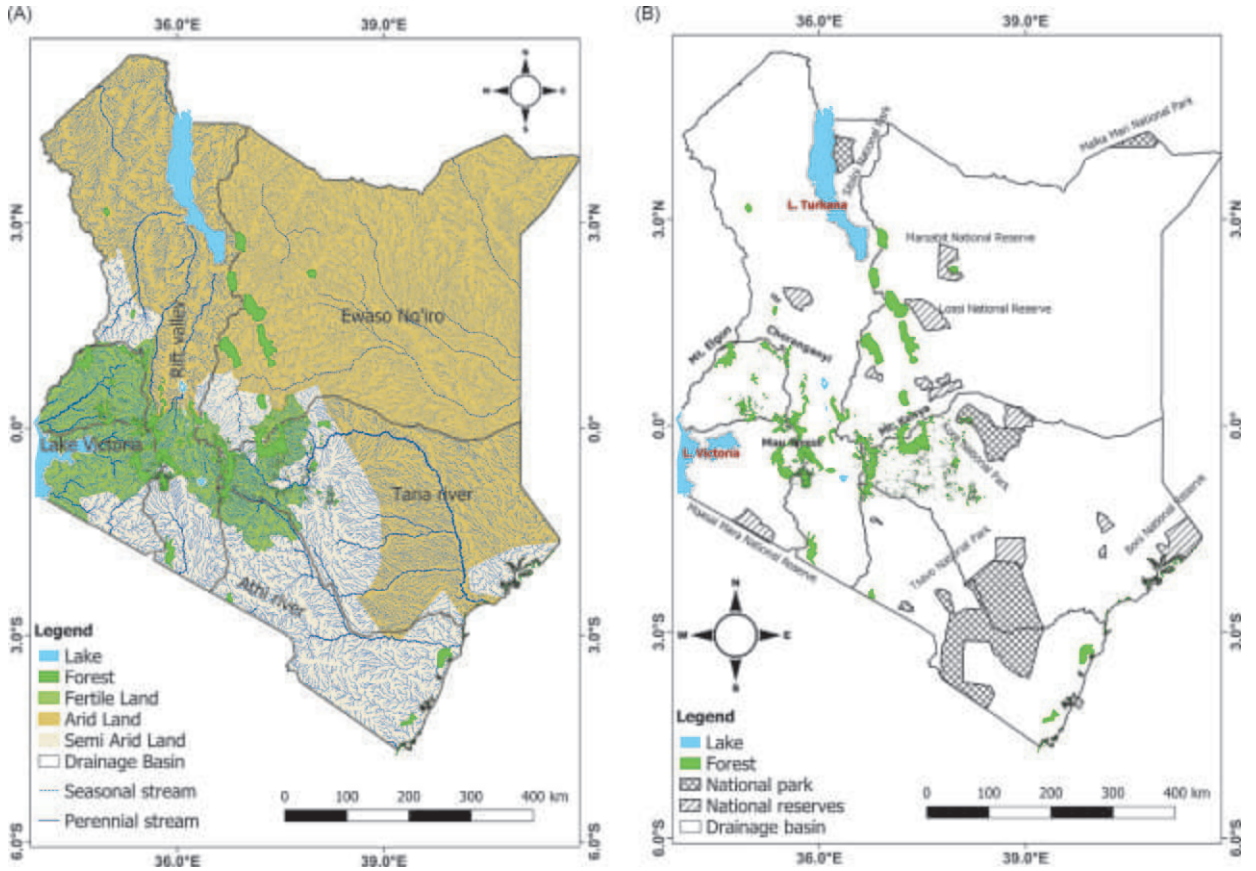

Fig. 2 Kenya landscape (A) land cover and (B) protected areas.

through semi-arid land into the ocean while Tana basin traverses both semi-arid and arid land (Fig. 2A). The two basins not only host over 40% of the Kenyan population with major dams and irrigation schemes (Langat et al., 2019), but also largest protected areas such as national parks and reserves in the plains (Fig. 2B), dominated by grassland (Tamooh et al., 2014; Marwick et al., 2018). The Rift valley basin exhibits high temporal and spatial variability in rainfall. Its headwaters originate from the Cheranganyi, Mau and Aberdare forests with fertile agricultural land and extends northwards into arid land before draining into Lake Turkana and southwards through semi-arid land into Lake Natron (Fig. 2A). The basin attracts birdwatchers due to the string of alkaline lakes which attracts flamingos, pelicans, and many other species. Lastly, the Kenyan side of the Lake Victoria drainage basin stretches through fertile agricultural land into the second largest freshwater lake globally, except the mid-stream of Mara River basin which is a semi-arid area bordering Tanzania and within the Maasai Mara National Reserve. The headwaters of Lake Victoria basin originate from Mount Elgon, Kakamega, Cheranganyi and Mau Forests (Fig. 2A). The region is considered as the food basket for the country since it is very productive, but also is a densely populated basin, with more than 500 persons per square kilometer (World Bank, 2016; Sayer et al., 2018; Olaka et al., 2019).

Land use in Kenyan watersheds

The headwaters through terminus watersheds for the five drainage basins have experienced fundamental environmental and ecological changes especially due to change in land use and land cover (Krhoda, 2006; MEMR, 2012a, b) with majority of the land being pastoral in the semi-arid zones and agricultural in the humid zones (UNEP, 2009). Average land area under cultivation has increased over the last decades as a result of clearing forests, farming in marginal lands and conversion of humid rangeland to farmlands causing an increase in competing land uses including forestry and wildlife conservation, new cultivation methods and cropping systems as well as the introduction of irrigation schemes, sedentary farming and livestock management (UNEP, 2009). Competing land uses is compounded by the fact that over 89% of the country is Arid and Semi-Arid Land (ASAL) occupied by roughly 38% of the country's population (Republic of Kenya, 2012; Bedelian et al., 2019), while the remaining 11% being non-arid land occupied by more than half (62%) of the country's population, and mostly under agricultural activities. The country depends on agriculture as its primary source of income; consequently, direct and indirect contribution of agriculture accounts for 51% of Kenya's GDP, 60% of employment and 65% of exports (Birch, 2018; World Bank Group, 2018). Agriculture also supports about 80% of Kenyan population (UNEP, 2009).

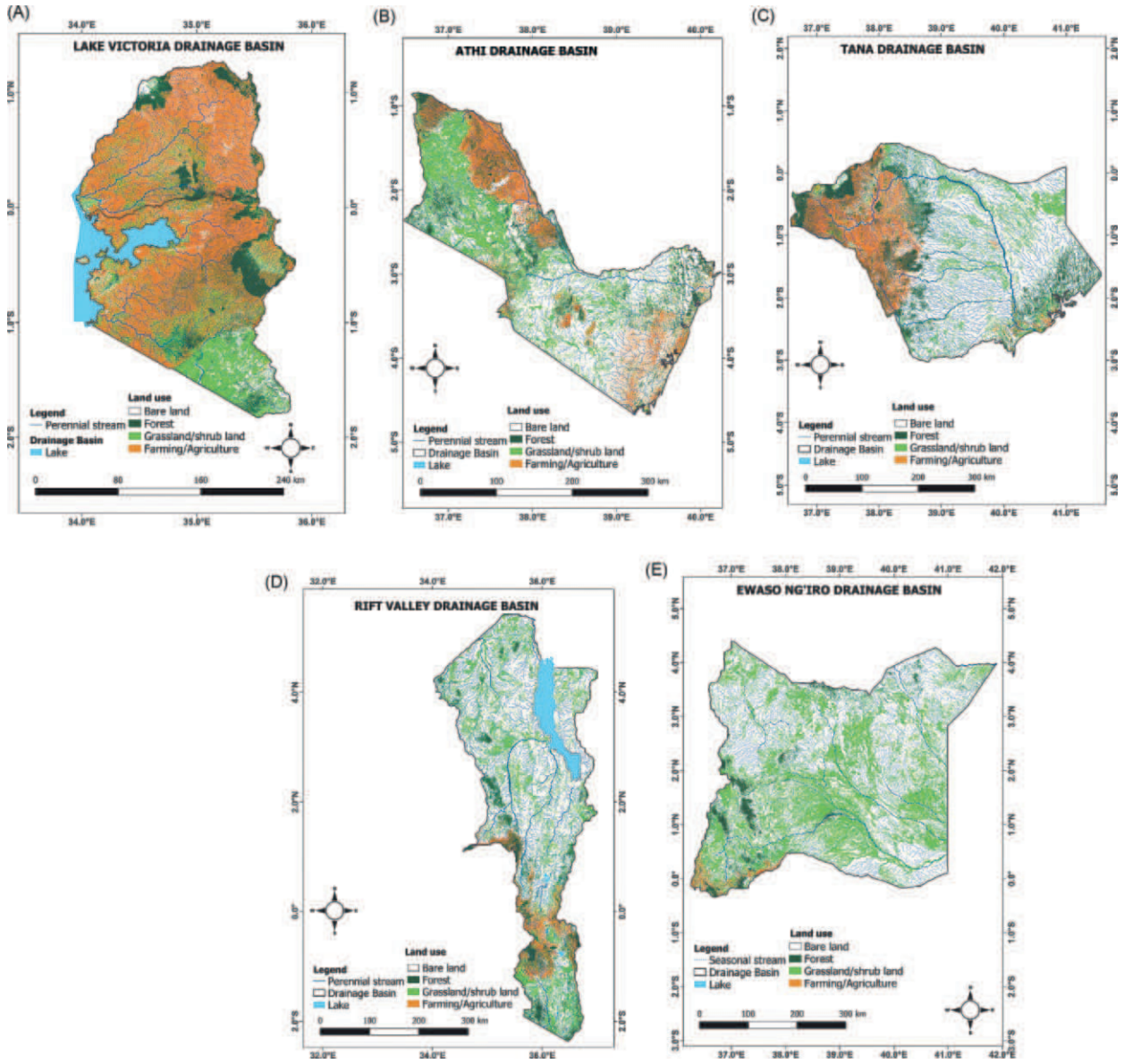

Fig. 3 Agricultural land use patterns at Kenyan drainage basins (A) Lake Victoria, (B) Athi river, (C) Tana river (D) Rift valley and (E) Ewaso Ng'iro.

Most of the agricultural production (subsistence and commercial) is concentrated at the headwater watersheds of the five drainage basins (Fig. 3) thus impacting downstream water availability for different uses. Agricultural production ranges from small- and medium-scale cultivations to mechanized large-scale cultivation systems, characterized by the high use of fertilizers, pesticides and herbicides, as well as supplementary irrigation. Agricultural activities are mostly concentrated (i) throughout the Lake Victoria basin (Lake Victoria Basin Commission and GRID-Arendal, 2017; Achieng et al., 2021) with the largest proportion of agricultural activities (Fig. 3A), (ii) at the upper and mid reaches of Athi and Tana basin (Kauffman et al., 2014; Langat et al., 2019) with considerable proportion of agricultural land use (Fig. 3B and C) and (iii) upper Rift Valley (Kuiper and Greiner, 2021) and Ewaso Ng'iro basins (Lanari et al., 2018) with the least proportion of agricultural practice (Fig. 3D and E). Athi and Tana basins also have many irrigation schemes and major hydropower stations resulting in competing water demand and scarcity (Langat et al., 2019) while Rift Valley and Ewaso Ng'iro basins are largely bare arid land with seasonal rivers (Fig. 3D and E).

Impact of land use and drivers of ecosystem change

Kenya has seen rapidly growing populations over the last six decades, from 10.9 million in 1969 to 47.6 million in 2019. The population is youthful (75.1%), largely rural (68.9%) and depends on natural resources for livelihoods (KNBS, 2019). Majority of

the population lives within the non-arid land and around the forests at the drainage basins, consequently impacting on land use and causing pressure on watershed resources (Table 2). At the headwaters and forested land, deforestation, forest degradation and encroachment are driven by (i) agricultural extension subject to population pressure, rural poverty, and limited alternative sources of income, (ii) excision, resulting from poor governance, political interference, and weak institutional capacity to protect forested land, (iii) wood extraction for commercial logging and extraction of forest products for subsistence and income, (iv) livestock grazing, and (v) infrastructural development (Ongugo et al., 2014; Achieng et al., 2017).

Drivers of land use change at the midstream to terminus watersheds vary with the drainage basins but range from settlements, urbanization, damming and hydropower production, pastoralism, mining, conversion of wetlands into farmlands (Table 2) and a multitude of other emerging demands on watershed resources (Mulinge et al., 2016) which has led to water crisis of unprecedented scale at the arid land and downstream of the basins (Wamuyu, 2014; Schilling et al., 2012; Providoli et al., 2019). Furthermore, increased competition and conflicts between different user groups, namely large-scale commercial farms, smallholders, pastoralists, large-scale ranchers, and wildlife conservation among others, result in water scarcity, degradation, human encroachment, illegal abstraction and overexploitation of watershed resources (Table 3). Consequently, the amounts of land in the agriculturally productive highlands and the productivity of these lands are declining due to growing populations and other socio-economic variables (poverty, knowledge, attitudes and perceptions, culture and gender imperatives).

Transboundary issues are also growing in importance since all of the drainage basins are shared resource with neighboring countries such as Ethiopia, Somalia, Tanzania and Uganda. Catchment activities in one country impact on resources in another. In most of the region, rapidly evolving socio-economic dynamics are propelling demand upstream, which in turn is threatening downstream supplies. The impacts and potential remedies are even more complex when watershed resources are shared internationally. A major complexity faced at the basins is that watershed management and governance processes take place at different spatio-temporal scales and societal levels which involve a multitude of actors. The societies in these regions have to find sustainable sub-basin management solutions; however, the decisions they make impact on others far away. Connection between social and institutional development, the available information base, legal requirements and policy development processes should be smoothly weaved to support each other for informed decision-making and effective action in the watersheds.

Policy, legal and institutional framework

Implementation of good governance for watershed resources serves as a precondition for the successful watershed management and interventions. In Kenya, the promulgation of a new constitution in the year 2010, anchored on sustainable development, rule of law, and protection of ecologically sensitive areas and devolution of power and resources, led to review and alignments of laws and policies, as well as creation of new institutions and structures for watershed governance. The Constitution established two levels of Governments: National and Counties with clear functions though with mutual interactions and intergovernmental structures to ensure smooth operations and dispute resolution between the two levels of Governments. Devolution aims to facilitate the involvement of stakeholders and enhance public participation at different levels of the watershed and sharing of resources (including power) in relation to natural resources management, especially at the grassroots-level. Thus, in Kenya, Natural resources management function is therefore a concurrent jurisdiction between National and County Governments as espoused in the Fourth Schedule of the Constitution as well as Articles 6(1) and Article 185 (2) & 186 (1) for County and National Governments respectively. The two-tier governmental functional boundary is also provided in Article 187 (2) of the Constitution of Kenya 2010.

Government Ministries in watershed management include Ministries in charge of Water, Sanitation and irrigation; Agriculture, Livestock, Fisheries and Cooperatives; Wildlife and Tourism; Environment and Forestry (that hosts Climate Change Directorate); and Petroleum and Mining operating at national level, among others (Table 4). All these sectors are mirrored (replicated) at the county-level, and require capacity strengthening by the National Government (human, financial and technological capacity) for their proper functioning, in line with function Number 32 of the National Government under the Constitution. It is also important to note that within each of these line ministries, there are a number of Semi-Autonomous Government Agencies (SAGAs) and independent Constitutional Commissions and offices that work closely with the ministries in discharging the relevant natural resources management and development mandates.

Other institutions, especially State cooperations such as Kenya Forest Service, Kenya Wildlife Service, Kenya Water Towers Agency, National Environment Management Authority and Kenya Fisheries Service as well as National Land Commission are also involved and have a major stake in conservation, development, and sustainable management of the terrestrial and aquatic resource in the watersheds (Mwangi et al., 2015) from the National to the Community level. For instance, the institutional framework for Water Sector under Water Act 2016 is shown in Fig. 4 (Puzyreva and Roy, 2018).

However, governance in watershed management still faces major challenges including data sharing, overlapping functions and responsibilities between or among state cooperations, inadequate funds for cutting-edge research to inform policies and regulations, or limited skilled personnel and shortage of essential facilities. Other challenges include perennial conflicts among different communities, especially pastoralists in drylands experiencing little rainfall and water shortage, and change in land cover in agriculturally productive land. The drainage basins also traverse many county governments that exhibit physical, socioeconomic and ecological diversities hence varying watershed management (priorities as well as conflicts) at community level within a watershed.

Table 2 Major land use and drivers of ecosystem change at the drainage basins.

Basin and Basin area (sq. km.)	*Major land use*	*Pressure*	*Impact*
Lake Victoria North 32,384 sq. km. Lake Victoria South 18,613 sq. km.	Fishing, large-scale farming, Mining, harvesting papyrus reeds, brick making, forestry, pastoralism, conservation, national reserve, tourism and recreation, irrigation, power production/energy, water supply, national reserve, artisanal products	• Inappropriate land use and overutilization • Conversion of wetlands to agricultural land • Unsustainable exploitation of resources • Land subdivision and fragmentation	• Pollution • Loss of land cover • Invasive species • Reduced water quantity and quality • Loss of biodiversity • Flooding • Reduced fisheries
Rift Valley 138,459 sq. km.	Conservation, mining, fishing, forestry, pastoralism, energy- geo and hydropower, ranching, irrigation, tourism and recreation,	• Urbanization • Inappropriate land use • Conversion of land for agriculture • Unsustainable exploitation of resources • Increased demand for resources • Land subdivision and fragmentation	• Pollution • Soil erosion/siltation • Loss of land/forest cover • Overgrazing • Reduced quantity and quality of water
Ewaso Ng'iro 213,731 sq. km.	Large scale commercial farms, pastoralism, ranching, wildlife conservancies, oil and gas exploration, forestry, grazing, water supply, fish farming, tourism	• Inappropriate land use • Overutilization of water • Conversion of land to agriculture • Overstocking of livestock • Settlements • Loss of catchment forests • Increased demand for resources • Reduced water levels • Land subdivision and fragmentation	• Pollution • Soil erosion/siltation • Overgrazing • Reduced water volume
Tana 120,925 sq. km.	Large scale farming, conservation, irrigation, pastoralism, mining-sand, fishing, quarrying, forestry, hydropower generation, recreation, water supply	• Inappropriate land use • Overutilization of water • Conversion of land to agriculture • Overstocking of livestock • Settlements • Loss of catchment forests • Increased demand for resources • Reduced water levels • Land subdivision and fragmentation • Damming	• Pollution • Soil erosion/siltation • Overgrazing • Reduced water volume • Loss of critical habitats and species • Reduced hydrological capacity • Increased river salinity as a result of damming • Reduced fisheries production
Athi 67,337 sq. km	Wildlife conservation area (Nairobi National Park Amboseli, Tsavo East and Tsao West, Shimba Hills), industrial use, farming (subsistence and commercial), pastoralism, livestock ranching, limestone, fishing, forestry, energy-wind and thermal water supply, natural conservation and recreation, irrigation, sand harvesting, dry season grazing, cultural and spiritual use, watering points for livestock, wastewater treatment, fishing	• Over-exploitation of surface and groundwater resources • Wetland resource degradation • Unregulated diversions of river channels • Catchment degradation due to overgrazing and sand harvesting • Land use changes for settlement and agriculture • Climate change and variability	• Acute water scarcity due to high water demand • Limited ground water recharge • Changing river regime • Pollution of water resources from industrial effluents, and agricultural and domestic waste

Modified from MEMR (2012a) *Kenya Wetlands Atlas*. Nairobi, Kenya: Ministry of Environment and Mineral Resources, https://na.unep.net/siouxfalls/publications/Kenya_Wetlands.pdf.

Watershed governance

Legal and institutional frameworks play a key role in sustaining environmental goods and services at the watershed scale. They act as both carrot and the stick for effective governance, especially in enhancing natural resources stewardship. While polices are tied to politics, having strong policies does not necessarily translate into sustainable watershed resources management, if (political) goodwill is lacking at national and subnational (county and ward) levels. Goodwill fosters effective implementation and ensures resourcing for specific actions for green growth, resilient economies and ecosystems. Equally, policies and legislative regimes that give birth to strong institutions to regulate human behavior on ecosystems and watershed resource use and interactions, are key to sustainable development. This is core in setting good governance principles relating to sustainable watershed resources use, equity and equality, rule of law, access to and control of resource as well as conflict management.

Table 3 Water management challenges in Kenyan drainage basins.

Drainage basin	*Primary challenges*
Athi	Acute water scarcity due to demand exceeding availability
	Pollution of water resources from agro-industries and waste disposal
	Catchment degradation due to overgrazing and sand harvesting
	Over-exploitation of surface and ground water resources.
Ewaso Ng'iro	Acute water scarcity due to demand exceeding availability
	High salinity of groundwater in certain areas underlain by basement rocks and colluvial deposits
	Catchment degradation due to overgrazing, poor farming practices and encroachment into wetland areas.
Lake Victoria	Degradation of water resources from both point and non-point sources of pollution
	Catchment degradation through soil erosion, siltation, landslides, deforestation, destruction of springs and human encroachment into the watershed
	Depletion of water resources through planting of exotic trees
	Frequent flooding along the shores of Lake Victoria.
Rift Valley	Degradation of water resources from both point and non-point sources of pollution
	Illegal abstractions and over-exploitation
	Quarrying and mining along river banks
	Human encroachment into and destruction of the watershed.
Tana	Acute water scarcity
	Degradation of water resources from both point and non-point sources of pollution
	Catchment degradation in Mount Kenya and the Aberdare Range slopes, soil erosion and overgrazing in the lower parts of the region
	Human encroachment into the watershed
	High salinity of ground water (due to salt water intrusion) in the lower Tana due to over-exploitation
	Increased water resource demand owing to urbanization and industrialization.

Modified from MEMR (2012a) *Kenya Wetlands Atlas*. Nairobi, Kenya: Ministry of Environment and Mineral Resources, https://na.unep.net/siouxfalls/publications/Kenya_Wetlands.pdf.

Local community participation and involvement in sustainable utilization of resources within watersheds are also very important, especially where the resource is the primary source of income and food (livelihood). Conflicts between resource use demands and conservation are evident due to rare alternative source of livelihoods. Community participation and involvement enables local people to identify and prioritize their environmental problems accurately, ensure efficient resource allocation, promote greater respect for decisions made with local inputs such as rules for resource use, allow for easier monitoring of resource use and give marginalized and vulnerable groups greater influence on local policy (Larson, 2003).

Understanding of hydrological basins at the watershed scale and their intersection with local populations for effective conservation and management of the landscapes and the natural resources is extremely important. This is only possible with well formulated studies on the landscape with integration across disciplines and involving the community within the watershed as well as the incorporation of technological advancements into watershed management. Cutting-edge research to inform governance is currently weak due to limited skilled human resource in the region. Very few studies exist on assessment, monitoring, mapping and modeling of these ecosystems to correlate them with the socioeconomic and geo-political imperatives to establish impacts and ecological changes. This disconnect and lack of intersection analysis, is possibly the genesis of all the challenges in Kenyan watersheds. Natural resources including watersheds are still managed with the traditional 'conservationist' approaches, giving little attention to social, economic and political dimensions – the key good governance ingredients - in land-based resources management and development.

Conclusion

Kenyan watersheds are rich ecosystems supporting diverse aquatic and terrestrial communities. The fertile lands flourish with human population practicing subsistence and commercial agriculture while, the arid and semi-arid land is populated with pastoralists and wildlife. Change in land cover, especially due to agriculture and deforestation are the major socioeconomic and environmental drivers of ecosystem degradation. Their impacts on the watershed include pollution, soil erosion, siltation, loss of land cover, reduced water quality and quantity, reduced hydrological capacity, acute water scarcity, biodiversity loss and loss of critical habitat among others. Despite the established policies, legal and institutional instruments and infrastructure, with improved governance in watershed resource due to decentralized government and devolution that facilitates the involvement of stakeholders and enhances public participation at different levels of the watershed management; skilled human resource and cutting-edge research are still imperative in understanding the hydrological basins at the watershed scale and their intersection with local populations for their effective conservation and management.

Table 4 Policy, legal framework and institutions involved in watershed governance in Kenya.

Policy	*Legal Framework*	*Governance on Water Catchment*	*Institution*
	The Constitution of Kenya 2010	The supreme law that guides human development, environmental and land-resources management and conservation in the Country. It facilitates justice and entrenches the protection of human rights (in all forms including social, cultural, environmental and political) for purposes of achieving ecologically sensitive development and use of natural resources	Government of Kenya (GoK)
Forest Policy 1968; Forest Policy 2020	The Forest Act 2016	This law guides and coordinates actions toward development and sustainable management, including conservation and rational utilization of all forest resources for the socio-economic development of the country areas.	Ministry of Environment and Forestry/Forest Service (KFS)
Water Policy Sessional Paper I of 1999; Sessional Paper No 1 of 2021	Water Act 2016	Provides the legal and institutional framework as well as action plan for coordinating sub-sectors in water resources development and management	Ministry of Water & Sanitation and Irrigation
Several (draft) policies	Agriculture Act (Cap 318; rev 2012)	Seeks to promote and maintain a stable agriculture, and guide conservation of soil and its fertility and to stimulate the development of agricultural land in accordance with the accepted practices of good land management and good husbandry.	Ministry of Agriculture, Livestock, Fisheries & Co-operatives
The National Wildlife Policy 2020	Wildlife Conservation and Management Act 2013	This guides the country toward securing a healthy and resilient wildlife, Kenya's heritage, by providing efficient and effective policy, legal and institutional framework for the conservation and management of Kenya's wildlife resources	Ministry of Environment and Forestry
		framework for the conservation and management of Kenya's wildlife resources including habitats/ecosystems	Kenya Wildlife Service (KWS)
	County Governments Act No 17 of 2012	Specifies the functions, powers and responsibilities of, and that guide, County Governments in service delivery including those that relate to natural resources/watershed management	County Governments
Sessional Paper No 7 of 2016 on Mining and Mineral policy	Mining Act 2016	Vests mineral resources under the custodianship of the National Government and guides all mineral operations and development in all land categories such as parks and forest reserves in Kenya	Ministry of Petroleum & Mining
	Regional Development Authority Acts	Facilitates basin-based regional planning, socio-economic and ecologically resilient development	Regional Development Authorities
Session Paper 6 of 1999	EMCA Act No. 8 of 1999 (amended in 2015)	This is the motherboard/main framework law that guides and co-ordinates activities related to the management and conservation of the environment including natural resources such as wetlands and riparian lands	Ministry of Environment and Forestry/ National Environmental Management Authority
	Fisheries Management and Development Act No 35 of 2016	Promotes and coordinates activities relating to conservation, management and development of fisheries and other aquatic resources to enhance the livelihood of communities' dependent on fishing. It establishes the Kenya Fisheries Services	Ministry of Agriculture Livestock, Fisheries & Co-operatives
Sessional Paper No 3 of 2009 on the National Land Policy	Land Act No. 6 of 2012 (rev 2016); National Land Commission Act No 5 of 2012 (rev 2015); Community land Act No 27 of 2016 and Land Registration Act No 3 of 2012	These are the main laws governing land in Kenya that foster the realization of sustainable land and natural resources management and administration including the protection of ecological sensitive areas such as wetlands, riparian lands, water catchment areas, forests and biodiversity hotspots.	Ministry of Lands and Physical Planning and the National Land Commission

Modified from MEMR (2012b) *Masterplan for the Conservation and Sustainable Management of Water Catchment Areas in Kenya Ministry of Environment and Mineral Resources*, https://www.preventionweb.net/files/34692_conservationmasterplanfinal.pdf.

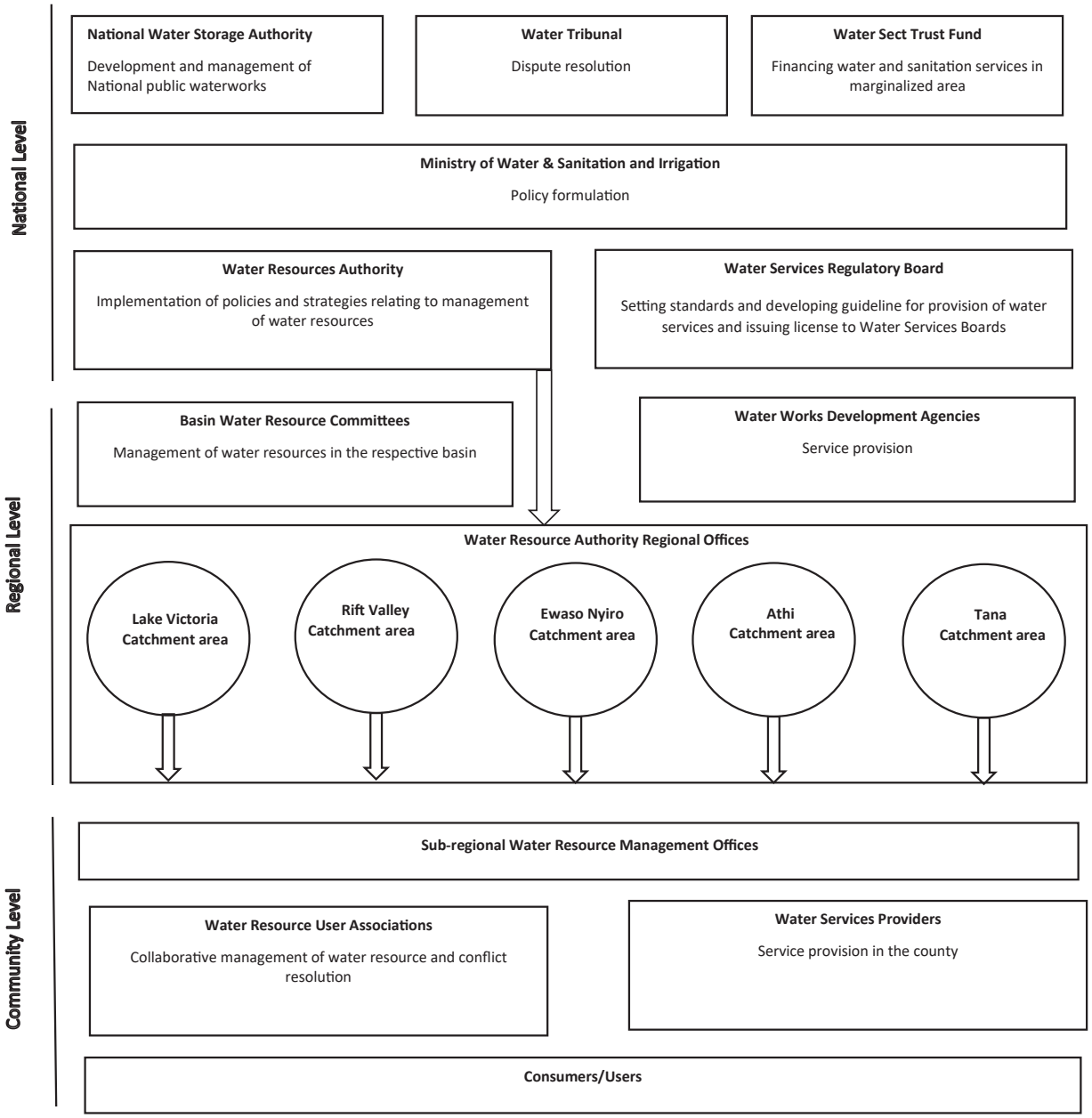

Fig. 4 Institutional framework for water sector under the Water Act; 2016. Modified from Puzyreva M and Roy D (2018) *Adaptive and Inclusive Watershed Management*. International Institute for Sustainable Development. https://www.iisd.org/system/files/publications/adaptive-inclusive-watershed-management-kenya.pdf.

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Societal Values of Inland Fishes

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Catherine Febria and Gail Krantzberg.

Glossary

Artisanal fishery A community- or household-based fishery that is part of the local tradition and often uses traditional methods for capture. Artisanal fisheries differ from large-scale commercial fisheries in that the harvest levels are low with small amounts of capital invested and simple technology. They have small or no fishing vessels, operate from or close to shore, and harvest mainly for local trade and consumption. Often synonymous with small-scale fishery.

Commercial fishery A fishery where harvest enters a market-based system to be traded or sold. It can be economically valued more easily and is often part of a value-added supply chain.

Environmental flows The water quantity, quality, and flow regime required to sustain freshwater and estuarine ecosystem integrity and derived social benefits. Also known as e-flows.

Flow regime The temporal changes of flow within a river or stream, including the predicted pattern for low and high flows as well as the magnitude, duration, and rate of change of water levels. Factors that influence a flow regime are rain, snow melt, watershed size, geology, land and water use, and vegetation type.

Freshwater biodiversity The variety and variability among living organisms found in and around freshwater ecosystems, measured within and among species, and within ecosystems.

Inland fishery A fishery operating in inland waters for food, income, or recreation which may or may not involve harvest.
Inland waters Land-locked waters, including lakes, ponds, rivers, streams, creeks, springs, canals, reservoirs, and wetlands.
Recreational fishery A fishery where the principal motivation is recreation, tourism, or sport (i.e., competition). It may or may not involve harvest.
Small-scale fishery A fishery with simple technology. Typically, harvest is locally traded and consumed. Often synonymous with artisanal fishery.
Subsistence fishery A fishery where harvest is consumed by fishers, their families, or shared with others without formally entering a market or commercial economy. Often found in communities that rely on fish as their main source of nutrition; almost exclusively small-scale and artisanal.
Water quality A measure of the chemical, physical, and biological condition of water, usually with respect to a particular use.
Water quantity A measure of the amount of water in a system, typically expressed in terms of total yield and flow regime (pattern) over a specified amount of time.

Introduction

Inland fishes and freshwater biodiversity are all around us. The vast majority (87.5%) of human populations live within 3 km of a river (Kummu et al., 2011); yet, the societal value of inland fishes and aquatic biodiversity is often neglected. Perhaps this is because inland fishes and freshwater biodiversity are 'out of sight, out of mind,' just below the water's surface. Or perhaps, because inland waters have been so integrally tied to the rise of human civilizations, the societal value of resources within or supported by these systems is taken for granted. This neglect cannot discount the significant contributions these services provide (Table 1). Inland waters are home to more than 50% of all fish species (>18,000 species), more than 25% of all vertebrate species (Fricke et al., 2020). Inland fisheries employ approximately 60 million people as fishers and in post-processing jobs (over 50% are women; FAO, 2018). More than 90% of inland capture harvest is for human consumption and 43% comes from low-income food-deficit countries, where fish provide vital micronutrients and animal protein to communities that have few alternative sources (Funge-Smith, 2018). Inland fisheries have an estimated economic value of up to USD 122 billion, which is compounded when the value is weighted by the local gross domestic product (Funge-Smith, 2018).

This chapter seeks to explicitly acknowledge the immense societal value of inland fishes through examination of the human benefits of conservation and sustainable management of inland fishes and their ecosystems. These benefits can be broadly categorized into nine societal services: 1. Livelihoods and subsistence income; 2. Commercial income; 3. Food and nutrition; 4. Recreational services; 5. Cultural services; 6. Educational and scientific opportunities within fisheries; 7. Biodiversity and ecosystem function; 8. Regulation and indicator of freshwater quality; and 9. Regulation of freshwater quantity and natural flow regimes (Fig. 1). Around the globe, these services vary in their relative importance to different communities (Fig. 2). For instance, inland fisheries provide critical contributions to food security and nutrition in certain regions and recreational opportunities in others.

The natural environments that support these services are under extreme threat. Freshwater ecosystems are considered the most endangered in the world (Tickner et al., 2020 and references therein). Of the 29,500 freshwater dependent species so far assessed for the International Union for Conservation of Nature (IUCN) Red List, 27% are threatened with extinction. Freshwater species display very high levels of endemism, meaning they are often only found in one location, which may increase their risk of extinction (Collen et al., 2014). Major threats include: habitat degradation, flow modification, water pollution, overexploitation, invasive species, disease, hydropower development, and climate change (for more comprehensive discussions, see Dudgeon et al., 2006; Reid et al., 2018). While most of these drivers are external to inland fishes and freshwater biodiversity, tensions among societal services can also arise and threaten derived benefits, as different stakeholder groups prioritize different services. Typical key stakeholders in inland waters include recreational and commercial fishers, consumers of freshwater fish, community members who utilize freshwater

Table 1 Selected statistics on global inland fisheries and biodiversity summarized from Funge-Smith (2018), Funge-Smith and Bennett (2019), FAO (2020), and Fricke et al. (2020).

Catch	
Total annual catch	12.0 million tonnes (12.5% of total global capture fishery production)
Proportion for human consumption	>90% of total inland fishery capture harvest
Harvest from Low-Income Food-Deficit countries	>43% of total inland fishery capture harvest
Economic value	
Estimated economic value (including non-market use value)	USD 108 billion – USD 122 billion
Employment	
Estimated number of fishers	16.8 million – 20.7 million
Estimated number of fishing post-processing jobs	8 million – 38 million
Percent of women in fishing the workforce	>50%
Biodiversity	
Number of inland fish species	>18,000 (>50% of all fish species; >25% of all vertebrate species)

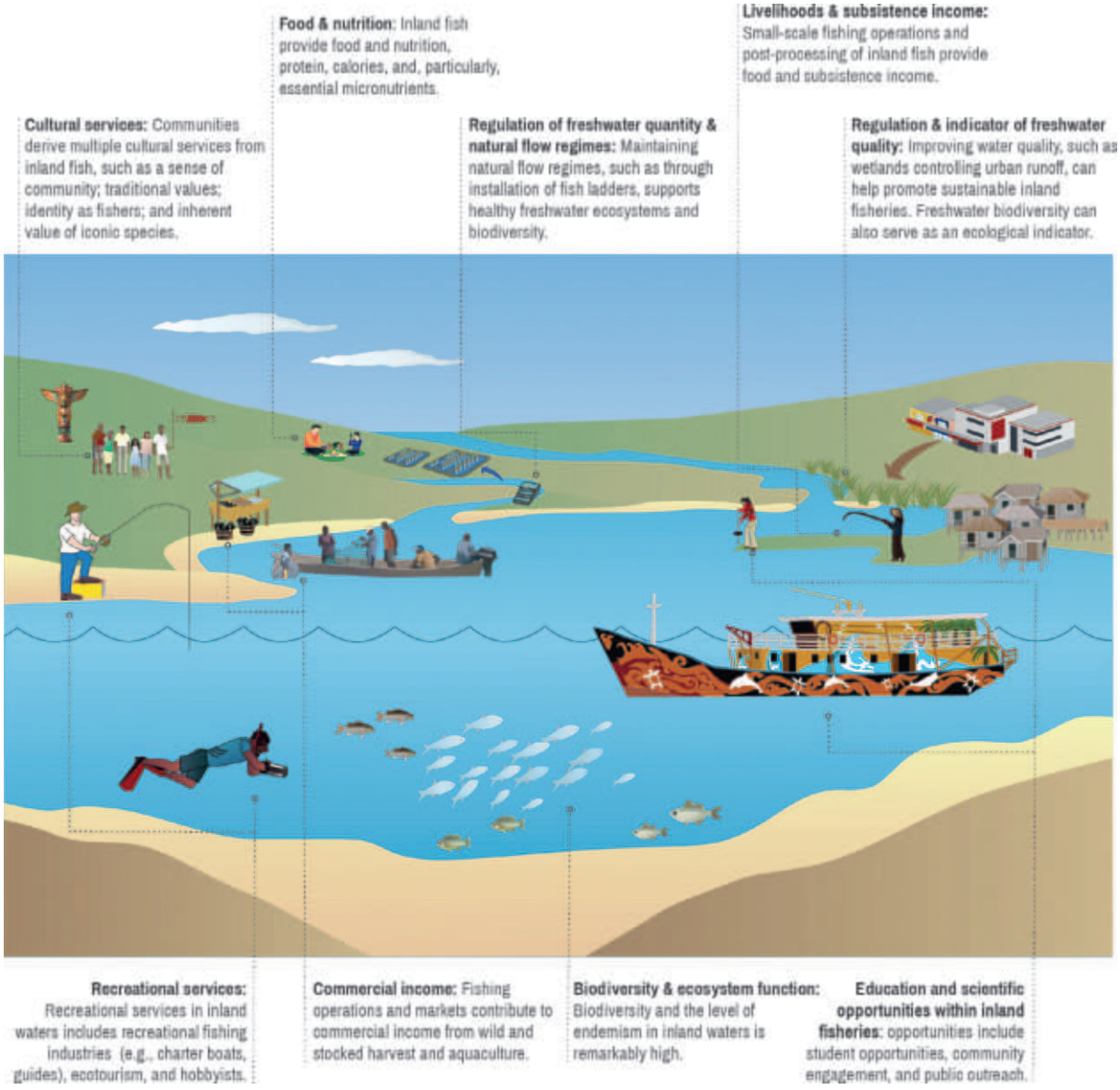

Fig. 1 Inland fishery services across a hypothetical landscape: livelihoods and subsistence income; commercial income; food and nutrition; recreational services; cultural services; educational and scientific opportunities within fisheries; biodiversity and ecosystem function; regulation and indicator of freshwater quality; and regulation of freshwater quantity and natural flow regimes.

resources for consumption and recreation, and stakeholders with wider interests, including regulatory agencies that require efficient methods for assessing aquatic environments. Services gained from maintaining fish in inland waters, for example, can conflict with the benefits of harvesting fish from those systems. However, working from a holistic, ecosystem-based perspective, conservation and sustainable management of all nine societal services can ensure that the persistence of one service does not threaten or degrade benefits derived from others now or in the future.

The following sections aim to highlight the global importance of inland fishes by service. Each section includes a general description of the service, key stakeholders, threats, and a specific case study to exemplify the service.

Livelihoods and subsistence income

Inland fisheries utilize wild fishery resources in rivers, streams, floodplains, wetlands, lakes, inland seas, canals, reservoirs, and even rice fields. They represent a relevant livelihood providing poverty alleviation, income, and employment to more than 60 million people worldwide (Fig. 3; Béné et al., 2016; FAO, 2018). Inland fisheries can be a primary livelihood or can be used to support the acquisition of inputs and goods from other subsistence activities such as agriculture, beekeeping, and raising livestock. Individuals

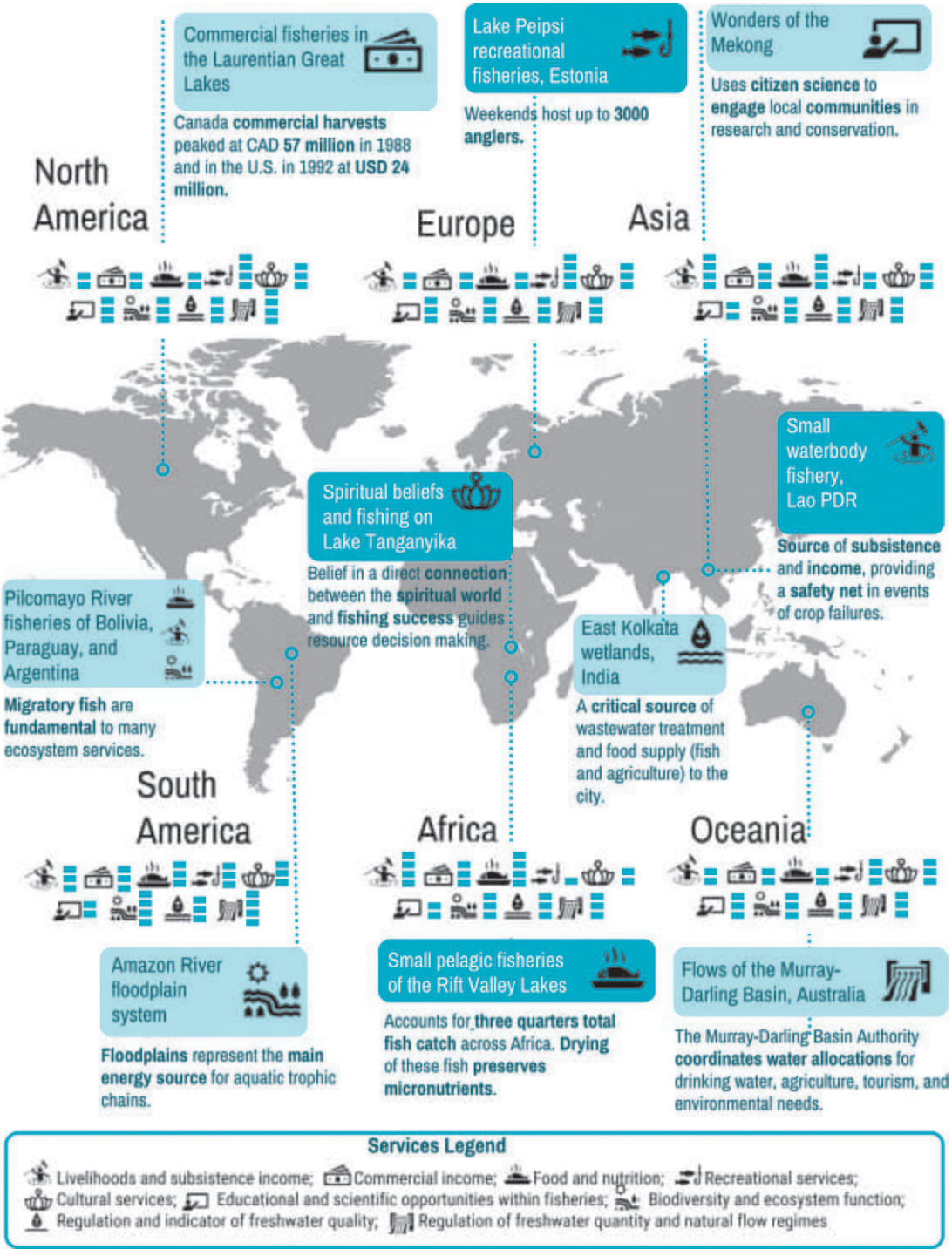

Fig. 2 The relative importance of inland fishery services at a continental scale including highlighted case study examples: livelihoods and subsistence income; commercial income; food and nutrition; recreational services; cultural services; educational and scientific opportunities within fisheries; biodiversity and ecosystem function; regulation and indicator of freshwater quality; and regulation of freshwater quantity and natural flow regimes.

linked to commercial fisheries are fishers, traders, processors, and informal and formal fish sellers in markets. As a low-cost opportunity for subsistence and livelihood support, inland fisheries can serve as social safety nets, offering alternative options when primary income sources fail. In addition to wider threats to the physical environment and fish populations, subsistence use of inland fisheries may be threatened by commercial encroachment, changes in governance arrangements, or the development of recreational fisheries over subsistence use.

Fig. 3 Inland fisheries provide livelihoods and subsistence income. (A) Native fishers with ancestral gear in the Pilcomayo River. (B) Woman repairing nets in Nepal. (C) Woman sorting fish on traditional drying racks on Cape Maclear, Lake Malawi. (D) Fishers on the Mekong River. (A) Courtesy Claudio Baigun; (B) courtesy Julie Claussen; (C) courtesy Gretchen Stokes; (D) courtesy Abigail Lynch.

Case study: Small waterbody fisheries in southern Lao People's Democratic Republic (PDR)

Small waterbody fisheries in southern Lao PDR provide an example of the different ways that inland fisheries can contribute to livelihoods and subsistence income. Small floodplain waterbodies are a common feature of the rural landscape in southern Lao PDR, playing an important, direct role in the livelihoods of almost all rural households and providing a safety net on occasions of crop failures. Within this landscape, perennial waterbodies are a particularly important source of aquatic resources in the dry season, when ephemeral water resources begin to disappear. Subsistence fishing in small waterbodies is an almost universal activity in Lao PDR and accounts for at least 70% of the fish acquired by rural households (Garaway et al., 2006). While most small waterbodies are available to villagers at all times for subsistence fishing, some may serve as a means to generate village income, with access to these locations being more restricted. The nature of restrictions varies among villages; examples include fishing days, where the waterbody is opened for fishing by particular fishing gears on purchase of a ticket, and organized collective harvesting and sale of fish by a small group selected by the village authorities. Leasing the use rights for a waterbody is also common and provides a means for villages to raise income while passing on the responsibility for organizing the harvesting to the leasing group. Where few alternative places to fish exist, regulations in these income-generating waterbodies may provide opportunities for individual subsistence fishing, albeit with a restricted set of gears.

Commercial income

Harvesting, processing, distribution, and sale of inland fish from wild-capture, stocked, and aquaculture systems generate revenue for people around the world (Fig. 4). For farm-raised fish, income is also derived from the rearing and propagation of commercially valuable fish, in addition to income provided by jobs related to the functioning of the aquaculture facility. The supply chain for

Fig. 4 Inland fisheries provide commercial income. (A) Aquaculture pens growing chambo (*Oreochromis lidole*) in Lake Malawi. (B) Fisher uses gillnets in the Parana River. (A) Courtesy Gretchen Stokes; (B) courtesy Trice Castillo.

inland fish often involves several intermediary actors (e.g., wholesalers, distributors) and serves both local and global markets. Major stakeholders are the commercial fishers, fish farmers, agri-businesses that run aquaculture facilities, other actors in the fisheries supply chain, and fish product consumers. Also, recreational fisheries provide valuable jobs and revenue derived from bait and gear sales, boat rentals, among other associated industries. Members of governance institutions are also key stakeholders and benefit from management and enforcement duties. Such institutions include those related to fisheries management as well as those focused on food quality, safety standards, and environmental quality. It is increasingly difficult for fishers to make a living solely from commercial fishing. Income from small-scale fisheries, in particular, is generally low, especially when the supply chain has multiple intermediaries. It is usually difficult for fishers to obtain a fair price and this generates inequitable value chains. While the dockside prices for many fish species have remained constant over the past few decades, commercial fishing costs have significantly risen. Additionally, commercial fishers often are competing for access to fishing grounds with recreational water users.

Case study: Commercial fisheries of the Laurentian Great Lakes

Commercial fisheries play an important economic and cultural role for coastal communities located along the shores of North America's Laurentian Great Lakes. Lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) have long been an

important part of the cultural heritage of First Nations and Tribal communities in the region. The abundant fishery resources in the Great Lakes were also a key driver for later European settlement and development of this region. Together, lake whitefish, lake trout, and percids (e.g., walleye *Sander vitreus*) were the commercial fish species most targeted for harvest. Dockside value for Great Lakes commercial harvests landed in Canada peaked in 1988 at approximately CAD 57 million and peaked in the US in 1992 at approximately USD 24 million (Brenden et al., 2013). Since these peaks, dockside value has steadily declined. This decrease is, in part, due to the declining abundance of fish populations as a result of developments in fishing technologies that led to increased fishing efficiency, introduction of invasive species that compete with native fish for resources, and decreases in habitat and water quality, among other factors. Although the current state of commercial fisheries in the region is a specter of what it once was, the activity continues to be an important source of income and livelihoods to coastal fishing communities. These fisheries are often multi-generational enterprises and are deeply embedded in local communities. The fish harvested by these fishing families are generally sold to local restaurants and markets. Great Lakes fish are also sought after by many tourists to the region.

Food and nutrition

Inland fisheries are an important, yet often underestimated, contributor to global food security and nutrition (Fig. 5). Over 90% of global inland fish catch is used for direct human consumption (Welcomme et al., 2010). Capture fisheries provide the equivalent of the total dietary animal protein for 158 million people each year (Funge-Smith, 2018), and are particularly important for hunger and malnutrition alleviation among many of the world's poorest and most vulnerable populations. They also supply a critical source of micronutrients essential for human growth and development, especially in geographies reliant on starches as their primary food source. Proteins and lysine found in fish provide a source of amino acids necessary for growth; vitamins (A, D, B) that are important for cardiovascular health, energy production, vision and tissue growth; and minerals (calcium, zinc, iron, iodine, phosphorus, selenium) that support bone, blood and muscular health (Youn et al., 2014). Omega-3 fatty acids and calcium from consumption of fish meat and bones are especially important for pregnant and lactating women in low-income countries without access to dietary supplements. Storage methods (e.g., dried, preserved) for inland catch can provide year-round food access to nutrients that would otherwise be unavailable. Inland fisheries are also an important component of global food production systems, often serving as a buffer for crop failure or agricultural loss due to pests or certain extreme weather events. Indirectly, livelihoods provided by inland fisheries employment (e.g., fishing, processing, selling) supply income for trading or purchasing food staples and other necessities in the marketplace. Key stakeholders of food and nutritional services include subsistence and small-scale fishers, supply-chain workers (e.g., processors, market vendors, transporters, traders) and consumers of fish or fish products. Aquaculture or agricultural workers may purchase feed for fish or livestock made from fish unsuitable for human consumption. Threats to inland fisheries are numerous: flow modification for irrigation and power generation, introduction of non-native species, habitat degradation, fragmentation, eutrophication, water pollution, and overharvest have all contributed to declines in fish populations worldwide, and thus threaten food security in regions of high nutritional dependence. For example, a 90% loss of fish catch resulted from the construction of two dams built for agricultural irrigation on the Senegal River, and ultimately led to malnutrition without sufficient agricultural food compensation (Pirot et al., 2000). Similar consequences are expected if there is continued unmitigated damming of the mainstream Mekong River (Dugan et al., 2010). In light of a changing climate, recognition of the efficiency and sustainability of wild-caught inland fisheries (e.g., no irrigation, feeding, or land clearing required) is vital, in addition to consideration of the economic and ecological cost of replacing fish protein and micronutrients with alternative food sources.

Fig. 5 Inland fisheries provide essential and cherished food sources. (A) Smoked vendace (*Coregonus albula*) are highly valued in the Lake Peipsi region. (B) Fish for sale, Lake Malawi. (A) Courtesy Aimar Rakko; (B) courtesy Gretchen Stokes.

Case study: Small pelagic fisheries of the African Rift Valley Lakes

Small pelagic fishes, common to East Africa's tropical rift valley lakes, account for nearly three quarters of all fish catch across Africa (Kolding et al., 2019). For example, dagaa (*Rastrineobola argentea*) accounts for 60% of fish catch in Lake Victoria; kapenta (*Stolothrissa tanganicae*, *Limnothrissa miodon*) contributes 60–80% of catch in Lake Tanganyika, Lake Kariba and Cahora Bassa; and muziri (*Neobola bredoi*) and ragoogi (*Brycinus nurse*) comprise 80% of Lake Albert's fish catch (Kolding et al., 2019). The region's small pelagic fish value chain is distinguished by having high yield, high nutritional value, and being ecologically sustainable. Most small pelagic species tend to be short-lived, and highly productive (e.g., replacing harvested biomass up to five times per year). The highly perishable nature of small pelagic fish requires drying, salting, smoking, or frying to reduce post-harvest loss. Unlike larger fish that require more labor-intensive post-processing to remove guts, small pelagic fish can be easily dried on large racks in the sun in just a few days. One major nutritional advantage of this practice is that sun-dried pelagic fish can be consumed whole, thus preserving micronutrients in the head, bones, and intestines of the fish. Sun-dried fish can be stored without refrigeration for months, providing long-term food security for low-income families. Thousands of tons of dried pelagic fishes are traded annually both locally and to neighboring countries via wholesale markets for human consumption, feed production, pharmaceutical and food supplements, and other byproduct uses. Although previously viewed as food for the poor, sale and consumption of pelagic fishes has gained popularity across social classes due to the nutritional benefits and rapid processing time. Remaining challenges in the supply chain include the potential for disease from improper drying, contamination in transport, and limited quality control.

Recreational services

Recreational services supported by inland fishes, which include recreational fishing, snorkeling, boating, photography, and ornamental fish trade, are prominent across the globe (Fig. 6). Estimates of visits for recreational services (e.g., freshwater fishing, enjoyment, photography) to the world's freshwater lakes vary among waterbodies located in different regions, but are, for example, considered high in the Laurentian Great Lakes in North America, Lake Titicaca and the Pantanal in South America, and Lake Toba in Eurasia (Sterner et al., 2020). Riverine fishes and other aquatic biota are also highly valued for recreation, such as the Murray crayfish (*Euastacus armatus*) and Murray cod (*Maccullochella peelii*) in Australia. In addition, flagship species can play an important role in recreational tourism, such as Peacock bass (*Cichla* spp.) in Brazil. Inland fishes provide direct recreational services to a diversity of stakeholders, including fishers and hobbyists, and indirect services to the tourism industry, including boat and tackle shops, grocery stores, lodging, gas stations, and local governments in the form of fishing licenses or access revenue. In the United States alone, freshwater angling contributes USD 41.9 billion to the gross domestic product (ASA, 2018). Despite its importance, recreational fishing is often not evaluated as an ecosystem service or for its socio-economic impact in countries that do not closely manage their inland fishery resources. Given the importance of recreational services to stakeholders in many different regions, management and conservation of inland fishes and biodiversity resources is needed. Threats to recreational fisheries include overfishing, invasive species, pollution, and climate change, among others. Recreational fisheries can also negatively impact freshwater ecosystems, by polluting riparian areas, removing vegetation, or modifying shore areas (e.g., hardscaping for ease of access). Understanding the threats to and impacts from recreational services for inland fishes and biodiversity is key to maintaining and conserving these services.

Case study: Lake Peipsi recreational fishery

Lake Peipsi is a popular recreational area on the Estonian-Russian border. The lake's fish stocks are remarkably high, which makes the lake economically important for both commercial and recreational fishers. Ice fishing (e.g., catching fish with hooks on a frozen body of water) is an extremely popular leisure activity in the region. A typical winter weekend can host up to 3000 anglers fishing on the Estonian side of the transboundary lake, the most frequented area for winter fishing (Orru et al., 2014). The ice fishing period may last from a few days to up to 4 months, depending on how long sufficient ice cover lasts. Ice fishing is defined as a hobby; however, interviews with fishers show that financial gain from the sale of fish is an important incentive for retired or unemployed persons in the coastal villages of Lake Peipsi, where there are few employment alternatives. The landings of winter angling can be considerable in the case of long ice-cover periods, when anglers may fish out approximately 40% of the total annual harvest of Eurasian perch (*Perca fluviatilis*), the most popular target species, roach (*Rutilus rutilus*), and ruffe (*Gymnocephalus cernuus*) from the lake (Orru et al., 2014). The caught fish are used mainly for domestic consumption or are exchanged in a barter economy where they generate some economic benefits. Yet, enjoying nature, relaxing from everyday worries, the feeling of excitement from catching fish, and the company of other fishers were all estimated to be more important to anglers than other benefits (e.g., the financial or food gain from ice fishing; Orru et al., 2014).

Cultural services

Globally, numerous cultural services exist due to the significance of inland fish and fisheries within a community. Unlike provisioning services where there is direct monetary value associated with the activity, cultural services are considered invaluable.

Fig. 6 Recreational services supported by inland fishes are diverse. (A) Winter angling on Lake Peipsi. (B) Brightly-colored cichlids draw visitors to ecotourism in Lake Malawi National Park. (A) Courtesy Peeter Kangur; (B) courtesy Gretchen Stokes.

These include, but are not limited to, individuals experiencing a sense of community through cultural icons, spiritual and religious values, identity as fishers, and the enjoyment of the aesthetic beauty of fishes. The ornamental fish trade for the aquarium industry, for example, is based on the cultural service of the aesthetic beauty that fishes provide. Fish as cultural icons often play multiple roles as artforms, signifying the importance of fish in a society, and as religious allegory. For example, in the Mithila Region of Nepal and India, Madhubani art depicts a distinctive smiling fish which symbolizes fertility and abundance. Just north of this region, Tibetan Buddhism has the *Sernya*, a pair of large golden fish that represents happiness, spontaneity, and freedom of movement (Beer, 2003). In some cultures, fish have been the foundation for their very existence. Consider First Nation Tribes and their deep relationship with salmon, which have shaped their spiritual and ethnic identities (Willard et al., 2020). Cultural services also include aesthetic appreciation and inspirational pursuits (e.g., art, music, storytelling), so any individual with exposure to inland fish and fisheries could be considered a stakeholder. Worldwide, a diverse range of stakeholders have the potential to foster a deep environmental stewardship for the species and traditions they hold dear. In places where human and aquatic resources are intimately linked, cultural values are often overlooked or undervalued (e.g., Lowe et al., 2019). Festivities, traditions, and regionally-specific events that are related to inland fish or fisheries often have little preservation power in the face of larger economic development, such as damming of rivers, or industrial growth.

Case study: Spiritual beliefs and fishing on Lake Tanganyika

East Africa's Lake Tanganyika is a place where fish, economics, and culture are closely connected. The lake sustains a major inland fishery among its four surrounding countries. Here, fishers believe there is a direct connection between their spiritual beliefs and customs and their fishing success. They hold that certain sacrifices, prayers, rituals, and charms influence their fishing outcomes (Lowe et al., 2019). This link between the spiritual world and fishing is what guides fishers in their decision-making regarding the lake's resources, and influences fishery management decisions, regulations, and compliance. Understanding and respecting these connections is a critical component of effective management in these communities, where fishers believe that the health of their fish population is driven by the spiritual world.

Educational and scientific opportunities within fisheries

Because of the diversity of research areas encompassed within fisheries, there is a broad range of educational and scientific opportunities available within the field (Fig. 7). These opportunities range from formal education and outreach (e.g., capacity building among fisheries professionals, mentoring and engaging students in fisheries programs) to community engagement and public outreach among non-fisheries professionals (e.g., via social media outlets, citizen science projects). Key stakeholders for initiating and leading these efforts include local communities, policymakers (at multiple levels of government), and conservation organizations and nongovernmental organizations (NGOs). Some educational opportunities, such as World Fish Migration Day (https://www.worldfishmigrationday.com), were started locally by individuals who wanted to raise awareness of migratory fish species. Due to their efforts, and the importance of migratory fish in communities around the world, World Fish Migration Day has now grown into a global event that occurs every two years and offers a range of educational and outreach opportunities to communities worldwide. People tend to take their local sources of freshwater for granted, due to a lack of education and awareness of the links between the health of freshwater ecosystems and human wellbeing. While some programs are specifically designed for educational outreach, others are one component of a larger program. World Fish Migration Day, International Day for Biological Diversity (https://www.cbd.int/idb), World Water Week (https://www.worldwaterweek.org), and World Rivers Day (https://worldriversday.com), are all examples of focused efforts to raise awareness of a specific topic of concern.

Case study: Wonders of the Mekong Project

Larger education initiatives are often designed to target multiple stakeholders. The Wonders of the Mekong Project aims to maintain the ecological, cultural, and economic integrity of the Mekong River and delta system, a biologically rich system that supports the livelihoods of over 70 million people in East and Southeast Asia (Hortle, 2009). The Mekong faces a wide array of complex challenges from a growing human population and accelerating regional development. The Wonders of the Mekong Project recognizes that education is a key component and uses a multi-faceted approach including educational storytelling, multimedia communication, outreach for children, social media, recognition of community leaders, and community workshops. These efforts are designed to reach a range of ages and audiences on a variety of topics that will promote a sustainable future for the Mekong region. While many of these educational efforts take a passive approach to teaching, other Wonders of the Mekong programs are designed to directly involve individuals in conservation-oriented activities. Community science (also referred to as citizen science) initiatives are an educational method employed by conservation organizations, museums, and environmental agencies, among others, to directly include lay people in a research or conservation program. These efforts train laypeople to make scientific observations, maintain equipment, record data, or provide reports. Through this direct connection with the resource, individuals can gain a deeper understanding of the freshwater resource and serve as an ambassador for the Wonders of the Mekong Project within their own communities.

(A) (B)

Fig. 7 Inland fishes contribute to research and education. (A) Research vessels in Monkey Bay, Lake Malawi. (B) Students sample fish habitat using transect measurements in Virginia, USA. (A) Courtesy Gretchen Stokes; (B) courtesy Gretchen Stokes.

Biodiversity and ecosystem function

Healthy ecosystems, including natural physical conditions (i.e., floodplain connectivity) as well as functional and structural biodiversity, support sustainably-harvested inland fisheries. Inland fishes support ecosystem function, and the loss or decline of key species can result in disruption of nutrient and organic matter cycling and transportation (e.g., McIntyre et al., 2007). For example, sabalo (*Prochilodus lineatus*) in the Pilcomayo River of South America play a key role in sustaining several subsistence and commercial fisheries as they complete a seasonal migration from lowland swamps to upstream spawning grounds (Baigún and Salazar, 2019). Given that ecosystem roles of inland fishes are often poorly understood, biodiversity itself provides a societal service in the form of functional redundancy, providing "insurance" that ecosystem processes remain intact despite unanticipated species loss or ecological surprises. Key stakeholders include recreational and commercial fishers, consumers of inland fishes, community members who rely indirectly on processes supported by functioning freshwater ecosystems, as well as the resident organisms. Habitat degradation and fragmentation, overexploitation, invasive species, flow modification, inappropriate land use, hydropower, and pollution are primary threats to biodiversity and ecosystem function. Emerging threats range from impacts of climate change to the effects of evolving and growing technologies (e.g., nanomaterials and microplastics) on fishes and habitats.

Case study: The Amazon River-floodplain system

The Amazon River-floodplain is a fluvial macro-system where natural ecosystem function is critical to maintaining many societal benefits. The system is strongly tied to flood pulses and the ecological role of the floodplain. Specifically, floods trigger primary and secondary production in the floodplain by exchanging and allowing the flux of organic and inorganic matter, nutrients, fruits, leaves, fish larvae and seeds, derived from forests and flooded lands. In vegetated floodplain habitats, especially in nutrient- and sediment-rich rivers, lacustrine environments represent the main sources of primary energy production that support the aquatic food chain. Fishes migrate to and from floodplains, increasing productivity in the main channel. Longitudinal movement of fishes also plays an important role in ecosystem function: species migrations provide nutrient transport from mainstem channels to less-productive tributaries, while Amazon catfish migrations restructure foodwebs through the addition or subtraction of a top predator (Winemiller and Jepsen, 1998). The wellbeing of rural people who depend on Amazon River ecosystems is inherently tied to the exploitation of migratory fishes. The main disruptive factors that compromise ecosystem function and hydrological processes relate to 76 existing dams, mostly in the headwater areas (Andes Mountains), with 288 more dams planned for the basin (Latrubesse et al., 2017). In addition, land-use changes associated with gas, petroleum, and minerals extraction coupled with road construction have provoked massive deforestation, affecting water quality and runoff (Leitão et al., 2018). Such combined impacts have led to increased disruption of ecosystem function, loss of biodiversity, and could ultimately threaten the sustainability of fisheries. Further, additional degradation is likely to result in surprising and unpredictable changes to societal benefits as poorly-understood ecosystem processes are fundamentally altered by species loss.

Regulation and indicator of freshwater quality

An indirect service of sustainable inland fisheries is the protection, maintenance, or construction of fish habitat, including environmental conditions, connectivity, and water quality. Freshwater fishes can directly contribute to improving water quality through their role in facilitating ecological processes such as recycling nutrients as happens with migratory fishes in cold temperate rivers or tropical rivers and lakes such as Lake Tanganyika. In addition, an easily overlooked value of inland fishes is their role as ecological indicators. Fish respond rapidly to disturbance and changes in environmental conditions. Given that fish are relatively easily observed as compared to other freshwater indicators (e.g., excessive nutrients or pollutants), fish-derived metrics are often used to shape policy and management. For example, the Index of Biotic Integrity (IBI; Karr, 1991) is a commonly used assessment tool which examines local fish assemblages to identify aquatic habitat perturbations. Key stakeholders include recreational and commercial fishers, consumers of freshwater fish, community members who utilize freshwater resources for non-consumptive uses, and other diverse stakeholders, including regulatory agencies that require simple methods for assessing aquatic environments. Threats include land-use change (e.g., urban, agricultural) that degrades water quality, aquatic environment changes that impact fish communities and exacerbate the effects of nutrient and pollutant loading, and species invasions and introductions that disrupt natural ecosystems. Threats are exacerbated where a lack of support for aquatic environmental management occurs.

Case study: East Kolkata Wetlands

Kolkata, the capital of West Bengal with a population of approximately 15 million, is located in the Ganges Delta. Adjacent to the eastern edge of the city lie the East Kolkata Wetlands, which encompass over 12,000 ha of urban and peri-urban wetlands. These wetlands perform important ecosystem services based on natural ecological processes, including wastewater treatment and food supply, providing the city of Kolkata with around one-third of its daily fish supply. The East Kolkata Wetlands originated as a brackish swamp of the Bidyadhari River. Traditionally the area was used for rice cultivation and subsistence fishing. As the city expanded during the colonial period, challenges with managing human waste increased. The wetlands emerged as a more

eco-friendly sewage management alternative to direct waste disposal in the Hooghly River. Over time, the role of the wetland in regulating water quality has evolved, with up to one million cubic meters of wastewater passing through the wetlands daily (Bhattacharya et al., 2012). The changes in the wetland environment created opportunities to develop wastewater-based agriculture and fish production. Natural processes within the ponds decompose organic wastes and support plankton production and fisheries. Critically, urbanization and the need to regulate freshwater quality have continued to result in changes in the wetland environment and the nature of the fisheries. Diversion of anthropogenic wastewater into the wetland has changed the environment, and the management of water flow and quality has enabled a shift from a capture-based fishery system to one dominated by pond-based aquaculture production.

Regulation of freshwater quantity and natural flow regimes

In lotic environments (i.e., rivers, streams, and creeks), flow regimes shape the structure of the habitat, the composition of the biodiversity, and the ecological processes of these systems. For example, the success of fish spawning and recruitment can be tied to the natural rhythms of flowing waters. Spring floods and flow pulses in temperate rivers often act as an environmental cue to initiate spawning migrations, while sustained water levels in upper reaches of tributaries can help ensure larval fishes have a chance to enter the mainstem of the river or enter a lake or floodplain lagoons before those areas become stranded by reduced flow. Thus, the maintenance of intact and natural lotic environments, including their floodplains, supports healthy inland fisheries. Globally, many stakeholders are interested in large riverine habitats for human benefits such as food provisioning and livelihoods, hydroelectricity, freshwater, flood mitigation, irrigation, transportation of goods, as well as recreational boating and angling. As a result, it is estimated that >75% of the largest river systems in North America, Europe, and the former Soviet Union are moderately or strongly regulated (Dynesius and Nilsson, 1994) and that only 37% of the world's 246 longest rivers remain free flowing (Grill et al., 2019). Given the competition for freshwater resources, there are many threats to the regulation of freshwater quantity, flow timing, and variability, as physical manipulations directly alter the natural flow regime. Impoundments such as dams convert flowing environments to lake or reservoir habitats, disrupting ecological processes and aquatic communities including inland fishes and their prey. Determining how to prioritize interests of competing stakeholders becomes a management challenge.

Case study: Water allocations in the Murray-Darling Basin, Australia

The Murray and Darling Rivers of southeastern Australia are highly regulated to supply diverse stakeholders with critical water resources. For 40,000 years, the rivers of the 1,061,469 km^2 Murray-Darling Basin have been central to the cultures and livelihoods of 40 Aboriginal Nations (Rutherfurd et al., 2020). In the late 1800s, European settlers began developing irrigation structures, and plans for larger storage and distribution projects began after a decade of severe drought starting in 1892. Beginning with the River Murray Waters Agreement in 1914, river regulators have sought to balance the complex water needs among user groups and across legislative boundaries, which includes parts of four states and the capital territory. Today, the Murray-Darling Basin Authority (MDBA) coordinates water allocations among the diverse, and often competing, needs of an AUD 24 billion agricultural sector, an AUD 8 billion tourism industry, 2.6 million basin residents, as well as the environmental needs of fish, other animals, and plants native to the basin, and the cultural flows owned by Indigenous Traditional Owner groups (McLoughlin et al., 2020). In 2012, the MDBA began implementing a basin-wide plan that maintains baseline environmental flows necessary for fish and other aquatic life, establishes sustainable diversion limits, and allocates water rights among user groups. Because the basin has highly variable climate and rainfall patterns, the total allocation of water available to users changes each year, with highest priority given to drinking water supply in times of drought. Critical to the MDBA Basin Plan is the ability of regulators to adapt management to changing user and environmental conditions, as water supply to the basin has declined over the past 20 years.

Synthesis

Inland waters are highly varied and often dynamic. From seasonal watershed inputs to resident fish and human communities, these elements can, and frequently do, change. Most inland fishery services share the characteristic of being highly responsive, for better or worse, to basin management, particularly in transboundary watersheds. Progressively through time, and even seasonally, the services and benefits from inland fishes and biodiversity are different for inland systems. Regionally, these benefits are highly diverse and, in some cases, the benefits can be in direct conflict. Commercial fisheries (i.e., wealth-generating) can frequently be at odds with subsistence (i.e., welfare-motivated) or recreational (i.e., wellbeing-focused) fisheries; recreation and tourism can impact conservation; and introduced species can alter relationships among native fish species. Tensions can arise between the benefits from fish conservation (which can involve *restricting* access) and benefits from fisheries (which usually involves *enabling* access) because inland fishes are a limiting resource. However, most frequently, the threats to all services derived from inland fishes arise from external sectors and sources. Fish biodiversity and fisher livelihoods, for example, both depend on functioning aquatic ecosystems, which in turn are highly dependent on land and water use at the basin scale. Rather than pit the diverse array of services derived from inland fishes and freshwater biodiversity against each other, a unified front can lead to mutual benefits and "win-win" scenarios for all of the societal values (for more, see Phang et al., 2019).

Improving science, policy, and management for these vital societal services provided by inland fishes will require a number of key knowledge gaps to be addressed. The importance of inland fish to food security, nutrition, and economies is poorly known, and likely grossly underestimated. Beyond the fisheries, more information is needed on the impact of climate change and human developments on freshwater ecosystems and the effectiveness of regulations to maintain or improve water quality. The extent to which climate change together with land-use changes will alter the quantity, flow timing, variability, and connectivity of these environments and how resilient fish communities are to these changes is still largely unknown. These science information gaps are particularly severe for smaller-scale inland fishery systems.

Prioritizing these complex problems at a policy level often requires cohesive and comprehensive efforts to educate various constituents about inland fishes, freshwater biodiversity, ecosystem function, and the services they support. Though several valuation studies have been conducted, many policymakers still do not recognize the full economic, societal, and conservation contributions of the societal services provided by inland fishes. For example, the role that fish and fisheries plays in societies are often confined to a specific area or region. Once outside these inner circles, awareness can be limited on how fish are woven into the various components of a culture.

Translating these priorities to management may require a realignment of focus. Much of the current emphasis in fisheries management is directly on the fish and the fishers. The broader social and economic contributions that inland fisheries make, for example, through income generating opportunities and services remains an important gap. Likewise, understanding the cumulative effects of co-occurring stressors on inland fishes and freshwater biodiversity is an ongoing need for sustainable ecosystem management (as is described in the following case study).

Case study: The Pilcomayo River fisheries of Bolivia, Paraguay, and Argentina

Inland systems are often a complex integration of services and reflect the interaction between environmental features and anthropogenic impacts. The Pilcomayo River, a transboundary, free-flowing river crossing Bolivia, Argentina, and Paraguay, and ending in several diffuse swamps, is a notable example where human and ecosystem benefits directly overlap. Both the aquatic life and the humans that live there have adapted to the highly dynamic and seasonal nature of this river. Large amounts of sediment are transported during the summer flood pulses promoting remarkable changes in the river landscape by forming new channels and filling or isolating older ones, while contributing to the flooding of swamps and wetlands downstream. The Pilcomayo River is inhabited by several species of migratory fish, with the sabalo playing a key role in sustaining several subsistence and commercial fisheries along the basin (Baigún et al., 2019). The fisheries are highly seasonal and are strongly associated with the migratory movements during the autumn, when the water recedes into the lowland swamps obligating this species to migrate upstream to reach the spawning grounds in the middle and upper watershed (Baigún and Salazar, 2019). These fisheries play a fundamental role in the food security of poor river dwellers, including Indigenous and local people, and support a well-developed small-scale commercial fishery that has a strong impact on local economies during the catch season. However, the sustainability of the fishery could be severely threatened by reduced flood pulses due to adverse climatic conditions, loss of lowland swamps, mining pollution, channelizations for irrigation, small dams, and dikes (Smolders et al., 2002). Fisheries and livelihoods in unstable river systems such as the Pilcomayo will depend on avoiding alteration of the natural balance between sediment dynamics and hydrological regime to allow fish populations to complete their life cycle.

Conclusion

Inland fishes and freshwater biodiversity may be all around us, but their societal values are still often ignored in important decision-making arenas. Conservation of freshwater resources requires integrating not only different disciplinary perspectives but also improvements in water and land governance. However, freshwater governance is often dominated by other societally important sectors including agriculture, energy, and water for drinking, sanitation, and hygiene. Rivers are often perceived as generating economic activities (e.g., trade, tourism, and transportation) rather than as bodies of water that also generate other valuable ecosystem services, including fisheries. The lack of awareness of rivers as dynamic systems made up of channels and floodplains that need to be interconnected has led to many rivers losing their floodplains in favor of agricultural activities or urban development. Inland fishery services are impacted by these decisions at local, national, regional, and global levels. By joining this conversation, the inland fisheries sector can help increase recognition of the societal values of inland fishes and biodiversity and explore opportunities for improved outcomes for the aquatic ecosystems and the communities that depend on them around the globe (for more, see Cooke et al., 2016).

Acknowledgments

All authors are members of the international InFish Research Network (http://infish.org). We thank Kate Malpeli for an internal U.S. Geological Survey review and the Editors Febria, Krantzberg, and Mehner for their constructive feedback. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Societal Values, Water and Public Policy

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Catherine Febria and Gail Krantzberg.

Glossary

Ecosystem A geographic area or scale where all living organisms exist together in a network of life.
Environmental rights The right of all living things to natural resources that enable life including air, water, food and shelter.
Environmental stewardship The responsible protection of the natural environment through conservation and sustainable practices to enhance ecosystem health and human well-being.
Human rights Universal rights of individual human beings that are inherent to us all regardless of geography, nationality, gender, ethnic origin, race, religion, language, or any other status.
Hydrosolidarity Multi-dimensional values and ethics for guiding and solving water governance challenges.
Personal values The attitudes and beliefs held by an individual.
Public opinion An aggregation of individual views, attitudes, and beliefs about a particular topic as expressed by a significant proportion of a community or population.
Societal values Collective attitudes and beliefs held by societies at different scales.
Water ethics The philosophical and moral aspects of human relations and interventions with water.
Water footprint The amount/value of water used by an individual, community, business or jurisdiction.
Water governance The social, economic and political arrangements used to value and manage water at various scales.
Water values Economic, social, ecological and cultural dimensions of water and its meanings.

Introduction

Societal values related to inland waters are part of our daily lives. Our daily routines, behaviors, and travels reflect our water values as citizens. Water sustains all life and human existence. People around the world consume and interact with water, want to be near water, seek travel destinations based on water, own property close to water, and have long-standing rituals and sacred relations with water. John Stanmeyer's photography and imagery clearly depicts how water is revered in human cultures and religion across the globe (2010). Photographer Edward Burtynsky's book *Water* (Burtynsky et al., 2013) and films *Watermark* and *Anthropocene* (Baichwal and Burtynsky, 2014; Baichwal et al., 2018) powerfully outline how human values continue to result in behaviors and actions that negatively impact water. Dams, irrigation, drilling for groundwater in aquifers, are all obvious reflections of societal values related to water over the past 100 years.

In the international realm water values and ethics take different forms in different culture and jurisdictions. Humans have complex relationships with water. A paradoxical example is the pilgrimage to the Ganges in India, a river that is spiritual and supports over 400 million people, yet is one of the most polluted in the world.

There are clear conflicts in our values related to water across the globe and at the heart of these conflicts lie water uses and policies. In Western societies, our values, rights and uses of water take the form of rules of use and behavior that ultimately are codified in law. In non-Western societies, they may take the form of beliefs and rights that develop into customs of behavior with the

social sanction of the community (Priscoli et al., 2004). Individual and collective actions are the foundation of different societal water values. Failures to fully value water in all in its different forms and uses is considered a root cause, or a symptom, of the political neglect of water and its mismanagement (WWAP, 2012).

Across the world, there is increasing recognition that societal values and human uses and behaviors related to water are at the heart of improving water governance and stewardship. This increased awareness of the centrality of water values to water governance is reflected in the United Nations 2021 World Water Development Report, Valuing Water (UN, 2021). The inclusion of this chapter and Thematic Section in the 2nd edition of the Encyclopedia or Inland Waters reflects the growing recognition that water values are at the heart of both water science and governance. This chapter reviews the scholarship and developments related to societal water values, water governance and public policy. It begins with an overview of water values and ethics at the global scale. It then reviews various approaches which embody different sets of water values. In this section examples and illustrative cases from inland waters in Canada and the North American Great Lakes region are used to outline the complexity of societal values and the various alternative approaches that underpin water uses and governance related to inland waters. The chapter outlines how many different approaches and values are simultaneously at play in various societies and jurisdictions around the world. Finally, the chapter underscores how human-centered societal values underpin most water governance and policy regimes and how many actors and organizations are urging jurisdictions and policy-makers around the world to take a more values-centered approach to water governance, particularly in the context of climate change, population growth, and unsustainable human uses and abuses.

Societal values, water and policy on the global scale

Water values are becoming centrally important in many societies around the world. Scientists stress how water values will only become more important over time. International organizations and global policy actors realize that the value of water to human beings is increasing. Conflict and crises related to water are evident in both water-abundant and water-scarce regions of the world - in both inland waters within nation state borders and in transboundary regions where water is shared. But what are water values and ethics?

The social value of water resources remains relatively poorly explored and understood because it is abstract (Wu et al., 2019, 74) and includes water as part of ecosystems and values related to supporting human life and uses. Using a social-ecological systems approach (Holling, 2001; Folke et al., 2010), the social value of water is complex and includes physical, social and psychological dimensions which affect social and individual well-being including economic, mental and spiritual meanings (Wu et al., 2019). Water values are also closely bound to culture and reflect beliefs about economic efficiency, social equity and environmental protection, the need to provide for future generations, esthetic and spiritual concerns, the role of government in society, and the human right to water (Gober, 2018, 91).

Water values are held by individuals, groups, cultures and societies. How societal water values are defined depends who is doing the defining, the context, and which change and differ across cultures, communities, space and time. Water values and their interconnections influence decisions made from individual to higher levels of social organization (Euzen and Morehouse, 2011, 239). For purposes of this chapter we use a simple definition, from the 2007 United Nations High Level Panel on Water, *Principles on Valuing Water* report - "valuing water means recognizing and considering all the diverse benefits and risks provided by water, and encompassing its economic, social, and ecological dimensions as well as its diverse cultural and religious meanings" (UN, 2007, 3).

Water ethics focuses on interventions and consequences of human impact on ecosystems of which humans are a part of. The "human factor" in water systems is at the core of ethical considerations (Grunwald, 2016, 12). Scholarship on water ethics has been motivated by environmental concerns and related to the field of environmental ethics (Grunwald, 2016; Stefanovic and Adeel, 2021). Although inherently anthropocentric (Grunwald, 2016), water ethics includes eco-centric principles often included in sets of ethical principles related to water in societies (Groenfeldt and Schmidt, 2013; Grunwald, 2016). Water ethics also focuses on criteria to assess human uses and behaviors and explores the options for more responsible water societies and governance (UNESCO, 2004).

Valuing water is a shared responsibility of us all (Gober, 2018, 91). Generally, there is not a distinction made between societal values related to inland vs. coastal waters, surface vs. groundwater, or values in systems of abundance vs. scarcity. Values are the basis of formulating water policies and clearly reflected in international agreements, domestic laws and policies, and in collective action (Johns, 2021). Societal water values thus include both values and ethics which are reflected in language, arts, discourse, human behaviors, collective actions, international agreements, and public policies.

Since the 1990s there has been 'an ethical turn' (Schmidt, 2011; Groenfeldt, 2019a, b) and there have been increasing calls for a "new water ethic" on the global stage. In the 1992 Dublin Statement on Water and Sustainable Development, the UN formally stated their view that all humans have the right to access clean water and sanitation at an affordable price, introducing a focus on water equity (Whiteley et al., 2008) and articulated several guiding principles for water (WMO, 2018). UNESCO's Ethics of Freshwater Survey in 2000, subsequent *Best Ethical Practices in Water Use* (UNESCO, 2004), and the International Law Association's Berlin Rules on Water Resources in 2004 further advanced the focus on water values and ethics (Dellapenna, 2004). Several UN resolutions also contain value statements and ethical principles for water based on human rights and environmental concerns (Rossi, 2015). Scholars have documented several international developments related to the rising concerns of ethical water issues and several key concepts, such as hydro-solidarity and Integrated Water Resource Management (IWRM) that include principles, values, and ethical dimensions (Matthews et al., 2007; Rossi, 2015; Schmidt, 2011). Hydro-solidarity as a concept features a

growing conviction that human and environmental welfare are inseparably linked (Gerlak et al., 2011, 252). It is a concept that is "all encompassing, multi-dimensional guiding ethic for solving water-related problems" (Falkenmark, 2005: 40) and includes calls for greater dialog around water values, beyond the dominant technical, economic, and political discourse.

Those at the forefront of calls for new water paradigms, values, and ethics generally are calling for more inclusion of social, cultural and environmental values of water – beyond the traditional economic and capitalist market foundations of water values and ethics.

Anthropologist David Groenfeldt, founder of the Water-Culture Institute in the United States and the global coordinator of the Water Ethics Network, has long been an advocate of the need to integrate values, ethics, and Indigenous and traditional cultural values into water governance and policies (Groenfeldt, 2003, 2019a,b; Groenfeldt and Schmidt, 2013). Groenfeldt and many other scholars who focus on water values and ethics, have advocated for a global water charter that "will be applicable at any scale where there is a governance body with decision-making authority" (Water Culture.org, 2014). This work culminated in the recommendation at the 2012 World Water Forum for a global Water Ethics Charter.

The proposed Charter is a moral statement intended to inform and guide public policy. It lays out general ethical principles which are intended as guidance for the development of operational policies and practices in specific contexts (Charter Draft 2.0: 2) (Table 1).

In the draft Charter, several central principles and concepts are articulated including: water ecosystems have inherent rights, and intrinsic value over and above their utilitarian value to people; water is intimately connected to society, forming a socio-ecological system that addresses social needs and provides opportunities; and social arrangements are instrumental for both socially just and economically effective water management. However, there has been no formal advancement of the draft Water Ethics Charter since version 2.0 was developed in 2015.

Around the same time as calls were being made for a global water charter, in 2015 the United Nations launched its 17 Sustainable Development Goals with 169 associated targets. Goal 6 reaffirms a global policy goal of ensuring availability and sustainable management of water and sanitation for all by 2030. In addition to these efforts, in 2015 the Organisation for Economic Co-operation and Development (OECD) Water Governance programme developed 12 water governance principles that were endorsed by OECD member countries. Three key components are at the core of these principles: effectiveness, efficiency, and engagement. Values and ethics are not explicitly part of the principles or the OECD's 36 Water Governance Indicators (OECD, 2018). The OECD's water governance indicators are grounded more in institutions and engagement of interests rather than being focused on societal values, however water vales are implicit in the OECD's reports.

The most recent United Nations latest World Water Development Report (2021) is entitled *Valuing Water* and focusing on the question: what is water worth? (UNESCO, 2021, 9). The report launched on World Water Day in 2021 in several languages, outlines current methodologies and approaches to the valuation of water using five interrelated perspectives (see Table 2).

Although the UN report is very comprehensive, it is not clear if the list in Table 2 reflects a hierarchy of water values. The report does outline that these interrelated perspectives are complex; must be complemented with varied experiences from different global regions; there are different approaches to understanding values related to water; and there are opportunities to reconcile multiple values of water through more integrated and holistic approaches to governance (UN, 2021). The report highlights and details some of the fundamental tensions related to different societal values and uses of water across many different contexts, including contexts of abundance, scarcity and very poor water quality.

Finally, the report itself does reflect dominant Western anglosphere values and perspectives on water.

Despite these important international policy developments and achievements, to date, there is no universal or widely accepted or applied set of values, principles, or ethics related to water policy and decision making for inland, coastal or ocean waters. Scholars

Table 1 Goals and aims of a global water ethics charter.

The aim of this Charter is
(1) to educate water policy makers, water users, and the public at large about their moral responsibilities in making choices which involve water directly or indirectly
(2) to foster an ethical attitude toward water bodies, and in so doing,
(3) to improve water management and governance

Source: Charter Draft 2.0: 1.

Table 2 United Nations *Valuing Water* 2021.

Five interrelated perspectives on water values:
i) valuing water sources (in situ water resources and ecosystems);
ii) valuing water infrastructure for water storage, use, reuse or supply augmentation;
iii) valuing water services, mainly drinking water, sanitation and related human health aspects;
iv) valuing water as an input to production and socio-economic activity, such as food and agriculture, energy and industry, business and employment; and
v) other sociocultural values of water, including recreational, cultural and spiritual attributes.

Source: UNESCO (2021) *The United Nations World Water Development Report 2021: Valuing Water*, p.1.

and practitioners continue to advocate for water values and ethics. The co-edited book entitled *Global Water Ethics: Towards a Global Ethics Charter* (Ziegler and Groenfeldt, 2017) and the recent edited book *Ethical Water Stewardship* (Stefanovic and Adeel, 2021) both contain contributions from international group of scholars calling for water values and ethics to be the foundation of water governance. Entrenched water paradigms and values in societies, economies and political systems across the globe, present significant challenges to embracing a values-centered approach to water governance.

In summary, there has been growing international and scholarly attention to water values, ethics and water valuation. Despite the growing number of scholarly publications and reports by international organizations espousing the virtues of a values-centered approach, sovereignty for water governance remains deeply embedded in the authority of nation states and dependent on human behavior. Across nations and jurisdictions, some laws and policies reflect water values and ethics based on valuing water in its natural, uninhibited, and free-flowing state, but other laws and policies clearly reflect the value that water is something to be controlled as a resource valued primarily for its human and economic uses. As noted in the UN *Valuing Water* report, there are many different approaches to understanding societal values related to water. For purposes of this chapter, the next section reviews some of these and provides illustrative examples and cases from Canada and the North American Great Lakes region.

Alternative approaches to societal values, water and public policy

There is growing awareness that a new set of values must be at the heart of water policy change if societies across the globe are to pursue more sustainable water policy paths and desired end states (Van Nijnatten and Johns, 2020) and a fundamental shift is required away from political liberalism and capitalist values that have dominated societal values related to water for the past 100 years (Schmidt, 2012, 108). There are many different approaches based on different sets of water values in the scholarly literature. It is beyond the scope of this chapter to offer a fulsome review of the various approaches however instead this section reviews some common approaches for understanding societal water values related to inland waters, human behavior and public policy.

Indigenous water values and stewardship

Indigenous peoples hold the view that water is more than a commodity or resource to be managed. Water is life. Indigenous cultures around the world recognize the spiritual nature and inherent value of water. Although water has different meanings across various Indigenous cultures and communities, Indigenous peoples share some fundamental values related to water. Many are associated with spirituality and creation stories. These stories vary from nation to nation, but as a fundamental component of the earth, water plays a central role in each of them. Indigenous organizations and activists have been formally advocating for incorporation of Indigenous values into water policy on the global stage since the Indigenous Peoples' Kyoto Water Declaration at the World Water Forum in 2003. Scholars have also been articulating that "insights from Indigenous communities' more holistic and long-term relationship with water could help define such an ethic" (Norman, 2018, 243).

Internationally, there is also some recognition that a gendered element exists in water values and ethics frameworks. Women in many communities have special responsibilities related to water, yet are rarely involved in strategic and policy decisions on water resource management (Priscoli et al., 2004: 18). Women have a special relationship with water, since, like Mother Earth and water, they have life-giving powers (McGregor, 2012). Honoring water means honoring the fact that water is life, the lifeblood of the land and of Indigenous peoples and cultures (Walkem, 2007: 310–311). For Indigenous peoples, water teaches us that everything is cyclical. It is deeply embedded in key Indigenous worldviews, such as the seventh-generation principle: the recognition that all living things are interconnected. Water bodies need to be valued for their own sake rather than merely for what they can give to humans (Walkem, 2007: 314). "Decisions relating to water must treat it with awe and reverence rather than merely one more resource to be managed, controlled, exploited and used" (Walkem, 2007: 316).

In Canada, over the past 15 years, water problems have been at the forefront of growing awareness of water inequities in society. Tragic water events such as long-standing boil water advisories, the evacuation of Kasheshewan in 2005 due to contaminated water, and the shocking reality that the majority of First Nations communities have problems accessing clean reliable drinking water, have led the UN and several environmental groups and Indigenous groups to demand action and policy change. The Assembly of First Nations and the Chiefs of Ontario have tried to formalize these proposals in formal water statements and declarations (Chiefs of Ontario, 2008; AFN, 2018). Indigenous water activists have made global impacts yet their plight has been very frustrating in term of generating political action in Canada. However, awareness of Indigenous water values is growing (Table 3).

These cases from Canada show a growing recognition that there are "important differences between the philosophies and worldviews that guide decision making in Indigenous and Canadian societies" (Walkem, 2007: 315). Indigenous laws and culture have much to teach us about emphasizing limits to human use, limits to science and technology, and moving beyond short-sighted water policies (McGregor, 2012). Traditional ecological knowledge needs to become more central in water policy (McGregor, 2012). Indigenous values related to water have both advanced thinking about water values and ethics, both by placing a common emphasis on the interconnectedness of water and other aspects of life (Matthews et al., 2007). Norman (2018) argues that a new water ethic based on Indigenous values could incorporate three precepts: (i) treat water as sacred; (ii) consider rights and responsibilities together; and (iii) practice hydrophilia - love and know your waterways (Norman, 2018).

Table 3 Indigenous Water Values in Canada.

Josephine Mandamin and the Great Lakes Water Walks
For thousands of years, Indigenous peoples have held Turtle Island and the Great Lakes as a sacred gift to be respected and valued. The Mother Earth Water Walkers are an example and testament to Indigenous water values. The first water walk by 77 year old Anishnaabe grandmother Josephine Mandamin to raise awareness about water pollution and abuses occurred in 2003 around Lake Superior and covered more than 1300 km. It inspired an annual water walk that seeks to remind people in the Great Lakes region and across Canada about their responsibilities related to water. At the time of her death Josephine Mandamin had walked over 25,000 km and these annual water walks continue to highlight Indigenous values related to water. Each walk works to raise awareness about water and to change the perception of water from that of a resource to that of a sacred entity.
Chiefs of Ontario Water Declaration
In 2008, the Indigenous organization, Chiefs of Ontario released their Water Declaration as First Nations on Turtle Island and occupants of the Great Lakes region from time immemorial. This declaration includes clear statements of Indigenous water values and rights. The text in the document clearly outlines the relations, values, conditions and rights that many of Canada's Indigenous peoples hold related to water. https://www.afn.ca/uploads/files/water/08-10-00.pdf
Indigenous Youth Water Activist Autumn Peltier
At the age of 12 Autumn Peltier Anishinaabe water youth activist and member of the Wiikwemkoong unceded territory on Manitoulin Island in Lake Huron in the Great Lakes, gained national attention when she confronted Canada's Prime Minister Justin Trudeau during the 2016 First Nation's annual meeting expressing her concerns about the long-standing boil water advisories and lack of safe drinking water in various Indigenous communities across Canada and Trudeau's support for controversial gas pipelines. In 2018, at the age of 13, she addressed world leaders at the UN General Assembly on the issue of water protection. Her words on the global and national stage embody Indigenous water values. In 2019 she was named the chief water commissioner in 2019 by the Anishinabek Nation, a position previously held by her great-aunt Josephine Mandamin. She is considered a "Water Warrior" using social media and her voice share Indigenous water values in the world and Canada to change water governance.

In the past several years there seems to be a slow progressive global movement to recognize that Indigenous peoples have much to offer in terms of teaching modern societies about water values. For Indigenous peoples, human rights are secondary to the roles and responsibilities humans should have as caretakers of ecosystems. This societal values approach has different implications for water governance and stewardship than those who advocate for a more anthropocentric approach based on fundamental human rights. This also relates to the UN Declaration on the Rights of Indigenous peoples, which Canada has been slow to adopt but is an important example of the close relationship between land, water and human rights.

Water values and human rights

Over the past two decades, considerable efforts have been made to advance water values and ethics on the international front related to water as a fundamental human right. In 2002, the United Nations Committee on Economic, Social and Cultural Rights adopted General Comment No. 15, stating that "the human right to water is indispensable for leading a life in human dignity. It is a prerequisite for the realization of other human rights" (UN, 2002). In 2010, the UN General Assembly explicitly recognized the human right to water and sanitation through a formal resolution: it acknowledged that clean drinking water and sanitation are essential to the realization of all human rights (UN, 2012) and this approach was also included in the Millennium Development Goals (MDGs).

There is now a substantial literature on water as a human right. As of 2015, some 52 countries had accepted the human right to water and sanitation in their laws and policies (Brunner et al., 2015) and South Africa has the right to water in the constitution. At the core of the human right to water is a normative principle of water access for all (Schiff, 2016), water as a public good, and the view that the state should ensure equal access and citizens have rights to clean water (Prieto, 2021, 11). This human-right-to-water view has an inherently anti-privatization and anti-commodification value set and a core component of the human rights framework is that water pricing and water allocation should be determined within the framework of social equity and the state must ensure equal access and distribution (Prieto, 2021). The scholarship on water as a human right is also closely aligned with the concept of water equity (Whiteley et al., 2008; Goff and Crow, 2014) and includes both individual and collective rights.

This approach consists of inherent human values related to water but is also aspirational in water governance as water rights and access are not equitable. Human rights are not equitable for all people. There is a significant body of literature highlighting how and why water security and access are not equitable in many societies. Those with lower socio-economic means, women, people of color, youth and other marginalized publics do not have equitable access to water (Donoso et al., 2021). The focus on drinking water (Goff and Crow, 2014) has also had negative consequences in terms of equity. In addition, private property is also viewed as a human right and there is an inherent tension between private water values and public water access (Prieto, 2021, 14). In addition, human rights are "ideals to which governments can and should aspire, but they remain just that—ideals—unless states internalize their implementation and take compliance" (Schiff, 2016, 277).

The Canadian case is again useful for illustration purposes. In an excellent case study by Schiff (2016), it is clearly documented that from 2002 to 2012 Canada opposed international moves to formalize water as a human right. Only after years of global pressure and consistent and dedicated lobbying by the Council of Canadians did Canada finally recognize the human right to water in June 2012 at the UN Conference on Sustainable Development (Karunananthan and Willows, 2012). Following this agreement, the challenge was for NGOs to continue applying pressure to the Canadian government in the hopes that it would internalize its international commitments within domestic water policy (Schiff, 2016).

Using the case of long-standing violations of basic human rights to clean water in many of Canada's Indigenous communities and the decades long boil water advisories, Schiff presents compelling evidence that outwardly Canada appears to be complying with its international water rights commitments but upon closer analysis has only superficially, rather than substantively, altered its behavior regarding water provision in Indigenous communities since its 2012 international acknowledgement of the human right to water (Schiff 2016). Despite enacting the Safe Drinking Water for First Nations Act (SDW Act) in 2013, her research provides convincing evidence that there has been a '*masquerade of compliance*' rather than true internalization of an emergent international human rights norm related to water (Schiff, 2016, 278). Almost 10 years later, this remains the case, despite a change in government in 2015, a formal commitment to national recognition and responsiveness to the Truth and Reconciliation Commission Calls to Action, and a formal commitment to eliminating all boil water advisories by 2021. At the time of writing, the landscape in Canada is an evolving one and the Trudeau government has stated that Indigenous engagement will be a key pillar in the establishment of the new Canada Water Agency and the long-overdue update of the Canada Water Act. However, sadly, Indigenous peoples are still being denied a fundamental human right to clean water in Canada.

Societal water values, infrastructure and the built environment

In addition to Indigenous and human rights approaches, there are a number of alternative approaches to water governance based on societal values that relate to core human uses of water, wastewater and stormwater services. Broadly these societal values are articulated related to water infrastructure and sanitation. For illustrative purposes, we highlight three such approaches in this section.

The first approach is what some scholars and practitioners refer to as the necessary value shift required in water governance systems from the 'hard path' to 'soft path'. The hard path refers to water societies and policy regimes that rely on centralized, engineered infrastructure and related decision-making values including: dams and reservoirs, pipelines and treatment plants, water departments and agencies where natural *sources* of water are typically shared, but the *end use* is not (Wolff and Gleick, 2002: 1, 7). Some even argue that this hard path in water policy leads us to an impoverished environment, undemocratic decision making, with growing social, political, and economic costs (Christein-Smith et al., 2013). Other scholars have made water values more central to the soft path arguing the soft path involves social choices and cultural values. In Canada, Oliver Brandes et al. argued over a decade ago that "a new script for water management is emerging" (2007) and that a new set of water values is shifting water policy in Canada from a hard path to a soft path (Brandes et al., 2007: 292). In this perspective, "[s]oft path analyses and strategies are explicitly normative establishing the values of sustainability and equity as social goals and promoting the changes in technology, institutional structures, and personal consumption patterns needed to achieve those goals" (Brandes et al., 2007: 293). While the soft path features some different ideas and values related to water policy and management (Brooks et al., 2009), it does not contain a set of ideas that fundamentally challenge the dominant anthropocentric policy frame that is centered on human use and economic development values. These values are also reflected in both the green infrastructure and "one-water" approaches.

The second approach is generally referred to as the shift from gray to green infrastructure related to uses of inland waters. Gray infrastructure forms the backbone of water systems in many communities and cities across Canada. It consists of engineered systems for managing water and connecting residents, industries, and a wide range of users to water and wastewater systems. Sewage, or used water, is channeled through gray infrastructure to treatment facilitates and then, in most cases, to receiving bodies such as rivers and lakes. These systems, which have been at the heart of water policies in Canada since before Confederation, underpin what Jamie Benedickson has called our "culture of flushing" (2007). In the past 20 years, the concept of green infrastructure has evolved in policy and scholarly discourse and research. Green infrastructure includes a wide range of natural vegetative systems and green technologies that provide many environmental, economic, and social benefits. At the core of this discourse related to water is the idea that a new set of values related to water is central to making the shift from gray to green infrastructure. Faith is placed in small systems, innovative technologies, and green infrastructure installations that reflect a fundamentally different set of water values. A growing literature explores the challenges of using and implementing a green infrastructure approach, particularly given the dominance of gray approaches ossified in policy regimes and evidence that there is not a shift in values occurring but more of a slow integration with gray approaches (Dhakal and Chevalier, 2016, 2017; Johns, 2019).

A third approach is what is referred to as the "one-water" approach (USWA, 2017). It builds on IWRM approaches on the global scale, but attempts to integrate new values related to water use in the future. Similar to green infrastructure approaches, the one-water approach challenges the conventional water paradigm and the dominant paradigm of centralized and siloed systems as well as short-term and fragmented views of water (Mukheibir and Gallet, 2014). The Water Research Foundation in the US has outlined that this approach requires a new blueprint for water users and the water industry by removing the value, technological, policy and management barriers traditionally separating water, wastewater, stormwater, and water reuse (WRF, 2017). The values that underpin 'one-water' approaches are fundamentally conservationist and anti-waste. The approach draws on global models of closed water systems, water recycling, and water-reuse technologies and policies. Recent scholarship on the circular economy is also reinforcing the values of not wasting water and valuing water for multiple and repeated uses, rather than single uses that return water to the natural environment. This approach is also based on faith in technologic futures. The main principle is that humans are stewards who hold some specific responsibilities related to water but that technology offers a new frontier for shifting and improving human uses of water through more integrated and responsible systems.

Economic valuation approaches

Some of the most common approaches to understanding and thinking about societal values related to inland waters stem from economic valuation approaches. Societal values that are more anthropocentric start from the human use values of water. Indeed, the United Nations states that "economics is the most widely applied framework for valuing water" (UNESCO, 2021, 21). There is a voluminous literature on economic and ecosystem services valuations of water. For purposes of this chapter, these two broad approaches to societal values are briefly reviewed in this section.

It is not surprising that the dominant societal water values are fundamentally economic values. In addition to the reality that the major water uses globally and in most nations are agriculture, industry and energy, the global water industry has an estimated value of over US$300 billion (Fidelity International, 2017). The S&P Global Water Index included more than 50 companies from around the world that are involved in water related investment businesses and research indicates that investment in the water industry is motivated by strong historical and anticipated future rates of return through various investment strategies and assets (De Duonni et al., 2019, 109). These powerful economic realities mean that societal values that underpin water economics in capitalist economies are fundamentally based on water use, extraction, technologies, commodification and public and private profits from water.

Societal water values based on economic valuation are inherently based on property rights, land rights, riparian rights, water rights and water entitlements. In the most market-based forms this take the form of tradable rights to access an exclusive share of a water resources, water entitlements and water access that are regarded as assets that have the potential to provide substantial returns to investors (De Duonni et al., 2019, 94). Economic valuations and the wide range of methods used to value water in the world reflect these values (UNESCO, 2021).

In Canada and the Great Lakes region, these historical water rights and values underpin both water quantity and quality policy regimes. They are institutionalized into water governance institutions and policies at all levels (Sproule-Jones et al., 2008). These water values are also embedded in citizen behavior related to water use and for many citizens their primary interactions with water are transactional and economic. There are some important variations in systems of abundance vs. systems of scarcity related to economic valuation approaches that are evident in Canada and other jurisdictions.

In the proposed Water Values Charter, economic water values are included as economic principles that should guide water use. As outlined in Table 4, they incorporate primary human-centric water values but when combined with the other sections of the Charter a more wholistic and ecological set of values is proposed.

There are also some tools that try to enlighten citizens around the values they have for water using the approach. For example, the water footprint is a tool used as an indicator of freshwater use that calculates both direct and indirect water use of a consumer or producer, and can be calculated for a particular product, for any well-defined group of consumers or producers, and for individuals (Hoekstra and Mekonnen, 2012). Tools such as these highlight the increasing awareness that some citizens and jurisdictions have related to their impact on water, and the multi-dimensional value that water has beyond strict economic value.

There is increasing recognition that societal values of inland waters must include both monetary and non-monetary values. This is reflected in the concepts of natural capital, blue-accounting, and ecosystem services. Ecosystems services are the benefits that people obtain from healthy ecosystems (Pardy, 2014). The concept provides both a value-orientation and a methodology for the economic and social valuation of such benefits. Common understanding of the value of ecosystems was greatly assisted by the 2005 Millennium Ecosystem Assessment which provided an essential typology of four categories of ecosystem services (Millennium Ecosystem Assessment, 2005) and the World Resources Institute (WRI) guidance on methodologies for review of ecosystem services.

Scholars and policy practitioners from jurisdictions around the world are using ecosystem service valuations to try to forefront ecological values in systems where economic values of water dominate. Ecosystem services valuation has been used by policy makers and water managers at the transboundary scale as well as at the local scale to force comprehensive reflection and thinking about societal water values related to inland waters. This approach inherently put ecosystems and the ecosystem approach at the heart of water valuation. It also highlights that many societal water values are at play and forces a dialog related to the inherent values that healthy ecosystems provide to humans that need to be recognized and valued properly. While ecosystem service valuation is primarily used by practitioners, when combined with tools such as the water footprint calculator, it can also be used to reveal and assess water values at the individual level.

Water values, public opinion and public policy

Most citizens express the value of water in their daily lives and recognize the value of water to their individual health, their livelihood, their communities, national identity and global well-being. Public opinion research reflects these social perceptions and

Table 4 Economic principles and water use.

Water Ethics Charter economic principles which should guide water use:
• User-pay and polluter-pay principles;
• Principle of cost-recovery for water services;
• principle of fair, transparent, and efficient financing arrangements for water-related investments;
• Principle of monitoring and sharing information about the status of water stocks (feeding into the principles of education and knowledge governance).

Source: Water Ethics Charter Section 3b.

Table 5 Key findings from Canadian water attitudes survey.

Highlights from the 2017 National Survey

- Almost all Canadians (93%) "strongly agree" (59%) or "somewhat agree" (34%) that access to water is a human right
- 45% of Canadians continue to view freshwater as Canada's most important natural resource
- More than half of Canadians "strongly agree" that water is an important part of Canada's national identity
- 60% feel freshwater is very important to Canada's national economy; another 34% say it is somewhat important
- 79% are "very" or "somewhat" concerned about water conditions on First Nations reserves.
- Nearly half of Canadians "strongly agree" that commercial enterprises should pay the full cost of delivering and treating the water they use (49%) and obtain licenses for groundwater use (48%), and that there is a need for stricter rules and standards to manage water use by industries and municipalities (45%)
- Canadians feel they are individually making reasonable efforts (86%) to conserve freshwater
- 92% think that developing stricter rules and standards to manage water use by industry and municipalities is the best way Canada can better protect and manage freshwater

Source: RBC National Canadian Water Attitudes Survey, 2017. http://www.rbc.com/community-sustainability/_assets-custom/pdf/CWAS-2017-report.pdf.

Table 6 Societal water values: the Great Lakes case.

- 90% of respondents indicated it is very important that the health and water quality of the Great Lakes basin be protected
- 35% felt governments should be responsible for protecting the lakes; with 29% indicating responsibility should be shared by all (governments and individuals)
- 84% indicated the very important role of individuals and households in protecting the health and water quality of the Great Lakes
- 59% felt there are too few rules, regulations and actions in place to protect the Great Lakes
- 51% indicated they would be willing to pay more to protect the lakes if it resulted in higher costs of consumer items;
- 25% indicated they would be willing to pay $20 more per month on their water bill to protect the Great Lakes; but 30% indicated they would not be willing to pay more
- 46% indicated they use the Great Lakes for leisure or recreational purposes each year; with 91% indicating it is very important that the lakes are of sufficient quality for leisure and recreational purposes
- 80% indicated actions should be taken now to ensure the health and water quality of the lakes for future generations

Source: International Joint Commission (2021). *Great Lakes Regional Poll, draft report to the Water Quality Board*, February 2021. Great Lakes Regional Poll.

values around the world. Unfortunately, the World Values Survey does not include any questions related to water values (WVS, 2021). However, there are many public opinion surveys and polls that do try to gauge human values related to water. Two examples will be reviewed in this section: the Canadian Water Attitudes Survey and the Great Lakes Regional Poll.

For 10 years the Royal Bank of Canada, under its Blue Water program, conducted national surveys of Canadians about their values and perspectives on water. Consistently Canadians reported that they significantly valued water. As outlined in Table 5, the vast majority of Canadians feels water is a human right, that it is one of Canadas most valuable natural resources, that they are concerned about water inequality related to Indigenous peoples and water is central to the Canadian economy. Significant numbers of Canadians also feel governments play an important role in regulating water use and leading water protection. Although the RBC discontinued this poll in 2017, more recent polls of Canadians as residents in the Great Lakes region show these values related to water also hold in the shared context of the Great Lakes region.

A poll of 4550 residents of the Great Lakes region indicates citizens place a high value on the water quality of the lakes. As outlined in Table 6, high percentages of residents feel it is very important to protect the lakes, both governments and citizens are responsible for the lakes, and that they value the economic and recreational benefits provided by the lakes.

The poll also asked many questions about issues facing the lakes and provides some interesting insights into water values, ethics, and behavior. Residents reported most concerns with pollution (41%), invasive species (18%) and algae (8%). Although respondents clearly view individuals, governments, and industry as having responsibilities for water in the Great Lakes, there is not a lot of knowledge about how their own values and behaviors connect to the protection and state of the lakes. However, some populations seem to have particularly high levels of awareness grounded in a different set of values. The IJC's most recent poll included 500 Indigenous participants. Survey results show consistent and strong support for Great Lakes protection as well as high levels of awareness of the lakes and the issues affecting them. Some 49% of Indigenous respondents reported that the ways they engage with the lakes were threatened because of the poor health and water quality of the lakes (IJC, 2021).

Societal values, water and policy: Knowledge gaps

From this review of some of the alternative approaches to understanding societal values related to inland waters it is evident how societal water values are critically important in water science, governance and stewardship. As outlined in the sections above, many organizations and coalitions around the globe are in favor of developing new principles, guidelines, charters, and standards to support different water values and better water stewardship. There have been increasingly calls for making water values and ethics more central in water governance and policy at the global scale (Groenfeldt, 2019a, b; Stefanovic and Adeel, 2021) and in countries

Table 7 Six imperatives for a new water ethic.

1. meet basic human needs to enhance equity today and for the future
2. safeguard ecosystems by allocating sufficient water resources
3. encourage efficiency and conservation of water resources
4. establish open and participative decision-making processes
5. respect system complexity and emphasize precaution
6. 6. see multiple sustainability benefits from water centered initiatives

Source: Matthews, C, Gibson, and Mitchell B (2007) Rising waves, old charts, nervous passengers: Navigating toward a new water ethic. In: Bakker K. (ed.) Eau Canada: The Future of Canada's Water, 335–358. Vancouver: UBC Press (353).

such as Canada (Stefanovic and Adeel, 2021; Johns, 2021). The main knowledge gaps relate to deepening our understanding of the importance of water values and how they vary across societies, cultures, and watersheds. A secondary knowledge gap is learning more about how societal values interface with governance and public policy.

A values-based approach requires some faith that our beliefs may legitimately change over time, with new knowledge and evidence. Groenfeldt and Schmidt argue several policy approaches can be used to integrate a values-based perspective into water policy and enhance "explicit attention to underlying values" (2013:14). One fundamental step toward such change is to make values an explicit part of policy processes and discourse. Charters and statements are viewed as a way to align individual, organizational, and broader policy goals. If used as part of a broader values-based approach to policy development, implementation, and evaluation, they can be the source of what Groenfeldt and Schmidt call a more "explicit attention to underlying values" (2013).

In Canada, scholars such as Matthews et al. (2007) argue that there are some basic components of a new water ethic. Based on the scholarly literature, they argue six imperatives from the literature that must underpin a new water ethic (Table 7).

They argue that a new water ethic in Canada must be "incorporated into mainstream legislation and regulation, policies, programs, and project planning decisions so that, gradually, these underlying ideas become the assumed normal framework for water-related choices" (Matthews et al., 2007: 353). However, they also note that "a new water ethic is no magic wand" (2007: 355). There is very little evidence that Canada is explicitly placing water values at the heart of water governance and policy (Johns, 2021), although the recent federal government's announcement of its intention to create a Canada Water Agency and year-long public consultation has clearly generated some important discussion about water values in Canada, particularly related to Indigenous peoples and values.

One of the most common ways for policy practitioners to incorporate a values-based approach in everyday discourse and decision-making is through the use of a values lens. Lenses require policy practitioners to explicitly view policy from a certain perspective. They tease out underlying values that are embedded in policy processes, language, and documents. The water footprint and ecosystem services valuation approaches and tools discussed above are examples. Another example is the Water Culture Institute's Ethics-Based Decision Support Tool for guiding technology, policy, and investment decisions in the water sector (Water Culture.org, 2016). "It is intended for cities, watershed, and river basins, but could be applied at any level. Through a process of interviews and facilitated workshops, water stakeholders are guided through a process to document their priority values about local water and water ecosystems. The tool orders these values into a systematic framework, which can then be incorporated into existing local water governance arrangements" (Water culture.org, 2016). Another example is the Water Culture Institute's Handbook for Crafting a Local Water Ethics Charter (Water Culture.org, 2017).

The development and use of such tools are based on the assumption that policies are more likely to be developed, adopted, and implemented successfully when a values-based approach is used that engages a diverse set of policy actors with different sets of water values in dialog. The potential exists to develop similar tools to move toward more reflection, discussion and knowledge about current water values to improve water policy outcomes and governance in the future.

Conclusions

There are numerous, and often competing, ideas and values related to water globally and in different jurisdictions. A review of some alternative approaches in this chapter highlights that in any given society or jurisdiction, there are multiple values and approaches at play in the public debates, discourse, science and policy. The illustrative examples and cases from Turtle Island, specifically Canada and the Great Lakes region, highlight how these different, and often competing, values co-exist and underpin water policy. This review also highlights how there is a need for values to be reconciled, and the trade-offs between them resolved and incorporated into more equitable water governance and decision-making processes. No water governance systems and public policies are value neutral and a focus on societal water values related to governance and policies in various jurisdictions and watersheds reveals the complexity of water values.

A focus on water values and ethics explicitly recognizes that different governance constellations have the effect of legitimating certain normative positions while undermining others (Schmidt, 2012: 61). Some argue that the true driving forces behind water

governance and management are always economic and political powers, and that any attempt at change will not be successful (Rossi, 2015: 100). However, a societal values-based perspective places some faith in policy change and the central role of values in fostering that change, whether gradual or radical. Public policy scholars have demonstrated that by focusing on who participates in policy discourse, which existing ideational policy frameworks and values are dominant, and how alternative ideas are ignored or marginalized in the policy process, practitioners and scholars can become more aware of the ideas and values that are institutionalized in public policies and overcome barriers to policy change (Roe, 1994; Schmidt, 2008, 2011). Water ethics scholars affirm that moving toward a new water ethic requires "understanding the ethics we have" and making a concerted and intentional effort to incorporate more and stronger ethics into policies. It requires "defining the ethics we want," "making ethics explicit," and "comparing and debating competing ethical paradigms" as key parts of moving toward alternative water values and a new water ethic (Groenfeldt, 2019a).

The imperative of centering water values in governance and public policy will only become more important. Future water stress, crises and conflict, climate change and digital water futures are going to make societal water values increasingly significant. Reductions in time and space will also make water values more global. The way forward, therefore, will be to further develop common approaches to valuation where feasible, but also to prioritize improved approaches to compare, contrast and merge different values, and to incorporate fair and equitable conclusions into improved policy and planning (UN, 2021, 1). Effective water governance acknowledges competing values and adjudicates public disagreements about the meaning, purpose, and value of water (Gober, 2018, 91). By examining societal values related to inland waters on which humans and ecosystems depend, water governance systems will be better able to learn and adapt to looming water challenges.

The long-term success of governing inland waters will depend on how water values and equity are integrated into future water governance approaches.

Knowledge gaps/future research

This chapter attempts to make a contribution to broadening the study of inland waters at the interface between water values and public policy. There is also considerable scope for future interdisciplinary research that might focus on:

- intersectional approaches to valuation, policy and equity
- social and environmental justice related to water values
- Analysis of water laws and legislative values in specific jurisdictions
- comparison of water values across regions and watersheds
- water values related to coastal waters and oceans
- how water values may vary related to surface and groundwater
- analysis of water values in global public policy and international organizations
- the interface between societal water values and science
- Indigenous water values and knowledge

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Freshwater Governance and Resilience

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Catherine Febria and Gail Krantzberg.

Glossary

Adaptation An incremental change that allows the system to retain its basic functions and characteristics.
Adaptive cycle The cycle of development and decay of a social-ecological system over time.
Anthropocene An unofficial geological epoch, referring to a new human-dominated period of the Earth's history.
Complex adaptive system A special type of system that is complex (i.e., it is made up of multiple interconnected elements) and adaptive (i.e., it has the ability to change and learn from the experiences).
Equity Fairness in access to and use of natural resources, and also in their decision-making.
Governance A set of actors and formal and informal mechanisms to coordinate a social practice towards a collective goal.
Human agency Ability and power of individuals to think and act independently and to make their own free choices.
Management Day-to-day actions and decisions to conduct or supervise a system.
Panarchy A nested set of adaptive cycles that influence each other.
Persistence Capacity of a system to resist change and maintain the same functions.
Power Ability to take part in and influence decision-making processes.
Resilience Capacity of a system to absorb disturbance while maintaining its essential structures, functions and identity.
Social-ecological system Integrated system in which human society, and its multiple cultural, political, social, economic, institutional and technological expressions, interact with ecosystems.
Transformation Radical change to shift a system into a new state.

Introduction

Water issues are largely issues of governance (Rogers and Hall, 2003; OECD, 2011). That is, the decisions we take to set directions for, and manage, water resources have enormous implications for water quality and availability. A system can be pristine, but if poor direction-setting and day-to-day management occur, over time that system will likely degrade. Similarly, a freshwater system with serious challenges may be improved with consistent decisions that have a positive impact. In this chapter we focus on freshwater governance and management from an integrated social-ecological systems perspective, and how it connects to the concept of resilience.

An integrated social-ecological systems perspective on water systems

Humans are undoubtedly having unprecedented impacts on ecosystems, and this includes freshwater systems (Steffen et al., 2007). Geologists are contemplating a decision to deem our current time the era of the Anthropocene, acknowledging that humanity has become a major force for global change (Lewis and Maslin, 2015). We see the impacts of humans on freshwater systems in many ways, including pollution, distribution and availability, the rise of invasive species and habitat degradation. Humans are closely interconnected with freshwater systems-we recreate in them, we draw on them for our needs, we build in them, next to them, we enjoy their beauty, we redirect water, add to it, take away from it. These interactions are just that—interactive. Recognizing that human and ecological systems are highly interconnected, we can refer to them as 'social-ecological systems' (Berkes and Folke, 1998; Colding and Barthel, 2019). Freshwater systems respond to our uses and impacts and change, which causes us to respond to those changes, and so on.

Complex adaptive systems

Social-ecological systems—that social and ecological systems are highly intertwined and are constantly interacting—represent a type of complex adaptive system. 'Complex' refers to the many parts of a system and the interactions both within the parts of the system, at a range of geographic extents and institutional levels and across time. These interactions can have unpredictable outcomes. 'Adaptive' means that the system is capable of changing in response to interactions, including purposive actions by humans to adjust to changing conditions, so that the system behavior as a whole is determined from the many interactions among the parts of the system, both human and ecological. This behavior is not always consistent over time—a major disturbance can have impacts that result in a re-organization of the interactions within the system—but interactions are path dependent. Path dependency means your current behavior is dictated to some extent by previous behavior. For example, we are more likely to sit in the same seat in a classroom over repeated visits than to change seats each time we enter the room. Understanding freshwater systems as complex adaptive systems is critical to how we define resilience and the suite of options we see as possible for freshwater system governance (Biggs et al., 2012; Bohensky et al., 2015).

Social-ecological systems example: Wetlands and agriculture

Let us consider an example (adapted from AgWeek, 2012) to help illustrate these concepts: A farmer drains a series of wetlands to convert them into agricultural land and to therefore increase crop production. The water that would have accumulated in those wetlands is now distributed across the surrounding area. In the following year, the farmer's land and surrounding fields experience more flooding which negatively impacts crop yield. The farmer, after a few years of consistently wet land, decides to install physical infrastructure to create better drainage for the land to support crop production. Now, the water flows very quickly off the affected land and floods an adjacent field. The farmers of adjacent land also put physical infrastructure in place to drain their land and as a result, periods of wet weather result in very substantive releases of water from these fields, which greatly increases flooding downstream. This new flooding prompts the region's government and residents to come together and discuss ways to mitigate flood impacts by managing water releases from their individual fields. As long as farmers work in a coordinated way (in deciding for example about the timing of water releases), flooding is minimized.

From the above example, it is clear that human / social systems and freshwater systems are closely connected and interact, with feedbacks influencing future conditions and decisions. This way of thinking about the relationship between humans (and the social system within which they operate) and ecosystems is called a 'social-ecological systems' perspective.

When we view freshwater systems as being interconnected with social systems, then the importance of our decisions and actions becomes clear. And, the ways in which we act, who we involve in decision-making, how the decision-making process is structured, and the flexibility to adapt or transform how we interact with freshwater systems are all critical to the quality of those social-ecological interconnections. The remainder of this chapter will describe current understandings of freshwater management, freshwater governance and finally, freshwater resilience as an overarching concept that requires appropriate management and governance in social-ecological systems and in light of our potential entry into an era defined by human impact on the planet.

Water management and governance

Decision making and actions related to freshwater are called 'management' and/or 'governance'. Freshwater management is defined as "the activities of analyzing and monitoring water resources, as well as developing and implementing measures to keep the state of a water resource within desirable bounds." (Pahl-Wostl, 2015, p. 27). Freshwater governance consists of the formal and informal institutions and processes by which multiple actors work together to set rules for water (and to set desirable outcomes) (Rogers and Hall, 2003; Lautze et al., 2011). Governance is a more encompassing concept than government. Governance includes government as well as informal and non-governmental mechanisms. Water governance is defined as "the social function that regulates development and management of water resources and provisions of water services at different levels of society and guiding the resource towards a desirable state and away from an undesirable state." (Pahl-Wostl, 2015, p. 26). In essence, it sets the directions or scope of work for water management. A boat analogy can be useful to understand the difference: management is like the rowing or propulsion mechanism, while governance is like the steering mechanism or direction setting towards a collective goal. The two work

hand-in-hand to maintain a desirable trajectory. Likewise, governance and management work together to impact (positively or negatively) freshwater systems and their trajectories. However, the boundary between management and governance is much less obvious than the distinction between rowing and steering. Actions and decisions blur the line and so we bring these terms together for the purpose of the chapter and refer to both together as 'water governance' from here forward, recognizing that this broadly refers to the actions and decisions that impact freshwater systems.

What is 'good governance'?

Governance is generally assumed to exist for the betterment of society. Early approaches to water governance emphasized the role of government and regulation for solving problems. These approaches are referred to as 'command-and-control' and tended to work well in situations where there was a defined issue (e.g., a pollutant entering a waterway) and a known source (e.g., an identified polluter with a specific location of pollution). However, many freshwater issues are complex (that is, they have multiple component parts that interact in sometimes unpredictable ways, and no one person or entity has full information/knowledge about them) and approaches that focus only on government decision-making and action are considered insufficient to address complex issues (Holling and Meffe, 1996).

There is no one definition of good water governance. However, there are generally accepted conditions that are exhibited in good governance approaches. These include: participation and inclusiveness, openness and transparency, accountability and integrity (corruption control), predictability provided by the rule of law, efficiency and effectiveness, and adaptability (Rogers and Hall, 2003; Lautze et al., 2011; Jiménez et al., 2020). Good water governance recognizes that no one authority or person has the potential to fully understand freshwater systems, and that meaningful participation by a wide range of actors (e.g., governments, civil society, private sector, Indigenous government) benefits governance outcomes. Further, addressing issues at the level in which they occur while coordinating with other decision-making bodies within and across levels of organization (e.g. from local to international)—called polycentric governance—is usually desirable.

How governance is connected to resilience

Resilience, as used here, has its roots in ecology. Buzz Holling, widely considered the originator of the concept within this field, used resilience originally as a way to explain and understand the capacity of ecosystems to persist within a specific state despite changes, or disturbances, to the system (Holling, 1973). From this initial thinking, resilience has expanded to the consideration of how humans, or social systems, interact with ecosystems (that is, a social-ecological system). 'Social-ecological resilience'—the application of the concept of resilience to social-ecological systems—is now its own topic of study and lens in which to view systems generally, and water systems (including freshwater systems) more specifically. Governance is a core consideration in resilience when we approach it from a social-ecological systems perspective because the processes of decision-making and the structures we as societies have created to do so (both formal like governments and laws and informal like networks of individuals with similar interests and unwritten rules of social behavior) have enormous implications for how freshwater systems function, and are affected by ecosystem dynamics. These feedbacks occur in ongoing cycles, leading to the building or degrading of resilience (Gunderson and Holling, 2002). Governance processes and structures that support social-ecological resilience include:

- Inclusive participation in decision-making, considering diversity and equity.
- Effective and strong leadership.
- Polycentric governance (described in more detail in Section "Resilience principles").
- Consideration of social memory (i.e., the accumulated experiences and knowledge within the system to cope with uncertainties and to build resilience).
- Capacity for self-organization (i.e., the ability of actors in localized interactions to form emergent 'order').
- Adaptable and flexible decision-making processes and institutions.
- Precautionary risk management.
- Inclusive considerations of system needs, benefits, and tradeoffs (Plummer et al., 2014; Plummer and Baird, 2020).

We will address the multi-faceted nature of resilience first, then how systems build and degrade resilience over time in the following section.

Resilience definitions and principles

Resilience, ultimately, is about how 'disturbances' (i.e., changes—whether known or surprising) affect the social-ecological system. Disturbances can be planned, for example, a policy decision made by a government that has impacts on freshwater systems such as expanding or contracting wetland protections. Disturbances can be surprising, for example, an extreme weather event that was not predicted that has major impacts on shoreline erosion. Disturbances can also be acute (quick to occur and short-lived) or more chronic in nature (slower to emerge, lasting a longer time). Further, disturbances can occur, and have impacts on, multiple levels,

from local to global. For example, a single occurrence of an invasive species introduced to one location in a freshwater system such as the Great Lakes may have much larger impacts on the system if the conditions are conducive to their propagation. Conversely, decisions made at a national level about programs or funding may have very specific impacts at the local level. Due to the complex nature of disturbances (their variety, predictability, and durability) and their impacts, it is difficult or impossible to predict all disturbances and plan for them. However, thinking about freshwater governance in terms of resilience offers a way to manage uncertainty and surprise, and to deploy coping mechanisms.

Definitions of resilience

Resilience has different interpretations depending on how you answer the question: 'Resilience of what?' (Walker and Salt, 2012; Rodina, 2019). If the focus is on, say, infrastructure within a system (e.g., a dam), then resilience is likely about withstanding or resisting disturbance. This is what is commonly referred to as 'engineering resilience'. If the focus is on communities (e.g., a specific group within a city) then resilience is likely about persisting despite, or adapting to, disturbance. This is referred to as 'community resilience'. There are many different ways to answer the question 'resilience of what?' and several definitions of resilience that address the diverse interests in it. In this chapter we focus on the resilience of social-ecological freshwater systems (a type of complex adaptive system) and so we adopt a definition of resilience that is consistent with that focus: the ability of social-ecological freshwater systems to persist, adapt or transform in the face of constant, and sometimes surprising change, in order to continue to support human wellbeing (Plummer and Baird, 2020; Folke, 2016).

Resilience terms

In the definition of resilience above, we use the terms 'persist,' 'adapt,' and 'transform.' Each of those terms are explained in turn here (Baird et al., 2020a):

Persistence: the capacity to resist change (that is, absorb or withstand stresses) as a result of a disturbance. The goal of persistence is to maintain the same functions of the system post-disturbance as existed pre-disturbance. For example, several Areas of Concern (rivers and watersheds where water quality has been substantially degraded over time) within the North American Great Lakes have been 'remediated' to a previous standard of water quality through government-initiated Remedial Action Plans (Hartig et al., 2020; Baird et al., 2020a).

Adaptation: the ability to adjust or change how a system responds to disturbances in order to maintain the same functions over time. These changes are usually incremental in nature and meant to maintain the current system, which distinguish them from transformations (below). For example, the Saint John/Wolastoq River Basin that extends across parts of Quebec, Canada and Maine, United States and much of New Brunswick, Canada is a stressed watershed that still provides well-being to people and contributes to ecosystem health. The system requires additional adaptive capacities to continue to provide well-being over time, and especially in light of increasing impacts of climate change (Baird et al., 2020a).

Transformation: major shifts in how resources, authority and power are structured and interact within a system, usually in response to a major disturbance that makes the current system structure no longer feasible to maintain. Transformations represent a holistic re-organization or the system, everything from people's values and beliefs to how decisions are made to how societies connect with ecosystems are changed. An example of this is the Cowichan Watershed in British Columbia, Canada, where system-level change is being actively pursued to manage the watershed differently, emphasizing Indigenous authority and preparedness for the surprises that climate change is likely to impart (Cowichan Watershed Board (CWB), 2018; Baird et al., 2020a).

Depending on the system's ability to function in a way that provides human wellbeing (including long-term ecosystem health), there may be one of these goals: persistence, adaptation, or transformation that becomes most important. Resilience can be built or shaped in ways that supports these goals.

Resilience principles

What is social-ecological resilience as it relates to freshwater systems and governance? There are seven principles that are important to resilience (Biggs et al., 2012). A few notes are worthwhile here: first, that these principles relate to the social-ecological system. The focus of this chapter is on freshwater system governance and so the explanations of the principles were developed with governance as the focus. Second, that these principles have somewhat fuzzy boundaries: there is some overlap and certainly relationships among them (e.g., such that increasing one principle also increases another) (Biggs et al., 2012). A graphic illustration of the principles is presented in Fig. 1.

1. *Maintain diversity and redundancy*: Diversity refers to the variety of elements and their relative abundance within the system, while redundancy refers to overlap in terms of the functions of those elements. These two concepts seem to oppose each other but actually work together. Diversity and redundancy working hand-in-hand provide options for how to respond to a disturbance. For example, if there are multiple non-governmental organizations (diversity) working to conserve a wetland area, and their work overlaps somewhat (redundancy), then if one or two lose their funding (disturbance) then conservation work continues and other non-governmental organizations may be able to address the gaps left by those organizations that lost funding.

   However, very high levels of diversity and redundancy can reduce the effectiveness and efficiency of governance, and even undermine resilience. High diversity increases the complexity (e.g. more groups involved in governance) and potential difficulty in responding to changing conditions, and high redundancy means a lot of overlap in governance roles and responsibilities which can be costly. Conversely, low diversity and redundancy mean that there are fewer response options and adaptation to change may be difficult. Accordingly, a balance must be struck.

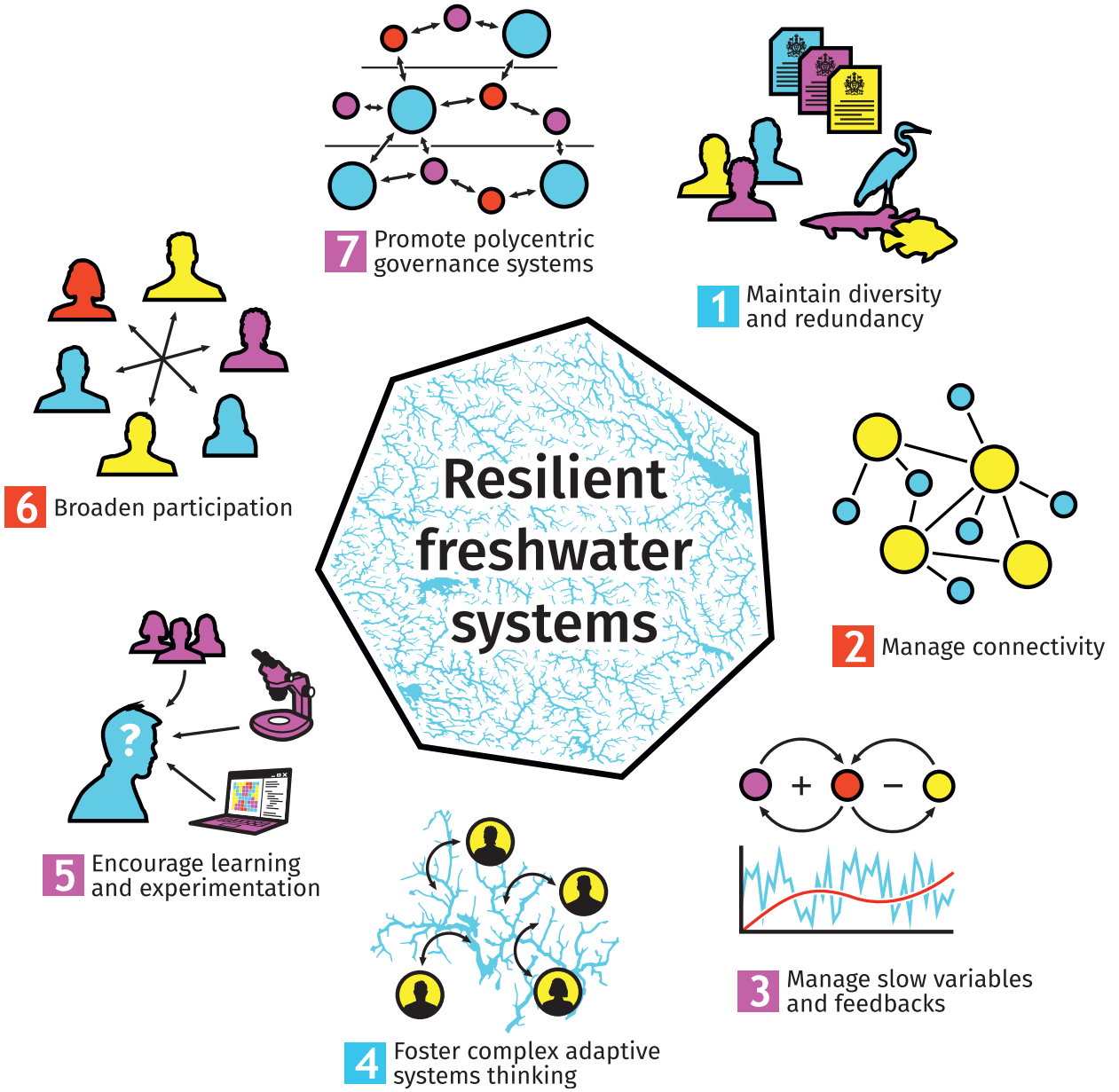

Fig. 1 Resilience principles as they relate to freshwater systems (created by Jesse Reib).

2. *Manage connectivity*: Connectivity is the structure and strength of interactions or relationships among parts of the system. We can think about this in terms of a network where connections can relay information (credible or not), support collaboration, and result in learning, among other functions. When considering freshwater systems as complex adaptive systems, it is important to build (and manage) connectivity among groups (decision makers and others with a stake or rights to the system) to enable better understanding of the system and decisions for its governance. No one perspective is sufficient to govern freshwater systems in isolation because they are complex. Further, connectivity across levels (from local to watershed and beyond) is important to ensure that local issues are represented at higher decision-making levels and that policies and programs developed at higher levels do not have adverse consequences at lower levels. Finally, more connectivity is not always better. Depending on the specific system and context, more or less connectivity may be needed. Too much can hinder the ability of new ideas to enter the network and create a rigid and self-reinforcing network of communication. Too little can result in a fragile network where communication and ideas do not flow between those who would benefit from being connected.
3. *Manage slow variables and feedbacks*: Slow variables are just that, variables that change slowly—so slowly, in fact, that the changes may not be noticeable. However, incremental changes can accumulate over time and suddenly have major impacts on a system. An example of this is incremental changes to the legal system, that on their own have little impact on freshwater conservation. Over time, however, these incremental changes may lead to an opportunity for a private company to exploit freshwater in a way

that was not possible before. Monitoring changes in slow variables is one form of feedback, as it ensures that knowledge of changes is kept current and provides the potential for assessing change over time. Feedbacks are the interactions between the slow variable and other system parts that lead to further changes in the slow variable. In the example above, a feedback might be an environmental watchdog group that reports on changes to the legal system, which might lead to heightened public concern and potentially reversal of decisions. Governance of slow variables and feedbacks requires connections to other resilience principles: broadening participation in governance to access relevant knowledges about the system when making decisions; connectivity to access information and maintain a suitable level of monitoring at the appropriate levels and scales (geographic, temporal, etc.), and adaptability to shift decisions/approaches if feedbacks indicate changes are needed.

4. *Fostering an understanding of social-ecological systems as complex adaptive systems*: This principle relates to, and brings together, the sections above that discuss freshwater systems as interacting and intertwined social and freshwater systems (social-ecological systems), how these systems have many, many interacting parts, are self-organizing (the behavior of the system as a whole is defined by the behavior and interactions of the parts), and are unpredictable (complex adaptive systems), and how worldviews and human agency interact to determine how we act and what governance approaches we support (e.g., human agency). The suite of approaches that we view as feasible in governing freshwater systems is dependent on how we understand the systems themselves. A complex adaptive systems perspective is consistent with social-ecological resilience and creates the capacity to govern in a way that supports resilience.
5. *Encourage learning and experimentation*: Learning about the system—especially learning that happens as a result of interactions with others who hold different knowledge and/or perspectives than our own—is important for responding to disturbances, no matter the goal (persistence, adaptation or transformation). Creating opportunities for learning is key to realizing this principle, and several other principles (managing connectivity, maintaining diversity, broadening participation) support this principle. Repeated interactions among those who are learning from each other builds relationships and trust and can enhance the ability of the system to respond to disturbances. Experimentation is the manipulation of parts of the system to understand how it changes outcomes. It is a key way that we learn about the system, and is particularly important when considering adaptation. In order to adapt, changes must be made, but because the system is complex and sometimes unpredictable, experimenting allows us to try different manipulations and compare outcomes to understand how best to respond to disturbances/changes. Both learning and experimentation serve to reduce the degree of uncertainty in the social-ecological system.
6. *Broaden participation*: Bringing more, and more diverse perspectives to governance is widely considered to improve decision-making in complex adaptive systems, like freshwater systems, through enhancing legitimacy, promote a more fulsome understanding of system dynamics, and increasing the capacity for monitoring. Who should be involved is a complicated question to answer—it depends on the specific system and who holds a stake or rights within it. How participation occurs is another complicated question: participation can range from being informed to partnerships among actors to full citizen control (Arnstein, 1969). Further, participation can happen at multiple different stages of governance, from setting goals to creating policies to evaluating outcomes. Despite the complex array of considerations of participation, broadening who is involved can result in increased cooperation among participants, increased transparency of governance processes, and increased ability to include relevant information in decision-making. There are clear linkages between this principle and maintaining diversity and encouraging learning and experimentation.
7. *Promote polycentric governance systems*: Polycentric governance refers to multiple centers of decision-making at different levels that are independent but work together towards common goals. Decision-making may happen by governments, non-governmental organizations, and others. Connections among centers of decision-making are most effective when they are horizontally connected (multiple centers that exist at the same level [e.g., municipal governments] interact with each other) and vertically connected (multiple centers that exist at different levels [e.g., municipal governments, watershed organizations, Indigenous governments] issues that jointly affect them. This principle is related to all others, as polycentric governance either exhibits the principles (e.g., maintaining diversity and redundancy) or enables them (e.g., encouraging learning and experimentation).

Additional considerations to the resilience principles

In many of the resilience principles, there is an underlying theme that is not explicitly stated, but deserves attention. A focus on equity, power dynamics and human agency is central to governance for resilience of freshwater social-ecological systems. Questioning the 'resilience for whom' is important. Whose wellbeing matters most? Which individuals' and groups' interests and preferences should be targeted? When is it deemed suitable or desirable to keep a social-ecological system in its current state? When is transformative change deemed relevant or necessary? Resilience is in fact a normative concept. This means that, for example, a resilient freshwater system may be good and desirable for a certain group of the society, but at the same time bad and undesirable for other groups. So, it is necessary to make normative choices, and it is important to understand who benefits and who loses, and how we can strike a balance among the interests. Governance is key to understand this social-political dimension of resilience. It helps us understand who is and should be involved in freshwater related decision-making processes; who has and/or should have the power, freedom, and agency to actively participate, to retain or enhance freshwater resilience, and ultimately shape the future of freshwater systems (Cinner and Barnes, 2019). By understanding inequities and power dynamics in governance of freshwater systems, we can better address them and enhance the ability to build good governance of freshwater that aligns with social-ecological resilience principles.

The role of individuals and human agency

The focus so far has been largely on governance structures and processes—the ways in which we organize ourselves in society and the rules by which we make decisions. However, individuals have important roles to play in social-ecological resilience of freshwater systems as well. The fourth principle of social-ecological resilience—fostering an understanding of social-ecological systems as complex adaptive systems—emphasizes that the ways in which we as individuals understand the world around us is important. Our 'worldview,' or the way in which we see and understand the world and how humans and ecosystems relate to each other, will determine in large part the ways in which we think decisions should be made (who should be involved and what they should consider) and the suite of options that are appropriate for governing freshwater systems (Bohensky et al., 2015; Baird et al., 2020b). Our worldview can either enable or create barriers to social-ecological resilience.

Human agency—the ability and power to act based on one's will—is of central importance in individual roles in social-ecological resilience. Agency can be exhibited through decisions in our daily lives through to political actions we take without decision-making authority (e.g., engaging in more environmentally friendly practices in our home, voting for a particular political party aligned with our values and beliefs, or engaging in environmental activism) and through the actions of those who do have decision-making authority (e.g., advocating for policies that support freshwater conservation measures, developing programs to support others' work in freshwater management/resilience). Human agency and worldviews intersect: the types of actions taken by individuals are generally reflective of their worldviews. The individual actions taken, whether by those in positions of authority or not, can have impacts on the larger system. For example, individual votes in an election in a democratic nation together decide who (and whose agenda) will govern that nation.

An important note on human agency is that it has constraints, and those constraints differ among individuals (as described above) (Baird et al., 2020b). We can use the ability to vote again as an example. The opportunity to vote based on an individual's values and beliefs is dependent on several factors: citizenship/residency status, whether they live in a democratic nation or not, age, ability to vote (access to transportation, financial means and time to allocate to voting, etc.). Certain groups within societies have less agency than others and thus their worldviews may be less represented in governance.

Resilience, governance, and panarchy

The ways in which social-ecological systems, as complex adaptive systems, function and system elements interact and change over time can be considered an 'adaptive cycle' (Gunderson and Holling, 2002). This cycle "describes the processes of development and decay in a system" (Garmestani and Benson, 2013, online) through four phases that can result in system reorganization in relatively the same configuration (persistence or adaptation) or in a new configuration (transformation). This cycle can happen at the local level (e.g., a single location along a creek), regional level (e.g., a watershed) and at broader levels (e.g., global) and adaptive cycles at these different levels operate on their own time scales, and also interact and can impact each other (called 'panarchy'). For example, a single point of pollution in a waterway can contribute to much larger water quality issues downstream over time once a threshold is exceeded, and global climate changes can have local effects on water temperature and aquatic habitat.

Resilience contributes to how a social-ecological system moves through the phases of the adaptive cycle. For example, a high degree of resilience can maintain a system in a state of conservation of resources for a long period of time, despite internal and/or external disturbances. While an ecosystem cannot expect surprises (disturbances) or anticipate their impact, social systems hold this potential (Angeler et al., 2014). Accordingly, resilience can be 'managed' through society's actions and decisions. The extent to which resilience is present in governance systems (see Sections "How governance is connected to resilience" and "Resilience principles" above) has impacts on how the social-ecological system is managed and moves through the adaptive cycle.

Conclusion

Governance and management—the decisions and actions taken to set direction and interact with freshwater systems—are central to freshwater problems. This is in part because of the entangled nature of human systems and ecosystems—together forming a 'social-ecological system' that is complex and adaptive. The disturbances that act upon the social-ecological system, and the interactions among components of it, can be difficult or impossible to predict. But, understanding the nature of the system, and its web of interactions, helps us to consider how we can address governance and management in a way that aligns with it.

The 'what,' 'who' (and 'for whom'), and 'how' of freshwater governance and management is critical for freshwater resilience. We outline seven principles of social-ecological resilience-based governance/management in this chapter: maintaining diversity and redundancy; managing connectivity; managing slow variables and feedbacks; fostering a complex adaptive systems mindset; encouraging learning and experimentation; broadening participation; and, promoting polycentric governance. We add to this an emphasis on power, equity and human agency, and highlight the role of individuals as potential change agents to build resilience at the system level.

Knowledge gaps/future research

- Applying the coupled and inseparable social (actors and institutions) and ecological (water resources) perspective in water resilience;

- Integrating all relevant actors in the water governance and enhancing the interactions among the different levels of governance (individual, local, regional, national, and international);
- Focusing on participatory, equitable, legitimate, and transparent characteristics of governance for water resilience;
- Addressing and dealing with power relationships and individual human agency in water governance and water resilience;
- Addressing trade-offs among actors in the water governance process for water resilience;
- Studying social learning (i.e., how knowledge is built, shared, and used in group settings) in water resilience research and practice;
- Bridging the water resilience science and policy gap to better align the goals, definitions, and approaches around water resilience;
- Overcoming challenges of multidisciplinary perspectives in order to operationalize social-ecological resilience in water sector.

Acknowledgments

Julia Baird acknowledges her support from the Canada Research Chairs program. The authors wish to thank Catherine Febria for constructive comments on an early draft and Jesse Reib for the development of the figure.

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The Gender Gap: Women as Authors and Leaders in International Publications in Fisheries Science

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Catherine Febria and Gail Krantzberg.

Glossary

Gender gap Is the difference between or among genders owing to gender. In this case, the gender gap incorporates differences in citations and first authorship for women compared to men.
Gender Is a person's internal sense of being a woman, a man, some combination of man and woman, or neither man nor woman, including a range of identities and expressions. Gender is distinct from a person's assigned sex at birth and is often independent of physical or secondary sexual characteristics.
Impact gap Is the difference in the significant effect between or among groups. In this case, the impact gap is the difference between impact of women versus men across their citations in 18 fisheries journals, especially as it relates to a scientist's reach within and beyond their field by influencing management, policy, or society.
Impact Is used to describe researchers having a significant or major effect within and beyond their field by influencing management, policy, or society.
Minoritized individuals Are defined as being of the minority by a dominant group in society, most often white, cisgender, heterosexual men.
Productivity gap Is the difference in productivity levels between or among groups. In this case, the productivity gap is the difference between productivity of women and men in publications in 18 fisheries journals.
Productivity Is the effectiveness of productive efforts (output per unit of input) leading to results and benefits.
Sexism Is prejudice, stereotyping, or discrimination against a person on the basis of their perceived sex; or behavior, conditions, or attitudes that foster stereotypes of social roles based on sex.

Introduction

Productivity and impact continue to be important qualities to evaluate a successful science career, especially as they relate to a scientist's reach beyond their field by influencing management, policy, or society. Productivity and impact are traditionally measured by the number of articles published, especially in the prestigious position as lead author (Sekercioglu, 2008; West et al., 2013), and the number of times each article is cited by others (Franck, 1999; Biagioli, 2003; Bornmann and Daniel, 2008), respectively. However, gender imbalance between men and women in science has been a widely recognized issue for decades, with women having shorter careers and higher dropout rates (Blickenstaff, 2005) leading to an overall reduced productivity and impact (Huang et al., 2020).

Globally, for every article with a woman first author, there are nearly two (1.93) articles first-authored by men in science (Larivière et al., 2013). Differences in the sustainability of women's careers is proposed to explain these numbers (Huang et al., 2020). Reasons for such gender imbalance are deeply rooted in social, cultural, and legal norms, owing to differences in family responsibilities, work absences, resource allocation, isolation, sexism, racism, workplace culture, lack of women leaders, and gender stereotypes. Indeed, the gender gap is a paradox, as the inclusion of women and diverse people leads to more productive (Horta, 2013) and innovative teams (Østergaard et al., 2011) that produce high-impact research (Freeman and Huang, 2015), yet they are not consistently included. Consequently, understanding productivity and impact by gender and other identities is important for identifying continued barriers to inclusion and advancement of minoritized individuals, but also because these metrics provide the foundation of the current reward system.

The science of management and conservation of inland waters (i.e., fisheries, aquaculture, and aquatic science communities) has broadly affirmed the importance of diversifying its workforce, including gender diversity (Arismendi and Penaluna, 2016; Abernethy et al., 2020; Gopal et al., 2020). These efforts raised awareness of the need for competitive advantages and innovation, expressly as the field faces unprecedented challenges from complex human-environmental issues related to inland waters. Specifically, diversity is part of what makes people who they are (Batavia et al., 2020), and the science of inland waters depends on people. For example, women make up half of the fisheries workforce and play a prominent role in fisheries and aquaculture economies around the world, including in small-scale fisheries, yet women are unrecognized in official statistics, policies, and development programs (Gopal et al., 2020). As sciences of inland waters are called to diversify, demographic information related to productivity and impact will also increasingly be relied upon to inform decisions about equality, advancement, and the status of women.

If there is a shift in fisheries of inland waters to include more women and in leadership roles, especially women of color, we predict a paradigm shift toward the infusion of new ideas, which could only improve the management and conservation of inland waters. For example, women represent around 30% of the professional workforce in fisheries science across federal and academic positions in the United States, which is 20% less than expected if considering the pool of qualified talent (Arismendi and Penaluna, 2016). The number is even lower for women in in the professional workforce in leadership positions such as full professor, where representation is around 15%. In addition to career level, a gender gap has been noted in fisheries science, including in the representation of women authoring the most-cited articles in the field (up to 21% of most-cited articles had female representation: Branch and Linnell, 2016) and holding influential positions in academic collaboration networks (Arismendi et al., 2021). To understand why these discrepancies exist for women, we raise a critical question: what is the current state of productivity and impact of women in fisheries science? And what can be done to close the gender gap in the field?

To address this need, we conducted a bibliometric analysis of 15 years of publications in international English-language journals with a focus on freshwater fisheries science, which is a key part of managing and conserving inland waters. One of the main goals of this research was to extract basic information about lead author and number of citations from primary research, and to assign binary gender to author names to understand the effect this factor on productivity and impact in fisheries science. Doing so will help us to understand disparities between women and men involved in fisheries science publications beyond the most-cited fisheries references (Branch and Linnell, 2016). We were unable to quantify gender diversity beyond the male-female dichotomy, which does not represent the full range of gender identities, owing to the lack of available data on nonbinary and gender-nonconforming fisheries researchers. Drawing on the large body of diversity scholarship outside of fisheries, we discuss the challenges of including women in fisheries science, the risks of not including them, and long-standing problems of success related to productivity and impact.

Overview of recent fisheries science literature and gender assignment

Our focus on authorship information limited our analysis to the publishing careers of scientists, and consequently does not capture aspects of teaching, administration, mentoring, or government-related research activities. For example, women in academia have been shown to spend a disproportionate time on "invisible" work, which leaves less time for them to work on tenure and promotion (Social Sciences Feminist Network Research Interest Group, 2017). We extracted authorship information of published articles from the Web of Science database (WoS) focusing on 18 fish-related journals (Mather et al., 2008; Table 1) between 2006 and 2020 (WoS uploaded electronic information of complete first names, when available, starting in 2006). Although the Web of Science does not index the entire journal literature in fisheries sciences, it provides a reliable sample of citations comparable to broader citation indexing services such as Scopus (Archambault et al., 2009). As our study was comparative in nature, complete citation counts were not required. We included all regular publications (those identified as "*articles*" in WoS) and considered "*articles*" and "*reviews*" from specialized journals that focused on reviews, including *Fish and Fisheries*, *Reviews in Fish Biology and Fisheries*, and *Reviews in Fisheries Science and Aquaculture*.

From each article published between 2006 and 2020, we extracted the following fields: journal, WoS accession number (unique identifier), year of publication, names of authors (surname and first name), and the number of citations (up to 15 January 2021). Although gender includes a range of identities and expressions, we are only able to assign gender as female or male based on first names using the genderizeR package (Wais, 2016) in R statistical software (R Core Team, 2017) and GenderAPI (https://gender-api.com/). These tools assign the probability of a first name being female or male based on large database of names (>6 million). We validated this gender assignment procedure using the membership list of the American Fisheries Society, AFS (pers. comm. Eva Przygodzki, 2015). We used 6542 AFS members who voluntarily provided demographic information including surname, first name, and gender. We tested our gender assignment procedure using the AFS names and then contrasted the degree of agreement between the predicted gender from this procedure and the actual gender for AFS members. Our procedure identified the actual gender in 97.6% of the cases ($n = 6542$) for men ($n = 4925$) and 96.8% from women ($n = 1617$), although there is gender diversity that we were unable to capture, which we discuss in more detail in the discussion.

The year that each journal included in our analysis was founded ranged from 1872 (*Transactions of the American Fisheries Society*) to 2000 (*Fish and Fisheries*; Table 1) and the journal impact factor ranged between 1.04 (*Fishery Bulletin*) and 6.79 (*Fish and Fisheries*). Half of the 18 journals were founded by professional societies or other organizations. We tested the association between the age of the journal and the proportion of women lead authors using a simple Pearson's correlation analysis. We performed a similar

Table 1 Journal information, including year founded, impact factor, society/organization that the journal is associated with, number of articles used in analyses, and % of articles used in the analyses for 18 journals included in our analyses.

Journal Name	*Year Founded*	*Impact Factor (2019)*	*Society/Organization*	*Number of articles (2006–2020)*	*% of articles with lead author gender assigned*
Aquaculture	1972	3.23		8662	79%
Canadian Journal of Fisheries and Aquatic Sciences	1901	2.85	Natural Research Council, Canada	2693	92%
Ichthyology and Herpetology	1913	1.16	The American Society of Ichthyologists and Herpetologists	1197	95%
Ecology of Freshwater Fish	1992	1.95		936	65%
Environmental Biology of Fishes	1976	1.52		1964	90%
Fish and Fisheries	2000	6.79		645	96%
Fisheries	1976	2.70	American Fisheries Society	474	92%
Fisheries Management and Ecology	1994	1.73		789	18%
Fisheries Oceanography	1992	2.20	The International Journal of the Japanese Society of Fisheries Oceanography	635	81%
Fisheries Research	1981	2.15		3449	82%
Fisheries Science	1932	1.17	The Japanese Society of Fisheries Science	1929	93%
Fishery Bulletin	1881	1.04	U.S. Dept. of Commerce, NOAA	575	92%
Journal of Fish Biology	1969	1.50	The Fisheries Society of the British Isles	4447	16%
Journal of Fish Diseases	1978	2.32		1845	20%
North American Journal of Fisheries Management	1981	1.49	American Fisheries Society	1686	94%
Reviews in Fish Biology and Fisheries	1991	4.40		568	86%
Reviews in Fisheries Science and Aquaculture	1993	3.76		362	87%
Transactions of the American Fisheries Society	1872	1.44	American Fisheries Society	1841	91%

analysis between the journal impact and the proportion of women lead authors. Lastly, we used a simple Mann-Whitney rank sum test and a Yates continuity correction to compare the median of article citations (one time or more) by binary gender. Similarly, we used a Kolmogorov-Smirnov Test (K-S Test) to compare the overall distribution of citations by binary gender.

Representation of women in publications of fisheries science

We were able to extract 34,697 articles between 2006 and 2020 from WoS. Some articles were excluded from our gender analysis because first names were incomplete (3.8%) or not provided (24%). Some journals have not adopted the use of a full first name in the article and some people intentionally use initials, resulting in our inability to assign gender. Thus, our gender analysis is based on 24,857 articles. Collectively, these articles have been cited 411,116 times (as of 01/15/2021). These articles represent a total effort from 157,024 individuals.

During the past decade and a half, around 30% of the fisheries articles published in fisheries science journals were led by women, whereas men led approximately 70% (Fig. 1). However, lead authorship by gender varies by journal, with women leading more articles in the *Journal of Fish Disease* (46%) and leading the fewest in the *North American Journal of Fisheries Management* (19%; Fig. 2). Pearson's correlation analysis showed that the proportion of women lead authors was not associated with the age of the journal (P-value = .79) or its impact factor (P-value = .85). Journals from publishing companies had slightly higher participation of women as lead author (33%) compared to journals associated with professional societies or organizations (27%). Similarly, 30% of total citations of woman-led articles were from publishing companies, relative to 25% from professional societies or organizations.

The proportion of articles with single authorship was higher for men (5%) than for women (2%) across fisheries journals. However, women lead authors include the same relative number of coauthors on their articles (3–6 coauthors) as those led by men (Fig. 3). Citations for articles by gender vary by journal, with woman lead authors being cited most in *Reviews in Fish Biology and Fisheries* (34%) and the least in *Reviews in Fisheries Science and Aquaculture* (14%; Fig. 4). Overall, women are undercited relative to the proportion of articles that they lead, except for *Reviews in Fish Biology and Fisheries* and *Ichthyology and Herpetology*(Fig. 5).

Articles published across these 18 fisheries science journals had an average of 11.8 citations per article. There were statistically significant ($T = 72{,}113{,}635$; $N_1 = 6667$; $N_2 = 15{,}450$; P-value $< .001$) differences between the number of times that articles with a

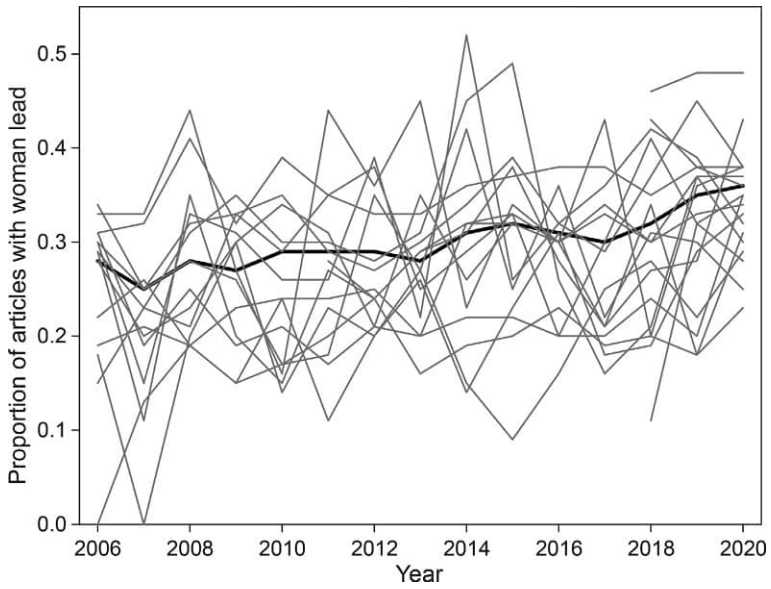

Fig. 1 Proportion of articles with woman lead over time from 2006 to 2020. Each gray line represents a single fisheries journal and the black line is the mean.

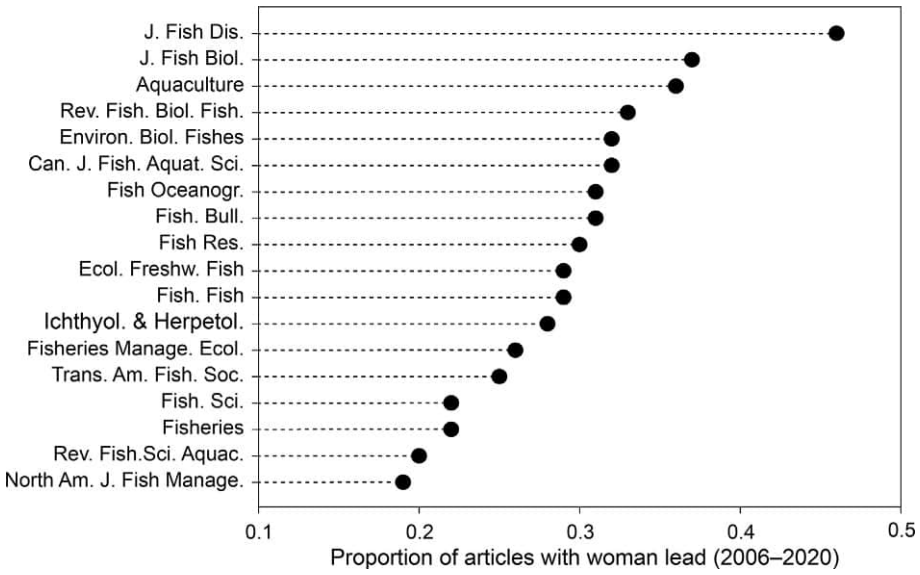

Fig. 2 Proportion of articles with woman lead by journal from 2006 to 2020.

woman lead author were cited versus a man lead author (Fig. 6). Similarly, only 10.6% of articles led by men authors had no citations compared to 12% of articles led by women authors. In general, the proportion of highly cited papers (30 or more citations) was dominated by men lead authors, as is shown by the different citation distributions by gender ($D = 0.027$; P-value $<.05$). More articles led by men authors (0.8%) had >100 citations compared to articles led by women authors (0.6%).

Identifying the gender gap for the management and conservation of inland waters

To advance women in science, the gender gap has been proposed as a 'productivity gap' (e.g., Abramo et al., 2009). We suggest that the productivity gender gap is not affecting women in fisheries science, at least superficially, because women publish in fisheries as lead author proportionate to their presence in the fisheries science community (~30%; Arismendi and Penaluna, 2016). The fact that women are keeping up in productivity is remarkable considering the barriers and biases that they face in their careers, including interactions with editors and peer reviewers (Bornmann et al., 2011). Similarly, research output of Spanish postdoctoral scientists shows no differences in publications by gender (Borrego et al., 2008). This is mirrored by results of professors in universities in the

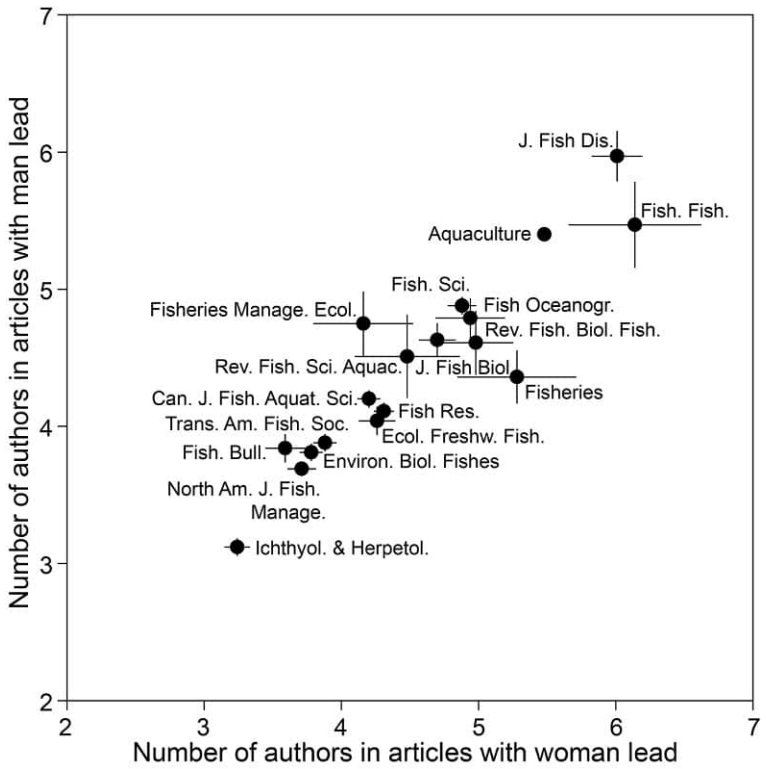

Fig. 3 Relationship between mean number of authors in articles with woman lead and mean number of authors in articles with man lead across 18 journals from 2006 to 2020. Each point represents the mean values for a journal with standard error.

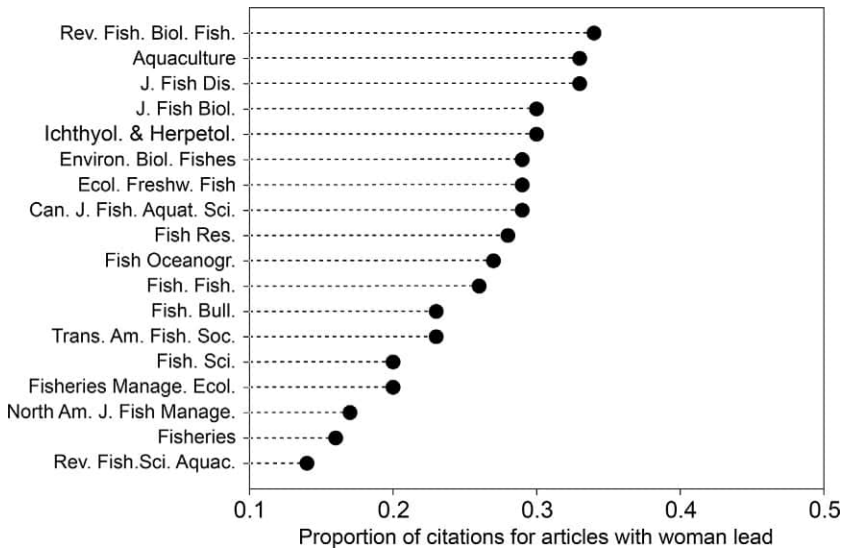

Fig. 4 Proportion of citations for articles with woman lead by journal from 2006 to 2020.

province of Quebec, Canada, where there are no differences in productivity between men and women until age 38, when women receive less funding, have fewer publications, and have less impact compared to men (Larivière et al., 2011). If women in fisheries are producing research at the same level as men, then the fisheries science community may consider improving the recruiting and retention of women in fisheries positions to achieve gender parity, in addition to addressing social, cultural, and legal aspects that contribute to the gender gap.

Women in fisheries have low numbers of citations relative to their productivity, suggesting that there is an 'impact gap' in fisheries, in addition to issues of recruitment and retention, rather than a 'productivity gap'. As impact incorporates the major effect

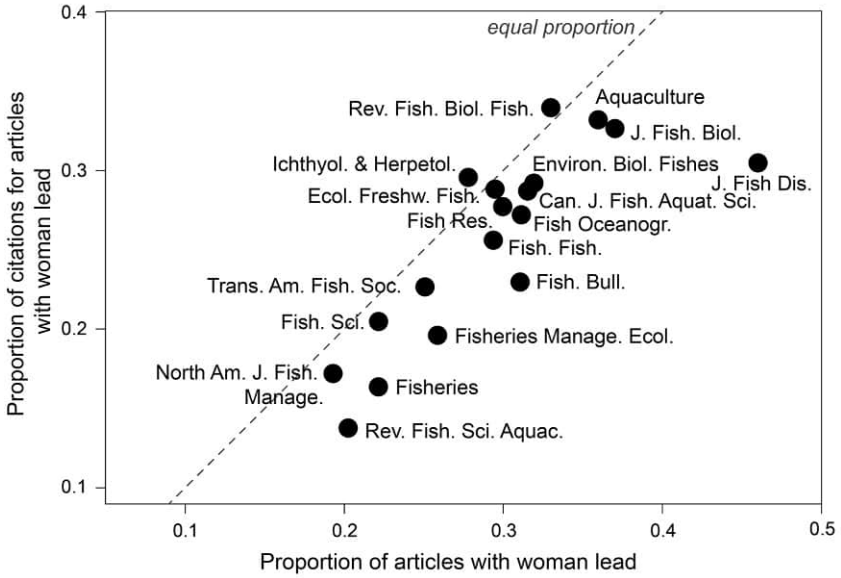

Fig. 5 Relationship between proportion of articles with woman lead and proportion of citations for articles with woman lead by journal from 2006 to 2020. Dotted line shows 1:1 relationship.

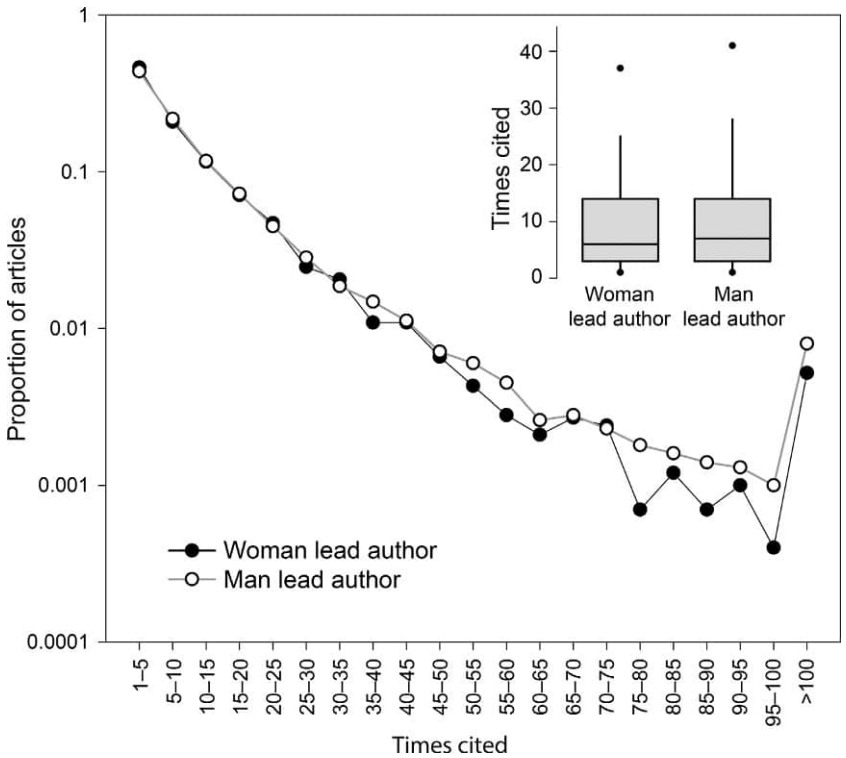

Fig. 6 Proportion of articles with woman lead author relative to man lead authors over time from 2006 to 2020. Inset shows number of times that articles are cited for articles led by women relative to those led by men.

of a person and their work both in their field and beyond by influencing management, policy, or society, our findings suggest that the reach of women is not as far as that of men. The challenges of impact for women fisheries scientists reflects the broader societal challenges that women face to both serve and be viewed as leaders. For example, the 'Matilda effect', a bias against acknowledging the achievements of women scientists whose work is attributed to their male colleagues, has been an ongoing problem for women for centuries (Rossiter, 1993). When considering co-authorship roles, women contribute to science by performing the experimental work disproportionately more often than men (Macaluso et al., 2016), and even when women are lead authors, they are less likely

to be the corresponding author, as demonstrated by Fox et al. (2016) for the journal *Functional Ecology*. When looking at impact, the most-cited fisheries articles come from men, with only 21% of most-cited articles including women coauthors (Branch and Linnell, 2016). We also show that articles that are highly cited are disproportionately led by men. Collaboration networks from top women researchers in the US fisheries science academic network show that top-ranked women have smaller networks than men, but their roles in the network are influential to the structure of the network (Arismendi et al., 2021). Collectively, we suggest that women are devalued relative to men, which makes it difficult to reach high-status or high-impact positions in their careers.

The value system in science could shift to broadly include metrics of justice, equity, diversity, and inclusion instead of continuing the perpetuation of citations and impact factors (Davies et al., 2021). This would help us to reimagine the fisheries science workforce as a collection of paths that change and adapt to the needs of the individual with a foundation of mentoring, which may also increase job satisfaction. For example, mentoring relates to more than a two-fold increase in job satisfaction for fish biologists in the USDA Forest Service (Penaluna et al., 2020). By broadening the value and rewards system in science, we would also add value to career pathways or duties that are not focused on publishing, including managers, private industry and policy makers, and it would make more visible work related to mentoring, relationships, and communication. If there were to be a shift in our scientific value systems, then inland fisheries science professionals would be additionally valued for contributions that influence aspects of mentorship, diversity, and well-being.

Single authorship was minimal for both women and men in fisheries, suggesting that fisheries science is inherently interdisciplinary, but the productivity and impact of women in fisheries varied by journal. In the journal *Fisheries*, there were some binary gender differences during the review process; articles led by women were published less often than expected by chance, suggesting bias (Handley et al., 2015). Overall, women publish less in journals associated with professional societies and organizations suggesting that women probably are less comfortable in those spaces and/or there is bias in the review process. We suggest that journal editorial teams should look for ways to increase the number of submissions and improve participation of women in their journals. They may strategically solicit and incentivize submissions by women, include women and people of color on their editorial boards, publish who is part of their editorial boards on their website, offer double-blind reviews, and require reviewers to check an agreement box that their reviewer comments will not be disrespectful or discriminatory.

The true gender diversity of fisheries science professionals includes people beyond the male-female dichotomy, such as nonbinary and gender-nonconforming individuals who identify as both male and female at one time, as different genders at different times, as no gender at all, or dispute the very idea of only two genders (Richards et al., 2016). For example, the prevalence of nonbinary genders was 1.8% in natal men and 4.1% of natal women in two separate data sets in one study (Van Caenegem et al., 2015) or as high as 35% in another study asking participants about their gender (Joel et al., 2013). The marginalization that transgender or nonbinary scientists face extends to the lack of information that we have about them related to their identities, professional roles, and successes in science. The victimization and stress from discrimination that these people face can be even higher than for women (Richards et al., 2016). Societal and institutional changes may be warranted to start quantifying the prevalence of nonbinary fisheries science researchers, including attention to safety and inclusion.

Although our study focuses on one dimension of social identity, there are additional barriers and specific challenges that people with multiple identities face, including able-bodiedness, race/ethnicity, age, class, country of origin, religion, or sexual orientation that could be explored. The interconnected nature of social identities leads to overlapping and interdependent systems of discrimination and disadvantage. Crenshaw (1989) posits that considering only one dimension of someone's being distorts the multidimensionality of their experience limiting our understanding of the issue, and rather by considering such intersectionalities the dynamics are more appropriately understood. If more information about social identities is known about people involved in inland waters, then a deeper understanding of who we are and how many lives are touched worldwide is possible.

Talented women have been and are leaders and role models in inland waters, including fisheries and aquaculture (Murphy et al., 2020; Zatkos et al., 2020). They continue to inspire new generations of women and girls to enter the field, or other fields of science. If we want women to be making high-level decisions about the management and conservation of inland fisheries, then we may invite them to the table where those decisions are being made and show that we value their experiences, ideas, and expertise.

Conclusions

The status of women in fisheries science publications brings attention to the broad problems that still exist globally, from low representation of women at all career levels, but especially in leadership roles, to discrimination and lack of access that affects career opportunities. To design science so that it represents everyone, we need to include women in conversations and in making decisions. Consequently, the fisheries science community may want to recruit women into fisheries positions, and particularly leadership, and put practices in place to retain them. Putting women in leadership roles is a first step in addressing gender inequalities in fisheries as it may also be important to rectify social, cultural, and legal issues more broadly. Women, like all people, are interested in being heard, and a key part of that is to accept and validate women's experiences, ideas, and expertise (Crandall et al., 2021). Consequently, it is increasingly important for researchers to devote time to issues that affect women in fisheries, to be better prepared to meet the ever-growing challenges facing society, and the management and conservation of inland waters. Binary genders do not represent the complete diversity of fisheries investigators. Accordingly, to understand more deeply about the complete diversity of genders in fisheries science, we need to create support systems and cultures of inclusion to recruit and retain people with diverse gender identities.

Knowledge gaps

- To address gender issues, or any diversity issue, information and data must be collected by asking individuals directly for information, and more than the English-speaking world may be considered. There is an information gap related to intersectional identities of people, including gender, race/ethnicity, sexual orientation, age, career/job, disability, and marital status (this may be particularly important for women who have small-scale fisheries).
- Additional information about people involved in inland waters would provide the opportunity for a deeper understanding of how many lives/sectors inland waters touches globally. For example, are there differences in representation of people if they are from countries in the Northern Hemisphere versus the Southern Hemisphere?
- To more deeply understand gender identities in fisheries and aquaculture, one would (a) have to recognize the legacy of oppression that affects nonbinary and gender nonconforming communities and (b) need more information than someone's name and presumed gender. Increasingly, as younger researchers enter the profession, names may not necessarily reflect a binary gender (e.g., Avery, Taylor, Skyler, McKenzie, Teal). Additionally, to capture racially, ethnically, and nationally diverse researchers whose names derive from many languages, a much larger database of first names is needed.
- Gender-diverse scientists need better protections against discrimination and harassment before we can expect them to publicly self-report. First steps can include offering a write-in option for gender and by offering non-gendered options for titles/honorifics such as Mx.
- With the information that is obtained from WoS, we are unable to determine whether women are not submitting articles to certain journals, or whether they remove their submission or are rejected during the review process. This type of information could be collected by journals and would offer insights to minimize bias during the publication process.
- We found that women publish less in journals associated with professional societies and organizations suggesting that women probably are less comfortable in those spaces, but that relationship should be evaluated more explicitly.

Acknowledgments

We thank Catherine Febria, Gail Krantzberg, Lee Cerveny, Farallon Broughton, and Kathryn Ronnenberg for their comments on the manuscript. Kathryn Ronnenberg also edited figures.

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https://www.mianpo.org/—Minorities in Aquaculture
http://kuahawaii.org/—Kua'āina Ulu 'Auamo (KUA)

Value Proposal in Freshwater Systems-Theoretical Frameworks and Operational Measures

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editors Catherine Febria and Gail Krantzberg.

Glossary

SDGs The Sustainable Development Goals or Global Goals are a collection of 17 interlinked global goals designed to be a blueprint to achieve a better and more sustainable future for all. Set up in 2015 by the United Nations General Assembly they are intended to be achieved by the year 2030.

Value Worth, usefulness, or importance in standing or in comparison and a principle or quality that is intrinsically desirable by individuals or shared by many.

Water security The capacity of a population to safeguard sustainable access to adequate quantities of acceptable quality water for sustaining livelihoods, human well-being, and socio-economic development, for ensuring protection against water-borne pollution and water-related disasters, and for preserving ecosystems in a climate of peace and political stability (UN-Water, 2013).

Introduction

Water is essential for safe and balanced living, but freshwater is facing a global crisis due to exploitation, pollution, and climate change (Islam, 2017). While, clean water, fresh air, and a pristine environment are increasingly considered valuable natural assets, over the past five decades, population growth, intensifying industrialization, and agricultural advancement have profoundly altered natural ecosystems and stressed water quality and availability. In addition, the challenges from climate change impacts exacerbate the water risks, and increase the exposure of communities and populations, particularly in vulnerable settings (Evans et al., 2012). Global freshwater use has been growing at about 1% annually since 1980, especially in developing countries. In 2015, the annual global water withdrawal was noted as 4500 billion m^3 (WWAP, 2015). By 2030, the lack of water usage efficiency combined with increasing economic productivity is predicted to result in global water use close to 7000 billion m^3. Other projections show that by 2030 the global water demand could increase by 40% and 55% by 2050 (WWAP, 2014). Water is an indispensable component of a wide range of economic activities. Therefore, the increase in demand will likely come from the growth of industrial and domestic use, energy production, and agriculture. The water demand already exceeds available supply in many regions, particularly in developing nations with rapidly growing regions viz., Asia, North Africa, the Middle East, and Sub-Saharan Africa (FAO, 2017).

The water demand-supply dynamics is largely impacted by various globalization trends such as trade flows, change in production and consumption patterns, etc. either directly or indirectly. Septon et al. (2019) reflect on the multiple perspectives of water values such as economic, social, and cultural values in connection with understanding the water demand-supply dynamics stating that these interlinkages are critical for maintaining socioeconomic and political stability in communities and states. The increasing interconnection of water with various sectors also calls for the integration of diverse stakeholder perspectives while

shaping water management plans and policies. Defining 'water values' universally remains a challenging task due to context-based socioeconomic, sociocultural, and sociopolitical settings. Moreover, the western paradigms rooted in technological progress and the hegemony of the market economy have been playing a key role in influencing the notion of values (Euzen and Morehouse, 2011). Concurrently, in the globalizing economies worldwide, the valuing process is no static phenomenon, though the placement of water within the existing valuing systems is primarily focused on economic interests. The growing perspective of industrialization-based growth notions had made it tough for environmental, social, and cultural perspectives to be appropriately integrated into the 'value' proposal operational strategies.

Water is a vital source of life and thus embodies a diversity of interests and has various classifications or value propositions placed on itself by context or by definition. It is within this understanding that a wide variety of 'values' emerge. When looking at the importance of 'water' solely with an economic lens, the pressures posed by climate change and environmental stresses are not property reflected or adequately addressed. Management of water resources equitably and sustainably is becoming a demanding task due to discord and limited to non-existent collaboration between economists and other disciplines engaged in sustainable development agenda implementation. For example, no economists were involved in a special section on "Ecosystem Earth" published in science (April 2017) that encompassed discussions of population, consumption, agricultural production, land use, human behavior, collective action, and policy (Vignieri and Fahrenkamp-Uppenbrink, 2017).

Additionally, in the age of climate emergencies the environmental protection agenda can be best addressed through discussion of emerging and continuing flawed economic growth paradigms that undervalue nature's contribution to people as highlighted in recent global assessment report on ecosystems and biodiversity compiled by the United Nations (UN) agencies, global experts, regional and national researchers (IPBES, 2019). The challenge of the water crisis is that it is altered with various climate-related events and, in turn, can influence geopolitical balance and political stability in communities and states. For instance, persistent climate change-induced extreme flooding faced by Ecuador's indigenous people that live in resource-scarce settings of the Amazon region (Gabay, 2020), added stress and triggered conflict between communities, in some cases precipitating people to move and migrate. Haarstad's (2012) commentary on the episodes of environmental conflict in Brazil, Chile, Ecuador, Peru, Bolivia, Uruguay, Colombia points to the concept of environmental personhood as an emerging dimension in the value proposal narrative. Capturing and synthesizing these diverse elements in the 'value proposal' for freshwater, this synthesis highlights the need to deconstruct the complex interlinkages, the theoretical density as well as operational measures of this framework while planning water security and economic development agendas. Besides, it proposes an explanation based on arguments and case examples to exhibit the value narrative with an integrated perspective that suitably incorporates the environmental, spiritual, and cultural dimensions of water (Fig. 1).

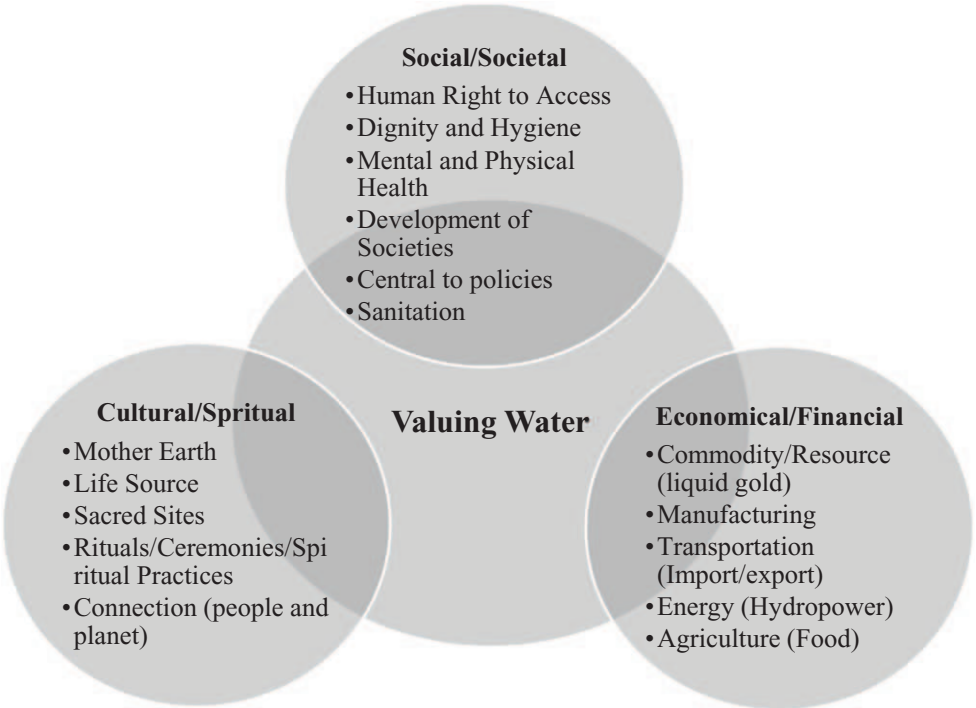


Fig. 1 Overview of dimensions that apply in assessing and addressing multiple values of water. Source: Collated by authors from different information sources.

Understanding multiple framings of 'valuing water'

Water is not only part of many economic and industrial processes; it is also essential for human life and wellbeing and is critical to food production. In April 2016, the UN and the World Bank Group (WBG) during the High-Level Panel on Water (HLPW) called for a comprehensive, inclusive, and collaborative form of leadership, which is necessary for developing, managing, and improving water and sanitization related services (Government of the Netherlands, 2020). The outcome of this HLPW was the '*Making Every Drop Count*' document released in March 2018. In this document the recommedations regarding the necessary collective betterment in understanding, valuing, and managing water. The overarching intent was to bring about systemic change that lay outside the margins and into the core of significant water challenges; and trigger the deconstructionism of how water is valued in practice, policy, finance, and behavior (Government of the Netherlands, 2020). The Bellagio principles and the Valuing Water Initiative (VWI) were launched in tandem to boost the implementation and adoption of outlined principles. VWI explains practical applications of valuing water principles to policy, business practices, and behavior across contexts, sectors, organizations, institutions, and agencies. And states that such a process needs collaborative initiative developed around four pillars centered on intervention and activities, as shown in Fig. 2. In this section, the focus is on Bellagio's Principles and UN Human Right to Water Resolution, underlined as examples of guiding frameworks that considers ecosystem and social objectives in tandem and allows integration of multiple 'water values' in the designing operational management measures in various sectors of the water domain.

The Bellagio's principles

Billions of people lack access to safe water and sanitation services. This crude fact calls for emphasizing the need for a collective and collaborative agenda to manage water resources and deliver necessary provisioning services to growing populations. Noting the importance of collective action, in May 2017 in Bellagio, the preamble of these principles was set on the recognition of eight key aspects: first, water is precious, fragile, and hazardous with the capacity to sustain or destroy life, societies, and economies, and these capacities act in interconnection with land, air, and energy resources. Water is not just a substance but an element with multiple values and meanings usually expressed in spiritual and cultural terms. The heritage of water language, norms, and artifacts provide deep perceptions, making it essential that stakeholders' relations and participation is duly acknowledged and represented in water management and governance measures. Furthermore, to ensure that water is available for multiple uses by various users, the supporting infrastructure, institutions, agencies, and policies systems remain important. And, transforming water from a natural resource to provision services, recycling, and reuse should be given appropriate consideration and thoughtful planning.

Second, making all the values of water explicit can provide recognition and platform to conventionally overlooked dimensions, and an alternative vision to the existing generalized cost-benefit approach to managing water demand and supply. In addition, focus on collective decisions and trade-offs while shaping sustainable solutions can help to overcome inequalities and bolster institutions and infrastructural innovations.

Third, creating initiatives through a collaborative process and building champions and ownership at all levels by presenting unique and mutually reinforcing concepts that consider water as necessary for equitable and inclusive human development.

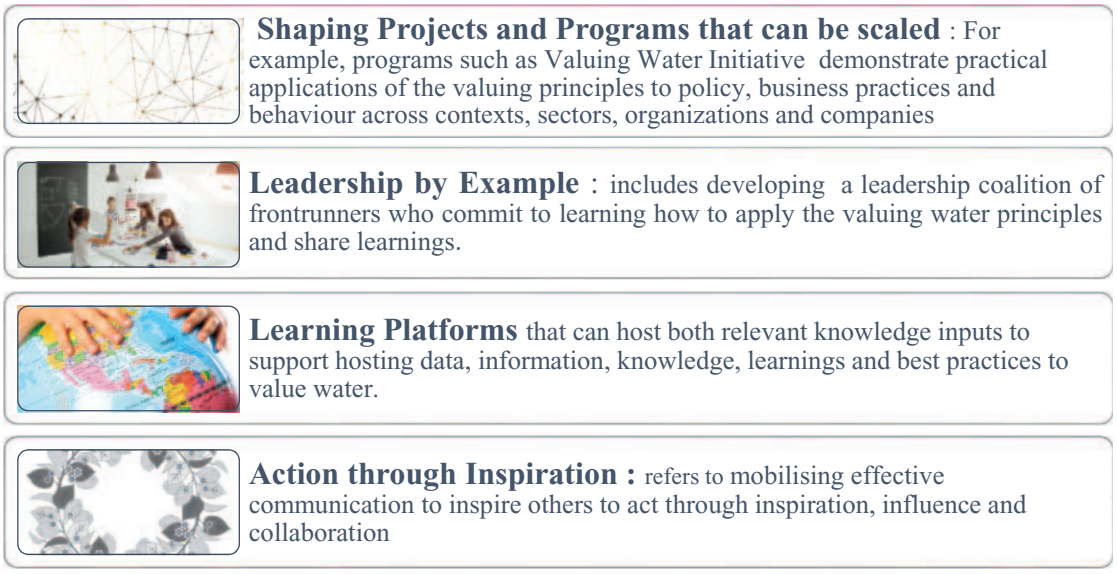


Fig. 2 Summary of aspects that are key in scaling and operationalizing valuing water concepts and frameworks. Created by authors adopting from Valuing Water Initiative.

Fourth, acknowledging that the world's freshwater systems face a mounting set of crises and threats from multiple direct and indirect drivers such as overuse, pollution, and impacts of extreme events, droughts, and floods and that these resources are finite while water demands are escalating.

Fifth, realizing and counting multiple values of water toward aggregation of various benefits provided by water in the economic, social, and ecological domains, local to national scales, and settings of social and cultural establishments is crucial.

Sixth, the valuing water perspective can stabilize the complex supply-demand dynamics through informed and balanced decisions on water allocations both for human and ecological wellbeing. Different ways apply to such a process, including but not limited to regulation and economic instruments, waste management, reuse, and recycle (green/gray infrastructure) systems, and restoration of water sources through efficient procedures and policies.

Seventh, efficient water management offers a ground for transforming risk to resilience, poverty to wellbeing, and degraded ecosystems to restorative landscapes through collaboration across sectors, communities, and states, and particularly for transboundary water systems.

Eight, the need for action, takes note of vast changes and innovation, and prospects to focus on human development-related challenges such as poverty, resilience building, management of shared resources, and underlying components of wellbeing. Furthermore, it takes into consideration the necessity to define practical roles or applications, for example, active and participatory stakeholders' consultations, agenda on common property resource (water) management, resource allocation strategies, resolving of resource-related conflicts, and supporting future investments in the water sector.

To understand the value perspective further, note that in the common understanding most of the value proposal surrounding the water systems point to the economic value. This understanding is often based on different variables and contexts such as quantity, time, location, and quality. This value notion is also affected by the climate crisis and the disaster events such as droughts that in turn can significantly impact the hydrological systems. For instance, water availability, referring in the terms of quantity is influenced by dry condition/droughts and change in rainfall patterns. The state of existing knowledge on valuing water is disaggregated. A standard guideline such as Bellagio's Principles that reckon spiritual, environmental, and cultural dimensions and outlines five principles, as shown in Fig. 3 offers a promising option toward holistic understanding of value proposal for freshwater systems. The critical element in this set of Principles include:

(a) recognizing water's multiple values by knowing the interconnectedness concerning human need, spirituality, economic well-being, and freshwater viability for and by different stakeholders carrying of that knowledge in the decision-making process and plans in the water sector.
(b) building trust through reconciliation of multiple values in an equitable, transparent and inclusive manner;
(c) protecting the source of water such as watersheds, rivers, and aquifers, associated ecosystems must be protected from pollutants and other stressors while managing the challenges related to water scarcity, adhering to the normative aspects of sustainable development agenda, in the current context of sustainability pathway for the water related SDGs);
(d) steering better-informed decision-makers regarding water-related issues by empowering communities and populations, strengthen their capacity through education initiatives, focus on public awareness surrounding water's essential role and intrinsic value;

Fig. 3 Key dimensions of Bellagio's Principles in the valuing water context. Figure by authors adapted from Bellagio's Principles documents.

(e) fitting investments and encouraging innovative mechanisms that draw on local, traditional, and indigenous knowledge and practices and apply to multiple facets of the complex water-food-energy nexus can serve helpful to realize full potential and value of water within by institutions, business, public sector unit in provision and infrastructure and the information and knowledge landscape on water.

Aligning to the discourse set by Bellagio's Principles is the United Nations resolution of universal access to clean, safe drinking water and sanitation declared as a fundamental human right. On 28 July 2010, through this Resolution [64/292], the United Nations General Assembly acknowledged the human rights dimension in the water sector and called upon states and international organizations to provide financial resources, support capacity-building and facilitate technology transfer to support countries and communities, in particular developing countries and people and populations living in vulnerable settings. The key dimensions of this resolution are outlined in Fig. 4.

Fig. 4 The important element of the *human right to water and sanitation* resolution of the United Nations (UN, 2010) toward access to safe water and basic sanitation is a legal entitlement, rather than a commodity or service provided on a charitable basis. The resolution emphasizes on accelerating the achievement of basic and improved levels of water access and to better manage inequalities and to focus on empowering communities to take part in decision-making processes.

Valuing Water and enabling change

Human existence and wellbeing depend on nature and its contributions in various forms. As a valuable natural resource, water directly contributes to human beings' daily life activities and life quality. It is essential to assess the variables and risks in a systematic manner in order to accomplish valuing water goals. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) introduced the concept of nature's contribution to people (NCP), emphasizing the importance of dynamic approaches to the assessment or valuation of NCP. The diverse value of NCP to the context of people's sense of identity, spirituality, and meaningful life is quite important as well, though the decision making often concentrates on instrumental assets of NCP like food, water purification, and flood prevention, among others (Pascual et al., 2017).

Furthermore, IPBES, with its recent publication, the Global Assessment Report (2019) recognized the immense benefits humans receive from wide-ranging access to natural assets like water, energy, food systems and other relevant materials to economic development process that are directly or indirectly harvested from nature. Over time, unregulated extraction and over exploitation of natural resources have adverse impacted and resulted in high declination of nature's capacity to allow contributions in different stages and formats and to regulate a good quality of life and implementation of the 2030 Agenda for Sustainable Development Goals (IPBES, 2019). It is vital to address these emerging challenges, which demand an enhanced knowledge of multiple values associated with nature and NCP. The emerging focus on 'values' also helps to move toward a more sustainable global community by communicating with a wide range of audiences for the policy and decision-making process (Pascual et al., 2017).

IPBES also commissioned a methodological assessment of diverse conceptualization of multiple values of nature and its benefits at the sixth session in Medellin, Colombia (IPBES, 2018). This initiative is targeting high-level discussion of stakeholders at the IPBES Plenary, its ninth session in 2022 (UNEP, 2020). The objective is to facilitate a strong foundation for knowledge and exchange for long term and efficient valuation of natural resources systems and to support decision-makers across various sectors in the development of policies and strategies that integrates coupled socioecological systems.

Another initiative in this direction is the World Business Council for Sustainable Development (WBCSD) publications on water valuation that help to clarify how businesses could establish their water valuation framework (Fig. 5) and supports them in undertaking a water valuation exercise while guiding scoping, planning, and embedding valuation into business processes across areas of operations, marketing, and reporting (Morgan and Orr, 2015).

'Valuing Water' is a nebulous domain, right from valuing rainwater and freshwater ecosystems to valuing water bonds or valuing water purification membranes, one can use different ways to express and ideate. To dissect the importance of the term, while adopting a business lens, it is evident that the financial impacts from water risks can be paramount. Take, for instance, the information provided by mining companies in 2018. The analysis covering >3000 mining sites worldwide points to the suite of the risks for countries, communities, basins, and companies and notes the spatial concentration of water risks as among various factors of interest and notes > USD20 billion of water-related financial risks, that have negatively impacted their operations (Morgan and Dobson, 2020). Such impacts can be drastic for a region or community with limited or no capacities to mitigate and adapt, for instance, 50% of the active and operating mines producing chromite globally are in South Africa's Limpopo basin and more than half of active and operating platinum mines are also in the same region. A significant scale of spatial crowding of commodity operations in specific regions is clearly a call of concern on many fronts and for the water sector.

Furthermore, the financial value of water risks is not of appropriate concern to all investors and companies, resulting in misinformed investment choices that unfavorably affects long-term business growth. The well-being of the communities and the environment is also influenced when water is judged solely based on economic value. The value proposal of the water beyond the financial and economic aspects is of utmost importance to ensure a water secure future for states and communities. To support this vision, '*Valuing Water Database*' a free resource containing over 100+ tools was launched in 2019 and integrated into WWF Water Risks Filter (Morgan, 2019). Amid the multiple water valuation methods and tools that have emerged in the past two decades, a rising need to comprehend how these methods vary and correspond toward enhancing the capacity of businesses, investors, government, and users is noted. The 2030 Water Resources Group (WRG) established multi-stakeholder partnerships to collectively manage the scarce water resources to benefit people, ecosystems, and economies. The report '*Valuing Water, Enabling Change*' tracked

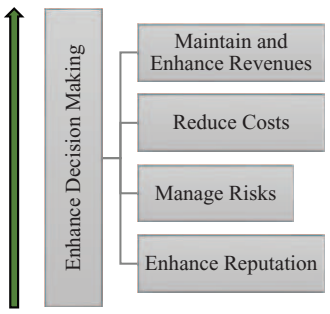


Fig. 5 Summary of WBCSD's Water Valuation Framework. Source: Modified based on Morgan A and Orr S (2015) *The Value of Water: A Framework for Understanding Water Valuation, Risk and Stewardship.*

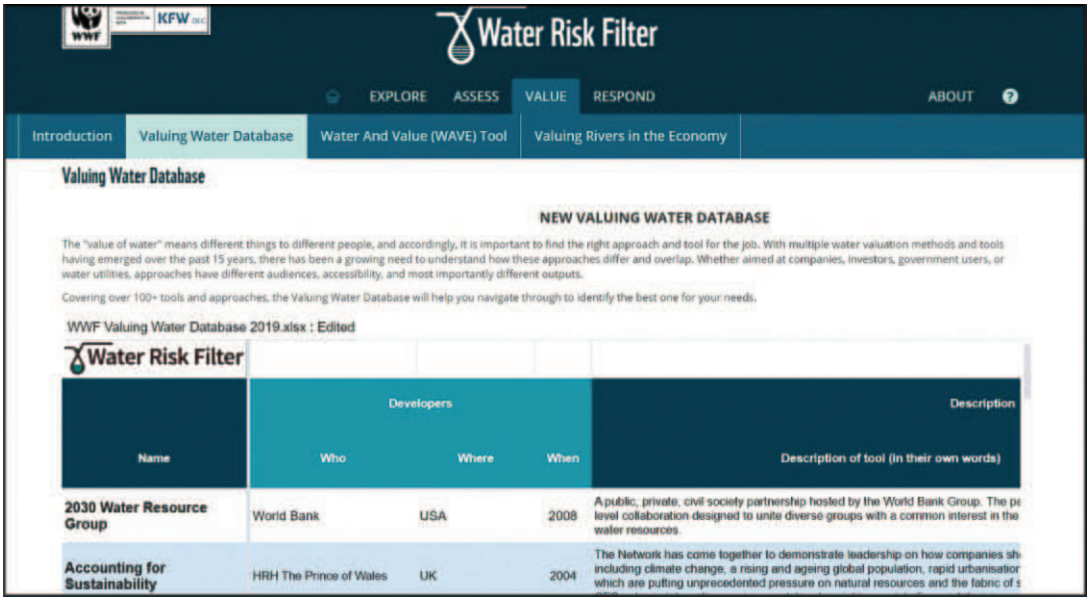


Fig. 6 Valuing Water Database at WWF Water Risk Filter. Source: https://waterriskfilter.panda.org/en/Value/ValuationApproachFinder.

the activities and impacts between July 1, 2019 and June 30, 2020 at the country level and provided a strategic approach for action (World Bank, 2020a,b). In the current context of the global pandemic situation, the 2030 World Water Resources Group hosted by the recent World Bank Annual Report endorses that the acceleration of adequate actions taking note of the valuation of water risks pointing it as a prevention strategy for COVID-19 (World Bank, 2020a,b) (Fig. 6).

Environmental personhood

The Anthropocene, an unofficial unit of geology, often describes the most recent period in Earth's history that is a period in which human activity has and continues to impact the global change and rampant degradation of ecological systems is seen. Amid this era of environmental change, the climate emergency with extreme events has prompted human societies, states, and populations to act for the restoration and protection of our natural heritage. The valuing water narrative also captures the framing of 'environmental personhood' as a viewpoint towards outlining operational measures. Presented as a legal concept that designates certain environmental entities' status as a regular person, this concept also extends to corporations (corporate personhood). In the contemporary environmental conservation scholarship, the concept is nearly 50 years old, when in 1974, Christopher D. Stone collected essays in a book titled 'Should Tree Have Standing? Toward Legal Rights for Natural Objects' (Bryant, 1975). The argument is, if an environmental entity is a 'legal personality,' it cannot be owned and has the right to appear in court, and it should be noted that by considering water a legal personality in the western lens, it is then legally valued. Some countries have already taken this concept to application—examples include the Whanganui River in Aotearoa, New Zealand; Lake Erie in Toledo, Ohio, and Vilcabamba River in Ecuador. In 2019, Toledo, Ohio, passed the Lake Erie Bill of Rights to protect its waters (Samuel, 2019).

This concept recognizes nature as a living, breathing force and allows creating space for all stakeholders, particularly indigenous peoples, to voice their concerns and perspectives, thus allowing a holistic approach to a complex problem related to water and the climate crisis. For the Anthropocene construct to be inclusive, the value systems of native people allow confrontation and acknowledgment of 'social nature' (Burke et al., 2016). In that framework the emerging set up of 'environmental personhood' calls for an ontological shift i.e. humans and nature are bound together, leaving us indistinguishable, into a complex but singular 'social nature.'

In indigenous settings around the world, the connection with nature (water, land, soil, and all dimension of the natural capital) is paramount. The social and cultural value of indigenous people and communities reflects on the healing power of nature and reflects on the circle of moral concern and encompassing partialities beyond the human species. Take for instance the case of New Zealand, the Whanganui River for >700 years is home for Whanganui tribes who managed, cared for, and depend on, calling it '*awa tupua*' meaning their river of sacred power. With European settlement in the mid-1800s, the traditional authority to manage the river was substituted by the nation-state decree. The inventions under that tenure included the use of dynamite to create an easy passage for tourism, gravel mining, and effluent dilution. Given such course of events in the modern era of river management, on March 20, 2017, New Zealand recognized in law what local and indigenous people such as Maori had widely supported i.e., the declaration of the river as a living being. This new legislation declared 'Te Awa Tupua,' the river and all its physical and metaphysical element as an indivisible, living whole, to henceforward holds all the rights, powers, duties, and liabilities of a legal person.

Water, energy, and food nexus—the value proposal

Few points are presented to expand on the value of water in the food sector. Modernization of irrigation systems have upgraded and improved the capacity of the production system to respond to the increasing food security needs, alongside the institutional, organizational, and technological changes and reforms governing the water-supply and demand dynamics through improvement in operation, maintenance, and management of canal irrigation and systems (Facon, 2005). These emerging management practices promoted or/and involved active participation both from government institutions and farmers, and inclusion of the stakeholders in decisions regarding the level of service and co-management. The private sector's emerging role in financing irrigation is another important and developing aspect toward improving the efficiency of water use as Eshete et al. (2020) highlights this point in the assessment for the Ethiopian region. In general, the evaluation of water resources for various uses and related allocation policies depends on the clarity of sectoral demand management.

In the 'value proposal' for freshwater systems, water pricing is a key attribute. For example, the agricultural sector in Ghana, Africa, noted decline in the past years (Dzanku and Aidam, 2013), thus impacting the national GDP and employment opportunities for the rural people, more so as the country specializes in the production of high-value crops such as cocoa, coffee, oil palm, cashew, and rubber. It is reported that seasonal variability in precipitation, particularly in the dry season, renders heavy reliance of the farming community on irrigation supply, and in recent years irrigation is noted as dominant source of water resource consumption in the country (FAO, 2016). Amid escalating water scarcity in the region and growing water demand of the agricultural sector, ensuring economic returns on freshwater use required fresh insights (Soto Rios et al., 2018). To mitigate the situation, as a short-term strategy, the urban farmers explored the use of wastewater to meet irrigation demand for vegetable production (Amponsah et al., 2015), however the health outcomes of such an intervention was not carefully evaluated. Therefore, the need for alternative options and careful measure of trade-offs while designing operational measures to address the value proposal to water is persisting. As valuation of water for food production at the cost of health outcomes could prove to be an unsustainable option.

In this above case, different systems and models to price water were debated as an option. The Multi-Analysis Tool for the Agricultural Sector (MATA) approach selects areas according to their resource characteristics (for example, land, labor, capital, and management), takes note of farmer management decisions while providing a framework for water pricing in the agriculture sector. The corresponding socioeconomic and agroclimatic environments are integrated into the tool along with the central assumption that income maximization is a priority for the farming community. The tool helps to understand trade-offs, specifically by adopting 2 cedi/m^3 (0.43 US dollar/m^3) annual volumetric rate as a measure that attracts farmers to a conscious use of freshwater resources and rationale for investment in water-saving technologies (Aidam, 2015). That said, public investment and policies need to recognize innovation and smart programs by providing proper incentives and an enabling environment for financing efficient water use systems and an integrated 'value' perspective.

In a similar context, the 'energy intensity analysis' by Hussey and Pittock (2012) points to water distribution systems that enable the identification of regions and districts where large amounts of energy are required to deliver water.

Narratives on water security and economic development

The water security and economic development interlinkages also involve objectives of safeguarding water needs for populations, household and livelihood requirements, and overall conservation and restoration of ecosystems. Therefore, securing water availability and allocations for sectoral needs such as food and energy production, industry, transport, and tourism are critical challenges in water management and governance. During past decades economics of water use, distribution and allocation received increased attention from academic, private, and policy communities. A crucial development report showcased trends of many regions worldwide focusing on water availability, noting that water security will remain a key catalyst for economic growth and sustainable development (World Economic Forum, 2017). Economic growth refers to an increase in the production of goods and services of economic value in a temporal domain. It is traditionally measured as the gross domestic product (GDP) linked to sustainable water management in multiple ways. Hence, the focus on water security is not only relevant to achieving sustainable development but necessary. However, there is no one concept or narrative to outline a clear agenda of water security. The working definition by UN-Water (2013) "*the capacity of a population to safeguard sustainable access to adequate quantities of acceptable quality water for sustaining livelihoods, human wellbeing, and socioeconomic development, for ensuring protection against waterborne pollution and water-related disasters, and for preserving ecosystems in a climate of peace and political stability*" provides a guiding framework framing while reflecting the vital need for efficient water use at economies of scale. Further, the emerging understanding of the various value and knowledge systems related to water management calls for water resources protection and priority attention to wastewater management, recycling, and reuse mechanisms (WWAP, 2019; Avellán et al., 2021). The general conceptual layout of water security (UN Water, 2013) clearly emphasizes the interconnectivity of multiple water needs-sectoral, environmental, and economic growth (Annexure).

The economic evaluation of water is generally shaped around the key dimensions of supply and demand dynamics, alongside the mechanisms for water quality management systems, storage infrastructure, and delivery or provisioning systems. These aspects are also crucial for the planning of water security for states and communities. Let's say, contamination of water resources is a water quality issue that renders a suite of risks to threat to human and ecosystem health. While the developed economies have been

experimenting since the mid-20th century to invest in improving the water resources systems, in some developing countries, the costs of treating urban and industrial waste far exceed their technical and financial capacity. Note a simple explanation- each cubic meter of on-site recycled water embodies one cubic meter that will not have to be withdrawn from a surface water source or groundwater. Reuse and recycling water and wastewater systems could also consider integrating industrial and municipal sewage/waste treatment agendas (WWAP, 2017). For example, reclaimed water can be used in industrial cooling and power generation, boiler feed, and extinguishing. Although the recycling and reuse approach is gaining popularity as an effective method of saving and valuing water both in industrial and municipal settings and is being integrated with the circular economy/circularity (Avellán et al., 2021) framework, the emerging theoretical and foundational knowledge is yet to demonstrate potential in societal well being and sustainable development vision. Besides, framings such as 'water auditing' has been developed that refers to the industrial sector or manufacturing facility, where water supplied to the plant is used for various activities and allows to measure how much water is used in each process and the water footprint of the entire chain/cycle production are being employed by various sectors of water use. The rainwater and evaporation rates impact the audit process, rendering information toward evaluating the water balance. It is acknowledged that an enhanced understanding of these framings could help to redefine the operational efficiency in water use.

Regional and national agendas for valuing water

People often understand the 'economics of water use' in a limited way; to enhance understanding in this direction the 'National Water Security Index' (NWSI) by Asian Development Bank includes five dimensions: household water security, economical water security, urban water security, environmental water security, and resilience to water-related disasters (ADB, 2013) and provides good insight into profiling the water security for various economic and non-economic sectors. Herein, the agriculture-focused subindex considers the different aspects of water security relating to food production, such as irrigated agriculture, import of water, and large storage structures like a dam. Also, mitigation and adaptation focus on disasters such as floods and drought risk for agricultural lands. The industrial-focused subindex is referred to as the financial value of industrial goods relative to industrial water use or consumption. The energy-focused subindex considers the use of overall hydropower and the ratio of hydropower to total energy supply. The direct connections between water and economic growth need in-depth investigation both for emerging and developing economies to evaluate their freshwater use, allocation, distribution plans, and policies. However, for several countries, especially in the developing world, crises related to access, availability, and quality of freshwater resources can unfavorably influence economic growth. Consequently, new technologies and business models need to be applied. International relations for knowledge sharing need to be established to ensure better capacity for sustainable use of water resources (Molden, 2007) and a water-secure future for people and societies.

The Inter Press Agency, during the Fourth Consultation of the HLPW (United Nations, 2017), noted that experts and policy-makers within the context of 'Valuing Water' alluded that regional cooperation is a must to resolve long-standing water problems in South Asian countries like Bangladesh, Bhutan, China, India, and Nepal, and to harness the full value of water (Islam, 2017). Focusing on several water-related diseases, including cholera and schistosomiasis, remains widespread across many developing countries. Only a tiny fraction (in some cases less than 5%) of domestic and urban wastewater is treated before its release into the environment. Although the rapidly growing cities in the developing countries are projected to become significant sources of nutrient emissions, South and East Asia, parts of Africa, and Central and Latin America are forecasted to become the hotspots for high nutrient emissions' increase in surface water systems (WWAP, 2019). Therefore, focusing on managing the ecological health of aquatic systems remains closely tied with tackling human health and the sustainable development agenda's goals, and the valuing water perspective.

The sense of urgency in tackling economic and development objectives and having an agenda alleviating the water crisis is increasingly noted in many countries' national agendas. At the national scale, the example includes the United States Bureau of Reclamation's water resource projects from 1930 to 1970 that reflected on the positive impacts on regional economic growth in the Southwest USA, particularly in regions experiencing water scarcity (Cicchetti et al., 1975). Another example is Spain, the largest semi-arid land in the European Union, which has outlined a complex multi-goal management approach to water security and develops water policies that address ecological, socioeconomic, and sociopolitical issues. Nevertheless, due to existing political instability in the past years, a comprehensive water policy is yet to materialize (Global Water Partnership, 2010). In a different part of the world, the Indus River, a transboundary water resource shared between India and Pakistan, provides an example to examine how in shared water systems, managing water for sectoral/economic needs poses complicated and multifaceted challenges. The Pakistan Council of Research in Water Resources reports that water shortage is dramatically increasing. The World Economic Forum (WEF) states that the country may deplete its water resources by 2025. Pakistan's economy is heavily reliant on agriculture, mainly irrigation-based production. Interventions like a dam could provide a solution for the pressing water needs. In rural Sindh and Baluchistan region, communities people walk several miles for daily water needs. However, transboundary water politics is complex, posing as a limiting factor as agreements of water sharing are not reflective of social, cultural, and humanitarian value systems (Adeel and Wirsing, 2016).

Case study: Water value perspectives in South Asia with focus on Nepal

Nepal is ranked among the top 40 water-stressed countries worldwide by the recent World Resources Institute report, having an average of 40–80% of the available water extracted every year to meet the annual demand. According to the institute's Aqueduct

Water Risk Atlas, the country faces 2–4 cm of groundwater depletion per year (Mandal, 2019). Thus, evidence shows that water demand increases significantly in Nepal, and access to safe and adequate drinking water is key to sustainable development agenda implementation. More than a quarter of the population has access to basic sanitation; those without access rely on local surface water sources like rivers for bathing, washing dishes, and clothes. Children under the age of 5 are the most affected by waterborne diseases, with an estimated 44,000 children dying every year. The public lacks awareness and education on safe drinking water rights and proper sanitation requirements; and domestic-industrial wastewater treatment plants need to be widespread (Ghimire, 2019). About 91% of Nepal's population drinks from an improved water source, however, recent studies also indicate *Escherichia coli* and total coliforms pollution is detected in water sources.

The study attributes the pollution of water resources from the human and animal densities, farm animal waste, manure application and livestock grazing, and the poor management of wastewater treatment plants and calls for better investment and focus on low-cost techniques to manage drinking water quality toward better health outcomes (Malla et al., 2018). Corrective actions in the water supply system and provisioning systems not connected to regulated piped networks (Slaymaker and Bain, 2017) also needs attention.

The Pokhara Metropolitan City (PMC) of Nepal's effort to respond to valuing water toward enhancing drinking water security is a pilot initiative research-based study '*drinkPani*' (Photos from the field shown in Fig. 8). The initiative intends to bridge the gap between water utilities and communities in information flow on water supply and quality, involving Youth as key actors and information and communication tools as the primary measures to navigate the path to reach policymakers for evidence-informed decision making. As part of ongoing research where 'water supply and quality monitoring are managed by using emerging technologies,' key-actors, the youth [Young Water Volunteers], are assigned official 'water clubs'- named *drinkPani are* provided

Fig. 7 (A) Residents of Kathmandu (Nepal) have faced water scarcity for years reflecting the need to strengthen water security (availability, access and affordability); (B) This photo shows a local woman washing dishes in the Bagmati River in Kathmandu, Nepal and available literature reflects on the gender disparities in water and sanitation sector at the community level. (A) Source: Mandal C (2019) *Climate and Environment: Nepal should reconsider water consumption patterns and protect its resources, new study warns* [WWW Document]. Kathmandu post https://kathmandupost.com/climate-environment/2019/08/15/nepal-should-reconsider-water-consumption-patterns-and-protect-its-resources-new-study-warns. (B) Creekmur N 8 (2016) Typhoid Fever Bacteria Detection in Fecal Contaminated Kathmandu Drinking Water. Climate Vulture. Available at: https://climatevulture.com/2016/07/31/typhoid-fever-bacteria-detection-in-fecal-contaminated-kathmandu-drinking-water/ Image Source: https://www.worldhunger.org/articles/links/images/riverinnepal.jpg.

Fig. 8 (A) School students receiving outdoor training to use field kits to test water are different points of the supply system (B) trained students as Young Water Volunteers (YWVs) taking water samples at household level (C) YWVs receiving training to use different water test kits in a local laboratory (D) YWV using mobile application for collecting water supply and quality data as a reporting tool. Source: Gautam, 2019, Location: Nepal.

with intensive training and tools for water sampling, test, data collection, reporting, and sharing under 'Youth-led Participatory Sensing'- YPS Model. The website manages information flow and the web application (app) quotes Gautam (2020).

Concluding points

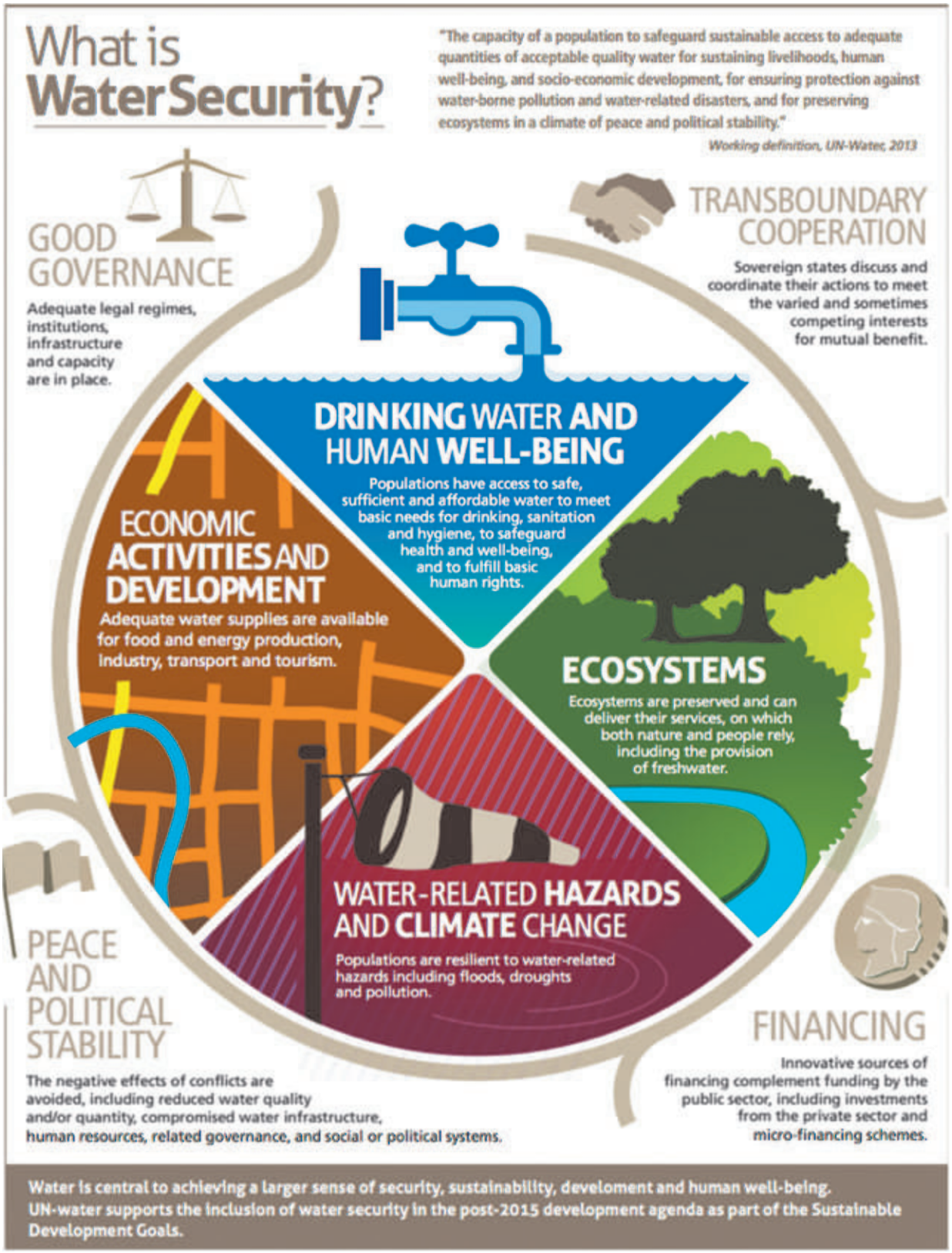
The framing of 'valuing water' is diverse, complex, and multifaceted; however, gradually, countries and communities are acknowledging and/or integrating multiple conceptualizations of values that apply to the water sector. Understanding these multiplicities from an economic and non-economic standpoint could help assess prior and current water use trends and likely future freshwater management trajectories. The existing knowledge surrounding valuing water is disaggregated. To this need, existing guidelines for managing water values' such as Bellagio's Principles and ongoing programs like the VWI, have potential. Additionally, the water security notion provides a useful perspective to design, plan, and address sectoral water needs with an integrated perspective. Thus, diverse values and aspects associated with water can be protected. Additionally, the concept of 'environmental personhood' provides a framing for *the* creation of valuing human rights to a valuing non-human entity rights holder and extending it to valuing nature, and by extension, water. Endowing water resources with this value proposition reflects the willingness to integrate multiple value systems, including but not limited to local and indigenous value and knowledge systems. The holistic approach to 'valuing water' can allow for a more equitable exchange of power and, in turn, access to political resources for effective management of freshwater resources via an optimal balance in economic growth and sustainability targets.

Knowledge gaps/future research

- In order to acknowledge and manage the 'value proposal' in the water domain, integrated approaches to managing food security, energy needs, and water security simultaneously remains a gap that should be addressed collectively and in participatory manner through a multi-stakeholder approach.
- Decision-makers should better put together interconnected challenges in the water, food, and energy nexus and design integrated freshwater-related policies and planning measures.
- Design mechanisms and tools that allow for assessing trade-offs while designing operational measures to address the value proposal to freshwater management systems.
- The interlinked sectors of water, food, and energy need can seek better ways of effective decision-making to optimize benefits, address financial barriers, and identify potential new partnerships.
- Promote research and development of smart and innovative strategies that allows integration of multiple values and knowledge systems in operational frameworks of water infrastructure, planning, and capacity development.

Annexure

UN Water (2013) water security conceptual framework emphasizes multiple dimensions that should be considered for inclusive planning and participatory management of water resources.


What is Water Security?
"The capacity of a population to safeguard sustainable access to adequate quantities of acceptable quality water for sustaining livelihoods, human well-being, and socio-economic development, for ensuring protection against water-borne pollution and water-related disasters, and for preserving ecosystems in a climate of peace and political stability."
Working definition, UN-Water, 2013
GOOD GOVERNANCE
Adequate legal regimes, institutions, infrastructure and capacity are in place.
TRANSBOUNDARY COOPERATION
Sovereign states discuss and coordinate their actions to meet the varied and sometimes competing interests for mutual benefit.
DRINKING WATER AND HUMAN WELL-BEING
Populations have access to safe, sufficient and affordable water to meet basic needs for drinking, sanitation and hygiene, to safeguard health and well-being, and to fulfill basic human rights.
ECONOMIC ACTIVITIES AND DEVELOPMENT
Adequate water supplies are available for food and energy production, industry, transport and tourism.
ECOSYSTEMS
Ecosystems are preserved and can deliver their services, on which both nature and people rely, including the provision of freshwater.
WATER-RELATED HAZARDS AND CLIMATE CHANGE
Populations are resilient to water-related hazards including floods, droughts and pollution.
PEACE AND POLITICAL STABILITY
The negative effects of conflicts are avoided, including reduced water quality and/or quantity, compromised water infrastructure, human resources, related governance, and social or political systems.
FINANCING
Innovative sources of financing complement funding by the public sector, including investments from the private sector and micro-financing schemes.
Water is central to achieving a larger sense of security, sustainability, development and human well-being.
UN-water supports the inclusion of water security in the post-2015 development agenda as part of the Sustainable Development Goals.

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EMERGING METHODS AND TOPICS

Section Introduction: Exploring the Exciting New Landscape of Inland Waters Research

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Introduction

The study of inland waters has a robust and long history. However, what is most exciting to us (and many scientists), are the newest scientific questions that require us to develop different perspectives of freshwaters, engage with new areas of study, and develop or apply new approaches and methods. That's what this encyclopedia section *Emerging Methods and Topics*, is all about—the new frontiers that are advancing the understanding and management of inland waters.

Some of these new perspectives and questions are the result of emerging technologies opening new areas of research. Many of these questions come from our heightened understanding of the pressures facing our freshwater resources in the face of global changes, such as land use intensification, climate change, and the spread of exotic species. These global changes that are inextricably linked with humans, requiring us to interrogate the belief that science (and scientists) is objective and to embrace new ways of transforming knowledge and translating that new knowledge to those beyond academia. Therefore, many of these questions require limnologists to collaborate with experts in the social sciences, humanities, and communication sciences. The emerging approaches and methods required may be brand new, requiring algorithm or technology development and partnering with those in fields such as statistics, computer science, and engineering. Alternatively, these approaches and methods may already exist in those disciplines, but haven't yet been applied to understand inland waters.

This *Emerging Methods and Topics* section brings you chapters that highlight some of those exciting new questions being asked, perspectives being developed, and methods and approaches either being developed or applied to inland water research and management. These chapters are written by emerging leaders in limnology, mainly early-to-mid-career scientists who are pushing the boundaries of their specialties to answer important questions that are just now surfacing. The chapters are arranged to introduce you to a new perspective, research question, or area of research and then to share some of the new approaches and methods being used by those taking such perspectives, asking those questions, and developing these new areas of research.

First, we bring you a chapter that shifts our perspective of inland waters. We like to use a medical analogy when thinking about this perspective change. In the past, many limnologists were like medical doctors, studying and managing individual bodies of water, watersheds, or water-rich regions. More recently, some limnologists have become more like epidemiologists, seeking to understand and manage entire populations of inland waters. In *Macrosystems Limnology and Beyond: Re-Envisioning the Scale of Limnology*, the authors describe the importance of this perspective. We then follow that chapter with a series of five chapters that share approaches, tools, and methods that help advance this broad-scale perspective (i.e., high-frequency sensors; remote sensing; machine learning; research teams, networks, and networks of networks; and citizen science, crowdsourcing, and social media).

Next, we bring you a series of three chapters introducing you to some interesting new areas of inland waters research: dust and fog effects, understanding the soundscape (i.e., ecoacoustics), and fungi in the Anthropocene. Finally, we end the section with

three chapters that share exciting new approaches, tools, and methods to better understand and manage organisms in inland waters (i.e., environmental DNA or eDNA, electronic tagging and tracking, and fatty acid markers and foodweb tracers). Below, we provide a short summary of each chapter of the *Emerging Methods and Topics* section to pique your interest and prompt you to turn to each respective chapter to learn more about the future of inland waters research and management.

Macrosystems limnology and beyond: Re-envisioning the scale of limnology (McCullough et al., 2022)

This chapter discusses the emerging field of *macrosystems limnology*, which recognizes freshwater ecosystems as components of larger, integrated systems influenced by aquatic, terrestrial, and atmospheric components and processes at multiple scales of space and time. This field has its content roots in landscape limnology, biogeography, and systems science, and has been advanced with data from long-term monitoring networks, government monitoring programs, large compilation databases, coordinated snapshot surveys, remote sensing, and citizen science. The aim of macrosystems limnology is to uncover patterns that exist and the underlying processes operating at different levels of biological organization and across scales of space and time. A macrosystems perspective could be instrumental in predicting how freshwaters will respond to global changes and guide regional to continental (and even global) management efforts.

Creating and managing data from high-frequency environmental sensors (Rose et al., 2022)

This chapter discusses the relevance and applications of high frequency sensors for advancing limnological research. High frequency sensors facilitate fast and repeated sampling of ecological phenomena, even where it is impossible to make manual measurements (such as in sites that are not easily accessible), which has resulted in many insights into ecosystem dynamics. The chapter describes a range of sensors and outlines practical considerations for their use in data collection. In addition, the authors discuss key sampling concepts and their ecological implications and challenges, as well as some disadvantages of fast sampling rates such as increased dataset complexity, power consumption, and storage requirements. The chapter outlines practical considerations in sensor choice and management, including sensor type, system design, cost, and measurement variables. Rose et al. also explain the challenges associated with these methods, such as harsh environmental conditions, and explore considerations for ensuring data quality and adequate data management.

Remote sensing of inland waters (Tyler et al., 2022)

This chapter provides an overview of the principles and applications of earth observation (EO) technologies (e.g., satellite or airborne remote sensing) for monitoring water quality. The chapter describes ways to characterize water color and how light propagation, optical complexity, and water typology affect EO estimation of water color. Additionally, the chapter explores the evolution of remote sensing platforms and defines the criteria for selecting sensor and platform developments. Platforms discussed are spaceborne, airborne, drone, in situ above-water, and in situ subsurface sensors. The criteria discussed include size of distinguished objects, range, number and width of spectral bands, number of digital levels used to express collected data, and the interval between the different resolutions. The authors also discuss additional applications such as estimating chlorophyll *a*, phycocyanin, turbidity, and total suspended matter. Monitoring algal blooms, brownification, and primary production at both national and global scales using remote sensing can provide critical information for lake management.

Machine learning for understanding inland water quantity, quality, and ecology (Appling et al., 2022)

This chapter provides an overview of machine learning (ML) models and their applications to the science of inland waters. ML is the development and application of models that adapt and can analyze and draw inferences from patterns in large amounts of data. The authors describe many aspects of ML models, including their characteristics and how they compare with process-based and empirical models, ways to determine model trustworthiness, ways to choose among model classes, and ways to understand and interpret model results. They focus on four classes of ML approaches that are gaining in popularity when studying inland waters - neural networks, classification and regression trees, clustering and dimensionality reduction methods, and model interpretation techniques. The authors provide examples of ML model applications for predicting and understanding inland waters, including the prediction of water quality, quantity, and ecology across space or time.

Teams, networks, and networks of networks advancing our understanding and conservation of inland waters (Read et al., 2022)

This chapter discusses the important role of people working together to advance inland water science and management and provides case studies demonstrating the importance of teamwork for advancing knowledge. Teams, networks, and networks of networks lie at the forefront of inland water research, management, and conservation. This is largely due to the multi- and interdisciplinary and complex nature of inland water research and management. The chapter examines the role of teams, networks, and networks of networks in the

research and management of inland water resources, discusses aspects of team building and maintenance and their respective roles in propagating successful research and management, and methods for successful social connections within teams, networks, and networks of networks. The authors explain that teams, networks, and networks of networks may include individuals within the same or different organizations, but that they are bound together by a common goal, and that trust is the foundational tenet for success. Effective team and network dynamics are critical for effective flow of information, allocation of resources, coordination of logistics, knowledge generation and sharing, as well as building and engaging in collective action.

Citizen science, crowdsourcing, and social media advance our understanding and conservation of inland waters (Latimore and Lowry, 2022)

This chapter discusses how increasingly important it is for inland waters scientists and managers to engage with diverse audiences. The chapter focuses on three rapidly expanding methods for public engagement: citizen science, crowdsourcing, and the use of social media. These methods produce large amounts of reliable data; often represent cost-effective approaches to increase research scale, public relevance, participant knowledge of content and the scientific process; and empower participants to engage in stewardship and decision-making processes. The authors point to the recent growth of these approaches and provide case studies highlighting the use of these methods in both scholarship and application. Participation of non-scientists can result in more relevant research questions, can produce a richer set of data and knowledge, generate innovative solutions to complex conservation problems, and increase scientific literacy and public support for research and conservation work.

Dust and fog effects on inland waters (Brahney et al., 2022)

This chapter describes a new research area, that of the roles of fog and dust in the transportation of atmospheric nutrients to inland waters. Human activity (such as construction) is a major agent of dust generation and fog is critical in the deposition of dust into aquatic ecosystems. Nutrients carried by dust may alter the chemistry of the affected aquatic systems with negative effects on the ecology and behavior of microbial, phytoplankton, and zooplankton communities within. Fog is likely to have indirect impacts on inland waters through scattering and absorption of incoming light, and hydrologic and biogeochemical impacts on adjacent catchments. The authors discuss the process of dust and fog formation, controls on dust and fog composition, nutrient bioavailability, common measurement techniques of dust and fog, and provide case studies that exemplify the effects of dust and fog on water chemistry and the ecology of inland waters.

Freshwater ecoacoustics (Linke et al., 2022)

This chapter discusses ecoacoustics, an emerging interdisciplinary field that investigates the ecological relevance of environmental sounds. It examines fundamental differences between bioacoustics and ecoacoustics and highlights applications of the latter in aquatic systems research. The chapter discusses biotic, abiotic, and anthropogenic sources of environmental sounds. Biotic sounds discussed commonly emanate from insects, fish, and plants; abiotic sounds include flow turbulence, sediment transport, and river flow; and anthropogenic sounds include water transport, recreational water parks, and mining and construction activities. After highlighting problems with traditional sampling methods, the chapter makes a strong case for the need of ecoacoustics to improve understanding of aquatic soundscapes. The chapter concludes by highlighting knowledge gaps, technical challenges, and relevance of ecoacoustics to society.

Inland water fungi in the Anthropocene: Current and future perspectives (Grossart et al., 2022)

This chapter examines the biological, chemical, and physical effects of pollution on inland water fungi. Fungi species have different mechanisms of assimilating and breaking down the pollutants. For example, some fungi have extracellular enzymes that break down pollutants from human environments. The ability to process and detoxify anthropogenic pollutants qualifies fungi as an indicator of ecosystem health. The authors explore the diversity and ecology of aquatic fungi and fungi-like organisms, and highlight the emerging topic of fungi-virus interactions. The authors also highlight the effects of micro plastic pollution on aquatic fungi and the roles of fungi in decomposition of micro plastics. Micro plastics are commonly generated from urban environments and washed into inland waters. However, some fungi assimilate micro plastic pollutants in aquatic environments. Understanding the ecological roles of aquatic fungi is critical in examining the negative feedback loops of human pollution to human health.

Environmental DNA advancing our understanding and conservation of inland waters (Seymour, 2022)

This chapter explores the application of environmental DNA (eDNA) for sampling freshwater animals. The use of eDNA is an emerging modern technique facilitated by recent advances in molecular techniques that is rapidly gaining popularity within

freshwater ecological research. The method relies on extraction of free floating DNA samples in the environment without targeting a particular organism. The extracted samples are released by animals (e.g., as fecal material) into the environment and eDNA traces the source animal species. The chapter discusses concepts related to the accumulation of eDNA and its extraction from freshwater environments. The author discusses the use of eDNA for monitoring of organisms (including fish, macroinvertebrates, and diatoms), which would otherwise be laborious and invasive. He also highlights the importance of eDNA methods for detection of rare and invasive species and monitoring disease spread.

Electronic tagging and tracking of animals in inland waters (Cooke et al., 2022)

This chapter discusses the use of electronic tags to track inland water animals. This approach can be used to understand several aspects of aquatic animal ecology (such as habitat use and interspecific interactions), behavior (such as movement, migration, and dispersal patterns), and environmental conditions (many tags measure components such as depth and temperature). The authors describe biotelemetry and biologging as the major tools used to track inland water animals (e.g., radio and acoustic telemetry, Passive Integrated Transponders (PIT) tags), and provide example applications to study a diversity of animals ≥ 10 g body mass including invertebrates, amphibians, reptiles, waterbirds, fish, and some mammals. The authors discuss how information generated from animal tracking is used in the evaluation of conservation programs, including tracking animals reintroduced into the wild from captivity.

Fatty acid-markers as foodweb tracers in inland waters (Makhutova et al., 2022)

This chapter describes the use of fatty acid (FA) markers to trace the fluxes of matter and energy through foodwebs. The authors describe FAs and their use as foodweb markers in aquatic ecosystems, describe and compare the FA-marker analysis with other methods for studying aquatic animal diets, and describe the identifying characteristics of FAs in the main taxonomic groups of organisms inhabiting freshwater ecosystems (bacteria, algae and other photosynthetic eukaryotes, non-photosynthetic eukaryotes). The chapter also describes how FAs have been used to understand the feeding spectra of many aquatic consumers and have contributed to scientists successfully differentiating between external and internal sources of organic matter in inland waters (i.e., allochthonous versus autochthonous inputs). FA-marker analysis has facilitated discoveries such as selective feeding of filter-feeders, diet variability of detritovores, and adaptations of feeding behavior to changing environments.

Acknowledgments

Thank you to Thomas Mehner for inviting me to edit this encyclopedia section and Paula Davies for keeping us all on track. The lake health analogy with epidemiology was co-created with KSC's co-director, Patricia Soranno. I appreciate Allie Shoffner for her editorial support. Hats off to all of the authors who have contributed their time, energy, and brilliance to this section during a global pandemic and a time of social and environmental crises.

Macrosystems Limnology and Beyond: Re-Envisioning the Scale of Limnology

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Big data Massive volumes of data, often of many varieties, that are not readily handled by the usual data tools and practices and present unprecedented opportunities for advancing science and informing resource management through data-intensive approaches (Hampton et al., 2013).

Component Biological (e.g., species, populations, communities), geophysical (e.g., climate, physiography, hydrology, geochemistry), and social (e.g., political systems, economies, cultures) variables and phenomena that span timescales ranging from days to millennia. When interacting with one another and with phenomena at other spatial or temporal scales, these components constitute a macrosystem (Heffernan et al., 2014).

Cross-scale emergence A macrosystems interaction where local-scale components interact and accumulate across broad geographic space to produce macroscale phenomena (Heffernan et al., 2014). Example: The additive effects of dam construction on individual stream reaches that result in highly fragmented river networks and impair migratory fish habitat. A single dam on a stream segment may not have a large effect on fish populations, but the cumulative effect of multiple dams on a stream network can significantly reduce habitat connectivity and adversely affect fish populations.

Cross-scale interactions A macrosystems interaction where processes at one spatial or temporal scale interact with processes at a different scale and result in unexpected ecosystem responses (Heffernan et al., 2014; Soranno et al., 2014). Example: The relative role of local wetlands as nutrient sinks and sources depends on regional setting. In regions with high levels of agriculture, local wetlands may act as a nutrient sink preventing excess nutrients from entering receiving lakes and streams, whereas in regions with minimal agriculture, local wetlands may act as a nutrient source to receiving waterbodies (Fergus et al., 2011).

Landscape limnology The spatially explicit study of lakes, streams, and wetlands as they interact with freshwater, terrestrial, and human landscapes to determine the effects of pattern on ecosystem processes across temporal and spatial scales (Soranno et al., 2010).

Macroscale feedbacks Macrosystems interactions where one macroscale component can amplify (positive feedback) or diminish (negative feedback) the effects of another macroscale component. These feedbacks can promote thresholds or alternative stable states in freshwater ecosystems (Heffernan et al., 2014). Example: The positive macroscale feedback loop between rising air temperatures and methane emissions (a potent greenhouse gas) from freshwater ecosystems. Rising temperatures caused by high greenhouse gas concentrations can promote methane emissions from warming, stratified lakes and melting permafrost. This reinforcing macroscale feedback leads to greater greenhouse gas levels, which then promote warmer air temperatures and conditions that result in freshwater ecosystems releasing more greenhouse gases.

Macroscale Regional to continental extents with distances spanning hundreds to thousands of kilometers (i.e., larger than landscapes; Heffernan et al., 2014).

Macrosystem A set of interacting biological (e.g., species, populations, communities), geophysical (e.g., climate, physiography, hydrology, geochemistry), and social (e.g., political systems, economies, cultures) components that range in spatial extent from very fine to very broad and that can interact over very large distances and can span timescales ranging from days to millennia (Heffernan et al., 2014).

Macrosystems ecology Study of diverse ecological phenomena at the scale of regions to continents and their interactions with phenomena at other scales (Heffernan et al., 2014).

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Macrosystems limnology Study of freshwater ecosystems (rivers, streams, lakes, reservoirs, wetlands, and groundwater) that explicitly recognizes the important role of integrated terrestrial, aquatic, and atmospheric components and processes operating at multiple spatial and temporal scales from the local watershed to regional, continental, and even global extents (this article).
Open science The concept of transparency at all stages of the research process, coupled with free and open access to data, code, and papers (Hampton et al., 2015).
Scale The spatial or temporal domain of study, reflecting data resolution (i.e., grain size or measurement frequency) and extent (i.e., study area or length of study) (Turner et al., 1989). Scale often refers to spatial or temporal hierarchies in ecological studies (e.g., local or continental for spatial scale and decadal or centennial for temporal scale).
Teleconnections Macrosystems interactions that connect geographically distant and otherwise disconnected regions via the movement of materials, organisms, energy, or information. Example: Anthropogenic acidification of freshwater ecosystems. In the 1970s in North America and Europe, lakes in remote, pristine settings had abnormally low pH to the point that biota could not be supported. The cause of acidification was coal combustion emissions that were transported via atmospheric processes from distant energy plants to remote, poorly buffered freshwater ecosystems.

Introduction

The historical roots of limnology are grounded in local-scale, single-ecosystem studies that intensely study and/or manipulate a few waterbodies and their watersheds over time. While these studies have created foundational knowledge for limnology, there are limitations in how findings from individual systems may apply to other freshwater ecosystems, especially those located in different landscape and regional settings. Additionally, these localized studies are insufficient to address the pressing, long-term scientific and management challenges facing fresh waters at regional to global scales such as climate change, land use conversion, and invasive species. Alternative approaches are needed for limnology to meet these challenges at broad spatial and temporal scales.

We suggest that understanding freshwater responses to global change stressors (e.g., climate change, land use/cover change, invasive species) will be enhanced by taking an integrative, multidisciplinary, and multiscale perspective such as offered by the emerging subdiscipline of macrosystems limnology. We define macrosystems limnology as the study of freshwater ecosystems (rivers, streams, lakes, reservoirs, wetlands, and groundwater) that explicitly recognizes the important role of integrated terrestrial, aquatic, and atmospheric components and processes operating at multiple spatial and temporal scales from the local watershed to regional, continental, and even global extents (Glossary). With advances in ecological knowledge and theory, the emergence of global change stressors, and the "big data" era of ecology embracing open science practices, limnology is expanding to regional, continental, and even global scales. In this article, we describe macrosystems limnology by describing the what, why, how, who, where, and when of this new era of limnology.

The what

Macrosystems limnology is a framework for studying and managing freshwater ecosystems (rivers, streams, lakes, reservoirs, wetlands, and groundwater) that explicitly recognizes that freshwater ecosystems are shaped by terrestrial, aquatic, and atmospheric components and processes operating at multiple spatial and temporal scales (Fig. 1). From this perspective, macrosystems limnology studies multiple freshwater ecosystems that generally span regional to continental extents to identify distributions (frequency, patterns) and multi-scale determinants and drivers (causes, risk factors) of ecological condition and processes. By identifying broadly occurring patterns and processes, the aim is to uncover general mechanisms operating at different levels of organization (Smith et al., 2008; Dodds et al., 2015, 2019) and overcome the limitations of local-scale studies that may have spatial and temporal contingencies specific to the local ecosystem and time of study (McGill, 2019).

It can be argued that a macrosystems limnology framework is necessary not only to understand freshwater ecosystem dynamics and properties that emerge from a set of multi-scale interactions, but also to predict how fresh waters will respond to global change. In fact, macroscale (i.e., regional- to continental-scale; Glossary) studies have increased in freshwater sciences over the past 20 years (Fig. 2). This trend mirrors a previously recognized shift in limnology toward more global-scale studies, accompanied by a growing recognition of the role of broad-scale phenomena such as climate change in aquatic biogeochemical cycling and aquatic ecosystem management, as well as greater availability of broad-scale datasets (Lapierre et al., 2020). This trend is expected to continue with advances in macrosystems theoretical frameworks, data and technology resources, open science culture, and the need to address pressing, broad-scale environmental problems.

Macrosystems limnology integrates and extends concepts, theories, and approaches from the fields of landscape limnology and macrosystems ecology. These ecological subdisciplines provide robust frameworks to guide and motivate the study of limnology across multiple spatial and temporal scales. From a landscape limnology perspective, freshwater ecosystems are viewed as discrete patches embedded within landscape mosaics composed of natural terrestrial, aquatic, and anthropogenic features that are

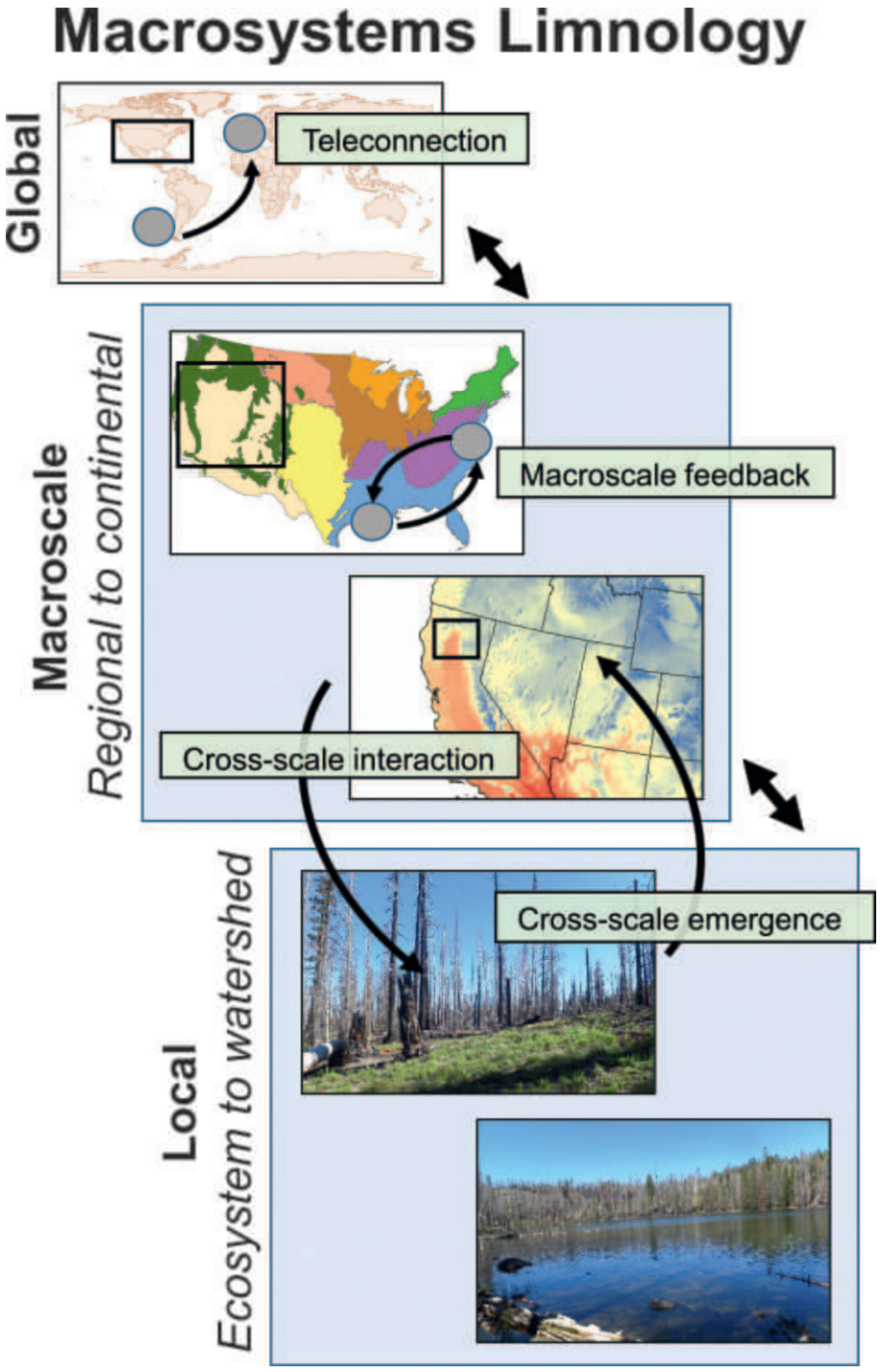

Fig. 1 Conceptual diagram of macrosystems limnology. Macrosystems integrate processes operating at spatial scales from local to global and at temporal scales from days to millennia. Macrosystems consist of various interactions within and across spatial scales, including teleconnections, macroscale feedbacks, cross-scale interactions, and cross-scale emergence (see Glossary for definitions and further examples). Shown at the macroscale are ecoregions (Herlihy et al., 2008) and regional climate (Daly et al., 2008). Ash from a volcanic eruption in Southeast Asia influences air temperatures in Western Europe (teleconnection). Precipitation influences forest growth and distribution, whereas forests also influence precipitation via transpiration (macroscale feedback). Fires are influenced by regional climate and local vegetation (cross-scale interactions), but individual fires across a given region also combine to influence regional air quality (cross-scale emergence). At the local scale (ecosystem to watershed), there is burned watershed vegetation and a nearby lake in California, USA. Photos: Ian McCullough.

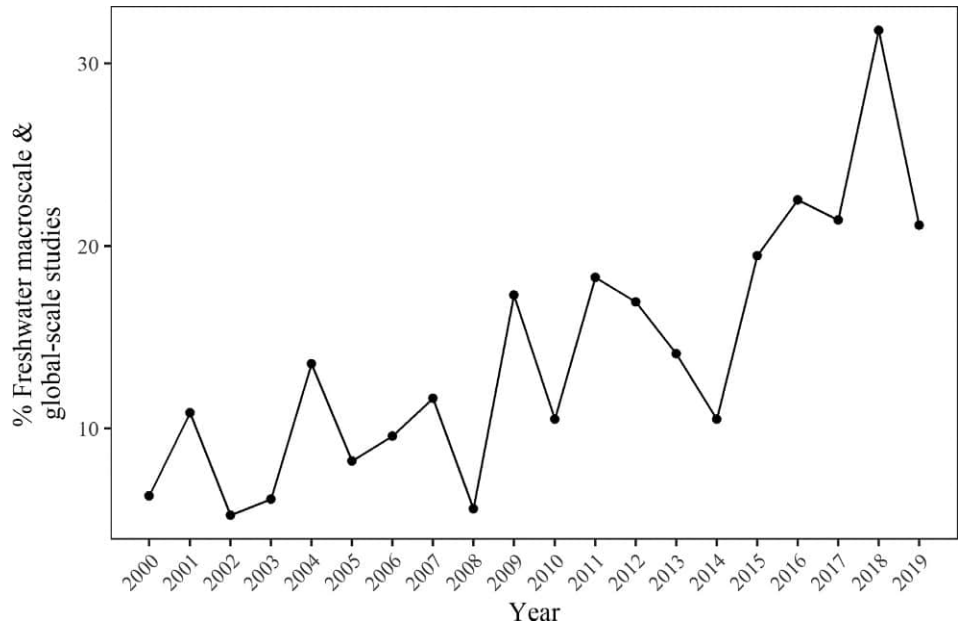

Fig. 2 Recent trend in macroscale (i.e., regional- to continental-scale) studies published annually in *Limnology and Oceanography* from 2000 to 2019, expressed as the percent of freshwater studies published in a given year conducted at macro- and global scales. We performed a spring 2020 Web of Science search using the following terms (and related forms of each using the * wildcard) "macroscale", "macrosystem", "region", "continent", "ecoregion", "subcontinent", "nation", and "global" to select studies conducted at large spatial extents. Marine and estuarine studies were excluded.

hierarchically structured and interact to influence freshwater ecological patterns and processes that emerge at different spatial and temporal scales (Soranno et al., 2009, 2010; Glossary). Freshwater ecosystems are generally the topographically low areas on the landscape that integrate terrestrial, aquatic, anthropogenic, and atmospheric processes structured at multiple scales. In addition, surface and subsurface hydrologic connections link freshwater ecosystems to geographically-distant landscape components and can enhance cross-ecosystem transport of materials, organisms, and energy. These properties make freshwater ecosystems particularly sensitive to global change stressors.

The macrosystems ecology perspective expands this landscape limnology view to consider explicitly the influence of macroscale phenomena operating at regional to continental extents (i.e., spanning hundreds to thousands of kilometers; Heffernan et al., 2014) on freshwater ecosystem properties and dynamics. Macrosystems consist of multiple biological, geophysical, and anthropogenic components that can interact across different spatial and temporal scales and result in emergent or potentially unexpected ecosystem properties in fresh waters that would be difficult to predict from local-scale observations alone (Heffernan et al., 2014; Soranno et al., 2014). These complex ecological relationships are important components of macrosystems and can be grouped into different classes: macroscale feedbacks, cross-scale emergence, cross-scale interactions, and teleconnections (Heffernan et al., 2014; Glossary). Macrosystems interactions can be defining characteristics of freshwater ecosystems and are a driving motivation for a macrosystems approach to limnology.

Integrating perspectives from landscape limnology and macrosystems ecology provides the framework for macrosystems limnology (Fig. 1). There are three key items that need careful consideration to address research and management objectives applying a macrosystems limnology framework. First, identifying the spatial and temporal resolution (i.e., grain size and measurement frequency) and extent (i.e., study area and length of study) is particularly important in macrosystems studies when scales extend beyond conventional watershed and season limits. Although scale is ultimately defined by the spatial and temporal characteristics of the phenomena of interest, it has frequently been constrained by observational data limitations that tend to be conducted at fine spatial scales and for short durations and thus may not accurately represent the full range of variability. Second, macrosystems are multi-scale, heterogeneous systems and to distill this complexity requires identifying ways to quantify biological, geophysical, climatic, and anthropogenic components that promote the patterns and trends of interest. Third, it is important to identify the disciplinary expertise (e.g., limnology, hydrology, climatology) needed for macrosystems studies because multiple drivers are hypothesized to affect freshwater ecosystems and thus macrosystems limnology often requires collaboration across multiple disciplines. With these three items defined, macrosystems limnology can be applied to understand and explain variation in freshwater ecosystems, responses to change, and prediction using scaling relationships at broad spatial and temporal extents. This macrosystems approach to limnology opens the door to address complex and challenging ecological questions facing fresh waters and provides a framework to support research and management objectives.

The why

Macrosystems limnology can lead to advances in understanding pressing environmental challenges facing fresh waters and guide management efforts. Current environmental challenges include both major causes of change in ecosystems (e.g., climate change, land use change, and invasive species) and major ecological responses to change (e.g., biodiversity loss, shifts in biogeochemical and hydrologic cycles, infectious disease transmission). Freshwater ecosystems are particularly sensitive to such phenomena because fresh waters integrate terrestrial, aquatic, and atmospheric processes over large geographic areas. We need a macrosystems framework to disentangle the effects of current global change stressors on fresh waters, which are complex and occur at, and interact across, multiple spatial and temporal scales (Fig. 1). Although many ecological questions can be answered at the local scale, understanding and predicting the consequences of global change for fresh waters require studies that contain numerous observations across wide ecological gradients, often over large geographic extents and long time periods.

The time scale at which global change stressors operate is often longer than that of a typical single study. For example, climate change studies should ideally last several decades to differentiate signal (i.e., response to climate change) from noise (i.e., response to interannual variation). Consequently, scientists should recognize that certain types of questions particularly benefit from long-term data and that in these cases there are potential limitations of relying predominantly on spatial data, as macrosystems studies often do. Therefore, long-term data should be incorporated into macrosystems studies when possible, particularly when investigating phenomena that operate over long temporal scales. Furthermore, long-term studies contribute disproportionately to both ecological knowledge and policymaking in a broad sense, demonstrating their value for both theoretical and practical applications (Hughes et al., 2017).

Studying freshwater ecosystems from a macrosystems perspective can also guide management efforts. First, and potentially most importantly, managers and natural resource agencies are often responsible for many ecosystems spanning large geographic areas. Therefore, developing management plans for ecologically diverse freshwater ecosystems in heterogeneous landscapes may necessitate identifying generalities to predict responses to multi-scale global change stressors. Results from single-ecosystem studies may be confounded by local factors (e.g., lake morphometry, watershed characteristics), making it unclear how such results apply across a more diverse group of ecosystems. Macrosystem studies, however, can reveal general patterns across wide ecological gradients and help disentangle the effects of multi-scale drivers. Further, given that managers often lack the resources to sample all ecosystems being managed, they may benefit considerably from the more generalizable findings of macrosystems studies. For example, researchers and managers are concerned about the spread and ecological impacts of aquatic invasive species in inland waters. Regional-scale models or frameworks that estimate the potential spread or impacts of aquatic invasive species represent a useful approach to scale up local-scale knowledge (e.g., local abundance, habitat suitability) and increase the efficiency and effectiveness of management interventions at the state or provincial level by identifying types of lakes that are most susceptible to invasions (Papeş et al., 2011; Vander Zanden et al., 2017). In a broad sense, an improved understanding of ecological responses to global change stressors across wide gradients can help managers anticipate responses of their ecosystems of interest to ongoing global change, which is also useful for communicating their plans and strategies to public audiences and policymakers.

The how and who

The move toward practicing macrosystems limnology was motivated by a combination of long-term monitoring networks, government monitoring programs, large synthetic databases, coordinated snapshot surveys, remote sensing, and citizen science. Numerous agencies, organizations, and people contribute to these programs and data products, including academic researchers across a wide range of disciplines, governments at different levels (e.g., city to national), and volunteers. Although these various actors often have different individual goals, all have collectively made important contributions to the growth of macrosystems limnology through data collection, open science, and knowledge development (Fig. 3).

Long-term monitoring networks generally entail intensive data collection at select ecosystems to document long-term ecosystem change. For example, the Global Lake Ecological Observatory Network (GLEON) operates standardized, automated sensors that collect high-frequency lake data (e.g., dissolved oxygen, water temperature) across over 50 lakes and reservoirs worldwide. GLEON began in the mid-2000s as an initiative among a relatively small group of scientists to share and combine lake datasets from across the globe. GLEON has since evolved into a diverse, grassroots organization of lakes, data, and people, involving researchers from many disciplines, practitioners, information technologists, students, and others. Today, membership is nearing 1000 people representing 61 countries and participating observatory sites exist on all continents except Antarctica (Hanson et al., 2016). Like GLEON, StreamPulse is a coordinated, global network (although mostly located in North America) aimed at measuring stream metabolism using automated, high-frequency data. Since the mid-2000s, StreamPulse has grown to over 200 member sites that openly share data through a centralized data portal (https://data.streampulse.org/). Other long-term monitoring networks such as the US Long-term Ecological Research Network (LTER) and the US big-science initiative National Ecological Observatory Network (NEON) collect long-term limnological data from a wide range of freshwater ecosystems across the entire US. Despite relatively few freshwater sites compared to global networks such as GLEON and StreamPulse, networks like NEON can make valuable contributions to macrosystems limnology through the use of standardized methods across a wide range of regional settings, as well as strategic co-location of observational and high-frequency instrument measurements. In addition to serving as one of the best sources for long-term limnological data, freshwater LTER sites such as the North Temperate Lakes (Wisconsin) and Arctic (Alaska) have also contributed rich foundational knowledge for limnology as a field through decades of research, data sharing, and training of scientists (Huang et al., 2020).

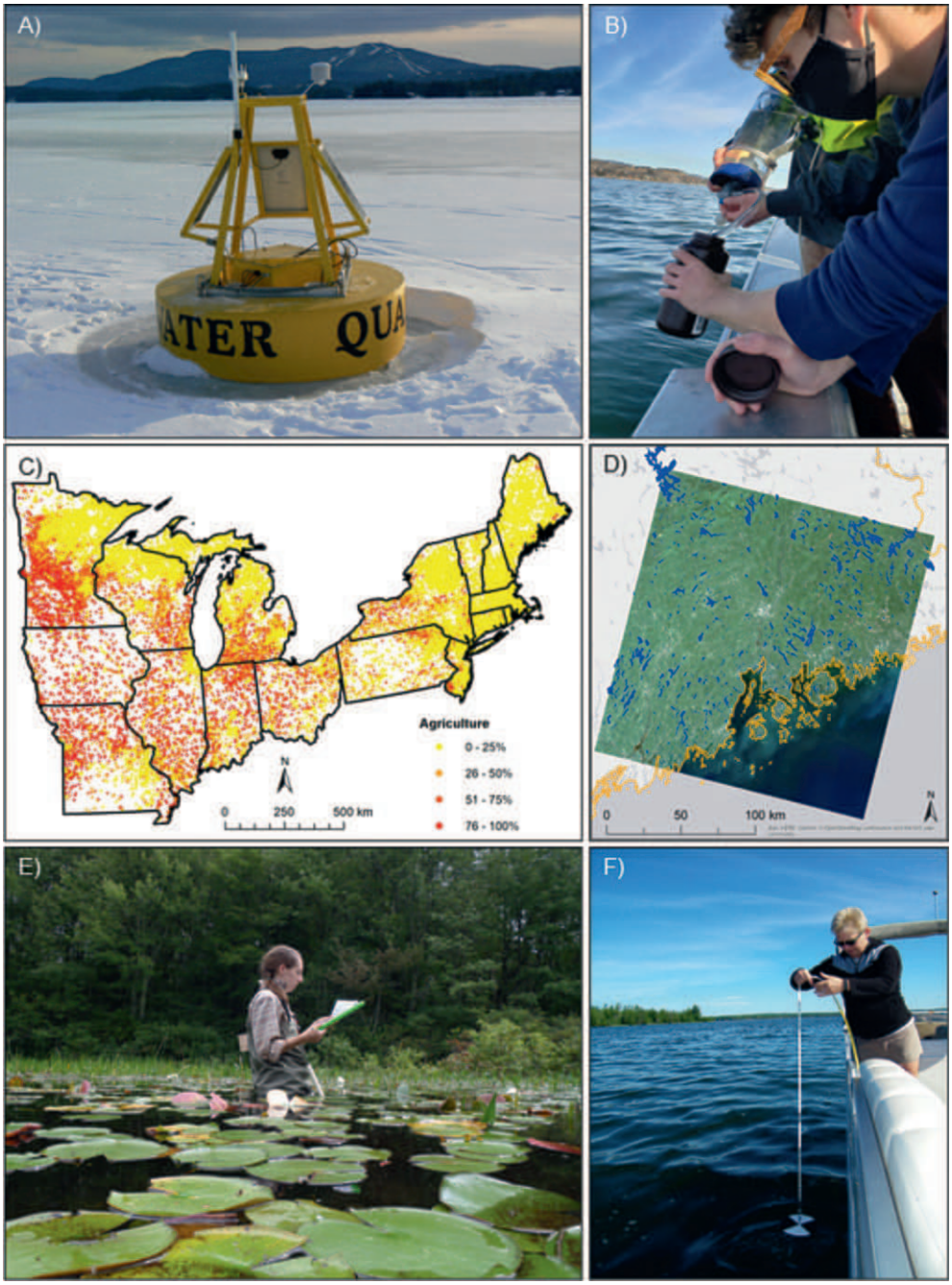

Fig. 3 The how and who of macrosystems limnology. (A) Long-term monitoring networks: this automated sensor on Lake Sunapee, New Hampshire, United States is part of the Global Lake Ecological Observatory Network and is operated by the Lake Sunapee Protective Association (photo: M. Eliassen). (B) Government monitoring programs: Lake County Water Resource Department scientists collect water samples from Clear Lake, California, United States (photo: A. DePalma-Dow). (C) Large synthetic databases: LAGOS-NE contains watershed ecological context data for approximately 50,000 lakes in the northeastern and mid-western US and lake water quality data from approximately 10,000 lakes compiled from various government, university, nonprofit, and citizen science monitoring programs (Soranno et al., 2017). Shown is lake watershed (represented as lake centroids) percent agriculture (row crops and pasture) in 2011 (Soranno and Cheruvelil, 2017b). (D) Remote sensing: shown is a true color composite Landsat 8 Path 11, Row 29 image from September 2018 of Maine, United States that can be used to estimate lake water quality variables. Lakes $\geq$4 ha are overlaid from Soranno and Cheruvelil (2017a). (E) Coordinated snapshot surveys: a scientist collects wetland data in Rhode Island, United States for the US Environmental Protection Agency's National Aquatic Resource Survey (NARS) (Photo: Tetra Tech, Inc.). (F) Citizen science programs: a volunteer measures lake water clarity using a Secchi disk in Lake Margrethe, Michigan, United States (Photo: Michigan Clean Water Corps).

Government agencies also operate some of the longest running limnology monitoring programs. These programs generally strive to maintain freshwater ecosystem services, often to ensure compliance with national, state/provincial, or local policies and standards. These efforts may entail maintaining water quality and quantity, limiting the spread of nonnative/invasive species, or managing commercial or recreational fisheries. Due to resource limitations and the desire to provide baseline data for as many individual ecosystems of interest as possible, government agencies often intentionally sample individual ecosystems relatively infrequently (i.e., annually at best). As a result, such programs often collect relatively little long-term data and are commonly biased toward particular types of ecosystems. For example, several state monitoring programs in the northeastern and mid-western US collected considerably less long-term ($\geq$15 years) lake water quality data than citizen science programs and were biased toward large lakes (although so were citizen science programs) (Poisson et al., 2020). Key challenges associated with using these data include public data access (i.e., not all programs publish data online with complete documentation) and different assessment, sampling, or laboratory procedures used by agencies or through time as instrumentation changes. For example, participating nations in the European Water Framework Directive have collectively assessed tens of thousands of rivers, streams, lakes, and groundwaters since 2000, but use different nutrient criteria for waterbody assessment, which can complicate international comparisons and efforts to pool data (Poikane et al., 2019). Nonetheless, government monitoring programs operating at national, state/provincial, or regional extents are currently among the largest data sources for macrosystems limnology.

There have been recent efforts to compile and standardize data collected by disparate government monitoring programs, as well as other sources, into large synthetic databases. Currently, two prominent examples are from North America. In the northeastern and mid-western US, LAGOS-NE is a database of lakes, water quality, watersheds, and landscape characteristics for 50,000 lakes (Soranno et al., 2017). LAGOS-NE contains lake water quality data from 87 separate federal, state, nonprofit, university, tribal, and citizen science programs. Constructing such large databases, however, requires enormous effort, such as contacting and communicating with data collectors, uncovering and reconciling different field/laboratory techniques, producing large amounts of metadata and documentation, and conducting quality assurance/quality control (QA/QC) (Soranno et al., 2015). Therefore, database engineers, computer scientists, and statisticians are valuable collaborators for database construction. Similarly, in Canada, the Canadian Lake Pulse Network is preparing the Lake Data Archive, a large database consisting of disparate historical datasets from across Canada (Huot et al., 2019). Likely owing to the steep challenges associated with compiling and harmonizing disparate datasets into large synthetic databases, such databases are currently rare. They may become more common in the future, however, as more data are published online in open repositories or are made available for sharing. Open science practices such as data sharing and data publication make possible the synthesis of disparate, local- to regional-scale datasets into larger, more complete databases that contain numerous observations distributed across wider ecological gradients and through longer periods of time than individual programs (Cheruvelil and Soranno, 2018). Given the necessary effort for producing large databases, such databases benefit from a culture of open science and in turn, represent some of the most powerful data resources for macrosystems limnology.

Coordinated snapshot surveys that seek to provide single observations across a large number of ecosystems at a particular point or window in time (Mantzouki et al., 2018; Pollard et al., 2018) are also becoming increasingly common. These programs are often motivated, coordinated, and supported by national governments. An example is the US Environmental Protection Agency's National Aquatic Resource Survey (NARS), intended to assess physical, chemical, and biological indicators in thousands of aquatic ecosystems across the lower 48 US states. NARS for inland waters encompasses the National Lakes Assessment (2007, 2012, 2017), the National Wetland Condition Assessment (2011 and 2016) and the National Rivers and Streams Assessment (2008–09, 2013–14, and 2018–19). A unique feature of the NARS program is the probabilistic sampling design developed by statisticians, which helps ensure that sampled sites are representative of a larger target population. This design facilitates population-scale assessment of ecosystem condition to meet policy and management objectives at national or regional scales. Similarly, the Canadian Lake Pulse Network sampled 680 lakes across Canada from 2017 to 2019 using standardized methods as part of an academic-government partnership (Huot et al., 2019). An example of an international collaboration is the 2015 European Multi-Lake Survey, which sampled 369 lakes across 26 countries to cover wider ecological gradients than exist in individual, often relatively small countries (Mantzouki and Ibelings, 2018). Disadvantages of snapshot surveys are the required high levels of planning, organization, and cooperation among numerous partners to cover broad spatial extents, which can be expensive and limit the frequency of surveys, resulting in little temporal data. Advantages of snapshot surveys, however, are standardized data with temporal coherence and broad spatial coverage across ecological gradients of interest, and that avoid the major challenges associated with compiling disparate data sources. Particularly when made publicly available, as the example programs described above have done or plan to do, snapshot surveys represent uniquely powerful resources for macrosystems limnology, especially when repeated to document changes over time.

Another promising approach for producing macroscale snapshots is through satellite-based remote sensing. Some of the earlier freshwater remote sensing programs were developed to help government agencies monitor waterbodies that they otherwise would be unable to sample frequently (Pulliainen et al., 2001; Olmanson et al., 2008). More recent research advances, particularly in image processing, have facilitated subcontinental-scale remote sensing of lake water quality (e.g., United States: Ross et al., 2019, China: Song et al., 2020). Compared to field-based snapshot surveys, however, remote sensing is currently only able to monitor a relatively small number of variables, mostly water clarity and to a lesser extent pelagic algal biomass, turbidity, dissolved organic carbon, and surface temperature. This limitation is related both to satellite resolution (spatial and spectral) and the need for large amounts of in situ calibration data, which are typically most available for a limited number of widely collected variables. Developing models that can be successfully applied across broad ecological gradients requires large amounts of in situ calibration data collected from ecologically diverse waterbodies. As such, remote sensing scientists must often rely on existing water quality

monitoring programs for calibration data collected at approximately the same time as satellite image capture. Public, well-documented observations such as those found in large synthetic databases represent a major calibration data source due to their spatial and temporal coverage, enabling use of historical satellite imagery to estimate long-term trends in water quality variables. As such, remote sensing, like other data resources for macrosystems limnology, also greatly benefits from a culture of open science.

Finally, citizen science is a main contributor to macrosystems limnology. Unlike state/provincial, national, or international monitoring programs, citizen science organizations are often motivated by individuals' desire for involvement in environmental stewardship and to protect the natural resources that they personally value (Bonney et al., 2009). Many citizen science groups are organized at local, regional, or state/provincial/national levels and train volunteers to use standard sampling techniques without professional supervision. Additionally, citizen science organizations are often jointly operated or supported by government agencies or academic research programs to increase data collection capabilities beyond what can be amassed without volunteer contributions. Given that limnological citizen science data have generally been found to be reliable (Hoyer et al., 2012; Scott and Frost, 2017), citizen science programs represent a major boost to macrosystems limnology, particularly when their data are made publicly available and are pooled across larger geographic areas in large synthetic databases (e.g., Poisson et al., 2020).

The where

Much of the research focus and data resources for macrosystems limnology have been concentrated in Europe and North America, largely reflecting the geographic roots of limnology as a discipline. These research traditions have fostered the growth and prevalence of long-term monitoring networks, snapshot surveys, and government and citizen science monitoring programs. Although providing a country-by-country assessment of where macrosystems limnology has been conducted is beyond the scope of this article, it is clear that such research and associated infrastructure is increasing in prevalence globally, including outside of North America and Europe. Examples include studies of invasive species spread in Kenyan lakes (Mergeay et al., 2005), land use effects on Brazilian Amazonian stream fish communities (Leitão et al., 2018), and patterns and drivers of ecosystem properties of Argentinian Patagonian lakes (Baigún and Marinone, 1995). There are also examples of national-scale efforts to synthesize disparate datasets (New Zealand rivers and streams; McDowell et al., 2009) and to establish standard field and laboratory methods and make data publicly available (Korean rivers and streams; Jiang et al., 2016) for macrosystems research. Studies such as these will build on our rich existing knowledge of high-latitude and temperate ecosystems and further our understanding of tropical and subtropical ecosystems, their contributions to global cycles, and how they are responding to global change stressors.

The growing subdiscipline of global limnology (Downing, 2009) also contributes to macrosystems limnology. Currently, global studies are often dominated by European and North American in situ data, biased toward larger ecosystems, and/or rely on remote sensing to attain global coverage (which also may bias studies toward larger ecosystems due to satellite image resolution). For example, global surface temperature trends in large lakes have been quantified using a combination of in situ and remotely sensed data (Sharma et al., 2015), whereas studies estimating global lake counts and area have relied entirely on remote sensing (Verpoorter et al., 2014; Labou et al., 2019). Global-scale remote sensing, however, provides numerous future opportunities to extend macrosystems limnology and high-frequency monitoring to regions and countries where regular field monitoring is difficult or impractical. Given the increasing availability of satellite imagery and growing interest in large synthetic databases, coordinated snapshot programs, and open science, it is likely that global-scale studies will become increasingly viable in the upcoming decades.

The growth of macrosystems limnology and global limnology reveals the high future potential for increased international collaboration, including sharing of data, methods, and expertise as part of an ascending culture of open science. Although the abilities to establish and maintain monitoring programs or to combine data from disparate studies and programs are major boosts to macrosystems limnology, international collaboration can potentially help redistribute necessary resources and support growth in underrepresented locations. As such, international collaboration may be particularly beneficial for smaller countries, including those with limited resources or where national-scale studies do not span particularly wide ecological gradients (as was the case with the European Multi-Lake Survey, which encompassed 26 countries; Mantzouki and Ibelings, 2018). Like coordinated snapshot surveys, collaboration that prioritizes methods compatibility across research sites helps ensure that all observations are equally valuable. International collaboration also can be particularly useful for remote sensing efforts by encouraging co-production of algorithms and sharing and reuse of in situ data across large geographic areas (e.g., LIMNADES program; Palmer et al., 2015) and for helping researchers link relatively coarse-resolution, remotely sensed global-scale datasets with finer-resolution continental- and regional-scale datasets within a macrosystems limnology framework. Collaboration and open science, which are key elements of the "how" of macrosystems limnology, are crucial for expanding this type of research across the globe.

The when

There has been a recent coalescence of many factors motivating macrosystems limnology, including the development and convergence of key scientific theories and concepts, major technological advances, and important shifts in scientific practices. The steady increase in macroscale and global-scale limnological studies over the past 20 years (Fig. 2) reflects the broad scientific recognition that macrosystems studies are increasingly necessary to address the current environmental challenges facing freshwater

ecosystems. By combining foundational theories and concepts from macrosystems ecology and landscape limnology, limnologists are currently better positioned than ever before to address major global change stressors facing fresh waters such as climate change, land use/cover change, and invasive species. Such stressors often operate at regional or larger scales, and so must be studied at these scales, but with the key recognition that various ecological processes combine to influence freshwater ecosystems at multiple spatial and temporal scales. A macrosystems limnology framework is necessary to tackle these challenges and emphasizes that traditional, local-scale approaches are insufficient to capture inherent variation in freshwater ecosystems and multi-scale drivers (and stressors) that shape ecosystem composition and function. Until recently, the scientific focus on single-system or single-region studies and restricted data and technological resources kept a macrosystems approach to studying limnology out of reach. As these barriers have come down, however, scientists are leveraging broad-scale and long-term datasets to understand and protect fresh waters better under changing environmental conditions. This recognition within the research community has been echoed within research funding agencies, resulting in increased allocations to macrosystems studies over time.

As limnologists have acknowledged the growing complexity of studying fresh waters under global change, recent advances in tools and technology also facilitate ongoing growth in macrosystems limnology. Macrosystems studies are inherently data-intensive and therefore require more data storage and computing resources than small-scale, individual researcher studies. Notably, increasing deployments of automated sensors and satellites provide an ever-increasing source of data, sometimes available in real-time, across broad geographic extents. Today, advances in cyberinfrastructure and data science expertise enable collection of coordinated, broad-scale snapshots and syntheses of disparate, existing data sources, and macrosystems limnology studies that were until recently, largely impractical.

Finally, as scientists, volunteers, automated in situ sensors, and satellites collect more and more data, we have also seen the shifting of scientific cultures to embrace collaboration within and across disciplines, open science, and data science in limnology. Many macrosystems studies now rely, sometimes exclusively, on data collected by other researchers to achieve desired spatial and temporal coverage. Additionally, the increasing availability of large datasets describing the ecological settings of fresh waters (e.g., downscaled climate, land use/cover) facilitates studies that consider numerous variables operating across multiple spatial and temporal scales. Although not all such datasets are currently public, investment in developing and maintaining public spatiotemporal datasets as part of a growing open science culture is highly promising for the future of macrosystems limnology. Coupled with the rise of open science and limnological big data, the multi-scale, integrative perspective of macrosystems limnology represents an essential framework for meeting the scientific and management needs for fresh waters under intensifying global change, both now and in the future.

Therefore, the time for macrosystems limnology is now. Across landscapes, regions, and continents, limnologists are in prime position to make major advances in both understanding and predicting responses of freshwater ecosystems to different aspects of global change. We must capitalize on the present and increasing scientific understanding, emerging technology and data resources, and growing culture of open science.

See Also: Emerging methods and topics: Citizen Science, Crowdsourcing, and Social Media Advance Our Understanding and Conservation of Inland Watersaters; Teams, Networks, and Networks of Networks Advancing Our Understanding and Conservation of Inland Waters

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Creating and Managing Data From High-Frequency Environmental Sensors

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Aliasing The inability to detect a phenomenon due to infrequent observations below the Nyquist rate.
Biofouling The colonization and growth of microrganisms on in situ sensors, which can often interfere with sensor operation.
Data versioning The creation of progressive iterations of a data set as it moves through a quality control process.
Integration time The amount of time a sensor is turned on and measuring the environment.
Integration volume The volume of water being observed by a sensor.
Nyquist rate (or Nyquist interval) The minimum sampling frequency necessary to detect a phenomenon. The rate is twice the frequency (i.e., observations are made twice as often) as the dominant scale of variation of the process being examined.
Sensor drift The process of increasing bias and/or decreasing accuracy in sensor measurements over time due to physical changes in the sensor.

Introduction to high-frequency sensors and data

Novel scientific insights are often built on technological advancements. Galileo Galilei had the telescope, Rosalind Franklin had X-ray crystallography, and contemporary aquatic ecologists and resource managers have a range of sophisticated tools at their disposal, including high-frequency sensors. Many environmental processes are poorly characterized by infrequent, manual measurements. Continuous and automated sensor measurements can generate observations on important aspects of aquatic ecosystems, supporting a deeper understanding of patterns and processes and the development of novel hypotheses. Near real-time environmental measurements can also support adaptive management and public engagement to improve scientific literacy. Complementing traditional manual methods of ecological research and management, as well as advancements in cyberinfrastructure and data processing, high frequency sensors are reshaping fundamental aspects of how aquatic ecology research and management are conducted.

In ecological sampling, "high-frequency" typically refers to measurement at sub-daily intervals, although in practice sampling may be as frequent as multiple times a second. High-frequency measurements are regularly contrasted with manual measurements, which require the presence of a person to collect, process, and or store samples, and which must often be processed in a lab at a later time. In practice, how frequent should sampling occur? In addition to practical considerations (e.g., regarding memory and battery life), there are important tradeoffs to consider when using high-frequency sensors. Signal processing theory posits that sampling

should be conducted at least twice the frequency (i.e., twice as often) as the dominant scale of variation of the process being examined. This concept is known as the Nyquist–Shannon sampling theorem, with the corresponding minimum sampling rate termed the **Nyquist rate (or Nyquist interval)** (Nyquist, 1928). Sampling at lower rates (i.e., coarser temporal intervals) can lead to what is referred to as **aliasing**. Aliasing occurs when samples are collected too infrequently, which results in the inability to detect an actual estimate of the frequency or magnitude of a response variable of interest. This phenomenon can be observed in videos when the camera frame rate (i.e., sampling frequency) is too slow, and things like the rotation of helicopter rotor blades occur at a similar frequency. In this example, the effect of aliasing of rotor blades is that they appear to be moving much slower, standing still, or even moving in the reverse direction than what they are actually doing.

Aliasing has important ecological implications for the minimum sampling rate for high-frequency sensors. For example, imagine a research program designed to study zooplankton diel vertical migration. This phenomenon is generally characterized by a downward migration of some zooplankton species during the day and an upward migration at night to avoid fish predation and exposure to damaging ultraviolet light (Lampert, 1989; Williamson et al., 2011). Consistent with light cycles, a full diel vertical migration cycle (downward movement, then back up to the original starting position) typically occurs once every 24 h. Before conducting their field research, researchers estimate the frequency at which they need to collect measurements of the vertical position of zooplankton in the water column. They want to minimize their sampling frequency to reduce the workload (zooplankton sampling requires quite a bit of manual labor), but sample frequently enough to adequately characterize the magnitude of diel vertical migration. If the researchers were to only sample once every 24 h, observations of zooplankton vertical position would show that the zooplankton were in nearly the exact same location in the water column at every time point, and therefore the diel vertical migration would not be discernible from other drivers of variation of zooplankton vertical position. The Nyquist-Shannon sampling theorem posits that to characterize a phenomenon like zooplankton diel vertical migration that occurs at frequency of 24 h, the researchers should sample at a frequency of at least every 12 h.

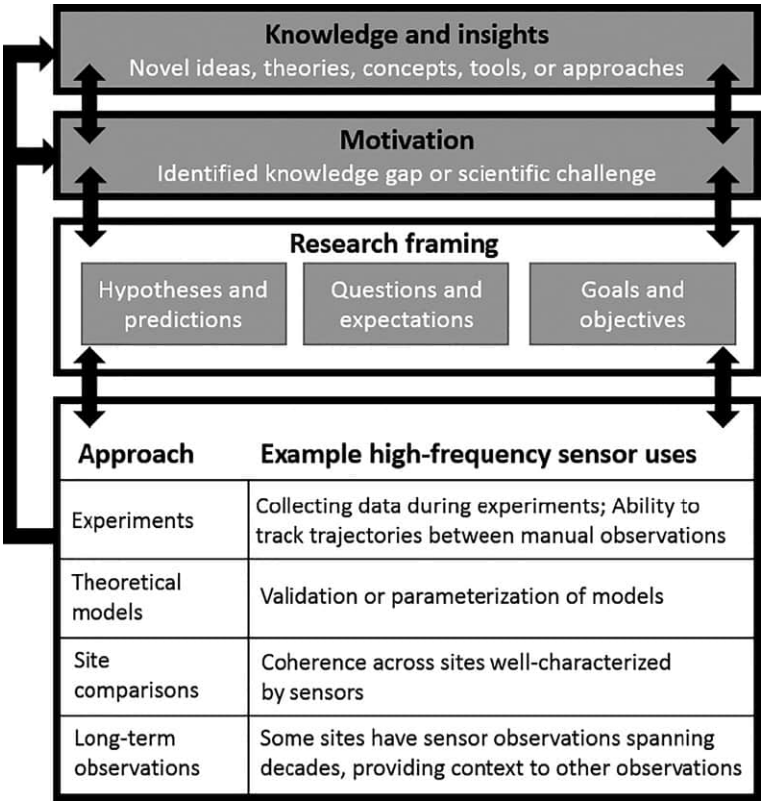
One challenge of using the Nyquist-Shannon sampling theorem to choose a sampling interval is that the maximum or dominant frequencies of many ecological phenomena are not known. Like zooplankton diel vertical migration, many ecological phenomena vary over a 24-h cycle. Thus, sampling every ~12 h can serve as a general guideline for the minimum sampling frequency recommended for most ecological observatories, unless there are other important tradeoff considerations (e.g., data storage or power; see Section "Sensors, platforms, & configurations"). Furthermore, given the possibility of even higher-frequency cycles (e.g., seconds to hours) in many phenomena, there can be substantial benefits to sampling much more frequently than every 12 h. Ecosystems are dynamic across many orders of magnitude in temporal scale. At a sub-daily time-scale, for example, variations in weather and organism behavior can introduce substantial heterogeneity in many measurements. Thus, many researchers often set high-frequency sensors to sampling intervals at the scale of several minutes (e.g., an interval of one to fifteen is common). Increasing the sampling rate (relative to, e.g., every 12 h) enables researchers to study diverse ecological phenomena without much prior knowledge of the dominant scales of variation, and thus avoid aliasing potentially important dynamics. Additionally, more frequent sampling has other potential benefits, such as a greater ability to calculate statistical attributes with greater accuracy and identify potential interferences (e.g., shadows on light sensors, when sensors are pulled from the water).

Despite the advantages of fast sampling rates (e.g., at the scale of 1 min to 1 h), there can be important tradeoffs that reduce the benefits of even-faster sampling rates. First, very high sampling rates can introduce data set complexity and management challenges. For example, increasing a sampling rate from once every 12 h to once a minute increases the number of data points generated every day by 720-fold. Although it is possible to downsample a dataset post-hoc, researchers must be prepared for a data-deluge if sampling rapidly, and especially if sampling at sub-minute time-scales (Porter et al., 2012; Rode et al., 2016). High sampling rates (e.g., sampling intervals at the scale of seconds to minutes) may not be useful unless researchers also have the corresponding technical capacity to ingest, manipulate, process, analyze, and visualize massive data sets. Additionally, faster sampling rates increase power consumption and data storage requirements at the point of data collection. In a power- or storage-limited environment, fast sampling rates may not be achievable. However, the additional power and memory required for some sensors is minimal, and often the most limiting factor to sub-minute sampling rates is technical capability in data handling.

There are other practical considerations that reduce the benefits of further reductions in sampling interval. For example, many sensors require time to equilibrate in situ (i.e., in its aquatic sampling location). If a sensor is moving through the water column (e.g., on a profiler—see Section "Sensors, platforms, & configurations"), a minimum equilibration time may be needed, for example, for the diffusion of gasses through gas permeable sensor membranes. Often, this can take several minutes if there is a steep concentration gradient and the user wants to have near 100% measurement accuracy. Additionally, sampling at the scale of seconds often means that sensors are running nearly continuously. This means that there is limited or no down-time for removal of accumulating substances on sensor surfaces (e.g., with mechanical wipers) and the potential for organisms that respond to the sensor lights to increase (see QA/QC section for further details). Accordingly, many observatories do not collect or log data at sub-minute time scales. Nevertheless, these challenges must be evaluated against any potential future utility of additional time-resolution in the measurements being undertaken.

Observations and hypotheses using high-frequency sensors

High-frequency sensing holds substantial potential to complement and extend traditional methods and has already demonstrated its utility in numerous research applications. However, a criticism of high-frequency monitoring is that it can represent a surveillance-based approach to conducting science that is not necessarily guided by specific questions or robust experimental



Approach	Example high-frequency sensor uses
Experiments	Collecting data during experiments; Ability to track trajectories between manual observations
Theoretical models	Validation or parameterization of models
Site comparisons	Coherence across sites well-characterized by sensors
Long-term observations	Some sites have sensor observations spanning decades, providing context to other observations

Fig. 1 Conceptual diagram of the scientific process as an iterative process, including the role of high-frequency sensors in research. Table at bottom describes example roles of high-frequency sensors during the data collection phase. Adapted from Elliott KC, Cheruvelil KS, Montgomery GM, and Soranno PA (2016) Conceptions of good science in our data-rich world. *Bioscience* 66(10): 880–889. https://doi.org/10.1093/biosci/biw115.

design (Lindenmayer et al., 2018). Indeed, the production of large volumes of observational data can enable research based on data exploration and discovery, which contrasts with a traditional hypothesis-driven approach to scientific discovery and the creation of knowledge. However, despite the bias against data mining, high-frequency sensing can serve an important role in understanding ecosystem dynamics, especially when science is viewed as an iterative process (Fig. 1; Elliot et al., 2016). For example, a first step in understanding an ecosystem is often to collect data, and it is important that measurements are objective and verifiable. Traditional lower frequency ecological monitoring can be insufficient to generate enough observations for events that occur infrequently or change rapidly. Rapid and frequent monitoring of ecosystem dynamics such as changes in turbidity or dissolved organic matter in response to storm events can be impractical to near-impossible without high-frequency sensors. Without sensor data, hypotheses that explain dynamics at short time-intervals may not otherwise be created.

In addition to providing initial data to support the creation of hypotheses, high-frequency sensors can serve an important function in testing hypotheses. There are multiple ways ecologists test hypotheses, including using experiments, theoretical models, site comparisons, and long-term observations (Carpenter, 1998). High-frequency sensing can be used in all of these approaches, depending on the nature of the research question and mode of conducting the research (Fig. 1). For example, high-frequency sensors can also play an important role in providing contextual information to understand research conditions (e.g., during experiments, site comparisons, or long-term observations) and, when applicable sensors exist, in testing hypotheses directly.

Research and monitoring applications

High-frequency sensors provide the capacity to autonomously and frequently characterize ecological conditions. Thus, a primary advantage and use of high-frequency sensing is in situations where it would be difficult or near impossible to make manual measurements. This can include applications where high-frequency observations are desired or required (e.g., every minute for months-long deployments), but it also applies to inaccessible sites. Accessibility can be limited due to, for example, distance (e.g., remote field sites such as mountain lakes), as well as for difficult or hostile conditions such as under-ice deployments. In fact, there is historically a dearth of research on under-ice ecology due in large-part to the difficulty in conducting manual sampling-based research in such environments (Hampton et al., 2017).

Many ecological processes and characteristics exhibit substantial variability at short-time scales. For example, while lake near-surface water temperature is often assumed to be a slowly changing characteristic, measurements from high-frequency sensors demonstrate that it can vary many degrees over the course of a day (Woolway et al., 2016). More generally, high-frequency

monitoring enables the characterization of phenomena that exhibit high temporal variance. There can be tremendous value to characterizing variance at short intervals, as there can be abrupt changes in ecological state that have long-term implications (Pace et al., 2015). For example, disturbance events, by definition, are short-term punctuated events such as severe storms that can alter the structure and functioning of aquatic ecosystems, sometimes for years to decades afterwards (e.g., Blaen et al., 2016; Jennings et al., 2012; Klug et al., 2012; Lin et al., 2022; Perga et al., 2018). Tracking dynamics during disturbance events and immediately thereafter often requires the use of high-frequency sensors. Additionally, high-frequency measurements can be used as indicators of impending large and persistent changes in ecosystems (i.e., regime shifts), irrespective of disturbance event impacts. For example, in an experimental manipulation of nutrients designed to stimulate the formation of harmful algal blooms, researchers found that features of high-frequency time-series data, such as variance and auto-correlation, were predictive of impending cyanobacterial blooms (Pace et al., 2017).

In addition to the value of high-frequency monitoring to understand short-term events, these sensors also provide important contextual information to understand long-term trends. This can be as simple as tracking conditions (e.g., in temperature, conductivity, or other variables) during a months-long experiment or understanding the degree to which a one-time manual sampling value was representative of conditions during a longer period. In this fashion, high-frequency monitoring improves the ability to understand ecosystem dynamics between lower-frequency samples. When correlations can be drawn between high-frequency observations and other difficult to measure attributes, high-frequency data can be used to infer other features. For example, high frequency sensors have been used to estimate methyl mercury concentrations (Bergamaschi et al., 2011) and estimate ecosystem metabolism characteristics, including gross primary production, ecosystem respiration, and the balance between these, net ecosystem production (Staehr et al., 2012).

High-frequency sensing is also useful to ground truth measurements or predictions from satellite based imagery or ecosystem models. For example, hydrodynamic models are often dependent on a time-series of meteorological observations to drive the model, and outputs are validated against in situ observations of water temperature. Ecological and biogeochemical models are likewise often validated against high-frequency observations of characteristics such as dissolved oxygen, conductivity, chlorophyll, and dissolved organic matter fluorescence. An advantage of high-frequency sensors over traditional manual observations is that temporal (and/or spatial) variability can be quantified in both sensor measurements and model output. Comparisons of variability across orders of magnitude in time scales provides the capacity to improve model forecasting accuracy and reduce uncertainty (Kara et al., 2012).

In addition to research applications, high-frequency monitoring is increasingly a component of water quality management programs and a mechanism for stakeholder engagement, especially when data can be provided online and in near real-time. Many high-frequency sensors exist that complement traditional managed-for characteristics, including turbidity, dissolved oxygen, water clarity, chlorophyll, and phycocyanin (see Table 1). For example, many jurisdictions have water quality mandates such as maximum turbidity levels. High-frequency sensors make it easy to rapidly assess water quality conditions and immediately respond to out-of-compliance occurrences. High-frequency monitoring can also increase the likelihood of observing out-of-compliance readings even if water quality conditions are, on average, favorable. This is because the more frequent sampling provides better characterization of the full distribution of conditions, including rare events (e.g., high turbidity levels). In this case, a running (e.g., daily) mean may be more appropriate than relying on individual time point observations. High-frequency sensors can also be used for adaptive management when telemetry enables near real-time access to the data. For example, reservoir managers may select water withdrawal depths based on water quality conditions, or turbidity monitoring could be used to avoid out-of-compliance conditions during dredging. Finally, high-frequency sensors can be a means to engage the public. Just as weather forecasts provide real-time data on outdoor conditions, so too can many in situ sensors. For example, sailors may want on-lake wind speed and direction measurements, and fishermen may want information on dissolved oxygen and temperature to identify the likely depths of cold-water species.

Sensors, platforms, & configurations

Sensors

It can be argued that high-frequency sensing is not only a contemporary approach to ecological research and monitoring. For example, various methods to characterize river flow volume in an automated fashion have existed for over 100 years. However, the recent expansion of high-frequency ecological sensing emerged from contemporary advancements in sensor, battery, and storage technologies. Today, there are many types of high-frequency sensors used to study aquatic ecosystems. Sensors are generally categorized by whether they are in situ (i.e., underwater) or ex situ (e.g., above surface) measurements, by the type of characteristic(s) they sample (physical, chemical, and/or biological) or by the underlying technology they employ. A detailed list and description of high-frequency aquatic sensors is available in (McBride and Rose, 2018; see Table 13.1). Here, Table 1 provides a broad summary of many types of high-frequency environmental sensors used in research and monitoring of inland waters.

Sensor selection can be a challenging part of study design, with a sometimes overwhelming amount of options of manufactures, models and measurement principles (i.e., the underlying technology) available for many variables. For example, while most commercial dissolved oxygen sensors for underwater applications use optical technology, there are other types of technological options available (McBride and Rose, 2018). Optical sensors have come to dominate the market owing to their long-term stability; however even among optical sensors there are multiple measurement principles (e.g., fluorescent intensity versus lifetime

Table 1 Summary of many types of high-frequency environmental sensors used in research and monitoring of inland waters.

Variable	*Typical units*	*Typical underlying technology*	*Popularity*	*Price*
Chlorophyll	RFU	Fluorescence using LED excitation and emission detectors tuned to chlorophyll pigment	Common	$$$
Conductivity	$\mu S\ cm^{-1}$	Current between electrodes is conductivity dependent	Common	$
Dissolved carbon dioxide	$g\ m^{-3}$	Non-dispersive infrared detector (NDIR)	Uncommon	$$$$
Dissolved methane	$g\ m^{-3}$	Non-dispersive infrared detector (NDIR)	Rare	$$$$
Dissolved organic matter	RFU	Fluorescence using LED excitation tuned to peak C	Common	$$$
Dissolved oxygen	% saturation or $mg\ L^{-1}$	Optical: quenching of fluorescence signal dependent on oxygen concentration; several other technologies exist	Common	$$$
Methane	$g\ m^{-3}$	Non-dispersive infrared detector (NDIR)	Rare	$$$$
Nitrate	$g\ m^{-3}$	Spectral absorbance signature in deep UV	Rare	$$$$
Oxidative/reduction potential	mV	Voltage between electrodes	Common	$
pH	unitless	Electric potential between electrodes is pH dependent	Common	$
Phosphate	$\mu g\ L^{-1}$	Wet chemistry	Rare	$$$$
Phycocyanin	RFU	Fluorescence using LED excitation and emission detectors tuned to phycocyanin pigment	Common	$$$
Phycoerythrin	RFU	Fluorescence using LED excitation and emission detectors tuned to phycoerythrin pigment	Rare	$$$
Solar radiation	$\mu E\ m^{-2}\ s^{-1}$	Silicon photodetector	Common	$$
Tryptophan	RFU	Fluorescence using LED excitation and emission detectors tuned to peak T	Uncommon	$$$
Turbidity	NTU, FNU	Light source with detector at an offset angle, often 90°	Common	$$
Water level or depth	m or Pa	Hydrostatic pressure measurement in sensing diaphragm	Common	$$
Water temperature	°C	Thermistor or integrated circuit	Common	$

RFU, relative fluorescence units; NTU = nephlometric turbidity units; FNU = Formazin Nephelometric Units. Price range $ to $$$$ roughly equates to <$1000 to > $10,000 US.

luminescence methods), materials quality, and measurement response times (a few seconds to several minutes) that affect price, longevity, and data quality. There are some objective resources available that provide sensor evaluations for their stated characteristics and sensitivities. For example, the Alliance for Coastal Technologies (https://www.act-us.info/) provides evaluations of many types of in situ aquatic sensors. Additionally, scientists in NETLAKE (Networking Lake Observatories in Europe) assembled a series of factsheets that summarize many important aspects of sensor selection and deployment (Laas et al., 2016). Finally, it should be noted that caution is warranted in reviewing older resources, as technologies and best practices can advance quickly.

There is no single agreed-upon suite of sensors or configurations, as differences in priority research questions and monitored variables, budget, conditions of the site (e.g., depth, productivity, remoteness), sensor accuracy requirements, and spatial coverage needs all impact the suite of sensors selected and the manner in which they are deployed and maintained. Despite the range of variables that need consideration, many sites share a similar suite of common measurements. The most common variables measured at high-frequency are dissolved oxygen and temperature (Meinson et al., 2015). Temperature is typically measured at multiple depths, with greater vertical resolution near the surface where conditions are more dynamic. Often, other chemical and biological sensors are bundled together on a sonde (also known as a multi-probe; see platforms and configurations section below for more information), but the specific sensors selected depend on the priorities for the site. Commonly measured variables include pH, oxidation reduction potential (ORP), conductivity, turbidity, fluorescent dissolved organic matter (FDOM), and pigment fluorescence (e.g., chlorophyll *a*nd/or phycocyanin). FDOM sensors are also referred to as peak C fluorometers, based on the excitation and emission wavelengths used to quantify the signal (Carstea et al., 2020; Coble et al., 2014). Regardless of the specific sensor, it should be noted that many in situ sensors do not conform to the same measurement principle used for laboratory analyzes of the same variable (see Section "Processing and interpreting high-frequency sensor data", data corrections).

Other sensors include fluorometers to measure phycoerythrin, tryptophan, refined fuels, rhodamine, and optical brighteners/fluorescent whitening agents. Many of these sensors are not particularly common in freshwater ecology research and monitoring but can be easily added to many sondes and serve particular functions. Phycoerythrin is predominantly used in marine applications, but this accessory pigment is also found in some freshwater cyanobacteria (e.g., Harrison et al., 2018). Tryptophan fluorometers (also known as peak T fluorometers) are common in wastewater research and monitoring, but less common in aquatic ecology research (Baker et al., 2015; Carstea et al., 2016, 2020). Rhodamine sensors are commonly used in dye tracer studies that seek to understand water movement and storage dynamics (Runkel, 2015). Refined fuels and optical brightener sensors are often used to study specific types of anthropogenic impacts on aquatic ecosystems.

Another common sensor measurement both above surface and below is solar radiation. When deployed underwater, light measurements are often made at two or more depths using photosynthetically active radiation (PAR) sensors (measuring wavelengths from 400 to 700 nm), enabling calculation of a light attenuation coefficient (Kirk, 1994). Light attenuation regulates numerous aspects of aquatic ecosystems, including the depth range of photosynthesis and the distribution of heat in the water column (Rose et al., 2016). In most deployment configurations, light sensors are mounted on underwater arms away from the

surface buoy or float to avoid shading effects. Temperature measurements may also enable estimation of light attenuation during calm day-time conditions when heat gain differences between sensors at multiple depths can be solely attributed to light attenuation (Read et al., 2015). This enables greater use of temperature sensors, which are one of the most deployed sensor types.

In addition to light, some of the most common above-surface measurements include meteorological conditions (e.g., air temperature, barometric pressure, wind speed, wind direction, relative humidity, and multiple forms of precipitation). Meteorological sensors are often used to provide contextual information on conditions regulating water quality or to provide data to implement models of hydrodynamics and/or water quality. One of the most common applications of high-frequency sensors is to understand lake metabolism (Meinson et al., 2015; Solomon et al., 2013), where gas flux models are typically parameterized using wind speed measurements (Cole and Caraco, 1998; Dugan et al., 2016; Klaus and Vachon, 2020). Sensor height is an important consideration in many situations because of the importance of wind speed (and direction), and the potential for platform listing in waves, which can affect wind speed measurements. Often, most meteorological variables are measured together in an integrated weather station that is located on a pole above a lake buoy at a height of ~1.5–2 m above the water surface. Sensor height is then often normalized to 10 m for various calculations and comparison across sites (e.g., Cole and Caraco, 1998; Liu and Schwab, 1987). Rotation of the platform (common in single mooring-line deployments) can make wind direction measurements meaningless if an on-board compass is not part of the system. These integrated systems can be fairly robust and often contain no moving parts but can be sensitive to damage or fouling by birds. Bird-spike kits can reduce this problem, but some species are quite persistent.

In addition to these relatively common sensors, there are a number of less common to rarely deployed sensors. These include, for example, wet-chemistry sensors to measure phosphate. In situ spectrophotometers or spectrofluorometers can also be deployed to characterize a number of water quality attributes that may be inferred from light absorbance data made across ranges of the electromagnetic spectrum, such as nitrate, dissolved organic matter concentration and quality, and turbidity (e.g., Puiu et al., 2015). Additionally, there are some sensors that characterize multiple phytoplankton groups based on different fluorescence signatures or images (e.g., Fossum et al., 2019; Kring et al., 2014), and still others that characterize dissolved gasses (e.g., CO_2, CH_4). Acoustic doppler current profilers (ADCPs) can sample at very high frequency and be used to characterize water movement, gas flux, and particle size and movement including organisms. The use of sensors that passively sample aquatic acoustics is not widespread but shows promise for various applications such as fish species identifications (e.g., Browning et al., 2017; Noda et al., 2016). There are even sensors capable of conducting complex genomic analyzes in situ (Scholin et al., 2017). Most of these sensors are uncommon in sensor deployments, often due to the high cost associated with complex instrument designs. In some cases, the equipment can also have high detection limits, be sensitive to interference, or be difficult to maintain, thus requiring a high degree of expertise and specialization.

Data from high-frequency sensors are usually recorded by a data logger or computer before use. Sensors use many different communications standards. These can be broadly divided into analog (voltage, e.g., 0–5 V or current, e.g., 4–20 mA), and digital communications protocols (e.g., SDI-12, RS232, RS485 MODBUS, ethernet, I2C, 1-Wire). The data logger should have compatibility with the signal standards employed by the desired sensor suite, although a vast range of aftermarket signal converters are available. Different signal standards have unique pros and cons related to ease-of-use, robustness, cable length/capacitance, and susceptibility to noise. Serial standards that allow connection of multiple devices to single data lines (e.g., SDI-12) are user-friendly and can greatly reduce wiring complexity, but may increase the vulnerability of all connected sensors to faults in one sensor connected to the same bus. Oversight or otherwise involvement of qualified and experienced personnel are important for successful design of robust measurement systems, adequate circuit protection and grounding. Issues related to signal-to-noise (i.e., the strength of a process being measured relative to background variations in the measurement) or incorrect sensor/logger configuration can take months or years to detect and correct, by which time a great deal of expensive, ultimately unusable data may have been collected.

Platforms and configurations

The simplest design for collecting high-frequency sensor observations requires a sensor, a power source, and a device to store (i.e., data logger) and/or transmit the data. Platforms can take multiple forms, including stationary buoys, vertically profiling buoys, portable autonomous multi-probes and sondes, and vehicles (Figs. 2–4). High-frequency sensor platform designs correspond to the manner in which sensors are powered, data are logged, and the mobility of the system (Table 2). In many cases, multiple platforms are used at the same site. For example, a stationary or profiling buoy may be deployed during the stratified open-water season, and autonomous internally-logging sondes may be deployed under ice. Together, this approach enables year-round characterization of a waterbody.

While high-frequency sensing enables detailed characterization of environmental variables, the approach does not necessarily permit broad spatial coverage. The actual volume of water (and its constituents) being observed by many common sensors each time they turn on is often quite small (e.g., perhaps one cubic cm). However, depending on the degree of homogeneity of the environment and movement of water past the sensor (and/or the sensor through the water in the case of profiling systems), the actual volume of water being measured can be much larger. This sensed volume is referred to as an **integration volume** and is dynamic. Faster water movements correspond to greater movements of water and its constituents past a sensor, and therefore also increase the integration volume. The integration volume is also sensitive to the **integration time**, which is a measure of the amount of time a sensor is turned on and measuring the environment.

Integration time can be contrasted with sample frequency. A sensor can be programmed to turn on to measure the environment for a relatively long period (i.e., have a long integration time), such as measuring for 15 min, and reporting a measurement every

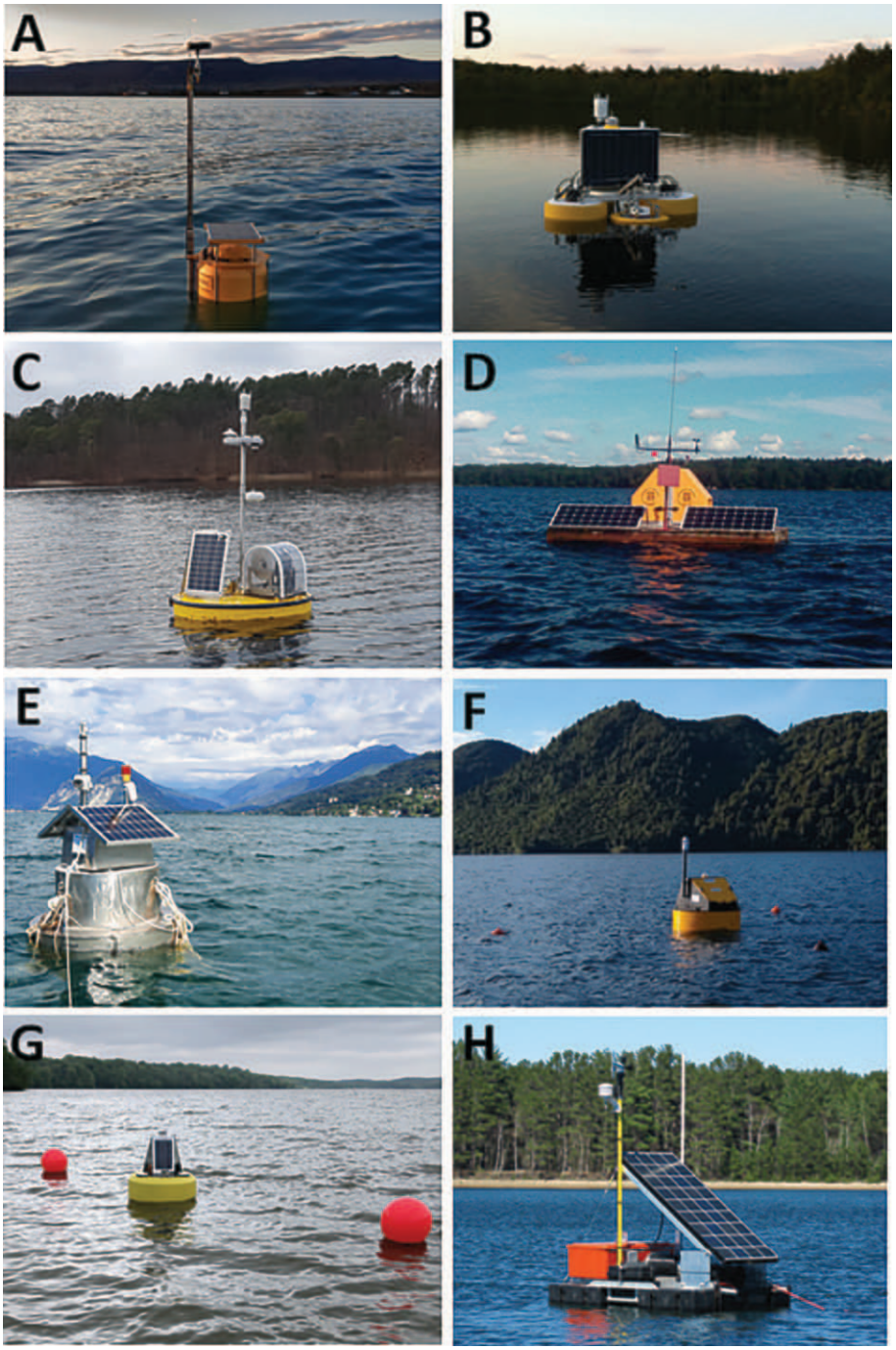


Fig. 2 Example buoys in lakes around the world, demonstrating a range in designs. (A) Argentino Lake buoy, Argentina; (B) Lake Lacawac, Pennsylvania, United States; (C) Lake Stechlin, Germany, (D) Lake Erken, Sweden; (E) Lake Maggiore, Italy; (F): Lake Okareka, New Zealand; (G) Acton Lake, Ohio, United States; and (H) Crystal Lake, Wisconsin, United States. Buoys A, E, and G are stationary buoys; all others are vertical profilers. (A) Credit: Alejandro Vitale, (B) credit: Jennifer Brentrup, (C) credit: Hans-Peter Grossart, (D) credit: Don Pierson, (E) credit: Michela Rogora, (F) credit: Chris McBride, (G) credit: Mike Vanni, (H) credit: Kevin Rose.

15 min (i.e., a 15-minute sample frequency). This is functionally similar to sampling continuously, but only reporting a measurement every 15 min. This contrasts with very fast sampling rates and logging, such as measuring and logging every second. An advantage of long integration times and less frequent logging is that the approach can reduce the variance in observations by taking more measurements before reporting. Additionally, a lower logging frequency reduces the size of the dataset and simplifies the burden on data storage, transmission, and management. A downside is that higher frequency measurements, and the variance they display, can provide additional information about the system or sensors. For example, sampling and logging dissolved oxygen every second can provide information to understand how long a sensor takes to reach equilibrium (e.g., if it is on a vertical profiler

Fig. 3 (Left) High-frequency sensors (dissolved oxygen, FDOM, and chlorophyll fluorescence) removed from a eutrophic lake after 11 months of autonomous sampling reveal substantial biofouling. Despite this growth, sensor faces were still clean due to wiping at a 6-h interval. (Right) The face of an underwater PAR sensor was still clean after 11 months of in situ sampling and the same frequency of wiping in an oligotrophic lake. Note the difference in overall fouling on sensor bodies pulled from eutrophic versus oligotrophic waters. Credit: Jenna Robinson.

Fig. 4 Example underwater vehicle. This model is tethered to a surface control system and includes an on-board sonde measuring variables such as conductivity, dissolved oxygen, fDOM, and chlorophyll fluorescence. Credit: David Winkler, Lake George, New York United States.

Table 2 Common deployment designs depend on the desired mobility of the sensors and the way sensors are powered and data is logged.

	Internal power & logging	*External power & logging*
Stationary sensors	Autonomous sondes and probes	Surface buoy with static sensors
Mobile sensors	Autonomous vehicles	Vertically profiling buoy

moving through the water column). It can be important to understand whether a sensor that is reporting a value every 15 min is reporting the mean of 15 min of continuous measurement or a single (instantaneous) measurement once every 15 min.

A typical deployment on many lakes is a stationary surface buoy with sensors that hang underwater, just below the buoy, typically 1–2 m below the water surface (e.g., Fig. 2). In addition, it is common for a string of temperature sensors to be deployed, which enables frequency characterization of water temperature from many depths throughout the water column. Often, stationary buoys are moored with a two or three-point design, are solar powered, and contain an on board data logger and communications equipment, to provide the option for near real-time data. While inexpensive compared with mobile sensor deployments, stationary buoy deployments are often more expensive than sondes and autonomous probes, but provide the capability for longer deployments (e.g., due to on board power production) and near real-time data telemetry.

Contrasting with surface buoys and sensors are vertical profilers (e.g., Fig. 2). This configuration usually consists of a surface buoy that contains a sonde, which is hung from an onboard winch and moored with two or more lines. Often, the winch cable also provides power and communications with underwater sensors and enables a single line to connect underwater sensors to the buoy's power supply (e.g., batteries and solar power) and logger. Vertical profiles can look similar to stationary buoys but are often

substantially more expensive than traditional buoy deployments with stationary sensors, but enable full-water column characterization (e.g., Brentrup et al., 2016). However, an equivalent sensor deployment (i.e., with many stationary sensors hung throughout the water column) would be even more expensive and therefore this design is a cost-effective solution when full-water column monitoring is a priority. Weaknesses of this design are the high cost and need for substantially more power and oversight due to moving parts. The system must also have a way to identify the depth of the sensors (e.g., include a depth or pressure sensor). Additionally, short sample intervals (e.g., every min to 15 min) are often not possible due to the fact that the sensors must move through the water column and equilibrate at each depth. For example, if a vertical profiler is sampling every meter through a 20 m deep water column and the equilibration dwell-time at each depth is 2 min, then a max sample rate at any given depth is 40 min. Vertical profilers also usually require substantially more power than stationary equivalents. Conversely, because profiler buoys use the same individual sensor(s) to cover the entire water column, maintenance demands related to the calibration and cross-validation of multiple sensors for the same measurement variable are eliminated, and the relative accuracy and thus comparability of measurements at all depths is ensured.

Internally logging autonomous probes and sondes are another approach to sample single depths or sites (Fig. 3). There are a number of integrated autonomous sensing systems, often referred to as sondes, that provide power and logging capability in either single or multi-sensor platforms. These systems also often store sensor calibration data to correct sensor measurements. The ability to provide power and data logging in a relatively small and inexpensive package enables underwater sondes to be used in a range of conditions, such as extended under-ice deployments. Deployment designs are flexible and can include bottom mounted systems or single mooring line systems. Sensors can also be deployed relative to the bottom, which can be important in some situations (e.g., to make sure sensors stay below seasonal ice cover). However, these systems usually lack the capability to transmit data back in near real-time, and power is typically limited to the capacity provided by onboard batteries. The inability to transmit data means that sensor failures may not be detected for weeks, if not months. Furthermore, if sensors are lost before retrieval (e.g., due to a mooring line failure or vandalism), data are also lost. Additionally, the inability to recharge batteries means that batteries must be changed frequently when power-hungry sensors are used. However, it is also possible to have extended deployments with other sensors that do not consume much power. For example, a dissolved oxygen logger may log measurements for over a year at a 15-min interval on two AA lithium-ion batteries. Due to the relatively low price of autonomous probes and sondes, they represent a smaller up-front cost than many other platforms, and complex sensor networks can thus be built out over time. Indeed, many sondes can be configured to accept external power inputs and transmit data to an external logger. However, if many autonomous sensors are used, internal clock drift (i.e., inaccurate time keeping) over time can present a problem to synchronizing data streams after long deployment intervals.

Vehicles are a general class of sensor platforms that can drift, drive, or glide horizontally across a waterbody surface, or in the case of underwater vehicles, move both horizontally and vertically (Fig. 4). There are many related categories of vehicles, including autonomous surface vehicles (ASVs) and autonomous underwater vehicles (AUVs), which are sometimes called underwater drones or unmanned underwater vehicles (UUVs). Depending on the design, AUVs are also sometimes referred to as gliders. Power sources are often from internal batteries, but can be from other sources, including tethers. AUVs facilitate a three-dimensional characterization of many aspects of aquatic ecosystems (e.g., Robbins et al., 2006). Relatedly, manual (e.g., on or towed behind human-piloted craft) use of high-frequency sensors for spatial studies is more common (e.g., Crawford et al., 2015). However, autonomous vehicles are relatively underutilized for high-frequency data collection in inland waters due to high costs, often large size and weight, and potential regulatory hurdles in many jurisdictions. However, despite their high cost, vehicles can be cost-effective if the alternative is a high-density network of stationary autonomous in situ sensors.

Platform design considerations

Site selection is an important aspect of platform design and configuration. Ideally, the site(s) should be broadly representative of the inland water habitat of interest, while also maximizing accessibility and minimizing the potential of vandalism or unintentional damage. Local regulations may require that sensor platforms be clearly marked and visible both night and day, particularly where powered craft operate. Relevant authorities should be consulted to gain consent for the installation, approve the desired location, coloration and lighting, radar or other navigation aids. On public water bodies, signage and clear markings can reduce the chance of vandalism and encourage engagement with the public about what is being measured, and how/where data are available (e.g., displayed online) and being used. Wind and wave conditions at the site need to be well understood and the platform and moorings designed or chosen carefully to suit. At exposed locations, moorings designed by qualified engineers are advisable or may be required. The platform should be stable enough to withstand even the largest of likely storms, and to accommodate sufficient power generation and storage for the required measurement regime and associated hardware. Sites that are exposed to harsh field conditions (e.g., strong winds and waves) should be checked regularly for equipment wear and tear.

Sensors and associated hardware (e.g., navigation lights, data loggers) require power. In certain deployment configurations, AC line voltage can be provided to the site. However, more often, sensors and buoys require batteries and on-site power generation, usually from solar panels, but also occasionally from wind turbines. Calculating a power budget to start and operate sensors and all associated hardware is an important consideration when designing a system. The aim of a power budget should be to ensure that batteries are never completely drained and a sufficient amount of backup/emergency power storage is available at all times. Collation of manufacturer specifications for current consumption of all hardware is a starting point. Often, a warm up time may be required for the sensor to work properly and should be accounted for in power budgeting. Where solar generation is to be used,

the light climate and its seasonality at the site needs to be well understood, as well as temperature effects on storage capacity. Additionally, solar panels are not always at the ideal orientation in direction or angle to maximize energy production and fouling or wear and tear can reduce generation.

Data telemetry and analytics

Many deployment configurations enable the near real-time transmission of sensor data. One exception is when a configuration is completely subsurface (e.g., under ice). Telemetry can be achieved using radio (including recent IoT approaches, e.g., LoRa), cellular network, or satellite. Radio is generally the cheapest option, but can require a clear line-of-site between an internet connected base station and the data logger. A cellular network connection typically requires an onboard modem and a monthly fee. It works well where cellular signals are sufficient to send text messages. Satellite telemetry is a good option for very remote deployments where real-time data acquisition is a priority, but is substantially more expensive than radio or cellular telemetry. High-gain cellular antennas, which can increase weak signals, are worth considering before committing to satellite communications.

The frequency of data transmission varies among sites, but transmission usually occurs at least once daily. Data transmission can be one of the largest power consumers on a buoy, and therefore endpoint intelligence that prioritizes data collection over transmission during power limited circumstances can be valuable (see next paragraph for more details). The provisioning of data in near real-time can be used to conduct automated altering for various purposes, such as the collection of manual measurements during disturbance events.

Analytics can be built into some data loggers. Alternatively, small single-board computers (e.g., Arduino or Raspberry Pi) can be deployed on a sensing platform, which enables logging as well as analytics at the site of data collection. Example applications include stopping logging (and transmitting) solar radiation measurements at night when there is no light. More complex decision making can enable automation to improve data quality or quantity given pre-determined events or dataset characteristics. For example, systems can be set to increase the sampling frequency of lake water quality measurements when stream inflow rates or precipitation measurements exceed predetermined thresholds. Additionally, some sensors such as dissolved oxygen sensors can take up to several minutes to equilibrate, with the specific amount of time depending on factors such as the depth and dissolved oxygen concentration gradient. When dataloggers have the capacity to analyze sensor data in real-time, they can adjust sensing to maximize the value of the data being generated. For example, analytics can enable the dwell-time (i.e., the amount of time a sensor is equilibrating) to be dynamic, as the system can recognize when measurements stabilize following movement into waters with a different dissolved oxygen concentration. This type of adaptive sampling allows the sensor and datalogger flexibility in how it captures and stores data. Advanced decision-making methods, including machine learning or more complex rule-based decisions, can not only greatly increase deployment durations, but can provide greater characterization of dynamic and rapidly changing phenomena.

Processing and interpreting high-frequency sensor data

Sensor versus laboratory-based measurements

While many high-frequency sensors share a measurement variable name (and units) with a related laboratory measurement, they often depend on a fundamentally different technical process to make a measurement. For example, in situ sensors such as turbidity, FDOM, chlorophyll, and phycocyanin all share laboratory analogs with similar names, but use fundamentally different ways to quantify the variables (see Table 3). Other high-frequency sensors such as temperature, dissolved oxygen, pH, and conductivity are directly comparable with laboratory-based measurements. When methodological differences exist between field and laboratory samples they can result in different sensitivities and biases. Therefore, when laboratory and in situ high-frequency measurements have the same name, they may not be directly compared or assumed to represent the same quantity.

Some in situ sensors represent a hybrid between more traditional in situ high-frequency sensor designs and laboratory-grade measurements. Sensors can be equipped with complex fluid handling and processing systems, effectively enabling laboratory methods, and the established standards they rely on, to be performed in the field. For example, some laboratory methods have been automated, miniaturized and packaged into environmentally hardened housings, enabling reagent-based measurement of phosphorus or applying qPCR to understand genetic diversity within ecosystems. For these sensors, direct comparisons with laboratory measurements may be possible.

A general preconception is that laboratory-quality instruments provide higher levels of precession and accuracy compared with in situ analog sensors and are thus considered the "gold standard" of measurement of many characteristics. Thus, in the next section we focus on known biases, sensitivities, interferences, and other data quality issues that challenge the reliability of high-frequency sensors and comparability to laboratory-based measurements. However, in situ sensors contain some advantages and laboratory measurements are not uniformly superior to high-frequency sensor-based measurements. For example, the process of collection, processing, storage, transport, and preservation from the field to a laboratory can introduce biases, errors, and uncertainties that reduce sample integrity.

Table 3 Interferences or other problems that affect the degree to which high-frequency aquatic sensors are comparable with traditional laboratory measurements.

Sensed variable	*Lab analog*	*Interference or problem*	*References*
Fluorescent dissolved organic matter (FDOM)	Dissolved absorbance (e.g., a_{254}, a_{440}), spectral slope (e.g., $S_{275–295}$) and/or dissolved organic carbon concentration	Temperature bias; inner filter effects; turbidity interference; relationship between fluorescence and lab analogs not necessarily uniform through time or across sites	Watras et al. (2011), Downing et al. (2012), Carstea et al. (2014), Lee et al. (2015), Saraceno et al. (2017), de Oliveira et al. (2018), and McKay et al. (2018)
Chlorophyll fluorescence	Chlorophyll *a* concentration or total chlorophyll concentration	Temperature bias; Inner filter effects; Non-photochemical quenching; Zooplankton interference; variable response due to cell size, biovolume, and cell agglomeration	Serra et al. (2009), Watras et al. (2017), Xing et al. (2018), Lucius et al. (2019), Moiseeva et al. (2019), Kuha et al. (2020), Moriarty et al. (2021), and Liu and Georgakakos (2021)
Phycocyanin fluorescence	Phycocyanin concentration or cyanobacterial cell counts	Temperature bias; inner filter effects; turbidity interference; detritus containing degradation products can also fluoresce; possible interference by other pigments; variable response due to cell size, biovolume, and cell agglomeration; potential of light-induced quenching is debated	Zamyadi et al. (2016) and references therein, Watras et al. (2017), Cremella et al. (2018), Hodges et al. (2018), and Rousso et al. (2021)
Tryptophan fluorescence	Tryptophan concentration	Temperature bias, inner filter effects; turbidity effects	Khamis et al. (2015), Wasswa and Mladenov (2018), and Goffin et al. (2020)
Turbidity	Turbidity or total suspended solids	Inner filter effects; particle size, geometry, and chemistry influences relationship	Downing and Lehr (2005), Daphne et al. (2011), Hannouche et al. (2011), Spackman Jones et al. (2011), Snyder et al. (2018)
Nitrate (UV optical)	Nitrate	Inner filter effects, particle scattering	Pellerin et al. (2013) and Snyder et al. (2018)

Data quality

There are multiple challenges associated with the process of collecting high-frequency sensor data that can impact data product quality. High-frequency sensors are susceptible to a range of issues associated with exposure to potentially harsh and variable environmental conditions. Some of the most common issues encountered during sensor deployments include biofouling, physical shock or damage, sensor drift, interference with non-target substances, variable temperatures or light, and excess electrical noise. **Biofouling** is the colonization and growth of microorganisms on sensors that can degrade their performance (Fig. 3; see also Section "Biofouling"). **Sensor drift** is the process of increasing bias and/or decreasing accuracy in sensor measurements over time due to physical changes in the sensor. Some individual sensor technologies also have known biases specific to a sensor type that require additional correction to make them relatively comparable with established analogous laboratory measurements (e.g., Table 3). While many of these challenges are not unique to high-frequency sensor data, the large volume of generated data poses an additional hurdle to ensuring data reliability and integrity. While manual identification of erroneous or otherwise biased data points is feasible with certain low frequency datasets, complete manual review and correction of large high-frequency datasets becomes nearly impossible. As high-frequency sensor datasets continue to grow in size and complexity, automated methods for identifying potentially problematic data points are becoming increasingly important.

Quality assurance and quality control

Quality assurance (QA) and quality control (QC) are two terms often used interchangeably in data science, but have different meanings. QA is process oriented and refers to any process, protocols or procedures implemented to reduce or prevent erroneous or biased data points from entering the data record. QA steps are thus typically implemented before planned sensor deployments. In contrast, the emphasis of QC is on the data product and refers to post-collection methods to detect erroneous data within a dataset, and either flag, adjust, or remove observations to remove biases or errors.

Data quality flags are used to convey information concerning the quality of individual high-frequency sensor data points, which increases the integrity and reliability of data for downstream users (Campbell et al., 2013). The most common use of data flags is to draw the user's attention to suspect data that have failed some aspect of QC (Fig. 5). Flags can also be used to denote missing data, version level, method of data processing, or important events (e.g., calibrations or site visits). Simple data flags can be assigned using an initial automated filtering process (see Table 4), easing the burden for secondary manual reviews. Data flags can be human-readable descriptive character-based strings, or machine-readable numeric codes. There is no community-wide standard for data flagging definitions or use, and most data owners choose a flagging system that best fits the needs of an individual project. Whatever the flagging system used, definitions of each flag and the methods used to create them should be clearly documented in easily accessible metadata (see metadata section).

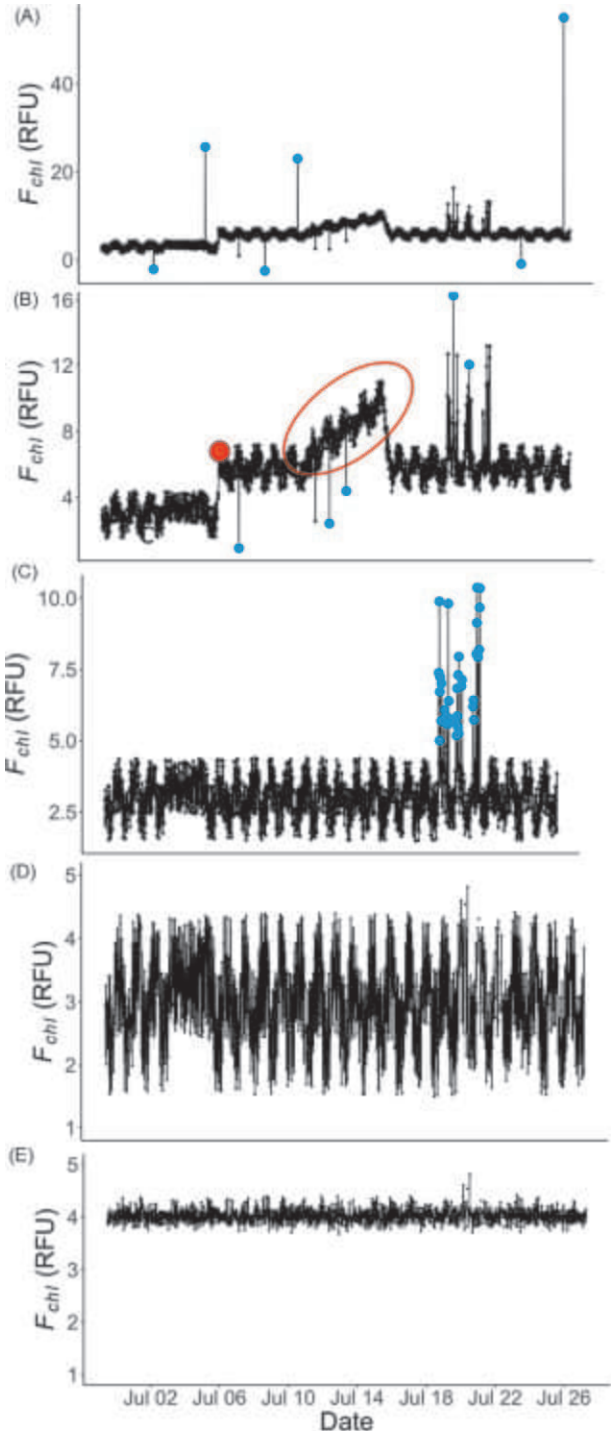


Fig. 5 Example of combined automated and manual data processing steps of chlorophyll fluorescence measurements from 1 month of measurements taken at a frequency of every 3 h. First (A), data are mechanically flagged using predetermined minimum and maximum value thresholds (blue dots). In (B), these initially flagged outliers are removed, enabling a rescaled y-axis; note the flagged step function increase (red dot; flagged by an automated "change-in-slope" filter), as well as a suspect upward trend in data starting Jan 13th (red oval; flagged as suspicious by manual review). Blue dots, representing data points that were mechanically flagged and removed. In (C), data blue dots in (B) have been removed for clarity and the step change previously flagged was identified as a calibration point. The data were adjusted between the two calibration periods (a Category 1 Correction). An unusual decrease in temperature was associated with the trend seen in B (red circle), and a temperature correction applied to the entire data set (Watras et al. 2017; Category 2 correction) removed the temperature bias. An automated analysis flagged additional data points (C, blue circles) that were later identified as fluorescence interference by zooplankton (Moriarty et al., 2021) and removed. (D) shows the dataset after these flagged points have been removed, when revealing a clear diurnal signal associated with non-photochemical quenching. A machine learning approach was applied (Lucius et al., 2020), resulting in a more accurate representation of chlorophyll at this site (E). Overall, 49 data points (2.4% of the month) were flagged and removed.

Table 4 Example data versions for high-frequency sensor data.

Level	*Data processing level*	*Description*
0	Raw	Unprocessed data and data products that have not undergone any alterations or annotations
1	Flagged	Actual data remain unaltered, but separate fields have been added to the original Level 0 data file, adding flagged data columns for each applicable raw data variable
2	Corrected	Dataset retains data flags from Level 1, but now may contain corrections, offsets, or complete removal. Additional flags are added to note these data alterations
3	Published	Data have undergone all levels of review and correction and are in a format suitable for publication and/or release to external parties

Regardless of the specific process, all steps should be clearly documented to enable repeat creation of data products.

Data flagging is an additive and annotative process where no data is changed; it is only described. It is good QC practice to maintain an unadulterated copy of the raw data file, before any initial flagging or filtering is begun. After an initial flagged dataset has been established, subsequent data products may include alterations or corrections of the raw data. Common data adjustments can include temperature or other bias corrections, corrections for sensor drift, various static offsets, or down sampling of data through various averaging methods (see data corrections section below). It is critical that such data manipulations be thoroughly documented, describing both the methods used and the reasoning behind the data alterations.

The creation of progressive iterations of a data set as it moves through a QC process is termed **data versioning**. Not only does versioning establish a well-defined provenance for all future data products, it offers protection from inadvertent or ill-advised changes to the original data values (Michener and Brunt, 2009). As an example of data versioning, Table 4 describes levels commonly applicable to high-frequency sensor data downloaded and initially stored in a simple text format (either .csv or .txt files). However, the specific steps taken in each data version depend on the needs of individual data users, the sensors used, and conditions experienced during sensor deployments.

The creation of metadata can be as important as actual data for understanding and using high-frequency sensor data. Metadata includes a description of the who, what, where, when, and why of a data set. This includes aspects of the study site and sampling location (e.g., depth, surface area, long-term mean water quality conditions); information on how samples were collected (e.g., whether samples are collected relative to surface or bottom); sensor information (e.g., manufacturer, model, and serial number); information on sampling design (e.g., sampling frequency, integration time, and wiping frequency); time stamp information (e.g., including possible GMT offset or daylight savings accounting), and QA/QC procedures. A robust QC workflow should include the ability to augment or add important metadata (calibration points, site visits, etc.) created at different points within the QC and versioning process. This would include metadata created through both automated processes or gleaned from manual reviews of either visual or tabular data. A published data set should be sufficiently described (i.e., documentation) such that it could be easily understood by external users with no knowledge of the original data collection, QA, or QC processes. Consistency in the collection, storage, and formatting of metadata is key in maintaining its usefulness. Maintaining a constant format allows for machine readable metadata, and easy ingestion of metadata into QC tools.

Before and during deployment

Assuring high quality of final data products begins before sensors are deployed. Pre-deployment, sensors should be calibrated according to manufacturer's recommendations within a range commensurate with the expected exposure conditions. Best practices for sensor calibration should also include a post-calibration check to confirm proper sensor functioning and quantify drift (see below for more information). Typically, a two-point calibration (e.g., where sensors are calibrated with a blank and a non-zero standard) is recommended. It should be noted that while some sensors, such as pH, dissolved oxygen, and temperature can be calibrated against known laboratory standards, other sensors, such as chlorophyll or phycocyanin fluorescence cannot be easily calibrated against standards due to the type of standard they rely on. For these sensors, calibration (e.g., using a known concentration of a fluorescing standard such as quinine sulfate or rhodamine) is used primarily to document and correct sensor drift over time (Earp et al., 2011).

Once a sensor has been properly calibrated and deployed, during the data collection process both internal (i.e., sensor drift, biases, electrical noise) and external factors (i.e., bio fouling, interferences, and physical impacts) can reduce data quality and reliability. If remote telemetry is available, near real-time sensor data should be regularly reviewed with a combination of mechanical inspection (see data cleaning and corrections sections below) and visual inspection by experienced personnel. Any suspected issues found as part of a real-time monitoring system should be recorded as part of the sensor metadata and investigated by field personnel promptly.

Site visits should be scheduled on a regular basis (and/or opportunistically, for example after disturbance events) to visually inspect sensors for damage and fouling. The recommended frequency of visits depends on many factors, but in general visits should be more frequent in high fouling environments (e.g., in more eutrophic or turbid environments), where there is a greater risk of damage from vandalism or natural variation in the environment (e.g., flooding), and when sensors are known to have a fast drift

rate. When regular site visits are not practical, deploying co-located replicate sensors can be a useful (but expensive) QA strategy. Not only will having replicate sensors minimize the chance of data loss due to sensor failure, data from duplicate sensors measuring the same environment can be used for detecting and correcting measurement errors.

The process of increasing bias and/or decreasing accuracy in sensor measurements over time due to physical changes in the sensor is referred to as **sensor drift**. This occurs due to factors such as internal sensor functioning changes or corrosion. The drift rate can be highly variable among various sensors. For example, sensors that utilize ion-selective electrode technology (e.g., pH sensors) drift rapidly and may require calibration at least every several weeks. In contrast, optical sensors measuring variables such as dissolved oxygen, FDOM, turbidity, chlorophyll fluorescence, or phycocyanin fluorescence drift relatively slowly and may only require a once-annual calibration. At a minimum, sensors should be calibrated immediately before and after deployment. However, it should be noted that more frequent recalibration is not necessarily better for assuring more accurate data, as calibrations can introduce greater uncertainty in measurements relative to the amount from sensor drift, especially for more stable (e.g., optical) sensors.

Biofouling

In highly productive warm waters (e.g., eutrophic lakes during summer months, Fig. 3), biofouling can be rapid, with visible growth in under a week (Delauney et al., 2010). Fouling in high turbidity environments due to sediment settling is also possible under some conditions. Like sensor drift, fouling can impact sensor measurements and therefore should be controlled as much as possible. There are multiple approaches to reduce fouling (whether biological in origin or not), including mechanical wiping, anti-fouling materials and chemicals, UV-C light, air blasts, and ultrasonic disruption (Delauney et al., 2010; Patil et al., 2007). Often, a combination of approaches is employed, with the most common approach being mechanical wiping and incorporation of antifouling materials (such as copper) into the sensor housing. After-market mechanical wipers are available that fit many third party high-frequency sensors.

When using a motorized wiper, choosing a wiping frequency should be given careful consideration. In general, warm and productive freshwater bodies will require frequent wiping, but minimum wiping intervals for an individual deployment area will need to be derived through experience. Fouling rates are seldom linear, and will often increase exponentially as biofilms are first established. Often, wiping can be much less frequent than sensing, at a frequency of hours to days. Additionally, there are potential downsides to wiping too frequently. Powering a wiper motor can be an energetically expensive task compared to the current draw of a typical sensor. Wiping a sensor face too often can also cause separate quality concerns. Sensor brushes have finite lifetimes, and over-wiping can cause premature breakdown of brush material. Sand, grit, and other detritus can foul sensor brushes, and over-wiping can also cause damage to delicate optical glass or sensor membranes (e.g., on dissolved oxygen sensors). The act of wiping a sensor also requires momentary pauses in data collection. Frequent sensor wiping can result in a cumulative loss in data fidelity, especially when sampling at higher frequencies. Finally, if wipers are powered by the same source as sensors, activating wipers can introduce unintended data distortions due to poor isolation of electrical components. This type of sensor bias can persist long beyond the wipe activation period (Fig. 6).

Data cleaning

Data cleaning, also known as data "wrangling" or "munging," refers to any method whereby a data set is fed into various QC processes capable of identifying, correcting, and potentially removing erroneous data points. Once raw sensor data have been collected and stored, data cleaning QC protocols should be implemented to ensure the final data product(s) are of the highest possible quality. In most QC workflows, there is a distinction between automated or mechanical QC procedures and those performed by a human researcher (i.e., manual). Automated QC methods are becoming increasingly necessary and common as the volume of data being collected by high frequency sensors grows rapidly (Campbell et al., 2013; Durre et al., 2010).

Most common automated QC methods rely on simple threshold or statistical attribute checks. For example, in the US, the National Ecological Observatory Network (NEON) has a well-documented initial QC checklist for sensor data consisting of six "plausibility tests" (Taylor and Loescher, 2013). These tests include checks for data outliers, variance, step changes, and missing

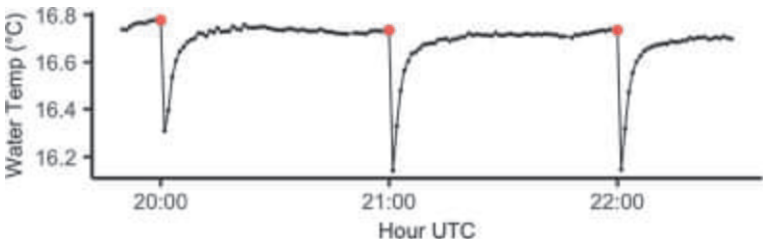


Fig. 6 Water temperature data from a wiped high-frequency sensor with a manufacturer reported accuracy of ±0.01 °C. Here, both the sensor and wiper were powered by a sonde. Water temperature data were collected at a 1-min interval, and the sensor faces were wiped every hour (red dots indicate when a wipe occurred). Temperature data can be seen to drop as much as 0.6C immediately following a wipe and took ~20 min to fully return to expected readings.

data, which are all common issues with high-frequency sensor datasets. The list below describes six quality control tests that are recommended for automated QC protocols of high-frequency sensor data (Campbell et al., 2013).

1. *Date and time*: Each data point must be associated with a timestamp. Time series sensor data should always be collected in chronological order, and this first step is a simple check that timestamps are sequential.
2. *Range*: Ensure measurements fall within an established upper and lower bound. Bounded limits are usually determined using previous knowledge of the system, or by absolute bounds (i.e., many sensors such as rainfall, PAR, wind speed, conductivity, or dissolved oxygen should never measure values below zero).
3. *Persistence*: When the same value is repeated with no change, it can be indicative of a sensor or system failure.
4. *Change in slope*: When evaluating a time-series, sudden changes in slope can indicate that a sensor was disturbed or malfunctioned.
5. *Internal consistency*: Many sensors that are commonly paired together have known relationships. This check makes use of these relationships and checks for consistency between co-located sensors. For example, a sensor recording snow accumulation when a co-located air temperature sensor reports temperatures of 20^0C should be flagged for QC concerns.
6. *Spatial consistency*: If available, comparisons of neighboring sensors can be helpful to evaluate data.

In addition to traditional statistical checks, more advanced methods from machine-learning and other computer science communities are increasingly being adopted for use with ecological sensor data. Methods specifically designed to work with time-series data such as Fourier transformations and wavelet analyzes (Cazelles et al., 2008), time series decomposition (Duan et al., 2018), symbolic representation (SAX; Ruan et al., 2017), or piecewise polynomial models (Gal and Anderson, 2010)can be used to help identify erroneous data points and trends associated with malfunctioning or failing sensors. However, despite the advantages of automated QC protocols, these approaches may miss unique situations. Thus, a combined automated and manual approach is often adopted, and automated processing checks and flags (see below) are typically reviewed by a person. Whether using an automated tool or developing manual check protocols tailored to a specific sensor and location, QC protocols should contain certain key functionality including data visualization, flagging, and metadata curation. An example data cleaning procedure is documented in Fig. 5.

Data corrections

There are many reasons raw high-frequency sensor data may need correcting, with many example reasons detailed here. Decisions to alter data should have a well-defined and defensible reasoning, and be well documented in accompanying metadata (see above). Raw data should always be maintained. Here, we define three categories of data corrections: (1) corrections associated with known and documented observations or incidents, (2) corrections associated with specific sensor technologies, and (3) corrections associated with unknown or undocumented observations in the data set itself. Sections below describe recommended protocols to correct data associated with category 1 and 2 issues. In contrast, category 3 issues emerge from unknown or undocumented phenomena. These issues often manifest themselves as curious patterns in the data or changes in statistical attributes over time. Accurately identifying these issues relies on local knowledge about a particular system, or well-defined relationships concerning the variable being measured for correction. While these issues may be flagged by automated QC protocols, researchers should be conservative when attempting to make data corrections in these circumstances and supply detailed metadata on the reasoning behind and methods used for corrective actions.

Corrections associated with known and documented observations or incidents: These correction types are the easiest to justify, as the underlying issue has been identified and should be documented in associated metadata. A common example of this type of correction would be those associated with calibrations. Issues discovered during pre or post deployment calibration checks (e.g., sensor drift or calibration errors) are easily documented, and provide solid justification to adjust data values. Changes in sensor data associated with field events or observations, such as physical movement of sensors during a site visit, are common during typical sensor deployments and can be easily corrected, assuming metadata are well-documented.

Corrections associated with specific sensor technologies: This type of correction is often derived from biases of certain sensor technologies that cause them to generate poor estimates of a variable in certain conditions. Corrective actions are often implemented to increase the comparability of the sensor output with an analogous laboratory measured variable. These corrections can be rooted in simple adjustments, such as correcting for barometric pressure when using a non-vented pressure transducer to measure water height. However, in many cases the corrections require more sophisticated post-processing techniques and site-specific adjustments. Many optical sensors are often subject to these Category 2 issues (Table 3).

The origin of multiple category 2 issues with optical sensors is associated with matrix effects. A matrix effect occurs when water and its constituents influence light in such a way as to bias a sensor's estimation of a variable. A common matrix effect is known as the inner filter effect, which occurs when light is absorbed after it is emitted from the sensor or following the stimulation of fluorescence. This leads to fluorescence being measured lower than it is at the source, and the effect typically increases with increasing DOC concentrations. However, the effect can also result from high concentrations of other light absorbing substances, including algal cells. Some sensors come equipped with FDOM sensors to correct for inner filter effect. Another matrix effect occurs in high turbidity waters, which scatter light and usually results in less light measured by the sensor's photodetector (e.g., Saraceno et al., 2017). The overall magnitude of matrix effects depends on both the properties of the water and constituents as well as

specifications of the sensors (e.g., path length, intensity and wavebands used for excitation and emission). Universal correction factors are therefore usually not possible and site-specific (and perhaps even season or event-specific) corrections may be necessary.

In addition to matrix effects, there are other factors that create category 2 issues and influence the degree to which many sensors can be used to accurately estimate laboratory analog variables. These issues include temperature-dependence effects (e.g., Watras et al., 2011, 2017) and fluorescence interference by zooplankton (Moriarty et al., 2021). Temperature effects are typically manifested as lower observed fluorescence measurements at higher temperatures. However, temperature also affects sensors other than fluorometers, too. For example, conductivity sensors exhibit temperature dependence similar to that of fluorometers. While this temperature dependence can be an important factor driving overall variation in sensor measurements, the temperature-specific coefficient can vary across sensors and manufacturers. Therefore, an instrument-specific calibration is recommended.

Fluorescence inference by zooplankton can occur because many zooplankton species are attracted to visible light (i.e., positively phototactic; (Storz and Paul, 1998) and thus are attracted to the excitation light source on some sensors at night (e.g., chlorophyll fluorometers; Fig. 7). High fluorescence interference by zooplankton increases both the mean and variance of nighttime chlorophyll estimates. The effect occurs when sensor light sources are on long enough such that zooplankton congregate at the sensor light source. This occurs when sensors are sampling frequently (e.g., every second) or integration times are long (e.g., 20 or more seconds; Moriarty et al., 2021). While this phenomenon has not been tested for in other types of sensors, it is likely to occur in phycocyanin sensors given excitation light sources are in the visible wavelength range. It is unclear if this phenomenon affects FDOM or turbidity sensors, as excitation light sources can be outside the visible range (depending on the sensor design). For example, FDOM sensor excitation light sources are often in the ultraviolet range where many zooplankton exhibit negatively phototactic behavior. Overall, the magnitude of the effect of zooplankton interference will vary depending on length of time sensor lights illuminate, the concentration of zooplankton, and the dominant zooplankton species, as phototaxis behavior is not universal (Moriarty et al., 2021; Overholt et al., 2015).

In addition to the above issues facing many sensors, FDOM and chlorophyll fluorescence sensors also face unique issues challenging the degree to which they can be used to estimate laboratory analog variables. First, FDOM sensors are frequently used to estimate characteristics of the dissolved organic matter (DOM) pool, including dissolved organic carbon (DOC) concentration, dissolved absorbance (e.g., a254, a440), and spectral slope (e.g., S275–295). DOM source and chemistry influences the relationship between FDOM and these other inferred characteristics, and the relationship cannot be assumed to be constant (Jaffé et al., 2012). Thus, often site-specific correlations may be necessary to accurately predict attributes of the DOM pool from fDOM sensors. In sites with substantial variations in DOM composition, corrections may even need to be season or event specific.

Chlorophyll fluorometers are sensitive to interference by non-photochemical quenching (NPQ; e.g., Serra et al., 2009). NPQ is a photoprotective mechanism common to most plants and algae by which potentially harmful excess light energy is dissipated as heat. NPQ is frequently observed during periods of high light intensity, and results in a decrease in the normal chlorophyll fluorescence signal as recorded by an in situ fluorometer. NPQ bias is frequently observed as a diurnal fluctuation in chlorophyll fluorescence values, with substantial reductions (upward of 90+%) in sensor-estimated chlorophyll in well-lit surface waters (e.g., Fig. 5). A common method to avoid the effects of NPQ when using high-frequency chlorophyll fluorescence as an indicator of chlorophyll or algal biomass is to only use nighttime data, as data collected at night is often assumed to be free of NPQ bias (Carberry et al., 2019; Rusak et al., 2018). While usually a sound approach, this method results in significant data loss and

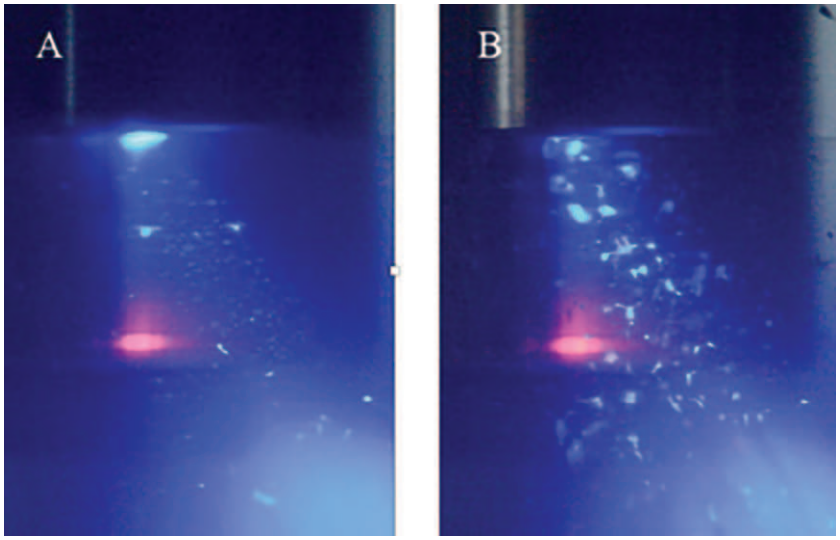


Fig. 7 Laboratory-based photographs of zooplankton responses to a YSI EXO2 chlorophyll fluorometer taken 5 s (A) and 50 s (B) after the sensor's blue (410–485 nm) LED was turned on, sampling (i.e., LED flashing) at a 4 Hz frequency. A large swarm of zooplankton can be seen congregating directly under the sensor face in B. See also Moriarty et al., 2021. The pink light visible in the images is a reflection from another optical fluorometer. Included video associated with this figure that shows fluorescence interference by zooplankton: https://drive.google.com/file/d/1kzQlLlJEGHwAHJAR1s8G03L3wCeXoCWj/view?usp=sharing.

eliminates the possibility of studying important daytime phytoplankton dynamics. Additionally, nighttime measurements can suffer from fluorescence interference by zooplankton under some sampling scenarios (see above). Multiple methods to correct daytime chlorophyll fluorometer data for the effects of NPQ have been developed (e.g., Liu and Georgakakos, 2021; Lucius et al., 2020; Rousso et al., 2021; Serra et al., 2009; Carberry et al., 2019; Xing et al., 2018), but often require the use of advanced methods or equipment, and may not be viable for all high-frequency sensor datasets. NPQ can be challenging to correct because many factors affect the amount of NPQ, including the species assemblage, cellular geometry, nutrient status, light exposure history and potential acclimation, temperature, mixing depth and rate, and incident light field. Thus, NPQ corrections should be carefully constructed on a site-by-site basis. Evidence that other sensors, such as phycocyanin sensors, are also sensitive to NPQ effects is mixed (e.g., Rousso et al., 2021; Zamyadi et al., 2016). Overall, NPQ is a substantial issue that must usually be addressed to accurately infer chlorophyll measurements from in situ fluorometers.

Beyond sensors and data: The power of ecological networks

The growth of high-frequency sensors in research and monitoring has spurred the development of ecological observatory networks (EONs) of people, data, and infrastructure. EONs, and the high-frequency sensor data that underpin them, are often associated with a high degree of collaboration and data-sharing. There are likely many reasons for this. First, the technical nature of the sensors requires expertise in diverse areas such as engineering, design, fabrication, cyber-infrastructure, data science, and ecology. Second, the volumes of data that are generated from high-frequency sensors provide the opportunity to ask many different types of research questions that are often beyond the scope of any single research organization. Third, once established, autonomous sensors and platforms continue to generate data at a low ongoing cost. When individual data points are inexpensive, there is a smaller barrier to sharing. Finally, the proliferation of high-frequency sensors has coincided with increased emphasis on understanding macrosystem-scale patterns in ecosystems, thus promoting the formation of EONs (Rose et al., 2017; Rüegg et al., 2014).

One such grassroots example is GLEON, the Global Lake Ecological Observatory Network, which is an inclusive community of people, lakes, data, and infrastructure dedicated to conducting and supporting lake research and management using high-frequency sensors (Weathers et al., 2013; Hamilton et al., 2015; Rose et al. 2016). A key strength of GLEON is the fact that the grass-roots nature of the organization and the prioritization of team science best practices means that the diverse community of individuals are empowered to lead research and other activities. Most network activities are underpinned by an evolving working group structure that enables teams to form and focus on topics where interests align. Members of GLEON have generated important insights into aquatic ecosystem dynamics using both high-frequency data (e.g., Solomon et al., 2013) and lower-frequency measurements using sensors (e.g., Jane et al., 2021). GLEON data have also been used in numerous ways to engage with stakeholders outside of academia to improve the understanding and management of lakes (Smyth et al., 2016). The grass-roots nature of GLEON means that individual sites often differ in many aspects, such as the types of sensors deployed, the frequency, depth, and duration of sampling, what other ancillary data that are collected, and the nature of who owns the data. The diversity in what and how data are collected and managed can often present a challenge to cross-site synthesis. The data management practices recommended herein can help reduce the barrier to effective use of network data. The overall rapid growth in community engagement and GLEON products highlights the power of network science.

Due to the complexity of high frequency sensor network data and the volume of data they generate, there have been considerable investments made in data processing tools, many of which are freely available (Read et al., 2016). These tools often help to (1) facilitate the QA/QC process or (2) assist in calculating derived characteristics, such as thermal stability indices from temperature measurements. Freely available tools to assist with automated QC include MATLAB based software (GCE Data ToolBox) capable of automating the collection and processing of high-frequency sensor data (Sheldon, 2008) and various R packages such as DriftR (Shaughnessy et al., 2019) and anomalize (Dancho and Vaughan, 2020). Additionally, the python based "ODM Tools" software packages have several QC-specific tools and were developed specifically for working with hydrologic and water quality data (Horsburgh et al., 2015). Freely available scientific workflow management software, such as Kepler, can be tremendously valuable in overall project management. Commercial time-series management platforms, including Kisters' 'WISKI' and Aquatic Informatics 'Aquarius', provide a range of native and customizable tools for detection of outliers or suspicious measurements.

Some software tools have been created to calculate derived indices from high-frequency sensor data. Some of the most popular examples are R packages such as Lake Analyzer (Read et al., 2011), Lake MetabolizeR (Winslow et al., 2016) and Lake Heat Flux Analyzer (Woolway et al., 2015). Lake Analyzer provides calculations of indices of mixing and stratification from depth-resolved measurements of temperature and other data including bathymetry and salinity. Lake Metabolizer provides estimates of lake metabolism from different types of metabolic models using time series measurements of dissolved oxygen, water temperature, and other variables. Lake Heat Flux Analyzer provides the capability to estimate surface energy fluxes such as sensible and latent heat fluxes, incoming and outgoing long-wave radiation, and surface momentum fluxes from time series measurements of water temperature and meteorological conditions. In sum, these tools enable the calculation of derived characteristics primarily associated with temperature and oxygen, the two most commonly measured high-frequency variables (Meinson et al., 2015). As other sensors become more common, associated processing tools that standardize output and estimate important derived characteristics will be increasingly valuable.

Conclusions

High-frequency sensing can provide numerous benefits in research, management, and outreach. There are many aspects to consider when planning a high frequency sensor deployment. There is rarely a single solution to a given technical problem, and there are important tradeoffs to consider in many aspects of sensor and platform selection and use. Additionally, deploying equipment and obtaining data is only a part of the challenge of effectively using high-frequency sensors to conduct research and management. Data management, including the creation and preservation of critical metadata, represents an important challenge and can be as important as the data itself in determining the long-term usefulness of data. Overall, high-frequency sensors greatly increase the capability of research and management. The ability to characterize ecological variability across massive temporal scales provides the capability to advance understanding of ecological processes and forecast future conditions. Growing cross-site syntheses, enabled by a growing culture of open and shared data, further facilitate insights into ecological dynamics across both time and space.

Acknowledgments

KCR acknowledges the support of NSF grants 1754265, 1761805, and 2048031, as well as Craig Williamson, Tim Kratz, Kathie Weathers, and Paul Hanson, whose support fostered his use of high-frequency sensors and involvement in GLEON. KCR and VM also acknowledge NSF grant 1655168 and New York State Higher Education Capital grant 7290. Data used in Figs. 6 and 7 were collected using equipment funded through the Jefferson Project at Lake George, which is a collaboration of Rensselaer Polytechnic Institute, IBM, and the Lake George Association. The authors also acknowledge the support and assistance of Dr. Kendra Spence Cheruvelil in bringing this chapter to fruition, assistance with gathering buoy photos by Eleanor Jennings and Alo Laas, and constructive input from Carl Watras.

See Also: Emerging methods and topics: Electronic Tagging and Tracking of Animals in Inland Waters; Remote Sensing of Inland Water Quality; Structures and functions of Inland Waters - Lakes: Ecological Consequences of Climate Extremes for Lakes; Lake Colors: Interpreting Apparent Optical Properties; Surface Mixed Layers in Lakes

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Remote Sensing of Inland Water Quality

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Absorption The disruption of the light beam that passes through.
Adjacency effects The scattering of light into neighboring pixels.
Apparent optical properties (AOPs) The reflectance characteristics of a medium that depend on both on the medium (the IOPs) and on the geometric (directional) structure of the ambient light field.
Atmospheric correction Removes the scattering and absorption effects of atmosphere on the reflectance measurements made by airborne or spaceborne sensors.
Atmospheric optical thickness (AOT) The optical depth or thickness of the atmosphere and is the vertical thickness from the earth surface to the top of the atmosphere.
Calibration The process of converting a signal from a sensor into a recognizable unit of measurement.
Downwelling irradiance The radiation from the sun that hits the earth's surface.
Earth observation Gathering information on the Earth's physical, chemical and biological systems through remote sensing platforms, which can be in situ, airborne or spaceborne.
Ensemble approach The selection of the most appropriate calibration for a given set of circumstances.
Inherent optical properties (IOPs) The various measures of the absorption and scattering properties of a water body.
Match-ups The number of coincident observations from airborne or spaceborne platforms with in situ measurements.
NADIR The point on the earth surface that is directly beneath the sensor.
Optical water types (OWT) A typology of water color that provides statistically distinct clusters of reflectance spectra, each characterized by discrete ranges of IOPs.
Overpasses Occurs when the field of view of a sensor passes a point of interest.
Radiative transfer models The modelling of the propagation of light through a medium.
Radiometric resolution The degrees of intensity that a sensor is able to resolve.
Remote sensing Acquiring information about an object from a distance.
Scattering The redirection of light by a substance.

 https://doi.org/10.1016/B978-0-12-819166-8.00213-9

Sky radiance The diffuse solar radiation that hits the earth's surface after being scattered by molecules or particulates in the atmosphere.
Spatial resolution The on the ground dimension that represents a pixel in an image.
Spectral bands The wavelength range over which reflected light is integrated for a sensor.
Spectral resolution The ability of a sensor to resolve fine wavelength intervals.
Temporal resolution The time taken to revisit or acquire data from the same point on the earth surface.
Transmittance The ratio between the incident light and the light that passes through the substance.
Validation The process of verifying the accuracy of a measurement.
Water-leaving radiance The upwelling radiance from water to the air following interaction with water constituents.

Introduction

Surface waters are a fundamental resource, providing key ecosystem services that support the way we function as a society as well as supporting life itself. Yet water is also the primary medium through which we are feeling the effects of climate change (UN Water, COP21), where increased episodes of extreme events and climate shocks (flooding and drought) often coupled with complex interactions with changes in the catchment, lead to the deterioration in water quality. At the global scale, this results in an increasing imbalance in the availability of clean, safe and sustainable water, exacerbating issues of poverty and hunger as well as biodiversity declines and carbon losses. Effective water management is critical to mitigate these effects but also enables us to sustainably manage water as a resource to blue and green economic growth opportunities. However, the inherently dynamic and heterogeneous distribution of water bodies across our landscape poses very real challenges for effective monitoring through conventional sampling and in situ techniques (Tyler et al., 2016). These issues are compounded further by inconsistencies in sampling and measurement strategies within and between organizations and nation states, constraining our systematic understanding of how surface waters are changing at local, regional and global scales (Carvalho et al., 2011; Palmer et al., 2015; Tyler et al., 2016).

There are estimated to be about 117 million lakes globally that cover around 3.7% of the planet's non- glaciated land surface (Verpoorter et al., 2014). Lakes have been described as 'sentinels, integrators and regulators' as a result of their sensitivity to climate change either directly or through changes occurring in their catchments (Williamson et al., 2009). Their importance in global biogeochemical cycling is increasingly being acknowledged (Bastviken et al., 2011; Cole et al., 2007), yet understanding of their role in transforming carbon is limited. Earth observation (EO) of lake color has an important role to play towards fully understanding the state and functioning of lakes within a global climate context and supporting sustainable management practices into the future.

The last 10 years or so has seen a rapid growth in the exploitation of satellite EO technologies for monitoring water quality (Tyler et al., 2016), shifting from the focus on individual lakes to the global scale. Three key developments that have enabled these advancements include: (i) the investment in ocean color remote sensing platforms that provide the sensitivities to detect and resolve constituents in water constituents that affect water quality; (ii) the computational solutions that allow us to resolve the optical complexity of inland and coastal waters for the reliable retrieval of water quality parameters (Spyrakos et al., 2018; Neil et al., 2019) and (iii) recent improvements in atmospheric correction to resolve the influence of the atmosphere in scattering the light reflected from water bodies, which tend to be dark targets compared to the adjacent land; examples include ACOLITE (Vanhellemont, 2019), POLYMER (Steinmetz and Ramon, 2018), C2X (Brockmann et al., 2016) and iCOR (De Keukelaere et al., 2018), which are among a series recently tested by Pahlevan et al. (2021). This change in capability has resulted in a step change in our ability to move the remote sensing science from observing individual lakes to enable the global population of lakes to be sampled and monitored from space with the accuracy that allows us to understand how these critical ecosystems are changing in response to climate change and changes occurring in their catchments. Here we will provide an overview of the principles and state of the art of the application of EO for water quality monitoring.

Using EO to detect water color

Water color is science of extracting information about the constituents within the water that affect its color. Water color can range from blue, through green to brown and yellow. The color of water is determined largely by the proportion of three main constituents, which we often refer to as optically active constituents (OAC) as they affect water color: (i) living phytoplankton measured by the chlorophyll *a* (ch*la*) pigment concentration; (ii) dissolved organic matter measured by the amount of color dissolved organic matter; and (iii) the amount of inorganic matter or Non Algal Particles (NAP) such as sediment measured as total suspended matter. Measuring these parameters allows us to understand the ecological status of inland waters and how they are changing with environmental pressures and the impact that might have on their ecosystems and the ecosystem services that these water bodies can provide.

Here we provide an overview of how light interacts with water and how we can use this to estimate the concentrations of these optically active in water constituents by classifying water into Optical Water Types through which computational methods for estimate optically active water quality parameters can be more reliably applied.

Light propagation

The estimation of water color by EO relies on the spectral shape of the radiometric signal, which can be detected by remote sensors deployed or onboard of drones, airplanes, or satellites. The radiometric signal detected is the sum of the interaction of several components such as: the atmosphere, the air-water interface, the dissolved and particulate material of the water column and, if visible, the waterbody's bottom. These components influence the remote sensing signal by transmitting, scattering and absorbing the light. Within the water column, light can be transmitted, scattered, or absorbed (Mobley, 2001).

These light interactions are defined as optical properties of water and are usually described in terms of their Inherent Optical Properties (IOPs) and Apparent Optical Properties (AOPs). AOPs are dependent on both the environment (the constituents in the medium) and the geometric (directional) structure of the radiance distribution (Mobley, 1994). In contrast, IOPs rely only on the biogeochemical properties of the environment, such as the absorption and backscattering of the major OACs such as phytoplankton pigments, CDOM and NAP.

AOPs are commonly used for the development of remote sensing algorithms to estimate water quality (Uudeberg et al., 2019). One of the most common AOPs is the remote sensing reflectance (R_{rs}) which is influenced by the response to the IOPs of phytoplankton pigments, CDOM and NAP within the water column (Kirk, 2011). Fig. 1 shows the variability of R_{rs} spectra from different coastal and inland aquatic systems. Because of the optical complexity of inland waters, remote sensing algorithms usually do not have the same performance for different water bodies. For example, algorithms developed over turbid shallow lakes will probably have a poorer performance in deeper clearer lakes.

Optical complexity and water typology

Earth observation methods in inland waters are often challenged by high optical diversity and dynamic variability. Inputs of external material (particulate and/or dissolved) into inland waters can decouple bulk optical properties from phytoplankton. This means that methods developed for waters where the phytoplankton community are the main sources of variability in water optical properties are not directly applicable to inland waters. A common strategy to work with the complexity of inland waters is to classify the derived remote sensing reflectance signal into Optical Water Types (OWT) which is an approach that has been used in several studies (Moore et al., 2009, 2014; Vantrepotte et al., 2012; Spyrakos et al., 2018; Botha et al., 2020). The traditional OWT classification defines water as Case 1 and Case 2 (Gordon and Morel, 1983) with the former being referred to as open ocean waters (dominated by phytoplankton) and the latter as coastal and inland waters (driven by a mix of different OACs which do not co-vary with each other).

However, this simplistic classification was not sufficient for inland waters, which can be very different from each other. Therefore, recent classifications of inland waters took the traditional classification to a new level based on statistical clustering of the apparent optical properties (AOPs), such as Rrs spectra, providing distinct Optical Water Types (OWTs) (Lubac and Loisel, 2007; Shi et al., 2014; Melin and Vantrepotte, 2015; Spyrakos et al., 2018). Another possibility was the cluster analysis to group IOP data derived from the inversion of the Rrs (Botha et al., 2020). The motivation to propose OWT classifications is to define which remote sensing algorithms may be better used for each OWT (Neil et al., 2019), which will improve the estimation of water quality parameters.

Evolution of remote sensing platforms

Since the beginning of remote sensing for inland water applications, the landscape has evolved significantly. Four major criteria define the requirements for sensor and platform developments to achieve a certain outcome: (i) minimum size of distinguishable

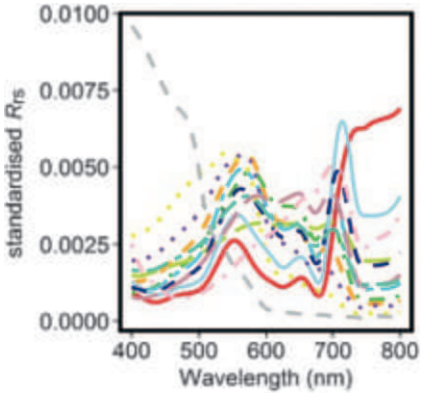

Fig. 1 Mean remote sensing reflectance spectra (Rrs) for each statistically distinct cluster of standardized remote sensing reflectances obtained for inland waters (Spyrakos et al., 2018).

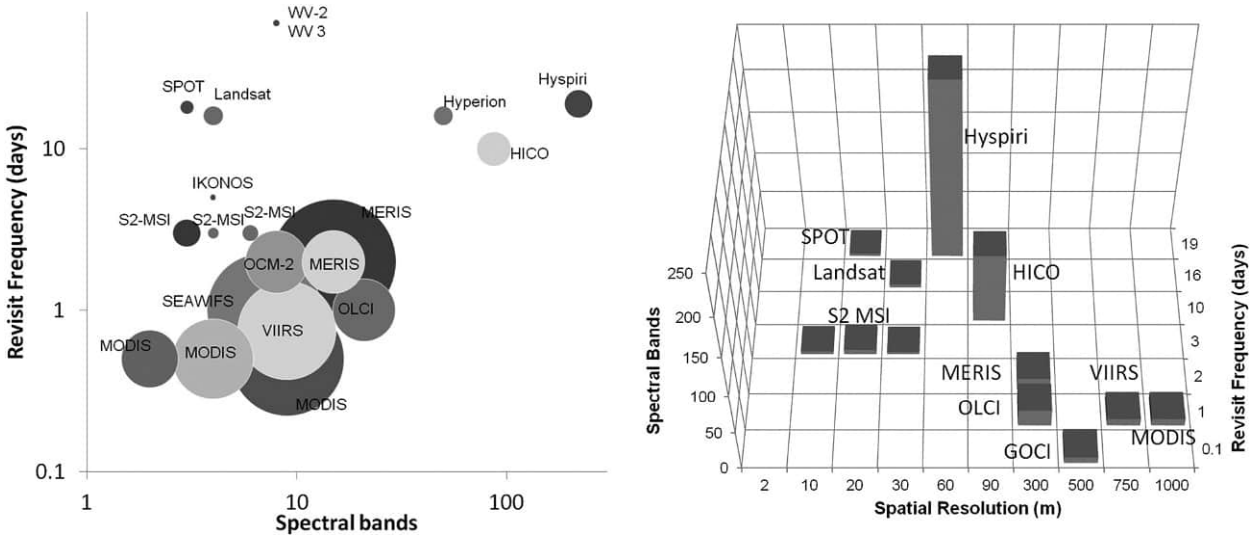

Fig. 2 Trade-off between spatial, spectral and temporal resolution of different satellite missions. Acronyms are provided for different satellite platforms, including: Envisat MEdium Resolution Imaging Spectrometer (MERIS); Hyperspectral Imager for the Coastal Ocean (HICO); and Hyperspectral Infrared Imager or HysplRI; Moderate Resolution Imaging Spectroradiometer (MODIS); Satellite pour l'Observation de la Terre (SPOT); Sentinel 2 Multi Spectral Imager (S2 MSI); Sentinel 3 Ocean and Land Colour Instrument (OLCI); and Visible Infrared Imaging Radiometer Suite (VIIRS). Source: Hestir E, Brando V, Bresciani M, Giardino C, Matta E, Villa P and Dekker A (2015) Measuring freshwater aquatic ecosystems: The need for a hyperspectral global mapping satellite mission. *Remote Sensing of Environment* 167: 181–195.

objects (spatial resolution), (ii) range, number and width of spectral bands (spectral resolution), (iii) number of digital levels used to express collected data (radiometric resolution) and (iv) the interval between image acquisitions (temporal resolution or revisit frequency) (Tatem et al., 2008). There is a trade-off between the different resolutions (e.g., the higher the satellite, the larger the area which can be covered at once, yielding a higher temporal resolution but at a reduced spatial resolution). Fig. 2 shows the trade-off between spatial, spectral and temporal resolution of various satellite missions. Here we provide an overview of the different remote sensing platforms that can facilitate Earth observation science of water quality monitoring.

Spaceborne

Satellite imagery has been used for decades to monitor inland and coastal waters. Initially, mainly ocean color sensors were considered, like SeaWiFs (launched in 1997), MODIS Terra and Aqua (launched in 1999 and 2002 respectively), MERIS (launched in 2002) and Sentinel-3 (launched in 2016). These sensors have spectral bands dedicated for water observations and have frequent revisit times (1–3 days). But their medium spatial resolution (100–300 m) hampers their use for observing smaller inland waters, like streams and narrow rivers or small lakes (Topp et al., 2020). As a consequence, land satellite missions became investigated for water applications. Although not designed for water (e.g., sensors are mounted pointing directly downwards (nadir), causing increased risk of sun glint contamination (Harmel et al., 2018)), the increased spatial resolution (10–60 m) has been shown to be an asset. Two successful examples are Landsat-8 (launched in 2013) and Sentinel-2 (launched in 2015) (e.g., Wang et al., 2019; Toming et al., 2016; Vanhellemont and Ruddick, 2015). But the temporal resolution (5–16 days for Sentinel-2 and Landsat-8 respectively) can be a shortcoming, increasing the vulnerability to cloud cover, reducing the observation frequency still further. Hyperspectral satellite missions provide hundreds of bands across the visible and near infrared parts of the spectrum allowing spectral shape to be observed and allowing new insights into water color remote sensing. Examples are the PRISMA (launched in 2019), EnMAP (expected launch 2022) and others.

The latest upcoming technology are CubeSats—small nanosatellites with standardized dimensions. CubeSats are made up of multiple cubic modules of 10 cm each side, weigh no more than 1.33 kg, and often use commercial off-the-shelf components for their electronics and structures. An example are the PlanetScope Doves (launched in 2013) by Planet (Planet Ltd, 2019). As they fly in a constellation, PlanetScope Doves can reach meter-scale resolution products at a daily revisit time. The spectral bands are suitable to derive water turbidity (Vanhellemont, 2019). Another example is the HYPer-Spectral smallsat for Ocean observation (HYSPO-1 and HYSPO-2) (both expected to be launched 2023), which will observe oceanographic phenomena through a small satellite with hyperspectral camera and intelligent on-board processing.

Airborne

Airborne remote sensing campaigns provide the excellent trade-off between spatial resolution (<10 m) and data coverage. This is in contrast to ground observations that are difficult to be used for regional scale monitoring and satellite data that have a relatively lower spatial resolution. With airborne remote sensing, data can be collected when the weather conditions and sun orientation are optimal. The platform is also ideally suited for testing new sensors and algorithm development. A lot of hyperspectral measurements occur from airborne platforms. With hyperspectral sensors it is possible to capture specific absorption features and backscatter peaks within a waterbody's spectral signature which provides new levels of precision to measure optically active constituents (Gholizadeh et al., 2016; Govender et al., 2007). Hyperspectral sensors consist of hundreds of narrow (1–10 nm) contiguous bands spanning visible to shortwave infrared spectral range. Since the 1980s, airborne imaging spectrometers such as APEX (Schaepman et al., 2015), CASI (Babey and Anger, 1989), AVIRIS (Vane et al., 1993) and others have been shown to provide accurate and quantitative information for inland and coastal water monitoring. The technology is ever evolving and new state-of-the art sensors are being generated. Two examples are the AVIRIS-NG (Chapman et al., 2019) which already conducted flights over Europe during the summer of 2021, and the upcoming Compact Wide-Field-of-View Imaging Spectrometer II (CWIS-II).

Drone

Drones are a relatively new and upcoming technology in the context of inland and coastal water monitoring. They have the advantage of being highly flexible in terms of use, can collect data over hard-to-reach areas and have a high spatial resolution. Fixed wings, copter-style airborne platforms and Vertical Take-Off and Landing (VTOL) are different aircraft designs. The copter-style systems have the advantage that they can hover over a certain spot, capturing dynamics at small scale, (e.g., Inflow of sediment plume in a harbor caused by tidal effects). Fixed wing drones have a longer endurance and can cover larger areas. While initially the focus for drone applications was to collect true-color images for visual observations, attention gradually shifted towards quantitative information such as turbidity, chla concentrations, macrophytes and more (e.g., Flynn and Chapra, 2014; Su and Chou, 2015; Larson et al., 2018; De Keukelaere et al., 2019). Technological innovations facilitating this shift include: a variety of conventional cameras and narrow-band imaging sensors (e.g., MicaSense Dual camera, with 10 spectral bands in visible and near infrared), irradiance sensors which are needed to measure changing light conditions. Real-Time Kinematic (RTK Global Positioning System (GPS) in combination with Inertial Measurement Unit (IMU; measures the roll, pitch and yaw of the platform) improve the projection of the images onto georeferenced maps.

In situ above-water measurements

The acquisition of high-quality in situ radiometric measurements is a primary concern for the calibration and validation of airborne and spaceborne remote sensing observations. The two main forms of radiometric data that are regularly measured synchronously with satellite overpasses include shipboard radiometric measurements to enable the computation of remote sensing reflectance and sun photometer measurements from aquatic and/or terrestrial stations for the derivation of properties such as Atmospheric Optical Thickness (AOT). These measurements can be obtained from small or large research vessels, ships-of-opportunity or from fixed platforms (e.g., jetties and buoys).

The in situ measurement of remote sensing reflectance can be achieved using a wide variety of instrumentation, methodologies and protocols. These include the manual use of single handheld radiometers used to consecutively measure the three constituent fluxes that enable the computation of remote sensing reflectance: (i) downwelling irradiance (usually via a reflective panel); (ii) sky radiance; and (iii) water-leaving radiance. However, this approach is rather onerous and can be subject to high uncertainties particularly under variable illumination conditions. Hence it has become common practice to employ a trio of radiometers making near-synchronous measurements of the three radiometric fluxes; in this case the downwelling irradiance measurement can be obtained by an upward looking radiometer fitted with a cosine diffuser. Regardless of the sensor(s) used for above-water radiometry, it is critical that measurements are made in the correct sun-sensor geometry to minimize the unwanted effects of phenomena such as sunlight on the quality of remote sensing reflectance (see Fig. 3). Further details on recommended instrumentation, sensor calibration, measurement protocols and data processing routines can be found in Zibordi et al. (2019).

In recent years, there has been a move towards more automated solar-tracking radiometry systems for the measurement of remote sensing reflectance that can collect data continuously during research cruises or while mounted on fixed platforms (e.g., jetties, lighthouse, buoys). The automated systems are designed to maintain an appropriate sun-sensor geometry by constantly adjusting the position of the sensors to optimize the solar azimuth angle. The use of automated radiometer systems is particularly advantageous during research cruises because it enables data to be collected continuously while the research vessel is underway and not only while it maintains a fixed station. In contrast, systems on fixed platforms enable high-frequency data to be collected at a single, well characterized station. Dedicated data processing routines have also been developed for quality control measurements made by automated systems. These automated approaches greatly increase the number of 'match-ups' between satellite overpasses and synchronous in situ measurements available for calibration and validation studies.

Measurements of properties such as AOT are important for the parameterization of atmospheric correction models for the processing of satellite data. These measurements are commonly obtained using sun photometers and, ideally, measurements should be made in parallel to radiometric measurements for computation of remote sensing reflectance. Sun photometers can be small, mobile, manually operated devices or autonomous (including robotic) systems often mounted on large research vessels or fixed

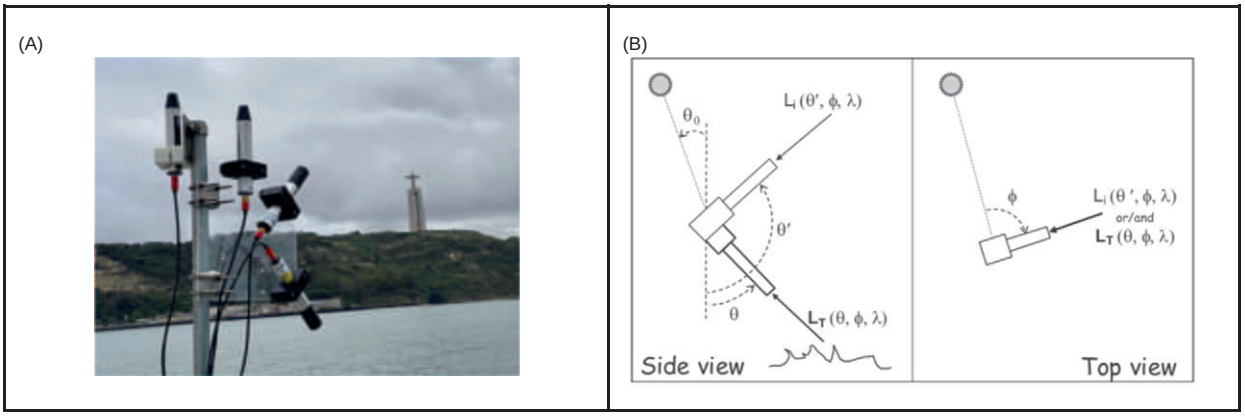

Fig. 3 (A) Three radiometers used for radiometric measurements to compute remote sensing reflectance (the fourth is a redundant downwelling irradiance sensor). (B) The recommended measurement geometry for above-water radiometry using a trio of radiometers has a sensor viewing angle (θ) of 40 degrees and a relative azimuth (φ) of 90 degrees (the third sensor measuring downwelling irradiance is not shown). From Zibordi G, Voss KJ, Johnson BC and Mueller JL (2019) *IOCCG Ocean Optics and Biogeochemistry Protocols for Satellite Ocean Colour Sensor Validatio 3: Protocols for Satellite Ocean Color Data Validation: In situ Optical Radiometry.* Dartmouth, NS: IOCCG.

platforms. The autonomous and/or robotic systems provide high frequency data, which increases the likelihood of match-ups with satellite overpasses while largely removing the need for manual operation. The NASA-led Aeronet network (https://aeronet.gsfc.nasa.gov/) is a global federation of robotic sun photometers for the measurement of atmospheric properties and imposes strict standardization of instruments, calibration, data processing and distribution to ensure high quality data are available for satellite validation studies.

In situ subsurface measurements

Subsurface measurements of both inherent (IOPs) and apparent optical properties (AOPs) are also widely utilized to aid the development, calibration and validation of remote sensing observations. Measurements of AOPs (i.e., subsurface remote sensing reflectance) are typically obtained using a set of profiling radiometers with two in-water sensors simultaneously measuring the downwelling and the upwelling radiance, while a single above-water radiometer measures the downwelling solar irradiance at the water surface to allow for changes in the illumination conditions to be corrected. These systems can be deployed manually from ships or autonomously from a profiling buoy. Further details on instrumentation, sensor calibration, measurement protocols and data processing routines can be found in Zibordi et al. (2019). One advantage of measuring subsurface radiometric fluxes is that it removes the need to measure and correct for reflected skylight, but the fluxes need to be numerically propagated through the air-water interface to enable comparison with satellite radiometry and this can also introduce significant uncertainties.

Subsurface measurements of the inherent optical properties (IOPs) are also used for the calibration and validation of remote sensing observations where algorithms directly retrieve such properties from the physical inversion of remote sensing reflectance. They are also essential to the quantitative understanding of underwater radiative transfer processes and the interpretation of above-water radiometric measurements whether measured by in situ, airborne or spaceborne sensors. The IOPs measured by in situ instrumentation include the spectral absorption (a) coefficients of dissolved and particulate matter and the (back) scattering (b or b_b) by suspended particulate matter (including both phytoplankton and non-algal particles) (example Optics Cage Fig. 4).

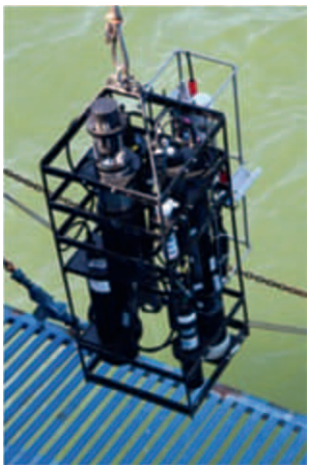

Fig. 4 Optics Cage housing instrumentation to characterize the IOPs of optically complex waters.

Spectral absorption and scattering can be measured using beam transmissometers (otherwise known as absorption and attenuation meters or simply 'ac' meters) or by point-source integrating cavity absorption meters (PSICAMs). Backscattering measurements are measured using dedicated meters, although commonly only at a limited number of wavelengths—although hyperspectral backscattering sensors have recently become commercially available; the so-called volume scattering function (VSF) can also be obtained by measuring scattering at multiple angles using specialized instrumentation. Further information on instrumentation for IOP measurements can be found in the protocols published by NASA (2002) and IOCCG (2019).

If the IOPs of all OACs are known, remote sensing reflectances can be computed through forward modelling of appropriate radiative transfer equations that provide an analytical route to interpret reflectance measurements. Moreover, mass-specific representations of the IOPs can be used to simulate the expected remote sensing reflectances for different optical water types and constituent concentration ranges, enabling large synthetic datasets of remote sensing reflectances to be established to support the development and parameterization of remote sensing algorithms. Sophisticated radiative transfer models such as Hydrolight can be used in this manner (Pyo et al., 2021), although the optical complexity of inland waters, and the large uncertainties associated with IOP measurements in turbid waters, can militate against this approach and various studies have reported difficulties achieving optical closure (quantitative agreement between modelled and measured spectra).

Water quality products from EO

The science of Earth observation of water quality now enables measures of the optical characteristics (reflectance) and water quality, e.g., turbidity, Total Suspended Matter (TSM), chla and CDOM to be accurately derived from remote sensing platforms. Here we provide an overview of examples of such products.

Aquatic reflectance

The removal of the atmospheric effects on the reflectance values is essential for water-color applications of remote sensing in inland waters, particularly for the estimation of biogeochemical parameters. Accurate atmospheric correction in inland waters is still considered challenging, as water has a low reflectance and the contribution of the atmosphere on the signal received by the satellite sensor represents 80% or more of the total at-sensor radiance. In contrast to typical open ocean atmospheric correction algorithms, for inland water, additional consideration is necessary, incl. (i) altitude of the inland water body, (ii) non-negligible reflectance in the near infrared region if the water contains high sediment concentrations, (iii) non-water spectra in the case of floating vegetation and (iv) adjacency effects originating from neighboring land pixels and affecting the spectral signal from water (Fig. 5). But several methods have been developed and now widely tested (Warren et al., 2019; Pahlevan et al., 2021) over a range of Optical Water Types found in inland waters. A number of water-targeting and land-surface AC processors (e.g., iCOR, POLYMER, ACOLITE, C2X) have been developed and used over inland waters. Selection of the AC processor used in different studies and applications is typically based on remote sensor, regionalities, its maturity and the derived products of interest.

Chlorophyll-*a* algorithms

Chlorophyll-*a* (chl*a*) is arguably the most commonly retrieved parameter in aquatic remote sensing studies, partly because it is such a well-established and widely used indicator of trophic state but also because it can be readily estimated using a range of multispectral ocean color satellites and some other high-resolution satellite sensors originally developed primarily for terrestrial applications. However, the retrieval of chl*a* concentrations over inland waters is generally far more challenging than over the open ocean and, as a consequence, the methods used are not only by necessity more numerous but also, in some cases, more sophisticated.

In ocean color remote sensing, most algorithms for the retrieval of chl*a*, whether based on simple empirical approaches or more complex analytical inversion methods, utilize ratios or other combinations of reflectance in the blue and green parts of the spectrum (so-called blue-green ratios). These methods are used to retrieve estimates of chl*a* in waters where phytoplankton are the only optically active constituents exerting a marked influence on remote sensing reflectance. This is the situation encountered in most 'Case I' OWTs that include open ocean waters, but algorithms that employ green-blue ratios have also been applied to inland waters, particularly in lakes with low to moderate chl*a* concentrations and low and invariant NAP and CDOM.

In the more turbid and complex OWTs (i.e., those that would be classically identified as 'Case II' waters), algorithms based in blue-green ratios generally do not perform well because the chl*a* absorption features that lie within the blue part of the spectrum are readily masked by the presence of high and non-covarying concentrations of CDOM and NAP. In these waters, it is more common to employ algorithms based on ratios or other combinations of reflectance in the red and near infrared parts of the spectrum. This avoids the confounding influence of other OACs in the blue spectrum while utilizing the measurable signal at red and NIR wavelengths that is encountered in more turbid waters.

The ability to exploit red-NIR wavelengths for chl*a* retrieval in inland waters is not sufficient to enable universal application of these methods. The high optical complexity encountered in inland waters, from CDOM-rich dystrophic lakes, through sediment-

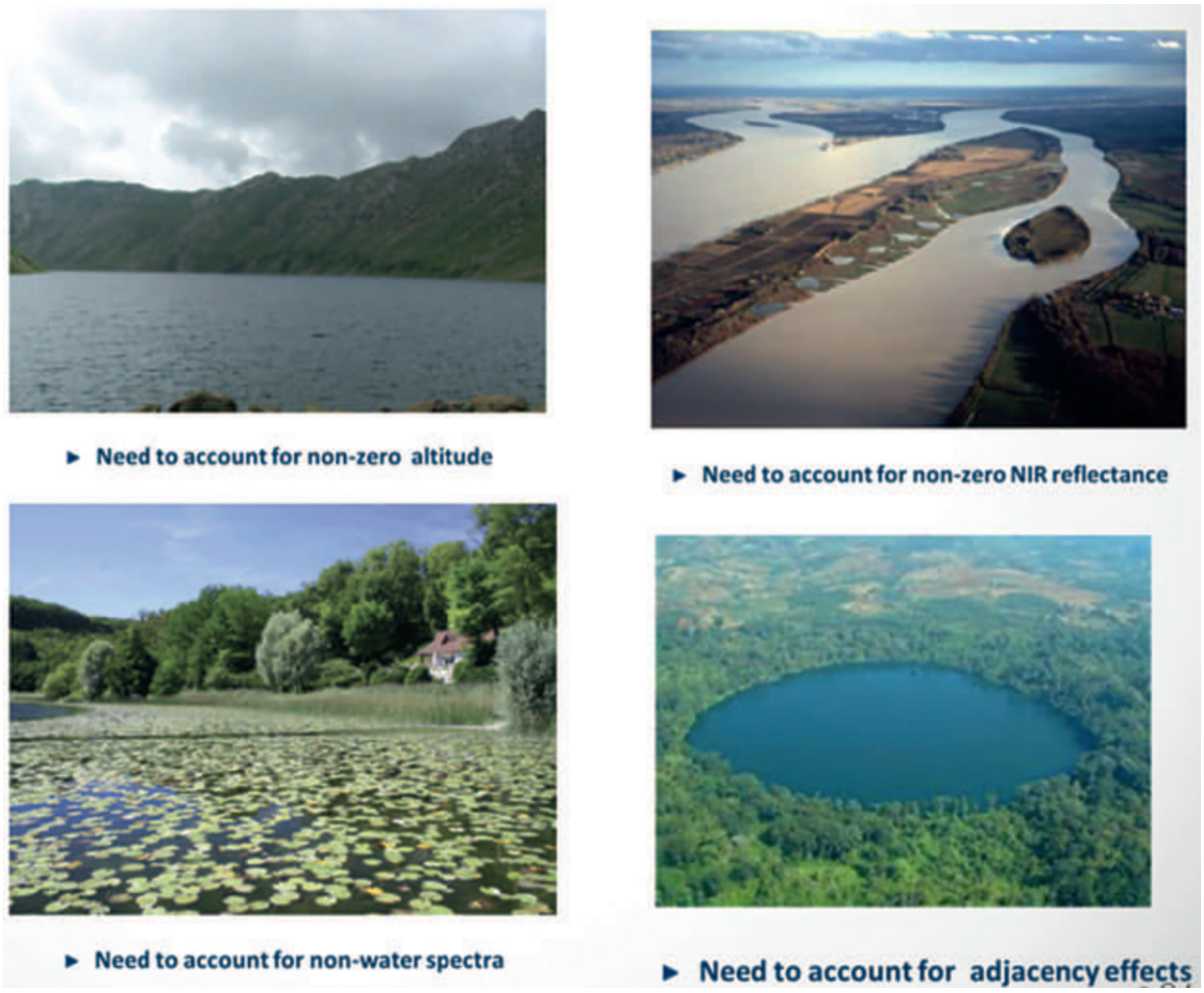

Fig. 5 Inland water bodies are complex and require atmospheric correction approaches which can handle different altitudes, non-negligible reflectance in NIR spectral region, presence of non-water spectra and adjacency effects caused by surrounding land pixels.

laden Alpine lakes, to algal-dominated eutrophic lakes, means that estimates of lake chl*a* concentrations often have far higher uncertainties than seen for ocean waters. It is also notable that no single chl*a* retrieval algorithm has universal application across a wide range of OWTs.

In an effort to improve the performance of chl*a* retrieval algorithms for inland waters, a variety of different methodologies have been employed. Simple empirical algorithms can be tuned using statistical approaches to reduce retrieval uncertainties for individual or small populations of optically similar waterbodies (e.g., Gilerson et al., 2010; Gurlin et al., 2011). In more challenging cases, more sophisticated analytical inversion (e.g., Hoogenboom et al., 1998) or machine learning approaches (Smith et al., 2021; Werther et al., 2021) have been applied and shown to outperform simpler methods. The use of ensemble approaches has also gained traction in recent years whereby the most appropriate algorithm (or algorithms) from a suite of models is dynamically selected based on the optical characteristics of the waterbody. This approach generally involves the pre-classification of the observed remote sensing reflectance to identify the dominant OWTs. This informs the selection and application of algorithms. Fuzzy classification approaches can also be used, with the resulting OWT membership function used to weight the retrieved chl*a* concentration. An example of this approach is described in Neil et al. (2019) and is used by operational services such as the UK Lakes Observatory (https://www.eo4ukwater.stir.ac.uk/) (see Fig. 6) and the Copernicus Global Land Service (https://land.copernicus.eu/global/products/lwq).

Phycocyanin algorithms

The development of algorithms for the retrieval of phycocyanin (PC) concentrations, and to a lesser extent phycoerythrin (PE) concentrations, as a marker for the presence and/or abundance of cyanobacteria has been a highly active area of research for over two decades. Numerous studies have demonstrated the diagnostic absorption and fluorescence characteristics associated with PC can be resolved in remote sensing reflectance signals (e.g., Gons, 1999; Wynne et al., 2008; Matthews and Odermatt, 2015) and used

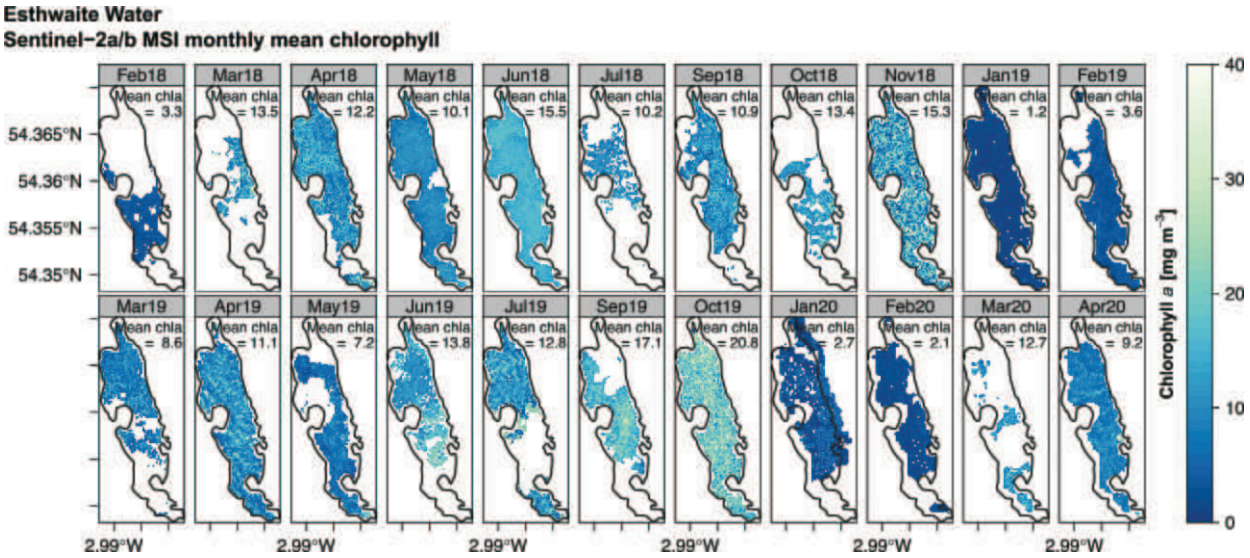

Fig. 6 Monthly aggregated chlorophyll-*a* concentrations in Esthwaite Water (2018–2020) from Sentinel-2a/b data retrieved using a processing chain based on the dynamic selection of algorithms from an ensemble following OWT classification. Data obtained and replotted from the UK Lakes Observatory (https://www.eo4ukwater.stir.ac.uk/).

to diagnose blooms dominated by cyanobacteria. Moreover, the magnitude of these features in remote sensing reflectance spectra can be quantitatively related to the concentration of PC in near-surface waters using empirical- and quasi-analytical algorithms (Simis et al., 2005; Hunter et al., 2009; Mishra et al., 2009; Li et al., 2015). The resolution of the diagnostic features associated with PC requires sensors to have a band centered at approximately 620 or 650 nm to capture the pigment absorption and fluorescence maxima (e.g., as per Sentinel-3a/b OLCI).

In recent years, significant improvements in the algorithms have been made (e.g., Qi et al., 2014; Matthews and Odermatt, 2015; Liu et al., 2018) and their performance has been rigorously evaluated in a number of studies (e.g., Ogashawara et al., 2013; Beck et al., 2017; Yan et al., 2018; Riddick et al., 2019) providing increased confidence in the data products generated. However, the uncertainties associated with the retrieval of PC are higher than those associated with the retrieval of chl*a*. This is due to the confounding influence of absorption by other phytoplankton pigments (e.g., chlorophyll *a* and chlorophyll *b*), the comparatively higher contribution of absorption by colored dissolved organic matter (CDOM) at the PC absorption maximum, and because the determination of phycocyanin in the laboratory and its relationship with cyanobacterial biovolume carries greater uncertainty.

Total suspended matter

Since Total Suspended Matter (TSM), chl*a* and CDOM constituents affect the color of the water, it is possible to detect their presence in water using remote sensing and to quantify their respective concentrations. Therefore, relatively simple global algorithms developed for open oceans are not applicable to these waters. TSM algorithms developed for inland and coastal waters range from purely site-specific empirical relationships between measured remote sensing reflectance and TSM to complex analytical methods.

The empirical approach is based on a statistical calibration and utilizes the relationship between spectral data and TSM measured (e.g., in situ TSM measurements). A large variety of empirical based TSM retrieval algorithms have been published. These empirical relationships have been set-up based on in situ reflectance data (e.g., Forget and Ouillon, 1998; Doxaran et al., 2002), satellite-derived reflectance (e.g., Miller and McKee, 2004), or atmospherically uncorrected at-sensor radiances (Onderka and Pekarova, 2008). Empirical relationships are established through linear (Forget and Ouillon, 1998; Binding et al., 2005), logarithmic (Siswanto et al., 2011), and exponential (Doxaran et al., 2003) regression analysis on the data. Both single band (Forget and Ouillon, 1998; Miller and McKee, 2004) and multi-band based empirical algorithms (Doxaran et al., 2002; Siswanto et al., 2011) have been developed.

Analytical approaches use sophisticated radiative transfer models to characterize the reflectance as a function of inherent optical properties (IOP) like absorption (a) and the backscattering (b or b_b) coefficients. A well-known bio-optical model is the one developed by Gordon et al. (1988).

To overcome the limitations of both the simple empirical approaches and the complex analytical methods, semi-analytical approaches are gaining more and more attention (Chen et al., 2013; Doxaran et al., 2012; Nechad et al., 2010). Semi-analytical methods have a strong theoretical basis. For instance, they consider the relationship between the absorption or scattering properties and TSM concentration, which they combine with statistical methods.

Turbidity

The turbidity of a water sample is an optical measure of the extent to which the intensity of light passing through water is reduced by the particles in the water. Turbidity is therefore strongly related to TSM. Turbidity can be expressed in various units, such as Formazin Turbidity Unit or FTU, Nephelometric Turbidity Unit or NTU. Turbidity is listed by the European Union as one of the prime water quality parameters to be measured regularly. Due to the fact that turbidity is an optical property, it is more related to reflectance through the backscattering than TSM. Measures of turbidity provide an indication of the potential health of the aquatic ecosystem and the potential impact on the quality of water, including the possible presence of other harmful constituents such as contaminants and pathogens.

In situ measurements of TSM are costly and are time-consuming as they require dedicated field campaigns in order to take water samples and these water samples need to be filtered, weighted and dried in an oven. Turbidity can be measured automatically using in situ turbidity meters which are often part of autonomous buoys like the Centre for Environment, Fisheries and Aquaculture (CEFAS) SmartBuoys. Turbidity meters can also be used on site, which allow a direct measurement of the turbidity of the water sample without much effort and specialized equipment. However, care has to be taken when combining turbidity data from different instruments or sensors as they might read light scatter from suspended particles differently, outputting different measurements for the same water sample etc. Some sensors are more accurate at low turbidity levels, while others offer the ability to measure a wide turbidity range.

Whereas there are many remote sensing publications on TSM, there are only a few focusing on turbidity (e.g., Warren et al., 2021). While the existing TSM algorithms are site-specific, algorithms proposed in the literature for turbidity retrieval are more globally applicable (e.g., Ouillon et al., 2008; Nechad et al., 2009; Vanhellemont et al., 2013; Dogliotti et al., 2015).

Color dissolved organic matter (CDOM)

CDOM is arguably the most challenging water quality parameter to retrieve from remote sensing reflectance, particularly from spaceborne sensors, yet it provides a valuable measure of dissolved organic matter content in water. CDOM has a near negligible contribution to light scattering in water bodies, but it strongly absorbs light at UV and blue wavelengths (a process that declines exponentially with wavelength towards the NIR spectrum). Hence waterbodies with high CDOM (but low phytoplankton and mineral particles) generally have uniformly low reflectance and thus changes to CDOM concentrations may exert little influence on remote sensing reflectance.

Moreover, algorithms for CDOM retrieval target blue wavelengths where the absorption maximum occurs (at least within the spectral sampling range of most remote sensing instruments). However, this part of the spectrum is also where the performance of atmospheric correction models is generally weakest resulting in significantly higher errors and uncertainties on remote sensing reflectance products.

In spite of these challenges, several studies have demonstrated it is possible to retrieve estimates of CDOM absorption from satellite radiometry. Much like the algorithms used for other OACs, approaches vary greatly, but several studies have developed empirical algorithms employing a combination of blue, green and (occasionally) red wavelengths. For example, Kutser et al. (2005) successfully mapped CDOM absorption coefficients across 34 Scandinavian lakes using multispectral satellite imagery and an empirical algorithm employing green and red bands.

Example applications of earth observation in inland waters

Algal blooms

One of the oldest applications using satellite imagery for monitoring algal blooms is the "Harmful Algal Blooms Monitoring Products" (https://coastalscience.noaa.gov/research/stressor-impacts-mitigation/hab-monitoring-system/) by the United States National Oceanic and Atmospheric Administration (NOAA). These products were used for quantifying algal blooms in coastal and lake regions of the United States and they were based on an integrated approach combining satellite remote sensing data with circulation and empirical models (Wynne et al., 2010, 2011, 2013). The ocean color sensors used in this application was the Medium Resolution Imaging Spectrometer (MERIS) for images acquired between 2002 and 2011, the Moderate Resolution Imaging Spectroradiometer (MODIS) for images from 2011 to 2016 and now the Ocean and Land Color Instrument (OLCI) from 2016 and continuing through future years (Stumpf et al., 2016). For a global application of satellite data to monitor algal blooms, there is the CyanoAlert (www.cyanoalert.com) which is a commercial service that automatically processes water quality information. This service provides satellite-derived measures of cyanobacterial occurrence and concentration, eutrophication, and additional water quality measures.

Brownification

Dissolved organic carbon (DOC) concentrations are increasing in many inland waters in the northern hemisphere (Roulet and Moore, 2006; Meyer-Jacob et al., 2019) and this is resulting in the browning of these aquatic systems. The brownification process has profound physical, chemical and biological repercussions affecting water quality, biological community structures and aquatic

productivity. Because of this issue, remote sensing has been used to monitor CDOM—the colored part of the DOC—which can be used as an estimator of DOC (Tranvik, 1990). Thus, satellite derived CDOM information can be used to assess DOC spatial and temporal distribution (Vantrepotte et al., 2015). An application using these principles is the LakeBrowser (https://lakes.rs.umn.edu/), which provides data for over 10,000 Minnesota lakes since 2002. The current version of this application is based on the automated imagery processing of Landsat 8 OLI and Sentinel 2 MSI sensors (Olmanson et al., 2020) and provides daily (when clear imagery is available) and monthly (May–October) median CDOM values.

Primary production

Remote sensing of primary production (PP) in inland waters has mainly been based on methodologies developed for oceanic and coastal waters (e.g., Behrenfeld et al., 2005; Westberry et al., 2008; Barnes et al., 2014). These range from simple empirical approaches that approximate PP as a function of the Chla to more complex models that estimate PP using knowledge of the underwater light field. The majority of remote sensing methods for PP in lakes require knowledge of Chl*a* but more recently, phytoplankton absorption or phytoplankton carbon have been employed to improve accuracy. Other inputs to the PP models such as downwelling, irradiance, diffuse attenuation coefficient and lake surface temperature can be taken from remote sensors. RS applications of PP have been primarily focused on larger (Deng et al., 2017) and optically deep lakes. Recent developments in field techniques for PP estimation and a revolution in EO capabilities have now started to empower RS applications of PP in smaller lakes and incorporate benthic gross primary production (GPP) to the models (Kuhn et al., 2020).

National and Global scale assessment

Successful implementation of EO approaches can now be achieved at the global and local scales. Examples of implementation can now be found that are operationalized, providing real opportunity for driving change in lake management at the local and global scales. Validation is critical to build confidence such that stakeholders will adopt these new approaches, although legislative changes are likely to be required to facilitate the incorporation of EO data into monitoring frameworks. Nevertheless, examples of operationalization exist around the world, where global processing is available through the Copernicus Land Service (Home | Copernicus Global Land Service), developed from the UK Natural Environment Research Council funded project GloboLakes (Fig. 7) and exploits Sentinel 3 OLCI and Envisat MERIS data.

Fig. 8 demonstrates an example of the UK Lakes observatory (UKLO). The service currently uses data from the European Space Agency's Copernicus Sentinel-2A/B satellites to produce weekly aggregated estimates of the phytoplankton chl*a* concentration at a 20 m pixel resolution (UK Lakes Observatory | eo4ukwater (stir.ac.uk). The processing chains used to support both the UKLO and the Copernicus Land Service use state-of-the-art approaches for the atmospheric correction of the satellite data and combines this with an ensemble of algorithms for the estimation of chl*a* which are implemented dynamically depending on the optical characteristics of the lake under observation. This approach has been shown to significantly improve the accuracy of chl*a* estimation over a large and diverse population of lakes.

Conclusions and perspectives

Significant progress has been made in the development of EO science in both the remote sensing platforms technology and more intelligent automated computation approaches to processing the remote sensing data. This has facilitated a step change in capability, transforming previous applications limited to individual water bodies to the reliable observation of many hundreds to thousands of water bodies globally. This now facilitates new ways of understanding how our inland water bodies are changing in response to pressures from climate change or from more direct human induced pressures occurring in their catchments. Such global assessments provide key insights into global biogeochemical cycles and are core to our water, food and energy security. This new capability is now also being recognized by water managers and the implementation of operational EO technology is being explored for routine monitoring purposes. At the international level, the opportunity now exists to provide water quality information for data poor regions of the world.

Despite these successes, development work is still required. The tendency of science and policy to focus research on more problematic inland water bodies that exhibit, for example, eutrophic characteristics has resulted in lakes of good ecological status to be under-sampled. As a result, more work is required to develop the EO capability for waters with low chl*a* concentrations, so that change can be detected early to support more effective lake management strategies and interventions. Greater coverage of in situ instrumentation for satellite calibration and validation is needed. The development of low costs instrumentation and citizen science approaches all play a role in supporting the interpretation of satellite data and filling data gaps where EO data has been unable to collect data due to weather conditions or the size of water body.

EO science is now sufficiently mature for the data to be used not only to reconstruct past events and changes in water quality statues as well as the current state of the environment, but critically provide the data to drive and update models for forecasting over the near term, in the same way that we can forecast the weather. This will be fundamental tool for water utilities to manage water and ensure secure water supply under increasing pressures from climate change and extreme events.

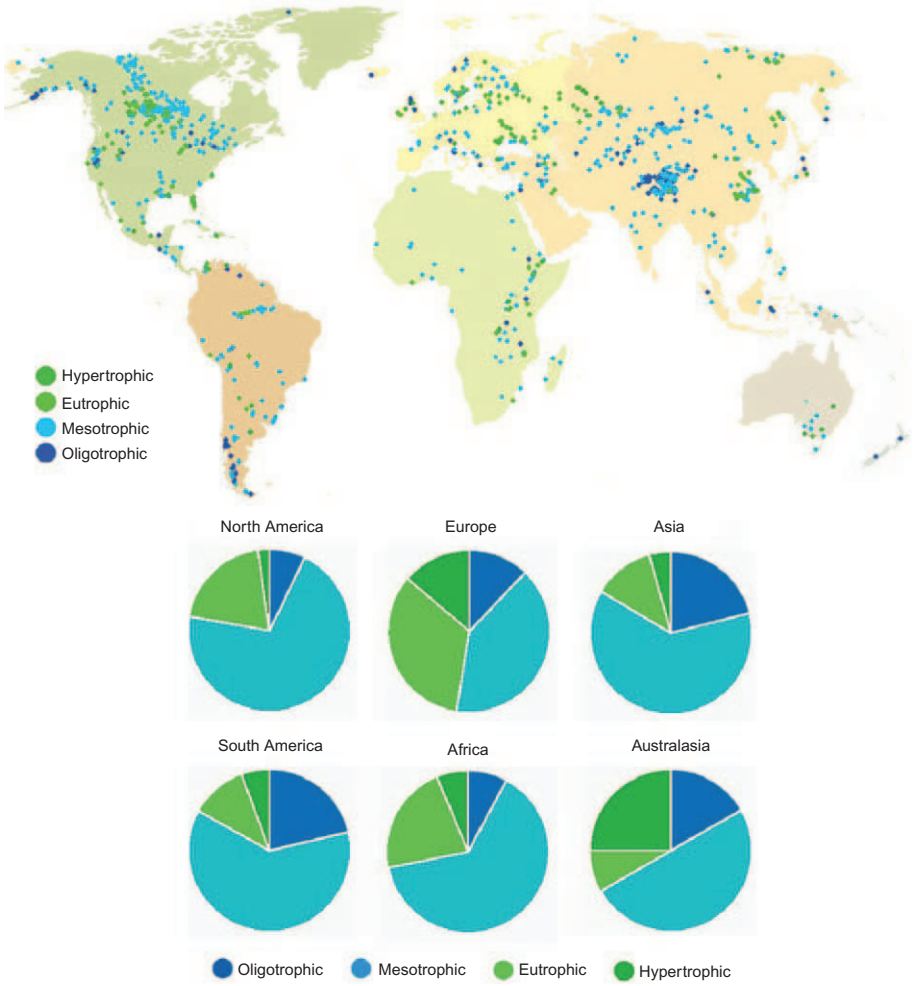

Fig. 7 Example output from the UKRI NERC Globolakes project, demonstrating global water quality coverage of 1000 lakes (Chl*a*).

Fig. 8 Example output from the UKLakes Observatory including a summary of lake water quality and change and detail EO data overlays and time series data.

See Also: **Emerging methods and topics**: Creating and Managing Data From High-Frequency Environmental Sensors; **Fundamental concepts and theories**: Trophic Dynamics and Food Webs in Aquatic Ecosystems; **Human pressures and management of Inland Waters**: Case Studies of (Semi) Constructed Wetlands Treating Point and Non-point Pollutant Loads to Protect Downstream Natural Ecosystems; Impacts of Large Dams on Harmful Algal Bloom Formation in the Tributaries of the Three Gorges Reservoir; The Best Management Practices in Agriculture for Protection of Inland Water Ecosystems; **Structures and functions of Inland Waters - Groundwater**: From Groundwater to Drinking Water—Microbiology of Karstic Water Resources; Groundwater Dependent Aquatic and Terrestrial Ecosystems; **Structures and functions of Inland Waters - Rivers**: Inland Waters—Rivers: Land Use and Water Quality

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Machine Learning for Understanding Inland Water Quantity, Quality, and Ecology

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Black box A model whose inner workings are not known to the user, whether because they are hidden or because they are too complex to readily grasp.
Design The use of human intelligence and knowledge to shape the structure, inputs, or algorithms of a model.
Discovery The use of algorithms to find values of model parameters, states, and/or equations that can suitably describe or reproduce observations.
Distillation Reducing large volumes of information to smaller ones.
Features The variables used as inputs to a model; also sometimes called predictors, dependent variables, or drivers.
Inference Discovering the model values - including parameters, equations, or internal states - that best fit the observations, with an interest in what the discovered values say about the real-world system and processes being modeled.
Knowledge-guided Rooted in machine learning while also formally incorporating knowledge of real-world patterns or processes; also sometimes called process-guided, physics-guided, theory-guided, or process/physics/theory/knowledge-informed.
Loss function A function quantifying the success of a set of model predictions, usually by comparison to observations; also sometimes called objective function or cost function. The *loss* is the output of a loss function for a given set of training examples.
Machine learning The use of algorithms that learn about the world based on feedback rather than relying on a human-defined set of facts or equations; abbreviated ML.

Prediction Estimating values of a dependent variable as a function of some inputs and a model; predictions may describe the past, present, or future at sampled or unsampled locations.
Process-based Primarily containing equations and parameters that are human-interpretable representations of physical, chemical, or biological processes.
Supervised Algorithms trained or calibrated to make predictions that closely match known outputs; contrast with unsupervised algorithms, which are trained to discover patterns in the data based on similarities among inputs.
Training The process by which machine learning models are iteratively modified until their performance minimizes the output of a loss function; roughly equivalent to model fitting or calibration for statistical or process-based models, respectively.

Introduction

Design and discovery

Limnology began with laborious field campaigns, from which observations were then used to develop empirical models to describe and explain patterns in aquatic ecosystems (e.g., Lindeman, 1942; Dillon and Rigler, 1974; Vollenweider, 1975). The advent of powerful new in situ and ex situ sensing techniques has given modern-day limnologists a much greater volume and variety of aquatic observations for testing theories and developing new models. At the same time, increases in computing power have opened the door to machine learning (ML) approaches that take advantage of this new wealth of data. A growing number of limnological studies now benefit from the strengths of ML models, which can include accurate predictions, short runtimes, and flexible equation structures that can capture non-linear relationships precisely (e.g., Hsu et al., 1995; Maier and Dandy, 1996; Fienen et al., 2013; Pacheco et al., 2017; Nolan et al., 2018; Kratzert et al., 2019c; Read et al., 2019).

ML models and their alternatives - process-based, empirical, and statistical models - take a great variety of forms and can be distinguished by the degree to which they contain two elements: *design* is the extent to which humans have manually specified the structure or parameters of the model to reflect current understanding, and *discovery* is the extent to which algorithms ingest observations to learn useful values of the model parameters, equations, and states (Fig. 1). For inland waters, design is guided by scientific knowledge of physical, chemical, biological, and ecological processes and patterns in aquatic systems; discovery is guided by data from in situ sensors, field samples and observations, remotely sensed images, etc. The strength of design is that it formalizes and enables tests of scientific theories, whereas discovery makes fuller use of the data and thus often yields the best predictions and may suggest new connections among variables. Both design and discovery can contribute substantially to our understanding of the natural world, especially when they are used in combination.

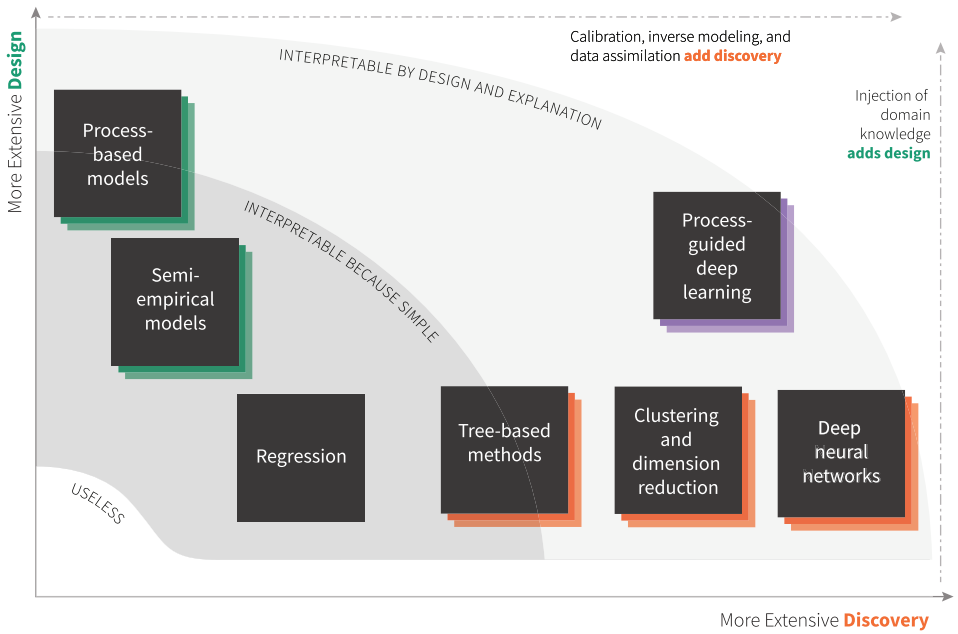

Fig. 1 Model types positioned by their use of design and discovery. Machine learning models may be purely discovery-based (orange) or can include design (purple), and they are distinguished from other model types by their capability for substantial data-driven discovery of model parameters, equations, and/or states. As discussed in Section "Interpretation techniques," the methods of interpretation by design and/or ML explanation have expanded rapidly in recent years such that it is now possible to derive some interpretive insights from nearly any model, and more for those discovery-based models that include some design.

ML models are distinguished from process-based and empirical models by their substantial use of discovery, which enables these models to benefit from large datasets. While substantial design is the distinguishing feature of process-based models, all models - from the simplest regressions to the most black-box-like ML models - contain some design in the form of expert-selected input variables and model structures that reflect expected relationships (Robson, 2014). ML models can be infused with additional limnological design elements in the numerous ways we will investigate throughout this chapter. Conversely, process-based and empirical models can be infused with discovery; this can be done by calibration, inverse modeling, or data assimilation, all topics that we leave to other texts.

Compared to non-ML models, ML models can offer greater prediction accuracy, faster training and execution times, and the flexibility to capture nonlinear relationships for which we lack good theory or direct observations (Solomatine et al., 2008; Shen, 2018; Reichstein et al., 2019; Sun and Scanlon, 2019). Despite these many benefits, ML models have seen only moderate adoption in inland water sciences, perhaps because newcomers to ML often worry that ML is severely lacking in two areas: trustworthiness and contribution to scientific understanding. We argue that both of these areas deserve rigorous attention when applying ML and yet are poor reasons to shy away from ML, because (1) trust and understanding can be earned by ML models, sometimes in ways that outshine non-ML alternatives; (2) trust and understanding are also challenges for non-ML models; and (3) the drawbacks of ML models are often outweighed by their benefits. We expand on these themes below and throughout the chapter.

Model trustworthiness

Models merit our trust when the outputs are accurate for all intended uses, often including application to new water bodies, time periods, aquatic communities, environmental conditions, or situations where data are sparse. Because we rarely have the right data to test a model for all intended uses, we often lean on a heuristic of process design: We tend to trust models whose equations and coefficients express processes as described in textbooks and the literature. However, this design heuristic is neither necessary nor sufficient. It is unnecessary because, as ML models have repeatedly demonstrated, transferable accuracy is achievable with black-box solutions and sufficient training data (DeWeber and Wagner, 2014; Kratzert et al., 2019b). It is insufficient because models are always imperfect: In addition to the omnipresent lack of perfect input data about ecosystem properties and drivers, even our most "process-based" models are always semi-empirical simplifications of the true processes occurring at ecosystem scales (Simon, 1962). In fact, it can be argued that given enough data, ML models containing more parameters than a process-based model are capable of representing limnological processes more completely.

Instead of relying on a heuristic of textbook-like equations, the growth of ML pushes us to judge trustworthiness based on (1) consistent accuracy across a challenging range of test conditions and (2) model inspection to determine whether the model respects known physical and biological constraints and cause-effect relationships. Similarly, we *create* trustworthy models not by keeping them tied to hypothesized processes but by training on larger datasets, following known best practices for ML model development and testing, and - perhaps most importantly for limnology - by injecting design into ML models to encode well-understood processes, physical laws, and reliable patterns, while leaving less-understood phenomena to be discovered by the algorithms.

Limnological knowledge can be designed into ML models at many points in the model structure and in the model development process (Fig. 2). All models permit - and in fact require - injection of knowledge-based design at the point of selecting and preparing input variables. Many ML models are capable of residual or hybrid modeling, i.e., ingesting residuals or outputs from other

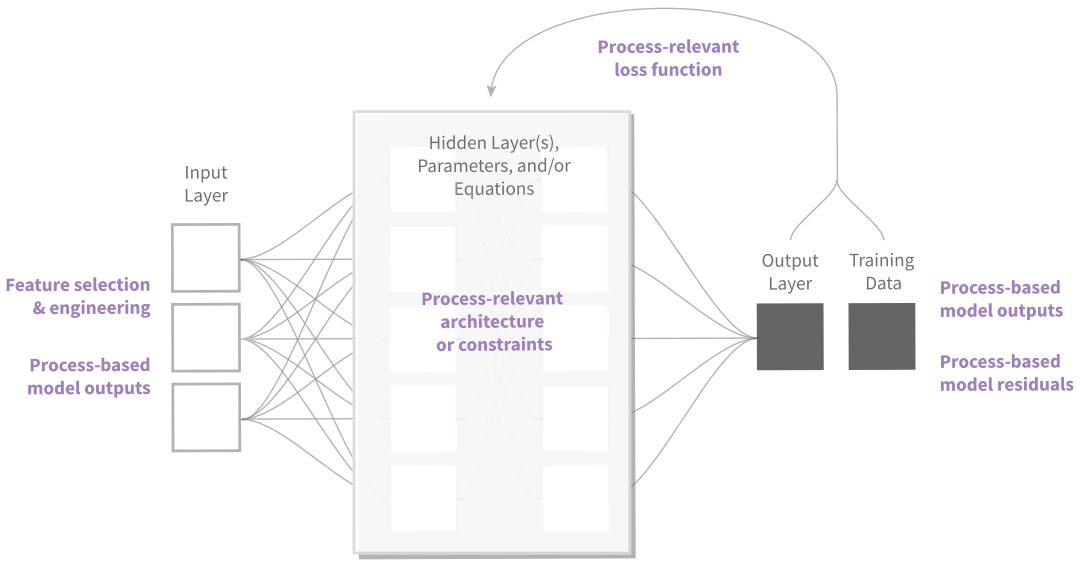

Fig. 2 Injection of limnological design into machine learning models can occur at the points (purple text) of the model inputs, architecture, training data, and/or loss function.

design-rich models and generating more accurate predictions of the same target variable. Some more advanced forms of design injection are limited to the more flexible model structures - for example, neural networks can be designed to assume temporal and/or spatial patterns in the inputs and outputs, and they can be trained or constrained to avoid violation of specific physical or biological rules. Specific modifications are discussed in detail in the Tools section of this chapter.

Discovery-driven models have proven so powerful at prediction that Anderson (2008) questioned the value of continuing to develop new research theories at all. However, theory-based design is a powerful complement to discovery-based models, enhancing model trustworthiness and utility when the two are used together. Further, outside a modeling context, theory remains an important means to discuss, teach, and engage meaningfully with our world. So, it is fortuitous that even as theory-based design improves the realism and out-of-bounds accuracy of ML models, ML models of all kinds can be used to build understanding, including new and revised theories (Mazzocchi, 2015; Nearing et al., 2020), as discussed in the next subsection. Theory and data will always be imperfect and incomplete, and the largest advances in limnological modeling will occur when flaws in either are identified and overcome by leveraging the other.

Pathways to understanding

Limnologists use models to improve understanding of inland waters - specifically, we seek the ability to concisely describe general aquatic patterns or processes via equations, natural language, or digestible images - i.e., we seek "intelligibility" (de Regt, 2017). Understanding of this form enables action: researchers can test hypotheses, develop new ones, and make predictions; environmental managers can choose and justify courses of action; and water users can appreciate and decide how to use water resources. Modeling typically supports understanding via pursuit of three major modeling pathways: *prediction*, *inference*, and *distillation* (Fig. 3).

Prediction asks, "What does the current model say about the world?" The goal of prediction is to estimate values of a dependent variable as a function of a model and some inputs, where the dependent variable is usually a property of the world such as water quality, a nutrient transformation rate, or the size of a fish population. Although predictions are sometimes too detailed for immediate understanding, they provide the raw material from which patterns can be discovered, theories proposed or tested, and understandable summaries derived (Douglas, 2009). Predictions also support water resources decision-making directly, by precisely estimating aquatic ecosystem states and process rates for decision-relevant locations and time periods.

Inference asks, "What do the observations tell us about the underlying process being modeled?" Here we use "inference" in the statistical sense to mean discovering the model values (parameters, equations, and/or internal states) that best fit the observations, i.e., "answer[ing] questions about the model in the light of the data" (Cox, 2006). Fitted parameters, equations, and states often yield understanding directly or can be distilled to something even more understandable. Inference using discovery-driven tools is sometimes called "statistical learning" and distinguished from "machine learning" by the user's objective (inference via statistics, prediction via ML; Bzdok et al., 2018), but because the tools are almost always the same, we consider data-driven inference using ML to be within this chapter's scope. We also expand the statistical definition slightly to include the use of one model to make inferences about another, where the second model may be data-driven, process-based, or even conceptual.

Distillation asks, "How can we say this more simply?" Distillation uses models to reduce large volumes of information to smaller ones. Distilled information may be directly useful to researchers or managers because it is more intelligible than the raw inputs, thus

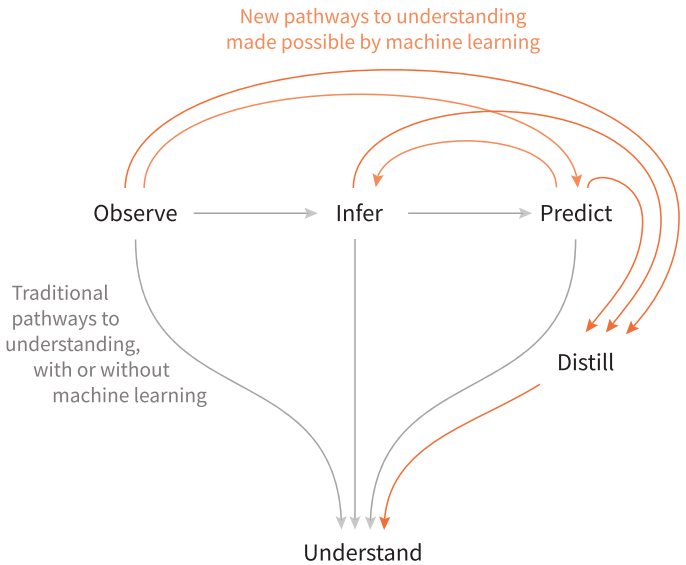

Fig. 3 Pathways from data to understanding. Some data can be directly understood. Process-based, semi-empirical, and traditional statistical models enable inference, which can directly provide understanding or can lead to understanding via predictions (gray arrows). Machine learning (ML) models can yield understanding by the same pathways as non-ML models but also introduce additional pathways, including predictions that bypass inference, inferences that emerge from predictive models, and ML-enabled distillation of observations, inferences, and predictions (orange arrows).

Table 1 Suitability of five major modeling approaches (columns) for three major modeling pathways (rows).

Objective	*Process-based models*	*Statistical models*	*Neural networks*	*Tree-based models*	*Clustering and dimension reduction models*
Prediction	**	*	***	***	*
	Simulation, out-of-bounds predictions	Regression, additive models, time series models	Prediction, recurrence, convolution	Random forests, boosting	Classification of new observations
Inference	***	**	**	*	*
	Calibration, inversion	Regression, hierarchical models	Attention, prediction of parameters	Decision trees	Cluster and dimension characteristics
Distillation		**	**	**	***
		Regularization, model selection	Autoencoders, regularization	Pruning	Simplification of inputs

Number of stars indicates level or frequency of suitability. Cells contain names of more specific methods for applying the approach to the pathway. Inference may also be addressed for all modeling approaches using model-agnostic interpretation techniques (see Section "Interpretation techniques").

enhancing understanding of pattern or process. In addition, distilled information may be used as input to subsequent models, thereby reducing computation costs for those later models (because the distilled inputs are smaller and simpler) or improving their accuracy (because the distilled inputs contain less noise). While inference and prediction are commonly recognized as the core pathways trod by modelers (Sanders, 2019), distillation is an important third pathway because it bridges the gap between raw data or model outputs and truly useful information.

Although ML models are sometimes criticized for failing to contribute to understanding, we argue that such criticism fails to recognize the several pathways by which modeling can inform understanding. We agree with the critics that little understanding would be gained by making inferences about ML equations and parameters that have little interpretable meaning (e.g., parameters in artificial neural networks or random forests). But ML models can support inference about meaningful limnological processes and states if we use ML differently - if we set the focal variables as the inputs or outputs of the model, or if we infuse certain parameters with meaning through strong doses of limnological design. And ML models are often *better* than non-ML models at prediction and distillation (Fig. 3, Table 1). As we describe specific tools and applications throughout this chapter, we will elaborate on the diverse uses of ML to build understanding.

Chapter overview

In this chapter we present four classes of ML approaches - neural networks, classification and regression trees, clustering and dimensionality reduction methods, and model interpretation techniques. We chose these four classes because we see much application of them in the recent literature and great opportunity for fusion of discovery and limnological design, especially for neural networks. There are many other ML approaches and variants on these approaches (e.g., Support Vector Machines) that are not covered in detail here. To learn more about these other options, please refer to a primer on machine learning methods written for ecologists (Olden et al., 2008) and a review of deep learning in the hydrologic sciences (Shen, 2018), and keep a watchful eye on new publications in this fast-growing field.

The main body of this chapter is divided into descriptions of these focal modeling approaches (Tools), guidelines for rigorous use of ML models (Implementation), and examples of how these approaches have been applied to meet goals for prediction, inference, or distillation for inland waters research and management needs (Applications). Recurrent themes throughout the chapter include gaining understanding of process or pattern, assessing model trustworthiness and prediction uncertainty, and injecting process design into model structures and the model-development process. We show that ML models, particularly when applied according to best practices and with heavy doses of both design and discovery, are powerful tools to support limnological investigation, understanding, and management.

Tools

Neural networks

Neural networks (NNs) are highly flexible black-box models that can mimic virtually any relationship between inputs and outputs, as long as the model and the training dataset are both sufficiently large (Goodfellow et al., 2016). The flexibility of NNs makes them suitable for any of the three modeling pathways (prediction, inference, or distillation), although their prediction accuracy is most frequently touted. As computing power and datasets have grown to enable ever more complex NNs, the resulting growth in predictive accuracy has driven the explosive popularity of NNs, with a turning point at a series of high-profile modeling competitions on tasks such as speech recognition, image classification, and time series modeling (LeCun et al., 2015). Deep learning, which employs NNs with multiple layers, has also risen in popularity within limnology (see Sections "Applications" and "Conclusion").

NNs are collections of connected variables, or *nodes*, where each node contains the weighted sum of its designated input nodes as transformed by an activation function such as a logistic curve (Fig. 4). Nodes are typically organized into *layers* to represent discrete

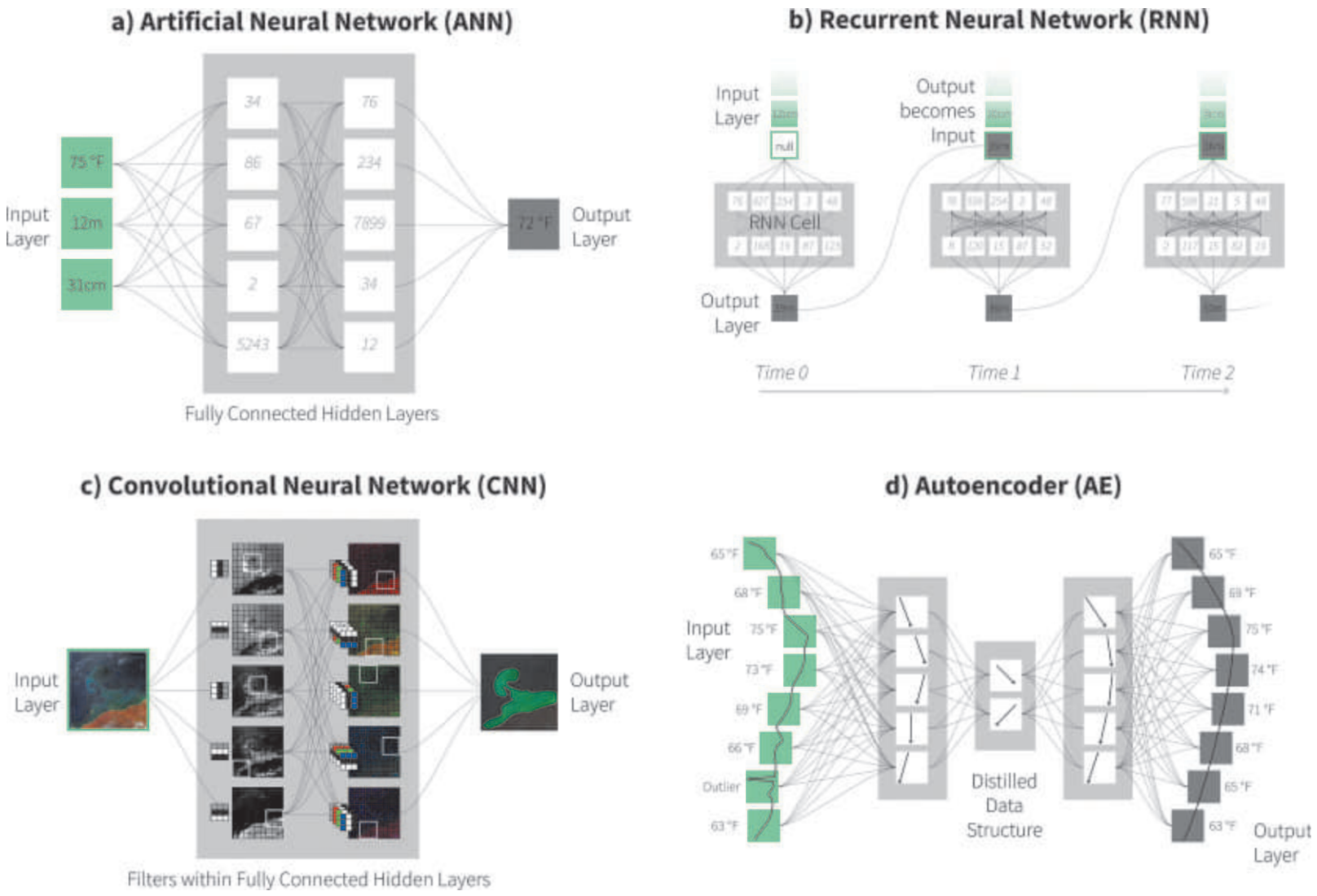

Fig. 4 Structure of (A) a basic NN, with expansions useful for (B) temporally correlated data, (C) spatially structured data, and (D) compression or de-noising of complex inputs. Within each panel, information flows along the curved arrows. Where arrows meet, values are combined by a weighted sum, the addition of a constant (bias), and transformation by an activation function such as sigmoid or tanh. Light gray rectangles indicate the conceptual gathering of nodes into layers. Green, white, and dark gray boxes represent input, intermediate, and output nodes, respectively.

stages of information flow through the network, where successive layers build from preceding layers to extract increasingly complex features, compute interactions among features, and ultimately generate predictions. NN parameters are initialized to random values and then iteratively trained until the model performance minimizes the output of a *loss function*, a function that returns a designer-specified accuracy metric such as the root mean squared error of predictions relative to observations. Model training follows an iterative process in which a set of trial predictions is generated, then blame for the *loss* (the output of the loss function) is apportioned among the parameters, then the parameters are each slightly adjusted in proportion to their blame, and then the next iteration is begun. The efficiency of this training procedure is what makes it practical for NNs to be substantially more complex, and therefore more flexible, than other ML modeling structures.

NNs can be a simple stack of fully connected layers (artificial neural networks, ANNs, Fig. 4A), or they can have more complex structures that are suited to specific prediction problems. Recurrent neural networks (RNNs, Fig. 4B) are useful for modeling time series of water chemistry (Li et al., 2019), temperature (Rahmani et al., 2020), quantity (Nagesh Kumar et al., 2004), community composition (Chon et al., 2001), etc. because they model whole sequences of inputs and outputs, using the same set of parameters for each transition between timesteps. RNN variants such as Long Short-Term Memory (LSTM) and Gated Recurrent Units (GRU) transfer more detailed information among timesteps, enabling a memory of recent and more distant past events and cumulative ecosystem status (e.g., snowpack depth; Kratzert et al., 2018). Raster-based convolutional neural networks (CNNs, Fig. 4C) apply to spatially structured datasets such as remotely sensed images and 2D representations of water bodies (Syariz et al., 2020). CNNs pass specialized parameter sets (kernels) over an input raster one spatially contiguous window at a time, extracting higher-level features from each window and representing those features in a new 2D layer that can itself be treated as a raster. Graph convolutional neural networks (GCNNs) allow spatial connections via a graph rather than a grid, which may be preferable for modeling systems such as river networks or food webs (Jia et al., 2021). Autoencoders (Fig. 4D) are a means of information compression or smoothing; the network is trained to re-predict the original inputs after passing data through one or more constrained hidden layers, which typically have fewer nodes than the input layer. After training, these constrained layers concisely represent the essential information and may therefore support inference about properties of the aquatic system (Li et al., 2020); alternatively, the modeler may be most interested in the final predictions for their smoothness or reduced noise relative to the original inputs. Other NN structures exist and continue to be invented, but ANNs, RNNs, CNNs, and autoencoders are readily and widely applicable for limnological modeling objectives.

Estimating Uncertainty: Many methods are available to quantify uncertainty in NN predictions (Kabir et al., 2018). For example, some NNs are trained to directly predict two or more moments of the probability distribution of each prediction (e.g., the mean and variance; Nix and Weigend, 1994). Alternatively, Bayesian NNs represent each node as a distribution and thus can represent uncertainty throughout the network (e.g., Graves, 2011; Blundell et al., 2015; Louizos and Welling, 2016; Pearce et al., 2018). Ensemble methods are another option, where the ensemble prediction is the distribution of predictions from many different instances of the NN (Tibshirani, 1996). Variation among the ensemble members can be obtained by training each member separately, e.g., with different initial parameter values or resampled training data (Dietterich, 2000), or by dropout from a single trained model, where a random subset of the weight parameters are set to 0 at the time of prediction (Gal, 2016).

Integrating Design: NNs are highly amenable to the injection of limnological process knowledge, especially when the NN structure already represents temporal or spatial dimensions of an aquatic ecosystem. Beyond that structural decision, Willard et al. (2020) describe the following approaches to adding design: (1) Custom loss functions can encourage physically, chemically, or biologically realistic values of internal model states and final predictions (e.g., Beucler et al., 2020; Jia, 2020). (2) The model architecture, i.e., the choice of layers and activation functions, can be designed to strictly enforce physical, chemical, or biological rules (e.g., Daw et al., 2020). (3) Model weights can be initialized, or "pretrained," to emulate a process-based model by treating process-based model outputs as observations (Read et al., 2019). (4) Models can be trained to predict the residuals between process-based model predictions and observations, rather than predicting the observations themselves. (5) NNs can be hybridized with process-based models, e.g., by passing the outputs from the process-based model as inputs to the NN (e.g., Karpatne et al., 2017), or chaining outputs from the NN into the process-based model, or embedding one model as an intermediate component of the other model. Applications of such methods for Earth system sciences have been recently reviewed (Reichstein et al., 2019).

Tree-based methods

Classification and regression trees (CART) algorithms (De'ath and Fabricius, 2000; Breiman et al., 2017) can represent very complex, non-linear, multivariate relationships and are most useful for building understanding via prediction (e.g., predicting groundwater pH from landscape features; Stackelberg et al., 2021) or *supervised* distillation (e.g., identifying syndromes of lake properties and warming rates, O'Reilly et al., 2015; or assigning phytoplankton species to functional groups, Kruk et al., 2017). CART algorithms lack some flexibility relative to other methods described here, especially in their ability to simulate spatial and temporal relationships among states, provide unsupervised distillation, or accommodate designed structural components to integrate limnological knowledge. However, CART algorithms excel at ingesting and predicting categorical variables, are often competitive with basic NNs for prediction accuracy, and are highly interpretable at the level of individual decision trees, which can be drawn and visually inspected.

CART algorithms are like NNs in that they obtain their flexibility from many connected nodes that each perform a simple calculation. Whereas each NN node is a weighted, transformed sum of preceding nodes, CART nodes are decision points within a tree of if-else statements, each of which is a split on the axis of one input variable. Terminal nodes ("leaves") of classification trees

predict class membership, while leaves of regression trees predict a continuous value as a simple average of the dependent variable from the training data for that node. Extensions of the regression tree include more complex functions at the leaves and sometimes the nodes, including using the last or all upstream predictors in a linear model to predict the continuous value (Quinlan, 1992).

Many popular CART algorithms use ensembles of trees, created largely by bootstrapping (bagging) or boosting methods. Bagging methods train many different trees and then report the average of the trees' predictions; for example, the random forest algorithm grows many trees by withholding random subsets of the inputs and randomly permuting a subset of features (Breiman, 2001). Boosting methods such as AdaBoost (Freund and Schapire, 1997) and Extreme Gradient Boosting (XGBoost; Chen and Guestrin, 2016) build an ensemble of trees whose predictions are added together, where each new tree is trained to predict the residuals of the sum of the previous trees' predictions. Ensemble CART methods perform well even for collinear predictors, high dimensionality data, and non-linear relationships between predictors and responses.

Estimating Uncertainty: Uncertainty in individual CART algorithm predictions can be estimated using method-specific algorithms, e.g., several methods for random forests (Meinshausen, 2006; Coulston et al., 2016; Mentch and Hooker, 2016; Zhang et al., 2020), ensembling for AdaBoost (Zhou et al., 2017), and quantile regression for XGBoost (März, 2019). Many of these approaches leverage concepts from Bayesian statistics, from which they gain uncertainty estimates and also benefits to model robustness and accuracy (e.g., Quadrianto and Ghahramani, 2015). Bayesian Additive Regression Trees (BART) combine boosting and a Bayesian approach that generates predictions from a probability distribution rather than a point estimate (Chipman et al., 2012). New methods continue to be developed for uncertainty estimation, such as the probabilistic models implemented as NGBoost (Duan et al., 2019).

Integrating Design: CART algorithms have a fairly rigid structure that limits the amount of knowledge-based design that can be injected. However, as with any model, modelers still use limnological knowledge when choosing which variables to input; knowledge-rich input variables may include derived variables that reflect important hydrologic or limnological properties. In addition, some algorithms and implementations offer opportunities to customize the training loss function (Chen and Guestrin, 2016) or constrain the output to be monotonic with respect to one or more input variables (Incer et al., 2018), permitting limited but intriguing opportunities to design knowledge into these aspects of the model.

Clustering and dimensionality reduction methods

Clustering and dimensionality reduction techniques provide understanding via distillation, i.e., they condense large, complex datasets into more manageable, interpretable, or otherwise useful forms (Borcard et al., 2018). Unlike most other ML models, the techniques described here use unsupervised learning: Rather than seeking to make predictions that match observable answers, they aim to reduce complexity while preserving the meaningful features of a dataset. Clustering methods classify similar observations into groups, which can yield insight about complex or high-dimensional data (e.g., quantifying changes in microbial community structure over time; Rubbens et al., 2021), reveal previously unknown structure in the data (e.g., identifying distinct seasonal patterns in stream photosynthesis rates; Savoy et al., 2019), or identify anomalies (e.g., detecting erroneous spikes and level shifts in water quality sensor data; Leigh et al., 2019). Dimensionality reduction methods compress high-dimensional data to fewer dimensions, which can be useful to reduce noise in data (e.g., remove distortion from underwater images; Fabbri et al., 2018), increase data-driven model performance by providing fewer and more meaningful predictor variables (e.g., simplify hyperspectral imagery to a set of independent variables; Dierssen et al., 2021), and aid in interpretation of results (e.g., describe effects of floodplain restoration on species richness of macroinvertebrates, macrophytes, and fish; Pander et al., 2018).

Methods for clustering include k-means clustering, Gaussian mixture models (GMMs), and hierarchical clustering (Scrucca et al., 2016; Bramer, 2020). In k-means clustering, data are grouped into k clusters by randomly selecting k data points to serve as the initial group centers, then iteratively adding nearby points to each group and computing the centers of the updated groups. K-means clustering performs best on groups that are spherical; GMMs overcome that limitation by describing each cluster with a different mean and standard deviation in each dimension, and allowing clusters to overlap, which allows clusters to take on complex shapes. Hierarchical clustering methods build trees by sequentially splitting or gathering data points into groups (divisive and agglomerative clustering, respectively). An important modeling decision for any clustering algorithm is the number of clusters to use (set directly for k-means clustering and GMMs or via tree depth for hierarchical clustering). This decision may be based on expert knowledge or by finding the value that minimizes within-group variance and/or maximizes between-group variance.

Dimensionality reduction techniques include time-honored linear transformation methods such as principal components analysis, linear discriminant analysis, and factor analysis; and non-linear methods such as isometric feature mapping, non-metric multidimensional scaling, locally linear embedding, t-distributed stochastic neighbor embedding, and uniform manifold approximation and projection. These methods have been joined by neural-network-based approaches such as autoencoder NNs (described above) and self-organizing maps (SOMs). SOMs are specially structured NNs that map multi-dimensional data points onto a 2-dimensional grid or honeycomb of nodes, simultaneously organizing similar data points spatially (a sort of "soft clustering") and reducing data dimensionality. Unlike most NNs, whose weights are adjusted based on their contribution to a loss function, the weights associated with each SOM node are iteratively updated until the map spans the full data space while preserving similarity among neighboring SOM nodes.

Estimating Uncertainty: Uncertainty in clustering and dimensionality reduction usually cannot be defined with respect to differences between predictions and observations because there is no "true" group membership or dimension definition to observe (autoencoders are a rare and partial exception). Instead, confidence in model output is assessed through goodness of fit, as

described by measures of group distinctiveness or preserved distances among samples (see 8.3 Model evaluation). Among clustering methods, GMMs shine with respect to uncertainty estimation because they naturally predict the probability that each data point belongs to its assigned cluster.

Integrating Design: Despite the data-driven, unsupervised nature of clustering and dimension reduction algorithms, design can be injected into these methods at the time of application. The researcher first chooses the variables to reduce, e.g., a set of potentially related biogeochemical measurements or gene abundances or a time series of model predictions across a set of sites that exhibit environmentally meaningful variation. For clustering algorithms, the researcher also selects meaningful measures of similarity, which may vary depending on the probability distribution, sparsity, or temporal or spatial structure of the data. Lastly, the researcher may apply expert judgment to the selection of model hyperparameters such as the number of clusters or dimensions to use, where the "right" number is often a compromise that explains substantial variance and yet is still simple enough to yield scientific insight.

Interpretation techniques

Model interpretation is useful for assessing trustworthiness and extracting insight from ML models. It has sometimes been assumed that ML models sacrifice interpretability for the sake of accuracy, but the inevitability of that tradeoff is belied by recent progress in ML model design (Rudin, 2019) and ML explanation techniques (Samek et al., 2019; Molnar, 2020) (Fig. 1). Process-based components of ML models are intrinsically interpretable, another point in favor of integrating design into ML. Additionally, ML models may be structured so that they explain themselves, e.g., by making predictions based on similarity of the current inputs to prototypes encountered during training (Chen et al., 2019). These structural approaches to interpretability are largely new to limnology, but the field of model explanation for artificial intelligence (called "Explainable AI" or "XAI") offers a slightly better-trodden and complementary approach to model interpretation. Having already addressed process-guided designs in Sections "Neural networks," "Tree-based methods," and "Clustering and dimensionality reduction methods," here we provide a taste of the current options in XAI.

When inspecting predictions one at a time, intuition suggests that there should be some quantifiable contribution of each input feature such that the prediction is some fixed intercept plus the sum of all features' contributions. Shapley values are these quantifiable contributions (Shapley, 1951). For a simple linear regression with normalized features, Shapley values are equal to the fitted coefficients, but for more complicated models, the calculation of Shapley values must consider many possible combinations of feature values to isolate the effect of the feature of interest. SHapley Additive exPlanations (SHAP; Lundberg and Lee, 2017) further generalize the Shapley value idea from the effects of individual input features to the effects of feature combinations, e.g., all the pixels in a specific fish in an underwater image.

SHAP values can be inspected at multiple levels of detail (Lundberg and Lee, 2017). For a single prediction, the direction and magnitude of the contribution of each input feature can be visualized in a stacked bar plot. From there, stacked bar plots can be positioned side-by-side for many individual predictions, with predictions optionally grouped by the similarity of the input feature contributions to reveal clusters of conditions for which different sets of input features drive the predictions (note the use of a clustering algorithm to distill the SHAP results, already putting into action the tools described above). Effects of each feature can be summarized as a single value giving the mean absolute effect of that feature (one way to measure feature importance); as a density plot showing the distribution of effects of that feature over all training examples; or as a scatter plot with one point per training example showing the feature's effect (SHAP value) versus the feature's value.

Fast estimation algorithms have made SHAP a leading interpretation method in recent years; however, SHAP values are still computationally expensive to derive, are less informative when features are correlated with one another, and can't answer the question, "If I increase this feature by 5%, how will the prediction change?" An approach that does better with the first and third of these issues is Local Interpretable Model-agnostic Explanations (LIME; Ribeiro et al., 2016), in which a locally linear model is fit around a single input example to intelligibly describe the sensitivity of that prediction to small changes in the inputs (even for models that are globally nonlinear). There are also alternatives to SHAP for estimating feature importance (Breiman, 2001; Fisher et al., 2018) and partial dependence (Friedman, 2001) or variants that deal more elegantly with interactive effects (ICE; Goldstein et al., 2015; ALE; Apley and Zhu, 2019).

While the above methods are model-agnostic or can be implemented for a variety of ML models, there are also interpretation methods specific to neural networks that offer additional forms of insight (Samek et al., 2019; Toms et al., 2019). We will highlight two such methods here. Integrated Gradients (IG; Sundararajan et al., 2017) quantify the rate of change in the output with respect to change in an input feature, using a discrete computation approach that reduces unwanted sensitivity of the interpretation to tiny variations in input values. Layerwise Relevance Propagation (LRP; Bach et al., 2015) produces relevance scores that indicate the contribution of each model node to the nodes in the next NN layer, where the sum of the relevance scores in any one layer of an NN is equal to the predicted value. LRP can describe complex NN architectures including those with recurrence (RNNs; Arras et al., 2019) and convolution (CNNs; Montavon et al., 2019). As with model-agnostic approaches to ML interpretation, the subfield of NN-specific ML interpretation is evolving rapidly, and new techniques continue to emerge.

Implementation

Choosing a model

Various modeling challenges are best met with different models. To select a core model for a specific science challenge, first consider the degrees to which data availability enables reliable discovery and well-understood theory enables sound design. Next, bear in mind that many limnological questions may be best addressed with a combination of models that fill different roles; for example, ML models may make inferences about process-based model parameters or may make predictions that serve as inputs to a model of any other type. Thus, the best set of models to address an inland waters science question will depend on the extent of current understanding, the availability of data, and the pathway by which each subtask will be pursued (Fig. 5).

- For *prediction*, discovery-rich models (e.g., tree ensembles and neural networks) of sufficient complexity can be very accurate in familiar conditions and are a clear best choice when theory is limited and data are abundant. Process-based, design-rich models may be less accurate in well-observed conditions but are often assumed to predict more reliably in new climates, geologies, etc. However, design and discovery need not be mutually exclusive: Process-guided neural networks have shown impressive accuracy in both familiar and new conditions, and both tree-based models and neural networks can be trained to emulate process-based models but with faster runtimes that make it feasible to explore predictions for many scenarios.
- For *inference*, very simple models or those whose design includes physically or biologically meaningful parameter values are the most rewarding, regardless of how much discovery is included. Simple decision trees and process-guided NNs are the ML models that best meet these criteria, while a wider variety of ML models can be used to make inferences about simpler statistical or process-based models. Lastly, model interpretation methods can be applied to any ML model to quantify the importance and effects of each input variable, describing relations between inputs and outputs that may yield insights into the limnological processes being modeled.
- For *distillation*, clustering and dimension-reduction models are good choices. Additionally, autoencoder neural networks, neural network regularization methods, and tree ensembles all provide built-in filtering or weighting of candidate predictors and constraints on model complexity, such that these methods can implicitly or explicitly distill input data down to the most important information. In general, ML models are substantially more useful than process-based models for distillation, because ML models can discover rather than assert the structure of complex data.

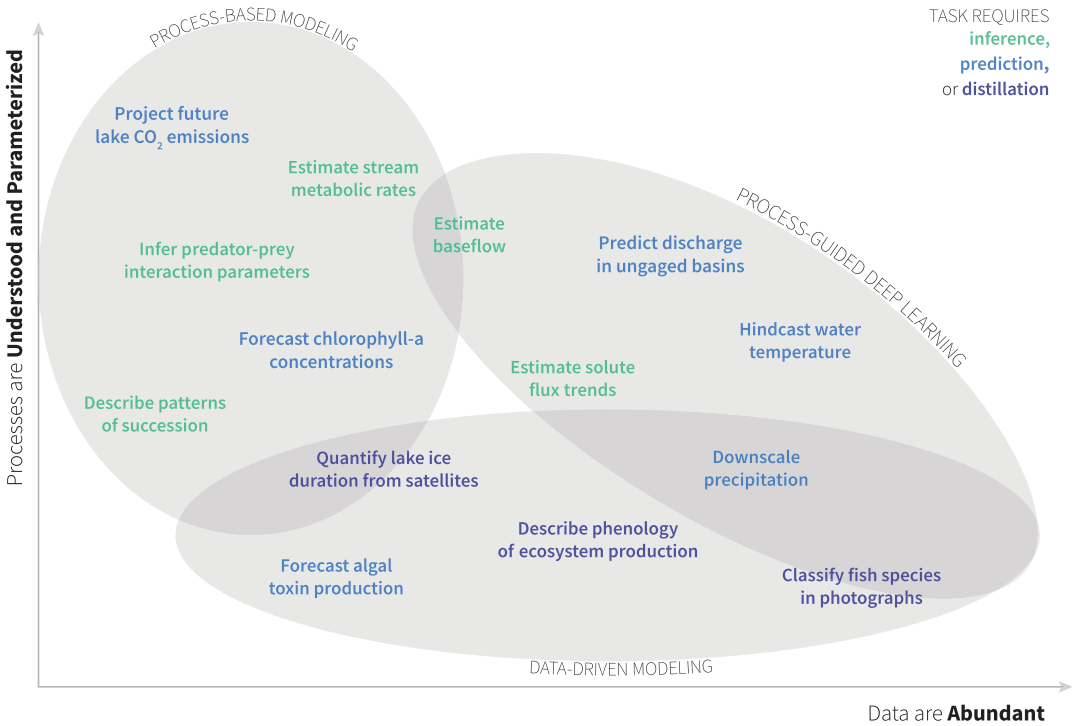

Fig. 5 Limnological research tasks (words in colors) begin with differing amounts of data (x axis) and knowledge of the underlying processes and parameters (y axis). Where the modeler's task falls on this plot can help in selecting a modeling approach (labeled gray regions, roughly corresponding to position in Fig. 1). The different tasks are colored according to whether the main goal of the task is to infer, predict, or distill, illustrating that each class of modeling approaches can serve several goals. Although the precise position of each research task can be debated, this figure illustrates the broad diversity of research tasks for inland waters with respect to theory, data, and beneficial approaches.

Ensuring reproducibility

Reproducibility ("re-performing the same analysis with the same code using a different analyst"; Patil et al., 2016) is essential to modern science, and applications of ML bring unique reproducibility challenges. One of the fundamental hurdles to clear is achieving reproducibility in the code scripts used to define and/or apply the ML models in a study. General guidelines for open and reproducible scientific computing are available elsewhere (Wilson et al., 2014; Gil et al., 2016), but a few guidelines are especially relevant to applying and experimenting with ML. First, if you are experimenting with variants in model structure, follow the Don't Repeat Yourself (DRY) rule: Write your code so that every variant can be run from the same code base, using concise arguments to specify which model variant is to be applied. When publishing for reproducibility, publish an archive of every model training and prediction run. Include well-explained source code, information about the software and hardware environment, hyperparameter values, inputs, raw outputs (if not too large), and summary and evaluation metrics. Lastly, report how you selected the hyperparameters (see "Model refinement" below); this is an often undocumented but important step in the modeling process.

Arguably even more scientifically important than computational reproducibility is replicability ("re-performing the experiment and collecting new data"; Patil et al., 2016). The odds of replicability are higher if you avoid over-tuning your model to match the dataset in hand. Specifically, at the very beginning of your project, divide the available data into three partitions: a training set, a development ("dev" or "validation") set, and a test set. Use the training data to train your model, select hyperparameters based on model performance on the dev data, and withhold the test data until the very end of your project, after you have fully developed your model, to provide an honest assessment of model performance. If data are limited, use a variation on the basic train-dev-test partitioning to make fuller use of the available data while still ensuring that test data have no effect on the selection or refinement of the model - e.g., use cross-validation to do training and testing on several overlapping partitionings. Ideally, the dev and test sets will each provide some surprises relative to the training set, representative of the surprises that would occur when applying the fitted model to an entirely new dataset - to make surprises more likely, split time series data into temporally contiguous chunks so that whole sequences of events remain unseen during training, and split geospatial data in spatial chunks so that dev and testing data are less spatially autocorrelated with training data (Ploton et al., 2020). To improve potential for both replicability and reproducibility, use the published model archive to identify which data were used for training, development, or testing, and document the rationale behind the selected data partitioning strategy.

Model evaluation

Rigorously evaluating model performance is the first step to building trust in an ML application. Model evaluation can be used to compare or choose among several candidate models, determine where each model fails, inform model refinements, and provide essential context for users of the model predictions. Post-hoc evaluation complements any uncertainty estimation method that may have been built into a model, allowing assessments of more diverse aspects of the model fit and providing a check on the uncertainty reported by the model.

For those models that predict observable states, prediction performance can be quantified with metrics such as root mean squared error, mean squared error, classification error, bias, or Nash-Sutcliffe efficiency. The accuracy of a model's uncertainty estimates can also be quantified, e.g., with the bracketing frequency metric. Alternatively, accuracy might be most usefully assessed with respect to values that are computed from the model predictions before being used by the target audience - for example, fisheries managers may be most interested in values computed from daily predictions, such as growing degree days, annual nutrient loads, or the probability of an algal toxin exceedance in a given week. Accuracy in predicting threshold exceedances may be assessed with Receiver Operating Characteristic (ROC) curves and/or Heidke Skill Scores (HSS), with the ROC curves providing a more nuanced view of event prediction by evaluating model sensitivity (false positive rate) against model specificity (false negative rate) for a range of thresholds (Shin et al., 2020). Continuous Ranked Probability Scores (CRPS) can also be used to evaluate probabilistic predictions and are analogous to mean absolute error (Gneiting et al., 2005; Thomas et al., 2020).

At the community level, accuracy of predictions (or of values computed from those predictions) on common datasets is a valuable means of comparing multiple models to one another. The inland waters community has made recent gains in data sharing through the publication of large, model-ready datasets such as GAGES-II (Falcone, 2011), LAGOS (Soranno et al., 2015; Cheruvelil et al., 2021), CAMELS (Addor et al., 2017), AquaSat (Ross et al., 2019), and DeepFish (Saleh et al., 2020). Development of more such datasets, and widespread use of them for model testing and reporting, would substantially improve our ability to identify top-performing models for limnological prediction.

For unsupervised ML models (e.g., those that provide clustering or dimension reduction), truth is often unmeasurable, and thus prediction accuracy cannot be directly assessed. Instead, clustering models are typically assessed by measures of distinctiveness such as the amount of variance within each group relative to the total variance of the data. Dimension reduction methods can be evaluated by their success in preserving the relative distances among the data points. Bootstrapping methods can also be used to compute the frequency with which a cluster appears over many resamplings of the data or to assess the robustness of conclusions drawn from dimensionality reduction.

Model refinement

Most ML models are defined by (1) a structure and training algorithm and (2) hyperparameters that specify variations within that general framework (James et al., 2021). Examples of hyperparameters (also called "tuning parameters" or "parameters") include the learning rate in neural networks, the number of candidate features per tree in a random forest, the possible shapes of the relationships among features in a Gaussian mixture model, and the map size of a self-organizing map. Although a sense of effective hyperparameter values can sometimes be pulled from published model applications or software defaults, optimal hyperparameter values are usually discovered by trial and error for each specific application. Data partitioning into training and development sets enables this trial-and-error exploration: Models are trained with a variety of hyperparameter values and then assessed on the development set to identify the most successful combination of hyperparameter values, where success is evaluated by a metric of the modeler's choice (e.g., root mean squared error). Because the number of possible hyperparameter value combinations is usually infinite, modelers explore a finite number of combinations and then accept the best of those options. This exploration can be done manually, with brute-force search algorithms such as random sampling or grid-based sampling of possible hyperparameter combinations, or using an additional layer of modeling ("surrogate modeling") to iteratively predict and explore promising regions of hyperparameter space (Feurer and Hutter, 2019).

Perhaps the most important consideration when tuning hyperparameters is the balance between underfitting (unnecessarily limiting the complexity of a model) and overfitting (excessively tailoring a model to the sample in hand). The flexibility of ML models makes them especially vulnerable to overfitting; fortunately, principled train-dev-test data partitioning and hyperparameter tuning are precisely the tools needed to find the right balance. Hyperparameters that affect underfitting and overfitting typically relate to model complexity and include the number of nodes and training iterations in neural networks, the depth and pruning methods for tree-based models, and the number of clusters or dimensions in distillation-focused methods. The values that best balance overfitting with underfitting are those for which accuracy is high for training predictions and yet only modestly worse for development predictions. Underfitting manifests as inaccurate training predictions, which can be addressed by adding model complexity or (if possible) providing additional input features. Overfitting manifests as substantially worse development predictions, which can be addressed by reducing or constraining model complexity, or (if possible) collecting more training data.

Model complexity is most obviously a function of the number of parameters in the model (neural network nodes, k-means clusters, etc.), but model complexity can also be reduced by constraining the range of values that each parameter can take on. Process-agnostic versions of this approach are known as regularization; a common example is to include a penalty term for the sum of all parameter values in the loss function used for model training, such that the model learns to achieve reasonable prediction accuracy with smaller and/or fewer parameters. Physical or limnological knowledge can also be used to guide parameter values toward a subset of the mathematically possible options; for example, a gradient boosting regression might be constrained to predict photosynthesis rates that increase monotonically relative to light intensity, and a neural network might be encouraged, via a loss function term, to predict changes in nutrient flux that conserve mass balance. Although neither of these process guidance examples constrains or penalizes parameter complexity directly, both indirectly limit the range of parameter values that the trained model is likely to include.

Reducing overfitting by collecting more observational training data is only sometimes an option in limnological modeling, despite major data-compilation initiatives (e.g., Soranno et al., 2017) and the continual expansion of public monitoring and remote-sensing datasets (e.g., Read et al., 2017; Topp et al., 2020). Fortunately, limnological expertise can be used to sensibly augment the training dataset, making up with quantity what is lacking in quality in the augmenting information. For example, when remote-sensing-based estimates of a variable can be used to complement in situ measurements, these two data sources can be assigned different weights, reflecting their known information quality, in the loss function that guides model training. Another effective approach is to embed information from the lower-quality, higher-volume data into a pretrained model, which can then be finetuned (i.e., trained further) with the high-quality data. For example, Kaya et al. (2019) finetuned a generic neural network image classification model, which had been pretrained on images of all kinds, to classify plant species. Synthetic data are also sometimes an option for pretraining or training a useful model; for example, synthetic images with realistic features and background can be used, or a model of depth to groundwater might be trained on synthetic observations of depth = 0 at the margins of streams and lakes. Similarly, Read et al. (2019) first pretrained a neural network on process-based model predictions of lake temperatures, then finetuned the model on in situ temperature observations. A distinct advantage of pretraining on process-based model outputs is that the ML model can learn from predictions for input conditions that have never yet been observed, allowing the ML model to learn from the process-based model about how to extrapolate to those new conditions in limnologically realistic ways.

Applications

Quality control

Raw data inevitably contain measurement error, whether due to human mistakes, sensor malfunctions, or environmental interference. Previously, human inspection was used to flag errant data, but today's larger and always-growing datasets can only feasibly be processed with automation. A major challenge in quality control (QC) is in distinguishing between errant measurements (e.g., biofouling of a sensor; sun flecks interfering with a remote sensing measurement) and surprising realities (e.g., an extreme algal bloom or sediment transport event), a task that ML models can perform either with no human intervention (for easier problems) or by directing human attention to the ambiguous cases (for harder ones). The line between "easy" and "hard" continues to shift as ML techniques improve, training datasets grow, and theory develops to guide QC targets.

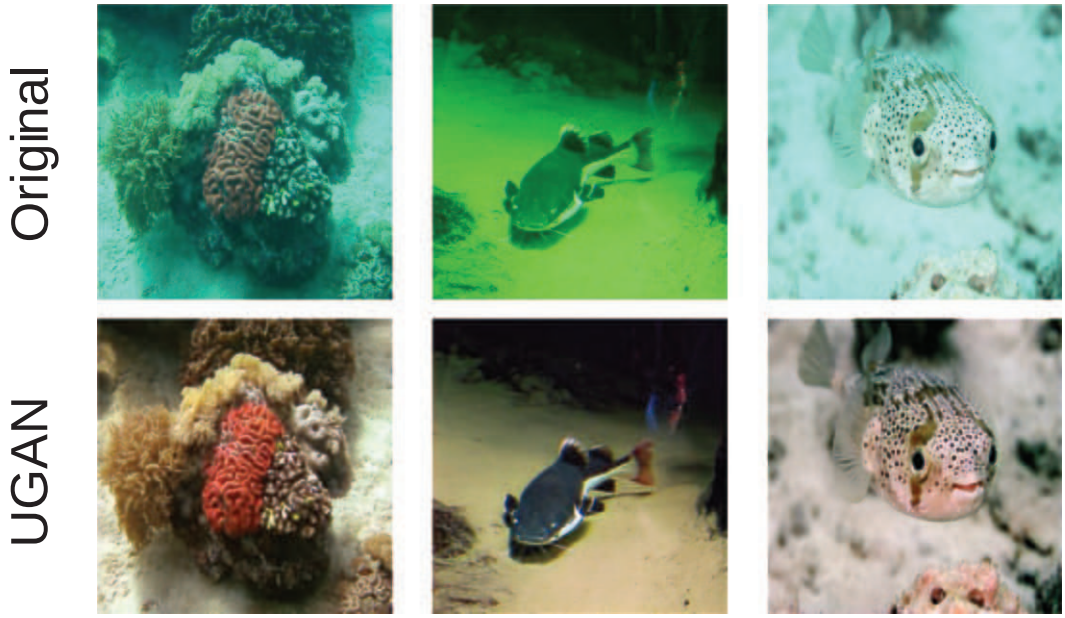

Fig. 6 Original distorted underwater images (top row) and images corrected with an underwater generative adversarial network (UGAN, bottom row). Modified from Fabbri C, Islam MJ, and Sattar J (2018) Enhancing underwater imagery using generative adversarial networks. In *Proceedings—IEEE International Conference on Robotics and Automation*. pp. 7159–7165. IEEE: Brisbane, QLD, doi: 10.1109/ICRA.2018.8460552.

ML methods for detecting data abnormalities primarily follow prediction or distillation pathways and can use a wide variety of model architectures. Supervised prediction methods can be used to predict ("reconstruct") clean datasets with fewer errant measurements. Both random forests and neural networks have been used for this purpose. Autoencoder neural networks are especially suitable because observational outliers are relatively incompressible and are thus greatly altered when the autoencoder compresses and then re-predicts the inputs (Zhou and Paffenroth, 2017). Generative adversarial networks can be used for the same purpose (e.g., for removing distortion from underwater images: Fabbri et al., 2018) (Fig. 6). As an alternative to prediction of clean data, categorical classification and clustering methods can classify data into regimes to enable algorithmic correction for some regimes and targeted expert intervention for others: Supervised classification can group data into modeler-determined regimes such as "clean," "common error pattern," and "needs inspection," while unsupervised clustering can assign data to algorithm-determined groups that the modeler can triage afterward. Both ML and non-ML approaches have been widely used to detect data abnormalities; see Pimentel et al. (2014) for a broad review and Kiran et al. (2018) for tools specific to video and imagery.

Preprocessing data for further modeling

Modern limnological models often ingest complex datasets: imagery from satellites, drones, cameras, or underwater videos, high-frequency observations from mobile or stationary sensors, and multidimensional inputs from rich public databases. Although ML promises a reduced need to simplify the features before building the model (because many ML models can filter the features themselves), this promise is not made for process-based or most statistical models, and in practice even ML models often show improved performance when given inputs that are already distilled to their most informative elements. Fortunately, specialized ML models for preprocessing can provide the link between complex raw datasets and data designed to be used by other models for inputs, training, or testing.

Preprocessor ML models can make use of prediction, inference, and/or distillation to extract information from raw data, reduce dataset complexity, and combine multiple datasets. For example, convolutional neural networks (CNNs) can learn to emulate human interpretations of images, enabling automation of labor-intensive tasks such as identifying fish species from underwater photographs (dos Santos and Gonçalves, 2019), classifying phytoplankton in flow cytometry images (Dunker et al., 2018) (Fig. 7), or estimating flood heights from social media images (Chaudhary et al., 2019). Alternatively, ML models can generate their own rules for data distillation, reducing an extensive time series to a smaller set of information-rich features (CNNs for soil moisture prediction: Feng et al., 2020) or identifying smaller, and thus more interpretable, sets of predictors (self-organizing maps for river salinity predictors: Bowden et al., 2005; feature selection for groundwater nitrate predictors: Rodriguez-Galiano et al., 2018). Some distillation activities make rare use of inference on ML models, learning values of ML parameters that have no *a-priori* meaning to humans but are identified as important by the distilling ML model and can be used effectively by subsequent ML models; for example, Peleato et al. (2018) used the values in the most-compressed layer of an autoencoder as the distillation of results of a multivariate water quality assay. Yet another approach to preprocessing combines multiple datasets in space, either interpolating

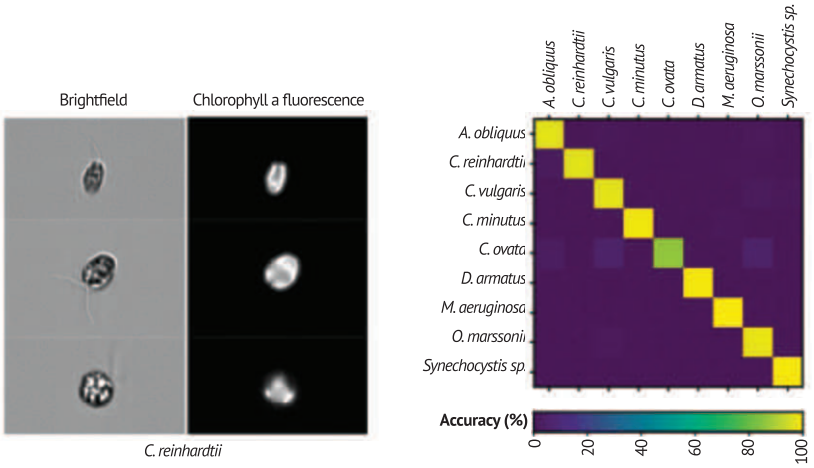

Fig. 7 CNN classifiers can be used to identify phytoplankton species from flow-cytometry images (examples in left panel). In the confusion matrix plot (right panel), rows give the true species, columns give the predicted species, and color indicates the percentage of images in each row that the model assigned to that column, such that a fully yellow diagonal and purple background would indicate perfect accuracy. Modified from Dunker S et al. (2018) Combining high-throughput imaging flow cytometry and deep learning for efficient species and life-cycle stage identification of phytoplankton. *BMC Ecology*, 18(1): 51, doi: 10.1186/s12898-018-0209-5.

from observed to unobserved locations (with random forest prediction: Mital et al., 2020) or combining spatial datasets of varying resolution to downscale a coarse data layer to finer resolution for subsequent modeling (with CNNs: Baño-Medina et al., 2020).

As with other applications, ML models for preprocessing can benefit from injection of limnological design. For example, fish species identification was more accurate when a CNN was trained to predict fish family and order as well as species (dos Santos and Gonçalves, 2019), and distinguishing between land and water pixels in a remote sensing image was more accurate when the classification was tied to estimated bathymetry such that deeper pixels were labeled "water" before shallower pixels (Khandelwal et al., 2016).

Exploring hypotheses

One common modeling goal is to gain insight about the drivers and processes underlying an observed pattern or prediction. With ML models, such insight is often obtained by post-hoc model interpretation techniques, although the use of ML to estimate parameters (next section) can be a complementary way to learn about drivers. ML models are well suited to explore poorly understood relationships between input features and predictions because they are typically robust to high dimensionality and redundant features, and they can capture feature-prediction relationships of any shape. ML interpretation techniques are valuable for generating hypotheses and confronting them with the available data (sometimes even employing formal causal reasoning, e.g., Nauta et al., 2019), thus nudging the field toward understanding of the many complex and hard-to-measure processes in inland waters. Hypotheses generated with ML may even be treated as prior beliefs to be merged quantitatively with the results of other experiments with data or process-based models (Tsai et al., 2020a).

Feature interpretation methods are often used to quantify the importance and effect shapes of features for a wide range of limnological response variables. For example, Worland et al. (2018) used feature importance (FI) to identify primary drivers of annual low stream flows, then used partial dependence plots (PDPs) to visualize the shapes of the effects of each primary driver. Similar approaches have been used to assess the relationships between newly proposed hydrologic metrics and depth to water table (Belitz et al., 2019); regional-to-local lake properties and water quality (Read et al., 2015); and potential drivers of groundwater nitrate concentrations (Ransom et al., 2017), fish reproductive success (Buston and Elith, 2011), and fish species richness (Franceschini et al., 2019). The shapes of relationships in PDPs have also been used to suggest thresholds in stream and watershed disturbance that trigger regime shifts in stream temperatures (Hill et al., 2013).

Neural-network-specific interpretation methods are not yet widely used in studies of water quality or ecology but have been recently embraced in the physical geosciences. Kratzert et al. (2019a) discovered memory nodes in a recurrent neural network whose states correlated over time with water storage states from a process-based hydrologic model; they then used Integrated Gradients to confirm that a node correlated with snow water equivalent was influenced by precipitation and minimum air temperature in early winter, a finding consistent with theory. Barnes et al. (2020) used Layerwise Relevance Propagation to identify those regions of global temperature and precipitation maps that were used by a neural network to predict the year of the maps, i.e., those regions that distinguished the climate in that year from other years (Fig. 8). Identifying the variables, times, and locations that a neural network is relying on for a prediction allows researchers to check for consistency with theory, explain errors, and examine the identified information for additional insights.

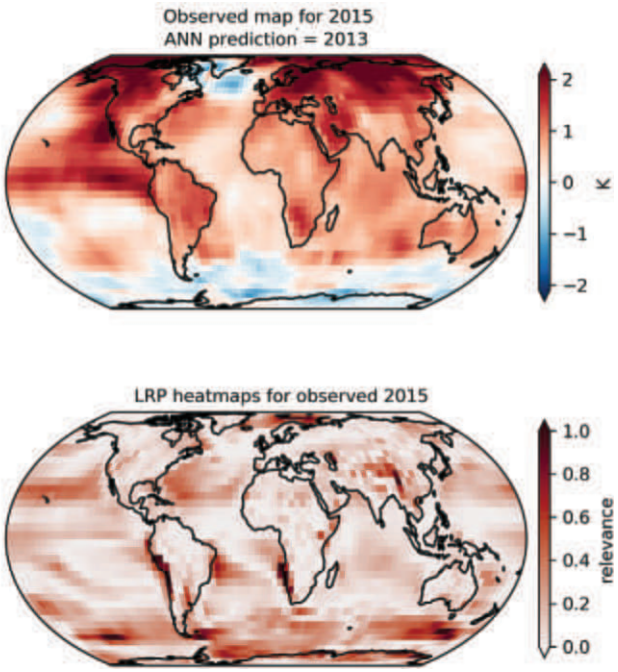

Fig. 8 Layerwise Relevance Propagation (LRP) can be used to propose regions of the globe where air temperature signals are most indicative of the year of an air temperature map. Top: temperature anomalies in 2015 relative to 1979–2099. Bottom: LRP heatmaps show the relevance of each input grid cell to the model's prediction that the map is from 2013, permitting exploration of features that are similar between 2013 and 2015 and different from other years. Modified from Barnes EA et al. (2020) Indicator patterns of forced change learned by an artificial neural network. *Journal of Advances in Modeling Earth Systems* 12(9), doi: 10.1029/2020MS002195, Fig. 10.

Estimating parameters and states

As a way of developing process understanding, modelers often work to refine qualitative descriptions of patterns into process-based or semi-empirical equations that describe relationships among inputs, outputs, and internally represented states. Further process understanding then takes the form of estimated values of the parameters or states used in those equations. ML models can assist in this estimation of parameters and states (collectively termed "variables" in this subsection). However, in contrast to the designed variables of process-based models, ML variables typically lack connection to known process equations, such that ML modelers have turned to creative techniques, either estimating the variables of process-based models or developing process-guided ML models that contain some interpretable variables.

One approach to the use of ML for parameter estimation is to train an ML model to emulate a process-based model, leveraging the quick prediction times of ML models to explore parameter space more rapidly. For example, Gong et al. (2015) experimented with random forests and neural networks as surrogates for a computationally expensive land surface model. They then used the surrogates in a parameter optimization algorithm to find suitable values of soil porosity and other parameters.

As an alternative to emulating a process model, an ML model can also be used to directly predict the values of variables within the process model. For example, Sun (2018) trained a generative adversarial network to predict a map of groundwater hydraulic heads from a map of aquifer hydraulic conductivities or vice versa, where hydraulic heads are more often observed (albeit sparsely) and hydraulic conductivities have historically been solved by inversion of a process-based model, i.e., running that model repeatedly with different conductivities until the predicted hydraulic heads match observations (Fig. 9). ML can also be used to develop transfer functions, i.e., functions that ingest widely measurable predictor variables and output parameter estimates. For mapping river basin characteristics (e.g., soil properties) to hydrologic model parameters (e.g., infiltration curve parameters), Feigl et al. (2020) used a text-generating autoencoder to discover the equation forms and coefficient values of transfer functions, and Tsai et al. (2020b) trained a recurrent neural network to itself act as a transfer function.

Lastly, although the approach is not yet common, ML training strategies and structures can be designed to encourage meaning in otherwise "black-box" states or parameters. For example, Jia et al. (2021) pretrained intermediate states of a neural network on the predictions of streamflow and water temperature from a process-based model, such that the final ML state predictions encoded estimates of these process-relevant state variables.

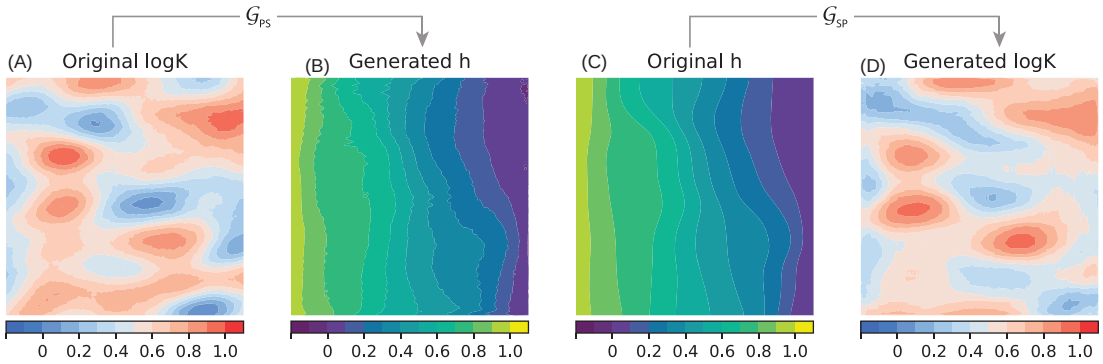

Fig. 9 Example of a generative adversarial network used to predict model parameters and states. There are two competing models in this example: one to predict groundwater hydraulic head states (B) from a set of hydraulic conductivity parameters (A), and one to do the opposite (C and D). Modified from Sun AY (2018) Discovering state-parameter mappings in subsurface models using generative adversarial networks. *Geophysical Research Letters*, 45(20): 11137–11146, doi: 10.1029/2018GL080404. Fig. 2.

Predicting, forecasting, and projecting

ML models are capable of highly accurate predictions and thus have been applied extensively to prediction challenges for inland waters (Maier and Dandy, 2000; Maier et al., 2010). Accurate predictions can fill knowledge gaps in space or time, facilitate scientific hypothesis generation, and support water resources decision-making. An example need for spatial gap filling is that lake water temperature models must usually be trained on a lake-by-lake basis using local observations but would ideally be leveraged for unobserved lakes. Willard et al. (2021) developed a gradient boosting regression model that uses lake features to select a trained lake model to use in predicting temperatures in a new, unobserved lake. For filling gaps in time, Toth and Brath (2007) and Kratzert et al. (2019b) have shown that NNs can predict streamflow with comparable or better accuracy than calibrated process-based models. ML models also excel at capturing nonlinear dynamics, which can be useful in identifying threshold responses; Hansen et al. (2017) fit random forest models of fish abundance and used the resulting nonlinear partial dependence plots to project how fish habitat would change under future climate scenarios (Fig. 10).

In addition to their accuracy, trained ML models also offer relatively fast prediction runtimes, making them efficient choices for generating predictions over large spatial or temporal extents or in real time, for robust uncertainty estimation via large ensembles of predictions, or for decision support applications that explore many potential scenarios. For example, Nolan et al. (2012) used an ML model to emulate a process-based model of the unsaturated zone to predict nitrate losses from agricultural fields throughout a large region of the United States. Fienen et al. (2013) used a Bayesian network model to emulate a large-scale groundwater model for adaptive management on an island threatened by sea level rise. The faster emulator allowed for uncertainty estimation and scenario testing for predicting depth to water table, a metric related to plover foraging habitat and access to freshwater for wild horses.

One concern for prediction using ML models is that they are data hungry and may not generalize well to new inputs such as climate scenarios that have never existed in the past. Incorporation of limnological knowledge can improve prediction accuracy and help ML models earn trust. For example, Franceschini et al. (2019) used knowledge of fish species interactions to develop an NN model that more accurately predicted the occurrence probabilities of a target fish species by including two meaningful intermediate variables, the occurrence probabilities of two secondary fish species. Noori et al. (2020) passed outputs from a process-based water quality model into an ANN to achieve more accurate predictions of riverine nutrient loads in and around Atlanta, Georgia. Read et al. (2019) showed that lake temperature models pretrained with a process-based model, and incorporating physical laws in the loss function, significantly improved performance of an RNN even under sparse data conditions. Recent work has explored real-time data integration into ML models to overcome data sparsity and noise issues and improve near-term forecasts of water resources such as streamflow (Feng et al., 2020).

Summarizing research results

In this age of sensors and powerful computers, it is common for observations and even model outputs to be too detailed for direct human interpretation. ML models can be used to impartially reduce a multidimensional result to two dimensions that can be visualized on a screen or printed page. Autoencoder neural networks are a potentially powerful tool for this application, as evidenced by their usefulness in distilling multivariate or timeseries data during preprocessing (see above), although we have yet to find examples of their use in interpreting water resources research results. Self-organizing maps have been used to summarize the multidimensional relationship between particle size and fluorescence properties in river water feeding to the largest freshwater lake in China (Yan et al., 2018) and to compress aquatic insect (chironomid) community data to a two-dimensional map that enabled (1) further clustering into three general community types and (2) comparison with concentrations of chemical stressors (Milošević et al., 2018).

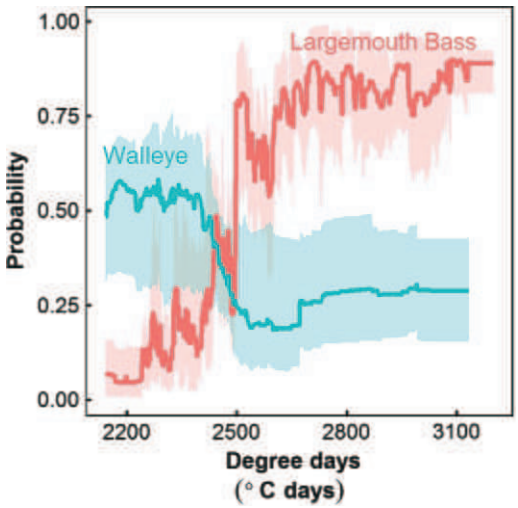

Fig. 10 Random-forest-based partial dependence plot showing the nonlinear relationships between mean lake temperature degree days (horizontal axis) and the probability of walleye (*Sander vitreus*) recruitment or high largemouth bass (*Micropterus salmoides*) abundance (vertical axis). In this plot, solid lines are median responses and ribbons are 25th–75th percentile responses to the degree day value across all possible combinations of the other predictors (lake area, conductivity, and shoreline complexity for walleye; lake order and Secchi depth for largemouth bass). From Hansen GJA et al. (2017) Projected shifts in fish species dominance in Wisconsin lakes under climate change. *Global Change Biology*, 23(4): 1463–1476, doi: 10.1111/gcb.13462. Fig. 1.

We have long organized our understanding into categories such as biomes, aquifer types, aquatic trophic classes, and lake stratification regimes, but the use of discovery rather than design to identify such states has the potential to hasten the development of new intuitions about how to make sense of inland waters and their drivers. For example, Pacheco et al. (2017) used a self-organizing map followed by U-matrix clustering to reduce continuous values in seven water quality dimensions down to six categorical clusters of water quality regimes observed along the Paraíba do Sul River in Brazil, which they then were able to tie to geographic location and local land use (Fig. 11). Savoy et al. (2019) used dynamic time warping to quantify the similarity between pairs of time series of photosynthesis rates in 47 rivers and then used hierarchical agglomerative clustering to identify four common patterns in the annual onset, peak, and decline of photosynthesis. Labels such as "Spring Peak River" or even just "Cluster 6" enable conceptual discussions that would otherwise be mired in numbers.

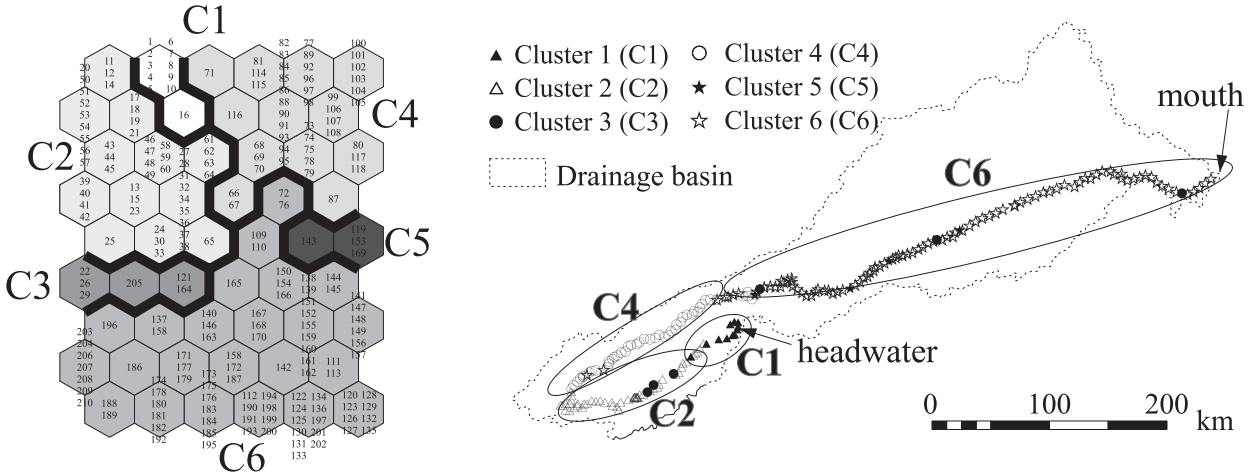

Fig. 11 Example of using a self-organizing map (SOM) to reduce seven continuous water quality parameters to six categorical water quality regimes. Left: Codes in the SOM honeycomb correspond to sampling sites where the number 1 represents the river source, and 210 the river mouth. Right: Map of the catchment and main river channel show the six clusters of the 210 sampling sites. Modified from Pacheco FS et al. (2017) Water quality longitudinal profile of the Paraíba do Sul River, Brazil during an extreme drought event. *Limnology and Oceanography*, 62(S1): S131–S146, doi: 10.1002/lno.10586. Fig. 2A–C.

Conclusion

Water quantity and quality models are central to an increasing number of policy and regulatory decisions, and deliberate selection of the best available ML, process-based, or statistical modeling approaches will be critical to address environmental problems and advance scientific understanding. As described in this chapter, shortcomings of ML models exist but are often overstated and similar to limitations of other approaches. Recognition of ML's value is reflected in the growing proportion of inland waters publications that mention one or more of the tools described in this chapter, although that proportion is still small and indicates room for continued growth (Fig. 12, left panel). Additionally, new research to inject limnological design into ML models is improving predictions and uncovering insights with fewer drawbacks, leading to the rapid recent growth in design-infused ML applications in inland waters and many other domains (Fig. 12, right panels).

The undeniable benefits of ML are creating opportunities for innovation in new dimensions of the aquatic sciences, including assembly and publication of datasets for benchmarking and training, versioned release of model codes for extension and reuse, and model development via interdisciplinary collaborations with computer scientists and technologists. There are also opportunities at the institutional level, where research incentives and resources could be better aligned with the pursuit of machine learning applications and innovation. Given the complementary nature of process-based, statistical, and machine learning modeling, the aquatic sciences are sure to gain by embracing ML models as one set of valuable tools for prediction, inference, and distillation.

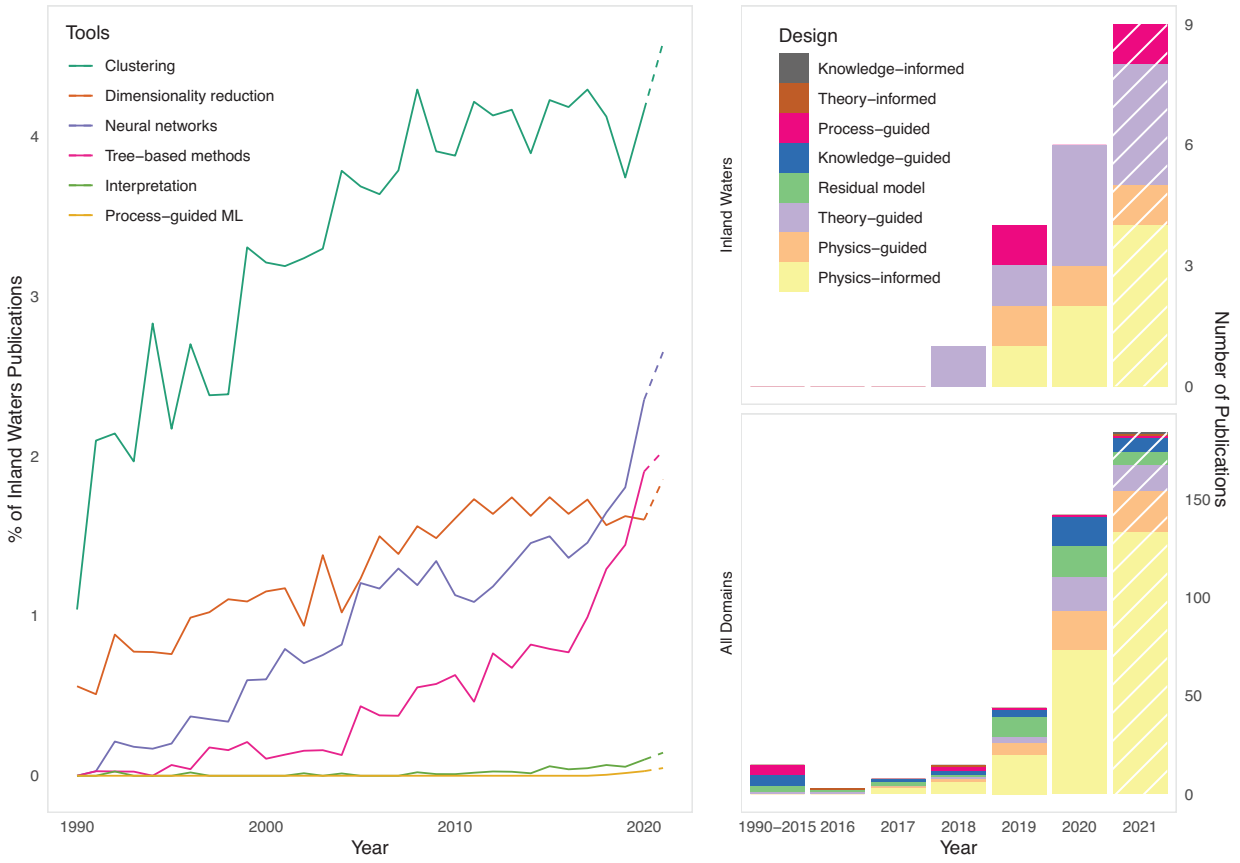

Fig. 12 Publication counts from Web of Science queries for inland waters publications mentioning one of the major tools described in this chapter (left panel) and machine learning (ML) with knowledge-guided design (right panels) for inland waters (top) or all domains (bottom). All major ML tools described in this chapter have become more popular over time, with neural networks, tree-based methods, interpretation, and knowledge-guided machine learning showing the most rapid recent growth. 2021 counts (dotted lines and striped bars) were queried September 5, 2021; counts were multiplied by 365/248 to project the 2021 totals in the left panel and left unmodified in the right panels. Methods in the keys are ordered vertically in the same order as they appear in the figure panels. Exact search terms included many specific approaches within each Tools category (left panel) and required some mention of ML or neural networks along with the text in the Design legend (right panels). Researchers have not yet settled on a consistent term for designed machine learning, hence the diversity of terms in the right panels; "hybrid" yielded many query results but was excluded because it ambiguously describes several methodological and biological concepts. Data from Web of Science, provided by Clarivate.

Knowledge gaps

- Additional core aquatic datasets and baseline performance metrics would support development and comparison of different model architectures, including process-based, statistical, and ML.
- The limnology community would benefit from a general understanding of the conditions under which ML models and process-based models are reliable for extrapolation.
- Establishing common patterns or practices for extracting interpretive insights from ML models would improve model trust and contribute to greater understanding of inland waters.
- Methods to integrate different data types (e.g., single-point data, continuous data, multi-dimensional data, and remotely sensed data) into ML models could improve accuracy and utility.
- Infusion of process knowledge into ML models is a concept in its research infancy, with much left to discover about techniques, potential and limitations, and best practices.
- The limnology community would benefit from a taxonomy by which researchers can communicate the mechanisms and extent to which approaches integrate limnological theory into ML models.
- In contrast to physical processes, biogeochemical and ecological processes can seldom be described with exact equations, such that new techniques may be needed to integrate empirical knowledge about those processes into ML models.

Acknowledgments

Ellen Bechtel transformed rough drafts of the conceptual figures into the polished diagrams we are proud to share here. Critiques by Matt Ross, Phillip Goodling, and Kendra Cheruvelil greatly improved the style and clarity of the text.

See Also: Fundamental concepts and theories: Eco-Evolutionary Dynamics in Freshwater Systems; Models of Animal Distributions in Inland Waters; Populations in Inland Waters; Regime Shifts and Tipping Points; Structures and functions of Inland Waters - Groundwater: "Importance of the Micro-scale for the Macro-scale—What Can We Learn From Groundwater Ecosystems?"; Structures and functions of Inland Waters - Rivers: Dispersal in Stream Networks: Meta-populations and Meta-communities

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Teams, Networks, and Networks of Networks Advancing Our Understanding and Conservation of Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Hydrologic network Interconnected bodies of water, waterways, and stores of water that comprise the hydrologic cycle.
Network of networks A collection of two or more unique networks, each defined by social, geographic, and temporal boundaries and distinct types of connections (e.g., governance, data gathering, information sharing).
Network A group or system of interconnected people or things (adapted from Oxford Language).
Science of team science The study of the processes by which science teams form, behave, communicate, and carry out scientific research.
Social network analysis Mathematical methods used to characterize the structure of networks in terms of edges (connections) and nodes (social actors such as individuals or organizations).
Social network The self-organizing webs of social actors (individuals, groups, or formal organizations) and the relational connections that bind them. In this article, social (human) networks are defined as groups with 12 or more people. Used interchangeably with "network."
Team science Science that is conducted in a collaborative, interdependent manner among individuals with a wide range of backgrounds, skills, and expertise.
Team A group of 3–11 people who interact and influence each other, are mutually accountable for achieving common goals, and perceive themselves as a social entity (adapted from McShane and Von Glinow, 2010).

Introduction and aim

As scientists across the world are working together to answer complex biological and ecological questions, they are forming larger and larger teams. Often, *teams* and *networks* are used interchangeably, but they are fundamentally unique ideas. Distinguishing between the two can help us understand how to improve the performance of increasingly large and complex scientific efforts. In ecological sciences, networks are used to describe more than large teams: a network is "a group or system of interconnected people or things" (Oxford Language Network, 2021). By this definition, inland waters research, management, and conservation is

inherently network-based (Fig. 1), from waterways themselves, to the teams of scientists conducting research, to the policies governing water management. Streams, lakes, wetlands, and groundwater are connected by a network of flowing water as *hydrologic networks*. Human-built infrastructure including drinking water distribution, sewerages, and stormwater management are connected via networks of engineered structures and built infrastructure. Human (social) networks monitor, research, and manage the infrastructure and hydrologic networks. And finally, governance of watersheds, municipalities, states, and nations affect the management function of each of the prior networks (and vice versa).

Consider the Great Lakes basin as a specific example of the network-based aspect of inland waters. Lakes Superior, Michigan, Huron, Erie, and Ontario are connected by a series of waterways including Saint Mary's River, Straits of Mackinac, Niagara River, etc. Built infrastructure such as locks, canals, and water diversions and returns for human use, are distributed across the watershed. Teams at institutions such as Michigan Technological University or the National Oceanic and Atmospheric Administration monitor and research the Great Lakes and connected waterways, and share information through networks such as the Great Lakes Observing System (www.glos.us). Management of the lakes is governed by policy set at the regional, national, or sometimes inter-governmental level. From hydrology to governance, the Great Lakes basin is made up of interacting networks.

Inland waters are inherently *networked*—and the human groups that research and manage them likewise reflect the same network structure. Therefore, these human networks have a particular opportunity to benefit from the understanding of social networks in human collaboration to achieve a goal. Understanding the effective functioning of teams and networks in inland water science will enable the more effective flow of information, resources, coordination, and knowledge creation necessary to address increasingly complex water resources challenges. This article explores the role of teams, networks, and networks of networks in the science of inland waters. Definitions and methods for the development and evaluation of these entities are provided. Case studies from inland waters science are used to illustrate real-world application.

This article sets out to address how to build and maintain *human* networks that can facilitate effective connections between people, knowledge, and data. In recent years, the evidence-based design of collaborative networks and teams in ecological science has increased (Cheruvelil and Soranno, 2018), and the potential effect of this on inland waters is especially great because of the highly networked aspect of inland waters research, management, and conservation. This knowledge must be leveraged to achieve research aims and advancements that would be impossible without crossing disciplinary and institutional boundaries (Fagan et al., 2018).

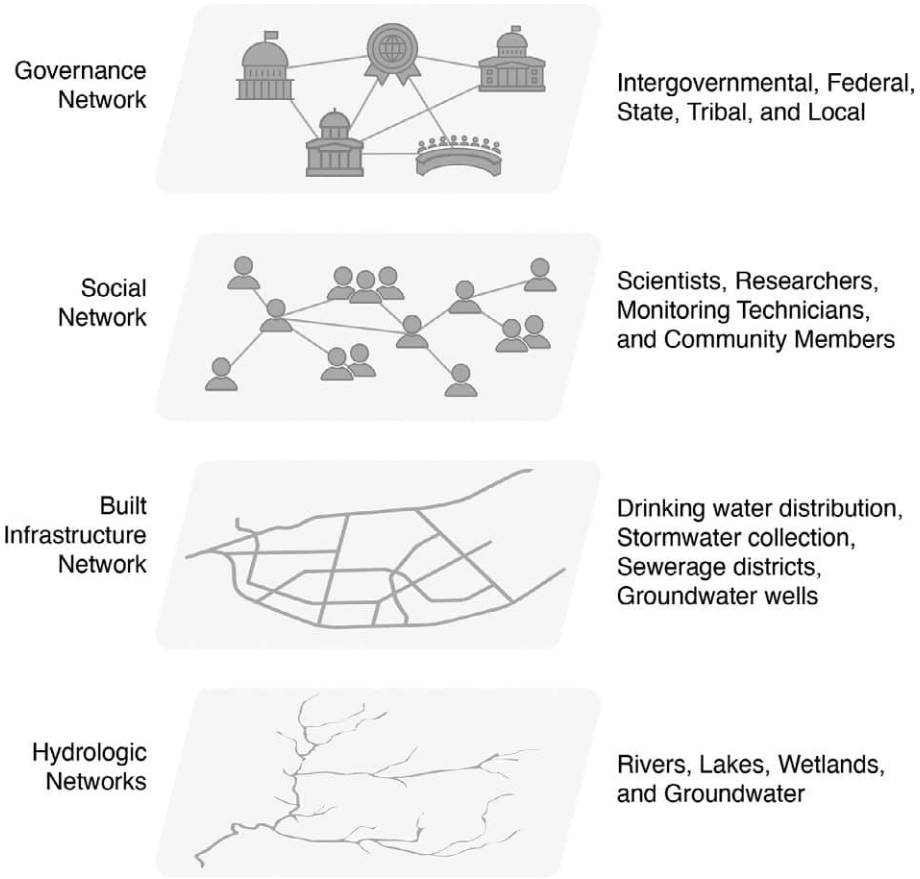


Fig. 1 Network aspects of water, built infrastructure, human (social) networks, and governance networks that relate to them.

The basics of teams, networks, and networks of networks

Before a discussion of the formation, maintenance, and attributes of teams, networks, and networks of networks, it is useful to briefly define these entities and the relationships between them.

Readers will be familiar with the concept of a *team*: a group of people who interact and influence each other, are mutually accountable for achieving common goals, and perceive themselves as a social entity (adapted from McShane and Von Glinow, 2010). In this article, a team is defined as a group of more than 2 and less than approximately 12 people (Box 1). Teams have long been used in the pursuit of science. The *science of team science*-the study of how science teams form and operate-has come out of two primary fields: organizational psychology and translational medicine. The science of team science has been an area of investment and active research since the late 1990s (Stokols et al., 2008; Hall et al., 2018). Although theories and knowledge of teams have developed in parallel in these fields, they agree on this: trust, communication, data and resource sharing, accountability, and cooperation are essential to reaching shared goals.

This article considers networks generally (e.g., interconnected waterways or coordinated data collection systems), but focuses most on *social networks,* within which humans or organizations are connected. Social networks are the self-organizing webs of social actors (individuals, groups, or formal organizations) and the relational connections that bind them. Although the structure of social networks has long been studied by the fields of anthropology and sociology, recent advances in computing have made it possible to study complex social networks in increasing detail and led to the development of more specialized sub-fields and breadth of fields using network analytic methods. Network analysis can be used to measure the formation, structure, performance, and resilience of networks of networks through time (Wang, 2016; Hall et al., 2018).

In practice, entire networks can make connections with other networks by forming new and beneficial connections between individuals across networks. This results in a network of networks, or a collection of two or more unique networks, each defined by social, geographic, and temporal boundaries and distinct types of connections.

Hereafter, teams, networks, and networks of networks are considered entities along a continuum of size (number of individual actors) and structural complexity (connections relating individuals). The value of the relationships between people is determined by the alignment of the connections with the objectives of the team, network, or network of networks.

Teams

What is a team?

Many drivers of change in inland waters-climate warming, pollution, hydrologic modification, and restoration-are large, complex, and interconnected; thus, responding to these changes requires broad interdisciplinary expertise. At the same time, advances in technology and data collection, compilation, and harmonization have given us more information about water than ever before (Cheruvelil and Soranno, 2018). These facts have contributed to the rise of *team science* in limnology-science that is conducted in a collaborative, interdependent manner among individuals with a wide range of backgrounds, skills, and expertise.

The potential for transformative science is maximized in research teams where individuals from different domains integrate their collective knowledge into new ideas and methods that go beyond those of an individual discipline (Stokols et al., 2008). The need for innovation across disciplines and the rise in team science is reflected by the increased funding of multi-principal investigator proposals for centers and research that are inter- or trans-disciplinary (National Science Foundation, 2013).

Sharing and integrating information across disciplines requires an environment of learning, and openness to learning requires trust (Tebes et al., 2014; Salazar et al., 2012). Successful and sustainable teams, therefore, are those teams that foster psychological safety–the shared belief among team members that interpersonal risk (e.g., proposing novel or risky ideas, asking clarifying questions, expressing lack of knowledge) will not come at a price (Edmondson, 1999). Psychological safety and trust are essential for team members to maintain the ability to interact and influence one another, to practice accountability, and to feel a part of a social entity.

Defining a successful scientific team is somewhat elusive, as the number of publications or citations are not holistic measures of success; success includes the effects on *science* and the *individual.* Morale and commitment to the team are additional ways to measure success; team members with high morale are committed to the cause and willing to do the work necessary for successful outcomes (He, 2012). Below are suggestions for how to foster these characteristics in your own science teams.

Methods for effective teams

Trust is the foundation of successful social connections (i.e., human relationships) that foster creativity, information exchange, and scientific advancements. Teams can intentionally build trust over time by creating shared experiences and by offering training in the interpersonal skills required to create positive relationships. Hierarchical relationships are inherent in many science teams, but activities that foster empathy or demonstrate diverse abilities and communication styles can build psychological safety among members with different amounts of power.

The ability of teams to perform a variety of tasks is not related to the maximum or mean individual intelligence, but rather on features like social intelligence (Woolley et al., 2010). Emotional intelligence or social sensitivity can be built through open discussions and recognition of differences in personalities, philosophies, backgrounds (Cheruvelil et al., 2014), and by practicing

Box 1 What differentiates a team from a network?

Everything from a tight-knit group of five scientists to a large, multi-institutional collaboration with hundreds of contributors might be called either a "team" or a "network." We want to distinguish between the two terms and focus our discussion on how viewing large teams as networks can help improve their management and development. All teams can be characterized as a network, but many networks are not teams because they may or may not be striving for a common goal, may not have a shared identity, and the boundaries of membership are less clearly defined. Because of a diversity of meanings and cultural context for the terms "team" and "network," it is important to technically define and distinguish between a team and a network.

Small groups, something less than 12 people, have the advantage of being able to more easily keep all members engaged, maintain communication between all members, and create clear roles and responsibilities for members.

Small work groups (teams) have the maximum number of connections per actor. Every actor has a connection to all other actors. This makes them unique networks because all nodes connect directly to each other.

The ideal size for a work team is 5–7 people because as teams get larger, they require more complex coordination and are more likely to become less productive because of social loafing (Forsyth, 2009). As small groups grow, dynamics begin to shift, and once teams get beyond 5–7, they often break into sub-teams of 3–6 members. As teams grow beyond half a dozen or so, they start to display new patterns, where members begin to work more closely with some members than others, have less frequent communication with the entire group, and have more complex work plans. It is at this stage that the concept of a network and the application of social network analysis to understand structure and function become useful.

Larger work groups (networks) have variation in the number of connections per actor. Actors have connections with one to five other actors. Darker shaded nodes indicates higher degree (number of connections with other nodes).

As the complexity of inland waters science grows, so too does the size and complexity of the groups needed to address them. With greater group size, network patterns begin to appear. In the networks that take on complex projects, much of the actual work tends to get accomplished in smaller work groups (or teams). Even though the social entity is a large network, the work group is likely to be a small team of 3–6 people where all members know each other, interact frequently, and have a well-defined scope of work in which each member has clear roles and responsibilities. The team or work group is a building block of the larger network structure.

Although the threshold at which a group transitions from a team to a network will vary, in this article a specific threshold is given. We distinguish and define *teams as groups of fewer than approximately 12 people and networks as groups of approximately 12 or more people* because increasing group size reduces the ability of individual members to interact with, influence, and hold accountable every other member, and to perceive belonging to the group.

reflexivity through sharing personal experiences and perceptions (Read et al., 2016). Allowing time to build personal connections and interpersonal skills will motivate commitment to the team and foster trust that all members are working toward the success of the team.

Box 2 Social network analysis.

Social network analysis uses mathematical methods to characterize the structure of networks in terms of edges (connections) and nodes (social actors, such as individuals or organizations). Network analysis is also referred to as graph theory (Wasserman and Faust, 1994).

A group of any size greater than three can be analyzed according to the methods below; however, we make a case in this article that more meaningful distinctions in network structure begin to appear when the number of actors in the group exceeds approximately 12.

Average Degree: In any network, degree is the number of edges (connections) that exist for a node (actor). The average degree describes the network as the average number of edges per node, or connections per actor, in the network. Higher levels of average degree are associated with more robust networks (Martin and Niemeyer, 2020).

Centralization: Networks that have a few actors with very high degree (many connections), while most of the network has actors with low degree (few connections), are described as having high centralization. These types of network graphs have a star-like structural pattern.

Closure: One common trait of networks is whether, in any triad, all three possible connections exist (a closed triad). Closure measures the proportion of all closed triads present as compared to all potential closed triads.

Degree Distribution: The degree distribution refers to whether connections among actors are evenly spread across actors in the full network, or whether some actors have very high degree (many connections) while others have very low degree (few connections).

Density: The proportion of connections that exist in a network to all possible connections that could theoretically exist. Smaller networks generally have higher density than larger networks.

Reciprocity: The likelihood of mutuality, or bi-directional, positive actions within a social network. When positive actions occur in both directions between two actors. Reciprocity is an important factor in building and strengthening sustained social connections.

Although diversity in the experiences and information each member brings to the team can foster creativity and interactions among group members that boost team performance (Hoever et al., 2012), diversity in values can create conflict and division of team members that creates an environment of distrust and low team performance (Jehn et al., 1999). Successful teams are both diverse and socially sensitive enough to manage their own diversity. Consider and make efforts to balance diversity in career stage, member incumbency (60–70% incumbent), domain expertise (>1 person per domain), communication mode, and viewpoints (Cheruvelil et al., 2014).

To feel invested in a team, members must have a shared understanding of team purpose and goals, and how they directly contribute to success (Bennett et al., 2018). Successful execution of science by a team depends on clear roles and responsibilities, management of tasks, and a means of accountability. The approaches used to manage and accomplish work can vary greatly within and across disciplines and cultures, and guidance for collaborative scientific management approaches have been defined (e.g., collaborative manuscript management sensu Oliver et al., 2018). The management approach selected will in turn influence how roles and responsibilities are assigned and tracked, which is essential for an accountability.

Effective communication allows the sharing and building of knowledge and trust, but can be difficult to establish and maintain, especially in new teams. Establishing communication includes establishing group norms (e.g., taking turns in group discussion and normalizing disagreement); effective meeting logistics that support all members seeing and hearing one another clearly; and the use of break-out groups to increase participation and engagement. Effective communication also includes having difficult discussions, and which can be enhanced by practicing skills related to recognizing and managing conflict (Read et al., 2016). The combination of shared expectations, optimizing the meeting logistics, and training in facilitation or conflict resolution all support effective communication and increase the likelihood of success of science teams.

Team science in inland water research

The need for team science in inland waters research is becoming more prevalent given an increasing number of disparate data sources, expanding spatial and temporal scales of interest, and new cross-scale and cross-system integrative approaches. Likewise, team science as an explicit research focus within limnology is also growing increasingly common.

Within the lake-centric part of limnology, the science of team science is being practiced and contributed to through graduate student training programs (Read et al., 2016), collaborative approaches to scientific writing (Oliver et al., 2018), the formation and maintenance of high performing science teams (Cheruvelil et al., 2014); recommendations around scientific reward structures (Goring et al., 2014); and around data collection and macrosystems ecology (Soranno et al., 2015).

Within river and wetland research, team science is less prevalent. However, new collaboratives around data sharing, such as a global network of intermittent rivers, have made mention of the importance of team science for accomplishing their goals (Datry et al., 2016). What is evident is that inland water research is moving into an era of being purposeful about the formation of these teams.

Team case study: Projections of climate change effects on Lake Tanganyika (CLEAT)

CLEAT is a transdisciplinary collaborative team with a goal of understanding how climate affects the East African Lake Tanganyika, the fisheries sector, and to make projections and recommendations for long-term sustainability. The project was funded through the Ministry of Foreign Affairs of Denmark. An initial team was formed for the proposal, but the team configuration and membership

evolved through time, which proved both a strength and a challenge to accomplishing project goals. A major challenge was bringing people together from different cultures, most of whom had not worked together, nor on this lake, before.

Structure of the team: *International, multicultural, medium*
- 13 individual members from three countries.
- Small core leadership team of three people.
- 23% early career scientists.
- Limnologists, modelers, fisheries consultant, social scientists.

Rules of the team: *Collaborative, transdisciplinary science*
- Leadership provided by small core of senior scientists.
- The scientific challenges and unique location motivated team participation.
- Project policies were collaboratively developed early and emphasized values, outlined authorship expectations, and had guidelines for data sharing.
- Emphasis was on building community through inclusiveness, communication, flexibility, and transparency.
- Entire team in-person meeting and social activities were important for building trust and social connections at the beginning of the project.

Outcomes of the team: *Publications, new fisheries policies*
- Multiple scientific publications.
- International media coverage of project.
- Engagement with policy makers and local organizations; additional non-project scientists and graduate students became involved directly or with related projects.

Networks

What is a (social) network?

A social network is a self-organizing web of social actors (individuals, groups, or formal organizations) and the relational connections that bind them. Because peer reviewed publications are increasingly produced by larger groups (Wuchty et al., 2007) distributed across more institutions (Jones et al., 2008) and political boundaries (Wagner et al., 2015), it can be useful to consider social network analysis and network properties to understand and improve group function.

The overarching structure of connections in a network determines how easily information or resources can flow or pass through a network, which then influences the ability of the network to accomplish work like creating new knowledge or coordinating collective action (Henry and Vollan, 2014). Network traits are defined by the pattern of connections between social actors (also referred to as nodes), and determine how easy it is for networks to share and create knowledge, adopt new knowledge, and coordinate for collective action (Henry and Vollan, 2014; Krebs and Holley, 2006; Phelps et al., 2012).

Network structures arise out of a variety of constraints, both physical and social, and are determined by the purpose of the network and the actions of individuals comprising it (Phelps et al., 2012; Marin and Wellman, 2011). Network structures are also shaped by individual choices and behaviors: actors may position themselves in a centralized role in order to retain or withhold information or power, or in order to aggregate information for the benefit of the outer actors or groups (Barabási and Albert, 1999; Henry, 2011). Social actors are more likely to form connections with those closer in geographic proximity, to other actors that are similar, and to actors that are connected to other actors (Barabási and Albert, 1999; Guimera et al., 2005; McPherson et al., 2001; Jasny et al., 2019). Network structures are also influenced by the social rules of engagement (e.g., normative expectations to share data freely) or required relationships (e.g., student committee membership), or the knowledge-based tasks networks have formed to achieve (Box 3) (Marin and Wellman, 2011). For example, when funders require a memorandum of understanding among a group of local agencies in order to be eligible to receive funding, the funder is making an intentional play to create network connections between a diverse set of actors. Individuals and organizations are only able to maintain a limited number of connections, and therefore, as new members join, existing connections may drop off or become less frequent connections, thus changing the patterns of connections in the network.

Box 3 Knowledge-based tasks for networks.

Network structures have differential effects on the ability of the network to accomplish various *knowledge-based tasks*:

- Flow of information or resources across the network
- Adoption of knowledge from one field of practice to another
- Integration of knowledge across fields
- Creation of new knowledge or innovation
- Solving complex problems
- Engaging in coordinated action
- Building capacity to mobilize for and engage in collective action

Table 1 illustrates how network structures change based on degree, density, centralization, closure, and modularity. These structures have varying opportunities and challenges for collaboration, knowledge sharing, and team performance (Table 1). See *Further Reading* for more detailed descriptions of how network structures enable or hinder creation, transfer, and adoption of knowledge and build capacity for coordinated or collective action.

Methods for effective networks

The considerations for forming effective teams also apply to forming effective networks. As in teams, trust is the foundation of network connections and plays a central role in the formation of relationships in a network, thus influencing the network structure (Phelps et al., 2012). Trust is the basis for the formation of individual connections, larger subgroups, as well as how knowledge and resources flow through a network (Levin and Cross, 2004). In addition, social network analysis can be used to help networks evaluate their capacity for knowledge-based tasks (Box 3) over time and understand how established processes and norms are supporting or degrading the intended network structure and achieving network tasks.

Some tasks are well suited to be parallelized and performed simultaneously, and in this case, the network structure and the assignment of work can be optimized to support this work. Research tasks such as data collection, data aggregation, modeling, and writing tasks may be best completed by a number of sub-groups (or *teams*) within the network and coordinated by a few lead scientists. Mapped as a network, this would resemble the hub-and-spoke network, where the lead scientists are acting as the hubs between teams.

When the goal of a network is to share and integrate knowledge, or create new knowledge and innovations, then a higher density core-periphery network may be more suitable. Consider the intensive, multi-day scientific events known as "annual retreats" or "workshops," where the goal is to integrate past work, iterate on knowledge, and create or revise a group vision that might be held by dozens of participants. These multi-day events could be used to cultivate greater density in the network and cultivate trust and team identity, by maximizing the opportunities for all network members to share information and to encourage the formation of social connections among participants.

When networks seek to make progress with specific tasks such as modeling or data analysis, while simultaneously advancing knowledge and innovation, then the network communication structure should allow for frequent within-team communication, with less frequent (but regular) opportunities to seek advice and share preliminary results. The corresponding network structure that optimizes both for accomplishing independent, parallelized, or sequential tasks, while advancing knowledge generation, is a multi-hub network.

Social network analysis can be used to strategically intervene when parts of a network—or single actors—fail. If a single actor becomes overwhelmed with requests for time or advice and is unable to perform their tasks because of collaboration overload (Cross et al., 2016), then that actor may become a limiting factor to achieving shared goals. In network structure, this would appear as high centralization, and the solution to this would be to encourage new connections to form to reduce the degree (number of connections) that are reliant on a single actor in order to accomplish their work.

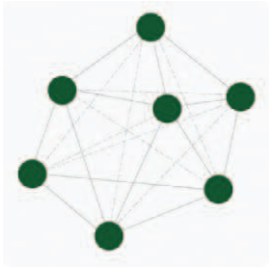
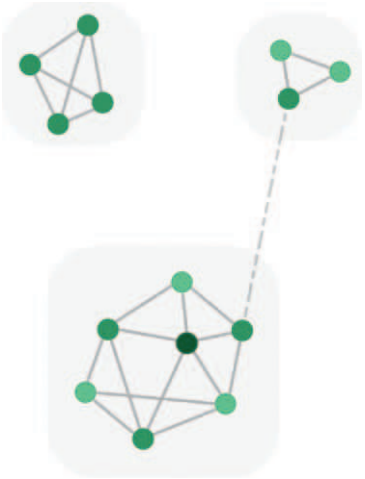
Networks in inland waters research

As the scale and scope of scientific research has expanded, so too have a variety of networks that focus on aquatic systems. Many of these networks share overarching research objectives but vary in their approach to accomplish knowledge-based tasks, which is in turn reflected in the network structure. Three tasks that aquatic networks appear to focus on singularly or in combination include (1) coordinated data collection and flow of information, (2) creation of new knowledge, and (3) building and engaging in collective action.

Networks designed around consistent data collection tend toward a decentralized hub-and-spoke model (Table 1), in which data sharing is the primary connection between actors, and governance and resource sharing from a central actor sustains the network. Government-sponsored inland waters networks in the United States that are designed for coordinated data collection and information flow include the National Ecological Observatory Network; U.S. Environmental Protection Agency National Aquatic Resources Assessments of lakes, streams, and wetlands; and the U.S. Geological Survey (USGS) National Streamgage Network. Information flow and communication occurs in support of the task of data collection. Information content from data collection flows from the less connected, outer actors toward the central actors, and governance (e.g., protocols, standards) tends to flow from the central actors to the outer actors. These networks have a strong emphasis on gathering data rather than on knowledge integration or new knowledge creation. Highly managed protocols and coordinated sampling lead to high quality datasets that are comparable across space and time, which facilitates data analyses by users of the network data.

In contrast, networks focused on creation of new knowledge tend to have core-periphery structures (Table 1), and the connections that bind the actors exist to optimize communication and resource sharing. An example of such a network is the Global Lake Ecological Observatory Network (GLEON; see case study below). These networks have more emphasis on bringing people together to integrate knowledge globally and for the creation of innovations in aquatic science and technology. The structure of the network, for which connections between actors are based on voluntary and non-standardized communication and resource sharing, heavily relies on trust. Knowledge networks with core-periphery structure may evolve more rapidly through time as compared to data collection networks, as new teams are created, new social connections are formed, and others senesce. Community-built tools and open science approaches are complementary to the core-periphery network structure and are a hallmark

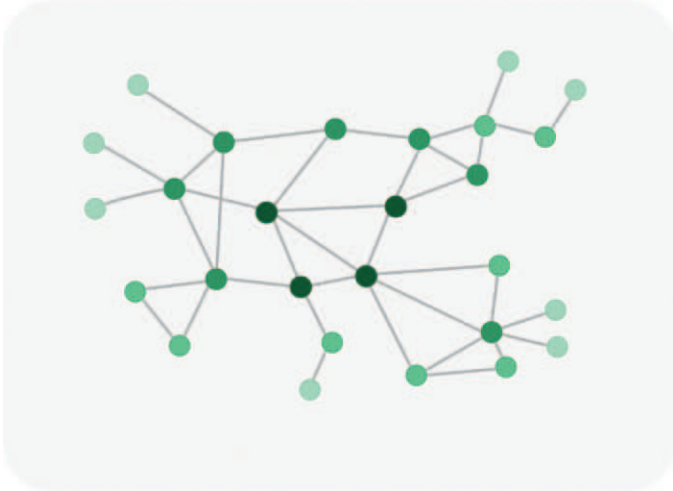
Table 1 Definitions, idealized example structures, attributes, and real-world examples of teams, networks, and networks of networks. Darker shaded nodes have higher degree (number of connections with other nodes), while lighter shaded nodes have lower degree.

Name, size, and description, idealized structure	*Traits and ideal uses (see Box 2 for definitions of traits)*	*Examples*
Team: 3–11 people; small, tight knit collaborative group. 	Average Degree: Moderate (3–6) Density: Moderate (>0.50) Closure: High (>0.60) Reciprocity: High (>0.50) Centralization: Low Modularity: Low Well-defined scope and objectives that can be accomplished by a small group	Projections of Climate Change Effects on Lake Tanganyika Team (CLEAT, see case study below)
Isolated Teams: More than 12, collection of small teams of variable size. No ties or very weak connections across teams. 	Average Degree: Low-moderate (1–3) Density: High within teams, low across full network Closure: High within teams, low across network Reciprocity: High within teams, low across network Centralization: Low within teams Modularity: High Work completed by separate teams, requires little coordination	Co-author teams contributing separate articles to a journal issue

Small Network: A single network including12–24 members in which all individuals have at least one connection. 	Average Degree: Low-moderate (1–3) Density: Low Closure: Low Reciprocity: Low Centralization: Moderate Modularity: Low-moderate	Grant-funded team with several co-investigators and their labs, requiring strong integration between groups
Centralized Network (Baran, 1964). Variable size, larger than 12 Also known as a *hub-and-spoke network* (Krebs and Holley, 2006). 	Average Degree: Low Density: Low Closure: Low Reciprocity: Low Centralization: High Modularity: High Used when a high level of coordination or standardization between actors is needed. The key feature of this network is the power held by the two key actors and the lack of connectivity among other actors. The hubs control information flow out to the edges of the network. This is an efficient network (e.g., emergency response) but vulnerable if either of the hubs is taken out of the network or intentionally limits information flow	U.S. Geological Survey National Streamgage Network National Science Foundation National Ecological Observatory Network U.S. Environmental Protection Agency National Lakes Assessment

(*Continued*)

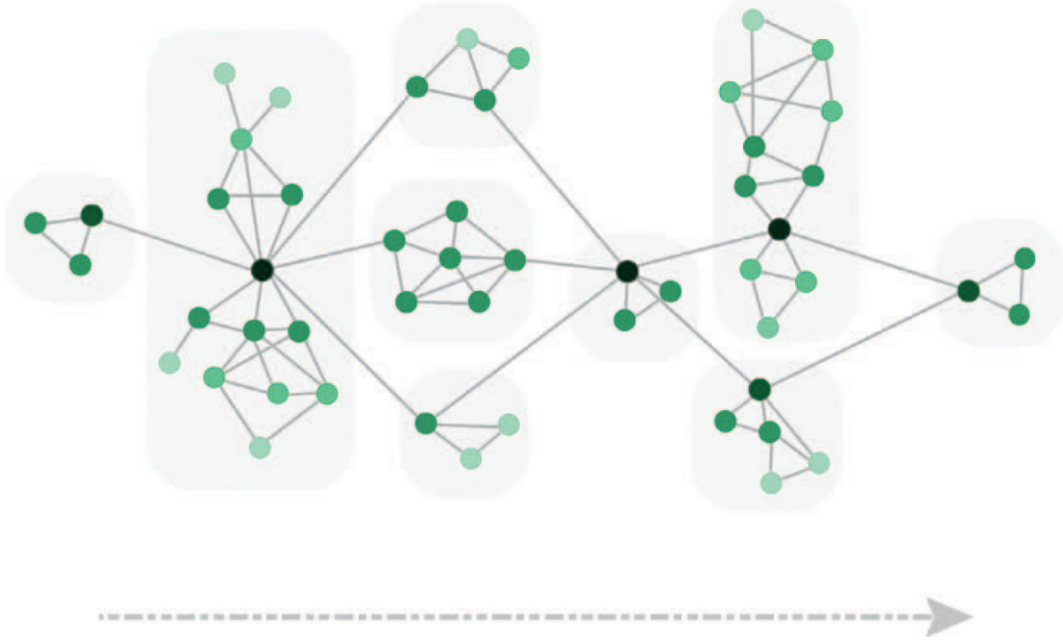
Table 1 (Continued)

Name, size, and description, idealized structure	*Traits and ideal uses (see for definitions of traits)*	*Examples*
Decentralized Network: Variable size, larger than 12 Also known as a *multi-hub network* (Krebs and Holley, 2006) 	Average Degree: Low Density: Low Closure: Low-moderate Reciprocity: Low Centralization: High Modularity: Moderate This kind of network may be formed initially for data collection or a more centralized, standardized purpose, but evolves to decrease centrality and increase density and closure. This network has a higher capacity to share knowledge and resources and be more resilient to loss of one of the hubs because there is more closure and less centralization (Baran, 1964)	National Science Foundation Long Term Ecological Research
Core-periphery: Typically two dozen or more, tightly connected core with sparse connections to the outside members (Borgatti and Everett, 2000). 	Average Degree: Low in periphery too high in core Density: High in core, low in periphery Closure: High in core, low in periphery Reciprocity: High in core, low in periphery Centralization: Moderate-high Modularity: Variable These networks are more resilient (due to the dense connections in the core), represent network maturity, and may improve the coordination capacity of the network (Krebs and Holley, 2006; Csermely et al., 2013) Useful for knowledge generation and innovation. Due to the centralization and density in the core, this type of network has increased capacity to move knowledge and resources across the network, coordinate collective action, and be resilient to change (Csermely et al., 2013)	Global Lake Ecological Observatory Network

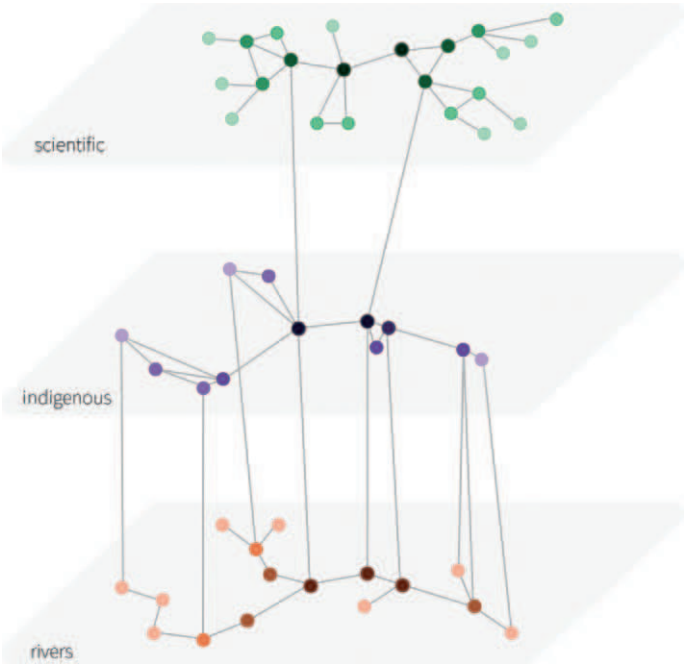
Small world networks: Small, densely connected groups with sparse connections between groups.		Average Degree: Moderate (especially within sub-groups) Density: Low across full network, high within clusters Closure: Low across full network, high within clusters Reciprocity: Low across full network, high within clusters Centralization: Moderate-high Modularity: High Used to coordinate and share information across sparsely connected teams or communities. Weak ties connect the groups to each other	American Society of Limnology and Oceanography

(*Continued*)

Table 1 (Continued)

Name, size, and description, idealized structure	*Traits and ideal uses (see for definitions of traits)*	*Examples*
Multi-team systems: A few dozen to hundreds of members, teams operate in parallel, and each has a unique focus and scope, but are all contributing to common overarching scope. Teams may be doing work that is dependent on the results from other teams, as indicated by the arrow 	Average Degree: Moderate (especially within sub-groups) Density: Low across full network, high within clusters Closure: Low across full network, high within clusters Reciprocity: Low across full network, high within clusters Centralization: High Modularity: High Used with a large and complex scope of work, requiring either specialization within small teams, or distribution of a large scope of work over many teams. The work of all teams contributes to a larger goal than the scope of each individual team. We define a multi-team system as a *network of networks* because of the separation of teams which may vary in size, network structure, and coordination with the larger goals of the network	Human Genome Project

Multi-level networks: Layers or levels represent unique types of network connections.	All network metrics (average degree, density, closure, reciprocity, centralization, and modularity) vary across the layers. Typically, contacts between layers are highly centralized and not highly dense, but this too varies by the purpose of the network connections across layers. Used to connect existing networks to each other. Each network has a unique purpose and types of ties (e.g., monitoring, governance, ecological). The structure of each layer is determined by its mission and context, ties are formed between layers to facilitate creation of something no layer can accomplish alone	Indigenous Observation Network



of some inland waters networks (Read et al., 2018). New connections built within this type of network are critical to developing new users of data and tools.

Finally, there are networks that focus on data collection, knowledge creation, and building capacity for collective action. The National Phenology Network has a focus on data collection and information sharing, but also on building the capacity to mobilize community scientists for collective action in support of the network's goals. Quality control of data is less emphasized as compared to the hub-and-spoke model described above. In contrast, the Long Term Ecological Research (LTER) network model not only functions as a hub-and-spoke network, but also incentivizes connections between different actors (LTER sites) via targeted cross-site funding. In this model, distributed place-based research stations collect high-quality, standardized data that are used primarily for pre-identified locally scaled research questions but the data are also publicly accessible. Within each location, knowledge creation, communication, and trusting social connections comprise the network connections.

Network case study: Global Lake Ecological Observatory Network

The Global Lake Ecological Observatory Network (GLEON) is a grassroots network of scientists, sensors, and data. The network has been funded by the U.S. National Science Foundation and various private foundations over time. GLEON is a core-periphery network that seeks to integrate knowledge across fields, create new aquatic science knowledge and innovations, and provide an optional platform for data sharing. GLEON seeks to enable connections between as many members as possible; however, also has a more sustained core of members with higher density, and with more sustained participation in the network through time.

Structure of the network: *Core-periphery*

- 500 individual members from 49 countries.
- 30% students.
- 60 member *lakes* from 34 countries on six continents.
- Members from academic, public, non-governmental and private institutions.

Rules of the network (excerpted from https://gleon.org/about/vision-and-mission): *Educational, collaborative, scientific*

- Steering Committee, Student Association, and Collaborative Climate Committee guide the long-term strategy, student services, and collaborative culture and practices of the network.
- Annual meetings rotate geographically to encourage new membership.
- Interdisciplinary lake science.
- Foster an empowered, diverse membership and facilitate informality, collegiality, and collaboration.
- Spark curiosity and share ideas, expertise, and data.
- Use transparency in decision-making, communication of results, tools, and products.
- Prioritize professional development of members.

Outcomes of the network: *Global lake research, technical and scientific advances, team-science fluent membership*

- Open data and community-built tools (Read et al., 2018).
- Effective pipeline for student training and career opportunities.
- 329 publications attributable to network collaborations between 2005 and 2020.
- Technical innovation resulting from GLEON-based collaboration between private sector and academia, driven by research needs.
- Training in team science (Read et al., 2016), sensor technology, data processing, and modeling skills.
- International networks for future opportunities (jobs, research collaborations).
- Appreciation for different cultures.

Networks of networks

What is a network of networks?

Beyond teams and networks, science frequently requires building connections between networks with different purposes and disciplinary alignment (e.g., monitoring, governance, analysis). These are networks of networks: interconnected networks where each layer is a unique network defined by social, geographic, and temporal boundaries and distinct purposes, e.g., governance, data gathering, information sharing. Networks of networks are often called multilevel networks (Lazega and Snijders, 2015; and see Table 1).

All of the knowledge about teams and networks described in previous sections also applies to the structure of networks of networks, but networks of networks are recognized to have uniquely transformative capabilities, and are being invested in by scientific agencies as a growth area (e.g., National Science Foundation AccelNET program).

By definition, networks of networks are interconnected by a small number of connections across networks; this structure makes them more vulnerable to the loss of those cross-network connections.

Methods for effective networks of networks

The process of forming networks of networks varies greatly depending on the networks that need connections to each other. Because networks of networks are composed of networks and teams, and rely on connections between actors through which knowledge and resources are shared, we speculate that the best practices for teams and networks also apply to networks of networks. However, in addition to the previous guidance, we hypothesize that the time needed for leadership and maintenance of key connects (cross-team, cross-network) scales proportionally with the complexity of the network.

Small world networks are an emergent property of human communities: because no explicit effort or design is required to build a small world network, the only prerequisite is a minimum number of individuals with opportunities to interact and form connections. In contrast, multi-team systems are used under moderate to highly organized circumstances, and in some cases to achieve very specific, coordinated outcomes where the work of one team is dependent on the previous work of another (see Table 1).

Multilevel networks form when independently-created networks become connected by relationships between individuals *across* networks; thus, these network of networks structures can be formed only when two or more networks already exist, and then become connected. The way that meaningful connections across networks are made and sustained are studied most frequently in the fields of environmental governance and resilience (Hahn et al., 2008; Hileman and Lubell, 2018). Thus, theories and applied knowledge about how best to design, manage, and study networks of networks are just beginning to appear in the literature (Brass and Borgatti, 2019; McGee et al., 2019). One of the unique features of networks of networks is that where any individual network structure might be resilient, the dependency of networks of networks on a small number of inter-network connections can make them vulnerable (Das et al., 2017). Because networks of networks are connected by actors, the loss of key actors or a connection can create a cascading failure. Networks of networks that have strong interdependent coupling may be less resilient than individual networks.

Support and training for the development of networks of networks can be found through organizations sponsoring inland waters research, including the National Socio-Environmental Synthesis Center or the USGS Powell Center.

Networks of networks in inland water research

Multi-team systems may be the most common form of networks of networks found in inland waters research. At this time, direct study of multi-team systems pursuing inland waters research objectives is not available, but it is likely that this network of network structure is present in the aquatic sciences: most natural science researchers in Norway conduct about 20% of their work in what would be described at least as multi-team systems (Kyvik and Reymert, 2017).

Multi-level networks can also be found in the field of inland waters. As a Federal agency, the USGS is a model of a national network of networks, as it incorporates a diverse set of networks including the National Water Quality Monitoring Network, the National Streamgage Network, the National Phenology Network, and others which have direct relevance for aquatic science; but the network of networks also features looser affiliation with other networks within USGS including volcano and earthquakes observatories. These networks within a network have been created within a bureaucratic framework and under an earth-science mission; largely, connections between the network are informal and consist of information sharing between a small number of individuals each embedded within one of the networks.

In contrast, the Indigenous Observation Network (ION; see case study below) is a multi-level network that has been created under a less formal setting: ION links an intertribal watershed council with a standardized community-based monitoring network and an indigenous knowledge network; this network of networks is designed for the co-production of new scientific knowledge. This multi-level network relies heavily on social relationships between a small number of individuals who span the three network layers.

The Consortium of Universities for the Advancement of Hydrologic Sciences, Inc. (CUASHI) is a network of networks that incorporates international partners and emphasizes integration of knowledge, creation of new knowledge, and data sharing. CUASHI's goal is to catalyze water-related research across institutions and disciplines. Institutions, rather than individuals, are members; currently there are more than 140 member institutions, with 20% from outside the United States. CUASHI primarily maintains infrastructure to support collaborative research and data sharing, but also provides training opportunities and hosts an annual meeting.

In the aquatic sciences, there is a growing demand for the creation of networks of networks beyond the naturally occurring small world networks, to multi-level networks in which layers are connected through formal linkages that can serve as "force multipliers and connectors to advance science." Recent investments by the NSF (e.g., the U.S. National Science Foundation's AccelNet Program and Coastlines and People Program) focus on connecting people, rather than infrastructure, in recognition of the importance of human relationships for creating networks of networks. The goal is to bring together networks that might not normally interact because the scientific context differs substantially. This approach is gaining ground within the aquatic sciences, with calls to strengthen connections between remote sensing scientists and limnologists to better understand lake ice dynamics, for example (Sharma et al., 2020).

Network of networks case study: Indigenous Observation Network

The Indigenous Observation Network (ION) is a multi-level network of networks that connects scientists, community monitoring groups, and indigenous knowledge networks. The ION links community-based water-quality and permafrost monitoring programs

that produce data from the Yukon River Basin in the United States and Canada. The Yukon River Inter-Tribal Watershed Council (YRITWC), an Indigenous non-profit organization, collaborates with the USGS, and the University of Alaska-Fairbanks to implement the ION. The ION was first established in 2006 to measure baseline water quality in the Yukon River Basin and has continued to collect hundreds of surface water samples annually to track effects from changing climate and land use. Today, ION has sampled >200 sites across the Yukon River Basin spanning the United States and Canada.

Structure of the network of networks: *Multi-level*

- Yukon River Inter-Tribal Watershed Council represents 76 Tribes and First Nations located in the Yukon River Basin that have signed the inter-tribal accord.
- USGS and YRITWC have agreed to collaborate on monitoring and science activities through a memorandum of understanding.
- U.S. Environmental Protection Agency—Indian General Assistance Program (EPA-IGAP) funds the surface water sampling of community members in the United States that participate in the program.

Rules of the network of networks: *Quality and conservation*

- Tribes and First Nation members of the YRITWC are the governing body committed to preserving and protecting the environmental quality of the Yukon River.
- Standardized training, field methods, quality assurance, lab analysis, and data publication is practiced across sites and by all community technicians.
- YRITWC consults with participating members on new site selection.
- Outside access to community members and collaborators is restricted by USGS and YRITWC project personnel so as to avoid stakeholder fatigue.

Outcomes of the network of networks: *Co-production of knowledge, conservation, and community engagement.*

- Research on long term water quality trends and other climate change effects experienced by Indigenous communities (Toohey et al., 2016).
- Demonstrated the generation of accurate, precise, and reliable water quality data by Indigenous community-based monitoring network.
- Provides rich opportunities for USGS engagement with Indigenous stakeholders.
- Provides opportunities for students and community members from traditionally underrepresented groups to engage in science, technology, engineering, and math (STEM) activities.
- Communities have greater trust in ION data than that collected by other entities because it is being collected by community members (Wilson, 2017).
- The ION allowed for deeper integration of Indigenous Knowledge with western science to understand climate change effects on this relatively under-studied (from a scientific perspective) region (Herman-Mercer and Schuster, 2014) by building long term trusting relationships.
- Communities have used the ION program to establish baseline monitoring and assessment required to establish conservation districts that further the YRITWC goal of preserving the environmental quality of the Yukon River.

Conclusion and synthesis

Trust is essential to the formation of human relationships, and these relationships in turn are the basis of meaningful connections in teams, networks, and networks of networks. Communication, data sharing, resource sharing, and coordination are impossible without trust; and without those functions, groups at all levels of organization cannot accomplish knowledge-based tasks including sharing and integration of knowledge, innovation, collective action, and more. The intentional formation of teams and networks, informed by the literature on the science of team science and social network analysis, can result in more productive and sustained performance. Creating and maintaining successful teams, networks, and networks of networks is dependent on both the structure and the culture of the entity.

Increasing the commonly-understood attributes of high performing teams and the ideal uses of various network structures will allow societies, universities, government agencies, and funders to improve team science and network building. A reward structure that recognizes and values the successful creation of teams and networks to accomplish inland waters research can incentivize more emphasis of team and network development in inland waters research. Because many reward structures focus on the products rather than the processes of team science, training for the social-emotional skills required to lead or participate in successful teams, networks, and networks of networks are not commonplace in natural and physical sciences graduate programs, and there are multiple generations of inland water science professionals working in teams or networks without such training. Outside of a few specialized graduate training programs that are limited in size and offered irregularly (e.g., NSF Research Traineeship program, GLEON), there are no common pathways for inland water professionals (particularly those outside of graduate school) to receive training geared toward improving team science outcomes.

At the writing of this article, networks of networks remain the least understood of the entities examined in this article. However, as humans face ever increasing global-scale environmental challenges related to water quality and availability, new connections across communities, research, governance, and management groups could help minimize the societal and environmental effects.

An understanding of the basis of teams, networks, and networks of networks, which all rely on robust, trusting human connections, will be essential to adapting to a changing planet. Inland waters research—and geosciences more broadly—can benefit from the knowledge acquired through social science research, and the integration of this to team and network formation; and we hope that this knowledge will contribute to meeting the global environmental challenges facing inland waters today.

Knowledge gaps

- Methods for developing and maintaining specific network structures and rules of engagement to accomplish various knowledge-based tasks.
- The effect of transdisciplinarity and convergent science on teams, networks, and networks of network structure and function.
- Methods for development and maintenance of multi-level networks and networks of networks.
- Rules of engagement for networks and networks of networks of various structures and purposes.
- Best practices for evaluating the success of teams, networks, and networks of networks outside of product-based metrics.

See Also: **Emerging methods and topics**: Citizen Science, Crowdsourcing, and Social Media Advance Our Understanding and Conservation of Inland Watersaters; Environmental DNA Advancing Our Understanding and Conservation of Inland Waters; **Social/societal values of Inland waters**: The Gender Gap: Women as Authors and Leaders in International Publications in Fisheries Science; **Structures and functions of Inland Waters - Rivers**: Biodiversity Conservation of Aquatic Ecosystems; Inland Waters—Rivers: Land Use and Water Quality; **Structures and functions of Inland Waters - Wetlands**: Ecology and Conservation of Wetland Amphibians and Reptiles; Patterns in Freshwater Fish Diversity; Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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Team Science

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Citizen Science, Crowdsourcing, and Social Media Advance Our Understanding and Conservation of Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Citizen science Participation of non-scientists in the process of scientific research, which may include the development of research questions and data-collection protocols; data collection, processing, and analysis; and interpretation and application of results. The term "citizen" here does not refer to the legal citizenship status of participants, but rather that participants are not professional scientists. Alternative terms include community science, participatory science, lay science, and public participation in science.

Crowdsourcing Leveraging a large unidentified group of people to perform predetermined tasks; a type of citizen science.

Social media Internet applications that allow users to create and share media and build connections with one another.

Introduction

Scientists and managers working on inland waters are increasingly recognizing the value of engaging diverse audiences. Participation of non-scientists from a variety of perspectives, places, and backgrounds in conservation research and implementation has been shown to have several benefits. For example, public participation in conservation research can result in more relevant research questions, can produce a richer set of data and knowledge, and generate innovative solutions to complex conservation problems. Further, public participation can increase scientific literacy and public support for research and conservation work.

Engaging broad and diverse audiences in conservation research and implementation requires the use of innovative communication and engagement strategies. Presently, funding agencies and foundations expect researchers and managers to incorporate public engagement into their work (National Science Foundation, 2015). Improvements in public access to, and comfort with, the necessary technology required for public engagement is also contributing to the growth in public participation. This is because technologies such as smart phones, web applications, and widely available access to the internet allow efficient data collection and transmission, validation of public observations, and integration of electronic sensor data, such as stream flow trackers, that can be collected and uploaded by public participants (Catlin-Groves, 2012; Dickinson et al., 2012). Rapidly expanding methods for public engagement in inland water research and conservation include citizen science, crowdsourcing, and the use of social media.

In this chapter, we explore the application, potential, and best practices for using citizen science, crowdsourcing, and social media to advance our understanding and conservation of inland waters.

Citizen science

Citizen science defined

Citizen science can be defined as "participation by the public in a scientific project" (McKinley et al., 2015). More descriptively, citizen science generally involves the participation of non-scientists in the process of scientific research, which may include the development of research questions and data-collection protocols; data collection, processing, and analysis; and interpretation and application of results (Silvertown, 2009; Miller-Rushing et al., 2012; Crain et al., 2014; Sanz et al., 2014; Thornhill et al., 2016). Science-based activities that do not result in new scientific knowledge, or those where results are not shared beyond the participants, are not typically considered citizen science. Such activities include educational or teaching activities where the outcome is known (Miller-Rushing et al., 2012).

Of important note are recent concerns raised about the implications of the term "citizen science," in that it can be interpreted as limiting participation to those holding legal citizenship in the country where the project is based (Eitzel et al., 2017). The word "citizen" in the case of citizen science is meant to distinguish amateur or non-professional participants from professional scientists, rather than the legal definition; however, some programs have chosen alternative labels, including community science, public-engaged science, participatory sensing, or lay monitoring.

History of citizen science

Amateurs (defined here as anyone who is not a professional scientist, regardless of level of expertise, Miller-Rushing et al., 2012) have long contributed to scientific endeavors. Throughout recorded history, people have asked questions and cataloged observations of the world around them (Miller-Rushing et al., 2012). As recently as just two centuries ago, nearly all science was conducted by people who made their living in some other way (Silvertown, 2009). As science professionalized, fields such as ornithology, archeology, and astronomy, where observational skills are equally or more important than access to expensive equipment, continued to benefit from amateur contributions (Silvertown, 2009; Dickinson et al., 2010). For example, public monitoring of bird populations can be traced back to the eighteenth century in Europe (Greenwood, 2007), and the Christmas Bird Count run by the National Audubon Society in the US has taken place every year since 1900, providing a vital source of ornithological data that allows conservationists to study the long-term status and health of bird populations (National Audubon Society, 2020, Fig. 1).

Citizen science has grown rapidly since the mid-twentieth century, an expansion that may be attributed to a combination of factors, including "environmental tragedies, shifts in policy making structures, affluence in society, governmental budgets, and expanded interests in partnerships" (Stepenuck and Genskow, 2018). The term "citizen science" came into broad use in the mid-1990s (See et al., 2016), including publication of a book of the same name (Irwin, 1995) that discussed the integration of citizen knowledge and scientific knowledge, and the use of the term by Cornell's Laboratory of Ornithology as an alternative to the phrase "public participation in scientific research" (Bonney, 1996). This growth of citizen science can also be observed in citizen science supported peer-reviewed scientific literature (Follett and Strezov, 2015).

Citizen science on inland waters

Volunteer monitoring of inland water quality has a strong tradition around the globe. Water-focused citizen science programs (often called volunteer monitoring programs) have a long history and are among the most common types of citizen science programs. For example, a national directory of US volunteer environmental monitoring programs published in 1998 included 772 programs, the vast majority of which focused on inland waters (Ely and Hamingson, 1998). These numbers continued to grow through the years; by 2013, 1676 volunteer water monitoring programs were in existence in the US, more than doubling the number of water-focused citizen science programs in just 15 years (Stepenuck and Genskow, 2018).

Among citizen science programs on inland waters, the most common focus is on rivers and streams (Fig. 2). In the earlier report, 76% of programs monitored rivers and streams, 34% monitored lakes and ponds, 22% monitored wetlands, and 11% monitored reservoirs (Ely and Hamingson, 1998). By 2013, volunteer water monitoring programs reported that 86% of responding programs monitored rivers and streams, while 43% monitored lakes and ponds. This focus on rivers and streams may be because public access at road crossings facilitates monitoring and makes boats typically unnecessary. Lake monitoring programs benefit from the presence

Fig. 1 Amateur birdwatchers have contributed data on bird populations and seasonality for centuries. Credit: Jen Owen.

Fig. 2 Streams are commonly monitored by citizen scientists due to their accessibility at road crossings and volunteer-friendly protocols to use aquatic invertebrates, primarily insects, as indicators of stream health. Credit: Jo Latimore.

of interested homeowners and homeowners' associations who have easy access to their lakes and an interest in maintaining lake health and associated property values (Stepenuck and Genskow, 2018).

Citizen science programs on inland waters in North America are led by local conservation groups, such as lake associations and watershed councils, as well as regional and national organizations like Trout Unlimited. Government agencies (local, state, federal, and tribal) are frequent sponsors of citizen science programs. Native American tribes have embraced citizen science approaches to combine indigenous knowledge and western science in projects like Indigenous Observation Network located in the Yukon River watershed in northwest Canada and Alaska (https://yukon.next.fieldscope.org/) and a program to detect aquatic invasive species on the Blackfeet Reservation in Montana (Hedin et al., 2021). Schools and universities also often support inland water citizen science programs, such as the Alliance for Aquatic Resource Monitoring (ALLARM, https://www.dickinson.edu/allarm) based at Dickinson College in Pennsylvania.

Types of citizen science programs

A key characteristic of modern citizen science is that participation is open to all interested participants, and not just those with the time and resources to pursue science as a hobby (Silvertown, 2009). This accessibility is due partly to the wide variety of participant roles along a spectrum of engagement, which can range from recording observations around one's backyard (e.g., The Great Sunflower Project, Domroese and Johnson, 2017) or within imagery accessed on one's computer (e.g., Zooniverse; Jones et al., 2018), to long-term engagement within a team of scientists and amateurs to develop a scientific project and apply its results. In fact, the multiple models for citizen science projects facilitate a variety of roles and a diversity of participants. Bonney et al. (2009) categorize citizen science projects into three broad categories: contributory, collaborative, and co-created (Table 1).

Examples of contributory citizen science projects on inland waters include using non-scientists to record water level data (e.g. CrowdHydrology; Lowry and Fienen, 2013), identify ephemeral streams (e.g. Stream Tracker; Kampf et al., 2018), monitor water clarity (Lottig et al., 2014), and submit samples or observations as part of the many lake and stream monitoring programs that are designed and led by professionals but engage the public (e.g., Michigan Clean Water Corps (MiCorps) Volunteer Stream Monitoring Program; Latimore and Steen, 2014). Collaborative citizen science projects involve the public in ways beyond data contribution; an example is the Michigan Clean Water Corps (MiCorps) Score the Shore program, which was designed by scientists with input from interested members of the public who expressed a need for nearshore lake habitat data to support lake conservation and management actions at the community level. These citizen scientists analyze their Score the Shore data with guidance from program scientists and many disseminate the findings to their homeowner associations and local decision makers (Fig. 3; http://www.micorps.net). Co-created programs are the least common, and examples of truly co-created citizen science programs focused on inland waters are not well-represented in the literature.

While citizen science projects can range from local to multinational levels, there are several clearinghouses where project information can be found that facilitate some analysis of participation. Within the United States, the three main clearing houses of citizen science projects are SciStarter.org, CitSci.org, and CitizenScience.gov. Databases within these organizations provide a

Table 1 Categories of citizen science projects, as defined by Bonney et al. (2009).

Category	*Description*
Contributory	Designed by scientists, members of the public contribute data
Collaborative	Designed by scientists; members of the public contribute data, may help refine project design, analyze data, or disseminate findings
Co-created	Designed by scientists alongside members of the public; at least some of the public participants are involved in most or all steps of the scientific process

Fig. 3 A volunteer in the MiCorps Score the Shore program records observations about lakeshore habitat conditions while boating around her lake. Credit: Jo Latimore.

starting point to analyze participation both within and across projects. By collecting information on the roles of staff, volunteers, and external scientists in nearly 300 US volunteer water monitoring programs, Stepenuck and Genskow (2018) determined that over half (53%) of the programs are collaborative; 29% contributory; and 14% co-created. An additional 2% were categorized as "collegial," operating without engaging professional scientists.

Goals and outcomes of citizen science projects

Just as the roles of participants in citizen science programs vary, so do the program goals and outcomes. The most common goals of citizen science programs in inland waters include community involvement, participant education, and collection of data (Table 2; Stepenuck and Genskow, 2018). To be successful, citizen science projects must have a sound scientific design and align with program goals.

An important scientific outcome of inland waters citizen science programs is the generation of an abundance of high-quality data. In a review of available lake data from seven US states, over half of the measurements of common water-quality parameters (water clarity, nutrients, and algal biomass) were provided by citizen science programs, and overall, 82% of all data over a 31-year period was collected by citizen scientists (Poisson et al., 2019). Citizen science programs also increase both the temporal and spatial scales at which scientific projects can occur (McKinley et al., 2015; Poisson et al., 2019). Participants often have access to private lands and water bodies that a research team may struggle to reach, and because participants often live near the study sites, they can collect data more frequently. Engaging participants who live near study sites allows for more frequent data collection over a larger geographic area than logistically feasible for a professional research team (Dickinson et al., 2012; Miller-Rushing et al., 2012; Latimore and Steen, 2014).

Because of the large number of observers across temporal and spatial scales, relative to professional monitoring, citizen science programs can be very effective in early detection of invasive species (McKinley et al., 2015; Johnson et al., 2020; Larson et al., 2020), environmental and phenological changes, issues that require management response, and the effectiveness of management actions (McKinley et al., 2015). Additionally, citizen science projects can be a cost-effective (though not cost-free) means for collecting data (Aceves-Bueno et al., 2015), an important factor when budgets and staff for environmental monitoring are limited. Further, engaging the public can help refine research questions by improving local relevancy and better incorporating human dimensions and the social aspects of ecosystem management (McKinley et al., 2015). Citizen engagement in environmental monitoring also influences the relationship between scientists and the public (Dickinson et al., 2010), potentially improving public support and funding for science-based management actions (Latimore and Steen, 2014).

Outcomes of citizen science programs can extend far beyond data collection. Citizen science programs can also benefit the participants and their communities, depending on program design, goals, and implementation. Participant outcomes may include increased personal knowledge (particularly about the scientific issue at hand, and about the scientific process generally), changed attitudes, and changed behaviors (Danielsen et al., 2005; Conrad and Hilchey, 2011; Jordan et al., 2012; Stepenuck and Green, 2015). While not a tangible outcome (Overdevest et al., 2004), personal knowledge gain tends to be the most reported benefit for citizen scientists. However, education is a very common goal among citizen science programs, so this is a positive finding (Stepenuck and Genskow, 2018). Among the most reported community outcomes is increased social capital; that is, improved networks of relationships among community members that enhance community functions. Other reported community outcomes include increased community awareness of environmental issues, increased citizen engagement in decision-making processes around environmental management and policy, improved adherence to natural resource regulations, and job creation (Overdevest et al., 2004; Danielsen et al., 2005; Conrad and Hilchey, 2011; Jordan et al., 2012; Aceves-Bueno et al., 2015; McKinley et al., 2015; Stepenuck and Green, 2015).

Table 2 Goals of US volunteer water monitoring programs, as reported by Stepenuck and Genskow (2018). Note that the percentages do not sum to 100 since each program can have multiple goals.

Program goal	*% of Programs reporting*
Involve community	91%
Educate the public	82%
Create a long-term data set	76%
Address lack of data	71%
Identify pollution problems	69%
Educate youth	65%
Create consistency in methods	56%
Obtain data to affect natural resource policy	51%
Study restoration outcomes	47%
Provide data for state/tribal water quality reports	43%
Address environmental crisis	27%
Answer a research question	17%

Challenges: Is citizen science right for your project?

While citizen science projects can be an effective approach to answering questions about inland waters, they are not without challenges. As noted above, citizen science projects can be cost-effective, but they are not cost-free. Depending on the program, necessary investments in staff and volunteers, data management tools, technology and equipment can be significant. Further, establishing organizational culture and policies that support citizen science may be needed (McKinley et al., 2015). Privacy can also be a concern in citizen science programs, especially those sponsored by or in partnership with federal agencies. For example, in the US, the Privacy Act applies to personal and location-based information, photographs, videos, and audio content. To comply, federal agencies must plan to either avoid collecting or storing personally identifiable information or develop an approved process for managing it (McKinley et al., 2015).

Volunteer recruitment and retention (i.e., keeping volunteers engaged after their initial participation and, if applicable, training) are critical to successful citizen science projects. Not all projects attract public interest. For example, projects involving charismatic animals or pleasant environments will draw more interest from participants than will opportunities to collect data in mucky swamps. Water bodies near college campuses or tourist destinations also attract more public interest than those in industrial areas, and in rural areas, the population of potential participants can be small (McKinley et al., 2015). To maintain volunteer interest, effort must be made to communicate project results and outcomes, respond to volunteer questions, and offer opportunities for future engagement that appeal to participants. For example, project results and outcomes can be shared in plain-language reports and presentations by project leaders at community gatherings provide opportunities for discussion. Such reports and presentations can also be used to recruit new volunteers and retain existing volunteers for future participation.

Data collected by citizen science programs is often subject to stronger scrutiny than that generated by professionals. Critics of citizen science data point to the lack of professional credentials held by the volunteers collecting the data, suggesting that they may be more likely to make procedural errors. Another common criticism is that volunteers are more likely to introduce personal bias into data collection and interpretation than professionals and have not been trained to avoid it (Latimore and Lawson, 2007; Cohn, 2011; Kremen et al., 2011). Although several studies have shown that volunteer monitoring assessments of inland waters are highly valuable and similarly reliable as professional assessments when volunteers are trained, protocols are clear, and quality assurance project plans are followed (Albus et al., 2020; Krabbenhoft and Kashian, 2020), demonstration of data quality and validity is a critical need for volunteer-based projects.

The strongest citizen science programs - those most likely to generate reliable data - are designed, implemented, and evaluated as rigorously as conventional science programs (McKinley et al., 2015). A range of methods can be used to certify data validity, with the most common reported as expert review (Wiggins et al., 2011). Development and adherence to a federally- or state-approved Quality Assurance Project Plan (QAPP) has been shown to increase the confidence that sponsoring agencies and external decision makers have in data generated by citizen science programs (Stepenuck and Genskow, 2018). However, QAPP development may be time-consuming and onerous since a QAPP lays out the goals of the project, field and lab protocols, and data handling, analysis, and reporting procedures. For each procedural step, the QAPP describes how volunteer compliance will be ensured, procedures for guarding against bias, and the process for resampling or rejecting problem data. The QAPP provides a procedural framework for program staff and reassurance to potential data users that these data are accurate and valid. The US Environmental Protection Agency provides QAPP guidance for volunteer water monitoring programs (USEPA, 2019).

The process of thinking through the necessary volunteer protocols and quality assurance steps "forces the program manager to carefully consider the reasons for collecting the data; the objectives for using the data; the needs and limitations of the methods, equipment, and personnel; and the need for contingency plans" (Latimore and Lawson, 2007), and for a particular question, may reveal that a citizen science approach is not a good fit. Projects that require specialized knowledge or training, expensive or complex equipment, great time commitments, or that take place in potentially hazardous conditions may not be suitable for citizen science (McKinley et al., 2015). Although citizen science projects can result in improved public participation in environmental stewardship and decision making, it is not always the most effective path to engagement. In fact, McKinley et al. (2015) argue that direct outreach can be more efficient and effective in stimulating engagement than citizen science projects.

Citizen science best practices

The current surge in interest in citizen science across many scientific disciplines has led to growth in associated scholarship supporting best practices, as well as many successful programs that serve as models. Several "toolkits" that compile resources and best practices for citizen science programs also exist (See Relevant Websites).

As with any scientific endeavor, a clear statement of the question or need to be addressed by the project is critical, as is the definition of goals and objectives. This framework guides the choice and development of data collection and handling protocols, project scale, and "job descriptions" for volunteer participants, program staff, and professional scientists. Clarity in project goals and objectives also supports development of an evaluation process through which realistic expectations can be set and the program can be regularly assessed and adapted, if necessary.

Resources and, in most cases, training of program participants are critical to ensure volunteer confidence in their roles and to ensure accurate, credible data and participant safety (Fig. 4). While some contributory programs may require no more than clear and concise instructions for submitting observations or reviewing imagery, many citizen science programs include classroom and field training programs, or pair inexperienced participants with seasoned, trained volunteers or staff who can guide and supervise

Fig. 4 MiCorps volunteers learn to identify aquatic plants during an in-person training session. Training is also offered online to increase accessibility and participation. Credit: Jo Latimore.

activities. If improved public capacity to engage in water resource management is a program goal, then resources or training in sharing program results should be provided, in addition to the training needed to collect or analyze data (Stepenuck and Genskow, 2018).

Assurance of data credibility is important for all citizen science programs, so methods for certifying data validity should be incorporated into program design. The most common approach for volunteer water monitoring programs is development of and adherence to a Quality Assurance Project Plan that is approved by a federal or state agency (see discussion above).

Attention must be paid to volunteer recruitment and retention throughout the project. Clear "job descriptions" for potential participants provide clarity of task and time commitment expectations. Offering a range of activities suited to different interests, abilities, availabilities, and levels of expertise allows a program to tap into a broad pool of potential participants; the option of one-time, low-effort participation can be an attractive option for participants who may then be inspired to commit to a more significant role in the program (Latimore and Lawson, 2007).

Understanding of the interests, availability, and motivation of current and potential project participants is valuable to match to program expectations. Helping the environment (Domroese and Johnson, 2017) and providing water resource information (Alender, 2016) motivate many participants in citizen science programs, perhaps less so than increasing personal knowledge (Nerbonne and Vondracek, 2003). Thus, it is important for programs to share with their participants specifically how results are being used to protect water resources or provide them with training and resources to use the results themselves. A review of eight US volunteer water quality monitoring programs revealed that volunteers are less interested in rewards or recognition for their participation, and more interested in hearing about the tangible results of their efforts (Alender, 2016).

Case study: Example of citizen science on inland waters: The Michigan Clean Water Corps

The Michigan Clean Water Corps (MiCorps) is the State of Michigan's volunteer lake and stream monitoring program. Formed in 2003, MiCorps incorporated two previously established citizen science programs: the Volunteer Stream Monitoring Program, launched in 1998, and the Cooperative Lakes Monitoring Program begun in 1974 that is the second-oldest statewide volunteer lake monitoring program in the US.

MiCorps is overseen by the Michigan Department of Environment, Great Lakes, and Energy, which has long recognized the value of public participation in collecting water quality data and engagement in the assessment and management of Michigan's lakes and streams. The MiCorps program is administered by a team of partner organizations, including academic and environmental stewardship organizations, which together bring the scientific, technological, and public engagement skills needed to run a successful, large-scale volunteer water monitoring program.

MiCorps mission

The mission of MiCorps is to network and expand volunteer water quality monitoring organizations statewide for the purpose of collecting, sharing, and using reliable data; educate and inform the public about water quality issues; and foster water resources stewardship to facilitate the preservation and protection of Michigan's water resources (MiCorps, 2021).

MiCorps goals

- Establish a volunteer monitoring network to facilitate communication, data and information sharing, common methods, and quality assurance practices.
- Promote and expand the volunteer monitoring network by identifying and assisting the development of new volunteer monitors and volunteer monitoring programs statewide.
- Educate the public about water quality issues and foster exemplary environmental stewardship.
- Gather and exchange reliable and meaningful water quality data for water resources management and protection programs at the state and local level.

- Establish an Internet-based program, including an enrollment registry, directory of member organizations, a data exchange platform, volunteer monitoring resources, training aids, and a newsletter.
- *Include a volunteer monitoring recognition program with a Certification of Recognition for each member organization and a Certificate of Participation for each volunteer member* (MiCorps, 2021).

All data collected by MiCorps volunteers, current and historic, is publicly available in the MiCorps Data Exchange online (https://micorps.net/about-data-exchange/). Program outcomes are shared with volunteers via written reports and regular communications.

The MiCorps Cooperative Lakes Monitoring Program (CLMP)

The CLMP offers participants a suite of parameters to monitor in their lake, including:

- Water transparency (Secchi depth)
- Total phosphorus (a productivity-limiting nutrient in Michigan lakes)
- Chlorophyll-a (indicator of algal biomass)
- Dissolved oxygen and temperature (determinants of many biotic species)
- Score the Shore (nearshore habitat assessment)
- Exotic Aquatic Plant Watch (aquatic invasive plant survey)
- Aquatic Plant Identification and Mapping (quantitative assessment and mapping of the entire aquatic plant community)

Participation in the CLMP is open to all. Most volunteers are lakefront property owners and learn of the program through direct outreach efforts through lake homeowner associations. Participants pay a small enrollment fee for each parameter they monitor, to partly cover program costs. The remaining costs are covered by state funds.

Quality assurance measures include participant training, volunteer-friendly protocols and equipment, and post-data collection handling techniques. Volunteers are trained directly by MiCorps program staff. A Quality Assurance Project Plan is adhered to and updated as needed.

The MiCorps Volunteer Stream Monitoring Program (VSMP)

The VSMP focuses on collections of macroinvertebrates as indicators of stream health, augmented by periodic physical habitat assessments. Participation in the Volunteer Stream Monitoring Program is open to all. Volunteer demographics vary widely. State funding allows for a competitive grant program open to non-profit organizations to launch and maintain their own programs. Training follows a "train-the-trainer" model, where MiCorps staff provide training to staff of participating organizations, who then recruit and train their own volunteers. Each participating organization develops their own Quality Assurance Project Plan, which is reviewed and approved by MICorps program staff.

MiCorps outcomes

MiCorps lakes and stream monitoring has advanced public understanding of inland waters, built public support for lake and stream research and management, and informed local management and conservation projects. Communities regularly turn to MiCorps data to assess status and trends in their local water bodies, researchers incorporate the data into regional and national assessments (Fuller and Jodoin, 2016; Poisson et al., 2019), and researchers cooperate with MiCorps volunteers on specialized research projects (Sarnelle et al., 2010). Both state natural resource agencies (the Michigan Department of Natural Resources and the Michigan Department of Environment, Great Lakes, and Energy) use MiCorps volunteer monitoring data to meet their planning and reporting responsibilities. MiCorps data regularly supports management decisions ranging from nuisance aquatic plant control to land use planning and assess the impacts of past changes to lakes and streams, including non-native species invasions and sewer system installations.

Crowdsourcing

Crowdsourcing defined

Citizen science can include crowdsourcing, which is a method of leveraging a large unidentified group of people to perform predetermined tasks (Dickinson et al., 2012). Within the context of citizen science, crowdsourcing is a way of outsourcing, in the most basic cases, tasks such as data collection, classification, and analysis to the community. The concept of crowdsourcing was first defined as a business practice to outsource a specific task to groups of people via the internet (Howe, 2006). In the hierarchical classifications of citizen science, crowdsourcing is considered a lower order method where participants come to the task pre-trained or needing little training. In many applications, crowdsourcing is anonymous citizen science where participants are not individually recruited to participate. While this anonymity can cause problems such as recurring issues of confidence in data quality, it can also be a strength as it is easy to upscale citizen science projects as there is no need for individual recruitment and training.

The original concept of crowdsourcing can lead to problems of training. Not fully knowing your participants makes it more difficult to design training and instruction platforms for crowdsourced citizen science. However, many crowdsourcing projects design research questions that are less complex, such as asking participants to compare observations to training images or report common observations like temperature. This approach allows citizen scientists to draw on their previous knowledge more than

learning new skills. When formal training is conducted in crowdsourcing, the training is typically performed through pre-recorded videos (e.g., CoCoRaHS; Reges et al., 2016) or through some sort of training exercise or games (e.g., CrowdWater; Strobl et al., 2019).

Benefits of crowdsourcing

The biggest benefit of crowdsourcing is the scalability in both space and time. With appropriate design and research objectives, crowdsourcing can open data collection to millions of participants at the continental or even global scale. This method also allows for multiple observations at a single location from multiple users, which provides repeatability that many other citizen science methods lack. Distributing the observations among multiple users at a single location also facilitates error analysis and allows a qualitative measure of each participant's accuracy as compared to the crowd. Based on the type of data collection, for example the use of mobile phones, it is possible to have users collect data at locations even professional scientists who may be conducting the research have not visited.

Crowdsourcing best practices

Crowdsourcing works best with well-defined research questions and simple sampling protocols. Complicated and multi-step observations can create barriers of entry that prevent participation from the crowd. This does not mean that specialized equipment (such as mobile phones or computers) cannot be used, but that this equipment needs to be accessible and familiar to the participants. Examples of situations where crowdsourcing works best include collecting images of streams (e.g., Crowd Water, crowdwater.ch) or cloud cover (e.g., Globe Clouds, observer.globe.gov) using mobile phones through web-based applications.

One concern when using a crowdsourcing approach is the quality control of collected data. Some methods use an oversampling approach for quality control, such as the example of image processing where more than one participant classifies an image (Hennon et al., 2015). If all participants agree on an image classification, it is deemed acceptable, whereas if participants disagree on an image, it is sent to an expert for further classification. This same quality control approach can be adapted to data entry. In the case of field measurements, traditional instruments such as weather stations or pressure transducers can be co-located in selected areas to allow for quality control. It is also possible to use a statistical approach to flag observations that may be erroneous based on related data (Wu et al., 2021). An example would be to flag measurements of stream turbidity if those observations were reported to have been collected at 2:00 AM. Quality control is a much bigger issue with field observations than image processing because experts cannot check the results. This highlights the usefulness of asking participants to take photos of field observations to help professional scientists verify these data.

Crowdsourcing of inland waters

Crowdsourcing of inland water represent a range of methodologies that can use existing or new infrastructure through passive and active participant recruitment. Passive participation can include data mining of existing social networks, describe in more detail below, to quantify human-nature interactions and prioritization of ecosystem function (Ghermandi et al., 2020; Angradi et al., 2018). Active participation can include crowdsourcing of water levels accomplished using physical water level stations at fixed locations (e.g., CrowdHydrology, Fig. 5; Lowry and Fienen, 2013) or virtual water level station at flexible locations (Seibert et al., 2019). The proliferation of mobile phones has exponentially increased the ability to monitor inland waters (Kampf et al., 2018; Malthus et al., 2020). However, it is more common that examples of crowdsourcing of inland waters are community-based projects

Fig. 5 Citizen scientist reporting water levels via text message on Amity Creek in Duluth, Minnesota. Credit: Andrea B. Crouse.

not necessarily reflected in the peer-reviewed literature. Examples include monitoring water clarity and quality (EyeOnWater.org; LakeForecast.org; lakeobserver.org), locating cyanobacteria blooms (cyanos.org/bloomwatch/), identifying river obstructions (river-obstacles.org), and image processing of invasive species (Zooniverse: Deep Lake Explorer). These examples highlight the richness and rapid growth of opportunities to monitor inland waters.

Social media

Social media defined

Another method used in citizen science and to broaden the impact of science is social media, which refers to internet applications that allow users to create and share content and build connections with one another, such as Twitter, Facebook, and Instagram. As of 2021, 72% of US adults used at least one social media platform (Pew Research Center, 2021). Social media is a growing tool for gathering and sharing scientific information, as well as engagement among professional scientists and with the public (Howell et al., 2019). Increasingly, citizen science programs use social media to raise awareness of their programs, recruit participants, and share outcomes (Catlin-Groves, 2012). More broadly, many scientists and members of the interested public are taking to social media to discuss scientific topics.

Benefits of social media

Wilson (2016) discusses several benefits of social media as a communications tool for professional scientists, including:

- Improved science communication - social media platforms require scientists to distill ideas concisely and clearly, in audience-appropriate ways
- Frequent and fast communication of results
- Broader awareness of scientific work and outcomes, which may lead to funding and other forms of public and private support for projects; innovation; and individual career advancement

Social media can provide a platform for two-way engagement between scientists and the public, opening pathways to explore and refine research questions, gather information and data, and share perspectives and experiences. This two-way engagement can advance research and add social relevance to scientific endeavors. A recent exploration of graduate student and faculty attitudes revealed a shared view that the public has valuable insights to contribute to their scientific fields, and that social media provides an opportunity for engagement (Howell et al., 2019).

Social media best practices

Recommended approaches and guidelines for scientific communication on social media coincide with those recommended for all types of science communication, with a few nuances. The approaches include: (i) Be clear and concise - some social media platforms limit the length of posts, so brevity is required. (ii) Include visuals - social media posts that include images or video show greater engagement (Ulloa et al., 2015). (iii) Communicate with integrity, respect, transparency, and honesty (Shiffman, 2019). (iv) Focus on quality messaging rather than social trends. Jumping on social media trends (e.g., popular hashtags, jokes, or memes) can help increase user engagement but should not be prioritized at the expense of delivering substantive and accurate content that is true to your science communication goals. (v) Share others' information when aligned with your (and your organization's) mission and goals (Wilson, 2016). (vi) Consider your audience. What are their interests and values? Why do they (or should they) follow you? Tailor your communication to suit your desired audience(s). (vii) Be open to respectful engagement with scientific peers (within and among disciplines) and non-scientists. Even the best-constructed social media post is only one-way communication of information until others comment – then it can become a truly social opportunity for rich discussion and exchange of ideas.

Practices for mining social media sites for scientifically relevant data are still relatively novel. A critical consideration for researchers in using these approaches is bias. For example, because not all people use social media and the preferred social media platforms vary by demographic (Pew Research Center, 2021), data mined from these platforms will be specific to the populations using the platform. For example, photos posted by Flickr users may not be representative of the locations visited by people who do not use Flickr (Keeler et al., 2015). Further, social media users may only post photographs or information about exceptional events (e.g., extreme floods, large fish caught), leaving researchers to resort to other means of collecting data about "normal" conditions.

Social media of inland waters

There are many ways social media is being used to further understanding and management of inland waters. For example, social media posts can be a rich source of data. Photographs and videos of organisms or environmental phenomena that are publicly shared on social media can be "mined" for information (Catlin-Groves, 2012). For example, Michelsen et al. (2016) analyzed YouTube videos of a cave popular with diving tourists to assess changes in water levels in the cave, leading to better understanding of hydrological changes in the region. Another study assessed the recreational and tourism benefits of improved water quality using

Fig. 6 Water Rangers uses social media platforms, including Facebook and Twitter, to create community and engage with their volunteers.

geotagged photographs shared by travelers on the photo-sharing site Flickr. By using the photographs as a proxy for lake visits, they were able to determine that people are willing to travel significantly farther, and thus spend more money, to visit clearer lakes (Keeler et al., 2015). Social media is also regularly used to promote participation and create community around citizen science and crowdsourcing programs. For example, the Canada-based Water Rangers program (https://waterrangers.ca/) uses Facebook, Twitter, and Instagram to promote participation opportunities, celebrate volunteer contributions, and share success stories (Fig. 6).

Social media can also be used effectively to increase public appreciation and understanding of inland water systems and their components. For example, a fisheries scientist created an annual Twitter campaign, #25DaysofFishmas, with the goal of increasing awareness about aquatic biodiversity in the Great Lakes of the US, using humor. The campaign has become an interactive forum for learning and sharing, with posts retweeted more than 8000 times and liked more than 25,000 times (Burdett et al., 2021).

Conclusion/synthesis

Application of citizen science, crowdsourcing, and social media approaches represent powerful opportunities for advancing understanding and conservation of inland waters. These approaches engage the public in dynamic and meaningful ways and generate an abundance of valuable data and information and can be used to address questions that may be unanswerable by traditional scientific means. The public and transparent nature of well-designed citizen science, crowdsourcing, and social media projects fit well into "open science" culture and practices, which are increasingly being recognized as beneficial to advancement of science and conservation. Most citizen science and crowdsourcing programs provide open access to data as a conscious choice and encourage engagement of both scientists and the public in at least some, if not most or all, stages of the scientific process.

The recent growth of citizen science, crowdsourcing, and social media approaches has also resulted in an expansion of the scholarship around practices and impacts, which, combined with examples of existing programs, provide a solid foundation for new and growing programs to emulate. This scholarship confirms that these approaches can result in accurate, reliable data about inland waters. Further, participants can become more knowledgeable about the issues facing inland water ecosystems and become more likely to engage effectively in public decision-making processes on water policy and management.

Knowledge gaps and opportunities for future research

- How extensively are citizen science and crowdsourced data used for the understanding and conservation of inland waters? Is there a significant gap between the collection of data and its use, and if so, what strategies could close that gap?
- What changes need to be made or metrics achieved for citizen science participation to become main stream in the professional science community? If transformative research and boarder impact have equal weight, why has citizen science not become the gold standard in our current research community?
- What characteristics of data-sharing platforms or structures best facilitate access to and use of citizen science and crowdsourced data?
- What are the primary motivations for citizen scientists to participate in the scientific process and how can professional scientists and managers build stronger participatory communities?
- What approaches of engaging nonscientists with scientific information on social media platforms are most effective in leading to knowledge gain and behavior change?

See Also: **Emerging methods and topics**: Environmental DNA Advancing Our Understanding and Conservation of Inland Waters; Teams, Networks, and Networks of Networks Advancing Our Understanding and Conservation of Inland Waters; **Social/societal values of Inland waters**: The Gender Gap: Women as Authors and Leaders in International Publications in Fisheries Science; **Structures and functions of Inland Waters - Rivers**: Biodiversity Conservation of Aquatic Ecosystems; Inland Waters—Rivers: Land Use and Water Quality; **Structures and functions of Inland Waters - Wetlands**: Ecology and Conservation of Wetland Amphibians and Reptiles; Patterns in Freshwater Fish Diversity; Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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Relevant websites

https://www.aaas.org/programs/center-public-engagement-science-and-technology/communicating-science-online—American Association for the Advancement of Science - Communicating Science Online.

https://www.epa.gov/citizen-science—US Environmental Protection Agency - Citizen Science for Environmental Protection.

https://youtu.be/G7cQHSqfSzI—Citizen science: Everybody counts. TEDxGreensboro.

http://www.crowdhydrology.com/—CrowdHydrology.

https://www.citizenscience.gov/toolkit/#—Federal Crowdsourcing and Citizen Science Toolkit.

https://micorps.net/—Michigan Clean Water Corps.

https://www.pewresearch.org/internet/fact-sheet/social-media/—Pew Research Center - Social media fact sheet.

https://scistarter.org/citizen-science—SciStarter: Overview and compilation of citizen science resources.

https://www.fs.usda.gov/working-with-us/citizen-science/citizen-science-toolkit—U.S. Forest Service - Citizen Science Toolkit.

Dust and Fog Effects on Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Acid neutralizing capacity (ANC) A measure of the overall buffering capacity of a solution against acidification.
Aerosols A suspension of solid, liquid, or gas particles in the atmosphere.
Dry deposition The deposition of dust and other aerosols by gravity.
Orographic Relating to the topographical relief of mountains. Orographic precipitation occurs when an air mass is forced to higher altitudes due to the presence of mountains, leading to condensation.
Persistent organic pollutants Toxic organic compounds that are resistant to degradation within the environment.
Wet deposition The deposition of chemicals via precipitation (rain, snow).
Xenobiotics Synthetic chemicals that is foreign to the body or to ecological systems.

Introduction

The atmospheric deposition of aerosols can occur in sufficient quantities to influence the water chemistry and aquatic communities of receiving inland waters. Although both dust and fog are natural phenomena, human activities have greatly influenced the production, composition, and distribution of these aerosols. For example, any activity that destabilizes soils can increase dust entrainment and influence dust composition. Some examples of land use activities that exacerbate soil erosion include agriculture, animal husbandry, and construction (e.g., Fig. 1). The chemical and aerosol composition of clouds and fog (hereafter fog) is usually more concentrated than rain and is influenced by urbanization and other sources of combustion products. Therefore, fog can play a role in the transportation to or removal of aerosols and soluble gasses from ecosystems.

The composition of dust and fog is influenced by both the composition of the generating source (e.g., the soil or water body composition) as well as chemical reactions that may occur along the transport path including sorting, adsorption, coagulation, nucleation, dissolution, precipitation, and in the case of fog, photochemical reactions. These atmospheric vectors have the potential to transport or export other constituents that may influence aquatic ecology, including metals, microorganisms, pathogens, plastics, and persistent organic pollutants. Both dust and fog can effectively transport nutrients but are likely to differ in their influence on aquatic chemistry. Because dust constituents are frequently alkaline, dust deposition will tend to increase the pH of receiving ecosystems. When downwind of pollution sources, fog can transport significant concentrations of airborne acids, which are

Fig. 1 Dust plumes arising from a tractor in Cache Valley, UT, US. Photo Credit: Patrick Strong.

Fig. 2 Fog in the Bitterroot Mountains, US. Fog can deposit nutrients and other constituents onto catchment surfaces. Source: Flickr.

deposited on surfaces within a catchment and can be subsequently transported to lake systems (Fig. 2). In the case of fog, water droplets generated from a lake surface can also be a vector for moving constituents out of the waterbody and into atmospheric systems.

Defining the minimum deposition rate of dust or other aerosols that could negatively influence an aquatic ecosystem, often described as a 'critical load', would be useful for land managers wishing to identify targets and/or predict whether a system may be affected by upwind activities. However, deposition rates of particulate aerosols onto catchments or lake surfaces may not be sufficient to predict the aquatic response. This is because catchment properties and antecedent lake conditions will also play a role in how an aquatic system responds. Catchment properties can either exacerbate or mollify the effect of deposition by either taking up the deposited nutrients/constituents or facilitating the transport to its aquatic systems. The antecedent lake conditions will also dictate the biological and/or chemical response to changes in atmospheric deposition.

Though the importance of dust in fertilizing soils and oceans over millennial times scales is well understood, only recently have scientists become aware that dust can meaningfully impact freshwater aquatic systems over annual to decadal time scales. This new awareness is in part due to the more recent decadal increases in regional dust emissions associated with land use. Globally, there are comprehensive networks aimed at measuring and monitoring atmospheric concentrations of particulates smaller than 10 μm as these are the sizes that influence human health. However, the bulk of the mass of particulates in local to regional dust sources is found in large size classes. Thus, we still know very little about the composition of atmospheric materials and their influence on receiving aquatic waterbodies. Below, we describe how dust and fog are generated, the controls on composition, the influence to aquatic systems, the role of catchment properties using the special case of mountain lakes, and we point to current knowledge gaps.

Dust generation and sampling

Atmospheric or eolian dust generally refers to mineral particulates that have been eroded from the Earth's surface and subsequently transported through the atmosphere. In contrast, particulate aerosols may refer to both dust and particulates that have formed within the atmosphere itself (e.g., photochemical smog). Dust particles are generated from a number of natural and human sources including soil erosion, industrial emissions (e.g., mining, fossil fuel burning, cement production), transportation, construction sites, biomass burning, residential heating sources, plant products (e.g., pollen), volcanic emissions, and synthetic particles like plastics (Piketh et al., 1999; Mahowald et al., 2008; Gesierich and Rott, 2012; Langmann, 2013; Allen et al., 2019; Brahney et al., 2020a) (Fig. 3). Because dust generated from such sources is transported through the atmosphere to aquatic ecosystems, for the purpose of this chapter, all particulate aerosols will be considered as atmospheric dust, regardless of source.

The production of dust from arid and semi-arid landscapes is a natural phenomenon and is controlled by two primary factors (Field et al., 2010). First, the soil surface must be exposed to erosive forces such as wind. Factors that limit soil exposure to wind include vegetation cover or other surface protectors such as cryptobiotic crust (Belnap and Gillette, 1998; Leys and Eldridge, 1998). Second, there must be sufficient wind energy for soil erosion and subsequent entrainment (Fig. 4). These biogeoclimatic drivers of dust production can be influenced by year to year variation in rainfall, storm tracks, and decadal drought (Prospero and Nees, 1986; Goudie and Middleton, 1992; Qian et al., 2002; Flagg et al., 2014). For example, in the semi-arid regions of the southwestern US, La Niña years lead to decreased precipitation, which suppresses the growth of grasses during the growing season. The loss of the stabilizing vegetation causes the soil to be more susceptible to erosion the following spring when storms and strong winds travel through the region (Okin and Reheis, 2002).

Human activities can exacerbate natural dust production in dust-producing regions and create new dust source areas by removing vegetation cover, water, and/or destabilizing surface soils (Neff et al., 2008; Mulitza et al., 2010; Munson et al., 2011;

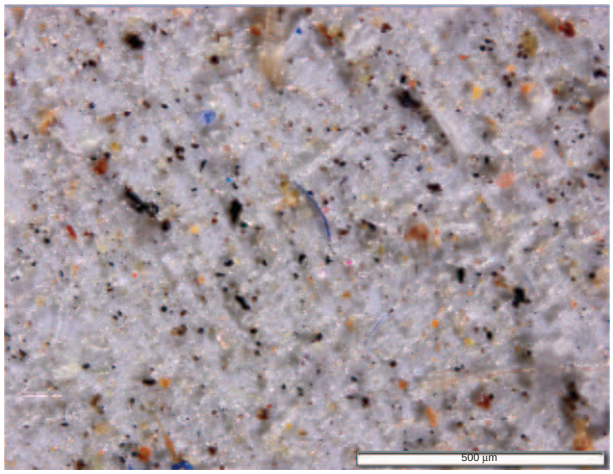

Fig. 3 Dust samples collected by Janice Brahney through the National Atmospheric Deposition Program (NADP http://nadp.slh.wisc.edu/). Visible particles are composed of minerals, amorphous organic matter, charcoal, pollen, car tires, and plastic. Photo Credit: Janice Brahney.

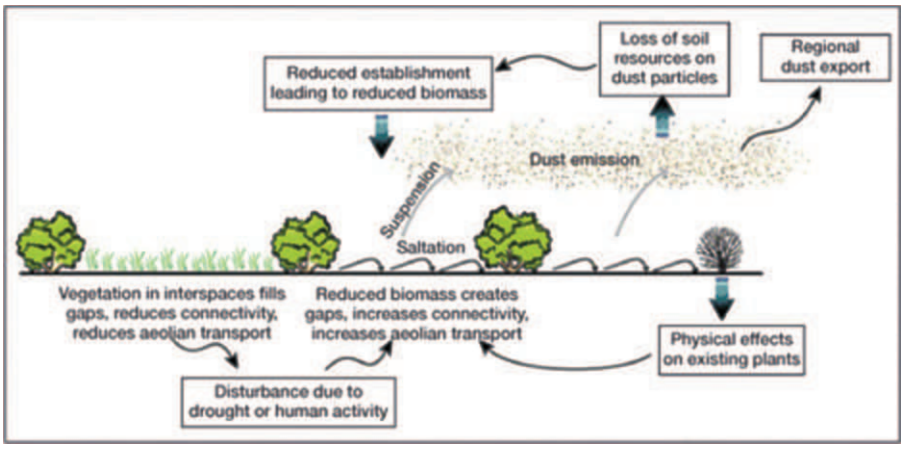

Fig. 4 The role of surface protectors and landscape disturbance on dust generated. Reproduced from Field JP, Belnap J, Breshears DD, Neff JC, Okin GS, Whicker JJ, . . . and Reynolds RL (2010) The ecology of dust. *Frontiers in Ecology and the Environment* **8** (8): 423–430.

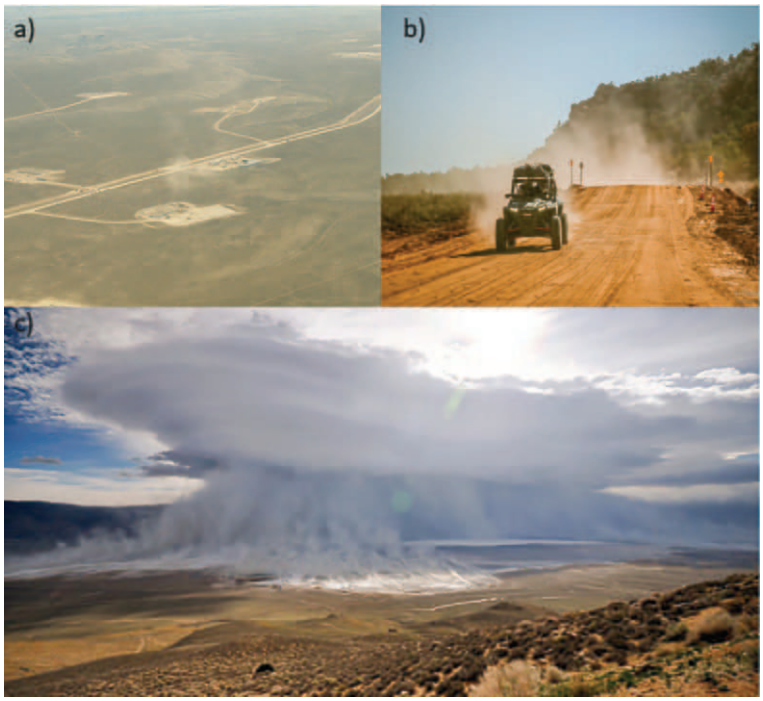

Fig. 5 Human activities and dust production (A) dust generated from well pads in WY, US, (B) dust generated from an ATV, (C) dust from the dry lake bed of Owens Lake, CA, US. (A) Photo: Dawn Ballou, (B) photo David G. Paul, (C) photo: Brian Russell, Great Basin Unified Air Pollution Control District.

Duniway et al., 2019; Brahney et al., 2019). Recent centennial and decadal increases in dust deposition have been linked to both drought and human activities (Neff et al., 2008; Brahney et al., 2013; Aarons et al., 2019; Arcusa et al., 2020). Human land-use activities that can aggravate dust production include agriculture and pastoralism (Neff et al., 2008; Lee et al., 2012; Brahney et al., 2019), water diversions (Saint-Armand et al., 1986; AghaKouchak et al., 2015; Indoitu et al., 2015), industry, roads, and construction (Morishita et al., 2006; Neitlich et al., 2017), oil and gas operations (Brahney et al., 2015a), biomass burning (Andreae et al., 1988), and recreation (Goossens and Buck, 2009) (Fig. 5).

The extent of the human fingerprint on Earth is enormous as more than 95% of the Earth's surface has been appropriated for the variety of land-uses listed above (Kennedy et al., 2019). Impacts of this human fingerprint are highlighted by a 50% diversion of the global runoff (Abbott et al., 2019). These diversions can lead to desertification and the complete or near-complete loss of large lake ecosystems whose lakebeds are then susceptible to wind erosion (Reheis, 1997; Larsen, 2014; Wurtsbaugh et al., 2017). Approximately 40% of the Earth's surface has been appropriated for pasture and crop production (Foley et al., 2005), which can exacerbate soil erosion through tillage or by reducing the threshold wind velocity required for soil entrainment (Leys and Eldridge, 1998; Goossens, 2004; Neff et al., 2005). The widespread fingerprint of human activity on the Earth's surface, combined with persistent and intensified droughts, led to an increase in global atmospheric dust generation in the 20th century (Mahowald et al., 2010). It is estimated that human sources make up 25% of the global 21st century dust production (Ginoux et al., 2012). This increase in the movement of material through the atmosphere has the capacity to significantly alter the natural biogeochemistry of receiving aquatic ecosystems.

Although dust emissions caused by humans have increased in recent centuries and decades, natural dust generation events are episodic and controlled by stochastic and climatic factors (Moulin et al., 1997; Prospero and Lamb, 2003). As a result, dust deposition rates in inland aquatic ecosystems are highly variable across space and time, which poses challenges to sampling efforts. To illustrate, 15 years of dust on snow data from the intermountain west has shown as few as three to as many as 12 dust events during the winter season with corresponding mass deposition rates ranging from 1.65 to 64.3 g m^{-2} $year^{-1}$ (CODOS, 2019). At a global scale, dust deposition rates range from 0 to 450 g m^{-2} $year^{-1}$ with the highest deposition rates influenced by proximal (<10 km) sources (Lawrence and Neff, 2009).

Dust sources are divided into three broad categories based on their proximity to dust deposition sites, namely "Local" dust sources originating from 0 to 10 km away, "Regional" from 10 to 1000 km, and "Global" from greater than 1000 km (Lawrence and Neff, 2009). Dust source distance influences the deposition rate and the spatial heterogeneity in deposition, the chemical composition, and the particle size distribution. Whether or not a researcher is interested in quantifying the effect of local, regional, or globally sourced dust will influence the types of samplers used and where they are placed on the landscape. Dust derived from local sources tends to have larger particles sizes and is likely transported closer to the ground surface than aerosols sourced from long distances. For example, Asian dust over North America is typically less than 2.5 μm in size and found between 500 and 3000 m asl (VanCuren and Cahill, 2002).

Fig. 6 Field deployed active (left) and passive deposition samplers. Photo credits: Jeff Perala-Dewey and Molly Blakowski.

Methods for sampling dust fall into two categories, namely passive and active sampling (Fig. 6). Passive sampling techniques rely on the gravitational deposition of particulates into the sampling apparatus (e.g., Reheis and Kihl, 1995). Bulk passive samplers collect particulates deposited both dry and with rain, whereas some samplers are designed to capture dry and wet deposition separately (Reche et al., 2018; Brahney et al., 2020b). Active sampling techniques use a vacuum to draw air through a filter and/or foam to capture gasses, aerosols, and dust (Hart et al., 1992). One advantage of active sampling techniques is that it allows for the separation of aerosols by their size (Büttner, 1988). A disadvantage is that active sampling methods provide atmospheric concentrations, not deposition rates. Concentrations may be more important for understanding atmospheric chemistry and the impacts to human health, but deposition is more relevant for quantifying and understanding the ecological implications of dust deposition.

Fog formation and sampling

Fog, or ground-based cloud, is comprised of water droplets whose size usually ranges from a micron to ~50 μm. These droplets, which are suspended in the atmosphere (Gultepe et al., 2007), are often referred to as occult precipitation (Weathers, 1999; Weathers et al., 2020). Occult precipitation is an apt description of fog behavior—fog hangs in the atmosphere—and also an indication of the complexities inherent to quantifying its deposition since it does not fall vertically like rain. Fog is formed via radiative cooling of moist air either as a result of advection over land from large water bodies or adiabatic expansion (e.g., upslope fog formation).

Of the three primary forms of atmospheric deposition—wet (rain, snow), dry (aerosols and gasses) and fog—fog sits between wet and dry: it is liquid, but because its droplets are suspended, its deposition is governed by meteorological conditions (e.g., windspeed) and receptor surface (i.e., vegetation) (Weathers and Ponette-González, 2011). Because of this, it is unlikely that direct deposition of fog to inland water surfaces is significant. Collection of fog water is usually accomplished via passive or active collection devices (Fig. 7). Passive collectors rely on wind to drive droplets onto collection surfaces, which are often inert strands or mesh, after which the droplets run down the surface into a collection bottle. Active collectors pull air into an opening and across a collection surface at constant speed. Advantages of using an active collector include that high windspeeds are not necessary to collect a sample of sufficient volume, and liquid water content of the sample can be calculated easily.

Dust and fog composition

Dust and fog composition are determined by the biophysical environment of the source region as well as other factors that alter its reactivity during transportation to deposition sites. The primary controls on dust composition are the parent geology and degree of soil development of the source region, as well as human land use activities. To illustrate, dust from arid regions such as the Sahara are typically poor in organic content comprising less than 1% of the dry mass (Eglinton et al., 2002), while dust generated from agricultural regions can contain much larger fractions of organic and nutrient-rich material, up to 67% (Malm et al., 2004). Dust may also change appreciably in composition during travel through the atmosphere due to sorting, scavenging, and chemical

Fig. 7 Passive (top) and active sampling of fog. Photo credit: Kathleen Weathers (top), Collett research group (bottom).

reactions. For example, the progressive loss of the larger size fractions due to sorting may lead to a loss of heavier and larger minerals such as zircons and silicates. Various gaseous and particulate emissions may also be scavenged by dust during transport through adsorption, coagulation, nucleation, dissolution, and precipitation reactions. As a result, dust produced in or passing through urban centers will have a composition influenced by combustion sources (fossil fuels, incinerators), volatile metals, and organic contaminants (Han et al., 2004; Marx et al., 2008; Xiong et al., 2017; Goodman et al., 2019) (Fig. 8). The chemical and biological composition of fog is often reflective of its regional environment (Weathers et al., 1988, 2020; Evans et al., 2019; Gultepe et al., 2007). Fog has been recorded to have up to a 100-fold higher chemical concentration than rain collected from the same location (Kimball et al., 1988; Weathers et al., 2020) (Fig. 9). Dust and fog can also contain synthetic compounds such as pesticides, fertilizers, or even plastics (Glotfelty et al., 1987; Allen et al., 2019; Brahney et al., 2020a). Finally, dust and fog can act as a vector for the transport of microorganisms including pathogens that can affect human and ecosystem health and functioning (Hervàs et al., 2009; Metcalf et al., 2012; CDC, 2013; Reche et al., 2018).

Dust and fog influences on aquatic system pH

The acid neutralizing capacity (ANC) references the ability of water body to resist, or buffer, changes in pH. Most natural waterbodies have pH ranges between 6.0 and 9.0 pH units and deviations higher or lower can fundamentally alter the ecology and chemistry of the waterbodies. Lakes with low natural ANC are sensitive to external inputs, like acid rain. Because dust is often, but not always, generated from sedimentary basins, dust often includes carbonate minerals and can therefor affect receiving water ANC.

Carbonate minerals such as $CaCO_3$ are readily soluble in even slightly acidic waters contributing ANC to both precipitation (Loye-Pilot et al., 1986; Rogora et al., 2004, 2016; Brahney et al., 2013; Kopáček et al., 2016) and aquatic ecosystems through the addition of the bicarbonate ion (Psenner, 1999; Tait and Thaler, 2000; Rogora et al., 2004). Fig. 10A shows a tight correlation

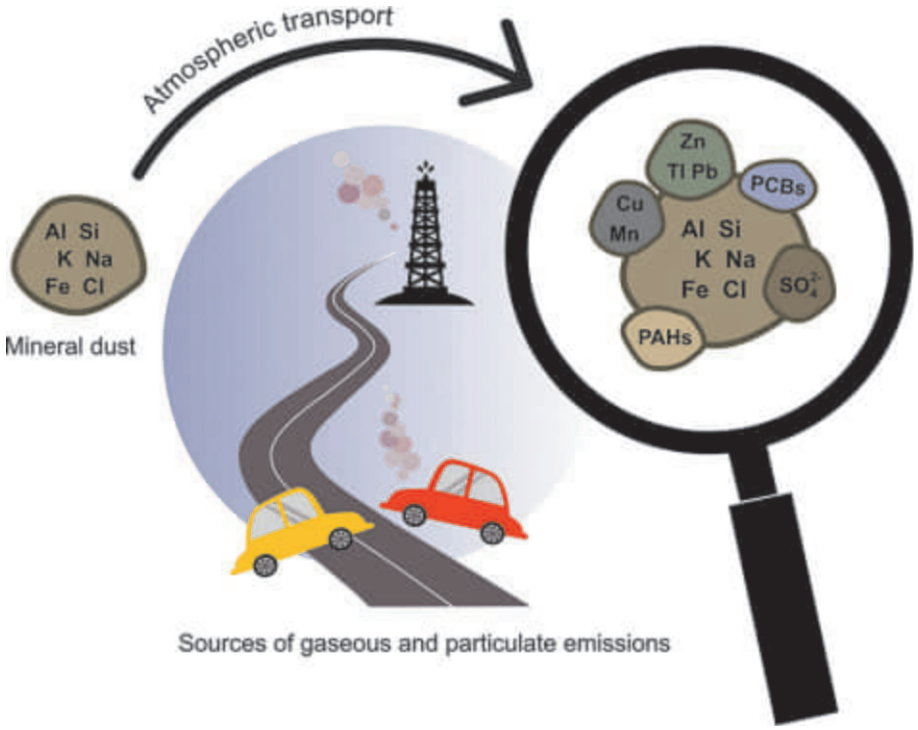

Fig. 8 During atmospheric transport, the reactive surfaces of dust can be modified by elements and compounds introduced to the atmosphere by human activities. Image credit: Molly Blakowski.

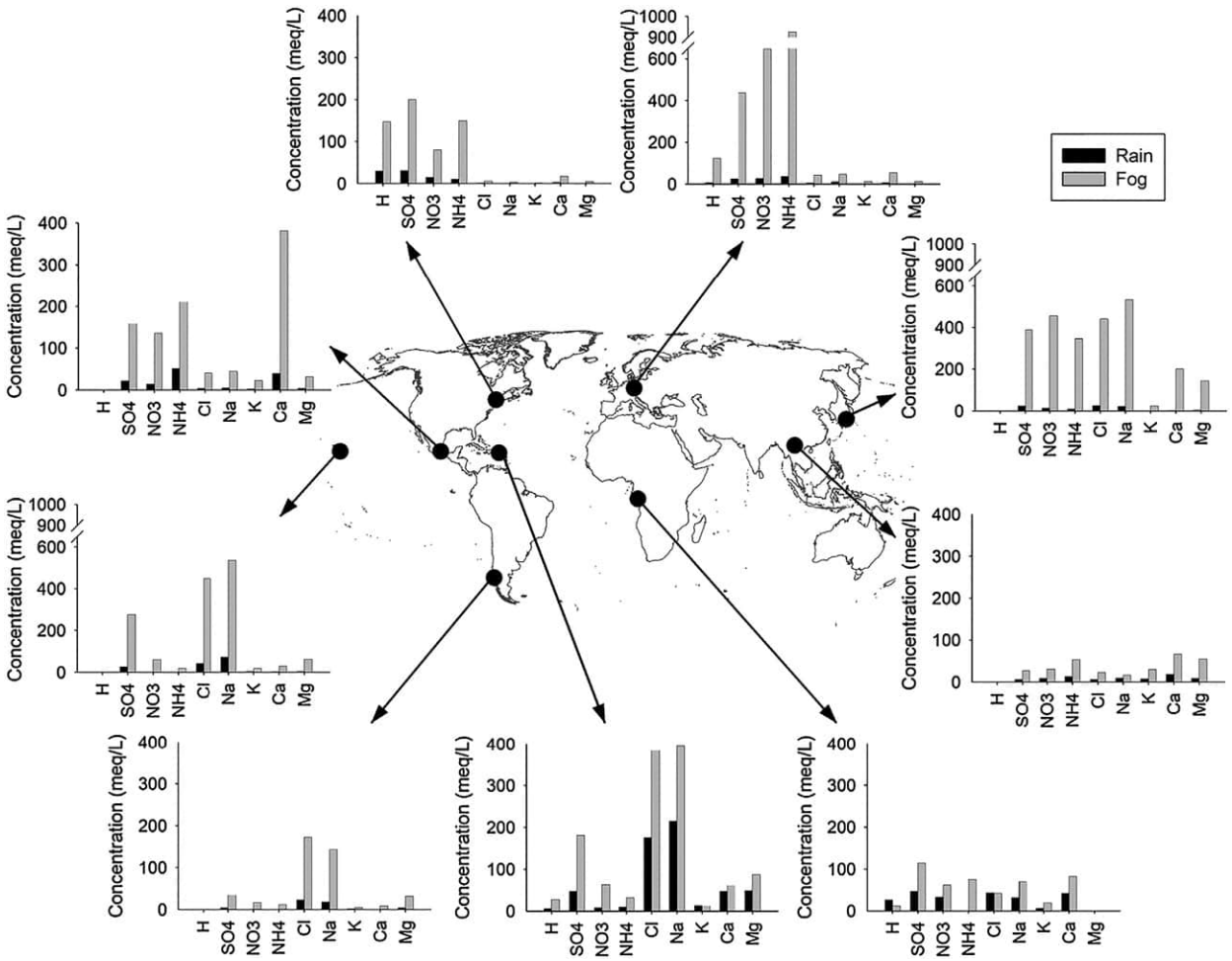

Fig. 9 The concentration of major ions in fog is considerably greater than concentrations found in rain water, even in arid regions. Image reproduced from Weathers KC, Ponette-González AG and Dawson TE (2020) Medium, vector, and connector: Fog and the maintenance of ecosystems. *Ecosystems* 23:217–229.

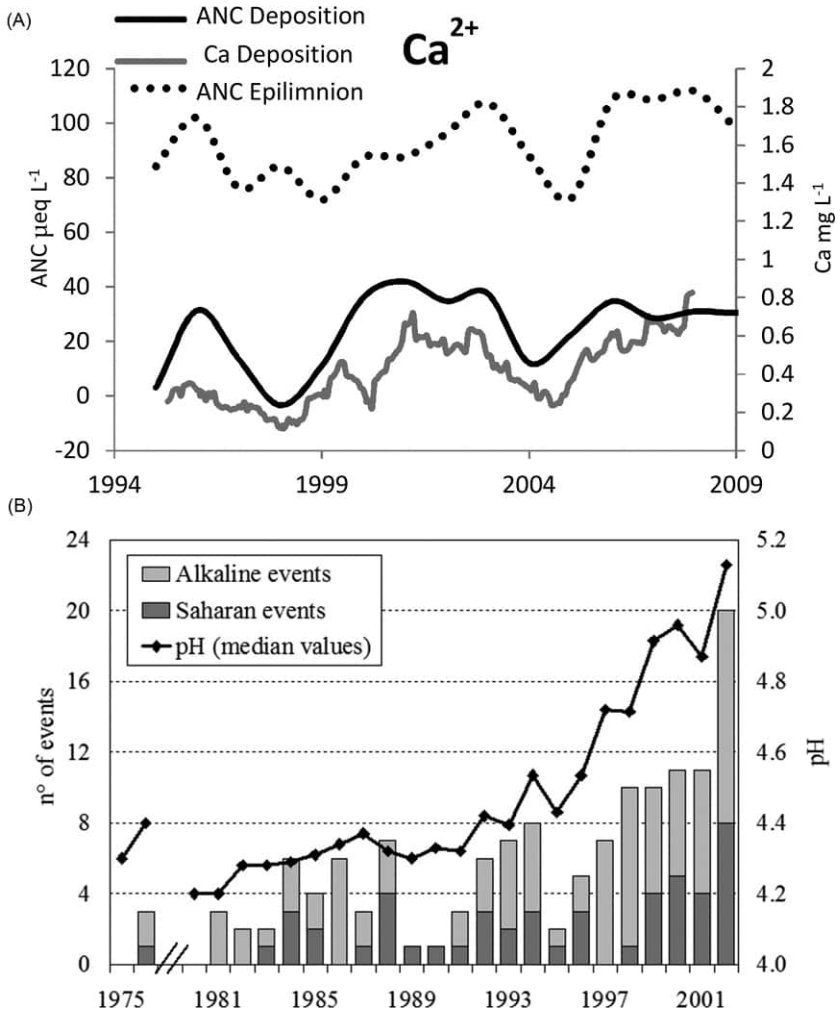

Fig. 10 (A) Temporal correlation between the Acid Neutralizing Capacity (ANC) in the Epilimnion of Blake Joe Lake, Wyoming with the dust (Ca^{2+}) and ANC in deposition (Brahney et al., 2014). (B) Temporal trends in Saharan dust events and the pH and alkalinity of precipitation in the Lake Maggiore region of Italy and Switzerland (Rogora et al., 2004).

between dust deposition, precipitation ANC, and the ANC of Black Joe Lake, Wyoming, illustrating the relationship between dust contributions and the buffer capacity of lake systems. Alkalinity contributions from dust may counteract acid deposition from other human activities. For example, the quartzite bedrock of the Uinta Mountains is naturally poor in ANC, yet these mountain waters have not experienced acidification despite their proximity to acid emissions. It has been speculated that dust contributions have buffered these aquatic systems that remain neutral to alkaline (Messer et al., 1982; Ellis et al., 2015). The effect of dust on lake recovery from acidification is illustrated in Fig. 10B. Elevated Saharan dust deposition from the 1990s onward is thought to have aided in the recovery of Lake Maggiore from acidification (Rogora et al., 2004).

The calcium carbonate content of dust ranges from 0% to 33% worldwide (Lawrence and Neff, 2009). However, due to its high solubility in water in some regions, the calcite content may rapidly disappear during transport, particularly if airborne acid concentrations are high (Jacobson and Holmden, 2006). Thus, the dust source composition, the distance traveled, and the presence of acid precursors in the atmosphere will influence the extent to which dust may neutralize acids in freshwater systems.

Dust and fog delivery of nutrients and metals to aquatic ecosystems

The transport of the key limiting nutrients such as nitrogen (in dust and fog) and phosphorus, carbon, and calcium to ecosystems may occur in both the organic and inorganic forms. Dust and fog may also be vectors for metals to ecosystems, some of which may be necessary micronutrients while others are considered toxins. Because it is aqueous, fog can effectively transport ions such as nitrates (NO_3^-) and ammonium (NH_4^+), and can trap and move particulates such as pollen, or particulate organic carbon from atmosphere to ecosystem (e.g., Fuzzi et al., 1997; Fenn et al., 2000). The bioavailability of nutrients, and thus their capacity to

influence inland waters, will vary with the composition of the particulate aerosols. For example, the water-soluble fractions of nutrients are immediately available for biological uptake whereas the organic or mineral bound fractions may become available over longer time periods. Dust can directly deposit nutrient and metals onto lake surfaces and some portion of the dust deposited within the catchment will be mobilized to the lake basin (Brahney et al., 2015a). Though fog is often enriched in elements (N, P, Ca, C) relative to rain (Fig. 9), direct deposition to lake surfaces is unlikely and it is not clear how efficiently fog deposition is transported into lake systems.

At present, a critical unknown is how the antecedent lake conditions will influence the response and bioavailability of deposited dust. Both pH and nutrient limitation can theoretically influence the efficiency of nutrient acquisition from dust particulates based on enzyme production and activation. Regardless, the atmospheric deposition of bioavailable nutrients will not only increase primary production but can also influence community composition through the alteration of N:P ratios (Elser et al., 2009a,b, Camarero and Catalán, 2012). For example, there is a strong linear relationship between the stoichiometry of nutrient deposition and that found in mountain lake systems (Fig. 11). These data suggest that direct atmospheric deposition is a primary control on mountain lake nutrient availability, which in turn influences production and species composition.

Nitrogen

Nitrogen deposition via rain and gaseous aerosols is well monitored and modeled around most areas of the world (Holland et al., 2005; Lü and Tian, 2007; NADP, 2019). Less is known about the contributions of nitrogen to receiving ecosystems from dry dust material as this fraction is rarely analyzed, although it is often modeled (Jia et al., 2016; TDep, 2019). Likewise, while fog has been shown to deliver proportionally large quantities of nitrogen to fog-dominated terrestrial ecosystems (e.g., Weathers et al., 2000a,b, 2020), little sustained, coordinated fog monitoring has been conducted. Furthermore, as noted earlier, while fog is chemically concentrated when compared to rain, direct deposition to inland waters is likely to be very limited.

In some areas, the dry fraction could potentially be an underappreciated component of the atmospheric nitrogen deposition (Neff et al., 2002; Cornell, 2011). The water-soluble organic nitrogen fraction has been shown to contribute approximately 25% of the flux of total nitrogen to Europe (Mace et al., 2003b; Cornell, 2011), 66% of the flux to North America (Neff et al., 2002), and up to 45% of the total nitrogen flux in the Amazon basin (Mace et al., 2003a; Cornell, 2011). Morales-Baquero et al. (2013) quantified wet and dry deposition of nitrogen associated with Saharan dust events, and found that wet deposition accounted for a larger fraction, with a Dry:Wet ratio of NO_3^--N at 0.56 and TN at 0.78. The bioavailability of particulate nitrogen is likely to vary according to dust composition, which is largely influenced by the climate and human land use patterns of the source area. For example, biomass burning and agriculture may contribute to the particulate nitrogen flux in areas where these practices occur, whereas, in the Mediterranean region, the organic nitrogen fraction has been linked to soil and dust sources (Mace et al., 2003b). Because dry deposition rates of nitrogen are generally modeled rather than measured and the spatial variability in deposition is high, overall uncertainties in the deposition rate of organic nitrogen and its waters soluble fraction can be large (Cornell et al., 2003).

Phosphorus

In contrast to atmospheric nitrogen, phosphorus has no stable gaseous form and thus atmospheric transport largely occurs as particulates. Important sources of atmospheric phosphorus include soils, biomass burning, and industrial emissions (Mahowald et al., 2008). Owing to the erodibility of the fine-grained, nutrient-rich fractions of soil, on average, dusts are enriched in

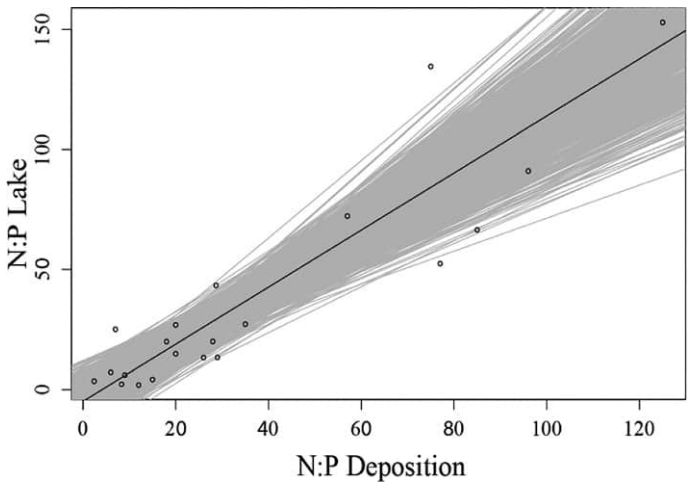

Fig. 11 The global relationship between the N:P ratio in atmospheric deposition and the N:P ratio in co-located mountain lakes. Each point represents the average within a mountain region spanning four continents (Brahney et al., 2015b).

phosphorus over average crustal concentrations by a factor of 1.6 (Lawrence and Neff, 2009). Thus, dust generally has the capacity to fertilize receiving ecosystems. Because fog can effectively scavenge and transport particles, total phosphorus concentrations measured in fog can be enriched compared to rain, and account for a sizeable portion of the mass flux of the nutrient to leaf surfaces in some areas (Vandecar et al., 2015).

Phosphorus concentrations in dust range from <1 mg g^{-1} to 5 mg g^{-1} (Tipping et al., 2014; Brahney et al., 2015b) but the form of particulate phosphorus will greatly influence the bioavailability of deposited phosphorus. Exchangeable and water-soluble phosphorus are the most bioavailable, while phosphorus bound in organic matter can be released in the water column when broken down by free enzymes and microbes. Phosphate bound to Iron (Fe) or Aluminum (Al) oxides or phosphorus locked up in the mineral apatite may not be biologically relevant over seasonal timescales but may become available through longer time scales.

The source of atmospheric particulates influences the forms of particulate phosphorus. For example, dust originating from the Sahara are dominantly minerogenic, with the organic fraction making up just 1% of the dry mass (Eglinton et al., 2002). Much of the phosphorus in this dust is tied up in apatite and iron minerals (Clausnitzer and Singer, 1996; Eijsink et al., 2000). Nevertheless, studies have shown that approximately 10% of the phosphorus in the Saharan dust becomes available within one hour, and an additional 30–40% within just 16 hours (Herut et al., 1999; Ridame and Guieu, 2002). Dust originating from agricultural or semi-arid soils, in contrast, can have organic concentrations that range from 15% to 67% by weight of dry mass (Dahms and Rawlins, 1996; Malm et al., 2004; Lawrence and Neff, 2009). Particulates from biomass burning may also be enriched in phosphorus (Newman, 1995; Boy et al., 2008; Ponette-Gonzalez et al., 2016). However, the concentration of P in emitted ash may vary with both the type of vegetation burning and the intensity of the fire (Maenhaut et al., 1996; Vicars et al., 2010; Vicars and Sickman, 2011).

Because phosphorus is a key limiting nutrient in aquatic ecosystems, the atmospheric deposition of this nutrient to remote sensitive aquatic ecosystems is of concern. The capacity for dust to affect phosphorus nutrient subsidies in mountain lake systems was first identified in the Austrian Alps (Psenner, 1999). Since then, other studies elsewhere in mountain regions of Europe, Asia, and the US have shown the effects of dust associated phosphorus deposition on controlling lake water nutrient chemistry, productivity, and species composition (Sickman and Melack, 2003; Morales-Baquero et al., 2006; Pulido-Villena et al., 2008; Tsugeki et al., 2012; Brahney et al., 2014). A 2016 study showed that oligotrophic (low phosphorus) lakes and streams in the continental US may be becoming higher in nutrients and the sites most affected were the most remote with the least amount of human influence within the catchment (Stoddard et al., 2016). This result suggests that phosphorus is likely entering these catchments via the atmosphere, potentially as dust. Lowland lakes are not exempt from the influence. For example, in regions with intense burning, even large lakes have been enriched in nutrients due to large atmospheric contributions (Tamatamah et al., 2005; Boy et al., 2008).

Research in the Wind River Range of Wyoming, US has provided strong correlational evidence that even at low deposition rates (e.g., <4 g m^{-2} $year^{-2}$), dust can transport phosphorus in sufficient quantities to affect lake systems. Because the dominant dust source to the Wind River Range is the nearby Green River Valley, a gradient in dust deposition across the range exists (Dahms, 1993; Dahms and Rawlins, 1996; Brahney et al., 2014). Dust affected lakes in the range had higher total phosphorus (TP) concentrations and up to two orders of magnitude greater primary and secondary production than nearby non-dust affected lakes (Brahney et al., 2014). Sediment core analyzes corroborated the spatial analyzes and showed temporal relationships between dust deposition and the diatom-inferred phosphorus concentrations in lakes (Fig. 12). This research highlights that while large dust storms or haboobs may generate public interest, smaller chronic emissions, which may not be visible via satellite, may lead to significant cumulative consequence in receiving water bodies.

There is a growing body of evidence that dust phosphorus can have measurable consequences in lake ecosystems Sickman and Melack, 2003; Reche et al., 2009; Vicars et al., 2010; Ballantyne et al., 2011; Camarero and Catalán, 2012; Brahney et al., 2014, 2015a,b). However, all but one of these studies (Reche et al., 2009) relied on correlational rather than experimental analyzes. Therefore, more research on the role of dust phosphorus is required to fully understand ecosystem impacts.

Calcium

Calcium is an important nutrient for many organisms in lake systems, but in particular for invertebrates, where the element makes up a key component of their shells and carapaces (Tessier and Horwitz, 1990; Wærvågen et al., 2002). Calcium leached from dusts into aquatic systems may be derived from a variety of minerals including feldspars, phyllosilicates, gypsum, dolomite, and calcium carbonate ($CaCO_3$). The dissolution of calcium carbonate and other dust minerals either in precipitation or in depositional water bodies can provide readily available calcium ions (Ca^{2+}) to remote mountain lakes (Pulido-Villena et al., 2006). For regions with catchments having low natural calcium abundance, this contribution may be a critical source of calcium to aquatic organisms with relatively high calcium requirements. Measured calcium carbonate concentrations from Chinese dust sources have ranged from 2% to 10% (Jacobson and Holmden, 2006), African sources from 2% to 20% (Guieu et al., 2002), U.S. sources from 1% to 25%, and up to 33% in parts of the Middle East (Singer et al., 2003). For example, in the Sierra Nevada Mountains in Spain, paleolimnological research showed that in the last ~50 years there has been an intensification of dust and Ca^{2+} inputs from the Sahara (Jiménez et al., 2018). This, combined with the effects of climate change, resulted in increased Ca^{2+} concentrations, which in turn, led to an increase in *Daphnia*, a Cladocera taxon, whose growth and reproduction can be impaired by low Ca^{2+} (Jeziorski et al., 2008). *Daphnia* is a keystone genus, and the expansion of their populations is an indication of significant environmental changes in this region, illustrating the role dusts may have in shaping community composition.

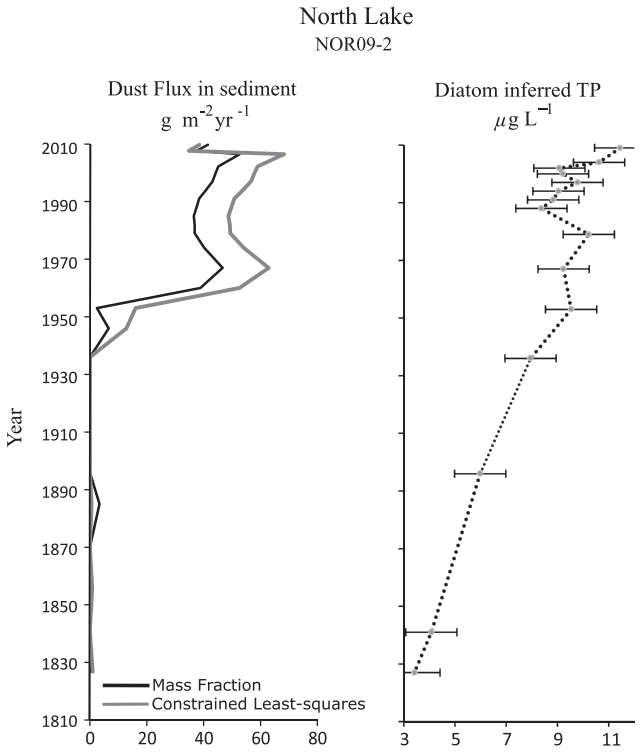

Fig. 12 Historical dust deposition rates to North Lake in Wyoming paired with diatom-inferred total dissolved phosphorus (TDP) concentrations.

Carbon

Dissolved organic carbon (DOC) concentrations in high-elevation lakes has been associated with the water-soluble organic carbon fraction of dust (Reche et al., 2009; Mladenov et al., 2011). Because alpine lakes are above tree line, terrestrial production and export of dissolved organic matter (DOM) is generally low and alpine lake transparency high. DOC not only serves as a substrate for microbial metabolism, but also adsorbs harmful ultraviolet radiation (UVR) that would otherwise act to suppress production. Thus, the dust-mediated transport of water soluble organic carbon (WSOC) can have both physical and biotic implications. A study in the Mediterranean reservoirs showed that dust transport of DOC into waterbodies reduced transparency and (UVR) penetration, and was associated with shallower mixing depths (de Vicente et al., 2012). Nutrient and DOC inputs from dust likely also support microbial growth in receiving water bodies (Pulido-Villena et al., 2008; Reche et al., 2009; de Vicente et al., 2012).

Metals

Along with macro nutrients (N, P, C, Ca) dust can transport trace elements that can act as either nutrients or toxins, depending on the concentration. Although several studies have quantified the metal concentrations within dust and the role of dust in transporting heavy metals such as As, Cd, Cr, Cu, Fe, Ni, Pb, Sb, Se, and Zn to aquatic systems (Sweet et al., 1998; Reynolds et al., 2014; Brahney et al., 2015a), there are no studies to date that directly examine the influence of dust-metal deposition on the ecology of lake systems. However, Goldman et al. (1990) attributed an increase in Lake Tahoe production during forest fires to nutrient and trace metal additions via ash deposition. Iron is critical for biological processes, including photosynthesis and nitrogen fixation, and may be limiting in some oligotrophic lakes systems (Vrede and Tranvik, 2006; North et al., 2007). Bhattachan et al. (2016) showed that dust iron (Fe) is more soluble than soil Fe and provided evidence that Fe in dust becomes more soluble through atmospheric processing, thus atmospheric processes may increase the bioavailability of soil macro and micronutrients. Future work might focus on quantifying the bioavailability of dust metal deposition to inland, oligotrophic systems, and the role of multi-element nutrient limitation on community composition and production.

Microorganism deposition to and export from inland waters

Dust and fog transport may represent a significant mechanism for the dispersal of microbes ranging from viruses to fungi across ecosystems, which have the potential to alter the function of resident communities (Kellogg and Griffin, 2006; Lindström and Östman, 2011; Yamaguchi et al., 2012; Reche et al., 2018). Microhabitats within dust and in situ sediment particles have been shown to enhance the survival of pathogens extending their range of influence (LaBelle and Gerba, 1982; Rao et al., 1984; Reche

et al., 2018). Further, microbes in coastal fog have been shown to resemble aquatic and terrestrial genera (Dueker et al., 2012; Evans et al., 2019), demonstrating that fog can be a vector of microbes from aquatic to adjacent terrestrial ecosystems.

Experiments in the Sierra Nevada and Pyrenees Mountains of Spain demonstrated the viability of transported taxa in laboratory experiments (Hervàs et al., 2009; Reche et al., 2009). However, the likelihood of establishment in a recipient habitat will relate to seeding pressure and the resident community composition (Jones et al., 2017). This microbe seeding may be particularly influential in mountain regions where the losses of perennial snowpack and glaciers have exposed new terrain and established new terrestrial and aquatic systems. Although atmospheric deposition of dust is likely to result in dispersal of microbes to inland waters (Peter et al. 2014), recent research suggests that fog may be a vector for microbial export from inland waters to adjacent terrestrial systems (e.g., Dueker et al., 2012; Weathers et al., 2020). Aerosols generated from lake surfaces have also been shown to contain cyanobacteria and associated toxins (Cheng et al., 2007; Banack et al., 2015; Olsen et al., 2018). The export and import of microbes to lakes and the ecological relevance of these processes are currently not well understood.

Aerosol effects on solar radiation

Dust and fog also have the ability to affect photosynthetically active radiation (PAR) in aquatic ecosystems. In fact, the greatest impact of fog on inland waters is likely to be indirect through its effect on PAR. Fog has been shown to reduce PAR and affect photosynthesis in terrestrial systems (Weathers et al., 2020). However, in terrestrial systems that are enveloped in fog, there is a counterbalancing effect on plant productivity through hydrologic modulation by fog: trees transpire less. In a similar way, dust can absorb PAR and it is likely that during periods of intense biomass burning, lakes experience diminished solar irradiance to a point where primary production is altered (Scordo et al., 2021) (Fig. 13).

Dust and fog effects vary by lake and catchment characteristics

The effect of dust and fog on water chemistry and biology in aquatic ecosystems will vary with catchment and lake characteristics. Geology, aspect, slope, catchment morphometry, and vegetation type and cover can all act to either mollify or exacerbate the influence of atmospheric deposition on receiving water bodies (Morales-Baquero et al., 1999). Steep, rocky slopes with poor vegetation cover can be very effective at delivering atmospherically deposited nutrients to waterbodies, whereas vegetation and soils can take up nutrients either effectively delaying the transport to the waterbody or preventing it altogether.

In steep mountain catchments, dust material can be mechanically focused into lake basins by either wind redistribution, or overland flow. However, catchment geology will play a role in the transport of phosphate as it binds tightly to available Al and Fe-oxide minerals, even when vegetation is poor. An abundance of these minerals within catchments may effectively immobilize phosphorus on the landscape (Vicars et al., 2010; Kopáček et al., 2011, 2015). Conversely, watersheds with poor soil development and a low abundance of Aluminum (Al) and Fe bearing minerals may allow for the effective transport of dust–phosphorus to lake basins (Tsugeki et al., 2012; Brahney et al., 2014).

Lake morphometry, including area, depth, volume, and fetch can influence whether lakes are more or less susceptible to the effects of atmospheric deposition. The addition of nutrients and other compounds can be diluted if the volume of the upper mixed layer of a lake (epilimnion) is relatively large, for example. Pre-existing lake conditions are also likely to influence the role of atmospheric nutrient deposition. Acidified lakes are likely to respond to a greater degree to dust alkalinity contributions and phosphorus limited lakes may see a greater increase in production than lakes that are predominantly nitrogen limited. Those hypotheses have yet to be explicitly tested.

Fig. 13 A lake enshrouded in fog to the extent that solar radiation reaching the lake surface is diminished. Similar effects may occur with excessive particulates in the air from smoke or inversions. Peter Dasilva/EPA, via Shutterstock.

A special case: Mountain lakes

Mountain lakes and their catchments are highly varied in their composition (Fig. 14). Thus, the response of any one lake to similar dust composition and deposition rates are likely to vary. Mountain ranges act as natural barriers to the atmospheric transport of material and orographic precipitation on windward slopes that may produce fog and effectively scrub the atmosphere of particulates. Mountain lakes tend to be particularly sensitive to atmospheric deposition due to their small, steep, and poorly vegetated catchments. These types of lakes are also excellent recorders of dust deposition due to enhanced mechanical transport of dust to lake basins. Further, a uniform and simplified geology of small catchments allows for the geochemical tracking of dust deposition rates in sediment core studies (Neff et al., 2008; Reynolds et al., 2010; Brahney et al., 2015a; Routson et al., 2016). Researchers can use the geochemical composition of dust and catchment bedrock as fingerprints and the relative amount of bedrock versus dust material that accumulates in a lake's sediment can be used to reconstruct historical dust loading. As such, mountain lakes provide an excellent context for studying changes in dust deposition and any associated effects on mountain lake chemistry and biology. Contemporary and paleolimnological analyzes in mountain lakes worldwide have shed light on long- and short-term dust histories as well as the variation in chemical composition, and influence on aquatic ecosystems through the atmospheric addition of alkalinity, nutrients, trace elements, contaminants, and organisms.

Research on the dust-mediated transfer of phosphorus to aquatic systems has primarily focused on oligotrophic mountain lake systems as they have few alternative watershed sources of nutrients (Morales-Baquero et al., 2006; Vicars and Sickman, 2011; Camarero and Catalán, 2012; Brahney et al., 2014). Similarly, the atmospheric deposition of N and its effect on aquatic systems is pronounced in mountain watersheds where natural concentrations are low and abatement through catchment uptake is limited (Baron et al., 2000, 2011; Wolfe et al., 2001; Nydick et al., 2003; Elser et al., 2009a). Thus, in mountain systems, a small change in atmospheric loads can result in a large change in absolute nutrient concentrations, causing mountain lakes to be more susceptible to the influence of atmospheric deposition than lowland lakes and those with large watersheds (Moser et al., 2019). For example, in the Sierra-Nevada Mountains of Spain, dust associated P deposition ranged from 24 to 38 $\mu g\ P\ m^{-2}\ day^{-1}$, a seemingly small contribution, yet this deposition rate had measurable effects on productivity, nutrient ratios, bacterial abundance, and plankton diversity (Morales-Baquero et al., 2006; Pulido-Villena et al., 2008; Reche et al., 2009). In fact, there is evidence suggesting mountain lakes may experience reduced functional diversity and a diminished efficiency in the trophic transfer of energy up the food web as a consequence of dust deposition (González-Olalla et al., 2018). Because mountain lakes are sensitive to such perturbations, a warmer dustier future may fundamentally alter mountain lake community composition.

Fig. 14 Mountain catchments and their lake chemistries are highly varied. (A) No name lake, British Columbia, (B) Gibson Lake, British Columbia, (C) North Lake, Wyoming, (D) Buster Lake, British Columbia. Photos: Janice Brahney.

Summary

Dust and fog have the capacity to influence the physical, biogeochemical, and biotic components of inland waters both directly and indirectly. Paleolimnological, modeling, and monitoring studies have shown that soil and biomass emissions have increased across large regions of the globe (Neff et al., 2008; Mulitza et al., 2010) and the resulting deposition has led to ecosystem shifts, such as elevated production, changes in pH, and associated changes in community composition. Because particulate emissions are tied to human land-use changes from pastoralism, food production, biomass burning, and the frequency and severity of drought, it is reasonable to conclude that with human population growth and climate change, eolian dust may become more important to aquatic ecosystems in the near future (Foley et al., 2005; Hudson, 2011; Trenberth et al., 2014). Fog is more likely to have indirect impacts on inland waters through scattering and absorption of incoming light, and hydrologic and biogeochemical impacts to adjacent catchments. However, in some systems and under certain conditions, inland waters may be a source of condensation nuclei for fog and thus result in an export of biotic or abiotic materials from inland waters to surrounding terrestrial systems.

Knowledge gaps

There are many knowledge gaps in our understanding of dust and fog deposition and subsequent direct and indirect effects on inland water ecology and ecosystem processes. Here we outline a few. While we know that what goes up into the atmosphere must come down, we know less about what is emitted, transported, and deposited when it comes to dust and fog. For example, there are few studies that have examined novel pollutants, pesticides (xenobiotics), nanoplastic, metals, or ash in either dust or fog, or what quantities of these chemicals make their way into aquatic ecosystems. Whether the aerosols and chemicals that are transported are also bioavailable to aquatic systems is also a major question. We know that dust can contain relatively high concentrations of nutrients, like phosphorus. However, phosphorus in dust can be found at mineral or organic exchange sites, bound within organic matter, or locked up in minerals. The ability for an aquatic organism to acquire dust-derived nutrients may also vary with antecedent lake properties, like pH and nutrient limitation. At present, the variability in dust composition and thus the bioavailability of dust-nutrients is not well quantified and there are limited studies evaluating how aquatic organisms respond directly to dust deposition in either controlled or in-lake experiments.

In recent years there has been an increasing interest in understanding to what extent materials move from inland waters to adjacent ecosystems via atmospheric transport. Of particular interest and concern is the transport of potentially toxic substances such as cyanotoxins. Further, several studies have shown that dust, and sometimes fog, can transport viable microbes to distal locations, and that the composite microbial community reflects the particle source area. However, whether or not the deposited microbes influence or shape the resident microbial community has not yet been addressed in the literature.

Finally, along with climate warming, dust on snow can change albedo and accelerate snowmelt (Skiles et al., 2018) leading to shifts in the pulse of water and nutrients to receiving water bodies. Changes in the timing snowmelt has led to shifts in periphyton communities in river systems. It is possible that dust-induced earlier runoff and nutrient delivery could impact lake ecosystems as well, but to date we are unaware of any research targeting this specific question.

See Also: **Fundamental concepts and theories**: Hydrologic Setting Affects Ecosystem Processes; Hydrological Cycle and Water Budgets; **Human pressures and management of Inland Waters**: Agricultural Pressures on Inland Waters; The Role of Wetlands in Mitigating Impacts From Diffuse Agricultural Loads; **Social/societal values of Inland waters**: Riparian Buffers and Land Cover Change; **Structures and functions of Inland Waters - Lakes**: Measurement and Variability of Lake Metabolism; pH of Inland Waters; Surface Mixed Layers in Lakes; **Structures and functions of Inland Waters - Rivers**: Inland Waters—Rivers: Land Use and Water Quality

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Freshwater Ecoacoustics—A New Addition to the Limnologists' Methods Toolkit

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Automatic call recognizer An application that uses various techniques (often machine learning or artificial intelligence) to automatically find acoustic events.
Autonomous Recording Unit A self-contained audio recording device that is deployed in marine or terrestrial environments for bioacoustical monitoring.
Bioacoustics The branch of acoustics concerned with sounds produced by or affecting living organisms, especially as relating to communication.
Ecoacoustics An interdisciplinary science that investigates natural and anthropogenic sounds and their relationship with the environment over a wide range of study scales, both spatial and temporal, including populations, communities, and landscapes. Ecoacoustics operates in all types of terrestrial and aquatic (freshwater and marine) ecosystems extending the scope of acoustics and bioacoustics.
Hydrophone A microphone designed to be used underwater for recording or listening to underwater sound. Most hydrophones are based on a piezoelectric transducer that generates an electric potential when subjected to a pressure change, such as a sound wave.
Passive acoustic monitoring (PAM) Is used to measure and monitor sounds emitted by organisms or ecosystems. It differs from active acoustic monitoring which often manifests itself by sonar emissions from research vessels.
Soundscape The acoustic environment as perceived by humans.

Introduction to aquatic bioacoustics and ecoacoustics

Environmental changes—both natural and human-induced—can be very difficult to monitor. Often remote locations can be only reached infrequently so changes in the environment that occur between sampling events can be hard to detect. Ability to detect change is also exacerbated in freshwater systems, for which specialized equipment and expertise are often needed. Freshwater species are about three times more likely to be endangered by extinction than terrestrial taxa, making it crucial to properly monitor these species (Almond et al., 2020). Bioacoustics and its sister discipline ecoacoustics are emerging non-invasive and real-time monitoring techniques that have been used to survey rare and endangered species' population trajectories and the impact of human activities on ecosystems (Sueur and Farina, 2015; Farina and Gage, 2017). Bioacoustics is analogous to biology—i.e., studying single species and the sounds they produce, including production mechanisms. Ecoacoustics is an interdisciplinary science that investigates natural and anthropogenic sounds and their relationship with the environment over a wide range of study scales, both spatial and temporal, including populations, communities, and landscapes.

Problem 1: Risks to fish health and habitat integrity. Classic techniques like netting and electrofishing can cause injury or even death in fish. This is inappropriate for sensitive or threatened species.

Problem 2: Bias. While all sampling methods are biased to varying degrees, a key source of bias is the act of sampling itself. It often causes fright responses of the target fish, making detection difficult.

Problem 3: Temporal variation. Usually single survey events are used to estimate ecosystem health and monitor population. This can only deliver a snapshot of the population at a single sampling time.

Fig. 1 Three key problems with traditional monitoring that ecoacoustics solves.

Ecoacoustics addresses three problems with more traditional sampling methods (Fig. 1). Apart from mitigating sampling-induced risk of damage to species and ecosystems as well as certain sampling biases, acoustic monitoring is able to autonomously detect continuous environmental change in an ecosystem. This is a major improvement on classic sampling techniques which often only entail annual or quarterly sampling.

In terrestrial systems, acoustic monitoring has been used to monitor wildlife populations for many decades. Historically, tape recorders were used to capture the sounds of nature by researchers like Aldo Leopold and Rachel Carson who used acoustics in behavioral and ecological studies. Sounds have been used to survey birds and amphibians since the 1960s, formalized in the Breeding Bird Survey of North America (Peterjohn and Sauer, 1999). These surveys were then manually processed by listening to the recordings to tally call types and frequencies. These manual survey processing techniques that resulted in studies optimizing call detection continued until the 21st century. The first auto-detection algorithms were developed between 1996 and 2005 with increased and accessible computational power as research computing moved from centralized clusters to home computers and laptops. Automatic processing revolutionized both bioacoustics and ecoacoustics as much larger data volumes could be processed.

Ecoacoustics is an emerging discipline studying the ecological relevance of environmental sounds (Sueur and Farina, 2015; Farina and Gage, 2017). It studies sounds at ecologically relevant scales including the individual, population, community and landscape (or soundscape). An acoustic population is composed of the songs of one species. An acoustic community is made up of different species producing sounds. Finally, a soundscape not only includes the acoustic community (biophony) but also geological sounds (geophony) such as wind or rain and anthropogenic noises (anthropophony) such as airplane or car sounds (Pijanowski et al., 2011). In this chapter, we discuss the history of bioacoustics in freshwater systems, as used to study both fish and invertebrates. We then describe abiotic sounds and introduce the holistic field of ecoacoustics. After a short primer on analysis techniques, we cover current challenges and recent frontiers in the field, before closing with a discussion of ecoacoustics as an engagement tool.

History of bioacoustics in inland waters

While even experienced freshwater ecologists are often unaware of the diversity in underwater sounds, the field of bioacoustics has a long tradition. In his Historia Animalium, Aristotle described the two key methods of sound production in fish in close to correct anatomical detail (Aristotle, 1910). Aristotle mentioned both stridulation ("rubbing motion of the gills"), as well as the use of the swim bladder ("an organ with air inside it") as sound producing mechanisms. In the 17th century, Izaak Walton noted that fish could hear and in the middle of 19th century sound production in fishes was also mentioned in communications to Charles Darwin by Fritz Mueller (https://www.darwinproject.ac.uk/fritz-m-ller). Mueller described sound production in 10 families, both by stridulation and vibration of the swimbladder. Ralph W. Tower—a professor at Brown University—in 1908 described the sound production mechanism of three drumfishes, as well as the sea-robin and toadfish in a groundbreaking and anatomically detailed study, paving the way towards an expanding field of research and on-ground applications (Tower, 1908).

The abundance of reference calls for fish is still greatly lagging behind reference calls for birds or anurans, despite a large effort by two researchers in the 1970s, Marie Fish and William Mowbray (Fish and Mowbray, 1970). The entire archive was digitized and is currently still shaping the backbone of the fish section within the Cornell's Macaulay Library sound archive. That said, the library still only harbors ~900 fish calls, as opposed to ~1.2 million bird calls, although this is hard to quantify as the taxonomic backbone for 'Actinopterygii' has recently disappeared from the library. Currently, a major drive to catalogue fish sounds is underway—on the aptly named 'FishSounds' platform (https://fishsounds.net/).

The science of behavioral aspects of fish sound and communication was driven forward by academics in North America and Europe including Arthur Popper, Michael Fine, Friedrich Ladich and Eric Parmentier, among many others (Ladich and Fine, 2006; Fine and Parmentier, 2015). In the early 2000s, a group of researchers led by Rodney Rountree and Joseph Luczkovich led the charge to drive an expansion of the field of applied ecoacoustics, especially of fish (Luczkovich et al., 2008). In recent years, researchers in the freshwater realm started to document calls, but also began to use acoustic data in behavioral and general ecological studies. For example a research group led by Rodney Rountree started cataloguing the sounds of six piranha species in the Amazon

(Rountree and Juanes, 2020) and a few Canadian studies looked at behavioral aspects of burbot (*Lota lota*) under arctic winter ice using acoustics (Grabowski et al., 2020). The science of building automatic recognizers and other processing options has also greatly progressed, starting with an automatic signal processing workflow for river redhorse (*Moxostoma carinatum*) spawning by a group of American researchers from the University of Georgia (Straight et al., 2014).

Fish bioacoustics

Fish have one of the highest diversities of vocal organs of any animal group, with many sounds made by the swim bladder—a gas filled organ that is mainly used to regulate buoyancy in the water column (Fig. 2). Similar to a plastic air balloon or a drum skin, the

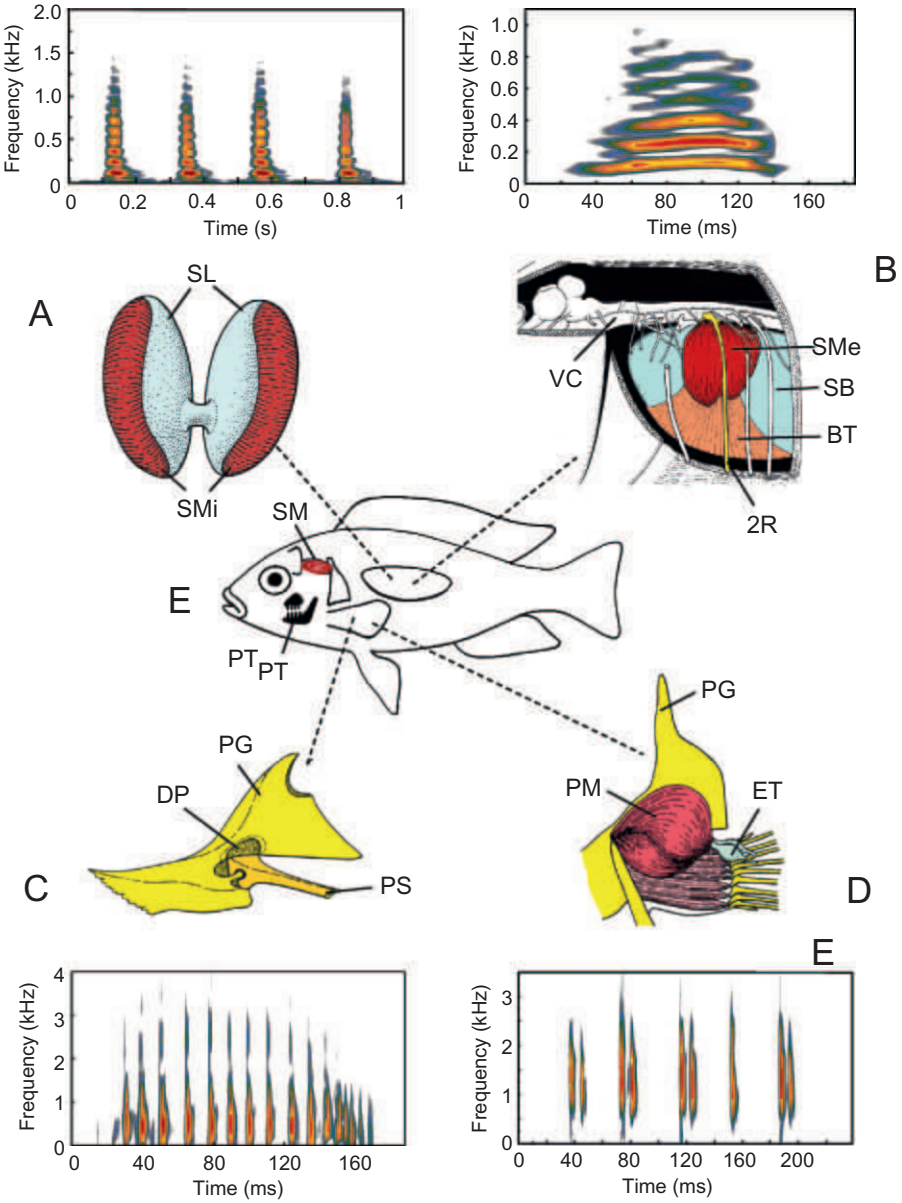

Fig. 2 Diversity of sound generating mechanisms in fishes and sonagrams of sounds produced by these mechanisms. (A) Intrinsic sonic muscles (SMi) attached to both swim bladder lobes (SL) in the Lusitanian toadfish *Halobatrachus didactylus*, (B) extrinsic sonic muscles (SMe) originating at the second rib (2R) and inserting on a broad tendon (BT) ventrally of the swim bladder in the black piranha *Serrasalmus rhombeus*, (C) in the stridulatory mechanism in catfish a ridged dorsal process (DP) of the pectoral spine (PS) rubs in a groove of the shoulder girdle (SG), (D) enhanced pectoral fin tendons (ETs) are plucked similar to guitar strings in the croaking gourami *Trichopsis vittata*, (E) Pharyngeal teeth (PT) stridulation in damselfish, sunfish, among others, and pectoral girdle vibration in sculpins by a sonic muscle (SM) originating at the skull and inserting at the dorsal part of the pectoral girdle. 2R: second rib, BT: broad tendon, DP: dorsal process of pectoral spine, ET: enhanced tendons, PG: pectoral girdle, PM: pectoral adductor muscle, PT: pharyngeal teeth, PS: pectoral spine, SL: swim bladder lobes, SM: sonic muscle, VC: vertebral column. All sonagrams show sounds produced in agonistic contexts. With permission from Ladich (2014).

vibrations of the swim bladder produce harmonic sounds, allowing it to be used as a resonator in sound production (Ladich, 2014). Sound production using the swim bladder includes a variety of mechanisms—hinting at convergent evolution—with the common feature being the perfect resonator of the swim bladder itself (Ladich and Fine, 2006). Some fish—toadfishes (Family: Batrachoididae) for example—have intrinsic muscles that trigger the vibration of the swim bladder to produce sound. Other taxonomic groups trigger the vibrations in the swim bladder by external muscles (Ladich, 2014). These muscles can be either directly attached to the swim bladder—for example in the family Terapontidae, a common family of freshwater grunters in Australia. The second mechanism, observed in Piranhas is an indirect connection via tendons or bony plates (Rountree and Juanes, 2020).

Not all sound production mechanisms involve the swim bladder. Catfish (multiple families in the order Siluriformes) rub a spine against the pectoral girdle—located under the pectoral fin—to produce a sound by stridulation (Ladich, 2014). The nature of this sound means that catfish can be heard above water as the production mechanism is not associated with the airfilled resonator that collapses above water. Other sound producing mechanisms around the pectoral fin are tendon vibration—often compared to plucking a guitar string, as well as vibration of the entire pectoral girdle in sculpins (Superfamily: Cottidae). Last, stridulation sounds can also be produced by grinding pharyngeal teeth, a second mechanism of piranha sound production, but also observed in damselfish (Family: Pomacentridae) and sunfish (Family: Molidae) (Fig. 2; Ladich, 2014).

Invertebrate bioacoustics

Aquatic invertebrates—especially insects—are one of the major components of the freshwater orchestra (Linke et al., 2018; Desjonquères et al., 2020). A wide diversity of insects and a few freshwater crustaceans are known to produce sounds underwater. This includes four orders of insects—Coleoptera, Heteroptera, Odonata and Trichoptera (Desjonquères et al., 2015). Sound production has been reported in one family of Asian Odonata larvae, one family of Trichoptera larvae, and two Coleoptera larvae species. Sound production in larvae is relatively anecdotal in contrast with sound production in Coleoptera and Heteroptera adults. Six families of Coleoptera and seven families of Heteroptera are known or suspected to produce sounds (Aiken, 1985).

Most insects and Crustaceans stridulate: they rub a tough ridge—the scraper—against a finely striated surface—the file. Most people are familiar with crickets producing sounds by rubbing their hind legs against their elytras; in the case of aquatic insects, a variety of body parts are involved. Most Corixidae produce sounds by rubbing a striated area of their front legs on the ridge of their head (Aiken, 1985). Other body parts involved in insect sound production include the abdomen, wings, various leg segments, and genitalia (in *Micronecta* sp. for example). Although stridulation is the most common mechanism of sound production in insects, some species produce sounds in other ways including muscle contraction (e.g., in a lesser diving beetle, *Acilius sulcatus*), or air expulsion (e.g., in the larvae of the great silver water beetle *Hydrophilus piceus* or the diving beetle *Cybister confusus*).

Aquatic invertebrates produce sounds for reasons similar to their terrestrial counterparts: sex, fear and food. Many insect signals are associated with reproduction. For example males produce signals to attract females and repel male competitors. Such is the case with water boatman males, *Palmacorixa nana*, which produce courtship signals to attract females. Females are attracted to the densest aggregations of calling males while males avoid those dense aggregations where they experience more antagonistic interactions. Some insect larvae and adults such as *Hygrobia* beetles produce antipredator squeaks when handled. *Hygrobia* beetles were even sold as 'squeakers' in London's Covent Garden Market (Aiken, 1985). Finally, some caddisflies in the family Hydropsychidae emit ultrasounds when fighting for their retreat and feeding territory (Vuoristo and Jansson, 1979).

Although invertebrates are one of the major components of the underwater orchestra, they remain a neglected focus of freshwater bioacoustic and ecoacoustic studies. A recent review of the literature highlights that they represent the focus of only a quarter of the freshwater acoustic studies while they are estimated to constitute almost 90% of the sound producers(Greenhalgh et al., 2020). This neglect is likely the source of our limited knowledge about the mechanisms and functions of sounds produced by invertebrates.

The sound of physico-chemical processes

Various physico-chemical processes produce sounds including flow turbulence, sediment transport and gas emissions (Linke et al., 2018). First, similar to wind in terrestrial environments, the water current in rivers and streams is an important source of sounds. Some may consider it as noise concealing animal sounds. Yet flow sounds can be rich and informative. These sounds result from flow turbulence and sediment transport and are thus indicative of geomorphological characteristics of the study locations (Tonolla et al., 2011; Lumsdon et al., 2018). Such sounds have enabled researchers to classify different river segments and habitat types, differentiate rivers with and without hydropeaking, and quantify water reaeration.

Another important component of freshwater soundscape comes from gas emitted by ecological processes such as organic matter decomposition, plant respiration and photosynthesis. Anaerobic decomposition of organic matter by micro-organisms may create methane pockets in the sediment that when released produce diverse bubbling sounds in standing water environments such as ponds and lakes (Linke et al., 2018). These decomposition sounds often co-occur with the sound of photosynthesis. Aquatic plants and algae release oxygen bubbles when photosynthesizing. These bubbles may produce ticking and whistling sounds when expelled in specific conditions (Freeman et al., 2018). Recent soundscape research shows that soundscape daily variation was related to oxygen daily variation, suggesting that such sounds may constitute important drivers of the soundscape (van der Lee et al., 2020).

Researchers are starting to uncover sounds related to physico-chemical processes. But this area requires extended research to better understand these sounds. Do different plant species produce different sounds? Do environmental conditions influence these sounds? Monitoring these sounds is likely to provide valuable insights towards the understanding of dynamics of ecological processes in freshwater environments.

Anthropogenic noises

In addition to being a tool for monitoring and assessment of natural components of ecosystem health, the soundscape can also assess the amount of anthropogenic noise present. As vocalizations have a communicative role for many soniferous animals, the incursion of human-induced noise can interfere with the normal functioning of an ecosystem. As with other aspects of freshwater ecoacoustics, knowledge regarding the impact of noise on freshwater ecosystems is sparse compared to terrestrial and marine environments, for which there is an abundance of evidence that noise has often deleterious effects.

In freshwater environments, anthropogenic noise comes from various sources including transport (boats but also cars on nearby roads and bridges), recreation (water parks), extraction (gravel pits) and construction activities. These noises can be present in a wide range of environments, including lakes, rivers and ponds. For example, in Irish lakes surveyed by Marta Bolgan and her colleagues, anthropogenic noise reaches sound pressure levels as high as 135 dB re 1 μPa (Bolgan et al., 2016).

Freshwater taxa suggested to be negatively impacted by noise include various species of fishes, invertebrates, and river dolphins (Celi et al., 2013; Popper and Hawkins, 2019). Mechanisms of disruption include interference with the communicative functions of animal calls; behavioral change in response to sound, for example provoking fear responses; physical damage to hearing mechanisms in the case of loud sounds such as pile driving, and possibly interference in echolocation function. Recent research has also investigated the effect of noise on feeding behavior of freshwater fish and has showed that immediate effects of noise include less efficient prey capture (Purser and Radford, 2011). Noise could thus impose disruptions on the whole trophic chain.

For suitable conservation policies to be developed, much more work needs to be done to assess and quantify the impact of noise on freshwater environments. Whilst there is widespread recognition of 'noise pollution' as a policy issue in marine environments (although virtually no binding regulations to address it), there has been little corresponding governmental attention in freshwater environments.

Ecoacoustics—Theory and analysis methods

Until recently, the study of animal sounds has focused on single species in controlled experimental settings. Lately, researchers are starting to adopt a more integrative approach to understand the importance of environmental factors in influencing acoustic behaviors (Short et al., 2020). For example, the presence of noise, other species, or rain may result in variation in acoustic behavior. Concurrently, recording the sound emanating from the environment has become technically easier with the advent of autonomous recorders. Ecoacoustics has resulted from these two paradigm shifts (Sugai et al., 2019).

The ecoacoustic understanding of acoustic communities is currently based on two main theories: the acoustic niche hypothesis and the acoustic adaptation hypothesis (Krause, 1993). According to the acoustic niche hypothesis, each species occupies a specific acoustic niche and this pattern is driven by the cost of overlapping with other species. Species sharing the same vocalizing environment, timing and frequency band, are thus expected to diverge in at least one of those dimensions (time, space or frequency; Krause, 1993). The acoustic adaptation hypothesis posits that animals vocalizing should optimize their signal such that it propagates well in their environment. Thus, animals vocalizing in the same habitat should acoustically converge towards optimal propagation. These two hypotheses are expected to result in two different patterns of signal co-existence (Morton, 1975). This question of constraints in acoustic community assemblage has generated much interest and tests for these hypotheses reveal conflicting evidence. Novel theoretical development suggests that the two predicted patterns (divergence or convergence) may result from a variety of other ecological and historical processes and should thus be interpreted with care just as any other ecological community pattern.

Ecoacoustics relies heavily on data collected by autonomous recorders over several days, months and sometimes even years. Data volumes are usually too large to be processed manually by listening. For example, the Australian Acoustic Observatory—an Australian-wide passive acoustic monitoring scheme—will collect recordings equivalent to a duration of 2000 years of recordings over 5 years (Roe et al., 2021). Ecoacousticians thus need to use automatic or semi-automatic analysis methods. There are two main approaches: acoustic indices and signal classification.

Acoustic indices are mathematical functions allowing quantification of certain characteristics of the spectrogram thought to be related to some aspect of bio- or acoustic diversity (Sueur et al., 2014). They are cost-effective tools to characterize the variation in animal sound production in recordings. There are more than 60 acoustic indices available. They have been applied successfully to detect acoustic and biological diversity; to distinguish soundscapes in different environmental conditions including different time (Linke et al., 2020a), different habitats (Fuller et al., 2015) and land management types; or to estimate population abundance (Borker et al., 2014). The efficiency of acoustic indices as indicators of biological diversity is under a lot of scrutiny. In aquatic environments, this scrutiny has different stakes. Most acoustic indices were developed with bird songs in mind and thus may not be the best tools to characterize acoustic diversity in freshwater environments composed mostly of rhythmic, non-tonal sounds from insects and fish. Yet, acoustic indices allow us to detect spatio-temporal differences in freshwater environments (Linke et al., 2020a).

Another approach to automatically process recordings is the use of automatic signal detection and classification. This approach usually relies on machine learning techniques to detect and classify acoustic signals. These methods can require a labelled training dataset in the case of supervised learning or be based on clustering methods that do not require labelled data (Ulloa et al., 2018). Such approaches are particularly efficient to detect specific signals emitted by single species. Machine learning techniques can also be used similarly to acoustic indices to classify different types of sound recordings and detect acoustic anomalies in a dataset (Sethi et al., 2020).

Recent developments in applied freshwater ecoacoustics

Automatic processing

Driven by a thriving research community and easier access to both computational resources and reference calls, recent years saw exponential growth in the development of automatic processing in ecoacoustic applications. Automatic call recognizers are a key technique for automatic processing. The term 'call recognizer' is an umbrella term for a number of auto-detection techniques, ranging from hand-coded custom algorithms to even 'point-and-click' windows in applications like Kaleidoscope (Wildlife Acoustics, 2019) or Raven (Cornell Bioacoustics Research Program, 2011). Many applied studies in ecoacoustics currently choose an intermediate path in which algorithms are implemented in a larger statistical or mathematical framework, such as Matlab, R or Python libraries (for example Katz et al., 2016).

An example of a hybrid approach is a recent study in which our lab developed call recognizers for eight frog species (within the genera *Litoria, Limnodynastes, Crinia and Neobatrachus*) to monitor environmental water allocations. We used an algorithm 'binary point matching' delivered via the R package monitoR (Katz et al., 2016). The algorithm develops a template by transforming a spectrogram into a binary representation. It then searches for a matching pattern in the dataset the operator wants to find the sound in. The core algorithm is coded in R and the user can optimize three parameters:

- The call template, which is the actual call that is used to develop the recognizer.
- The amplification—if the call is too quiet this can lead to a lack of detections, if it is too loud it can confuse the algorithm.
- The threshold, which triggers a detection.

For the frog study, we optimized these three parameters, which was the manual part building the recognizer. This is just one potential avenue; recent developments have also increasingly used AI and machine learning techniques that automatically classify all acoustic events.

In freshwater science, the first automatic recognizer was a simple pattern matching algorithm to analyze and monitor spawning noises in river redhorse in Georgia (Straight et al., 2014). Lately, underwater recordings from the endangered spadefoot toad (*Pelobates fuscus*) have been used to develop a call recognizer and give insight into the anuran species' ecology, especially in regard to the breeding season (Dutilleux and Curé, 2020). With improvements in technology, we predict that further call recognizers will follow soon, as clear call characterizations have recently been published for a range of fish taxa, for example piranhas and burbot (Grabowski et al., 2020; Rountree and Juanes, 2020).

Ecoacoustic analysis

Ecoacoustics usually researches the ecology of acoustic signals as organisms interact with each other, as well as their environment. Ecoacoustics has been developed by and for ecological practitioners. Summary indices are often used to simplify complex acoustic data, including the amplitude of the signal (M)—which is analogous to species abundance, or an acoustic complexity index (ACI), analogous to species richness, as well as an entropy index (H) which is analogous to Shannon's diversity index (Sueur et al., 2014). These acoustic indices have been used extensively in terrestrial applications, including studies monitoring ecological responses to environmental water allocations (Linke and Deretic, 2020).

Acoustic indices have been deemed good surrogates for acoustic events in underwater environments. Utility of different indices seems to be varying—depending on the signal and the system. The first study in freshwater systems (Desjonquères et al., 2015) found that the acoustic richness index (which is a combined index of acoustic entropy and overall sound pressure) best described 48 sounds in 3 ponds. In a similar study in British ponds, a whole suite of indices, including M, H and ACI were found significant in representing sound types (Greenhalgh et al., 2021). A study in waterholes from Australia (Linke et al., 2020a) found that ACI, filtered by frequencies can be related to a suite of signals, including a nocturnal insect chorus, diurnal variation in creek flow, as well as fish choruses that mainly occurred in the mornings. In flowing waters, Decker et al. (2020) combined these indices to describe acoustic variation in 12 Queensland rivers.

A new visual analysis method involves the use of false-color spectrograms, which are constructed from multiple acoustic indices (Fig. 3; Linke et al., 2020a). While summary indices could depict insect choruses, flow and fish calls, false-color spectrograms are also able to detect variation within these events. The nocturnal hemipteran choruses for example display complex interaction patterns between multiple species of hemiptera, but also rise and fall in diurnal creek flow (Fig. 3).

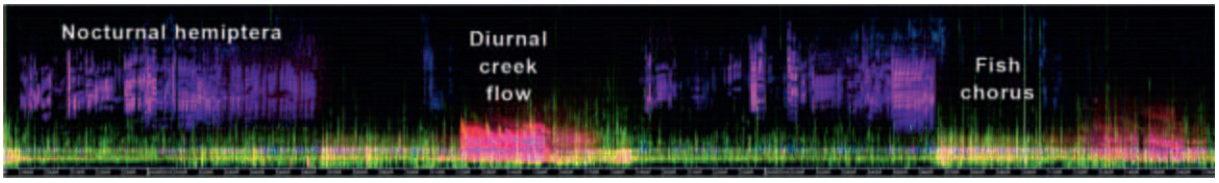

Fig. 3 False-color spectrogram of the diel variation in the Einasleigh River, Northern Australia described by Linke, Decker et al. (2020).

Linking sound to environmental condition

A limited number of studies have drawn links between frog and bird sounds and ecosystem condition in terrestrial and wetland settings (Linke and Deretic, 2020). However, a change in soundscapes does not automatically indicate the direction of change in an ecosystem. Soundscapes in degraded ecosystems for example, can become richer as ecological condition worsens, e.g., when pollution tolerant 'noisy' taxa start dominating the soundscape. Similarly, invasive species can increase soundscape complexity, while impeding ecological function. Previously, studies have investigated the response of bird and frog communities to disturbances (Fuller et al., 2015). This concept has even been extended to water-dependent terrestrial ecological communities in the United States and the Murray-Darling Basin. For example, in Australia, summary acoustic indices were utilized to track recovery of ecological communities in response to environmental water delivery as a restoration measure (Linke and Deretic, 2020). If we assume that an increased gradient of landscape complexity and good ecological condition will harbor higher species richness, it follows that the acoustic signal is enhanced by diverse complex communities.

The difference between aquatic and terrestrial applications of ecoacoustics is that only 20% of fish species and not all invertebrates are soniferous. Shifts in sonic activity will likely depend on the group of fishes. For example, an increase of the more pollution-tolerant Ariid catfish taxa will add to soundscape complexity, whereas displacement of more sensitive Terapontidae can reduce sonic activity. Therefore, an improvement in water quality is not directly related to an increase in sonic activity. Macroinvertebrates are important indicators of river health, but not all invertebrates produce sounds. While some sensitive taxa, e.g., caddisfly larvae, can be soniferous, the main classes of sound-producing organisms are aquatic hemiptera and beetles that have higher tolerances to warm water, low dissolved oxygen and mild organic pollution (Fig. 4). That said, dominance of very tolerant taxa e.g., chironomids and oligochaetes, will lead to a quieter soundscape. Thus, the most diverse soundscapes may be found at intermediate environmental conditions.

So far, few studies have linked acoustic measures to ecological condition in freshwater systems. A geomorphic link was established when comparing the sounds of pristine streams to streams that were impacted by sedimentation—mainly caused by grazing (Tonolla et al., 2011). Through the increased sediment input, gravel beds turned into sand beds and consecutively, the soundscapes were a lot quieter. Recently, a study from Holland related dissolved oxygen levels to underwater soundscapes. The change in soundscape was expressed not only by the proximate cause (i.e., roughness of the riverbed) but there was also a relation between sonic activity and dissolved oxygen (van der Lee et al., 2020). Listening to the invertebrate community, therefore demonstrated a first hint towards the validity of our theory of intermediate disturbance.

Knowledge gaps

Automated analysis of freshwater recordings is complicated by our general lack of knowledge regarding inland water soundscapes. Compared with terrestrial and marine environments, there has been relatively little history of freshwater acoustic analysis. In order to advance the field to the point of practical widespread application for conservation, a concerted global effort in recording, cataloguing, analyzing and sharing freshwater soundscapes is needed.

Over the last 5 years or so, automated analysis of data by computer algorithms has been revolutionized by a technique known as deep learning—a type of machine learning that leverages the increasing power of highly parallel computer graphics cards. Deep learning has been successfully applied to finding structure in complex data in a number of application domains, both supervised (with the help of human annotations) and unsupervised (without annotations). Deep learning has been recently applied in ecoacoustics for unsupervised learning in terrestrial and marine environments (Sethi et al., 2020), and supervised learning in freshwater environments (Guyot et al., 2021). The possibility of further using unsupervised automated analysis techniques in freshwater ecoacoustics is tantalizing, as it would facilitate a step-change in the volume of data analysis feasible.

Ecoacoustic monitoring generates high volumes of data. The logistical benefits of passive acoustic monitoring—namely the relative ease of long-term remote multi-site observation—tends to result in datasets much larger than typically encountered in ecology, sometimes of the order of PetaBytes. The storage and processing of such large datasets is a key challenge in ecoacoustic work

Fig. 4 Pollution tolerant taxa are responsible for key changes in aquatic soundscapes.

in any environment. Typically, studies will employ temporal sampling regimes (for example recording 1 min of every 10 min) and impose audio quality constraints by recording at low sample rates (for example 16,000 samples per second) to reduce data capture volumes. There is a trade-off, however, as such sampling regimes may miss rare but important events, the serial correlation patterns in acoustic indices are not generally known which confounds statistical inference, and high frequency sounds may be missed (Linke et al., 2020b).

The importance of spatial replication is increasingly being recognized in ecoacoustics generally. However, freshwater environments place greater demands in this regard, particularly in comparison to marine ecoacoustics. A foundational tenet of marine ecoacoustics is that sound travels far underwater, however this is not generally true in freshwater, particularly in shallow environments. On the contrary, sound there can be attenuated much more sharply than in terrestrial environments (Karaconstantis et al., 2020). Consequently, freshwater ecoacoustics can demand higher spatial replication and concomitant data storage and recording equipment requirements.

Because of the difficulties associated with data storage (Barclay et al., 2018), processing audio data in situ (i.e., at the recording site) is an attractive alternative where feasible. Running machine learning algorithms in real-time is sometimes possible, obviating the need to store all of the recorded audio. Instead, storing much smaller volumes of meta-data for species detection events and counts (for example) may be sufficient. Alternatively, processing may act as a filter to store audio only for periods of time deemed interesting. Algorithms for creating detection events and/or marking periods of time as interesting may include specialized species recognizers or more general anomaly detection approaches. Despite the steady increase in computational power of low-cost edge devices, processing on site remains challenging, as the machine learning algorithms typically employed push the capacity of these devices and add to the difficulty of providing power to long-term remote recording setups.

The sparsity of catalogued reference calls is a key obstacle to the practical application of freshwater ecoacoustic studies. In contrast to the rich catalogues of bird calls, freshwater acoustics has seen little representation in the leading international sound archives. The Cornell Lab of Ornithology's Macaulay Library does have some fish sounds (982, which represents 0.25% of the library, Linke et al., 2020b), however these are mainly from marine environments. This lack of reference material is challenging for researchers entering the field, as the emitter of an underwater sound is not obvious. In order for the field of freshwater ecoacoustics to advance, the international community should submit their documented and validated calls to the Macaulay Library, the Berlin Animal Sound Archive, the Paris sonothèque or other central bioacoustics repositories.

Ecoacoustics as a communications and engagement tool

The integrated nature of ecoacoustics calls for greater collaboration with other disciplines, including electronics, remote sensing, data science, humanities, and social sciences (Sueur and Farina, 2015). Collaborations between scientists and artists have become increasingly popular as environmental research calls for more effective methods to engage communities in the scientific process and its outcomes. Many of these collaborations can be categorized broadly as science communication, where artists are engaged to translate resulting data for accessible public dissemination. However, there is evident value in interdisciplinary research that brings together creative and scientific knowledge and perspectives to inform field work methods, analysis and outcomes. Freshwater ecoacoustics has benefited from various art science collaborations that have contributed to advancing the discipline and engaging communities in the process.

The rapid advancements of accessible and affordable digital technologies have resulted in numerous pathways for communities to directly engage with the emerging field of freshwater ecoacoustics. Creative projects, mobile applications and interactive experiences that engage communities in river soundscapes have the capacity to encourage environmental stewardship and inspire freshwater conservation (Gilmurray, 2017). Hydrophones capturing rich and immersive underwater soundscapes have been used in the context of creative work since the 1970s, with composers including Maggi Payne, Jana Winderen, Douglas Quin, Chris Watson, David Monacchi and Ros Bandt, all renowned for their creative projects that draw listeners beneath the surface of rivers, lakes and oceans. The resulting creative experiences have been a catalyst for communities to engage with freshwater ecoacoustics and facilitate local citizen science initiatives.

These interdisciplinary efforts have also strengthened engagement from those in the arts and humanities to promote the emerging discipline of freshwater ecoacoustics. Composer Rob Mackay has developed many creative projects and community engagement initiatives around hydrophones with recent examples including 'Red River: Listening to a Polluted River' (https://redriverpoetry.com/). This 18-month research project was funded by the United Kingdom Arts and Humanities Research Council and led by Dr. John Wedgwood Clarke. This project has included soundscapes, poetry, community events, workshops and showcases at conferences including COP26 in Glasgow. Another example is 'The Secret Sound of Ponds' presented at the Science Gallery Detroit, which is a collaboration between Benjamin Gottesman, David Rothenberg and Camille Desjonquères (https://detroit.sciencegallery.com/depth-exhibits/the-secret-sound-of-ponds). This project features an immersive sonic sculpture installation that was accompanied by a hydrophone building and recording workshop, freshwater soundscape data collection in the Detroit River and a live performance designed to connect people to the hidden life of freshwater environments through sound. The subsequent increased engagement in freshwater ecoacoustics has prompted students engaging in interdisciplinary pathways including science students creating podcasts with aquatic soundscapes and emerging sound artists such as David de la Haye who are using sound to raise awareness and cultural value of freshwater habitats.

Listening to rivers with hydrophones can help local communities understand freshwater biodiversity in accessible and engaging ways (Barclay et al., 2018). For example, the project 'River Listening' has developed new approaches for citizen science engagement with freshwater ecoacoustics that have inspired various communities to engage with hydrophone recording (Barclay et al., 2018). The project developed noninvasive recording techniques with accessible hydrophone kits and participatory workshops to engage local communities in the process and outcomes. Preliminary work in community engagement with freshwater ecoacoustics explored the possibilities of hydrophone recording through interactive workshops, recording expeditions, and art installations designed to draw attention to the sounds beneath the surface of rivers. The workshops explored methods for using acoustics to understand aquatic biodiversity and involved extensive experimentation with recording techniques, new technologies, and community collaborations to compare aquatic soundscapes and the most effective methods for recording in freshwater ecosystems. The resulting database of hydrophone recordings have informed the scientific research and a diversity of community events and creative projects disseminated the outcomes worldwide.

Various endeavors have been established within River Listening to encourage ongoing community engagement outside of scheduled workshops. These efforts include a customized digital platform, virtual sound maps with live streaming hydrophones, and a mobile application that allows communities to record, upload, and compare sounds in a global database (Barclay et al., 2020). These digital outcomes underpin the major creative projects and facilitate the collection of recordings for scientific monitoring. The central tools for public engagement around River Listening have been creative outcomes, including site-specific performances and installations that have toured internationally. The most effective tool for public engagement has been the River Listening Sound Walks, which require audiences to visit their river to experience the work. The sound walks involve a custom built mobile application that transforms the listener's phone into a sonic compass to guide them along the riverbank and explore the cultural and biological diversity of the river through sound (Barclay et al., 2018). The installation triggers geo-located soundscapes that are accompanied by images and text identifying the sounds that are drawn from a local database of hydrophone recordings.

Perhaps most importantly, the community engagement processes surrounding River Listening have acted as a catalyst to amplify First Nations voices and facilitate opportunities for Indigenous knowledge holders to take a leadership role in the projects. The River Listening project has had the great privilege of learning from Indigenous leaders such as Lyndon Davis, Brendan Kennedy and Anne Poelina in Australia (https://www.riverlistening.com/). In 2017, the Whanganui River in Aotearoa (New Zealand) was the first river in the world to be granted personhood and recognized as a living being. Anne Poelina has been leading the conservation and protection of the Mardoowarra (Fitzroy River) in Western Australia and has advocated for the river to be recognized as a living ancestral being. Poelina argues that healthy rivers are culturally located and there are Indigenous ways of knowing, being and doing based on nonlinear time, a located temporality, which connects people, rivers and place (Martuwarra et al., 2021). She believes that healing river ecosystems is a cultural endeavor and that listening, hearing and voicing rivers is a first, Indigenous step. Poelina, along with many First Nations leaders in Australia and beyond, believe that water management requires Indigenous-led restorative research and practices to ensure Indigenous values are recognized (Martuwarra et al., 2021).

Listening to rivers provides unique methods for bridging traditional knowledge systems, emerging science and creative practice when working directly with communities in freshwater management. The methods of engaging with freshwater ecoacoustics in the field can embrace Indigenous leadership and traditional knowledge, and the ongoing monitoring of acoustic sensors can be managed by local communities. The interdisciplinary pathways that continue to emerge in the field of freshwater ecoacoustics indicate that interdisciplinary collaborations are vital in engaging communities in listening to rivers and inspiring freshwater conservation.

See Also: Emerging methods and topics: Electronic Tagging and Tracking of Animals in Inland Waters

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Inland Water Fungi in the Anthropocene: Current and Future Perspectives

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Aero-aquatic fungi Fungi that need air exposure for sporulation to complete their life cycle. Consequently, they spend one stage of their life cycle underwater and another stage dispersed in the air-water boundaries.
Allochthonous organic matter Organic matter that is introduced into aquatic ecosystems from the terrestrial surrounding, e.g., plant debris, pollen, and leaves.
Anamorphic Asexual state of a fungus, which refers to the asexual morphotype of a fungus, also mitosporic state, i.e., a morphotype that forms spores only by mitosis.
Anthropocene The geological period during which humans have had a significant impact on the planet's climate and ecosystems. Most researchers state that it began at the start of the Industrial Revolution of the 1800s, when—for the first time—human activity had a significant large scale impact on carbon dioxide and methane in Earth's atmosphere.
Autochthonous organic matter Organic matter produced inside aquatic ecosystems, e.g., by algal photosynthesis and organismic biomass production.
Benthic shunt Fungal pathway in which (mainly terrestrial) organic matter is channeled by aquatic fungi in benthic biofilms to higher trophic levels of the aquatic food web.
Conidia Asexual reproductive units that formed from special cell (conidiogenous cells) developed from conidiophore.
Dark matter fungi Group of fungi that has been mainly characterized by sequence-based methods, related mostly to the early branches of the fungal tree, i.e., Aphelida, Rozellomycota, and Chytridiomycota (Grossart et al., 2016).
Emerging pollutants Synthetic or naturally occurring chemicals that are generally not controlled but could have adverse effects on human and ecosystem health.
Fungi-like organisms Represents all microorganisms in Oomycota phylum. They are morphologically very similar to fungi. However, molecular studies has revealed their vast evolutionary distance to fungi. While fungi are more related to animals, they are plant's close relative.
Hyphomycetes Fungi with long, branching filamentous structures called hyphae and that represent the main mode of vegetative growth in the form of mycelia.
Ingoldian fungi A fungal group honored for Ingold (1942) that is characterized by their ability for sporulation on plant materials underwater.
Microplastics Generally defined as plastic particles equal or smaller than 5 mm in length that result from both commercial product development (primary) and the breakdown of larger plastics (secondary microplastics). As a pollutant, microplastics can exert harmful effects on the environment, animal, and human health.
Mycoflux Fungal pathway in the pelagic zone of water bodies in which fungi lead to changes in organic matter aggregation or disintegration and thus affect organic matter cycling and sequestration.

Mycology Scientific field studying all aspects of fungi and fungi-like organisms.
Mycoloop A fungal pathway in the pelagic zone of water bodies in which parasitic fungi transfer inedible phytoplankton or pollen to higher trophic levels either via edible fungal zoospores of cell fragmentation and/or lysis.
Mycovirology Scientific discipline studying virus infecting fungi, i.e., mycovirus.
Mycovirus A virus that infects fungi.
OMICS era Phrase that relates to the current time period when the use of new molecular and biochemical tools such as metagenomics, metatranscriptomics, metaproteomics and metabolomics, arose to study organisms in the lab and field.
Plastisphere Term to describe a newly emerging microbial habitat created by the massive, anthropogenic introduction of microplastics to practically all environments.
Teleomorphic Sexual state of a fungus, in which two fungal nuclei unite and undergo meiosis, forming offspring with new genetic information.
Transient fungi Group of fungi that is passively introduced into water via high loads of fungal propagules from inflowing streams, rainwater runoff, and wind. These fungi exhibit no activity in the water, presumably due to unfavorable aquatic conditions or interactions with organisms.
Zoosporic fungi Synonym for chytrids and other basal fungi that possess a zoosporic stage during their life cycle.

Introduction

Fungi and fungi-like organisms (such as oomycetes) are key components of aquatic ecosystems, with parasitic and/or saprophytic lifestyles that influence biodiversity, food web dynamics, and the cycling of organic matter, nutrients, and energy within ecosystems. Yet, they represent an understudied group of aquatic microorganisms, largely neglected by aquatic microbial ecologists. In fact, historically *mycology* was separated from microbial ecology in all aquatic sciences. Studies of fungi are of great ecological and biotechnological interest because fungi have a large variety of polymer-degrading enzymes and detoxification mechanisms. However, the dramatic increase in the human population worldwide and subsequent increasing urban development and anthropogenic pollution has led to a severe modification of inland waters, with adverse effects on fungi. In this article, we highlight the multiple metabolic capacities and adaptive behavior of aquatic fungi to cope with these rapid environmental changes in the **Anthropocene**. We provide an overview of emerging topics in the field of aquatic **mycology** that are, to a great extent, related to the anthropogenic modification of inland waters, in particular **emerging pollutants**, including microplastics.

Diversity and ecology of aquatic fungi and fungi-like organisms

In general, fungi and fungi-like organisms (not necessarily the aquatic ones) have been phylogenetically and taxonomically separated (Fig. 1). However, several basic differences make it hard to treat all fungi the same. Therefore, the formal taxonomy-based classification system coexists with the "informal" ecology-based system which is polyphyletic. Thus, many classifications of aquatic fungi have been adopted (Goh and Hyde, 1996; Shearer et al., 2007).

Aquatic fungi

A recent estimate based on molecular evidence suggests a global fungal diversity of about 1.5 million species (Hawksworth and Lücking, 2017). Aquatic fungi form a taxonomically and morphologically diverse group in freshwater, brackish, and marine habitats. In parallel to their diverse lifestyles, community composition and abundance of fungi vary considerably with their aquatic habitats (Wurzbacher et al., 2010). Interestingly, about 96% of all fungal taxa have been recorded in temperate regions and fewer in tropical and subtropical regions (Rossman, 1994; Hawksworth, 2001; Duarte et al., 2016; Hyde et al., 2016). Therefore, the "true" number of fungi should be much higher, i.e., 2.2–3.8 million species, because a substantial fraction of the global fungal diversity has not been explored in-depth (Grossart et al., 2019).

The number of isolated and described fungal taxa is much lower than global estimates, including only 120,000–143,273 species (Fungorum, 2018; Wijayawardene et al., 2017). The majority of fungal species are related to the two phyla Ascomycota and Basidiomycota (ca. 96,000 species), which form the subkingdom Dikarya. Our current knowledge of fungal diversity is quite limited (Tedersoo et al., 2014), particularly in aquatic systems where the number of described species is low (ca. 3000–4000 species) as compared to terrestrial fungi (Jones et al., 2014). Consequently, the number of newly discovered fungal species in aquatic systems is predicted to increase (Voigt and Kirk, 2011).

Gessner and Van Ryckegem (2003) suggested that there are ca. 20,000 different species of freshwater fungi, yet only ~5% of the estimated fungal species have been described. The estimated number of species documented from different habitats and substrates include 622 fungal species of ascomycetes, 600 hyphomycetous fungal species from *Phragmites* litter (Gessner and Van Ryckegem, 2003), 531 asexual fungal species, 317 species on peat swamp (Tsui et al., 2001; Sivichai et al. 2002), and 183 trichomycetes. Also, zoosporic fungi comprise more than 500 species of chytrids and members of fungal-like organisms (Jones et al., 2014). All other

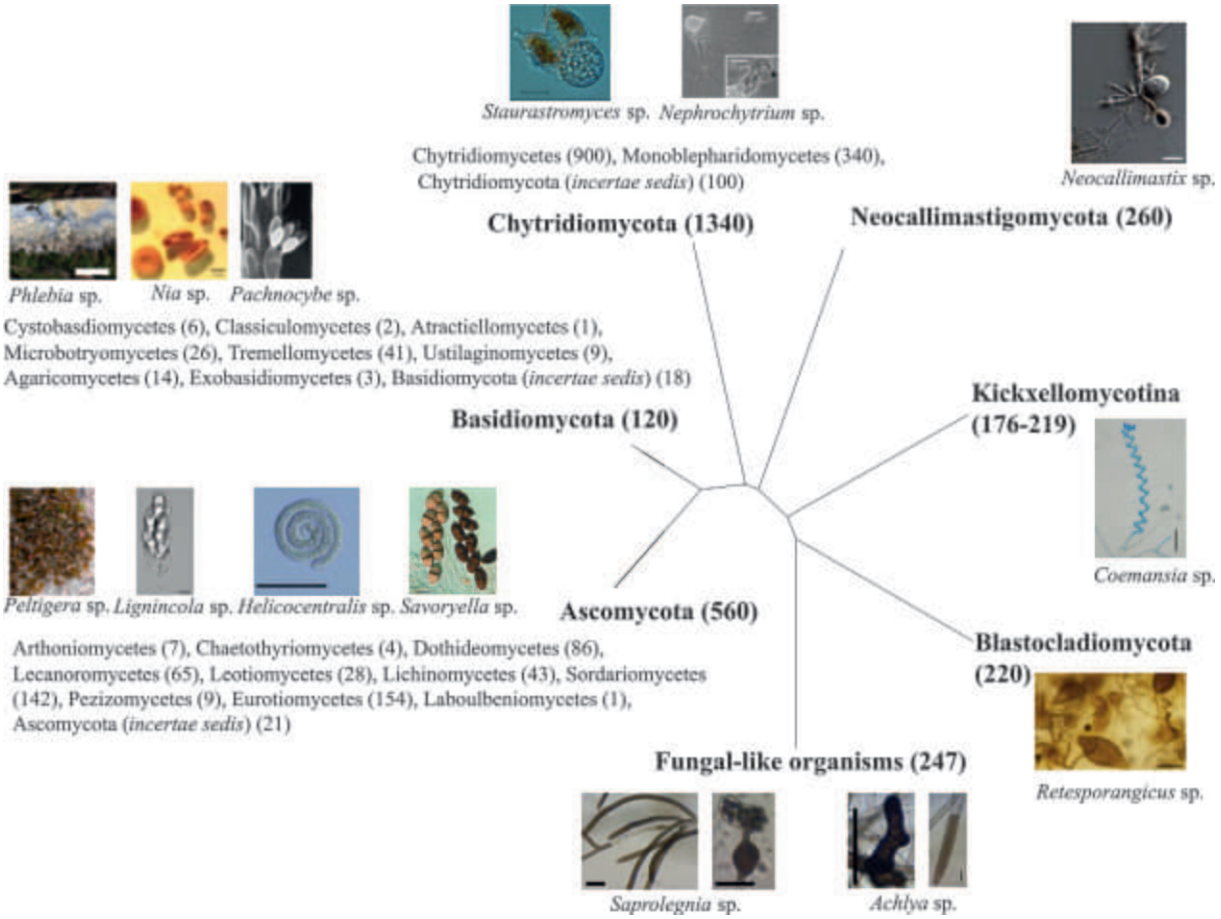

Fig. 1 Phylogeny of freshwater fungi and fungi-like organisms. The morphological and phylogenetic diversity of freshwater fungi and fungi-like organisms is illustrated. The numbers in parentheses stand for the currently identified species within each taxon. Ascomycetes are associated with dead stems and leaves of herbaceous and woody plants. They are mainly responsible for breaking down the lignocellulose constituents of plant cell walls. In contrast to their terrestrial diversity, freshwater Basidiomycota are less abundant. They colonize leaves and twigs in streams and rivers. They are known for basidiomata reduction, the passive release of basidiospores, and the production of branched conidia. Recently, the importance of true zoosporic fungi, including Chytridiomycota, Neocallimastigomycota, Kickxellomycotina, and Blastocladiomycota, has been highlighted. This is mainly due to increased awareness (both in morphology and phylogeny) for yet undescribed taxa (**dark matter fungi**). Many species are parasites and influence food web structure in freshwater ecosystems. Finally, fungi-like organisms, also known as "water molds," are some of the most devastating aquatic animal pathogens, responsible for massive mortalities of crabs, fishes, amphibians, etc.

fungal groups, however, are poorly described, including freshwater lichens with about 270 lichenicolous fungi and lichens, 226 fungal species on aquatic plants described as dark septate endophytes or endomycorrhizae, and 40 species of parasitic fungi. In particular, basidiomycetes are poorly documented in freshwater ecosystems, with only 41 non-yeast basidiomycetes and 74 basidiomycetous yeasts. The overall documented species richness of freshwater fungi (<4200 species) suggests that there are still many freshwater habitats and substrates to be surveyed (Jones et al., 2014).

In aquatic systems, three major types of fungi can be found depending on their growth and adaptation abilities in aquatic ecosystems: (I) terrestrial fungi that are often passively introduced into the water via high loads of fungal propagules from inflowing streams, rainwater runoff, and wind. This fungal group is known as **transient fungi** (versatile immigrants), which exhibit no activity in water - presumably due to unfavorable aquatic conditions or interactions with organisms (Dix and Webster, 1995; Voronin, 2014). (II) Partially adapted aquatic fungi that may be amphibious with one stage of their life cycle underwater and another stage dispersed in air-water boundaries (**aero-aquatic hyphomycetes;** Dix and Webster, 1995; Park, 1972 or periodic immigrants). (III) Fully adapted aquatic fungi (indwellers including Ingoldian fungi; Ingold, 1942) that can maintain their biomass in aquatic ecosystems with constant activity from year to year. They utilize substrates and nutrients available in water bodies, and most are capable of sporulating directly in water (Grossart et al., 2019).

Based on their morphology and lifestyle including different functional behaviors (independent of phylogeny), aquatic fungi are further separated into six major groups (Wurzbacher et al., 2010):

1. *Aquatic hyphomycetes* are recorded on decaying leaves and lignocellulosic debris in freshwater ecosystems worldwide. Aquatic **hyphomycetes** (Nilsson, 1964), also known as amphibious **hyphomycetes** (Michaelides and Kendrick, 1978), comprise **anamorphic** fungal taxa of ascomycetes and basidiomycetes (Shearer et al., 2007) that are specifically adapted to aquatic habitats via their reproductive systems by producing their spores in relatively large multiradiate (often tetraradiate), sigmoid or spherical conidia with tips usually covered with sticky mucilage (Read et al., 1992) to facilitate attachment to and colonization of a specific substrate. Aquatic **hyphomycetes** are categorized into two ecological groups according to their reproductive behavior (Goh and Hyde, 1996): (a) the **Ingoldian fungi** (Ingold, 1942) are characterized by their ability for sporulation on plant materials underwater and (b) the **aero-aquatic fungi** that do not sporulate underwater but need air exposure for sporulation to complete their life cycle (Wurzbacher et al., 2010). On the other hand, Goh (2003) provides another common group of aquatic hyphomycetes, i.e., transparent fungi with asexual reproduction (mitosporic) and dark conidia (coelomycetes) that have been recorded from various freshwater habitats. However, their conidial structure is not as well adapted for the aquatic ecosystems as the **Ingoldian** and **aero-aquatic hyphomycetes** (Goh and Hyde, 1996). These fungi include two ecological groups, namely, indwellers that are present only in freshwater environments (e.g., *Aquaphila*, *Canalisporum*, *Camposporidium*) and immigrants that occur in both terrestrial and freshwater environments (e.g., *Acrodictys*, *Acrogenospora*, *Arthrobotrys*) (Park, 1972).
2. *True zoosporic fungi* currently include phyla Chytridiomycota, Neocallimastigomycota, Kickxellomycotina, and Blastocladiomycota. They commonly occur as saprobes in the degradation of particulate organic matter of dead animals, pollen grains and plant litter as well as parasites of vertebrate animals, e.g., frogs, zooplankton and phytoplankton, or as symbionts in the mammalian digestive system. Consequently, zoosporic fungi have significant ecological roles in nutrient cycling and regulation of the populations of phytoplankton in aquatic ecosystems and also cause some economically important plant and animal diseases (Gleason et al., 2017). True zoosporic fungi typically occur in the pelagic zone of standing waters (Wurzbacher et al., 2010, 2016) and their reproductive units display primary adaptations to an aquatic lifestyle in the form of uniflagellated motile zoospores (Wong et al., 1998).
3. *Aquatic ascomycetes and basidiomycetes* (**teleomorphic** stage; develops sexual reproductive units including ascospores characteristic for ascomycetes and basidiospores for basidiomycetes) are microscopic fungi that decompose submerged woody material that falls into aquatic habitats. Since the 1990s, several studies concerning freshwater ascomycetes have been performed increasing the number of described species from 370 (Shearer, 1993) to 622 species (Cai et al., 2014; Shearer et al., 2014). Currently, about 675 species related to freshwater ascomycetes have been characterized and comprise several taxonomic groups (i.e., dothideomycetes, sordariomycetes, and leotiomycetes) ubiquitously found in freshwater on submerged and exposed woody debris (Jones and Pang, 2012; Shearer et al., 2014). The majority of freshwater ascomycetes form microscopic ascomata (less than 0.5 mm) and contain structurally water-adapted ascospores characterized by several sheaths or wall ornamentations covered by a gel-like sticky material that supports spore dispersal and attachment (Digby and Goos, 1987).
4. *Yeasts* are unicellular fungi with spherical or oval-shaped cells, representing a diverse group belonging to ascomycetes and basidiomycetes (Shearer et al., 2007) that are found mainly in the pelagic zone of freshwater habitats (Wurzbacher et al., 2010) and the pelagic and estuarine habitats of marine systems. Our understanding of their ecology and functions in aquatic ecosystems is still limited (Wurzbacher et al., 2010). However, they may play a similar role as heterotrophic bacteria generally referred to as the main (micro)organisms taking up and re-mineralizing dissolved organic matter.
5. *Glomeromycota* represent another under-studied group of aquatic fungi with little information on their ecology, composition and role in aquatic ecosystems (Goh and Hyde, 1996). The majority of glomeromycetes is terrestrial, except for aquatic trichomycetes (Shearer et al., 2007), and form a polyphyletic group which grows parasitically or mutualistically (order Harpellales) together with aquatic arthropods (Hibbett et al., 2007; Jobard et al., 2010). In addition, Glomeromycota are comprised of ecologically beneficial mycorrhizal fungi forming symbionts with the roots of aquatic macrophytes. These mycorrhizal fungi are characterized by the formation of special structures (vascular and/or arbuscular structures) inside the plant roots providing the plant with nutrients, e.g., phosphorus in nutrient-limited aquatic ecosystems (Wurzbacher et al., 2011).
6. *Fungi-like organisms* (Oomycetes, Straminipila) are well-documented (Wong et al., 1998) and considered the most ubiquitous aquatic "fungal" group characterized by biflagellate heterokont (two unequal flagella) zoospores (Dick, 1989; Shearer et al., 2007). Although Straminipila (hyphochytriomycota, Oomycota, and labyrinthulomycota) share similar morphological and physiological traits with true fungi (chytridiomycota, rosellomycota, and aphelida), their ecological functions and trophic strategies appoint them as false fungi (Alexopoulos et al. 1996; Beakes et al. 2014; Karpov et al. 2014).

Although cultivation is often biased, e.g., by sample handling and the choice of media, more fungal isolates from aquatic ecosystems are required to better characterize their genetics, physiology, and ecological role (Grossart et al., 2019). Yet, it remains difficult to characterize and estimate total fungal diversity at any given sampling site, often due to the lack of experience and qualified staff and suitable identification manuals, especially in tropical regions. There is a great demand to provide new techniques and strategies to isolate and assess fungal diversity and enable realistic site estimates for conservation purposes (Cannon, 1997 and Hawksworth, 2001). The application of different isolation techniques to the same waterbody may yield entirely different fungal communities (Abdel-Raheem, 2004; Sridhar et al., 2010). Whereas direct observation techniques can be used for investigations of growth of **zoosporic fungi**, aquatic **hyphomycetes**, and **teleomorphic** fungi on different substrates (Müller-Haeckel and Marvanová, 1979; Sparrow, 1968), the baiting technique is commonly used for isolation of **zoosporic fungi** and aquatic **hyphomycetes** from water samples using specific baits such as boiled sesame and hemp seeds (for oomycetes, fungal-like organisms), phytoplankton, pollen grains, and snakeskin (for chytrids) and plant leaves (for aquatic **hyphomycetes**) (Shearer and Von Bodman, 1983;

Shearer, 1972; Sparrow, 1968). Furthermore, the moist chamber technique can be employed to isolate **teleomorphic** fungi using woody blocks (Shearer and Von Bodman, 1983; Shearer, 1972). Finally, yeasts can be obtained by dilution plating of water or sediment on specific media (Fell, 2001; Kumar et al., 2011). Although most aquatic fungi remain uncultivated, new methods, baits, and media may isolate the entire fungal community in aquatic systems.

The phylogenetic relationship of aquatic fungi, including Ascomycota, Basidiomycota, Chytridiomycota, Neocallimastigomycota, Kickxellomycotina, Blastocladiomycota, and fungi-like organisms is given in Fig. 1. Recently, a new and surprisingly large fungal diversity has been discovered in aquatic habitats using molecular tools. These so-called **dark matter fungi** are mainly related to the early branches of the fungal tree, i.e., Aphelida, Rozellomycota, and Chytridiomycota (Grossart et al., 2016). Thus, considerable efforts to discover and evaluate their ecology and ecophylogenetics are needed. For example, their role as parasites or saprotrophs still needs to be identified and quantified (e.g., Banos et al., 2020). Whereas parasites exploit their living host for nutrition, saprotrophs use an array of excreted (extracellular) enzymes to digest their dead nutritional substrate directly (e.g., dead organism or other nonliving organic matter).

Current conceptual models indicate a multitude of different processes by which aquatic fungi transform and incorporate **allochthonous** and **autochthonous organic matter** into organismic biomass and transfer it to higher trophic levels. Recently, three major processes have been identified to describe the different ecological roles of fungi in the aquatic realm (Grossart et al., 2019): (i) **mycoloop**, (ii) **mycoflux**, and (iii) **benthic shunt**.

The **mycoloop** has been well described (Kagami et al., 2007, 2014) and refers to parasitic fungi that render inedible phytoplankton available to zooplankton grazers by producing zoospores or by fragmentation of large phytoplankton cells. The **mycoflux** relates to the important role of fungal interactions in organic matter and organisms that result in aggregation or disintegration of sinking organic particles, including living organisms and dead cell debris (Grossart et al., 2019). Most consequences of the mycoflux are still unknown, but we propose that they significantly affect the efficiency of the aquatic carbon pump and hence carbon sequestration. The **benthic shunt** describes how fungal colonization of (mainly terrestrial) organic litter and the formation of fungal biomass allows for an efficient transfer of this organic matter to macrozoobenthos on the sediment (Attermeyer et al., 2013). Macrozoobenthos represents an excellent food source for higher trophic levels in the pelagic zone, such as fish, and thus increases the efficiency of trophic transfer throughout the aquatic benthic and pelagic food webs. These three concepts take the various lifestyles and interactions (e.g., parasitism and saprotrophy) of aquatic fungi into account and highlight their ecological and biogeochemical importance in freshwaters. In sections "Aquatic fungi-like organisms" and "Fungi-virus interactions: An emerging topic" we describe two prime examples for interactions with fungi-like and fungi interactions with organisms and virus which until now have received only a little attention.

Aquatic fungi-like organisms

The fungi-like organisms represent non-fungal organisms from a taxonomical point of view but are often considered as a fungal group (Shearer et al., 2007; Grossart et al., 2019) given that they show ecological traits and functions in water similar to true fungi (Wong et al., 1998; Khallil et al., 2020). Aquatic fungi-like organisms are frequently found in the orders of *Saprolegniales* and (to a much lesser extent) *Peronosporales* within the class of Oomycetes. *Saprolegniales* has nearly 15 genera known as water molds causing destructive endemics in aquatic animals. *Achlya, Aphanomyces,* and *Saprolegnia* are the most dangerous threats to fishes and crabs across the world. In addition, *Pythium* and *Phytophthora* represent common parasitic genera in freshwater ecosystems although not all members of *Peronosporales* occur in aquatic environments. It's worth mentioning that zoosporic fungi are another term for describing both aquatic fungi and fungi-like organisms with motile spores (Wong et al., 1998; Dick, 1989; Shearer et al., 2007). Obviously, the word became obsolete when oomycetes and fungi got separated taxonomically.

Within the phylum Oomycota, oomycetes consist of two main assemblages including basal and crown oomycetes. Basal oomycetes as early-diverging ones are usually obligate parasites in marine ecosystems. Crown oomycetes, however, are considered to mainly occur in freshwater ecosystems. This group of fungal-like parasites has six orders with *Saprolegniales* and *Peronosporales* (see "Diversity and ecology of aquatic fungi and fungi-like organisms" section) as the biggest and most recent taxa, both including aquatic genera (Beakes and Sekimoto, 2009). Saprolegniales, or water molds, are well-known, exclusively aquatic organisms in freshwater ecosystems belonging to the phylum Oomycota. They are phylogenetically and systematically separated from the kingdom fungi and placed within the kingdom Chromista (Thines and Kamoun, 2010). Their positive association with water-related ecosystems is mainly due to their life cycle consisting of motile zoospores. The littoral zone, which is rich in **allochthonous organic matter** from animal and plant debris, seems to be their main niche (Marano et al., 2016). Their parasitic lifestyle on various species of fishes, crayfishes, etc. causes not only billions of dollars of damages to fisheries but also seriously endangers native aquatic animals (Van West, 2006).

Aquatic Saprolegniales such as *Achlya*, *Aphanomyces*, and *Saprolegnia* species are considered among the most widespread and dangerous animal pathogens worldwide (Bruno et al., 2011). Consequently, the multiple aspects of Saprolegniales pathogenicity in terms of ecology, diversity, as well as taxonomy, have been studied for more than a century. Several species of *Saprolegnia* and, to a lesser extent, *Achlya,* are responsible for drastic annual economic losses in salmonids and massive amphibian and crustacean mortality events, called Saprolegniosis (Hussein and Hatai, 2002; Fregeneda-Grandes et al., 2007). Their destructive potential is intensified by predisposing factors such as increases in mean temperatures, extreme drought periods, and aquatic contamination.

The species *Aphanomyces astaci* represents a key example of the destructive potential of parasitic Saprolegniales. This species causes the crayfish plague, which has been studied in terms of physiological adaptations and host responses toward parasitism since

the early 1960s (Unestam, 1965; Makkonen et al., 2012). The involvement of *A. astaci* in crayfish plague points to its crucial ecological role in freshwaters. Crayfish species significantly affect aquatic food webs and biogeochemical cycling via control of macrophyte biomass and growth, species richness, benthic primary productivity, etc. (Matthews and Reynolds, 1992). *A. astaci* is considered a significant threat to European crayfish populations that were transmitted to mainly Europe and other continents through the commercial exchange of American crayfish species (which are resistant against *A. astaci*, but transmit it) in the 19th century (Schrimpf et al., 2013). Now, *A. astaci* is listed among the world's 100 worst invasive species owing to the extremely high susceptibility of Non-American crayfish species (Luque et al., 2014).

Aside from parasitism, the ecology of Saprolegniales has been largely ignored with studies often limited to seasonality, occurrence, and correlation to various environmental parameters. Saprolegniales may be as common as their fungal counterparts in aquatic ecosystems since they may also colonize different **allochthonous** animal and plant debris in addition to being parasitic. This notion raises the question of whether Saprolegniales are as enzymatically active as fungi, making them important for **allochthonous organic matter** degradation. Interestingly, it has been shown that several genera in Saprolegniales behave opportunistically, quickly benefitting from the availability of small organic molecules while being ineffective in the degradation of more complex polymers (Masigol et al., 2019, 2020). This inefficiency is unlike fungi that can degrade a plethora of organic molecules by producing laccases and peroxidases. However, studies dealing with enzymatic capacities of Saprolegniales are rare and additional work is much needed to test whether ligninolytic inefficacy in Saprolegniales is universal.

Fungi-virus interactions: An emerging topic

One of the least studied topics in fungal ecology in inland waters is their interactions with viruses. In fact, little is known about the diversity of viruses in aquatic ecosystems, their relationships with fungal hosts such as their possible role(s) in regulating aquatic fungal populations e.g., chytrids after a diatom bloom, modes of dispersal, seasonal dynamics, and geographic distributions (Kotta-Loizou, 2019; Prussin et al., 2020). Yet, studies of viruses that infect economically important fungi (e.g., crop and aquaculture pathogens), reveal that **mycoviruses** are widespread in all major fungal groups and that most of them evolved at a very early stage of their fungal host's evolution and cause little or no apparent symptoms in their hosts (Ghabrial, 1998; Liu et al., 2012; Roossinck, 2015).

Recently, the number of reported **mycoviruses** has increased dramatically due to the use of high-throughput sequencing of fungal genomes and transcriptomes, which also allow the detection of their viromes (Nerva et al., 2016; Neupane et al., 2018; Ponsero and Hurwitz, 2019; Zoll et al., 2018). There are currently 12 classified and seven unclassified families of **mycoviruses** (Peyambari et al., 2021). The majority of **mycoviruses** are double-stranded RNA (dsRNA) viruses, while single-stranded RNA or DNA viruses are less common (Castón et al., 2020; Jiang, 2020; Li et al., 2020). The fungal viruses with dsRNA genomes, in most cases, encode for only two proteins: a capsid protein and an RNA-dependent RNA polymerase. Some families of dsRNA fungal viruses like Totiviridae can infect protozoa, while members of Partitiviridae can also infect plants (Liu et al., 2010; Yokoi et al., 2007). The broad host range of dsRNA fungal viruses, including hosts from different eukaryotic kingdoms, hints at their ancient origin (Peyambari et al., 2021).

Mycoviruses can be transmitted intracellularly during cell division, sporogenesis, or cell-to-cell fusion, resulting in life cycles generally without an extracellular phase. Each virus strain has a narrow host range, although certain viral families may have a broader spectrum of hosts. Most **mycoviruses** are asymptomatic, but those that reduce pathogenicity in fungal hosts are of great biotechnological interest for developing natural fungicides (Ghabrial et al., 2015; Preisig et al., 2000; Yu et al., 2013).

The effects of **mycoviruses** on aquatic fungal communities remain unknown, such as the virus-induced mortality that can provoke large-scale alterations of the fungal community structure and the subsequent impact on carbon and nutrient cycling, modification of fungal metabolism (e.g., by gene disruption or the introduction of new genes), and alteration of fungal fitness, e.g., by virus-borne toxins (Roux, 2019; Suttle, 2005; Wilhelm and Matteson, 2008). The associations of viruses with fungi should be explored with a higher resolution given the high diversity existing in the fungal kingdom. Of particular interest are the associations with early divergent fungi belonging to groups such as Chytridiomycota and Rozellomycota, which, despite being abundant in aquatic environments, have been relatively little studied.

In summary, the vast majority of **mycoviruses** in freshwaters (both in natural and urban environments) and their ecological roles remain poorly understood. Freshwater **mycovirology**, although accepted as a conventional research area, is less developed compared to human, animal, or plant virology (Kotta-Loizou, 2019). Due to their potential key role for freshwater fungi, **mycoviruses** deserve considerably more attention from aquatic microbial ecologists.

Aquatic fungi in the Anthropocene

Fungi inhabit a broad range of habitats (Grossart et al., 2019). In the case of those that inhabit natural aquatic ecosystems, there has been a growing interest in studying their diversity and ecology (Bärlocher and Boddy, 2016; Krauss et al., 2011), but much less is known about fungi in the urban aquatic environments (such as houses, hospitals, recreational parks and wastewater treatment plants) that are steadily increasing worldwide. Urban aquatic environments provide a series of conditions that result in a very different composition of fungal species from that found in natural environments. In other words, the human-build environment favors the enrichment of some fungal species, whose effects on environmental and human health are yet unknown. On the other

Fig. 2 Overview of habitats (in red circles) for aquatic fungi within urban environments. Houses contain numerous habitats for aquatic fungi, particularly in the kitchen and bathroom (e.g., sinks, tap water, showers, toilets, washing machines, and dishwashers), which are extensible to more massive constructions such as apartment buildings, hospitals, shopping malls, and industries. Aquatic fungi are also found in open spaces such as fountains, ponds, and swimming pools, as well as in wastewater treatment plants.

hand, these enriched species may be of great biotechnological interest. Few studies have been conducted to understand the diversity of fungi in different human-made aquatic systems, the effects of pollutants and human waste on fungal community structure, and the abundance of opportunistic pathogens (Assress et al., 2019; Biedunkiewicz and Góralska, 2016; Newbound et al., 2010).

Human homes contain numerous habitats for aquatic fungi, particularly in kitchens and bathrooms (Fig. 2). For example, fungal populations are regularly found in sinks, drinking water pipes, showers, and toilets (Flores et al., 2011; Gashgari et al., 2013; Hamada and Abe, 2009; Zhou et al., 2017). Aquatic fungi frequently occur in household appliances such as washing machines and dishwashers, where they adapt to extreme conditions of high temperatures, drastic changes in pH, high salinity, presence of detergents, and high shear forces (Babič et al., 2016; Raghupathi et al., 2018; Zupančič et al., 2016). House conditions, and thus habitat for fungi, are extensible to more massive constructions such as apartment buildings, hospitals, shopping malls, and industries (Steinberg et al., 2015).

Aquatic fungal communities have also been identified in habitats that are in close contact with humans such as fountains, artificial lakes, and swimming pools of public parks and recreational areas (Brandi et al., 2007; Jankowski et al., 2017). Fungi are found in the municipal systems designed for collecting and transporting wastewaters, including street gutters and sewers (Hervé et al., 2017; Yuan et al., 2020). Wastewater treatment plants (WWTPs), the endpoint for most of the waters from cities, provide aquatic fungi with a habitat that is better characterized than most urban aquatic environments, possibly for their sanitary and biotechnological interest (Assress et al., 2019; Espinosa-Ortiz et al., 2016; Matsubayashi et al., 2017; Wei et al., 2018).

Studies to date indicate that the majority of urban aquatic environments are dominated by a relatively small number of fungal taxa, i.e., opportunistic yeasts (*Candida, Cryptococcus* and *Rhodotorula)*, black yeasts (*Aureobasidium* and *Exophiala*), filamentous fungi (*Fusarium, Aspergillus, Cladosporium, Trichoderma*, and *Acremonium*) and some members of Cryptomycota. Interestingly, a common feature among many of these genera is their ability to form biofilms (Babič et al., 2017; Raghupathi et al., 2018; Zupančič et al., 2016). Although fungal diversity in urban aquatic ecosystems is likely lower than in natural ecosystems (Newbound et al., 2010; Wei et al., 2018), we propose that studying the diversity and ecology of fungal communities in human-disturbed environments is deserving of greater importance since approximately half of the world's population lives in cities and people spend about 90% of their lifetime in indoor ecosystems (Adams et al., 2013; Bello et al., 2018; Flores et al., 2011; Humphries, 2012).

Fungal metabolism and anthropogenic pollutants

Generally, fungi are characterized by a broad spectrum of extracellular enzymes (Harms et al., 2011) that allow them to break down highly polymeric substances consisting of very large molecules or macromolecules, composed of many repeating subunits. This metabolic feature renders fungi ideal candidates to break down natural polymeric substrates (Rojas-Jimenez et al., 2017) and anthropogenic pollutants that contain a large variety of macromolecules. Thereby, the high resistance against anthropogenic pollutants makes them ideal bioindicators of anthropogenic stressors in the environment. Aquatic fungi are ubiquitous and promising candidates for polymeric organic matter decomposition and humification of plant litter, which provides energy for microbes in various aquatic habitats (Webster et al., 1999). Aquatic **hyphomycetes** are considered one of the most prevalent microbial communities associated with emergent plant materials and submerged terrestrial plant residues in aquatic ecosystems, comprising 63–100% of total microbial biomass (Gulis and Suberkropp, 2003). These fungi exhibit a high degradation potential for lignocellulosic compounds due to their constant activity in a wide range of climatic conditions (Graça and Ferreira, 1995) and production of a wide array of extracellular ligninolytic enzymes such as cellulases, xylanases, pectinase, laccases and peroxidases (Harms et al., 2011; Rojas-Jimenez et al., 2017).

This degradation potential enables fungal colonization and growth and results in subsequent plant litter mass loss, skeletonization, and maceration (Bärlocher, 1998). The formed fungal biomass provides a significant feedstock for other aquatic heterotrophic microbes and higher trophic levels, leading to accelerated mineralization and transformation of plant biomass into humic substances (e.g., humic acids, fulvic acids, and humin) (Bärlocher, 1985). Furthermore, the quantity and quality of additional labile materials, such as algal exudates, determine the dominance of fungal groups within aquatic ecosystems and, consequently, terrigenous C turnover (Fabian et al., 2017). Moreover, environmental conditions and the fungi's enzymatic repertoire ultimately affect the rate of litter decomposition in streams (Benstead and Huryn, 2011). This relationship remains little studied for lacustrine environments (Grossart et al., 2019). Other polymeric compounds such as pollen grains and non-plant material, e.g., chitin and keratin, are mainly decomposed by chytrids and non-fungal oomycetes via the production of specific exoenzymes (Wurzbacher et al., 2014), resulting in fungal biomass and spore formation serving as a food source for higher trophic levels such as invertebrates.

Fungal processing of pollutants

One of the most evident traces of human activity on the planet is increasing pollution, which negatively impacts the biosphere. Today, the discharge of toxic liquids from urban and industrial activities carrying a large amount and variety of pollutants has reached dangerous levels in both freshwater and marine ecosystems. There are at least six pathways by which humans pollute freshwater ecosystems: (a) sewage, (b) nutrients and terrigenous materials, (c) crude oil, (d) synthetic dyes, (e) heavy metals, and (f) plastics (Häder et al., 2020). Fungi, as one of the most important and conspicuous components of aquatic microbial communities, are detrimentally affected by these pollutants. For example, species diversity and richness, functions, and physiology of aquatic fungi can be severely impacted by the ever-increasing discharge of pollutants into freshwaters (Krauss et al., 2003; Lecerf and Chauvet, 2008; Zeng et al., 2012; Op De Beeck et al., 2015). Yet, some aquatic fungi have developed a high capacity to deal with numerous environmental pollutants and are being used as part of environmental remediation strategies.

Many traditional pollutants are degraded by aquatic fungi, including surfactants (Mallerman et al., 2019; Nakamiya et al., 2005), 2,4,6-Trinitrotoluene (TNT) (Hoehamer et al., 2006), pesticides (Purnomo et al., 2011; Rodríguez-Castillo et al., 2019; Ulčnik et al., 2013; Wang et al., 2015) and other toxic persistent organic chemicals (Aranda, 2016; Marco-Urrea et al., 2009; Sun et al., 2016; Xu et al., 2014). However, the number of fungi that have been studied for their degradation capabilities is relatively small. Therefore, the likelihood to find new species with the potential for bioremediation of aquatic pollutants is high.

Aquatic fungi can use at least four mechanisms for processing and transforming a wide variety of pollutants in inland waters (Fig. 3). They are highly unspecific and can act independently or synergistically. The first mechanism involves the production of two main types of extracellular enzymes: peroxidases and phenoloxidases (Grinhut et al., 2011b; Majeau et al., 2010; Rodríguez-Rodríguez et al., 2019). The second consists of the production of low-molecular-weight redox mediators such as reactive oxygen species (e.g., singlet oxygen, peroxide and the hydroxyl radical) that also act extracellularly and with low specificity on the substrates (Grinhut et al., 2011a; Grossart and Rojas-Jimenez, 2016; Jensen et al., 2001). The third involves intracellular degradation by enzymes such as the cytochrome P450 complex (Haroune et al., 2017; Marco-Urrea et al., 2009). The fourth is related to the biosorption of compounds (Ulčnik et al., 2013; Xu et al., 2020) (Fig. 3).

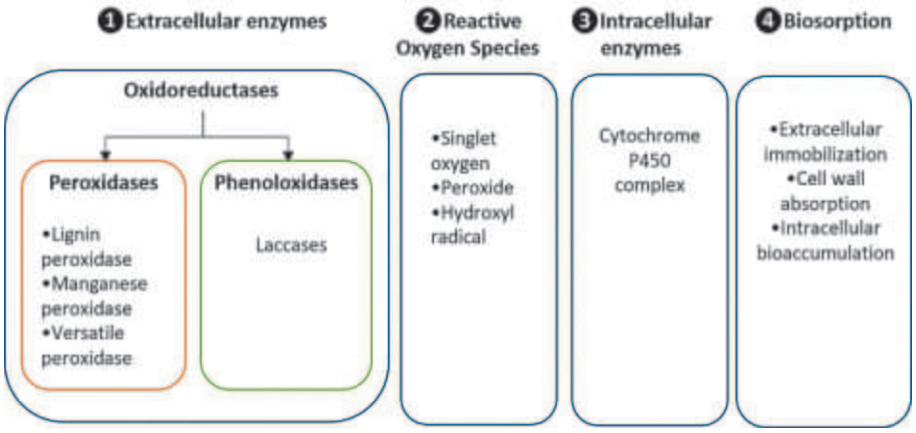

Fig. 3 Four mechanisms via which aquatic fungi process a wide variety of pollutants in inland waters. In general, these mechanisms are not specific for the type of molecules to degrade and can operate independently or synergistically. The first mechanism involves the production of two main types of extracellular enzymes: peroxidases and phenoloxidases. The second consists of the production of low-molecular-weight redox mediators such as reactive oxygen species that also act extracellularly and with low specificity on the substrates. The third involves intracellular degradation by enzymes such as the cytochrome P450 complex. The fourth is related to the biosorption (adsorption and absorption) of compounds.

Fungi possess enormous metabolic diversity, which makes them critical organisms for processing **pollutants** in aquatic systems (Grossart and Rojas-Jimenez, 2016; Harms et al., 2011; Krauss et al., 2011). Some of the most concerning are the so-called "**emerging pollutants**" that include synthetic or naturally occurring chemicals that are generally not controlled but could have adverse effects on human and ecosystem health (Llorca et al., 2016; Rodríguez-Rodríguez et al., 2019). Members of Basidiomycota and Ascomycota are capable of degrading pharmaceuticals, which are considered among the most diverse group of aquatic pollutants, including antibiotics, antidepressants, anti-cancer, antiepileptics, steroid hormones, and anti-inflammatory substances (Asif et al., 2017; Ferrando-Climent et al., 2015; Haroune et al., 2017; Kovalakova et al., 2020; Liu et al., 2016; Rusch et al., 2019; Silva et al., 2012). Moreover, aquatic fungi are capable of degrading various types of plastics (Ali et al., 2014; Deguchi et al., 1997; Jeyakumar et al., 2013; Krueger et al., 2015; da Luz et al., 2013; Wang et al., 2016) as well as accompanying contaminants such as plasticizing substances that can have endocrine-disrupting effects or carcinogenic effects on environmental and human health (Ahuactzin-Pérez et al., 2018; Ferrer-Parra et al., 2018; Loffredo et al., 2012; Skinner et al., 2009; Zhao et al., 2018).

In recent years, aquatic fungi have been studied and established as one of the most active groups of microorganisms for degrading synthetic dyes (Wesenberg et al., 2003). In fact, aquatic fungi degrade/adsorb dyes and intermediates such as aromatic compounds and mineralization of azo dyes (Papanikolaou et al., 2008). The high capacity of fungi, especially of white-rot basidiomycetes, to produce extracellular ligninolytic enzymes including laccase, manganese peroxidase, and lignin peroxidase (Gomi et al., 2011) renders them important for bioremediation measures.

In general, fungal dye decolorization is achieved in two ways: (a) biosorption and (b) biodegradation. In biosorption approaches, fungal biomass in wastewater is a byproduct of industrial fermentations. It contains amino, carboxyl, thiol, and phosphate groups in the cell wall, which can be applied for dye removal (Crini and Badot, 2008). In biodegradation approaches, fungi are used to degrade a wide variety of recalcitrant dyes via non-specific attachment of ligninolytic enzymes to the target substrate. Although results of biodegradation from lab-scale studies have been promising, their performance in the purification of various industrial effluents is little studied (Kaushik and Malik, 2009). The application of a broad spectrum of fungi resisting the toxicity of dyes allows for optimizing the overall biosorption and biodegradation ability at changing environmental conditions.

Increasing concentrations of heavy metals lead to deleterious impacts on fungal biodiversity, communities, and biological activities in aquatic ecosystems (Solé et al., 2008), including respiration, sporulation, and growth/biomass formation and fungal leaf-degradation rates (Krauss et al., 2001; Lecerf and Chauvet, 2008; Sridhar et al., 2000).

However, some aquatic fungi possess tolerance and resistant mechanisms for metal-induced toxicity through the production of extracellular and intracellular biomolecules (protein chelating agents, enzymes, slimes, and other metabolites) (Krauss et al., 2011). Furthermore, the structure of fungal cell walls possesses unique characteristics for heavy metal removal through adsorption mechanisms including; hydroxyl (OH), amino (NH), carbonyl (C═O), phosphate (P═O) groups in the fungal biomass, in addition to the porous nature with the high surface area cell wall (Braha et al., 2007, Hassan et al., 2018). Consequently, due to their high biosorption or bioaccumulation capabilities, aquatic fungi may play a critical role in the sequestration of heavy metal ions than bacteria (Massaccesi et al., 2002).

Case study: Fungal communities in the Plastisphere

The **Plastisphere** is a term used to describe the newly emerging habitat created by the massive introduction of microplastics to all environmental areas (Eckert et al., 2018). Microbiologists frequently study bacteria on plastics, but much less information exists for fungi (Amaral-Zettler et al., 2020). We suggest that fungi on plastic debris are an important emerging area of research (Fig. 4).

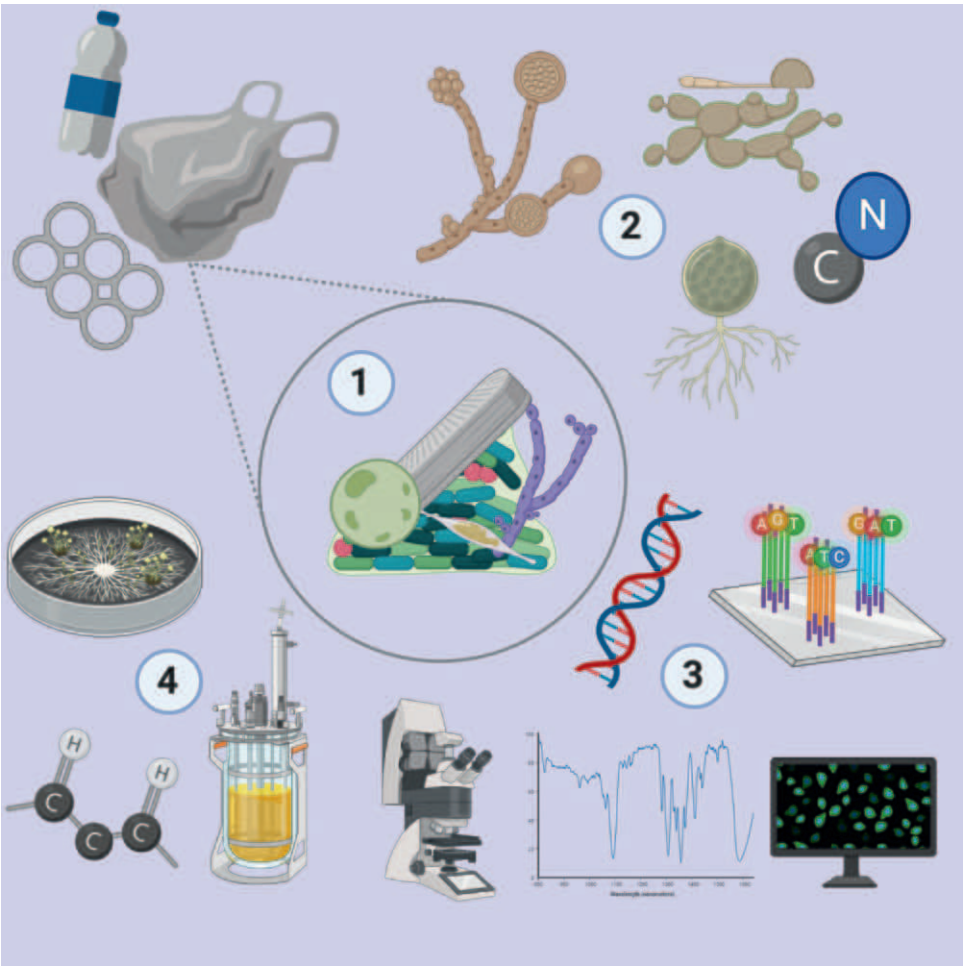

Fig. 4 There are many reasons and methods for studying fungi on plastic debris. (1) Plastic debris results in biofilm structures that include fungi, together with bacteria, green algae, diatoms, and other heterotrophs, termed the **Plastisphere**. (2) Fungi in the **Plastisphere** can include yeasts, filamentous, and parasitic fungi (e.g., some Chytridia). These groups contribute significantly to freshwater carbon and nitrogen cycling. (3) DNA-based sequencing technologies are well suited to decipher the fungal diversity within these biofilms. Other methods that combine fluorochrome-tagged genetic probes and spectral imaging techniques can help to observe and study different species of fungi within the biofilm structure and thus to determine their ecological role. (4) Isolation of fungi from the **Plastisphere** can lead to the discovery of new metabolic pathways of plastic polymer degradation.

Fungi are paramount to carbon and nitrogen degradation and transfer within aquatic food webs (Soares et al., 2017) and it has been shown that plastics have an impact on the heterotrophic activities of fungi (Arias-Andres et al., 2018). Furthermore, fungal parasites can control algae and cyanobacteria (Frenken et al., 2017), which are also present in plastic biofilms. Thus, it is important to know the implications of plastics on various ecological interactions and biogeochemical cycles.

In particular, fungi are well known for their xenobiotic degrading capacity, and more testing is needed to quantify fungal degradation of different plastic polymers (Brunner et al., 2018). Fungal metabarcoding and metagenomics will allow for great advances in the exploration of fungal biodiversity and functionality (Matsuoka et al., 2019) in the **Plastisphere**. Given the 3D structure of biofilms on plastic debris and the importance of interactions between fungi, algae, and bacteria, tools allowing for spatial and taxonomic analyzes should be included. For this purpose, methods that combine both high taxonomic and spatial resolution must be considered and adapted to studying fungi in the **Plastisphere** (Arias-Andres, 2020; Schlundt et al., 2019).

Fungi as bioindicators of ecosystem's health: A conceptual proposal

Structural bioindicators describe the composition or biodiversity of a given organismic group whereas functional bioindicators assess a specific function (e.g., the degradation of lignocellulose) or an ecosystem service (e.g., carbon or nitrogen cycling). Complex ecological indicators address the interconnection between structure and function through the food web (Parmar et al., 2016). Aquatic fungi are relevant bioindicators of freshwater ecosystem's health because of their role in the degradation of **allochthonous organic matter** (e.g., leaves falling from a nearby tree into a stream) in aquatic food webs (Baudy et al., 2019).

Fungal enzymatic tools for degrading lignocellulose (the main component of plant matter) are very well known (see "Fungal metabolism and anthropogenic pollutants" section) and explain their role from a biological point of view (Krauss et al., 2011; Rossi et al., 2017). For freshwater fungi, the most studied functional indicators are leaf litter degradation rate, biomass (ergosterol found in fungal cell membranes), and the capacity to produce spores for reproduction or sporulation (Bruder et al., 2016; Gomes et al., 2018; Krauss et al., 2011; Soares et al., 2017). Meanwhile, the most common group described in the literature are different spore (or conidia)-producing fungi, commonly referred to as "**Ingoldian**" or aquatic **hyphomycetes** (see above; Bärlocher, 2016; Baudy et al., 2019; Chauvet et al., 2016). The OMICS era is identifying more potential indicator groups (Ceci et al., 2019; Kettner et al., 2017).

Ecological indicators often involve changes in fungal community composition which, e.g., indicate high invertebrate feeding pressure (Baudy et al., 2019; Canhoto et al., 2017; Mora-Gómez et al., 2016). Consequently, specific fungal communities are well suited to serving as bioindicators of anthropogenic stressors and environmental change in aquatic systems. Differences among types of aquatic ecosystems (e.g., streams vs. wetlands), habitats (e.g., pelagic zone vs. sediment), and multiple stressors, however, need to be taken into account since they may affect the role of fungi as environmental indicators (Graça et al., 2016; Gulis et al., 2019; Ortiz-Vera et al., 2018; Röhl et al., 2017).

Two major and relevant anthropogenic stressors in aquatic systems, i.e., pollution and eutrophication due to nutrient input (N and P) (Reid et al., 2019) can be well detected by changes in fungal communities. Accordingly, the fungal community response to pollution and eutrophication is relatively well documented. Overall, eutrophication selects for specific tolerant groups (Bai et al., 2018; Samson et al., 2020), increases the abundance and diversity of fungal taxa, and lowers fungal sporulation rates and biomass (Pereira et al., 2016; Pietryczuk et al., 2018).

In contrast to eutrophication, the usage of fungal indicators to detect other factors is much less studied. For example, higher flow velocity increases fungal diversity (Fiuza et al., 2019) in running waters. In low-flow areas downstream of dams, there is a lower fungal richness and biomass production (Colas et al., 2016), probably due to sedimentation and lower concentrations of dissolved oxygen (Bruder et al., 2016). Salt concentration is well known to affect fungal community composition (Gonçalves et al., 2019). Thus increasing salinization due to climate change (Pesce et al., 2016) and run-off from salted roads in winter can be deduced from specific changes in fungal communities in parallel to a significant reduction in fungal sporulation and biomass (Canhoto et al., 2017; Gonçalves et al., 2019). So far, metal and chemical pollution effects on aquatic fungal communities are least analyzed (Barros et al., 2020; Pimentão et al., 2020), but indicate a high bioindication potential. Most of this information stems from rivers and streams, and the role of fungal bioindicators for anthropogenic stress in standing waters has been less explored.

Emergent metal pollution selects for specific species of tolerant fungi and affects fungal leaf litter degradation (Duarte et al., 2019), protein expression, and enzymatic activities (Barros et al., 2020). For synthetic chemicals, the scarcity of fungal models for ecological risk assessment of fungicides is noteworthy (Ittner et al., 2018; Ortiz-Cañavate et al., 2019). Other emergent contaminants have been evaluated for their effect on fungal communities and include antibiotics (Bundschuh et al., 2009), nanomaterials (Du et al., 2020), and microplastics (Kettner et al., 2017). In these cases, enzymatic activities have been identified as potential fungal bioindicators for chemical stress, in particular those related to lignin degradation (Rossi et al., 2017).

Conclusions and perspectives

In this article, we have highlighted the immense diversity and metabolic versatility of fungi and fungi-like organisms in natural and human-made aquatic ecosystems (Fig. 5).

Aquatic fungi are key organisms for organic matter cycling and the transformation and detoxification of anthropogenic pollutants, including synthetic dyes, aromatic hydrocarbons, and other polymeric and potentially toxic substances. Urbanization leads to increased inland water pollution affecting environmental and human health. We highlight the role of aquatic fungi in breaking down natural polymers such as cellulose, lignin, and chitin as well as more complex substances of anthropogenic origin such as antibiotics, anti-depressants, dyes, surfactants, hormones, and plasticizers, known as **emerging pollutants**. Thus, we demonstrate how aquatic fungi play an important ecological role in the cycling of nutrients and carbon and in mitigating the increasing effects of humans on the environment. However, there are still large knowledge gaps in the field of inland water **mycology**. It will be of paramount importance to further study the effects of **emerging pollutants** on the structure of aquatic fungal communities and their interactions with other organisms such as bacteria, viruses, and other eukaryotes. Finally, we need to better understand pollutant-fungi relationships, including those on microplastics, given the abundance, low degradability, and wide distribution of anthropogenic pollutants on the planet.

New technologies will continue to expand our knowledge and appreciation for aquatic fungi in natural and urban ecosystems. For example, the combination of molecular and advanced microscopy tools and new physiological and cultivation approaches will result in better characterization of fungal metabolic processes. This biotechnological research could also lead to discovering new pathways for the degradation of pollutants such as plastic polymers. Further, a deeper understanding of the ecological role of fungi and fungi-like organisms is required to identify new fungal bioindicators of anthropogenic stress. Filling these knowledge gaps is key to tackle the many challenges facing future environmental and human health due to urban development and anthropogenic pollution, including biodiversity loss and alteration of aquatic ecosystem functions.

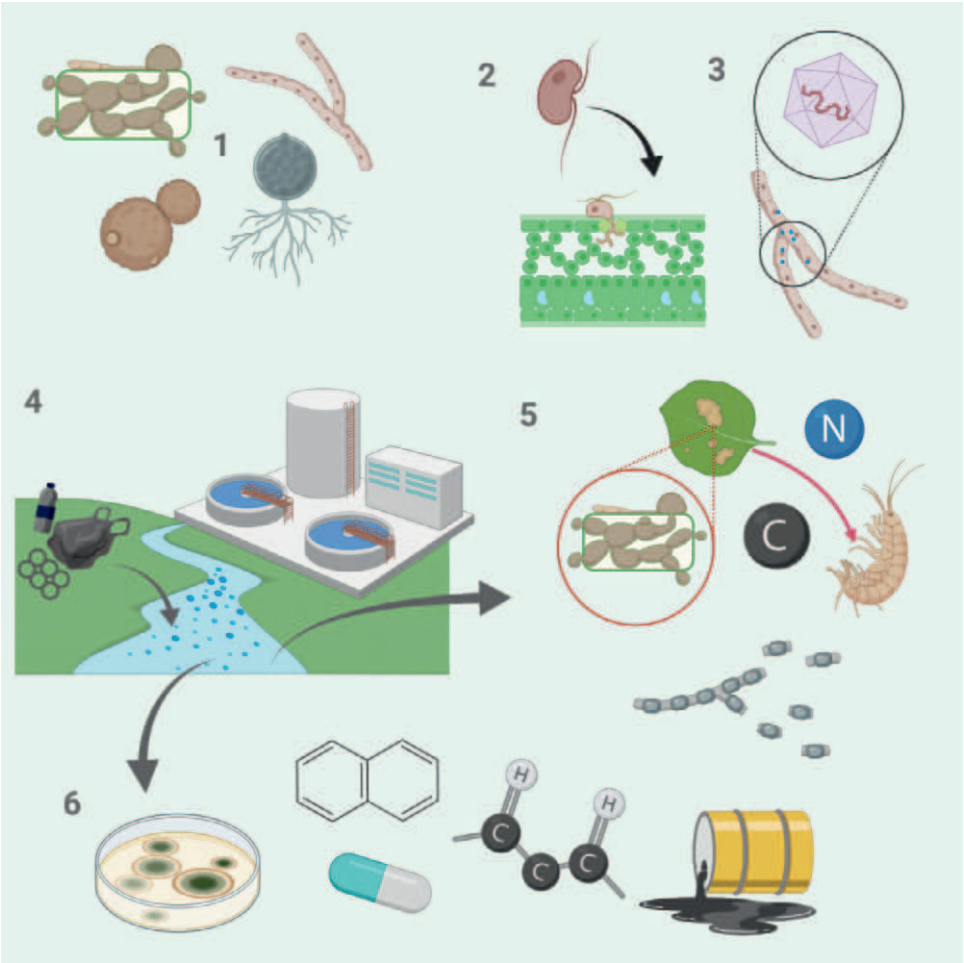

Fig. 5 We provide a summary of important and unexplored aspects of aquatic fungi in the **Anthropocene**. (1) Fungi in freshwaters display multiple lifestyles, e.g., saprophytic and parasitic, spore, and hyphae-forming species. All of them respond in an as yet largely unknown manner to anthropogenic stressors. Thus, further research is needed to better understand the fungal ecology and effects of inland water pollution in an urbanized world. For example, (2) fungi-like organisms such as aquatic oomycetes (some of which are prevalent plant and fish pathogens); (3) fungi-virus infections in aquatic systems; (4) increasing anthropogenic pollution via the release of nutrients, industrial chemicals, and urban waste into aquatic ecosystems effects; (5) fungal transfer of carbon and nitrogen from allochthonous organic matter to the aquatic food web, whereby sporulation (reproduction) rates act as common bioindicators of ecosystem health. Finally, (6) new fungal pathways for the biodegradation of emergent contaminants such as pharmaceuticals, persistent organic pollutants, and petroleum-based plastic polymers should be explored in new fungal isolates obtained from urban water ecosystems.

Knowledge gaps about fungi in the face of urbanization

- Anthropogenic effects of combined environmental factors and hydrologic conditions on fungal growth and organic matter transformation
- Changes in functional diversity of aquatic fungi in the presence of anthropogenic stressors such as eutrophication, warming, salinization, and emerging pollutants
- Loss of fungal diversity following habitat modification due to urbanization as a part of the global freshwater biodiversity crisis
- The ecological role of fungi-like organisms such as oomycetes in agricultural landscapes
- Fungi-virus interactions and their ecological consequences at increasing anthropogenic stress
- Specific fungal degradation processes of polymeric organic matter in urban environments
- Anthropogenic impact on biodiversity, ecology, and function of mycorrhizal fungi and endophytes in urban aquatic habitats
- Specific fungal degradation mechanisms of synthetic dyes and other anthropogenic pollutants
- Role of the emerging anthropogenic pollutant (micro)plastics as fungal habitat and substrate
- Role of fungi as bioindicators of anthropogenic stress and degradation of ecosystem state

See Also: Structures and functions of Inland Waters - Lakes: Fungi and Chytrids; Protists: Flagellates and Amoebae

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Environmental DNA Advancing Our Understanding and Conservation of Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Amplicon PCR amplified DNA fragment contained between two primer regions.
Barcode A specific region within a gene that is used to genetically identify individual species or other taxonomic levels.
Control samples field or lab comparison that matches the eDNA sampling type (e.g., sterilized water when aquatic eDNA is collected) and serves to assess false positives in downstream analyzes due to sampling contamination. Laboratory controls are used to assess contamination during lab analysis due to contaminated equipment.
Environmental DNA (eDNA) DNA isolated from an environmental sample (e.g., soil or water) that does not target a species or community of interest.
False negative When a species/taxon is not identified from a sample even though it is present.
False positive When a species/taxon is incorrectly assigned to a sequence due to contamination of the sample or incorrect assignment methodology.
Metabarcoding High throughput sequencing of PCR-generated sequence libraries, which allows for multiple unique sequences to be read from a single sample.
Polymerase chain reaction (PCR) A molecular technique used to replicate small (usually specific) segments of DNA.
Primer A short single-stranded nucleic acid (~20–50 base pairs) utilized in the initiation of DNA synthesis during PCR (e.g., extension stage of PCR). Primer specificity refers to how stringent the primer is binding to target DNA sequences.
Quantitative PCR (qPCR) A molecular technique that monitors the amount of amplification during a PCR via fluorescence.

Environmental DNA (eDNA)

Environmental DNA (eDNA) is a new technique and field of study with far reaching implications for environmental and biodiversity assessment within the fields of ecology, evolutionary biology, agriculture, disease control and beyond. Environmental DNA is defined as DNA extracted from an environmental sample that does not target a particular organism or set of organisms

(Bohmann et al., 2014; Seymour, 2019). The sources of eDNA are expected to be predominantly free-floating DNA that has recently left its species of origin through natural body secretion (e.g., shedding, molting, feces, urine, gametes), or as fragments released from decaying bodies (Jo et al., 2019; Moushomi et al., 2019). A major breakthrough in the utilization of eDNA was the discovery that once eDNA has been isolated from a sample it can be used to identify the species of origin using molecular methods (Ficetola et al., 2008). Since eDNA can be sampled from practically any environment imaginable, including water, soil, air, ice; the general concepts and methods regarding eDNA-based research can be broadly applied.

It is important to clarify that the definition of what constitutes an eDNA sample is debatable among researchers. In very broad terms, eDNA is often used to describe any DNA captured from environmental sampling, including bacteria and single cell eukaryotes or homogenization of bulk samples (e.g., insects from a trap blended together). However, it is important from a methodological standpoint to be aware of the environmental source and intended target because methods that work to identify bulk samples or bacteria communities are not always optimal for identifying non-target eukaryotes from water or sediment samples. To avoid confusion, this chapter will restrict the definition of environmental sampling to non-bulk sampling (e.g., water and sediment) and eDNA to eukaryote-derived DNA from environmental samples. Overall, this chapter provides a concise summary of eDNA concepts and applications in freshwater ecosystems, outlines the use of eDNA-based biodiversity assessment and the standard approach in using eDNA to sample freshwater environments, and offers insights into current pursuits using eDNA.

Biodiversity assessment in freshwater environments encompasses a diverse set of methodologies depending on the community or species of interest, sampling environment and the level of taxonomic identification required for a given study. Often methods are very specific to a set of species or environmental conditions, which can limit the ability, or effectiveness, of using the method across different sampling sites or time points. For example, sampling macroinvertebrates from streams is often conducted with kick-net sampling, which is only fully feasible if the depth of the rivers are shallow enough to traverse, to sample the middle of the river and both edges, and the substrate is suitable for adequately disturbing the riverbed. If the substrate is too coarse (e.g., boulders or bedrock) or fine (mud or silt), the method will often miss individuals within the environment. Additionally, seasonal conditions may alter a sampling site's physical characteristics (e.g., flooding, freezing or drought), thereby preventing subsequent or regular sampling.

In contrast, sampling for eDNA is more standardized for the type of environmental sample, be it water, soil or air, and can be consistently sampled regardless of the ecosystem type, season, or taxa of interest. The reliability of eDNA to detect communities has repeatedly been shown to be on par or better than traditional sampling methods (Valentini et al., 2016; Sales et al., 2020; Seymour et al., 2020). In addition, the standardized molecular and bioinformatics approaches used to process and analyze eDNA data are often faster and cheaper to routinely conduct compared to traditional taxonomic identification methods (Davy et al., 2015) and avoid the potential bias induced by using multiple or inexperienced taxonomic identifiers (Deiner et al., 2017). However, there are still several limitations, ongoing developments and potential pitfalls associated with the use of eDNA. For example, it is important that the environment is sampled in a structured manner, such as depth profile sampling within a lake or a sampling transect along the distance of a river, to account for eDNA movement within the environment (e.g., distribution/transport) (Li et al., 2019). This chapter serves as an overview to the understanding and practice of eDNA-based research in freshwater environments, particularly for new and interested researchers. It is not intended as a definitive statement on the subject, as the field is rapidly changing and many views and discussions are ongoing regarding the topic, some of which are highlighted below.

Freshwater environments

This section describes three important aspects of the use of eDNA in freshwater environments: The background and utilization of eDNA, how eDNA accumulates in freshwater environments and the processes that remove eDNA from the environment. Fig. 1 illustrates the factors that influence eDNA detection in natural environments.

Background of eDNA research and utilization in freshwaters

The methodological background for eDNA originated in the late 1970s and early 1980s with the establishment of the polymerase chain reaction (PCR) and DNA sequencing (Thomsen and Willerslev, 2015). PCR allows for the replication of targeted genetic sequences, which is important for eDNA since the concentration of target DNA in environmental samples is generally too low to be detected using visual or sequencing methods, unless PCR is first used. The development of quantitative PCR (qPCR) in the 1980s, which allows for real-time observation of a PCR reaction via fluorescence, provided a more accurate means to detect single species from eDNA samples. qPCR is still widely used today for population-level assessments and has well-established reporting guidelines and practices, referred to as the Minimum Information for Publication of Quantitative Real-Time PCR Experiments MIQE guidelines (Bustin et al., 2009).

Community-based assessments from eDNA, which are reliant on the development of DNA sequencing, have taken longer to develop methods and guidelines. Modern DNA sequencing allows us to determine the nucleotide order of a genetic sequence without the use of a reference genetic sequence. The development of DNA sequencing led to the development of DNA barcoding in the early 2000s (Hebert et al., 2003). DNA barcoding is a method of using a specific genetic sequence, often a specific gene or region within a gene, to identify species. Several DNA barcode reference libraries have been created, with the intent to catalog barcode sequences of all life on the planet, and are essential for eDNA studies that use high throughput sequence methods because we use these reference databases to link sequences detected in environmental samples to actual species identifications.

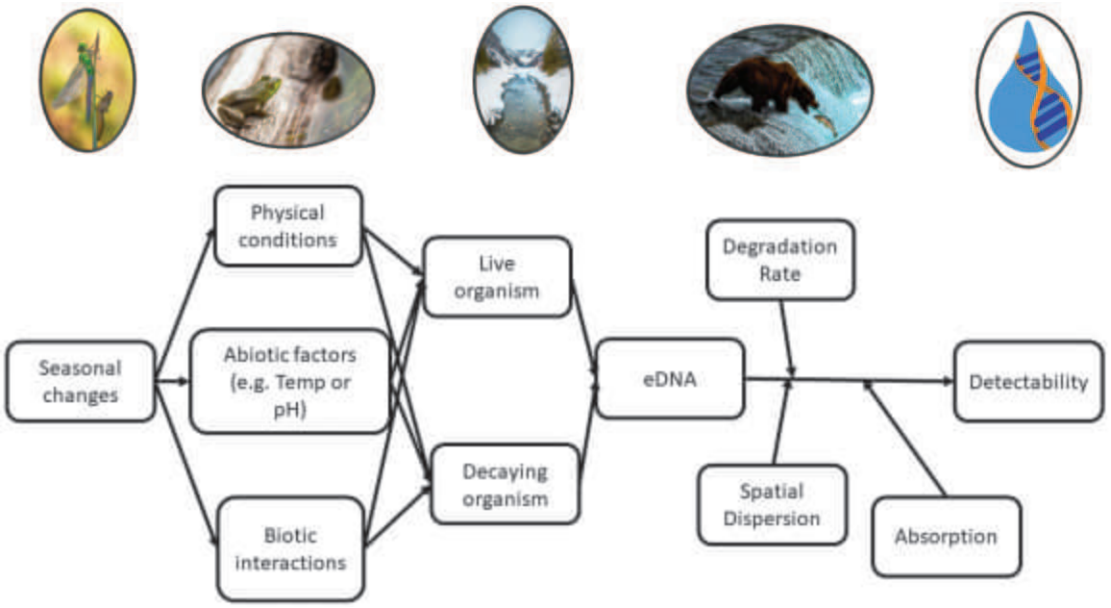


Fig. 1 Diagram showing the ecology of eDNA and how environmental, physical and biotic factors can influence eDNA detection. As eDNA is released into the environment, the tissues, cells and cell particles that are needed for sampling and detection are readily broken down, or absorbed, over time, meaning the detection of eDNA is time dependent. Many factors influence the detection of eDNA, such as seasonal changes to species activities or life stages, which will affect eDNA production, or differences in environmental conditions, such as chemical composition, which can affect degradation of eDNA. Environmental DNA may also readily traverse through waterways, meaning the detection of eDNA may not represent the specific location of the sample. Substrates may also bind eDNA particles making them undetectable, unless the substrate itself is sampled.

Using molecular methods to detect bacterial and fungal communities from environmental samples predates eDNA research, including using soil and water samples to detect microbial strains (Ogram et al., 1987; Fisher and Triplett, 1999) and permafrost to assess ancient fungal and pollen diversity (Eske and Alan, 2005). It is important to distinguish these earlier microbial and fungal studies from eDNA here, as eDNA entails detecting species and communities from genetic material that is not part of the target organism(s). Additionally, the concentration of targeted genetic material in eDNA is much smaller, compared to the high concentration of bacterial or fungal DNA found in environmental samples that require different methodologies (e.g., primer selection to avoid sequencing non-targeted species). The closely related field of ancient DNA (aDNA) uses a combination of museum and environmental samples (ice or deep sediment cores) to assess ancient communities and populations (Hofreiter et al., 2001). Apart from similarity in molecular methodological approaches, aDNA research has greatly influenced eDNA clean room and sample processing protocols, which are essential for ensuring data generated from eDNA samples is viable.

Interest in using eDNA for monitoring programs received a lot of attention, but was initially slow to take hold, as the method was largely untested. The first studies showing the application of eDNA, specifically multi-cellular eukaryotes, used water samples to detect American bullfrogs (*Lithobates catesbeianus*) in French ponds (Ficetola et al., 2008). The establishment of the silver carp (*Cyprinus carpio*) eDNA monitoring program in the United States is perhaps one of the most important eDNA applications to occur, as it established an important baseline for using eDNA as an established biomonitoring tool (Jerde et al., 2013). Additionally, the UK monitoring of the current great crested newt (*Triturus cristatus*), an important conservation species in Europe, was one of the first programs specifically designed to utilize eDNA detection (Biggs et al., 2015). With these and other subsequent successes, there is an ever-growing list of single species (i.e., population-based) eDNA programs across several countries and organization. Community-based eDNA assessments that rely on reference databases are less common but have been increasing since about 2014. Seminal works for key taxonomic groups include fish (Valentini et al., 2016; Hänfling et al., 2016), macroinvertebrates (Bista et al., 2017), and diatoms (Vasselon et al., 2017) and provide proof of concept matching eDNA biodiversity to traditional sampling methodologies. Presently many government bodies are planning to or have established community-based eDNA biodiversity assessment protocols for a wide range of species and biomonitoring communities.

An understanding of how eDNA is generated and remains in the environment is essential for utilizing eDNA-derived population and community information (Barnes and Turner, 2016). There are two important processes that affect eDNA in freshwaters: accumulation (or production) and removal (via transport and degradation). Environmental DNA is constantly being produced and subsequently degraded through biological and physical processes. The amount of eDNA present in the environment at any time varies depending on the abundance of the individuals and the intraspecific rate at which each species sheds or releases eDNA, either through bodily functions or via decomposition (Jo et al., 2017; Moushomi et al., 2019). While some species routinely shed eDNA via skin cell loss or excrement, other species may be poor shedders due to limited or timed molting or slow-decaying exoskeleton and can be difficult to detect at low population abundances, such as the American signal crayfish (*Pacifastacus leniusculus*)

(Dunn et al., 2017), and some invasive aquatic plants (Kuehne et al., 2020). Additionally, eDNA accumulation is likely to be affected by seasonal activity of individual species. For example, spawning times for fish can result in large volumes of gametes released into the environment, which may dominate other species eDNA detection and not be directly related to population sizes. Likewise, algal blooms can dominate samples and affect detection of other species such as diatoms and other primary producers. The timing of macroinvertebrate larval emergence may also affect the lateral transfer of biomass in lakes and streams, whereby pupae move from the benthos to the water surface, thereby affecting detection at different time points if not accounted for in the sampling design.

Once eDNA is produced, it can be transported away, particularly in rivers, or degraded. Degradation times differ depending on the environmental conditions; eDNA detection in lentic environments (e.g. lakes and ponds) can be up to 2 months, whereas in sediments it can be for several years (Barnes and Turner, 2016). Lotic eDNA will readily travel downstream once produced and can be detected several kilometers downstream in highly channelized settings (Deiner and Altermatt, 2014; Seymour et al., 2018), though downstream detection is much shorter in natural settings due to effects of dilution from river confluences and absorption from clay based substrates (Shogren et al., 2017). The rapid degradation of eDNA in water environments is thought to be due to hydrolysis as well as microbial activity (Barnes and Turner, 2016; Jo et al., 2019; Moushomi et al., 2019), although the exact processes are still unclear. Environmental DNA can last for several years in freshwater soil environments once it settles into the anoxic zone, as DNA can maintain its structure more easily under low oxygen conditions. Abiotic factors can also increase the degradation rate of eDNA in the environment (Strickler et al., 2015; Seymour et al., 2018) including low pH, high temperature, and potentially high UV exposure, although natural levels of UV are not expected to have significant effects on eDNA degradation rates (Andruszkiewicz et al., 2017; Mächler et al., 2018). The short term detectability of eDNA in water samples makes freshwater eDNA a measure of recent species presence, as opposed to long-term historical measurements from sampling sediments (Deiner et al., 2017). As such, water eDNA sampling is preferred for studies looking to assess the current community and populations inhabiting a site. However, sediment sampling may be more appropriate for assessing species that predominantly live within the sediment as their eDNA may not be visible or obtainable via water eDNA.

Using eDNA for biomonitoring and conservation

Freshwater biomonitoring generally focuses on routine monitoring of three main groups that are linked to environmental status: fish, macroinvertebrates, and diatoms. Detection and monitoring of these three groups can be labor and time intensive, which has led to increased interest in using developing eDNA-based biomonitoring methods and applications. Traditionally the monitoring of these groups differs substantially, with different research groups generally specializing on one group or another. Similarly, the adaption of eDNA for monitoring these groups, while more similar than the differences in traditional methods, has differed in their utilization and methods employed.

Fish biomonitoring

Fish biodiversity is, by far, the most studied within the eDNA research sphere, due to the economic importance of fisheries and relatively low diversity of fish communities compared to macroinvertebrates or diatoms, making validation of studies relatively easy. In addition, there is general widespread consensus that eDNA-based fish biomonitoring outperforms traditional sampling methodology, with the majority of studies occuringwithin lentic environments (Jerde et al., 2013; Valentini et al., 2016; Hänfling et al., 2016). From a conservation standpoint, eDNA sampling is advantageous over other methods because it is non-invasive, and no animals are harmed, compared to the several traditional sampling methods, such as electro-fishing, gill-netting, fin clipping that harm or kill fish. Combined with other non-invasive monitoring methods, such as hydro-acoustic monitoring, eDNA sampling offers a rapid and routine means to monitor fish population dynamics across the globe (Berger et al., 2020). A limitation of eDNA-based fish biodiversity assessment is the need to ensure that the sampling location (e.g., a lake) is either well-mixed or that the sampling has sufficient spatial coverage for the size and depth of the habitat of interest (Li et al., 2019).

Freshwater macroinvertebrate biomonitoring

Macroinvertebrates are a group of major interest for biomonitoring, particularly in river ecosystems where they are an important component of environmental assessment (Seymour et al., 2016) and indicators of functional change (Heino et al., 2004). Several recent studies have shown stark differences in data from eDNA methods and traditional macroinvertebrate sampling; however, the general biodiversity assessment patterns (e.g., assessment scores, inter-community variation) are often found to be similar (Macher et al., 2016). A major advantage of eDNA sampling over traditional macroinvertebrate sampling is the ability to sample water from any type of freshwater environment, including lakes, as well as both deep and fast-flowing rivers. Conversely, traditional kick-netting used for macroinvertebrate sampling is largely restricted to rivers that are traversable by foot and where the substrate is gravel or small-stoned. Macroinvertebrate communities can be assessed rapidly, compared to traditional taxonomic identification, by extracting and sequencing DNA from a kick-net sample (i.e., bulk sampling), though this should not be directly compared with eDNA sampling given the targeted approach of the bulk sampling method. It is suggested that the bulk sampling approach produces more reliable detection compared to sampling of aquatic eDNA, although community dynamics are equally well observed

(Macher et al., 2018). Moreover, collection of aquatic eDNA that utilizes a spatially structured sampling design results in a more representative biodiversity being sampled compared to benthic kick net samples, including increased detection of biomonitoring species that are traditionally difficult to assess, including Chironomidae (Seymour et al., 2021).

Diatom biomonitoring

Diatom communities are highly sensitive to changes in abiotic conditions, are routinely used for biomonitoring purposes in both lotic and lentic environments, and are generally the most sensitive to environmental change compared to fish and macroinvertebrates (Pandey et al., 2017). The importance of diatoms for biomonitoring are highlighted by their use in the European Union's Water Framework Directive (WFD) (Valentin et al., 2019), with similar efforts ongoing in Canada (Maitland et al., 2020). However, diatom identification is notoriously difficult compared to fish or even macroinvertebrates, which prompted a faster adaptation of molecular methods for diatom biomonitoring purposes compared to other biomonitoring groups. Single species assays are possible for some species; however, community spatial and temporal dynamics have received the most interest, particularly for biomonitoring purposes (Tapolczai et al., 2019). While some studies have used surface water for collection of diatom eDNA (Seymour et al., 2020), this might not be optimal over standard field sampling approaches that directly sample diatom by scrapping stones collected from river beds (e.g., bulk sampling) (Vasselon et al., 2017).

Detection of rare species and conservation efforts

There is an ever-increasing list of eDNA conservation efforts under development for several freshwater species (Mauvisseau et al., 2019; Belle et al., 2019). Perhaps the oldest example of an established eDNA monitoring program is the endangered great crested newt (*T. cristatus*) monitoring program in the United Kingdom (Biggs et al., 2015). Great crested newts require a network of ponds to form their home ranges, which can make it difficult to identify which ponds harbor newts at any given time. Given the endangered status of the great crested newt, land use changes that might affect great crested newt habitat require extensive habitat surveying. Given the high cost and difficulty in determining great crested newt presence using traditional methods (e.g., aquatic funnel traps, netting, torchlight, and egg counts), an eDNA-based monitoring program was established by Natural England (a UK environmental agency) to provide a more rapid and efficient monitoring protocol (Rees et al., 2014). Other notable conservation studies, for which eDNA detection is of interest, include Eastern hellbenders (*Cryptobranchus alleganiensis*) (Santas et al., 2013), freshwater pearl mussel (*Margaritifera margaritifera*) (Stoeckle et al., 2016), European eel (*Anguilla anguilla*) (Weldon et al., 2020), and wetland amphibian and fish communities (Kačergytė et al., 2021).

Detection of invasive species

Invasive species pose a threat to endemic biodiversity, as their establishment can lead to dislocation or extirpation of local, often rare, species. Early detection is crucial to effectively manage invasive species eradication and to prevent establishment (Mehta et al., 2007; Sepulveda et al., 2020). If invasive species become established, they are often very difficult to eradicate and can have negative effects on local biodiversity, threaten endemic species and incur huge economic cost (Sepulveda et al., 2020). The high sensitivity of eDNA-based assays can offer successful early detection of invasive species, even preceding early stages of invasions (Sepulveda et al., 2020). The standards and methods of invasive species eDNA development and implementation are very similar and are closely linked to those used in conservation biology. Some examples of invasive species that are routinely surveyed for using eDNA include the bluegill sunfish (*Lepomis macrochirus*) (Takahara et al., 2013), the New Zealand mudsnail (*Potamopyrgus antipodarum*) (Goldberg et al., 2013), and the red swamp crayfish (*Procambarus clarkii*) (Tréguier et al., 2014).

Detection and tracking of disease

An emerging aspect of eDNA research is the use of environmental samples to monitor and track the spread of disease vectors, including recent interest in using water samples to survey human coronavirus in waste water (Farkas et al., 2018; Randazzo et al., 2020). Additionally, eDNA is currently being used to assess the spread of polycystic kidney disease (PKD) (Carraro et al., 2018), an economically important disease in salmonids, and to help develop better spatial models for human pathogens such as cholera (Vezzulli et al., 2017) and schistosomiasis (Sengupta et al., 2019).

eDNA methodological workflow: From sampling to data

Sampling the environment and extracting eDNA

Detection of eDNA is done by sampling the environment of interest, particularly the material that the species or community of interest regularly interacts with. Sampling itself can be conducted by taking a sample of the environment such as using a digging device to sample the soil (e.g., shovel, sediment corer) or using a bottle to take a water sample. However, one must be aware that it is very easy to contaminate eDNA samples, with other eDNA sources being transferred by the sampling person or from unclean or reused sampling equipment. For example, if a person sampling for fish eDNA in a lake was fishing in a neighboring lake the day

prior, they could contaminate the samples they are taking as particles acquired the day before could be transferred from their person to the sampling container. It is therefore important to develop stringent sampling protocols for cleaning of persons and equipment and using disposable or single-use sampling equipment (e.g., gloves and sampling containers). The use of field controls/blanks to help identify any potential false positives that may arise from contamination are also strongly advocated. Field controls are previously prepared samples that resemble the field samples, such as a sampling bottle of autoclaved water, that should be brought into the field and processed in the same manner as the field samples. The results from the field controls can then be crosschecked with the field samples later to assess any potential sources of contamination.

Processing of the samples as soon as possible after collection is important to avoid further eDNA degradation. Water samples should be filtered for eDNA as soon as possible and the filters kept dry, preserved with lysis or fixing agents or frozen to avoid DNA degradation. Likewise, soil or sediment, once sampled, should be kept in cool and dark conditions for transport, either for laboratory analyzes or to freezers for longer-term storage. Environmental DNA extraction is generally done following modified DNA extraction protocols (Spens et al., 2017; Tsuji et al., 2019). Extraction of eDNA can be performed with modifications of commercial kits or using "home-brewed" methods (Spens et al., 2017; Lear et al., 2018). It is important to note that eDNA will be extracted at low concentrations, compared to extractions from bulk or tissue samples, in many cases resulting in only trace amounts of relevant DNA, with much larger concentrations of non-target DNA from other taxa, such as bacteria or single-cell eukaryotes. Additionally, inhibitors of downstream PCR reactions (for qPCR or metabarcoding) might be retained during extraction from environmental samples, such as humic compounds from soil (Matheson et al., 2010). Therefore, it is important to check for sample inhibition and consider using an inhibition cleanup step post-DNA extraction.

Generating data from eDNA samples

Once eDNA is isolated from the environmental sample, the DNA fragments need to be associated with the species or group of species (i.e., community) of interest. Currently, two molecular approaches are generally used to identify the eDNA fragments (Fig. 2): quantitative PCR (qPCR), also called real-time PCR, and metabarcoding. qPCR allows for a species-specific detection method using species-specific primers. Metabarcoding is a high throughput sequencing (HTS) method that allows multi-parallel sequencing within a single sample, allowing for community-based (e.g., multiple species) assessments from a single eDNA sample. The qPCR workflow is currently more standardized, cheaper and faster compared to metabarcoding, making it the preferred method for monitoring of rare species, detection of invasive species, or disease monitoring (Wood et al., 2019). Metabarcoding applications are newer, generate more data and allow for community level assessments, although single species can also be extracted from metabarcoding results (Deiner et al., 2017).

Using qPCR (single species)

qPCR methods can be used for several different applications, ranging from control laboratory experiments to species-specific detection in complex natural environments (Goldberg et al., 2015; Thalinger et al., 2021). The qPCR method can detect low levels of DNA in a sample, making it suitable for eDNA-based research. Droplet digital PCR (ddPCR) may also be used, which uses similar molecular chemistry as qPCR with increased sensitivity to detecting low concentrations (Doi et al., 2015). Currently, however, ddPCR machines are more costly to set up and implement, leaving qPCR still at the forefront for those looking to do standardized single species detection (Doi et al., 2015).

A full breakdown of the steps to create and validate PCR primers for reliable use in biomonitoring has recently been outlined by MacDonald and Sarre (2017). Briefly, special consideration needs to be taken to ensure the primers are species-specific so that false positives are not mistakenly identified during the data processing. Steps for creating qPCR primers should include *in silico* assessment for primer specificity, using software such as NCBI's primer blast (Ye et al., 2012), as well as laboratory test of the primers against target and non-target organisms. Depending on the intended application of the primers, either laboratory only use (controlled experiments) or for government biomonitoring programs, the test of the primers can be quite extensive in order to ensure that the primers are species-specific and avoid false positives. To ensure comparison of results across multiple samples and to quantify the copy numbers for each sample, a set of size standards needs to be included into each set of reaction runs. These size standards should contain known quantities of the target sequence that is being amplified during the qPCR run. Size standards can be created using DNA cloning (e.g., plasmids) or purchased as synthetic sequences from a company. The range of size standards to include into each run should capture the full range of values that is to be amplified from the samples. Particularly for eDNA studies, it is important to assess the limits of detection (LOD), which is the primer's ability to detect target sequences at low concentrations (Klymus et al., 2020). It is important to also be aware that some environmental samples may incorporate PCR inhibition, which can be assessed by spiking samples with known quantities of the cloned or synthesized size standard.

While there are many things that need to be considered to quality check and verify qPCR data, the whole process is relatively quick once the primers and protocols are established. The final data is readily accessible after each qPCR run and usable for analyzes immediately, whereas the data generated via high throughput sequencing will generally take several days to reach a similar usage point.

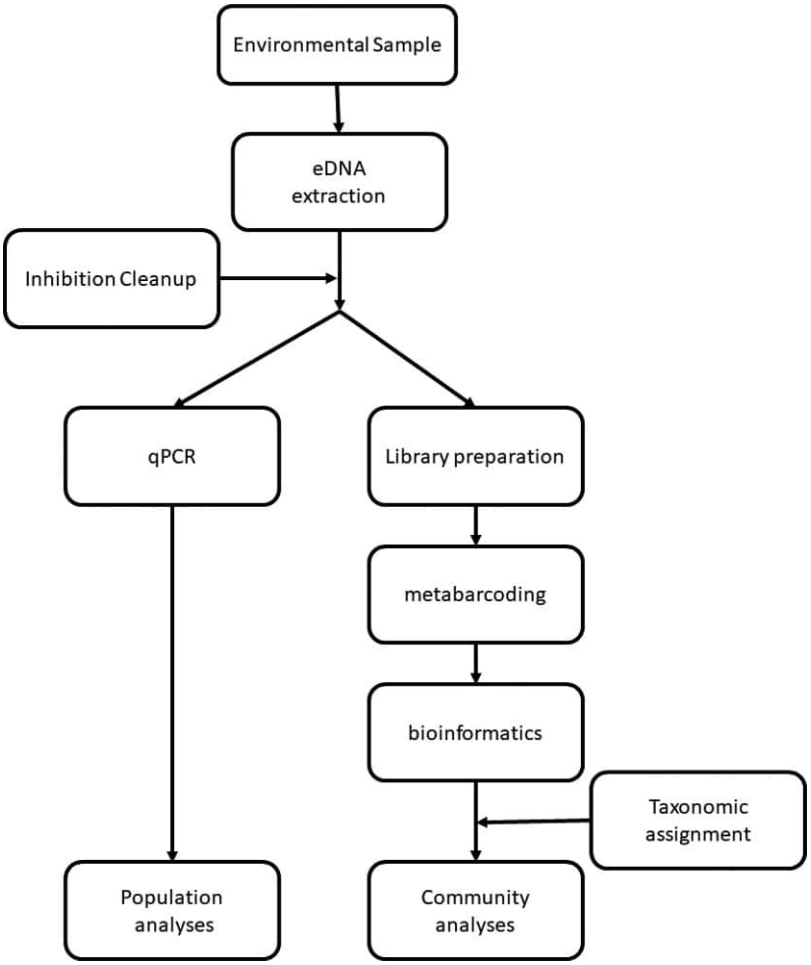


Fig. 2 Simplified workflow for single and multiple species detection using eDNA sampling. eDNA is extracted from environmental samples (e.g., water or soil). Depending on the quality of the extraction, it may be important to perform an inhibition cleanup prior to any PCR based method, although this is not always necessary. The general process for single species via qPCR follows standard qPCR procedures to generate population level data. The steps involved in multi-species eDNA assessment via metabarcoding includes preparing the genetic libraries from the extracted samples, performing the metabarcoding on a high throughput platform, using bioinformatics to quality check and process the sequence output and linking sequence information to taxonomy using a reference database.

Using metabarcoding (multi-species)

Metabarcoding entails using high throughput sequencing (HTS) to determine the sequence information from a pool of genetic material, which can then be linked to a DNA barcode database, hence the name metabarcoding (Deiner et al., 2017). The taxonomic diversity that can be detected from a metabarcoding analyzes is dependent on the specificity of the primers used and the reference database that is used to link genetic sequences to morphological taxonomy. No metabarcoding primer is perfect for all studies, with many different primers designed to capture different taxonomic groups (Cordier et al., 2019; Seymour et al., 2020). Some primers that work well with bulk sampling (e.g., insects blended together) will not work as well with eDNA samples because the primers will also sequence undesirable species, often protists or bacteria, that are more common (i.e., have more DNA available for sequencing) in the sample. With the increased interest in using eDNA, however, new primers are being developed that take into account the type of environmental sample and the desired taxonomic diversity (Leese et al., 2021). Generally, it is advised that primers perform better when they are specifically developed for each project, since they will be tailored to the regional diversity and environmental condition. However, the effort in designing study specific primers can be costly and time-consuming and several metabarcoding primer sets currently exist for a wide range of species that have been used across different studies, which may be suitable for a given project (Deiner et al., 2017).

After sequencing, the next steps require bioinformatics pipelines to perform quality checks, removing low quality reads, merging paired-sequence ends and checking for chimeras. The sequence reads are then grouped into clusters called operational taxonomic units (OTUs) or amplicon sequence variants (ASVs), depending on the pipeline and clustering algorithms being used (Porter and Hajibabaei, 2018; Tsuji et al., 2020). Once sequencing clusters (e.g., OTUs or ASVs) are created they can be analyzed directly, which is commonly done for bacterial or fungal diversity, or they can be linked to taxonomic identifiers using relevant reference databases (Hebert et al., 2003).

DNA sequencing reference databases contain the DNA barcode sequences for different species. Most publicly available libraries are incomplete, given the extensive number of species that require sequencing, with efforts ongoing to fill in the gaps (McGee et al., 2019). Three such databases are most commonly used. First, and the most iconic reference database, is the Barcode of Life Data System (BOLD), which curates species barcode sequences of the COI gene. Second is the substantial SILVA database for the small and large ribosomal subunits along with several smaller reference databases for other genes, including 12S (Mitofish), cytochrome *b* and rbcL (Weigand et al., 2019). Third, the NCBI database has the most diversity across available gene regions but these data are not as stringently curated compared to other reference databases. Despite this, the NCBI is highly accessible, compared to other databases, and is routinely utilized for generating personal reference sequence libraries for different gene regions (Hänfling et al., 2016; Fernández et al., 2018).

Once the data is formatted as either purely genetic cluster data or taxonomically linked community tables, it can be used similarly to other ecological analyzes. The read counts, which are the number of matching sequences recorded during the sequencing, will be available for each genetic cluster or taxonomic group. Read count numbers may provide some insight into the abundances of each group, however they are also generated due to variation in PCR efficiency. As such, caution should be made when using read counts in analyzes, as they do not represent abundances specifically, but will also vary artificially due to PCR chemistry. The most conservative approach is to convert the read count data to presence/absence, which is similar to how many traditional ecological analyzes proceed. There are alternative methods to convert read count data to semi-quantitative formats, such as relative read counts prior to additional analyzes; however, biases arising from the molecular methods may still persist (Lamb et al., 2019).

Future directions using eDNA

Environmental DNA is a tool as well as a field of study, which makes for an exciting and diverse set of future applications and research. Within the context of inland waters research, there are three key directions for eDNA research: network based analyzes, functional diversity assessment and use of alternative molecular methods. The description of these topics below is by no means exhaustive and the emerging foci are likely to change rapidly in the coming years.

Network analyzes

Ecological networks are a way to assess interactions among taxa across deep diversity pools, and have been linked to several aspects of metacommunity dynamics that are directly relatable to biomonitoring principles (Araújo et al., 2011). The scale of eDNA-derived data, particularly from metabarcoding, allows for the application of robust standardized analyzes to conduct network analyzes. Much research has been done to incorporate network-based approaches to link sample sites, either through time or space, which enables the assessment of environmental variables on network properties and the underlying biotic interactions, a key aspect for effective biomonitoring (Bohan et al., 2017; Seymour et al., 2020). In contrast to current biomonitoring assessments, eDNA-derived data has the potential to include a much wider range of taxa and indicator groups, which are currently excluded or simplified due to limitations of traditional taxonomic identification. Network-based eDNA assessment may further add to existing biomonitoring efforts by allowing for a finer-scale assessment, such as exploring differences in community dynamics among neighboring sites or evaluating moderate changes in environmental conditions (Cordier et al., 2017).

Although there is a need to ensure continuity between traditional and eDNA-based assessment methods, there should also be a forward-thinking approach that does not restrict eDNA research to simply confirming traditional expectations. Not only can eDNA data be used to assess environmental filtering on individual indicator taxa, allowing for comparable biometric data to traditional sampling, it can also be used to determine interactive qualities that are also linked to the stability and ecological complexity of habitats (Cadotte and Tucker, 2017). Additionally, the advancement of machine learning algorithms (Cordier et al., 2017) and newer abiotic monitoring systems, such as advanced mass spectrometry (Collins et al., 2021), combined with eDNA, potentially allows for a much deeper exploration of environmental samples for linking environmental effects to changes in natural populations and communities.

Functional diversity

Functional diversity has recently received increased focus in ecology, although it has long been recognized as an important factor in understanding the complete structure of an ecosystem (Young and Collier, 2009). More often biodiversity is quantified using species richness, which is the number of unique taxonomic units per site or sample. Richness is often positively correlated with heterogeneous environments, which is often attributed to higher levels of functional diversity (Cardinale et al., 2011; Donohue et al., 2013). Functional diversity directly quantifies the functionally disparate taxa within a community, and is becoming increasingly recognized as an important component of effective and more direct measure for linking community response to environmental change (Young and Collier, 2009). By measuring functional diversity, we get a better understanding of the characteristics within a community and can then relate these to environmental variation or to assess changes over time.

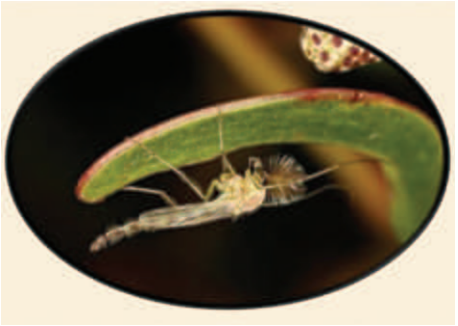
Environmental DNA research can further our understanding of functional diversity. For example, we can incorporate existing functional diversity of known species, such as feeding groups for macroinvertebrates (Moog, 2017), into eDNA data analyzes (Seymour et al., 2021). Attempts are also being made to detect variation in functional genes via transcriptomics directly from environmental samples (Taberlet et al., 2018).

Alternative molecular methods

A major interest in current eDNA research is to design methods that allow for estimation of abundances from high throughput sequencing (HTS). However, abundance estimates from HTS that use PCR (e.g., metabarcoding) are currently not reliable due to PCR amplifying sequences at different rates. Efforts are being made to incorporate PCR-free sequencing technologies with eDNA samples, such as shotgun sequencing (Ji et al., 2020), LAMP (Lee, 2017) and CRISPR (Williams et al., 2019). There are limitations to such applications at present, including incomplete reference databases, incompatibilities of some species to specific methods, the need for additional primer development, and the inability of methods to detect lower eDNA concentrations.

Another area of interest is to better understand the health of organisms sampled via eDNA. Currently, there is a lack of knowledge regarding the condition of the species when sampling eDNA, as the source of eDNA could originate from healthy, sick or dead organisms. The condition of the organism is important as different conditions may require different management strategies. As such, there is an increased interest in using eRNA, which refers to environmental RNA. The potential of eRNA may allow for aquatic health assessment via insights into organism functionality (Veilleux et al., 2021).

Case studies



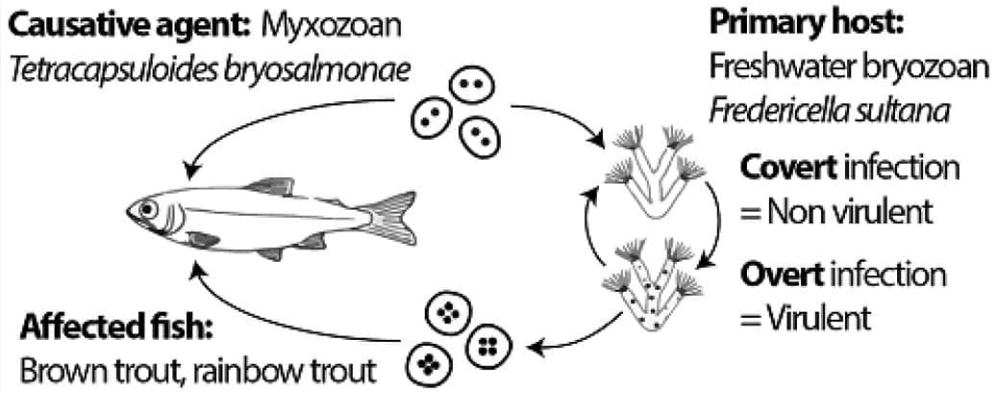
Bista et al. (2017) was one of the first to assess temporal dynamics of community diversity using eDNA, showing that eDNA can reliably depict temporal dynamics of Chironomidae communities. Chironomidae, informally known as non-biting midges, are a highly diverse family of flies with over 10,000 species globally. The larvae of Chironomidae are aquatic and form an important component of the benthic community of freshwater ecosystems, particularly in lentic or slow moving lotic systems. Chironomidae larvae predominately feed on algae, or small organisms, while serving as important food sources for fish, amphibians and larger predatory insects. Adult Chironomidae emerge, often en masse, from the surface of lakes or ponds by floating to the surface of the water as pupae and shedding their pupal skin (i.e., exuvia) as they transform into adults. As adults, Chironomidae serve as important food sources for bats and bird species, with some having evolved nesting strategies to coincide with annual cycles of Chironomidae adult emergences. Chironomidae are noted as important indicator species, meaning the presence or absence of key species is indicative of pollution.

However, traditional identification of Chironomidae species is notoriously difficult due to their small size and morphological similarity between species, which requires a high level of expertise to identify individuals to species level. Furthermore, sampling Chironomidae in lakes is mostly conducted by skimming exuvia from the lake surfaces during adult emergences, as sampling the lake bottom for larvae requires additional equipment and effort, and sampling from the edges of the lake will miss most species. Such traditional sampling limits observations to emergence times and does not capture the benthic community, which is essential for regular assessment. By using eDNA and monthly exuvia sampling of lake water Bista et al. (2017) compared emergence and biodiversity patterns of Chironomidae communities. Environmental DNA revealed much about the status of emerging species during their larval development times that had not been detected using traditional sampling through the winter months. Overall, these findings helped establish eDNA as a means to capture temporal trends in community biodiversity. Future efforts could look to compare surface and sediment eDNA to determine the overlap in community composition and dynamics.

Hänfling et al. (2016) presented a robust assessment of fish stocks in three large lakes in the United Kingdom and was one of the first studies to show that rank abundance comparisons across temporal eDNA sampling points was an effective means of assessing fish populations. Fisheries management is important for environmental assessment, societal enjoyment and economic stability. It is therefore important for agencies to accurately assess fish populations to apply appropriate management strategies. Fisheries managers use a wide range of assessment methods, which are often destructive or harmful to the fish, prompting many organizations to invest in non-invasive sampling methods.

Hänfling et al. (2016) looked to verify if eDNA metabarcoding was a viable means for routine monitoring of fish populations. The lakes used in the study have a long history of fisheries assessment, so their biodiversity and environmental condition linked to fisheries populations is well known. As such, results from eDNA assessments could be directly compared to current gill netting data as well as historical population structures. Hänfling et al. (2016) utilized a self-made reference database (freely available via their publication) that incorporated all fish species expected to live in or near the lake. Using a replicate transect sampling design, they compared the site occupancy of each fish species identified using two gene markers (12S and CytB). They showed that rank abundance of sequence reads reflected the rank abundance of species within the three lakes, suggesting read counts reflected differences in fish abundances. Additionally, they showed spatial preference for eDNA signal, whereby shore vs. off shore sampling affected the detection of different species (Hänfling et al., 2016). Overall, the key finding was that eDNA assessment of fisheries outperformed the traditional assessments methods, thereby providing a proof-of-concept for a non-invasive means of environmental assessment.

This study is an excellent example of a well designed and implemented eDNA research effort and has been followed by several other studies that have highlighted the importance of fisheries eDNA (Jerde et al., 2019; Miya et al., 2020). Additional work will look to improve on the ability to calculate abundances of different fish species from eDNA by incorporating biomass information directly from individual samples, such as proposed recently by Yates et al. (2020).



Lifecycle of Myxozoan Tetracapsuloides bryosalmonae

Carraro et al. (2018) is one of the first studies to apply river network based approaches to understand the spatial dynamics of eDNA in a river network. The study takes into account the transport time and spatial dynamics induced by flow to observe and model the biological distribution of the bryozoan *Fredericella sultana* and its parasite *Tetracapsuloides bryosalmonae*.

Tetracapsuloides bryosalmonae is of general interest to researchers and managers as it is the agent that causes proliferative kidney disease in salmonid fish. The life cycle of *T. bryosalmonae* involves seasonal cycles whereby the *T. bryosalmonae* persist in their primary host *F. sultana* throughout the year. During the summer, the *F. sultana* releases spores of *T. bryosalmonae* into the water, which infects fish through their gills. *Tetracapsuloides bryosalmonae* will grow and multiply inside the fish and during the autumn will leave the fish via being excreted with their urine to then infect other *F. sultana*. Effectively monitoring the timing and outbreaks of *T. bryosalmonae* life stages can therefore be essential for minimizing loss of fish to PKD.

Carraro et al. (2018) model highlights the importance of understanding the distribution of the target species and the hydrodynamics for effectively using eDNA for biomonitoring. Additional efforts to merge real time environmental data to project expected changes in species distribution will help managers gage what level of distribution is expected in combination with routine monitoring of key sampling sites along a given river stretch.

Concluding remarks

Environmental DNA is a rapidly growing field that is becoming more widely used. It has already made major inroads into freshwater science across academic, government and private sectors. Regardless of whether traditional or eDNA-based sampling is used, it is important to be aware of the use and application of eDNA, as many agencies and employers are rapidly looking to adapt eDNA methods where applicable. Environmental DNA research can also be seen as an opportunity for emerging scientists. The field is very new, which allows for new researchers to rapidly develop and implement novel ideas and studies. Combined with other emerging and developing research fields, eDNA based research offers a valuable doorway into modernized biomonitoring of ecosystems, environmental assessment, conservation biology, and many other potential avenues for understanding and discovering previously unobservable aspects of our natural world.

See Also: Fundamental concepts and theories: Biodiversity of Inland Waters; Invasive Species; Human pressures and management of Inland Waters: Biological Invasions: Impact and Management; Structures and functions of Inland Waters - Lakes: A Diversity of Primary Producers in Lakes; Structures and functions of Inland Waters - Groundwater: Biodiversity of Invertebrates in Springs; Springs—Groundwater-Borne Ecotones—A Typology, with an Overview on the Diversity of Photoautotrophs in Springs; Groundwater Metazoans; Structures and functions of Inland Waters - Rivers: Biodiversity Conservation of Aquatic Ecosystems; Energetics and Food Webs in Large Rivers; eDNA and Bioassessment of Rivers; Invasive Species in Streams and Rivers; Social/societal values of Inland waters: Societal Values of Inland Fishes; Structures and functions of Inland Waters - Wetlands: Benthic Invertebrates of Running and Stagnant Inland Waters; Worldwide Wetland Loss and Conservation of Biodiversity and Ecosystem Services

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Electronic Tagging and Tracking of Animals in Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Acoustic telemetry The transmission in water of ultrasonic energy or sound signals at frequencies generally in the range of 20–500 kH; requires use of a transmitter and hydrophone.
Archival logger A device that records and stores information (e.g., on depth use) until it is retrieved for downloading; a form of biologging.
Biologging Information is recorded and stored in an animal-borne device (archival logger) and information is downloaded when and if the logger is retrieved or in some devices stored until later transmission.
Biotelemetry The process of conveying information from one location to another, typically in a wireless manner; signal emanating from a device carried by the animal (transmitter) sends the information to a receiver.
Electronic tags A term that broadly captures the range of biotelemetry and biologging devices that can be attached to or implanted in aquatic animals.
Passive integrated transponder (PIT) Transponders are tags that send information upon interrogation only; tag consists of an integrated circuit chip and coil antenna which, when energized by a low-radio frequency (125–400 kHz) reader coil, transmits a unique identity code.
Radio telemetry Reception of data at a location remote from the source of the data, using radio-frequency electromagnetic radiation as the means of transmission; requires use of transmitter, antenna and receiver.
Receiver A device that collects (receives) information emitted from a transmitter, typically as either radio waves or acoustic waves.
Sensor An electronic component that can be incorporated into electronic tags to record various forms of environmental and biological information such as temperature, pressure (depth), acceleration, and electrocardiograms.
Telemetry array Deployment of automated telemetry systems to continuously track telemetry tags over long periods; variety of configurations that can be used for automated 2- or 3-dimensional positioning or simply presence/absence.
Tracking The process of locating tagged animals using either manual tracking approaches (e.g., by foot, boat, airplane) or use of a fixed telemetry array.
Transmitter An electronic device usually implanted or externally attached to a fish or other aquatic animal that transmits information to a receiver.

Introduction

Inland waters around the globe are home to diverse communities of fish and wildlife. Yet, life in freshwater is often cryptic as a result of turbidity, entrained air, algal blooms, emergent macrophytes, depth, and ice cover (Hussey et al., 2015). As such, even the most basic natural history is unknown and ecological data are lacking for many freshwater species. Fundamental questions such as (i) When do they breed?, (ii) What are their critical habitats?, and (iii) What are their environmental tolerances? remain largely unanswered for many species.

The advent of electronic tagging and tracking tools (i.e., biotelemetry and biologging devices; see Glossary for definitions) has enabled biologists to begin to unravel these mysteries of life in freshwaters (Cooke et al., 2013). Researchers use these tools to position individuals and recreate a path or network of movements for analysis. Calculating the time and distance between individual positions can contribute to improved understanding of the where, when, why, and how animals move, revealing information about an individual or a population, and how they interact with their ecosystem (Cooke et al., 2016a). The knowledge obtained from an animal's location in the environment, the timing of changes in their location, and the factors that might have driven those changes, can contribute to improved understanding of not only the life history of that species, but also to their conservation and/or management.

Animals move on a scale of centimeters to kilometers, and across microseconds to years, depending on various internal and external factors. For example, light levels and temperature may dictate the position of an organism in the water column, with fine-scale shifts in depth based on the time of day (Stangel and Semlitsch, 1987; Mehner et al., 2007; Mehner and Kasprzak, 2011), but also have been known to cue longer annual spawning/reproductive migrations (Jonsson, 1991). Aspects of the natural history of an animal can also be explored using telemetry, including any site fidelity, or homing behavior they may exhibit, the size of their home range and how this may change throughout the year and their lifespan (Minns, 1995; Tucker, 2010). Telemetry with biologging technology could also further our understanding of the resources an animal is selecting (e.g., depth, altitude, temperature, dissolved oxygen), and the bioenergetics of an individual, i.e., how they use their energy, and the various abiotic and biotic factors that can influence this energy expenditure (Cooke et al., 2016b).

Understanding animal movements, and how they may be affected by anthropogenic factors, can assist in management and conservation of fish and wildlife. Unfortunately, inland aquatic ecosystems suffer from issues concerning habitat/ecological fragmentation and connectivity (Grill et al., 2015; Reid et al., 2019). Telemetry can be used to determine the efficacy of passageways at dams, for example, at restoring the up and downstream connectivity (Castro-Santos et al., 1996; Aarestrup et al., 2003). Locally extirpated species can be captively bred and reintroduced. Tracking these individuals can allow for a better understanding of the success and ramifications of these reintroductions, helping inform conservation efforts (Peters et al., 2009; Wang et al., 2011; Brooks et al., 2019a). Knowing the location of an animal can provide information about the resources that the animal is selecting for (chemical, physical, biological), which can be beneficial when planning and monitoring habitat restoration efforts (Brooks et al., 2017). Fish and wildlife are often managed within a particular geographical area, i.e., a waterbody, a watershed, or a jurisdictional boundary; however animals rarely stick to these boundaries (Hussey et al., 2017; Brooks et al., 2019b). More broadly, temperature is a major driving force for any ectotherm and understanding how an animal may respond to changes in temperature, and the spatial scale of that response, will help better predict changes in animal distributions with our changing climate.

The tools

The tools used to track animals that live in inland waters can be divided into two categories; **(1)** *biotelemetry*, whereby the tag transmits a signal to a receiver that decodes and logs the information and (2) *biologging*, whereby the tag stores information generated from the tagged individual for later retrieval and downloading (see Table 1). Biotelemetry tags can be tracked manually (e.g., by boat, foot, aircraft, snowmobile) or by deploying automated receiving stations that log detections from tagged animals. Because biologging tags do not transmit data, they must be retrieved, either from the animal or the environment if the tag is shed, to download data.

Although revealing basic information on animal space use is a primary reason to tag animals, it is also possible to use both types of tags to incorporate various sensors that measure environmental conditions (e.g., water temperature, depth, light levels, pH), animal status (e.g., heart rate, acceleration), or even record images or ambient noise. Within these two broad categories of devices, there are many different technologies and configurations that allow scientists to answer questions about inland water organisms. However, every tool has its limitations (e.g., radio telemetry does not work in deep water, acoustic tags cannot be tracked on land, biologgers have to be retrieved and small animals cannot carry a large tag burden) and it is important that those limitations are understood prior to embarking on a study. In general, the objectives of the study, the characteristics of the system, and the biology of the focal animal dictate which tools make sense for a given study.

To track animals, they first must be tagged. Although the details of tagging vary widely among taxa, the most common approaches involve either external tagging (e.g., a backpack on a waterbird, glued to the carapace of a turtle or crayfish) or internal tagging (e.g., surgical implantation in fish and mammals). Protocols have been developed to ensure that researchers use techniques that minimize negative impacts on welfare of tagged animals (Withey et al., 2001). Investigators can refer to taxon-specific guidelines regarding the mass of devices that can be carried by animals before the tags cause undue energetic or postural burden.

Table 1 Overview of electronic tag types and their relevance to the study of animals in inland waters. See Cooke et al. (2013) for additional details on electronic tagging tools relevant to freshwater organisms.

Electronic tag type	*Ideal environments for deployment*	*Typical organisms studied*	*Common applications*
PIT tags	Shallow streams and rivers (<1 m deep); In and around fish passage facilities	Small invertebrates (e.g., dragonflies) amphibians (e.g., frogs) and fish; tags lack batteries so can be quite small	Space use of organisms in small systems; timing of migration; fishway efficiency studies; survival studies of small animals
Radio telemetry	Shallow rivers and lakes (<10 m deep)	Large invertebrates (e.g., crayfish), turtles and fish; Can be used to track aquatic animals that spend some time on land	Space use of organisms; timing of migration; winter biology studies including under ice; survival studies; energetics
Acoustic telemetry	Large rivers and lakes; Works best in >2 m of water but no maximum depth limit	Large invertebrates and fish; only works when animals are in water so best for animals that spend all their time in water	Space use of organisms; timing of migration; winter biology studies including under ice; survival studies; energetics
Biologgers	Can be used in any environment but must be retrieved to download data	Tends to be used on larger animals like turtles, fish and aquatic birds, but recent decreases in tag size are increasing options	Activity patterns; timing of migration; winter biology studies including under ice; animal-environment relationships; energetics

Tag size is determined largely by battery size, which is often the largest physical component of tags (except passive integrated transponder [PIT] tags, which do not have a battery as they are powered from external energy sources). Through time, tag size has decreased to the point where some battery-powered tags weigh less than 0.3 g and are the size of a grain of rice although their longevity may be on the order of days. Larger tags with larger batteries enable the tracking of animals across seasons and years. For the data to be representative of untagged conspecifics, it is essential to ensure that the tagging process and the burden of the tag do not alter the behavior, condition, or survival of tagged animals. However, trade-offs with device size relative to the size of the animal and study objectives are common.

Next, we provide an overview of the most common tools used in inland water systems for tracking freshwater animals. We direct readers to Cooke et al. (2013) and Lennox et al. (2017a) for more comprehensive reviews of technology. We exclude satellite tags from this discussion because they have rarely been applied to freshwater systems and have technical issues related to transmitting signals through water. In fact most satellite tags are limited to use with very large animals, and because their spatial resolution tends to be insufficient for understanding space use in freshwater systems (e.g., Kough et al., 2018). We also exclude technology that can solely be used on land (e.g., for tracking waterbirds or insects during flight) such as those that rely on harmonic radar (see Mascanzoni and Wallin, 1986).

Biotelemetry: Passive integrated transponder telemetry

Passive integrated transponder tags, or PIT tags as they are more commonly known, is a collective term for small electronic tags (Fig. 1) fitted to an animal that transmit data (a unique code) wirelessly via radio waves using radio-frequency identification (RFID). The tags comprise an encapsulation material, typically glass or food-safe plastic, which encases a coil antenna and integrated circuit that when energized transmits a unique code to a reader. The tags contain no battery and hence are in a passive state until energized. Read range of PIT tags is typically centimeters to meters, influenced by the technology used (full duplex (FDX) or half duplex (HDX)), tag size, environmental variables including temperature and habitat type, as well as specifics relating to antenna construction. As a result of their simple circuitry and absence of a battery, PIT tags are small, long-lasting, and relatively cheap, which provide for a number of inherent advantages when used in animal tracking studies including large sample sizes, longevity, and an ability to tag small animals weighing as little as a few grams. The application of PIT tags in aquatic animal studies has been reviewed for fish (Lucas and Baras, 2000) and more generally for aquatic animals (Cooke et al., 2013) and this information is synthesized below.

Once fitted to the study animal, the use of PIT tags can be grouped into three broad applications that vary in their level of future disturbance to the focal individual from: (1) mark-recapture that requires additional capture and handling, (2) manual re-location of the tagged individual in a field or mesocosm environment using a portable scanner, and (3) remote data logging using fixed stations. The use of mark-recapture methods enables estimation of population size and quantification of vital population statistics including mortality, survival, growth and movement (Gibbons and Andrews, 2004). The application of PIT tags to mark-recapture methods is not exclusive, with numerous external visual marks or tags, or natural (e.g., genetics, elemental ratios in the ear bones of fish) and chemical tags also readily applied. The advantage of PIT tags in mark-recapture methods is the use of a hand scanner to read a tag that enables digital data collection and retention of the tag over an external mark or tag.

Manual relocation of PIT tagged animals is undertaken with a portable scanner/datalogger and antenna combination and is well suited to small wadable streams and other restricted habitats. Recordings of unique tags are taken by passing an antenna over likely locations with minimal disturbance and no additional handling of the study animal. This method is suitable for determination of small-scale movements of aquatic animals and fine-scale habitat use, including tracking through ice (Linnansaari et al., 2007) or in

Fig. 1 A small (12 mm) PIT tag is implanted in a small-bodied fish. Photo credit = Steven Cooke.

complex habitats (Bubb et al., 2002). Novel applications include assessment of colonial waterbird predation on juvenile salmon through the field collection of PIT tags previously fitted to the salmon and subsequently located at breeding colonies (Collis et al., 2001).

Remote data logging using fixed stations is where PIT technology excels. When tagged animals undertake movements through restricted locations, enabling installation of an antenna that act as a "gate" or "door," the timing of movements can be determined. The technique, used extensively to monitor migrating fish movements through fishways, was pioneered by Castro-Santos et al. (1996) and is now applied globally to assess fishway efficiency (Cooke and Hinch, 2013).

Biotelemetry: Radio telemetry

Radio tagging has a long history of contributing novel insights to the ecology of fish, mammals, birds, turtles, and insects. Radio signals propagate through air and freshwater and are therefore widely used for tracking terrestrial, semi-aquatic, and aquatic animals. Radio tags are designed to transmit a wave of a defined frequency at an appropriate pulse interval, which is heard within a certain range by a compatible receiver (Fig. 2).

Tags can be configured with a coded signal indicating a unique individual on a given frequency. Coded signals allow a tracker to scan on a single frequency and find multiple fish without toggling through a prohibitive number of channels. When a large number of tags are deployed, coded signals can limit the channels an investigator needs to scan through, reducing the chances of missing a detection. Data logging receivers can be placed at strategic points in study systems and attached to a power source to toggle through radio frequencies and log the time and date of detection or carried by an investigator with a manual Yagi-type antenna to find an animal and record the coordinates of location. For linear systems such as rivers or corridors in between lakes, movement can be measured as the animal transits past the receiver in a series of one dimensional points; this has been applied successfully to the river migration study of various fish species, particularly salmonids (e.g., Thorstad et al., 2003; Thiem et al., 2013). Often, this requires paired receivers or directional antennas (e.g., upstream and downstream) to establish the direction of movement. In open two-dimensional systems such as lakes, multiple positions may be required to calculate a coordinate based on triangulation

Fig. 2 Manual tracking of radio tagged animals using a hand-held radio receiver and antenna. Photo credit = Eva Thorstad.

(Fish and Savitz, 1983). The frequency and spatial resolution of positioning will drastically influence the value of the data recovered from the study system and the ability to interpret the behavior of the tagged individual.

Designing radio telemetry studies can be challenging and has a variety of pitfalls. Radio telemetry can be challenged by interference from other local radio equipment. Detection efficiency will also vary as a function of environmental conditions such as water salinity and conductivity; water chemistry should therefore be considered when determining the suitability of radio telemetry for a project. Habitat features may also attenuate or block signals. Animals may also find hiding spots that generate false negatives in data. Occasionally, tags can disappear from a system and ruling out various pitfalls can help isolate a most probable explanation. Radio equipment, and the frequencies selected for the project, should be piloted at the study site to ensure optimal performance (e.g., Sullivan et al., 2019).

Tags can be attached in many ways (Thorstad et al., 2003), including externally through the musculature (e.g., fish), glued to fur (e.g., river otters) or carapace (e.g., turtles), harnessed or collared (e.g., beavers or mink), or internally implanted under anesthesia (e.g., fish; Fig. 3). Capture, handling, and tagging can all affect animal behavior and undermine the study if not rigorously studied. Predation, mortality, or straying of animals from the study system can introduce errors that are challenging to interpret and mitigating potential pitfalls is therefore important to improve interpretability of findings emanating from the study.

Radio telemetry is most frequently used for positioning animals, but additional sensors have been integrated to extend the information provided by the transmitters. Mortality sensors are sometimes integrated into radio tags to provide better resolution about the fate of tagged animals. Depth and temperature sensors have been developed, which can provide a third dimension to telemetry data. Lucas et al. (1993) tested the utility of heart rate loggers integrated in radio tags, although these sensors have not been developed much further in radio tags.

Biotelemetry: Acoustic telemetry

Similar to radio telemetry, acoustic telemetry involves the use of receivers to detect the position and movements of tagged animals, either with mobile tracking by people equipped with a receiver or using stationary, strategically positioned receivers (i.e., passive tracking; Fig. 4). However, rather than using radio wave transmissions, acoustic telemetry uses pulses of sound to transmit ultrasonic "barcodes" from tags that can then be deciphered by acoustic receivers. Acoustic telemetry uses short, fast, pulses of ultrasonic sound (low frequency) as signals (this technology is sometimes referred to as "ultrasonic telemetry"; Ogura and Ishida, 1995). Because sound travels much better through water than it does through air, acoustic telemetry is confined to the underwater world. It has become the most widely used technology for tracking fine and broad scale movements of animals in underwater environments, especially in marine environments and deeper freshwaters, where other tracking technologies like radio and PIT telemetry do not function well.

The largest acoustic transmitters that are routinely used are about twice the size of an AA battery, best suited for large animals like sturgeon, walleye, or snapping turtles. The largest tags can be programmed for 10+ years of battery life and have a strong signal that is easily detected by receivers. The smallest acoustic tags are about the size of a green pea, suitable for small species like gobies (Christoffersen et al., 2019) or juvenile salmon, which are routinely tagged on their outmigration from rivers (Deng et al., 2015). Acoustic tags are often surgically implanted into anesthetized animals and the smallest tags can now be injected (Deng et al., 2015). Acoustic tags are sometimes externally attached, either through the musculature (Raby et al., 2015) or in the case of turtles or some invertebrates, fastened to the carapace (Micheli-Campbell et al., 2013).

Once a tagged animal is released, it can be tracked using acoustic receivers positioned underwater. Typically, receivers are anchored to the bottom (seafloor, lake bed, etc.) and suspended in the water column by rope, with a float attached to the top of the receiver. Receivers can also be attached to existing structures (e.g., weirs, buoys), or cabled to an anchor point on shore. Acoustic

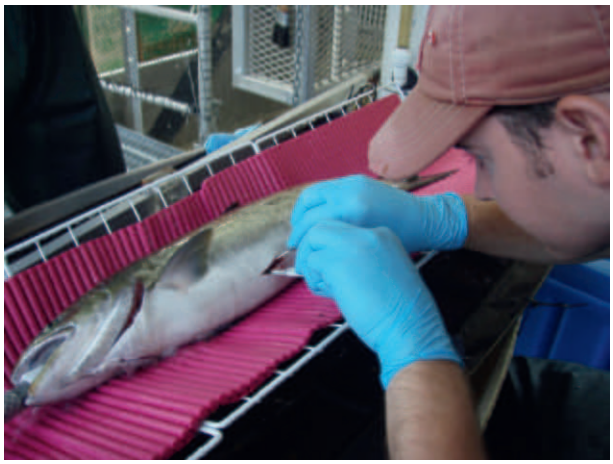

Fig. 3 Chinook salmon (*Oncorhynchus tshawytscha*) in British Columbia having radio transmitter surgically implanted in the coelom. Photo credit = Steven Cooke.

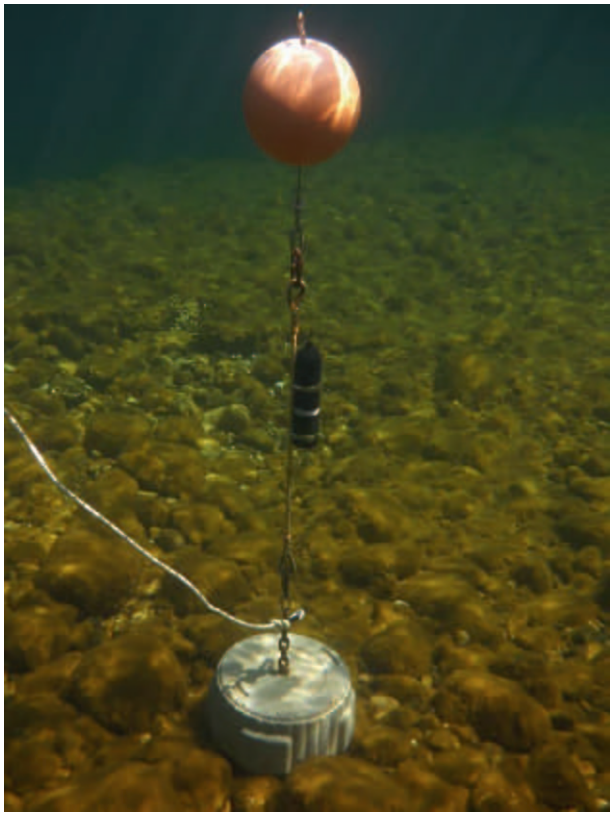

Fig. 4 Passive acoustic telemetry receiver deployed sub-surface to track fish in the Laurentian Great Lakes. Photo credit = Tom Binder.

receivers typically need to be retrieved for download and battery replacement every 6–12 months, but sometimes shorter or longer deployments occur depending on study design and receiver type. Receivers can, in many environments and with common tag types, detect tagged animals from 500 to 1000 m away or more. However, while ultrasonic signals can travel several kilometers through water, they can be impeded by ambient noise (ice, ships, other organisms, waves, etc.) and physical obstructions (bubbles, submerged vegetation), and they can "bounce" off of artificial or natural structures in ways that obscure the signal. Thus, how well tags are detected by each receiver is among the biggest technical challenges to consider by researchers using acoustic telemetry (Brownscombe et al., 2019). If a study is using an array of receivers that vary widely in their ability to detect tagged fish because of local physical conditions that affect acoustic signals, that variance can bias the apparent habitat use and behavior of animals (Kessel et al., 2014). In turn, researchers using acoustic telemetry sometimes put special emphasis on assessing the performance of their receivers (Klinard et al., 2019) and incorporate variation in their performance into how they interpret animal movement tracks (Brownscombe et al., 2020).

Biologgers

Biologgers are sensors that are attached to or implanted inside of animals to collect information about their environment (e.g., spatial position, temperature), and/or the animal's physiology (e.g., heart rate), or behavior (e.g., running, swimming, feeding), and store the information in memory on the device (Rutz and Hays, 2009). This storage facilitates continuous and high-frequency collection of the information derived from a diversity of sensors (e.g., acceleration, heart rate, magnetometer, temperature, dissolved oxygen, water speed, global position at up to hundreds of samples per second). These capabilities have enabled biologgers to be applied to diverse questions about a wide range of species inhabiting inland waters. For example, loggers containing varied combinations of acceleration, heart rate, temperature, and water depth sensors have been used to track the behavior and survival of fishes and turtles after exposure to stressors such as fisheries interactions (Algera et al., 2017; Gutowsky et al., 2017; Prystay et al., 2017; Lennox et al., 2018), as well as the metabolic costs of fish spawning behaviors (Clark et al., 2010; Prystay et al., 2019). Tri-axial accelerometers, which measure acceleration as a proxy for movement in three directions, can be used to remotely measure very fine scale behaviors, such as air breathing at the water surface by arapaima (Arapaima cf. arapaima; Lennox et al., 2018). One particularly exciting application of biologgers is in remotely estimating animal bioenergetics (Cooke et al., 2016b), which requires calibration between oxygen consumption and sensor output (e.g., heart rate or acceleration) with laboratory equipment (Clark et al., 2010) prior to deployment on wild animals.

Although biologgers enable continuous measurement at great resolution, the need to recover the device back from the tagged animal limits applications in inland waters to situations that allow for retrieval, which are often short-term studies within a constrained area. In semi-aquatic animals such as diving birds, biologgers including GPS, acceleration, and depth sensors are commonly used to assess movement patterns, foraging behaviors, and locations (Ropert-Coudert et al., 2009). In a more extensive study on fish, Raby et al. (2018) used temperature loggers to track thermal experience of walleye (*Sander vitreus*) over multiple years to understand how temperature influences movement patterns in Lake Erie, North America, with device retrieval facilitated primarily by large scale fisheries. To overcome challenges with device retrieval, biologger tag packages with timed pop-off devices can enable retrieval, although these packages are large and constrained in application to relatively large animals due to issues with tag burden (Broell et al., 2016).

The continuous, fine scale information that biologgers provide on animal behavior, physiology, and proximal environmental conditions makes them an important tool for understanding how environmental conditions impact individuals, which is used to scale to populations and entire inland water ecosystems. Continuing advancements in device sensor capacity, miniaturization, and retrieval mechanisms (Boyd et al., 2004; Block, 2005; Rutz and Hays, 2009), as well as integrating of other environmental measures and telemetry technology will be essential to understanding and mitigating the impacts of rapid environmental changes on biodiversity, ecosystem integrity and services provide by inland waters (Cooke, 2008; Cooke et al., 2012; Bograd et al., 2010).

Case studies

A networked approach to fish tracking across the great lakes

A comprehensive understanding of the ecology and biology of exploited freshwater fish is imperative to maintain population sustainability. The Laurentian Great Lakes ecosystem is large and geographically and limnologically complex, consisting of interconnected waterways, shallow, heavily vegetated and deep pelagic regions (Fig. 5). That complexity makes it difficult for fishery researchers to develop a comprehensive understanding of the movement patterns of Great Lakes fish, particularly those species exhibiting large-scale migratory behaviors such as lake sturgeon (*Acipenser fulvescens*), lake whitefish (*Coregonus clupeaformis*) and walleye (*S. vitreus*) (Scott and Crossman, 1973).

In 2010, the Great Lakes Acoustic Telemetry Observation System (GLATOS) network was established to provide fishery managers and decision makers with fish behavior information using acoustic telemetry technology not feasible with traditional fishery assessment gears (Krueger et al., 2018; Fig. 5). The GLATOS network relies on researchers working collaboratively throughout the basin to monitor fish movements at spatial-scales that otherwise would be cost-prohibitive or impractical if attempted individually. Individual researchers tag fish with acoustic transmitters internally and externally and deploy acoustic receivers to address project-specific objectives. Individual receiver detection data are shared with participating GLATOS researchers via a web-based data portal which serves as a basin-wide data repository. Although the receiver detection data are shared across the network, researchers only have access to transmitter detections associated with their projects (i.e., as investigator, co-investigator or

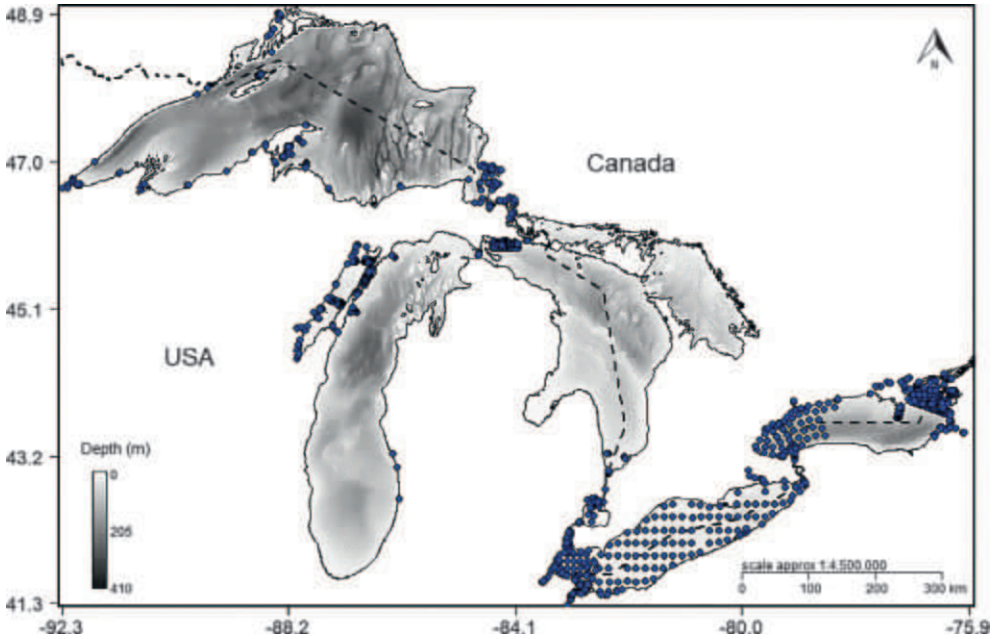

Fig. 5 Bathymetric map (in meters) of the Laurentian Great Lakes depicting the location of acoustic receivers (blue circles) deployed as part of the Great Lakes Acoustic Telemetry Observation System network (GLATOS). Dashed line represents the international border between Canada and the United States of America (USA).

collaborator). By participating in this manner, researchers monitor the movements of their tagged fish across the Great Lakes basin rather than being limited to the geographic extent of where they maintain receivers. Researchers have used the GLATOS network to understand population dynamics (survival and mortality), movement rates, habitat use, spawning ecology, and post-stocking survival of native and invasive fish populations across the basin. This information has been used by fishery managers to inform sustainable management of exploited fish, native species restoration, and invasive species control efforts (e.g., Binder et al., 2018; Raby et al., 2018; Kessel et al., 2018; Klinard et al., 2020).

Tracking Atlantic salmon across life-stages

The Atlantic salmon (*Salmo salar*) has a long history of being important for Indigenous peoples, recreational and commercial fisheries, and local cultures, and has been studied for more than 100 years. The Atlantic salmon has a diverse array of life-histories, most forms being anadromous with spawning and juvenile phases in fresh water and feeding migrations to the ocean. Even for this well-studied species, the development of telemetry has opened new research opportunities and provided new behavior knowledge during nearly all life stages that has continued to surprise us and helped solve management issues.

The typical upstream migration pattern by Atlantic salmon adults in rivers without large migration barriers consists of distinct migration, search and holding phases. As juveniles, they live within restricted areas, but can perform surprisingly extensive movements (Økland et al., 2004). However, less was known about the marine phase of this species until acoustic telemetry methods improved. Studies of the outward coastal migration showed a surface-oriented and relatively fast migration (e.g., Dempson et al., 2011; Barry et al., 2020). Recent studies of the ocean migration using archival and satellite tags have shown that Atlantic salmon use larger areas of the North Atlantic Ocean than previously known (Chittenden et al., 2013; Strøm et al., 2017, 2018).

Atlantic salmon populations have declined and are largely impacted by human activities. Telemetry is widely used to document the human impacts and identify management solutions, for instance related to migration barriers, power stations, fishways, aquaculture, hatchery-rearing and climate change (e.g., Hagelin et al., 2016; Moe et al., 2016; Frechette et al., 2018; Persson et al., 2019; Larinier et al., 2020; Silva et al., 2020). Telemetry has also been used to document high survival, but behavioral irregularities, after catch and release angling (Lennox et al., 2017b).

Tracking freshwater crayfish across habitats

The behavior and habitat use of freshwater crayfish has been studied through the application of both passive integrated transponder (PIT) tags and radio telemetry. Crayfish shed their exoskeleton (molt) as they grow, and the small size of PIT tags has enabled internal implantation that allows for molting to occur without tag loss (Bubb et al., 2002; Westhoff and Sievert, 2013). Larger species of crayfish can carry a heavier tag burden; therefore, radio tags have been glued externally to the carapace of numerous species for short-term movement studies.

The world's two largest freshwater crayfish species, the Tasmanian giant freshwater crayfish (*Astacopsis gouldi*) and Murray River crayfish (*Euastacus armatus*; Fig. 6), occur in Australia and can reach maximum weights of 6 and 3 kg, respectively. Manual re-location of radio-tagged individuals enabled researchers to determine movement distances over days and weeks to understand how the animals utilize their environment. Ryan et al. (2008) found that Murray crayfish continually occupied pool habitats, had overlapping home-ranges with other tagged crayfish species, and had no discernible movement pattern between day and night. Tracking the Tasmanian giant freshwater crayfish, Webb and Richardson (2004) found that despite occupying a comparatively

Fig. 6 Murray River crayfish (*Euastacus armatus*) with a radio tag attached to the carapace. Photo credit = Brendan Ebner.

smaller stream that was only 13 m wide and 2 m deep, crayfish walked up to 700 m in a single night, ranged up to 2.2 km over a period of months, and often returned to the same refuge location.

These and other crayfish species are increasingly being recognized as under threat from human disturbance. For example, Reynolds and Souty-Grosset (2011) identified that 151 of the 650 global species of freshwater crayfish species are threatened. Use of electronic tagging and tracking to understand crayfish behavior, preferred habitats, and the limits on dispersal and subsequent recolonization assists natural resource managers to prioritize recovery efforts. Numerous tools including biologgers, acoustic tags, and remote data logging using radio-telemetry (see Thiem et al., 2010) may provide novel insights in future applications of telemetry on this unique group of animals.

Tracking freshwater turtles across seasons

Turtle researchers primarily use radio telemetry to document movement patterns and habitat use, including overwintering habitats (e.g., Brown and Brooks, 1994; Litzgus et al., 1999; Markle and Chow-Fraser, 2017). At northern latitudes, freshwater turtles can spend nearly half of the year hibernating under water making the location and characterization of overwintering sites extremely relevant to the biology and conservation of turtles. Here, we illustrate how the identification of hibernation sites using radio telemetry has been critical for understanding key aspects of the ecology and conservation of a Canadian population of northern map turtles (*Graptemys geographica*).

Between 2004 and 2007, 51 turtles were fitted with radio-transmitters (Fig. 7) and tracked to quantify habitat use (Bulté et al., 2008) and movement patterns (Carrière et al., 2009). Turtles were also tracked in the winter while hibernating under several centimeters of lake ice. Winter tracking led to two large communal hibernation sites that played a major role in the design of subsequent studies of the populations. The two hibernation sites became the focal point of a long-term mark-recapture study from which fundamental demographic data were derived (Bulté and Blouin-Demers, 2009). Those data were then used to quantitatively assess the impact of mortality from powerboats on the study population (Bulté et al., 2010). The hibernation sites also served as a platform to test new techniques to study wildlife in the field. Map turtles mate at their communal hibernation sites. Taking advantage of these aggregations, Bulté et al. (2018) demonstrated the potential of underwater videography and 3D printed decoys to study the behavior of freshwater turtles in the wild. Moreover, the spatial data obtained from radio-telemetry was used to demonstrate that environmental DNA (eDNA) surveys can accurately pinpoint turtle hibernation sites (Feng et al., 2020).

Radio telemetry remains a cost-effective tool to locate hibernating turtles, and it can now be combined with a wide range of biologging devices such as small pressure sensors and accelerometers. Turtles are well suited for such deployment because most species are large enough to accept long duration devices, they have a hard surface on which they can easily be mounted, and they are generally placid and can be handled and fitted with devices with minimal risk to them and the researchers. The combination of radio telemetry and biologging will undoubtedly continue to yield novel insights on the hibernation ecology of turtles.

Challenges in platypus tracking

The platypus (*Ornithorhynchus anatinus*) is an extraordinary animal, with a unique composite of traits; it is an egg-laying monotreme mammal that is armed with venomous spurs and electric and tactile sensors at the tip of its duck-like bill to find macroinvertebrate prey species (Grant and Fanning, 2007; Bino et al., 2019). Platypuses are endemic to river systems along Australia's eastern mainland, Tasmania, and two islands, encompassing a wide range of environments, from tropical to alpine. Understanding

Fig. 7 Northern map turtle (*Graptemys geographica*) with radio transmitter affixed to the carapace. Photo credit = Greg Bulte.

Fig. 8 Platypus (*Ornithorhynchus anatinus*) implanted with a radio transmitter. The antenna is visible trailing the animal. Photo credit = Gilad Bino.

movement behavior of platypuses has been accomplished through repeated captures (Bino et al., 2015), radio telemetry (Serena et al., 2001), PIT tags (Macgregor et al., 2014), externally attached acoustic transmitters (Griffiths et al., 2013; Hawke et al., 2021a), and, most recently, implanted acoustic transmitters that offer longer tracking periods (Bino et al., 2018; Hawke et al., 2021b; Fig. 8). Accumulated knowledge from tracking movements by platypuses portray an animal with varying foraging and dispersal habits, occupying linear habitats between 0.5 and 15 km, but able to move over 40 km at times, which vary between breeding and non-breeding periods (Bino et al., 2019).

Tagging has been a challenge for platypuses. Unlike many other species, it is impractical to use collars or harnesses to hold telemetry devices on the platypus. There is a high risk of strangulation or drowning while platypuses forage among submerged roots and branches or when digging their burrows between tree roots (Grant and Fanning, 2007). Gluing tracking devices to the body is limited by short attachment periods given fur growth (Griffiths and Weeks, 2015; Hawke et al., 2021a). PIT tags offer lifetime tracking but have short detection distances (<1 m), limiting application to narrow streams (Macgregor et al., 2014). Therefore, there is still much to learn relating to understanding the species' habitat and foraging requirements, dispersal, and intraspecific interactions, warranting continued research that capitalizes on improvements in tracking technologies, particularly given increasing concerns over the species' deteriorating conservation status.

Knowledge gaps

Tracking data are broadly useful for inland waters animal management, species-at-risk monitoring, and invasive species control; yet, the potential of electronic tagging and tracking is still growing and there are a variety of important knowledge gaps to pursue.

- Tracking animals in inland waters largely relies on tags being detected by compatible receivers, and can contribute to biased estimates (e.g., Mourier et al., 2017). Therefore, detection efficiency of receivers is a pressing area for further research. Detection efficiency of receivers (especially acoustic ones) depends on environmental conditions (e.g., temperature, conductivity, noise, interference, macrophytes (Klinard et al., 2019; Weinz, 2020), and the configuration of receivers (Kraus et al., 2018).
- The effects of capture, handling, and carrying a tag on animal biology remains an active area of research and can drastically affect the results of tracking inland animals. Telemetry is often used to estimate vital rates such as natural and fishing mortality or estimating population sizes via mark-recapture, for which an accurate estimate of the tag effect is crucial (Crossin et al., 2017). Meta-analyzes of tag effects will be useful to provide guidance for well-known species but tag effects studies specific to the study system are always useful prior to embarking on a study.
- Analysis of tracking data can be laborious as it generates vast quantities of data. Determining how to best analyze and visualize data can be challenging (see Fig. 9 for examples).
- Positioning software (e.g., Baktoft et al., 2017) for triangulating positions and reconstructing paths are increasingly popular and extensions of these tools will drastically enhance the potential for information gain from aquatic telemetry systems.
- Tracking technology is still limited primarily to larger individuals, with smaller tags being limited in battery life. Continuing advancements in battery and sensor technology will enable greater understanding of a wide range of freshwater taxa over longer time periods. A recent study of immature dragonflies (from emergence to early flight) involved tagging and tracking using devices that weighed a mere ~16.5 mg (LeNaour et al., 2019) sets the new standard for tracking freshwater organisms (in this case during their life in riparia).

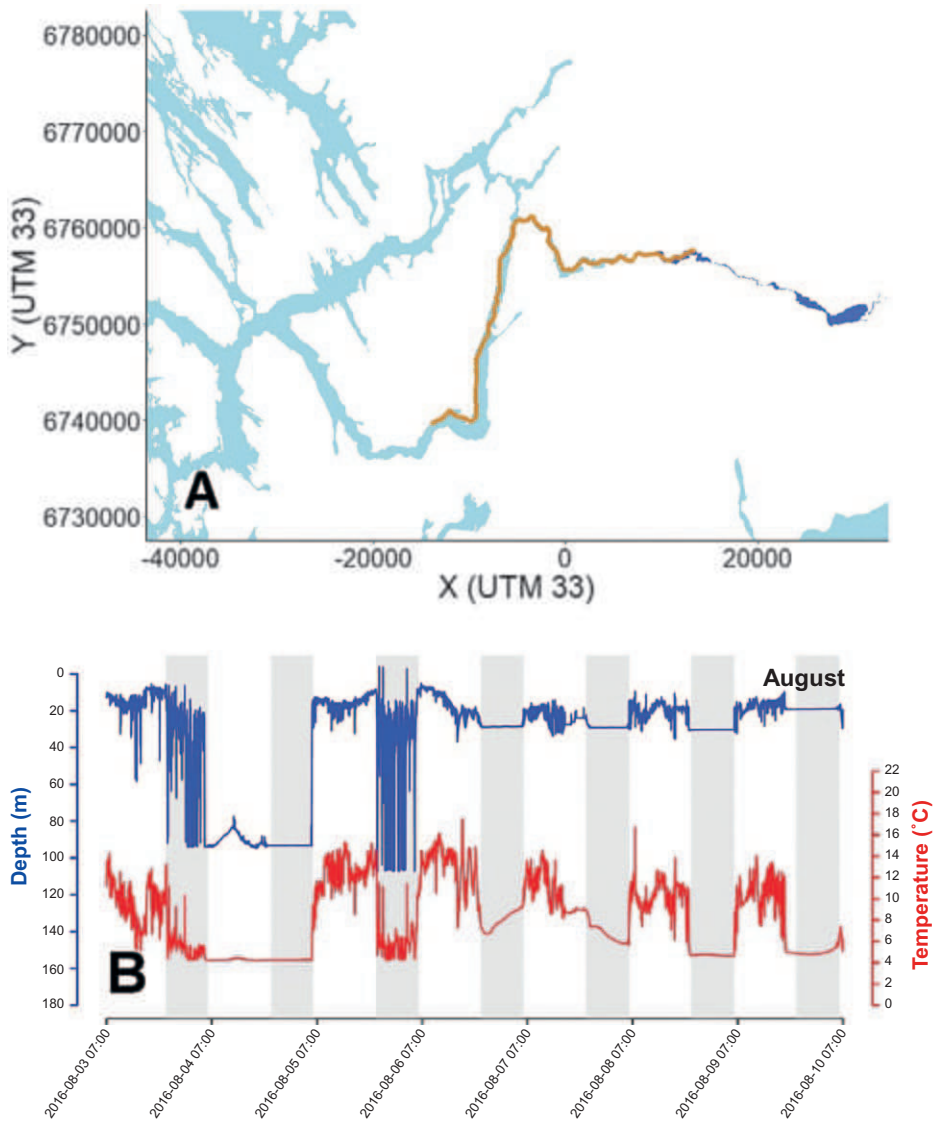

Fig. 9 Visualized samples of fish tracking data across the landscape (A) and in terms of depth and temperature (B) for two different animals. A: Spring outmigration (orange line) of a 52 cm long sea trout tagged in the Vosso River system in 2020 (Norway). The acoustic transmitter implanted in the trout was detected by multiple receivers during the river exit and fjord entry as it traveled eastward through the Osterfjord system in western Norway, which is a ring-shaped fjord around the island of Osterøy. The trout will continue to be followed as it moves through the summer and hopefully returns to the river to spawn again in the future. The detection data provide details of the timing and extent of movements between the freshwater and marine environments to better understand habitat requirements and exposure to anthropogenic stressors in multiple environments. (B) One week in the life of a 61 cm long lake trout in Lake Ontario (Canada/United States) in terms of depth (blue, left axis) and temperature (red, right axis) based on an externally attached data logger (see Raby et al., 2017 for detailed methods). Each x-axis tick is a 24 h period; shaded vertical bars represent nighttime (sunset to sunrise).

Conclusion

Freshwater organisms and ecosystems are in crisis. As such, there is an urgent need to develop strategies to protect and restore freshwater biodiversity (Tickner et al., 2020). Knowledge of habitat use, movement corridors, environmental tolerances, and survival rates are fundamental to developing science-based management and recovery plans (Cooke et al., 2016a). There are also many fascinating scientific mysteries that remain to be solved about freshwater species interactions, reproductive behavior, species-area relationships, and other fundamental aspects of life in inland waters. Electronic tagging and tracking tools are making freshwaters less opaque and providing a window into the underwater world (Hussey et al., 2015). These tools are not a panacea and are best used in concert with other assessment and research tools and techniques including habitat mapping, population assessment by mark-recapture, and individual sampling. In fact, electronic tagging and tracking has rapidly progressed from a niche area of research to one that is now embraced by hundreds of researchers and that is generating new knowledge to inform management of inland water biological resources.

See Also: Structures and functions of Inland Waters - Lakes: Fish Populations; Structures and functions of Inland Waters - Rivers: Aquatic Food Webs In Rivers; Invasive Species in Streams and Rivers

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Fatty Acid—Markers as Foodweb Tracers in Inland Waters

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This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvelil.

Glossary

Acetylenic FAs Fatty acids containing triple bonds.
Alkaliphiles Organisms that thrive in alkaline environments.
Allochthonous organic matter An organic matter that comes from outside the aquatic systems (e.g., leaf litter).
Autochthonous organic matter An organic matter that has been produced in the aquatic systems (e.g., algae).
Benthic organisms Freshwater or marine bacteria, algae or small animals living on, at or in the bottom.
Coenzyme A A coenzyme of acylation (the process of adding an acyl group to molecules). It has an important role in the synthesis and oxidation of fatty acids.
Conditionally essential nutrients compounds that can be synthesized by species in amounts sufficient to meet their physiological requirements in the absence of stress, disease, and other adverse factors.
Eicosanoids (prostaglandins, leukotrienes and thromboxanes) Signaling molecules, products of oxidation of arachidonic or eicosapentaenoic fatty acids.
Essential nutrients Compounds that cannot be synthesized by the species.
Fatty acid desaturases Enzymes that catalyze removing two hydrogen atoms from carbon atoms placed next to each other (C—C) in a fatty acid creating a double bond (C=C).
Fatty acid A carboxylic acid, containing a long aliphatic chain (>4 carbon atoms).
Halophile An organism that thrives in high salt concentrations.
Isotopic signature or isotopic fingerprint A ratio of isotopes of elements (C, N, H, etc.) in samples studied.
Long-chain PUFAs (LC-PUFAs) Polyunsaturated fatty acids with 20 and more carbon atoms.
Non-methylene-interrupted fatty acids Fatty acids that have two or more double bonds that are separated from each other by two or more methylene groups (—CH_2—).
Opportunism The ability of species to adapt to changing environments and thrive in them, e.g., by adapting feeding behavior.
Pelagic organisms Free-swimming or floating organisms in the water column.
Planktonic organisms freshwater or marine bacteria, algae or small animals floating in the water and unable to swim well enough to move against currents.
Stable isotopes Nonradioactive nuclides of one chemical element that contain different numbers of neutrons (e.g., carbon can contain 6 protons and 6 or 7 neutrons—stable isotopes ^{12}C and ^{13}C, respectively).
Sympagic organisms Aquatic organisms associated with ice. Ice algae and specific zooplankton communities inhabit such environments.
Sympatric species Two or more related species existing in the same geographic area.
Triacylglycerols Organic molecules containing three fatty acids esterified to a glycerol molecule.
Trophic fractionation A change in the isotope values of consumers relative to their food due to different rates of enzymatic reactions (during assimilation, synthesis and excretion of substances) involving the lighter and the heavier isotopes.

Introduction

Ecosystem functioning is based on fluxes of matter and energy in foodwebs. There are a number of methods for untangling foodwebs in aquatic ecosystems. In recent decades, fatty acids (FAs) have been widely used as foodweb tracers in aquatic ecosystems. Based on FAs, feeding spectra of many consumers have been specified. FA-marker analyses also contribute to differentiating between allochthonous and autochthonous (see glossary) organic matter inputs to foodwebs of inland water ecosystems. In this chapter, we describe FAs and their use as foodweb markers in aquatic ecosystems, describe and compare the FA-marker analysis with other methods for studying diets of aquatic animals, and describe the identifying characteristics of FAs in the main taxonomic groups of organisms inhabiting freshwater ecosystems (bacteria; algae and other photosynthetic eukaryotes; non-photosynthetic eukaryotes).

What are fatty acids and how can they be used to study foodwebs?

Fatty acids (FAs) are biomolecules consisting of straight or branched carbon chains. One end of the molecule is a methyl group (—CH_3) and the opposite end is a carboxyl group (—COOH). Additionally, FAs can be saturated or unsaturated. In saturated FAs, carbon atoms are linked by single covalent bonds. In unsaturated FAs, some carbon atoms are linked by double bonds or, sometimes, by triple bonds. Depending on the number of double bonds, unsaturated FAs are divided into monounsaturated (MUFAs) ones, which contain one double (triple) bond, and polyunsaturated (PUFAs) ones, which contain two or more double (triple) bonds. Usually, the structure of a FA is represented by the following formulas: e.g., 18:2n-6 or 18:2ω6, where 18 is the number of carbon atoms, 2 is the number of double bonds, n-6 or ω6 is the position of the first double bond from the methyl end of the molecule, and the second double bond is separated by two carbon atoms (or one methylene group, —CH_2—) from the first double bond (the 9th carbon atom here). Sometimes, FAs contain conjugated or non-methylene interrupted double bonds. Among branched FAs, the most common are iso and *anteiso*. The structures of typical FAs are shown in Fig. 1.

Fatty acids have many important functions within organisms, including structural, signaling, energy storage, etc. All cell membranes consist of a lipid bilayer, the molecules of which are mainly composed of the polar group and two FAs. Physical properties (e.g., fluidity) of cell membranes and their permeability mainly depend on the structure of FAs (chain length and number of double bonds). Some FAs, namely, arachidonic (ARA, 20:4n-6) and eicosapentaenoic (EPA, 20:5n-3) acids, play an additional role as precursors for eicosanoids (prostaglandins, leukotrienes and thromboxanes; see glossary) and other lipid mediators. Among FAs, EPA and docosahexaenoic acid (DHA, 22:6n-3) attract special attention of scientists, since they play an important role in many physiological processes in animals, including humans. For example, these PUFAs are necessary for the normal development of the cardiovascular and nervous systems. Many dietary FAs, such as some MUFAs (16:1n-7, 18:1n-9, 20:1n-9, etc.) and some PUFAs (16:2n-4, 16:3n-4, 16:3n-3, 18:2n-6, 18:3n-3, etc.), are often stored as part of triacylglycerols (TAGs) (see glossary). TAGs are usually used by animals as energy sources.

Bacteria, algae and plants synthesize a broader range of FAs de novo, when compared to animals. This is because animals have limited abilities to elongate and desaturate FAs. Animals, though, convert some dietary FAs to longer and more unsaturated ones. For instance, benthic mollusks synthesize non-methylene interrupted FAs with two or three double bonds from MUFAs, which is considered as an adaptation to their specific habitats or deficiencies in the physiologically important EPA and DHA in their diet. Mosquitoes produce 14:2n-6 and 14:3n-3, which very rarely occur in other organisms. Some fish species synthesize EPA and DHA when their diet lacks these PUFAs. Bacteria, algae, plants, and some animals synthesize specific FAs, which are transferred through foodwebs and accumulated in lipids (especially in TAGs) of animals of the higher trophic levels; they can be used as FA-markers of these organisms. By analyzing FA compositions of animals and finding FA-markers, scientists are able to identify their diets.

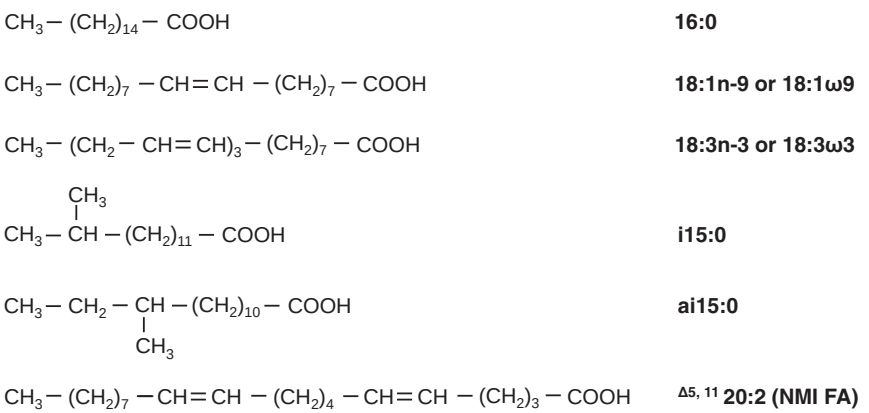

Fig. 1 The structures of typical fatty acids.

Comparing the use of FAs to other methods for studying foodwebs

There is no one ideal method for examining the diets of aquatic animals. All methods have limitations (Table 1). However, it is possible to choose the best method for your specific goal (Nielsen et al., 2018). Below, we briefly describe seven methods used in field studies and compare their advantages and disadvantages when investigating the diets of aquatic organisms of different trophic levels. The methods are: (a) visual gut content analysis, (b) controlled diet experiments, (c) DNA identification of prey items (hereafter the DNA-method), (d) stable isotope analysis, (e) FA-marker analysis, and (f and g) compound specific stable isotope analysis of fatty acids (FA-CSIA) and amino acids (AA-CSIA).

(a) *Visual gut content analysis*: When ingested items are not yet digested and well preserved, this method can provide information on ingested items such as species composition, their size, and the proportion of each item in gut content. When studying the diets of small organisms such as protozoa, rotifers, crustaceans, insect larvae, and worms, visual analysis identifies most of the gut contents as detritus, (i.e., unidentifiable particles). When studying fish diets, visual analysis of gut contents identifies organisms of higher trophic levels, like copepods and amphipods, as food items, but small or too soft organisms, like flatworms, remain unidentified. Fish guts sometimes contain sand, stones, and other inedible materials, as well as accidentally ingested animals (e.g., rodents), which do not make up a significant proportion of the fish's diet. One more important limitation of all methods based on gut content (visual gut content analysis and DNA-method) is the impossibility of estimating which items are assimilated. For example, some algae are not digested by fish during gut passage and are excreted alive, which is known as "viable gut passage". Thus, the algae will be mistakenly attributed to the animal diet. Despite the widespread use of visual analysis for examining animals' diets, this method has significant disadvantages compared to FA-marker analysis (Table 1).

(b) *Controlled diet experiments*: Controlled diet experiments were popular for studying animals' diets last century. The diversity of food items in natural ecosystems and environmental conditions cannot be fully reproduced in the experiments. Thus, it is hardly possible to extrapolate the results obtained in the laboratory to natural ecosystems. The use of flow cultivators removed certain limitations of closed tanks such as wall fouling, food sedimentation, food transformation in time, etc. However, viable gut passage of some algae (e.g., Cyanobacteria) was discovered using this particular method.

Table 1 Disadvantages and advantages of the most popular methods for studying trophic interactions in aquatic ecosystems.

Method	*Disadvantages*	*Advantages*
Visual gut content analysis (gut, stomach or fecal content)	1. Low taxonomic resolution (unidentified compounds) 2. Short term (no more than 48 h) 3. Taxonomic knowledge of potential prey items 4. Viable gut passage of ingested items	1. Identification of new or rare items 2. Identification of prey size and proportion
Controlled diet experiments	1. Limited result extrapolation to natural ecosystems 2. Inability to recreate natural conditions	1. Determination of the size of ingested particles
DNA identification of prey items (the DNA-method)	1. Short term (hours) 2. Libraries are not complete 3. DNA degradation during digestion 4. Unquantifiable 5. Environmental contamination 6. Viable gut passage of ingested items	1. High taxonomic resolution 2. Identification of new or rare items
Stable isotope analysis ($\delta^{13}C$, $\delta^{34}S$, $\delta^{2}H$, and $\delta^{15}N$, ‰)	1. Time determination (unclear time span and time-lag) 2. Low accuracy (the estimation of trophic discrimination factors is necessary) 3. Knowledge of isotope values of all items in the trophic chains 4. Diet resolution (3–5 items)	1. Determining of trophic position 2. Long time span 3. Identification of the assimilated items 4. Separation between allochthonous and autochthonous food sources
Fatty acid analysis	1. Time determination (unclear time span and time-lag) 2. Medium taxonomic resolution (no species identification) 3. Blind spot (not all food items have FA markers) 4. FA modification by consumers	1. Long time span 2. High accuracy 3. Identification of the assimilated items
Compound specific stable isotope analysis—fatty acids	1. Time determination (unclear time span and time-lag) 2. Measurement of isotope values of expected diets 3. Medium taxonomic resolution (no species identification) 4. Trophic fractionation (unknown for most organisms; possibly TF is not the constant) 5. A lot of controversial results	1. Identification of the assimilated items
Compound specific stable isotope analysis—amino acids	1. Time determination (unclear time span and time-lag) 2. Measurement of isotope values of expected diets 3. Medium taxonomic resolution (no species identification) 4. Different integration times of different amino acids	1. Identification of the assimilated items

(c) *DNA-method*: The most modern method for examining diets of aquatic organisms is the DNA-method. Unfortunately, many samples are needed to get comprehensive information on the diet of the organisms and this method provides information only about ingested, not assimilated, food. Different diet components (bacteria, animals, plants) require different modifications of the DNA-method, which makes the method more complicated and expensive than others (Table 1). The development of this method, including the replenishment of libraries with genetic data of new species, and quantitative assessments will be able to remove many of the disadvantages of this method in the future.

(d) *Stable isotope analysis*: The basis for using isotope analysis to study the trophic structure of aquatic ecosystems is the differences in the isotopic values of carbon ($\delta^{13}C$) between terrestrial and aquatic organisms (allochthonous and autochthonous food sources) and nitrogen ($\delta^{15}N$) between organisms of different trophic levels. Additionally, isotopes of other elements, such as sulfur and deuterium are less frequently used for untangling foodwebs in aquatic ecosystems. The differences in $\delta^{13}C$ between terrestrial and aquatic organisms are caused by substantial differences in $\delta^{13}C$ of atmospheric CO_2 (the source of carbon for terrestrial primary producers) and dissolved organic carbon (the source of carbon for aquatic primary producers). The differences in $\delta^{15}N$ between organisms of different trophic levels are caused by transformation of substances containing nitrogen that are consumed (e.g., amino acids) during metabolism. However, this method is limited by the impacts of food quality and quantity and the environment on the isotope values in consumers as well as the time-lag before the $\delta^{15}N$ or $\delta^{13}C$ of consumers' tissues have equilibrated the subsequent changes in consumers' diet (Table 1).

(e) *FA-marker analysis*: This method is based on using FAs as tracers of the organic matter transported through trophic chains. Many organisms, such as bacteria, algae, and some invertebrates synthesize specific FAs characteristic only of them. These specific FAs or FA combinations can be found mainly in groups of organisms that have genetic kinship. Tracking the transfer of specific FAs in foodwebs can be used to investigate trophic relationships in aquatic ecosystems (e.g., Desvilettes et al., 1997; Galloway et al., 2015). This method determines the groups of bacteria and algae that are part of even small organisms' diets, reveals the assimilation of bacterial, algal and animal organic matter by consumers, and indicates the primary carbon source for consumers. Many invertebrates and vertebrates that had been previously considered detritivores were found to exhibit food selectivity using FA-marker analysis.

(f and g) *FA-CSIA & AA-CSIA*: These methods are the combination of FA-markers/AA-markers and stable isotopes. Sometimes, food sources do not differ by FA-markers—i.e., the group of algae is the same, but these algae use different carbon sources (pelagic and subglacial/sympagic diatoms; see glossary). In this situation, by comparing the isotope values of carbon of the FA-marker in the consumer and in the algae from the pelagic zone and subglacial algae, it is possible to identify which algae the consumer prefers. Additionally, this method can be useful for investigating autochthonous and allochthonous utilization by organisms, which makes a significant contribution to understanding the carbon cycle in the biosphere. AA-CSIA is a more complicated, but similar method, to FA-CSIA. The AA-CSIA method includes not only carbon isotopes but nitrogen isotopes as well. However, there are limitations associated with revealing essential (see glossary), conditionally essential (see glossary), and non-essential amino acids for various animals. When using FA-CSIA & AA-CSIA methods, it is necessary to take into account the trophic fractionation that occurs in the consumers. Finding coefficients of trophic fractionation is not an easy task, which complicates the use of these methods (Table 1).

Although some authors propose integrating several methods to more accurately determine the diets of aquatic organisms, that approach may be laborious and expensive. Having studied the disadvantages and advantages of different methods (Table 1), we believe that the FA-marker method is generally sufficient, but sometimes we use additional methods to refine the results obtained. To correctly use FAs to determine the animal diets, knowledge of FA-markers of potential food items is necessary. Next, we will discuss the FA-markers of various groups of organisms.

The identifying characteristics of bacterial FAs

The diversity of the FA composition of bacteria was discovered in the middle of the 20th century. FAs began to be used for taxonomic identification of bacteria from phyla down to genus level as early as the 1970s. In fact, bacteria contain odd and branched saturated FAs (*iso* and *anteiso*), monounsaturated FAs, cyclopropane FAs, and FAs with OH-groups. FA composition of bacteria depends on their taxonomic position and environmental conditions.

Fatty acid synthesis (FAS) de novo in all organisms is carried out by cyclically repeating a series of reactions. Two types of fatty acid synthesis are distinguished: FAS I and FAS II (White et al., 2005). The first type of FA synthesis occurs mainly in non-photosynthetic eukaryotes, and the second type in most prokaryotes and photosynthetic eukaryotes.

Some bacteria are able to synthesize PUFAs, including long-chain ones (e.g., Metz et al., 2001; Bell and Tocher, 2009; Monroig et al., 2013). However, the PUFA synthesis in bacteria has a fundamentally different mechanism compared to animals and plants. Bacteria use anaerobic polyketide pathway. Different bacteria have different sets of enzymes for the synthesis of unsaturated fatty acids. As a result, different groups of bacteria have FAs inherent only to their specific group. FA-markers of the main groups of bacteria that are widespread in aquatic ecosystems have also been identified (Table 2). The generally recognized and widely used FA-markers of bacterial organic matter in water bodies are i13:0, ai13:0, 13:0, i15:0, ai15:0, 15:0, i17:0, ai17:0, 17:0, i17:1n-7, 18:1n-7 (Table 2).

Table 2 Fatty acid—markers of groups of bacteria inhabiting aquatic ecosystems.

Taxon/group	*FA—markers*	
Gram-positive bacteria	i15:0, ai15:0, 15:0, ai17:0, i17:1, ai17:1, 16:1n-9, 16:1n-5	Shaw (1974), Komagata and Suzuki (1987) and Wang et al. (2014)
Gram-negative bacteria	Cyclopropyl-FAs (cyc19:0, cyc17:0), 2- and 3- OH-FAs (3OH-14:0) C16 and C18 MUFAs, especially trans18:1n-7	Shaw (1974), Komagata and Suzuki (1987) and Grogan and Cronan (1997)
Sulfate reducing bacteria	Methylhexadecanoic acids (10Me16:0), i17:0, i15:1n-7, i17:1n-7, cyc17:0, 17:0, cyc19:0, i19:1n-7, 16:1n-7, 18:1n-7	Vainshtein et al. (1992) and Colaco et al. (2007)
Desulfobacter	10Me16:0	Mancuso et al. (1990)
Desulfovibrio	i15:1n-7, i17:1n-7, i19:1n-7	Colaco et al. (2007)
Methanotrophic bacteria	cis16:1n-8, trans16:1n-5, cis16:1n-6, cis18:1n-8 and cis18:1n-7	Bowman et al. (1993) and Le Bodelier et al. (2009)
Gammaproteobacteria	C16 MUFAs	Le Bodelier et al. (2009)
Alphaproteobacteria	C18 MUFAs	Le Bodelier et al. (2009)
Methylocystis	cis18:2n-7,12 and cis18:2n-6,12	Le Bodelier et al. (2009)
Acidophilic-thermophilic bacteria	Omega-cyclohexyl undecanoic, omega- cyclohexyl tridecanoic acids	Oshima and Ariga (1975) and Komagata and Suzuki (1987)
Alicyclobacillus (Gram-positive bacteria)	Omega-cyclohexyl FAs	Simbahan et al. (2004)
Iron-reducing actinobacteria	i16:0, ai17:0, i18:0	Itoh et al. (2011)
Mycobacterium, Corynebacterium, Rhodococcus and Nocardia	Mycolic FAs (C22-C60)	Erwin (1973) and Schweizer and Hofmann (2004)

The identifying characteristics of algal and other photosynthetic eukaryotic FAs

Photosynthetic eukaryotes are able to synthesize a wide variety of FAs. Unsaturated FAs are of the greatest interest as valuable markers. In algae and other photosynthetic eukaryotes, the introduction of double bonds into saturated FAs occurs after the incorporation of FAs into lipids in chloroplasts (prokaryotic pathway) or in the endoplasmic reticulum (eukaryotic pathway). In the eukaryotic pathway, C18 PUFAs are synthesized, while in the prokaryotic pathway, C16 PUFAs are synthesized. The introduction of double bonds into FAs in most algae occurs via the prokaryotic pathway, while in many higher plants, it occurs via the eukaryotic pathway. This means that algae contain more C16 PUFAs, while higher plants contain more C18 PUFAs. The photosynthetic eukaryotes discussed in this chapter are shown in Figs. 2 and 3.

Various taxa of photosynthetic organisms are distinguished by their sets of enzymes, resulting in the synthesis of different fatty acids. Among the FA profiles of photosynthetic eukaryotes and prokaryotes, individual FAs or sets of FAs have been identified that

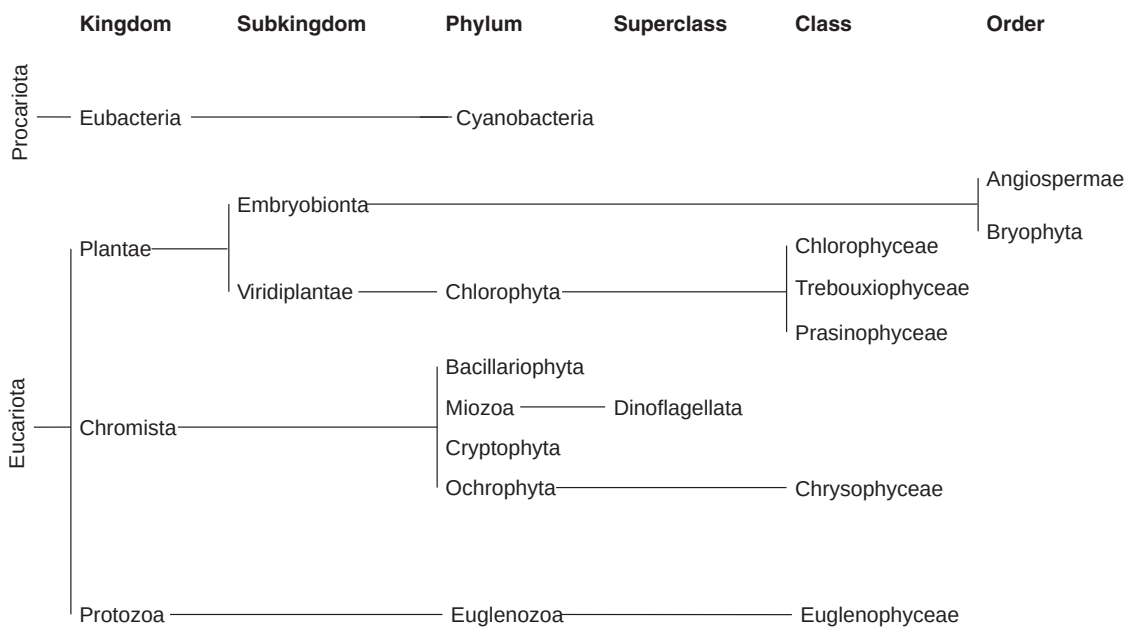

Fig. 2 A phylogenetic tree of the photosynthetic eukaryotes.

Fig. 3 The representatives of the photosynthetic eukaryotes (algae). Courtesy: Elena Kravchuk.

Table 3 Fatty acid—markers of photosynthetic eukaryotes and prokaryotes inhabiting inland waters.

Taxa/group	*FA—markers*	
Prokaryotes		
Cyanobacteria	18:2n-6, 18:3n-3, 18:3n-6	Ahlgren et al. (1992), Desvilettes et al. (1997) and Gugger et al. (2002)
Eukaryotes		
Chlorophyta	16:1n-9, 18:2n-6, 18:3n-3, C16 PUFAs of n-3 and n-6 (e.g., 16:2n-6, 16:3n-3, 16:4n-3)	Ahlgren et al. (1992), Napolitano (1999), Petkov and Garcia (2007) and Kelly and Scheibling (2012)
Euglenophyceae	18:2n-6, 18:3n-3, 20:5n-3, 22:6n-3	Taipale et al. (2013)
Dinoflagellata	18:5n-3 > 18:3n-3, 18:5n-3, 20:5n-3, 22:6n-3	Napolitano (1999), Bergé and Barnathan (2005) and Kelly and Scheibling (2012)
Bacillariophyta	16:1n-7/16:0 > 1, 14:0, C16 PUFAs of n-7, n-4 and n-1 (16:2n-7, 16:2n-4, 16:3n-4, 16:4n-1), 20:5n-3	Dijkman and Kromkamp (2006) and Kelly and Scheibling (2012)
Chrysophyceae	14:0, 16:1n-7, 18:1n-7, 18:4n-3, 20:5n-3, 22:5n-6, 22:6n-3	Ahlgren et al. (1992), Desvilettes et al. (1997) and Taipale et al. (2013)
Cryptophyta	18:3n-3 + 18:4n-3; 20:5n-3 + 22:6n-3	Desvilettes et al. (1997) and Guevara et al. (2011)
Angiospermae	18:2n-6, 18:3n-3, 20:0, 22:0, 24:0, 26:0	Shorland (1963) and Kelly and Scheibling (2012)
Bryophyta	Acetylenic FAs (6a,9,12–18:3, 8a,11,14–20:3)	Kalachova et al. (2011)

are specific only for a particular taxon. Currently, these FAs are widely used to study trophic interactions in aquatic ecosystems. FA-markers of the most common freshwater algal taxa and some higher plants are listed in Table 3.

Freshwater inland waters are mainly dominated by three taxa of photosynthetic organisms—blue-green and green algae and diatoms. Other taxa dominate for a short time or in a small number of ecosystems.

Blue-green algae (Cyanobacteria) are photosynthetic prokaryotes. Unlike most non-photosynthetic bacteria, they are able to synthesize PUFAs with 18 carbon atoms. FAs with a chain length of more than 18 carbon atoms have not been detected in cyanobacteria (Table 3).

Green algae (Chlorophyta) synthesize FAs of the n-3 and n-6 families, mainly with 16 and 18 carbon atoms. In most species, 18:3n-3, 18:2n-6, and 16:4n-3 dominate the PUFAs (Table 3). It is not usual for the majority of green algae species to synthesize FAs with chain lengths above 18 carbon atoms. In species of Prasinophyceae, FAs uncommon for green algae were found, namely, 18:4n-3, 20:5n-3 and 22:6n-3, while species of Trebouxiophyceae and Chlorophyceae had FA composition common for green algae. However, some authors have noted the presence of a significant amount of long-chain PUFAs (LC-PUFAs) (see glossary) in Chlorophyceae and other taxa. In general, findings of the FAs unusual for certain taxon may be associated with the erroneous identification of species; contamination of the samples of microalgae by other algae, e.g., the presence of diatoms attached to the surface of algae or plants (Fig. 4); or erroneous identification of FAs during chromatography using only retention times.

Diatoms (Bacillariophyta) synthesize a lot of specific FAs, such as C16 PUFAs of the n-7, n-4 and n-1 families (Table 3). Additionally, the high level of 14:0 and 20:5n-3 in many diatom species led to the use of these FAs as diatom markers. Most species of diatoms contain traces of C18 PUFAs. Like other taxa, some species of Bacillariophyta show specific FA profiles. Differences in FA levels in species of diatoms and in other algae may be explained by species specificity and different environmental conditions.

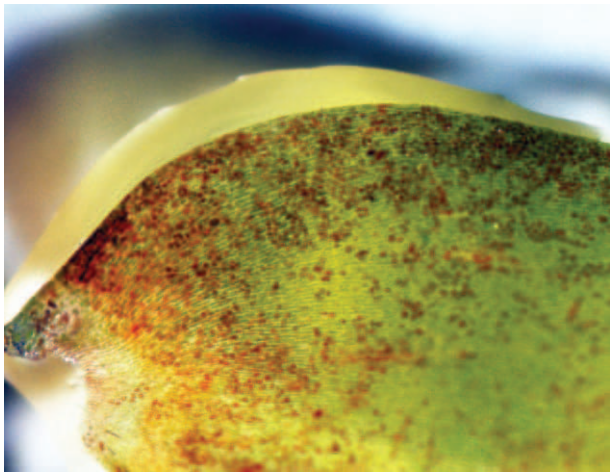

Fig. 4 Diatoms attached to the surface of the aquatic moss (Fontinalis antipyretica). Courtesy: Olesia Makhutova.

The presence of Cryptophyta in aquatic animals' diet is well recognized by a high level of 18:4n-3 in the consumers. The level of 18:4n-3 in Cryptophyta can reach approximately 10–20% of total FAs. Additionally, 18:3n-3, 20:5n-3, and 22:6n-3 dominate in cryptophytes, while the levels of other C20 and C22 PUFAs are very low in general. One more feature of cryptophytes is a high n-3/n-6 ratio (~20/1).

Dinoflagellates are typical representatives of marine phytoplankton, but they are also found in freshwater ecosystems. The presence of dinoflagellates in aquatic animals' diet is usually identified by significant levels of 18:5n-3 and 22:6n-3 (Table 3). However, some species demonstrate specific FAs. Phospholipids of two species of *Gymnodinium* contained unusual LC-PUFAs, namely 28:7n-6 and 28:8n-3, the level of which reached 2.2% of total FAs (Bergé and Barnathan, 2005).

It is difficult to determine the presence of other algal taxa, such as Euglenophyceae and Chrysophyceae, in diets of aquatic animals according to FA-markers. The proportion of these algae in animals' diet is usually low and these taxa do not contain specific FAs that would be found only in them (Table 3). Angiospermae or flowering plants are an important food source for consumers in littoral trophic chains. Similar to green algae, the main PUFAs of flowering plants are 18:2n-6 and 18:3n-3, which are mandatory compounds of photosynthetic membranes of eukaryotes. In addition to 18:2n-6 and 18:3n-3, aquatic plants contain long-chain saturated FAs with an even number of carbon atoms, namely, 20:0, 22:0, 24:0, 26:0, which are compounds of cuticle waxes. These FAs are widely used as markers of flowering plants and allochthonous organic matter in foodwebs of aquatic ecosystems.

Bryophyta is one more taxon that can be found in freshwater ecosystems especially in streams. *Fontinalis antipyretica*, the representative of Bryophyta, contains highly specific FAs, namely acetylenic FAs (see glossary), which were successfully used as tracers in trophic chains in the Yenisei River (Kalachova et al., 2011).

Case study: Selective feeding of filter-feeding crustaceans (Feniova et al., 2018)

The FA-markers of photosynthetic eukaryotes were successfully used in studies of the diets of invertebrates, including very small animals such as water fleas (*Daphnia*). *Daphnia* are filter-feeding planktonic animals, consuming all food particles of suitable size, and therefore are regarded as keystone species in freshwater planktonic ecosystems. However, a mesocosm experiment revealed that two sympatric species (see glossary), *Daphnia magna* and *Daphnia pulicaria*, had different feeding spectra. *D. magna* selectively consumed diatoms or flagellates and some allochthonous organic matter, while *D. pulicaria* selectively consumed bacteria and green algae (Fig. 5). This surprising result was verified in further experiments. Initially, *D. magna* and *D. pulicaria* were reared in laboratory cultures and fed green algae. According to the FA analyses, these two species did not differ in their FA composition, and markers of green algae adequately indicated their diet (Fig. 6). However, when placed in mesocosms with natural algal communities, *D. magna* switched primarily to diatoms and terrestrial organic matter, and *D. pulicaria* switched to bacteria (Fig. 6). This series of experiments strongly confirmed the relevance of FA-marker analysis for revealing the feeding spectra of small aquatic animals.

Using FAs to study non-photosynthetic eukaryotes

Non-photosynthetic eukaryotes have some specificity in their FA profiles. The non-photosynthetic eukaryotes discussed in this chapter are shown in Figs. 7 and 8. The synthesis of saturated FAs, mostly 16:0 and 18:0, in animals is located in cell cytosol and is linked with the acyl carrier protein (ACP). The subsequent elongation and desaturation are located in mitochondria and

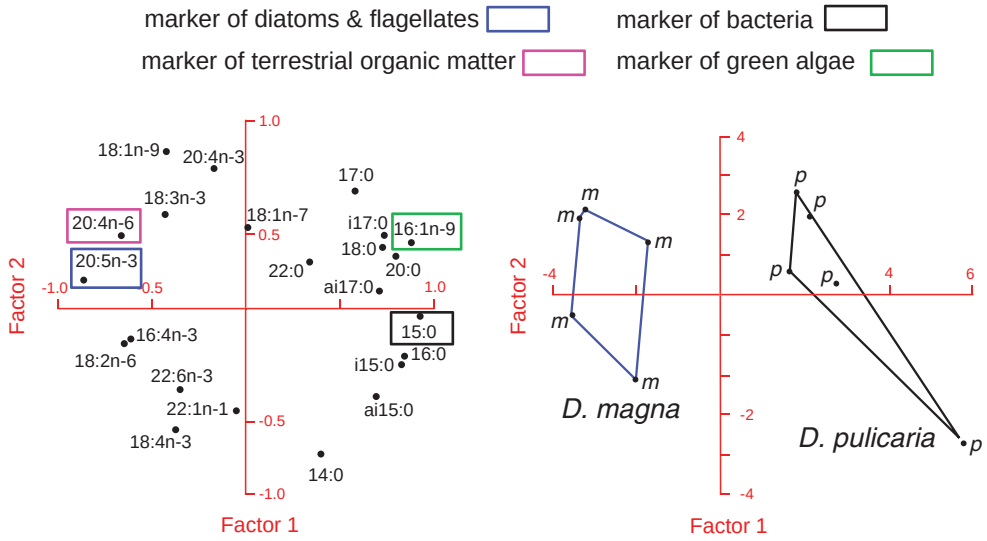

Fig. 5 Principal component analysis of FA levels in *Daphnia* from mesocosms. From Modified from Feniova I, Dawidowicz P, Gladyshev MI, Kostrzewska-Szlakowska I, Rzepecki M, Razlutskij V, Sushchik NN, Majsak N and Dzialowski AR (2015) Experimental effects of large bodied Daphnia, fish, and zebra mussels on cladoceran community and size structure. *Journal of Plankton Research* **37**: 611–625, with changes.

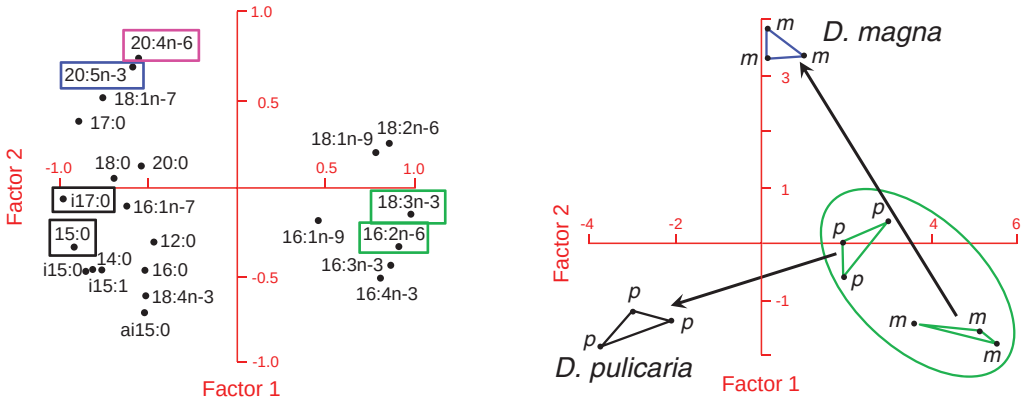

Fig. 6 Principal component analysis of FA levels in *Daphnia* from laboratory cultures (circled with green line) and from mesocosms (transition from laboratory cultures to mesocosms is designated with arrows). Colors for highlighted FA markers (15:0 and i17:0—FA-markers of bacteria; 16:2n-6 and 18:3n-3—FA-markers of green algae; 20:5n-3—FA-marker of diatoms and flagellates; 20:4n-6—FA-marker of terrestrial organic matter) are explained in Fig. 2. From Feniova I, Dawidowicz P, Ejsmont-Karabin J, Gladyshev M, Kalinowska K, Karpowicz M, Kostrzewska-Szlakowska I, Majsak N, Petrosyan V, Razlutskij V, Rzepecki M, Sushchik N and Dzialowski AR (2018) Effects of zebra mussels on cladoceran communities under eutrophic conditions. *Hydrobiologia* **822**: 37–54, with changes.

endoplasmic reticulum, respectively (Chan and Vogel, 2010). Non-photosynthetic eukaryotes contain enzymes, namely, acyl-CoA-desaturases, which incorporate double bonds into FAs bound with coenzyme A (see glossary). Animals have Δ9 desaturase and can effectively synthesize 18:1n-9. The majority of animals, excluding some ciliates, insects, and some other invertebrates, do not contain Δ12 and Δ15 (ω3) desaturases, which are necessary for synthesis of 18:2n-6 and 18:3n-3 from 18:1n-9 (Castro et al., 2016). Mammals and many other animals are not able to convert FAs of the n-3 family to n-6 and vice versa. Therefore, 18:2n-6 and 18:3n-3 are essential FAs for the majority of animals. Dietary 18:2n-6 and 18:3n-3 can be used as precursors for LC-PUFA synthesis, including physiologically important 20:4n-6, 20:5n-3 and 22:6n-3 (e.g., Tocher, 2015).

The main ways non-photosynthetic eukaryotes synthesize FAs are shown in Fig. 9. This figure highlights the diversity of the enzymes that non-photosynthetic eukaryotes can contain and the FAs that they are able to synthesize. Some enzymes are more universal than others and catalyze several reactions. Despite the presence of enzymes that catalyze the synthesis of 20:5n-3, 22:6n-3, and 20:4n-6 in animals, the rate of their synthesis is not high enough to maintain physiological processes in their bodies. Hence, these LC-PUFAs are partially essential for animals.

Fungi do not exhibit a high variability in FA composition. In fact, there are very few data on FA profiles of aquatic fungi, limiting characterization of this group as a whole. Some Hyphomycetales found in bottom sediments (Fig. 7), namely *Alatospora acuminata*,

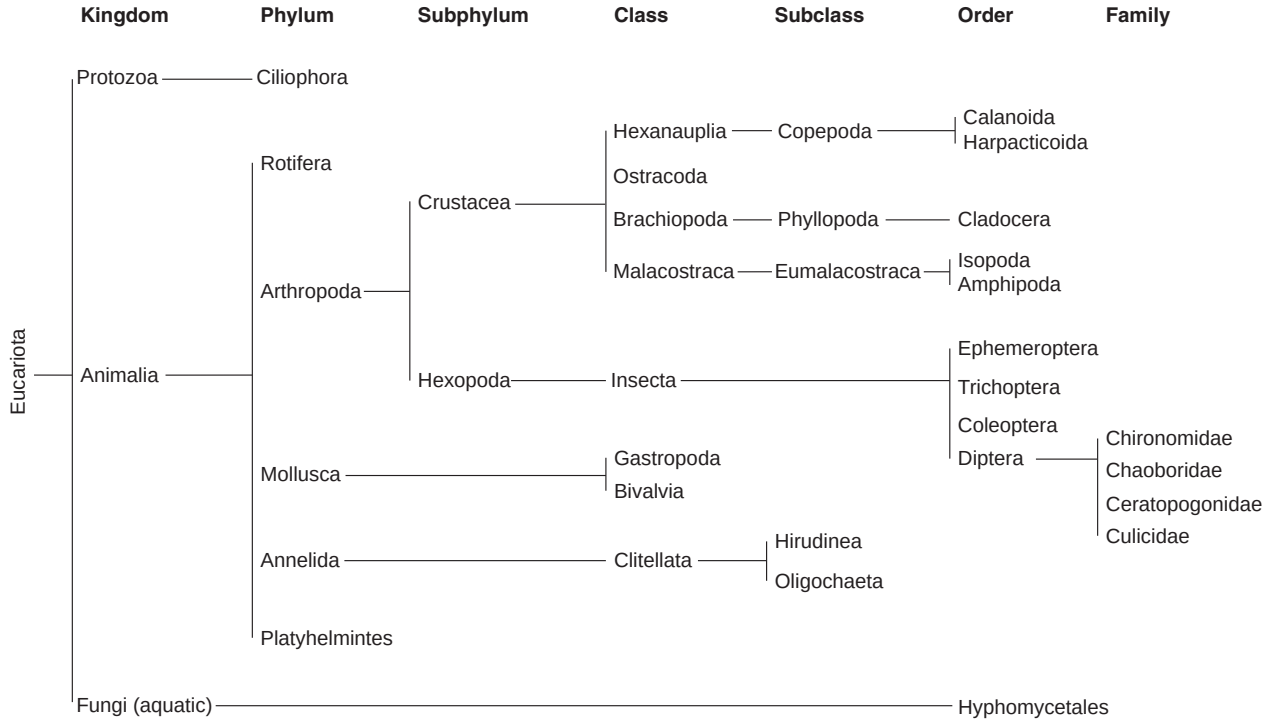

Fig. 7 A phylogenetic tree of the non-photosynthetic eukaryotes.

Heliscus lugdunensis, and *Tricladium chaetocladium*, synthesize C18 PUFAs of the n-3 and n-6 families (Arce Funck et al., 2015). Fungi may be an important source of essential PUFAs for invertebrates consuming detritus, which is usually poor in any PUFAs.

The FA composition of Ciliates (Ciliophora) and Rotifera (Fig. 7) has been poorly studied. The studied species do not contain specific FA-markers, with rare exceptions. In general, ciliates mainly contain 18:1n-9, 18:2n-6, 18:3n-6, and some other n-6 PUFAs, namely 20:2n-6, 20:4n-6, 20:3n-6, and 22:5n-6 (Desvilettes et al., 1997). Rotifera usually are rich in 16:0, 18:0, 18:1n-9, and n-3 and n-6 PUFAs.

Crustacea, namely Cladocera and Copepoda (Fig. 7), are the most dominant taxa of plankton in inland waters. They contain significant levels of 16:0, 16:1n-7, 18:1n-9, 18:2n-6, 18:3n-3, and 20:5n-3. In contrast to Cladocera, Copepoda contain high levels of C22 PUFAs, especially 22:6n-3. Specific FAs have been found in some species of Crustacea. For example *Limnocalanus macrurus* (Calanoida, Fig. 7) contains significant levels of unusual LC-PUFAs such as 24:4n-3, 24:5n-3, 24:6n-3, 26:4n-3, and 26:5n-3 (Hiltunen et al., 2014). Marine representatives of Copepoda, namely, Calanoida, store waxes esterified by 20:1n-11, 20:1n-9, 22:1n-11, 22:1n-9 (up to 10–15% of total FAs) (Scott et al., 2002). These MUFAs and LC-PUFAs are widely used as markers of marine copepods in trophic chains, including trophic chains of freshwater rivers and lakes containing semi-migratory fish. For example, a significant level of these MUFAs in semi-migratory fish reflects migration of fish from freshwaters to the sea.

FAs of some other crustaceans have also been identified. Although freshwater Isopoda (Fig. 7) are poorly studied, the benthic Ostracoda and Amphipoda (Fig. 7) are rich in both physiologically important n-3 LC-PUFAs—20:5n-3 and 22:6n-3. High levels of 22:6n-3 in freshwater and marine amphipods are associated with their carnivorous feeding habits. However, it seems that the high level of 22:6n-3 in amphipods indicates predation on animals rich in this PUFA. A 6-month experiment showed that *Gammarus lacustris* (a widespread representative of Amphipoda) individuals that consumed green algae and *Daphnia* (Cladocera that are deficient in 22:6n-3) had an absence of 22:6n-3 in their bodies. By contrast, when *G. lacustris* consumed copepods rich in 22:6n-3, its level increased to 8%. Amphipods also contain a significant level of 18:1n-9 and a high 18:1n-9/18:1n-7 ratio. Although some authors associate this with carnivory of amphipods, a high level of 18:1n-9 has been found in detritivorous gammarids (Legeżyńska et al., 2014). Thus, the use of 18:1n-9 as a marker of carnivory is questionable.

Mollusca (Fig. 7) synthesize specific FAs—non-methylene-interrupted (NMI FAs) (see glossary), which are widely used as their markers (Zhukova, 2019). Presumably, NMI FAs play structural and antioxidant (protection) roles in cell membranes. The ways of NMI FAs synthesis are shown in Fig. 9. In addition to NMI FAs, mollusks are rich in 20:1n-13, the rare isomer of 20:1. Bivalvia and Gastropoda differ in FA profiles. In contrast to Bivalvia, Gastropoda usually contain significant levels of n-6 LC-PUFAs, namely 20:4n-6 and 22:4n-6. The presence of specific FA-markers in Mollusca makes it possible to accurately discern the diets of fish and birds based on these invertebrates.

Fig. 8 The representatives of the non-photosynthetic eukaryotes (the aquatic invertebrates). Courtesy: Olesia Makhutova.

Case study: Adapt your diet or go extinct: Selective feeding of mollusks (Makhutova et al., 2013)

FA-marker analyses revealed differences in the feeding spectra of mollusks inhabiting the same aquatic ecosystem. Three mollusk species, *Dreissena polymorpha*, *Dreissena bugensis*, and *Unio tumidus*, were studied in the Kanevskoe Reservoir of the Dnieper River (Ukraine). *Dreissena* species, which settled on *Unio* shells and therefore were located in a higher layer than the fouled *Unio*,

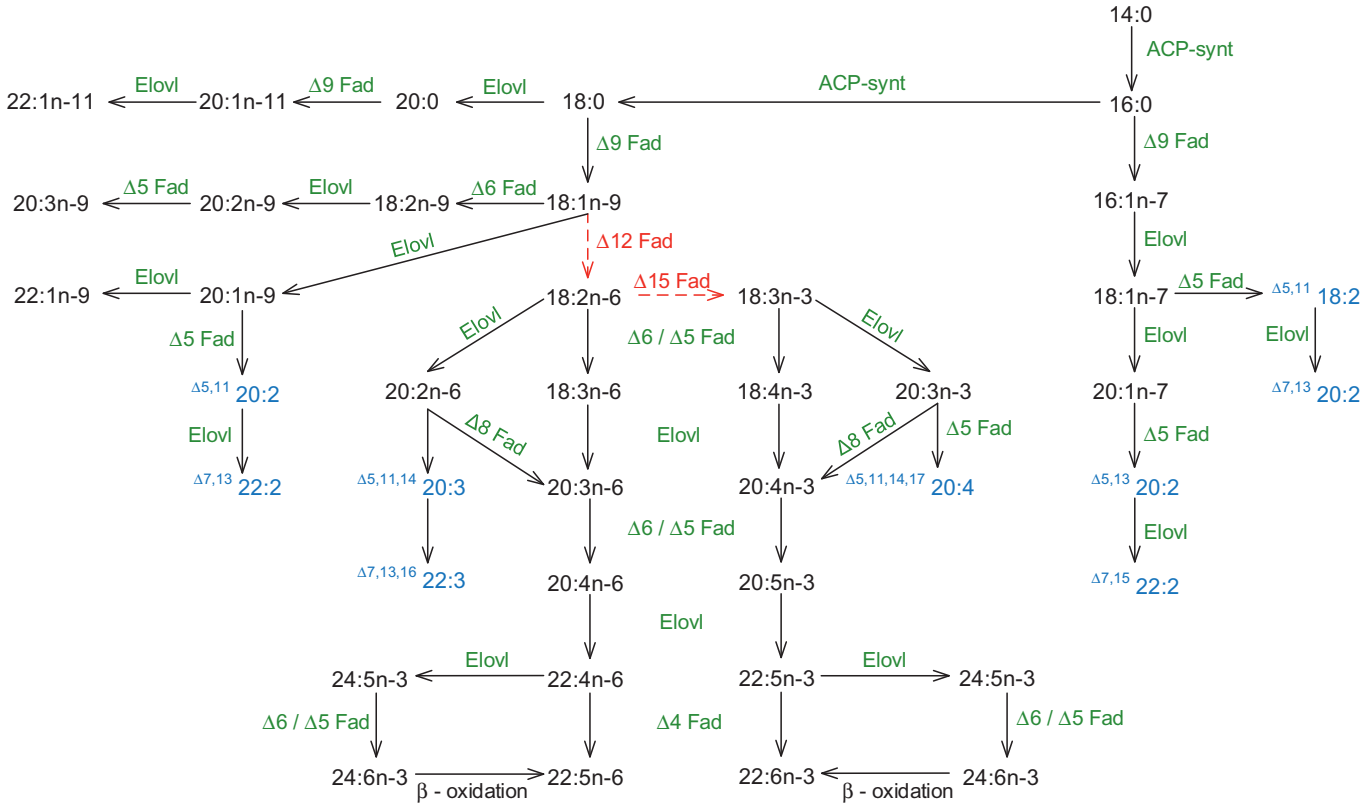

Fig. 9 The common ways of FA synthesis in non-photosynthetic eukaryotes. The enzymes, which are found in animals, are marked in green. The exceptions, which are very rare in non-photosynthetic eukaryotes, are marked in red, NMI FA are marked in blue.

preferably consumed more valuable food—planktonic algae and bacteria, while *Unio* mostly fed on detritus and benthic algae, which were of a lower food quality. The different feeding spectra of the mollusks and adaptations of *Unio* to benthic food might be the basis for the successful coexistence of the mollusks for a long time and prevent extinction of *Unio* due to *Dreissena*, as is the case in most waterbodies.

Insecta (Fig. 7) have diverse FA profiles. This diversity is explained by selective consumption of food (especially algae and bacteria) and synthesis of specific FAs. Larvae of nonbiting midges (Chironomidae, Fig. 7) usually contain FA-markers of diatoms, green algae, cyanobacteria, and other bacteria. For example, chironomids from Lake Biwa had high levels of 16:1n-8, 16:1n-6, and 16:1n-5—markers of methanotrophic bacteria (Kiyashko et al., 2004). Mayfly larvae (Ephemeroptera, Fig. 7) contain high levels of FA-markers of diatoms, whereas caddisfly larvae (Trichoptera, Fig. 7) FA-markers are dominated by green algae and diatoms.

Some species of Insecta synthesize specific FAs. For example, Mosquito larvae (Culicidae, Fig. 7) contain 14:2n-6 and 14:3n-3, which can be used as their markers (Sushchik et al., 2013). Caddisfly (*Apatania fimbriata*) larvae contain a number of short-chain PUFAs (12:2, 12:3, 14:2, 14:3) that they excrete with secretory fluid to scare away predators (Wagner et al., 1990). Among LC-PUFAs, only 20:5n-3 dominates in Insecta. LC-PUFAs with 22 and more carbon atoms are usually absent in Insecta or their level is negligible. There are some exceptions, however. In addition to 20:5n-3, glassworm larvae (Chaoboridae, Fig. 7) have a rather high level of 22:6n-3. When we studied the FA composition of various invertebrates inhabiting a fishless lake, we had been surprised to find rather high level of 22:6n-3 in water beetles *Dytiscus lapponicus* (Coleoptera, Fig. 7) because all previously studied predatory freshwater insect larvae like dragonflies and stoneflies only contained trace amounts of this FA (Makhutova et al., 2016). Then, we observed the beetles consuming gammarids that were rich in that FA and realized that gammarids were the sources of 22:6n-3 in beetles. Thus, some carnivorous insects may contain 22:6n-3 if their prey contain this FA.

In addition to the invertebrate taxa listed above, Annelida (especially Oligochaeta and Hirudinea) and Platyhelminthes (Fig. 7) are widespread in freshwater ecosystems. Oligochaeta contain a variety of FAs, including PUFAs. The level of 20:5n-3 can reach 22% of total FAs, while the level of 22:6n-3 is usually low. Another distinguishing quality of the FA composition of oligochaetes is a relatively high content of 20:1n-9, which can reach 10% in some species. The data on FA composition of Hirudinea and Platyhelminthes are scant. 20:2n-6 is considered a marker of freshwater Hirudinea because the level of this FA is rather high (~5%) only in this taxon. Some freshwater species of the family Planariidae (Platyhelminthes) contain a very high level of 22:5n-3 (~9%), which is unusual for invertebrates. Thus, 22:5n-3 is suggested as a marker of freshwater planarian.

Case study: Selective feeding of insect larvae inhabiting saline rivers (Zinchenko et al., 2014)

FA-marker analysis indicated that selective feeding could be a characteristic of benthic invertebrates that are commonly categorized as 'omnivores' or 'detritivores.' For instance, the larvae of three species of Chironomidae (*Cricotopus salinophilus*, *Chironomus salinarius,* and *Chironomus aprilinus*) found in two saline rivers within the basin of hypersaline Lake Elton) selectively consumed bacteria, diatoms, and some other microalgae from bottom sediments, but avoided consuming organic debris at a high degree of decomposition. Similarly, *Palpomyia schmidti* larvae (Ceratopogonidae, Fig. 7) inhabiting the same saline rivers selectively consumed diatoms and other algae, but avoided bacteria and decomposed dead organic matter.

Case study: Using photosynthetic and non-photosynthetic FA-markers to understand tadpoles' diets

FA-markers of all described aquatic organisms, namely, bacteria, algae, and invertebrates, are successfully used for studying diets of aquatic vertebrates. For example, the study of tadpoles' diet required the knowledge of FA-markers of various organisms. Whiles et al. (2010) found that although tadpoles in Illinois ponds (United States) obtained substantial amounts of food from heterotrophic sources, they displayed a high degree of opportunism (see glossary) in their feeding. The same species inhabiting different ponds had different diets. For example, *Lithobates clamitans* consumed detritus and plankton invertebrates in one pond; detritus and algae attached to submerged surfaces in another pond; detritus, plankton algae and aquatic insect larvae in a third pond. Two other tadpoles, *Rana arvalis* and *Pelobates fuscus*, cohabiting oxbows of the Khoper River (Russia), had differences in feeding spectra: *R. arvalis* primarily consumed bacterial food, while the diet of *P. fuscus* was based on cyanobacteria, green algae, diatoms, and higher plants.

Conclusion: Using FA-markers across taxa to understand foodwebs

There is no one ideal method for determining the diets of aquatic animals. However, scientists have discovered FA-markers for many taxa that are used in studies of trophic interactions in aquatic ecosystems (Fig. 10). FA-marker analysis has facilitated amazing discoveries such as selective feeding of filter-feeders, the diet variability of detritivores, and adaptations of feeding behavior to the changing environment. FA compositions of aquatic organisms are extremely diverse, providing many opportunities for further studies.

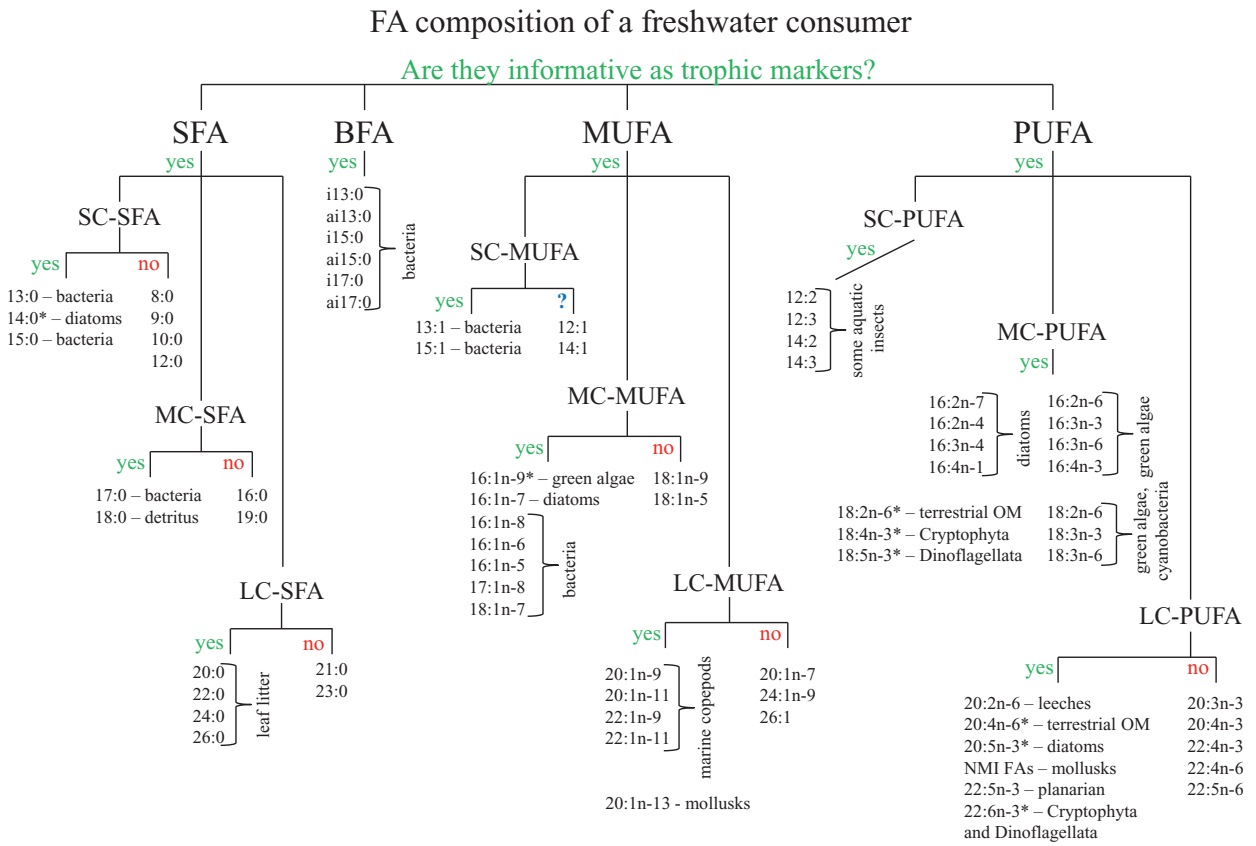

Fig. 10 The common FA-markers and non-marker FAs in a typical freshwater consumer. *: FAs that can be used as markers only if other FA-markers are also found. *SFA*, saturated FAs; *BFA*, branched FAs; *MUFA*, monounsaturated FAs; *PUFA*, polyunsaturated FAs; *SC*, short-chain; *MC*, medium-chain; *LC*, long-chain; *OM*, organic matter. The absence of the position of double bonds in some FA indicates their variability.

Future research

- Find FA-markers of other animal taxa,
- test recently proposed FA-markers,
- reveal the effect of changes in temperature, salinity, and other environmental factors on FA composition of aquatic organisms,
- develop a quantitative approach for estimating diets of aquatic animals using FA-markers.

See Also: Emerging methods and topics: Inland Water Fungi in the Anthropocene: Current and Future Perspectives; Fundamental concepts and theories: Parasites in Aquatic Food Webs: How and Why Environmental Gradients Influence Epidemics and Their Implications; Trophic Dynamics and Food Webs in Aquatic Ecosystems; Structures and functions of Inland Waters - Groundwater: Trophic Interactions in Subterranean Environments; Structures and functions of Inland Waters - Lakes: Benthic Algae in Lake Littoral Habitats; Lake Food Webs; Predation on Zooplankton; Protists: Ciliates; Structures and functions of Inland Waters - Rivers: Ecological and Evolutionary Consequences of Disturbance in Freshwater Ecosystems; Energetics and Food Webs in Large Rivers; Secondary Production in Streams; Structures and functions of Inland Waters - Wetlands: Restoring Riparian Peatlands for Inland Waters: A European Perspective

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INDEX

This index is in letter-by-letter order, whereby hyphens and spaces within index headings are ignored in the alphabetization, and it is arranged in set-out style, with a maximum of four levels of heading. Location references refer to the volume number, in bold, followed by the page number. Page numbers suffixed by *f*, *b* and *t* refers to figures, boxes and tables terms respectively. *vs*. indicates a comparison.

A

B

C

D

E

F

G

H

I

K

L

M

N

O

P

Q

R

S

T

U

V

W

X

Y

Z

SECOND EDITION

Encyclopedia of INLAND WATERS

VOLUME FOUR

ELSEVIER

ACADEMIC PRESS
An imprint of Elsevier
elsevier.com/books-and-journals

Set ISBN
ISBN 978-0-12-819166-8
9 780128 191668

Vol ISBN
ISBN 978-0-323-99123-0
9 780323 991230